THE GREEN TURTLE, *CHELONIA MYDAS*, POPULATION OF RAINE ISLAND AND THE NORTHERN GREAT BARRIER REEF: 1843-2001

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European history of the use of Raine Island and nesting green turtles is reviewed. Results of a diverse mosaic of investigations of the reproductive biology of the nesting population of green turtles using Raine Island and the adjacent islands are presented. These studies have focused on defining the fundamental characteristics of the breeding population, with more in-depth studies being conducted elsewhere. Studies at Raine Island have defined the species composition, morphology of adults, eggs and hatchlings, hatching and emergence success, sources of mortality of adults, eggs and hatchlings as well as the nesting environment. ❐ *Green turtle, Raine Island, population history, Great Barrier Reef.*

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There are four major green turtle, *Chelonia mydas*, breeding concentrations in Australia: Capricorn - Bunker Groups and adjacent islands in the southern Great Barrier Reef (GBR); Raine Island - Moulter Cay and adjacent islands in the northern GBR; Wellesley Group - eastern Arnhem Land in the Gulf of Carpentaria; and, the northwest shelf of Western Australia. These appear to be the only major rookery areas for the Australasian region where significant population declines are not already in progress for this species (Groombridge & Luxmoore, 1989). Raine Island, Moulter Cay and the other sand cays of the northern GBR collectively support the largest remaining breeding assemblage of green turtles in the world.

While world-wide there were once many other *C. mydas* rookeries of the magnitude of Raine Island - Moulter Cay, there may now only be a few: Tortuguerro rookery of Caribbean Costa Rica; Ras al Had in Oman; Northwest Shelf of Western Australia. Australia and, in particular the GBR, is one of the last strongholds for a once flourishing species worldwide.

Within a few years of commencement of our tagging at Raine Island it became apparent that many of the turtles were migrating from feeding areas outside of Australia. In addition, large numbers of *C. mydas* were being hunted for food, both at the village level and for commercial market, within the feeding areas supplying turtles to the Australian rookeries. So, while there has been almost total protection of the nesting females at the GBR rookeries for many years, the population is under a large but imprecisely determined harvest pressure. In many areas this harvest targets large females but in Torres Strait gravid females migrating to breed are preferred where they are available. The pattern that has developed this century with turtle harvests in other countries is that marine turtle population numbers will crash following several decades of intense harvesting. Given that the large harvests that target the Raine Island turtles have only been operating in the past 2 or 3 decades, concern must be held for the future stability of this population. Improvements in our basic understanding of turtle biology and significant improvements in marine turtle management are surely needed in these times of declining turtle populations in Southeast Asia and the Western Pacific Region (Limpus, 1997). This is particularly so, given that sustainable management of marine turtle populations subjected to large scale harvests has not been achieved in the 300 years since the elements of our modern understandings of green turtle biology were first described by William Dampier in 1717 (Masefield, 1906).

The turtle research at Raine Island in the years 1975-1979 was initially part of exploratory studies by the Queensland Government Conservation Agency (currently called Queensland Parks and Wildlife Service [QPWS]) to map the species composition, size and distribution of marine turtle breeding populations in Queensland. At that time it became apparent that there was a lack of fundamental information required to effectively manage a marine turtle

population in the face of large scale harvesting and guarantee its long term continuity. During the period 1979-1985, the Queensland Turtle Research Project undertook the development of new methodologies to address marine turtle population dynamics. These included: tagging methodology to enable turtles to be recognised over decades rather than a few years (Limpus, 1992a); capturing techniques for studying the turtles in their home feeding areas (Limpus & Read, 1985a); methodologies for sexing and assessing the reproductive status of turtles in their feeding areas (Limpus, 1992b); genetics research to determine methods of recognising the distribution and number of genetically discrete breeding units within our *C. mydas* herds (Norman et al., 1994a); and mark-recapture studies to provide the quantified life table parameters including fecundity, growth data, survivorship and recruitment, (Limpus & Chaloupka, 1997; Chaloupka & Limpus, 2002) that are necessary for developing good models for describing marine turtle population dynamics (Chaloupka & Limpus, 1996; Chaloupka, 2002).

This latter issue of understanding population dynamics is vital if we are to manage our turtle herds on a sustainable basis in the face of large scale mortality from harvest and other sources.

Recognising the potential threats to the conservation of the GBR *C. mydas* breeding populations posed by large scale harvesting within the Australasian region, QPWS placed a priority on studies of *C. mydas* in 1985. An integrated set of field studies was developed, bringing together a team of researchers with diverse skills, to investigate the population dynamics of eastern Australian green turtles. The study commenced in 1986 and became fully operational in 1987. At the core of the study has been the simultaneous study of *C. mydas* at each of its three eastern Australian rookery regions and at a series of feeding areas distributed throughout eastern Australia.

For logistical considerations, Heron Island within the southern GBR nesting area was selected as the primary study site for in-depth research of the reproductive biology of *C. mydas*. Access to the major nesting beaches of the northern GBR has been more difficult because of the remoteness of Raine Island and Moulter Cay and large expense associated with maintaining on-site studies there. Therefore, studies at Raine Island were planned as short term sampling studies rather than total season tagging census studies with an emphasis on quantifying those parameters considered to have unique values for Raine Island. It was also recognised that results of past intense studies from Bramble Cay in the extreme northern GBR would supplement results for the Raine Island area.

It is in the context of this complex mosaic of diverse, yet complementary investigations, that the present study of the *C. mydas* nesting population at Raine Island and adjacent rookeries is presented. It is part of a planned, long-term, integrated regional study of green turtles in the Australasian region designed to provide sound information that can assist in improving the conservation management of *C. mydas*.

METHODS

Data for this study was drawn from the historical and published accounts of Raine Island, from the results of interviews with fishermen and others who visited the island in recent years and from field studies undertaken at Raine Island in the period 1974 to February 2002. While the principal emphasis will be on Raine Island and its turtle population, the green turtle populations at Moulter Cay and the other islands in the northern Great Barrier Reef will also be considered.

SPECIES IDENTIFICATION. Turtle species identification was made from the available keys (Bustard, 1972 and Cogger & Lindner, 1969). These data have been modified into the field key used in the QPWS Queensland Turtle Research (QTR) Project (Limpus, 1992c).

TAGGING. Table 1 summarises the types of tags and their positions of application used in the present study. All tags were self-piercing self-locking flipper tags, serially numbered with a return address on the opposite side to the number. Monel tags: National Band and Tag Company, Kentucky; style 1005, #49 and #19; weight = 7g. Three series of monel tags were used, each being identified by the prefix to the tag number (Table 1). Titanium tags: Stockbrands Company Pty Ltd, Western Australia; #standard; weight = 4g, commercially pure titanium, grade 125, 1mm thick. These titanium tags have a locking mechanism resembling that of the monel tag style 1005 #19. Return address was to Queensland Parks and Wildlife Service. All titanium tags carry a T, I or K prefix to the tag number.

Tags have been applied to various positions on the trailing edge of the front flippers. Standard tagging positions (Limpus, 1992a) have been

TABLE 1. Summary of tag designs, return addresses, tagging positions and the number of tags applied per turtle. See Limpus (1992a) for further definitions. * Recaptured turtles from previous seasons or other studies were double tagged L3 and R3.

Tag series	Metal type or style	No. tags per female	Tagging position	Return address
No prefix	Monel #49	1	L1	Applied Ecology Pty Ltd
A prefix	Monel #49	2	L1 & R1	Applied Ecology Pty Ltd
X prefix				QPWS
Under X35000	Monel #49	1	L1 prior to 1978	
		1	L3 after July 1978	
Above X35000	Monel #19	1*	L3 after 1979	
T prefix, I prefix, K prefix	Titanium	1*	L3	QPWS

coded as follows: L = left front flipper; R = right front flipper; 1 = tag applied immediately distal to phalange 5 (after Bustard, 1968); 3 = tag applied through or adjacent to the most proximal axillary scale (= axillary tagging scale, Limpus & Reed, 1985a). Thus a tag can be described as having being applied at the L1, L3, R1 or R3 position.

COUNTING TURTLES. Counts or indices of the number of turtles ashore per night were established in one of the following ways:

a) Tally count. An instantaneous count of all turtles was conducted by several persons walking line abreast across the beach, for one circuit of the island between 2000-2300hr (a tally count usually took 40-60min. to complete). Counts commenced at least one hour after turtles had swimming access to the nesting beach across the reef flat after dark. During the summer nesting season the tides are such that on most of the nights, the majority of the turtles for the night will have beached within a few hours of darkness. A green turtle rarely lays and returns to the water in less than 3hr on the beach.

b) Tagging census. A count of all turtles ashore for the night based on tagging records. This was only attempted during periods of low density nesting (<400 females ashore per night).

c) Track count. A count of all turtle tracks for the night by species, based on a count just after dawn of the tracks that start below the previous nights high tide mark. Each track equals an 'emergence' and a 'return' component. This method has only been applicable on nights with a low density of turtles. At Raine Island, if there is an error it will usually involve some under-estimation. At localities visited for a single day only, tracks accumulated over several nights may be indistinguishable, resulting in the potential for overestimates.

d) Stepping index. Commencing with the Raine Island during the 1987 summer expedition, the opportunity was taken to evaluate nesting density equivalents to old reports from fishermen who spoke of having walked across the backs of many nesting turtles without having to step down onto the sand. When dense aggregations of nesting turtles were encountered on Raine Island beach between 2100-2400hrs, an agile average sized person stepped from turtle to turtle for as many steps as possible without stepping onto the beach. The number of turtles stepped on is defined as the stepping index of the nesting density. This was repeated at several places around the island on each night. It was not attempted on nights with rain when the carapaces were slippery.

MEASUREMENTS OF TURTLES, EGGS AND NESTS. The adult turtles were measured as follows. Curved carapace measurements were taken with flexible fibre-glass tape measure (±0.5cm prior to 1983; ±0.1cm thereafter) stretched tightly from edge to edge. Straight carapace measurements were taken with a steel tape measure (±0.1cm) and large wooden dividers with recurved ends. Measurements of standard length were made along the midline from the anterior skin-carapace junction to the apex of the posterior midline notch between the supracaudal scutes (curved and straight carapace length = CCL and SCL, respectively). Width was measured at the widest part of the carapace (curved and straight carapace width = CCW and SCW, respectively). These measurements correspond to those used in other major studies of marine turtles in Australia (Limpus, 1971; Bustard, 1972; Limpus et al., 1983a,b, 1984a). To allow for comparison with turtle studies in other areas, adults were also measured for the standard length measurement used by Professor Archie Carr, i.e. from the most anterior projection of the carapace over the shoulder to the tip of the most posterior projection of the carapace (= Carr's straight carapace length [CSCL] [Carr and Ogren 1960]; this is not a midline measurement). Adult turtles were weighed on Salter dial balances (±0.5kg). Females were weighed after completion of oviposition.

Clutches were counted and eggs measured within 2 hours of being laid and with a minimum of rotation and vibration of the eggs (Limpus et al., 1979; Parmenter, 1980a). Eggs and hatchlings were measured for mean diameter and straight carapace length, respectively, with vernier slide callipers (±0.01cm) and weighed on Pesola spring balances (±0.5g). No more than 10 eggs or hatchlings were measured per clutch. The emergence success of a clutch was assessed by excavation of the nest and recording the fate of the eggs by six classes: undeveloped = egg contained no obvious embryo (< Stage 17 of Miller, 1985); unhatched = egg contained a recognisable embryo (> stage 17 of Miller, 1985); predated = egg broken by crab; dead in nest = hatchling died after hatching, but below the beach surface; live in nest = hatchling was alive, but had not emerged from the nest (groups of live hatchlings just below the surface and not tangled in vegetation were counted as having emerged); emerged = hatchlings which successfully hatched and escaped from the nest to the beach surface (Limpus et al., 1983a,b).

Nest depths were measured with a fibreglass tape measure (±0.5cm) from the beach surface to the top of the upper most egg and to the bottom of the egg chamber (sinsu Bustard & Greenham, 1969).

Sand temperature was measured with a mercury-in-glass thermometer (±0.5°C) inserted horizontally into the sand 50cm below the surface. Core body temperatures of nesting turtles were measured by the Mrosovsky & Pritchard (1971) method. This required catching an egg immediately as it was oviposited and inserting a quick reading mercury-in-glass thermometer into the middle of the yolk.

NESTING SUCCESS AND CLUTCH DESTRUCTION. Two methods were used for estimating nesting success, here defined as the proportion of females ashore for the night that lay a clutch.

a) Following individual turtles. Nesting turtles were selected at random as they came ashore on the western end of the island at night and were followed until they returned to the sea. Their nesting success was recorded. This method of measurement was time consuming, as it required a person committed to maintain observation of an individual turtle, irrespective of how long it was ashore. Usually only one turtle could be followed on any one night. Each turtle had to be followed at such a distance that she did not respond to the observer's presence.

b) Using fixed sampling sites. Standard study sites were chosen on opposite sides of the island. Unless otherwise stated, each site was 100m in length and extended from the water line to the cliff line. On selected nights, within one or both of these sampling sites, a count was made of the number of turtles which entered the sampling site from across the waterline, the number of clutches laid within the area by these turtles, and the number of existing clutches that were dug into by the nesting turtles. Each data set required one person monitoring a sampling site for approximately 14hr continuously commencing at about 1600hr. Two rate parameters can be calculated from these data: nesting success (NS) and clutch disturbance (CD) by nesting turtles.

NS = Number of clutches laid / total number of turtles entering area

Nesting success was calculated on the number of turtles crossing the high water line on the assumption that lateral movements into and out of the sampling sites along the beach by turtles attempting to nest are approximately random and will cancel each other.

CD = Number of existing clutches disturbed / Number of new clutches laid.

When a turtle was found digging into an existing clutch, irrespective of where it was on the island, the number of eggs dug from the nest was counted. These counts provide a measure of the egg mortality per clutch disturbed (EMpDC) by nesting females. When compared to the mean clutch count for the rookery, this egg destruction can be expressed as the proportion of a clutch destroyed per clutch laid (clutch equivalent egg mortality = CEEM) CEEM = EMpDC × CD / mean clutch count.

ESTIMATION OF THE SIZE OF THE ANNUAL NESTING POPULATION.

Petersen Estimate. If a sample of the turtles ashore on Raine Island at night is marked so that they can be recognised in the water over the following days, and if the marked turtles are uniformly distributed among the unmarked turtles in the waters surrounding Raine Island, then mark-recapture data can be analysed using the Petersen estimate with Bailey's correction (Caughley, 1977) to provide an estimate of the number of adult green turtles in the waters surrounding Raine Island at that time.

In a population where M animals are marked

out of a total population of N animals and m marked animals are recaptured in a subsequent sampling of n animals:

$N = M(n+1) / (m+1)$

This estimate has a formal standard error of approximately:

$SE = [M^2(n+1)(n-m) / (m+1)^2(m+2)]^{1/2}$

The principal assumptions made in using this method are: 1) the marked turtles are uniformly distributed among the unmarked turtles that form the Raine Island breeding assemblage within the internesting habitat on that day; 2) there is a negligible rate of loss of the mark between marking and recapture; 3) the marks are easily seen on the swimming turtle; 4) all the females aggregated on Raine Island Reef are there to breed i.e. there are insignificant resident non-breeding female and immature male populations on Raine Island Reef; 5) there is equal probability of the tagged and untagged turtles moving outside the sampling area; and 6) there is negligible mortality of the adult turtles during the sampling period.

Two methods have been used to mark the Raine Island nesting turtles for mark recapture studies.

1) Standard turtle tags. Within a study trip, after several nights of tagging the nesting females on the beach, a search of sections of the surrounding Raine Island Reef was made to locate, count and visually check females for the presence or absence of a tag. Only those females checked were counted. Those seen in the distance but not checked were excluded from calculations. Monel tags applied to the L1 or R1 tagging positions (towards the distal ends of the front flippers) were readily visible on a swimming turtle. In 1979 the place of application of the metal tags was changed to the axillary area of the trailing edge of the front flippers (L3 or R3 tagging positions) to improve tag retention. This axillary tag placement resulted in a reduced visibility of the metal tag on the swimming turtle, especially for those not viewed at very close range. The poor retention rate of monel tags (Limpus, 1992a) made it unlikely that there was a significant proportion of remigrant turtles that would be counted in the internesting habitat as part of n but which were not part of M.

2) Paint marks on the carapace. Commercially available paint was use to mark the dry carapace of nesting turtles on Raine Island at night. Paint marks were at least 10cm long, applied by a 2.5cm wide brush or by a pressure pack can, were applied to the dry carapace of nesting turtles on Raine Island at night. Oil based enamel paints were used initially. Commencing in 1995, the paint used to mark the turtles was changed to white Wattyl Airpave™ (504-40100. BN:-451695-09) paint applied as single stripes with 5.0cm wide brushes. On the first night of painting, the stripes were longitudinal along the midline, on the posterior half of the carapace. If turtles were painted on a second night in the same trip, those marks were transverse stripes on the posterior half of the carapace. A turtle was selected for painting if: the carapace was dry; the carapace did not have a thick coating of algae; and the turtle was inland of the beach crest, and well within the nesting habitat. When applied in these conditions, the paint was observed to adhere well to the carapace surface for at least 48hr (enamel paint) or 96hr (Airpave). Using this marking system, the goal was to paint-mark as many turtles as possible on the island in a single night. A search was made for marked turtles among the turtles in the waters surrounding the island on subsequent days. Turtles seen were recorded by species and tail length. Those with long tails were scored as male, adult-sized short tailed turtles were scored as presumed adult female and those smaller than adult female (CCL <90cm for *C. mydas*; CCL <75cm for *E. imbricata*) were scored as immature (Limpus & Reed, 1985a; Limpus, 1992b). Counts were made of those females for which the presence/absence of the tag/paint mark could be definitely established.

Two types of in-water searches were made for the turtles.

1) Diving transects. Transects using SCUBA, or snorkel, were swum along the reef edge above the 10m depth terrace. Written records were kept on waterproof paper. During a diving transect, two persons were in the water, one counting and one on the lookout for sharks. The lookout carried a hand spear for warding off sharks and the recorder carried a line attached to a buoy at the surface. A third person maintained a dinghy adjacent to the buoy for rapid retrieval of the divers from the water, if required.

2) Speedboat transects. On days with clear, relatively calm water, transects were driven across the reef flat at the upper part of the tidal cycle and along the outer edge of the reef in search of turtles, using an outboard powered dinghy. By driving adjacent to the swimming turtle, it was possible to score it by species/size/sex/mark presence. A minimum of two persons were required in the speedboat, one recording and the other driving and counting. The

acceleration capability of the speedboat was vital. The boat had to be able to accelerate quickly to reach the turtle before its swimming disturbed others nearby, or before it escaped to deep water. Boats about 4-5m in length, powered with a 40-60HP outboard motor were best suited to this use in shallow water. Conventional 3.5m aluminium dinghies and inflatable dinghies fitted with 10-15HP outboard motors proved unsuited to the task.

In high density nesting seasons, it was impossible to obtain an absolute measure of the nightly number of females emerging on Raine Island, so the mean nightly tally count has been used in lieu of the number of turtles emerging per night. This under-estimates the actual number of turtles emerging nightly.

MORTALITY STUDIES. The number of dead and moribund turtles at each studied rookery was recorded on arrival. Subsequent adult mortality, particularly on Raine Island, was recorded daily. Previously encountered carcasses were identified by flagging them with coloured surveying tape or by paint marks. Moribund turtles were rescued where possible, especially those that had fallen onto their backs. These rescued turtles were counted as mortalities for the purposes of the study.

In December 1989, a group of turtles that had remained on the beach until at least mid-morning, and were in a location where all such turtles died naturally of heat exhaustion were selected for detailed study. Changes in core body temperatures of these moribund turtles was assessed by inserting a cannula through the inguinal pocket anteriodorsally, to the movement arch of the hind leg (as is done during laparoscopic examination of turtles). The cannula provided access to the abdominal cavity and allowed a thermometer probe, attached to a 50cm rod, to be inserted to lie above the gut and ventral to the lungs just posterior to the heart. The lead and readout unit were taped to the carapace and the turtles were allowed to move undisturbed on the beach until they died. Temperatures were read at half hourly intervals. Necropsies of these turtles confirmed the correct placement of the probes, and that no damage had been done to organs or blood vessels. The insertion of the probes did not contribute to the death of the turtles.

The daily census of dead and moribund turtles was conducted between 1500 and 1900hr. On occasion, freshly dead turtles were necropsied to assess oviducal contents and ovarian condition.

TABLE 2. Circumference of sand islands used by green turtles for nesting in the Far Northern Great Barrier reef. Circumference was measured at approximately mean high water spring tide level using a pedometer.

Island	Date	Circumference
Raine Island	1977 Dec	1799m
	1978 Dec	1764m
	1980 Jun	1808m
Moulter Cay	1976 Dec	1179m
	1977 Dec	1138m
Maclennan Cay	1978 Nov	885m
No. 7 Sandbank	1976 Nov	1755m
No. 8 Sandbank	1976 Nov	1816m
Bramble Cay	1977 Dec	748m

In December 1989 the core body temperature of some dead turtles was measured during necroscopy.

RECRUITMENT RATE STUDIES. We have introduced a new method for marine turtle studies for quantifying recruitment of new adults into the breeding population. Traditionally, recruitment of new adults into the breeding population has used long term total tagging census to identify all turtles with a past breeding history. After a total tagging census at a nesting beach that spans several mean remigration intervals, turtles that have not been previously tagged are identified as new recruit (Hughes, 1989; Richardson & Richardson, 1982; Limpus, 1985; Limpus et al., 1984b; Parmenter & Limpus, 1995). This has been an inappropriate method for the Raine Island population given the difficulties in tagging the entire nesting population, even in a single year. Within foraging area studies in eastern Australia, marine turtles have been assessed for recruiting into the adult breeding population using ovarian features, in particular scoring for the presence or absence of corpora albicantia. A corpus albicantium is a healed corpus luteum and a corpus luteum is formed by the release (ovulation) of a mature follicle from the ovary. The presence of corpora albicantia indicates that a female has bred in a past nesting season. Similarly the absence of corpora albicantia on the ovaries of a female with oviducal eggs indicates that she has not bred in a past breeding season and that she is in her first breeding season. Therefore the absence of corpora albicantia in the ovaries of females that have recently ovulated can be used to identify those females that are new recruits to the breeding population (Limpus & Limpus, 2003).

Ovaries were examined by direct examination via necropsy of nesting females that had freshly

died on the nesting beach or by endoscopy (Limpus & Reed, 1985b; Limpus et al., 1994c). For endoscopy of the breeding female, it was necessary to examine females ashore as they completed the laying of a clutch. Otherwise the presence of oviducal eggs made it very difficult to view the surface of the ovary clearly. Limpus & Limpus (2003) provide a key for scoring sex, maturity, breeding status and recruitment from gonad examination.

GENETIC STUDIES. Tissue samples were collected for genetic research in a variety of ways. Non-sibling hatchlings were sampled by collecting one hatchling per clutch from clutches which emerged within a two week period at any given rookery (Norman et al., 1994a). This ensured that no more than a single hatchling was sampled from any one female within the breeding season. To ensure that individual adult turtles were sampled only once, adult turtles with unique tag numbers were sampled for either muscle, blood or skin (Norman et al., 1994b; FitzSimmons et al., 1995). The methods for genetic analysis are described in these separate papers.

RESTRICTIONS ON STUDIES AT RAINE ISLAND. Raine Island and the adjacent islands have proven to be logistically difficult for long term and exrended period study due to remoteness. The number of personnel that can be deployed on the island for the turtle studies has been limited because of the need to minimise disturbance to the nesting colonies of sea birds that Raine Island supports.

The first trips to Raine Island for this study were opportunist. The Queensland Parks and Wildlife Service (QPWS) study was supported in part by research grants from the Australian National Parks and Wildlife Service during 1976-1979. In 1977 and 1978 the expeditions to Raine Island were supported by Applied Ecology Pty Ltd (AE) who provided a vessel to visit the island. In 1979 with the aid of a WWF grant a study of seas birds at Raine Island was commenced and one turtle researcher was able to accompany the bird study group. In 1981 the Raine Island Corporation became responsible for the conservation of Raine Island and commenced funding research expeditions to Raine Island. From 1981 to 1985 the Raine Island Corporation chose to place an emphasis on sea bird studies and the turtle research team was limited to one person on the island in any one trip except during December 1984, when 2 persons were present for the turtle studies. The sea bird research team assisted with turtle tally counts and incidentally with the other aspects of the study. Since 1985 the Raine Island Corporation has reduced its emphasis on sea bird studies at Raine Island and has funded the summer expeditions primarily for the turtle research with teams of 4-5 persons per trip. To maximise the data gathered on a trip, small numbers of other islands were surveyed for marine turtle nesting during transit to and from raine Island. Thus from 1975-1989, the majority of the islands between Princess Charlotte Bay and Cape York were surveyed at least once. These data provided a measure of the regional distribution of marine turtle nesting by species.

CLIMATE DATA. Regional rainfall and temperature data from the three long-term Coral Sea weather stations nearest to Raine Island (Torres Strait, Willis Island and Lockhardt River) were obtained from the Australian Bureau of Meteorology.

STUDY AREA

RAINE ISLAND. Raine Island (11°36'S, 144°01'E) is a coral cay on the leeward north-western end of a small detached reef on the outer edge of the northern GBR (Fig. 1). The island is approximately 80km offshore from the mainland, north east of Cape Grenville. Raine Island Reef lies in the eastern approaches at the Raine Island Entrance, a deep water passage through the outer barrier reef. The reef rises abruptly out of deep water with near precipitous cliffs to a narrow terrace at approximately 8m depth and is topped by an approximately uniform height reef flat that dries at the lower tidal ranges.

Raine Island, as described in recent times (Warham, 1977; Stoddart et al., 1981; King, 1986), approximates to the island as it was described in 1843 (Jukes, 1847). The island is approximately 1800m in circumference at the mean high water spring (HWS) tide level (Fig. 2, Table 2). The beach substrate is a white calcium carbonate sand composed of mostly fragmented coral and mollusc and foraminiferan skeletons (= star sand). Turtle and sea bird bones are obvious but at low density within this sand. The beach width measured from the high tide line to the low cliff line of the central rock platform varies from approximately 15m near the beacon to 90m on the southern side. Storms wash over the outer beach rim to flood the beach depression, as indicated by accumulated pumice in the floor of this depression.

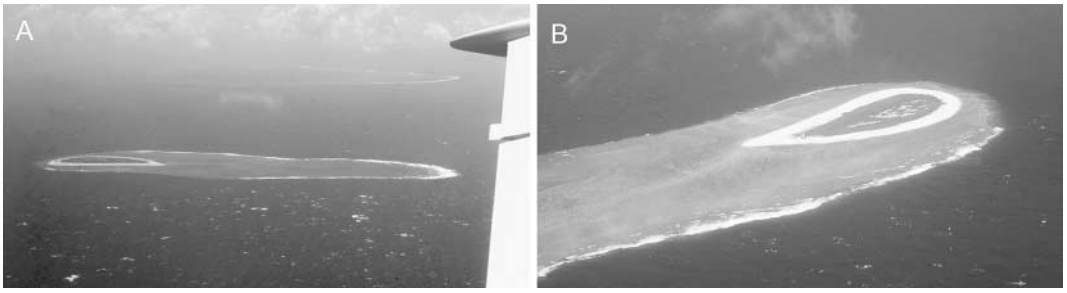

FIG. 1. Raine Island lies on the north-western end of Raine Island Reef. This small detached reef outside the main outer barrier reef marks the eastern boundary of the Raine Island Entrance. (8 April 1980). A, Raine Island and its reef, viewed looking north. B, this view of Raine Island shows a reduced beach vegetation cover outside the cliff line.

The island is devoid of trees. The inland portion of the beach is covered by grasses and herbs that vary in density and extent from year to year (Fig. 3). In breeding seasons with high density turtle nesting, the beach can be completely dug-over almost nightly and, as a result, can be essentially devoid of surface vegetation, e.g. following the 1974, 1984 and 1996 breeding seasons (Fig. 3A,F). Following such dense nesting seasons, the surface vegetation regenerates during and following the wet season, in the early to mid year. In a low density breeding season, there may be little disturbance to the beach vegetation (Fig. 3C) and it may be up to 0.5m high and extend over a half of the beach width at the commencement of the wet season. On all visits, the beach surface was uneven and cratered with turtle body pits of varying age.

The typical water line to cliff tracsect on the island, demonstrates a beach crest as an unvegetated outer ridge approximately 1 m above the mean HWS tide level. From this ridge the beach slopes downward into a depression before again rising to the base of the cliff line edging the central rock platform. The beach depression encircles the island except for a narrow rocky area adjacent to the tower. The floor of the beach depression can be up to 1 m below the outer beach ridge (i.e. at approximately the same horizontal level as the mean HWS tide) and slopes upwards in the seaward direction by as much as 13°.

The cliff line around the central rock platform (Figs 3, 4) ranged 1-2m in height and was usually a barrier to turtles climbing from the beach onto the surface of the central platform. At times, nesting turtles at the base of the cliff threw up sand rampways that provided temporary access onto the central platform by other nesting turtles. The position of the ramps constantly changed in high density nesting seasons as turtles dug away some ramps and formed others. These ramps provided access to the raised surface of the rock platform, especially in years of high density turtle nesting. This resulted in digging turtles creating patches of disturbed vegetation and bare sand on the adjacent rock platform surface adjacent to natural ramps (Fig. 3A). From time to time, nesting turtles would also undermine sections of the cliff to form small caves under the edge of the central platform.

The central rock platform consists of a cemented phosphatic limestone and has an approximately horizontal upper surface approximately 2m above the HWS tide level. A vegetated sand ridge of uncemented calcareous sand, rising to a variable height up to approximately 5m above HWS tide level and covered with grass and herbs, rims the rock platform and surrounds the central depression (Fig. 2). The floor of the central depression is the upper surface of the phosphatic limestone platform and has been modified by past guano mining.

MOULTER CAY. Moulter Cay, formerly called Pandora Cay (11°27'S, 144°00'E) (Fig. 5A), is a vegetated sand cay on the extreme outer barrier of the Great Barrier Reef, lying 14.5km north of Raine Island about 82km from the mainland coast at Cape Grenville (King et al., 1983b). The island measured approximately 1150m in circumference at the HWS tide level (Table 2). The calcareous sand beach was of very similar composition to that of Raine Island. The island had an outer unvegetated and an inner vegetated portion similar in width, elevation and topography to that of Raine Island. The small central rock platform of phosphatic limestone is partially bordered by a low cliff less than 1 m high

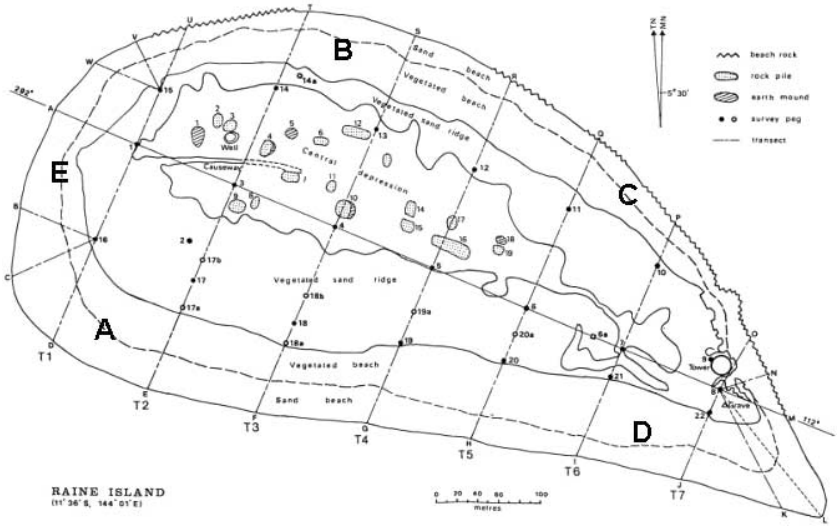

FIG. 2. Map of Raine Island, prepared by the late Brian King, showing the 100m interval grid lines. Study sites, 100m wide, for quantifying nesting success and clutch disturbance are designated by letters A to E.

at its maximum. As a result of this incomplete and low elevation cliff, no part of this island is protected from nesting turtle incursion. In the less dense turtle nesting seasons and following the wet season, the rock platform and the inner beach area has by a grass and herb coverage to approximately 0.5m high. There have been no trees established on this island in historic times.

MACLENNAN CAY. Maclennan Cay (11°22'S, 143°48'E) is a very small vegetated sand cay on a small reef inside the outer barrier of the GBR 32km northwest of Raine Island (King et al., 1983a) (Fig. 5B, Table 2). Its elevation is approximately 0.5m above the mean HWS tide level. The sand substrate of the island resembles that of Raine Island and Moulter Cay but there is no central rock platform. It is sparsely vegetated with grass and herbs and does not have established trees. The island is frequently washed over by storm surges.

NO.7 SANDBANK. No.7 Sandbank (13°27'S, 143°59'E) is a small unvegetated sand cay on the extreme outer barrier of the Great Barrier Reef approximately 37km east of the mainland at Cape Sidmouth and 7km south southeast of No.8 Sandbank (King & Limpus, 1983) (Fig. 5C, Table 2). The beach is composed of uncemented calcareous sand rising to less than 1m above HWS. The island does not have a central rock platform. The island has been devoid of trees during historical times.

NO.8 SANDBANK. No.8 Sandbank (13°22'S, 143°58'E) is a small vegetated sand cay on the extreme outer barrier of the Great Barrier Reef approximately 35km east of the mainland at Cape Sidmouth (King et al., 1983c) (Fig. 5C, Table 2). As with No.7 Sandbank, the beach is composed of uncemented calcareous sand rising to approximately 1m above HWS. There is no central rock platform on the island. The central portion of the island is covered with grass and herbsand the island has been devoid of trees during historical times.

GENERAL OBSERVATIONS ON THE OUTER BARRIER CAYS.

Trees. Seedling trees naturally germinated from beachwashed seeds (including *Barringtonia asiatica*, *Cocos nucifera* and *Nypa fruticans*) (Fig. 6) were found on the outer beach rim of Moulter Cay in December 1977 and Raine Island in December 1978. By December these seedlings were stressed and dying in the dry substrate of the outer beach rim. In most summers nesting turtles destroy any surviving plants on the outer beach rim of these islands. Any young tree that survived the digging of the nesting turtles would be used by perching sea birds and probably killed as a result.

Although Raine Island has been devoid of naturally occurring trees, some have been planted at various times by crews of passing boats, commencing with the visit of HMS *Fly* (Jukes,

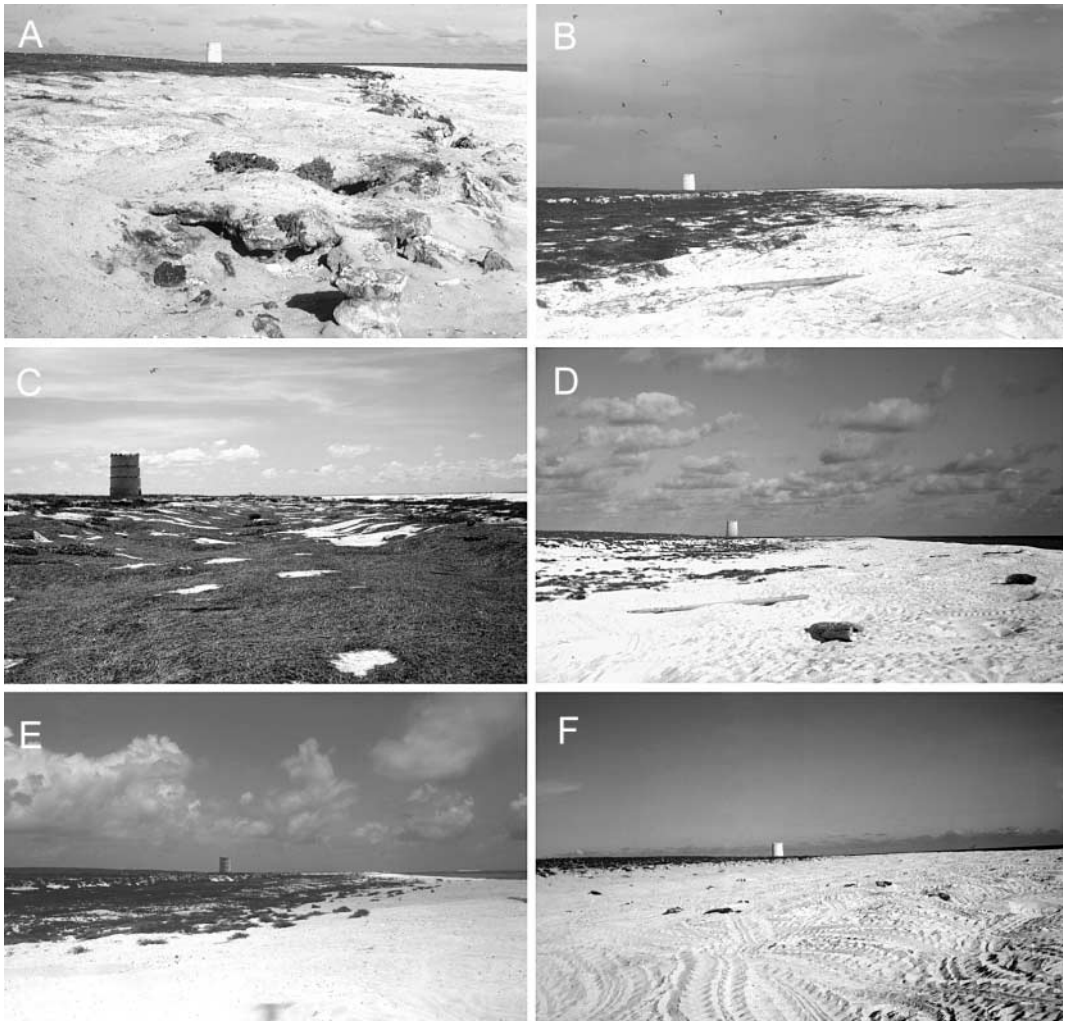

FIG. 3. Annual fluctuations in beach vegetation cover of Raine Island. Southern beach looking towards the beacon. A, 1974-75 breeding season, 1 March 1975. The beach is almost totally devoid of vegetation. Adjacent to sand rampways that gave access to the top of the rock platform for nesting turtles, the vegetation above the cliff line is also greatly reduced. B, 1976-77 breeding season, 3 December 1976. C, 1977-78 breeding season, 5 December 1977. This view illustrates the low level of disturbance of beach vegetation that can occur in years of very low density turtle nesting. D, 1978-79 breeding season, 2 December 1978. The same log is in the foreground as in B. E, 1980-81 breeding season, 5 December 1980. F, 1984-85 breeding season, 19 December 1984. This view illustrates the extreme level of disturbance of beach vegetation that can occur in years of very high density turtle nesting.

1847). The BBC documentary *Zoo Quest: The Birds of Paradise II. Raine Island* documents one such planting in July 1957. These trees have not survived in the long term. On the last occasion, six coconut palms (*Cocos nucifera*) were planted on the western sand dune of the central rock platform during 1980. Since 1976, any coconut trees found planted on these islands have been removed by QPWS staff.

Vertebrates. There are few species of animals resident on these islands that have an impact on the marine turtles. These outer barrier cays support no native terrestrial mammalian or reptilian inhabitants, except for Bramble Cay which supports a gecko and an endemic native

FIG. 4. Margin to the phosphatic limestone platform, Raine Island adjacent to the beacon where the rock platform had a well defined cliff margin.

rodent, *Melomys rubicola*. This is a small herbivorous rat that does not prey on turtle hatchling or their eggs (Limpus et al., 1983d). The gecko is *Hemidactylus frenatus*, a small insectivorous lizard that was probably introduced with the building materials or food parcels supplied to Bramble Cay during the 1970s when it was a research study site and egg collection site for the Torres Strait turtle farms. Goats were released onto Raine Island in the 1840s but disappeared from the island sometime late last century (Stoddart et al., 1981).

The extensive avifauna of these outer barrier coral cays has been reviewed in recent years: Raine Island (King, 1986), Moulter Cay (King et al., 1983b), Maclennan Cay (King et al., 1983a), No.8 Sandbank (King et al., 1983c), No.7 Sandbank (King & Limpus, 1983). However, most of the sea bird species, and in particular those that occur in very high density are not predators of the turtles. Observations of bird predation of the turtle hatchlings will be discussed in the section dealing with hatchling predation.

An estuarine crocodile, *Crocodylus porosus*, was observed at Raine Island on one occasion; it is commonly seen in low numbers on the inner shelf islands (Limpus, 1980c) and has been recorded preying on marine turtles elsewhere (Limpus et al., 1983b).

Invertebrates. Terrestrial crabs, all of which recruit to the islands from aquatic larval stages, have been scarce on Raine Island. Two species of ghost crab, *Ocypode cordimana* and *O. ceratophthalma*, occur at low density. These species occur on almost all islands in this area and have been recorded preying on turtle hatchlings and eggs. *O. pallidula* was collected from No.8 Sandbank. Two species of terrestrial hermit crab occur on these outer barrier reef cays. *Coenobita rugosus*, has been found at low density on Raine Island, Moulter Cay and No.8 Sandbank and in high density on No.7 Sandbank. The larger reddish coloured species, *C. perlatus* has been particularly abundant on No.7 Sandbank. These *Coenobita* spp. have not been observed interacting with the turtle hatchlings or eggs although *C. perlatus* is large enough to prey on hatchling turtles.

Oligochaete worms were recorded among hatched and unhatched eggs in nests at Raine Island in January 1997, December 1999 and December 2001. Specimens (N39131) collected 29 January 1983 by B. King were lodged with the Queensland Museum.

Climate Data. The north-western Coral Sea regional climate recorded at the three Bureau of Meteorology weather stations in closest proximity to Raine Island is characterised by relatively uniform maximum and minimum air temperatures year round. The warmer months coincide with a distinct summer wet season from December to April (Fig. 7). Mean monthly daily air temperatures are above 25°C year round and the mean monthly maximum air temperature did not exceed 35°C.

Eastern Australia and the Coral Sea region are subject to considerable variability in annual climate. This is illustrated by the variability in the monthly Southern Oscillation Index (SOI) (Fig. 8). Region rainfall, which has impacts on marine turtle nesting (Limpus et al., 2001), is under the influence of the regional climate fluctuations. Periods with a negative Southern Oscillation Index (SOI) are usually characterised by low rainfall while positive values are usually associated with elevated rainfall levels (Couper-Johnston, 2000). Examination of SOI fluctuations over the last 31 summers (Fig. 8) indicates that during the last six summers (since1996) there has been an atypical sequence of wet seasons. Indeed, based on positive SOI values, Raine Island since 1996 should have been exposed to 5 of the 6 wettest summers in the last 25yr (Figs 7, 8). It has been during this same period that flooding of the nesting habitat has become an obvious and regular event at these northern GBR rookeries. Photographs (Fig. 9A,B) demonstrate clearly that the water table can rise higher than the depth at which the turtle eggs have been laid. At this time we are not prepared to speculate as to whether this pattern of more regular wet summers is the result of long term climate fluctuation or of global warming (Manton et al., 2001).

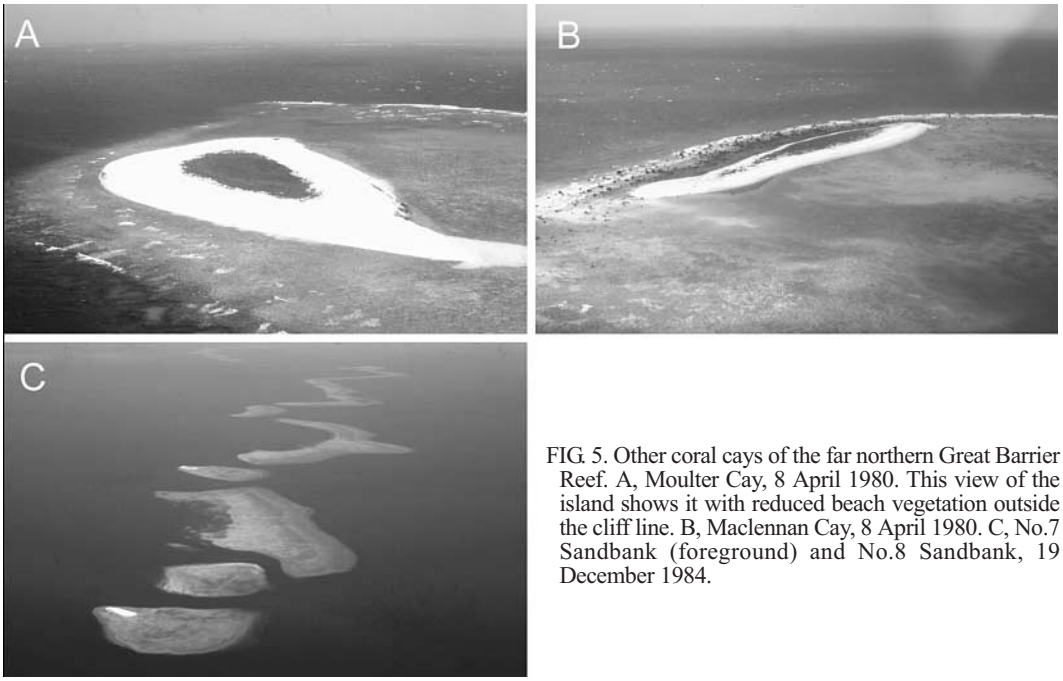

FIG. 5. Other coral cays of the far northern Great Barrier Reef. A, Moulter Cay, 8 April 1980. This view of the island shows it with reduced beach vegetation outside the cliff line. B, Maclennan Cay, 8 April 1980. C, No.7 Sandbank (foreground) and No.8 Sandbank, 19 December 1984.

HISTORICAL REVIEW OF PRE-1974 OBSERVATIONS OF TURTLES IN THE RAINE ISLAND REGION

The Raine Island Entrance from the Coral Sea through the Great Barrier Reef to Torres Strait was the focus of considerable navigational activity during the early to mid 19th Century. This, along with the large green turtle and sea bird populations associated with the adjacent islands (Raine Island and Moulter Cay) has resulted in numerous visits to the region by early Australian explorers, historians, sailors and naturalists. As a consequence there has been a considerable volume of natural history writings and observations on these islands.

FIG. 6. Seedling coconut palm, *Cocos nucifera*, growing on the outer beach rim of Moulter Cay, 3 December 1977.

Raine Island and adjacent Moulter Cay support one of the few remaining large breeding aggregations of *Chelonia mydas* in the world. In most areas where the species has bred in abundance in the past, the breeding populations have been greatly reduced, or taken to extinction by over harvesting at places such as Grand Cayman Island, Bermuda and Reunion Island (Groombridge & Luxmore, 1989). The current status of the turtle population that nests at Raine Island and Moulter Cay will be, in part, a function of the past history of human utilisation of the turtles and the islands. The following review of marine turtle records from these islands provides an historical context against which results of recent research can be compared and future change assessed.

The Queensland Turtle Research Project expanded to include systematic studies of the Raine Island *Chelonia mydas* rookery during the 1974-1975 breeding season. This then has been taken as the end point of the historical review of marine turtles in the Raine Island area. In this review, information has been brought together from diverse sources: published accounts of visits to the islands, interviews with fishermen

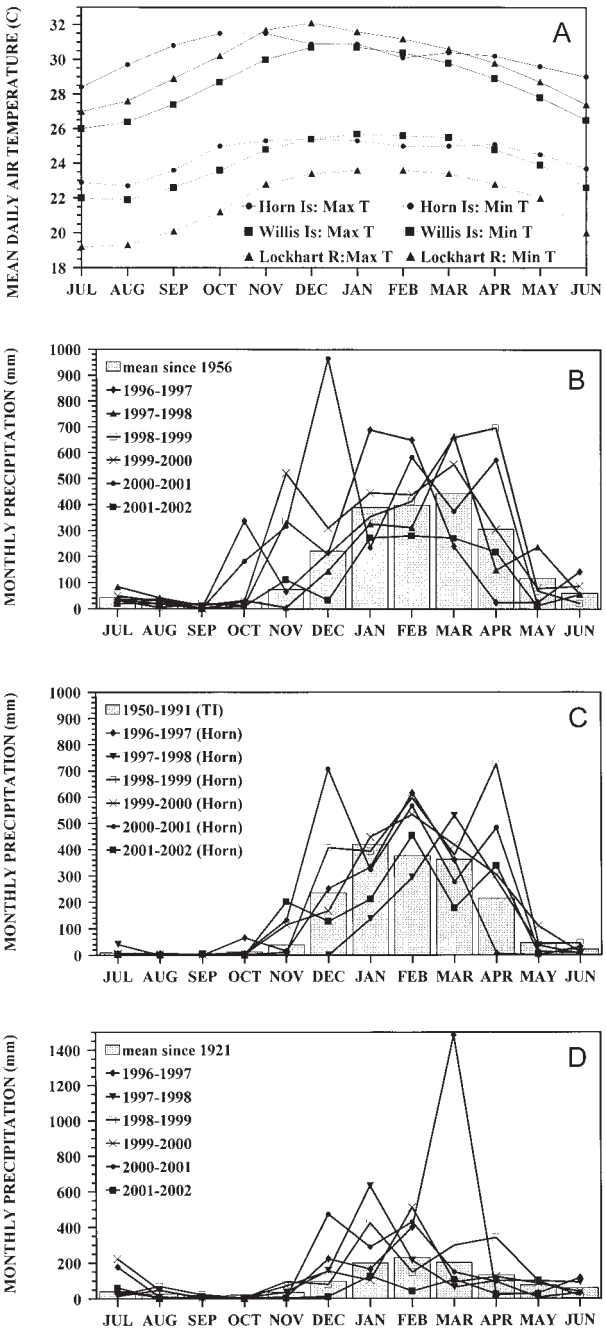

FIG. 7. North-western Coral Sea Regional climate data from Australian Bureau of Meteorology stations. A, monthly minimum and maximum air temperature data, Willis Island. B, monthly rainfall data from Lockhart River, NE Cape York Peninsula. C, monthly rainfall data from Horn Island and Thursday Island (TI), Torres Strait. D, monthly rainfall data from Willis Island.

and other visitors to the area, newspaper accounts of visits to the islands, and old photographs and documentaries. Together they contain a considerable body of knowledge, spanning 131 years of turtles at Raine Island and Moulter Cay. Also highlighted are some past misconceptions concerning marine turtle biology, including the belief that marine turtles could be systematically exploited on a grand scale.

HISTORICAL REVIEW. Raine Island was discovered by Thomas Raine on the HMS *Surry* in 1815 (de Salis, 1969). He did not land on the island and no reference was made to turtles.

Jukes (1847: 130-131) provided the first description of Raine Island and its natural history during the visit by HMS *Fly* on 29-30 July 1843. While the primary interest in the turtles was to provision the ship, Jukes provided some interpretation of the behaviour of the turtles at the island. They recorded a few turtle tracks on the beach, but did not capture any. Jukes was impressed by the large numbers of dead turtles and turtle bones on the island. He interpretation of the cause of their death was 'that when feeble, from sickness or age, the turtles have come here to die, and that those lying on their backs had died in a vain attempt to crawl up the broken bank into the interior of the island' (Jukes, 1847: 130). On 1 August 1843 he expressed a similar interpretation of why large numbers of turtles died at Moulter Cay (Jukes, 1847: 131).

HMS *Fly* and HMS *Bramble* returned during 29 May - mid September 1844 with a labour force of convicts to construct a navigation beacon on Raine Island (Jukes, 1847). The quarries dug during this construction work provided insights into the geology of the island and observations of fossil turtles and turtle eggs in considerable abundance (Jukes, 1847). Based on his observations of the fossil turtle eggs in nests, Jukes concluded that the rock forming the central elevated platform of Raine

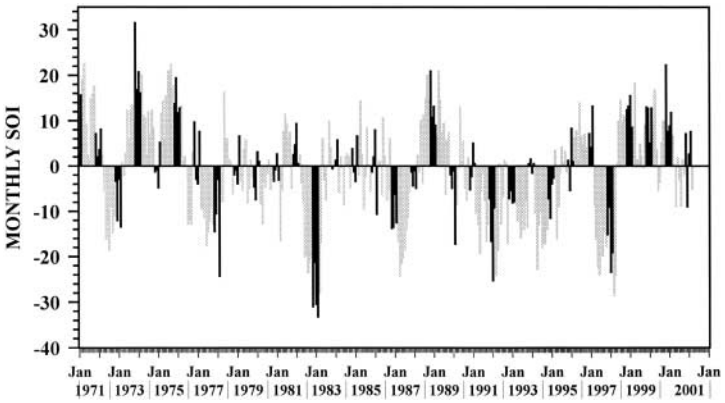

FIG. 8. Fluctuations in Southern Oscillation Index (SOI) over the 31 summers 1971 - 2001 (Bureau of Meteorology Australia, 2002). Summer SOI values (November - February) are shown in black.

Island had not been formed underwater and subsequently elevated.

MacGillivray (1846: 1474-1478), the naturalist on board HMS *Rattlesnake,* also visited Raine Island at this time and commented on the fossil turtle eggs in nests, citing them as evidence of the recent formation of this bed of sandstone 'only a few feet thick' where the rock for the tower was quarried. MacGillivray (1846) also made a number of original observations on the biology of the nesting turtles. All turtles visiting Raine Island and adjacent islands were '*green*' turtles which came to lay eggs, mostly at night. During June to August, single turtles came ashore at irregular intervals while the nesting density increased during September. He expressed surprise at the number of dead turtles on their backs which he interpreted as turtles that had fallen on their backs while endeavouring to climb the low rocky border of the island. He makes no reference to Dipterans associated with the turtle carcases, but notes the presence of 'several necrophagous Coleoptera'. Turtle bones were abundant enough on the island for him to note that 'noddies, *Anous stolidus*, used fragments of turtle shell and turtle bones among their nest building material'. While he wrote that hatchling turtles were 'preyed upon by various kinds of sea-fowls, from the frigate-bird down to the sooty tern', he only reported on one observation of a 'young turtle from the stomach of a tern which had swallowed it entire'.

An immature hawksbill turtle, *Eretmochelys imbricata*, was presumably collected during the 1844 visit by HMS *Fly*: British Museum specimen, register no. 46.7.27.6; immature with curved carapace length = 35.5cm; collected at Raine Island and presented by Lieut. Ince in July 1846 (A.F. Stimson in litt., 26 May 1977). This is the Boulenger (1889) specimen 'w'.

The crew of the *Heroine* went ashore on Raine Island on 28 January 1845 at daylight and 'obtained fourteen large turtles, each averaging four cwt.; also an immense number of eggs, and the crew killed birds out of number' (Mackenzie, 1845: 494).

FIG. 9. Raine Island during early December 1999 showing: A, the elevated water table level on the southern beach platform; B, a perched water layer in the central depression (flooding at this level is not tidal).

Sweatman (in Allen & Corris, 1977) was a clerk on board HMS *Bramble* with a responsibility for keeping records of provisions for the ship throughout its voyages and, as a result, his diary provides many quantified details of the occurrence of turtles. Crew members from HMS *Bramble* were on Raine Island during 28 April - 4 May 1845 when they caught 14 turtles. One was a live turtle which had fallen into the well near the tower and been trapped there for some time. He describes nightly patrols of the island at 2 hourly intervals to locate the nesting turtles, the walking of the turtles on tethers in the shallows to move them around to the anchorage end of the island by day and the novelty of riding on the turtles back in the shallows. Sharks were reported to attack the turtles being walked on tethers. Sweatman also describes abundant remains of dead turtles on their backs along the cliff.

Sweatman (in Allen & Corris, 1977: 55), in commenting on the food shortage on board HMS *Bramble* as she returned to Port Jackson on 9 July 1845, noted that 'Had it not been for the turtle caught at Raine's It. and the fish caught on the reefs we would have been destitute for food 3 weeks before'.

Stoddart et al. (1981) reported that the HMS *Heroine* was again in the vicinity of Raine Island on 5 August 1846 but there is no recorded attempt to collect turtles. However, the date of this visit is probably incorrect because the *Heroine* was recorded sunk on 24 April 1846.

On 24 July 1850 the HMS *Enchantress* was wrecked on Raine Island Reef. The crew went ashore on Raine Island and was rescued on 25 July 1850 by the by HMS *Lady Margaret* (Lack, 1953). The ship HMS *Constant* was also wrecked on Raine Island Reef on 12 July 1858 (Loney, 1980). There were no records of turtles being encountered by the survivors of either of these wrecks.

Rattray (1869) visited Raine Island in 1860 on board HMS *Salamander* and interpreted the phosphatic limestone rock of Raine Island as 'a thin layer of guano deposited by the numerous turtle and flocks of terns, gannets, and other aquatic birds that, like the former, make this their headquarters and favourite breeding-place'. The authors are unaware of any other report that attributes guano formation to turtle nesting activity. Given that turtles do not defaecate while on the nesting beach, this interpretation is presumed to relate to the incorporation of decaying turtles into the substrate.

In 1860, HMS *Herald* visited Raine Island twice (Denham, 1861): in April when supplies were left on the island; and 19 September to check on the condition of the supplies. There was no reference in Denham's diary to turtles or any other aspect of the island from either visit.

In 1862, Raine Island was leased for guano mining but there appears to be no reference to turtles in respect to this (Crowther, 1939).

In about 1874 a beche-de-mer fishery camp was operating on Raine Island and staffed by 2 whites, 2 or 3 Chinese, several Kanakas and some aboriginals from the adjacent mainland (Ellis, 1936). The duration of this operation was not stated but Ellis implied that they harvested turtles from the island to provision the crew.

Moseley (1879), in reporting on the 31 August 1874 visit of HMS *Challenger* to Raine Island, commented on the death of large turtles on the island. He interpreted the death of many turtles at the base of one part of the cliff as being the result of turtles coming ashore to lay eggs. He believed that they were unable to turn around or go backwards and hence died at the foot of the small cliff.

During 1890-92, Raine Island was extensively mined for guano with approximately 110 persons resident on the island at times and turtles were taken for food (Ellis, 1936). The total harvest was not documented: one turtle was killed daily during the nesting season to feed the European staff (about 10 people); eggs were also occasionally eaten; but the consumption rate by the approximately 100 Chinese labourers was not recorded. Ellis, the manager of the mining operation, provided the first account of the massed nesting by green turtles at the island: 'The coral sand beaches of Raine Island were visited by incredible numbers of green turtles during the summer months, for the purpose of laying their eggs. In the height of the season it was difficult to find a few yards of beach free from their broad tracks made the previous night, when perhaps more than a thousand would have come up'. Ellis's description also includes an account of the nesting behaviour of the turtles that agrees well with the recent technical description of green turtle nesting behaviour by Bustard & Greenham (1969). He gives a clutch count of 'eighty to a hundred or more' and an incubation period of 'about six weeks'. He provides a vivid account of the co-operative digging of hatchlings to reach the beach surface, the resting of masses of hatchlings near the beach surface until after dark,

the synchronous emergence of hatchlings from a nest and their vigorous dash for the sea. Ellis makes no reference to birds as predators of hatchlings but gives the impression that sharks took large numbers of hatchlings as they sped across the reef flat. The sport of riding turtles over the reef flat is commented on, and support is given to De Rougemont's claims that people could ride turtles in the sea (Maslen, 1977). The large numbers of nesting turtles were regarded as a nuisance as they dug up paths and disturbed people's sleep when they threw sand against the sides of houses during the night. Ellis also described turtles entering the central depression and dying of heat exhaustion during the day.

W. MacGillivray, an ornithologist, made several trips to Raine Island and the adjacent area during 1910-1913. On 30 October 1910 he recorded 'great numbers' of turtles on the beach at Raine Island and in the adjacent shallows (MacGillivray, 1910). During his 9-15 July 1911 visit to Raine Island he made no reference to turtle nesting or to bird predation on turtle hatchlings (MacGillivray, 1914). However, during his 4-12 December 1913 visit he provides a description of Raine Island and Moulter Cay under high density green turtle nesting conditions (MacGillivray, 1917). In this account, the crew were described leaping from the boat onto turtles for rides as hundreds of turtles swam past the vessel and, after the party landed, riding turtles down the beach into the water. MacGillivray described himself as 'absorbingly interested in the wonderful bird-life' of the islands during the day and 'tormented at night by the nesting turtles, who would persist in trying to walk over or under our sleeping shelter'. This negativity towards the turtles was not evident in his graphic word picture of massed nesting at Moulter Cay: 'In the moonlight we noticed thousands of turtles climbing the sand-bank, their wet backs gleaming with phosphorescence as they leave the water'. The whole surface of Moulter Cay was described as 'ploughed up by the tracks and pits of the reptiles, and the air is redolent with the odour of the dead'. At Moulter Cay he also described the destruction by nesting turtles of bird eggs in a large crested tern, *Sterna bergii*, nesting colony. *S. bergii* and silver gulls, *Larus novaehollandiae*, were recorded scavenging on turtle eggs dug up by nesting turtle during the previous night at Raine Island. Rufous night-herons, *Nycticorax caledonicus*, were recorded as numerous on Raine Island and identified as predators of the hatchlings (MacGillivray, 1918a). In his summary of brown booby, *Sula leucogaster,* nesting, MacGillivray (1918b) again voiced negativity towards the turtles when he described Moulter Cay as 'a large turtle-infested sand-bank'.

On 7 September 1950, the Order in Council of 15 December 1932 under the Queensland Fisheries Act was repealed. The 1932 regulation had put in place a closed season for the harvest of green turtles and their eggs during the months of October and November south of 17°S. In its place, this 1950 Order in Council declared a year round closed season for green turtles and their eggs throughout all Queensland. This was the first conservation management measure applied to the north Queensland turtle populations.

Our discussions with several people, including D. Duffey in 1974 and J. Dagie in 1978, who had been crew members of trochus luggers that operated out of Torres Strait, indicated that trochus luggers travelling south for trochus gathering in Great Barrier Reef waters, regularly travelled via Raine Island. Here they took on live green turtles as deck cargo as food for the crews. Many of these islanders have left their names inscribed in the interior wall of the beacon as the only record of their visit to the island (Bairstow, 1983).

Vince Vlassoff (pers. comm., 2 April 1981) visited Raine Island during a summer turtle nesting period in February - March of 1956 (the same year that Cyclone Agnes impacted north Queensland). During one night, his party counted turtles in several hundred yards of beach and extrapolated for the entire beach. They estimated 10-12 thousand green turtles for the night. They rescued about 10 turtles per morning from on their backs at the base of the cliffs. It was estimated that they 'could smell dead turtles from about 2 miles (3km) out to sea' (Fig. 10). The well was about 4ft (~1.3m) deep but had been filling up with dead turtles (Fig. 10D). Photographs taken on this trip provide the opportunity for the first independent validation of the species identification of the nesting turtles at Raine Island. Up to this time, it appears that no specimen of a green turtle from Raine Island or Moulter Cay had been lodged in a Museum. During this trip Vlassoff was accompanied by an Italian film crew from the Astoria Film Society. They filmed for an Italian documentary titled *La Grand Barrie*r. This documentary, if it still exists, would provide the oldest film record of the island

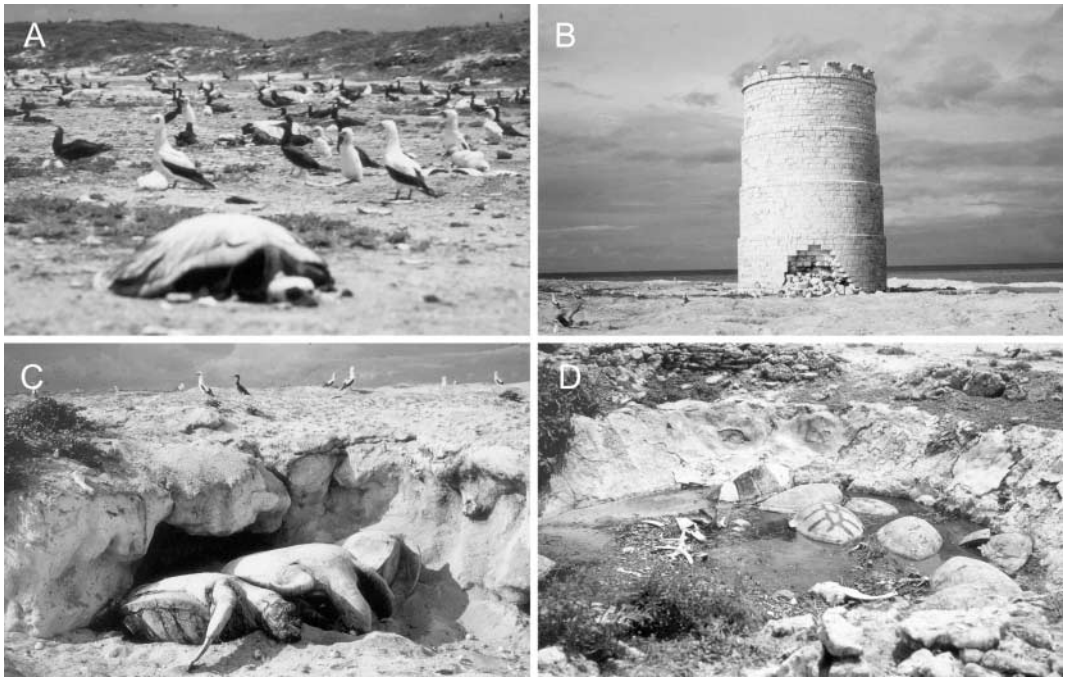

FIG. 10. Raine Island in February to March of either 1954 or 1956. Photographs by V. Vlassoff showing evidence of extremely high density turtle nesting for one or both of these breeding season. These are the oldest images located for Raine Island. A, numerous recently dead adult *Chelonia mydas* that had died from heat exhaustion within the central depression. B, the surface of the rock platform adjacent to the beacon was almost completely devoid of vegetation. C, a group of dead or dying adult female *Chelonia mydas* that had fallen over the cliff onto their backs. Note the relatively bare sand surface of the rock platform above. D, remains of 12 recently dead adult *Chelonia mydas* in the well at the western end of the central depression of the rock platform.

and its wildlife, including footage from a very high density turtle nesting season.

During 20-25 July 1957, Vince Vlassoff returned to Raine Island on his vessel, *Tropic Seas*, with a BBC Film Unit including producer David Attenborough (D. Attenborough, in litt. 4 April 1984; V. Vlassoff, pers. comm., 2 April 1981). The BBC documentary *Zoo Quest: The Birds of Paradise II. Raine Island* was filmed during this visit. This documentary provides a visual description of an island lush with grass cover across the rock platform. The images of dead turtles in the documentary were consistent with few turtles having died in the turtle breeding season some six months earlier. All except one carcass was a year or more old. There was low density turtle nesting during this winter visit with about twenty sets of tracks from nesting turtles counted in four nights. This documentary and photographs by D. Attenborough provide the first positive identification that the turtle species breeding at Raine Island in mid-year (winter) is *C. mydas*.

Changes in fisheries regulations in 1958 opened the way for commercial harvesting of turtles from the northern Great Barrier Reef. Records contained in the 1956-1958 Queensland Department of Harbours and Marine files indicate that the Cairns based Whittaker brothers (Snowy and Neil), of the fishing vessel *Trader Horn*, lobbied during 1956 and 1957 via their local member of parliament, G.W. Wallace MLA, to have permits issued to harvest turtles in north Queensland. They claimed that there were so many turtles nesting in areas of the Northern Great Barrier Reef that the turtles were unable to find places to deposit their eggs and consequently they dig out eggs previously laid by other turtles, and that on the following morning these are eaten by the birds. They further claimed that 'over a period of six to eight weeks, as many as 1,500 turtles visit Raine Island nightly' (B.W. Dick, in litt. 26 Feb. 1957, Brisbane). They suggested that the permit embrace the area from Olinda Entrance to No. 7 Bank, including Pandora (= Moulter Cay), Raine

Island, Ham Reef, Derry and Nos. 8 and 7 Sandbanks. Their concept of the biology of green turtles included the following ideas: turtle laying season extended from about November to March; less than 1% of the turtles hatched are males and therefore, unlike most other animals eaten by man, it was better that the females should be taken; it was appropriate to harvest the female turtle on the nesting beach as she headed back to the water because as long as the females lay once the turtles reproduce themselves; very few hatchlings ever live to become adults which weigh about 114kg; green turtles take only about four years to grow to adults (Anon, 1959a); there were so many green turtles in the area that they really needed thinning out; and the crew would save more than they killed, because they would take any hatchling that they found to the water and save them from death by birds (Anon, 1959b). Their political lobbying was successful, and on 4 September 1958, the Order in Council of 7 September 1950 under the Queensland Fisheries Act was repealed and a new Order in Council declared which restricted the year round closed season for harvesting green turtles to south of 15°S. The year round closed season for turtle egg harvest throughout Queensland was retained. This meant that turtles could be harvested without restriction in Queensland north of 15°S.

In addition to published material and correspondence, information regarding the Whittaker's turtle harvesting business was obtained from interviews in Cairns in August 1983 by CJL with Neil Whittaker himself and E. Gray who was a crew member of the *Trader Horn* for the first major turtle harvesting trip to Raine Island in January 1959. Neil and Snowy Whittaker's vessel for the turtle harvesting from Raine Island was the *Trader Horn*: displacement 70 tons, engine 115HP, overall length 72ft, beam 17ft, draft 7ft, wooden hull, built by Alf Hansen of Cairns (N. Whittaker, pers. comm.). She carried 7 dories and a crew of 12 (Anon, 1959a). According to Neil, the *Trader Horn* had a freezer capacity of about 50,000lb (22,700kg); most of the turtles were taken from Raine Island but some came from Moulter Cay; Moulter was hard to work when a swell was running; they had no problem capturing 100 turtles per night for slaughter on every trip; turtles were turned on the beach at night, killed and partly butchered on the beach next morning, loaded on a dory (Fig. 11A), transferred to the *Trader Horn* where the meat was washed on the deck and butchering completed (Fig. 11B); only meat (= muscle) was taken. According to E. Gray: the turtles were butchered at the island, at first by using an axe; the white crew did not like this job and were slow; the boat went to Thursday Island to employ extra native crew to slaughter the turtles; in the latter part of the first harvest many turtles were shot for butchering; and the meat was marketed through Cairns. Gray also observed that the green turtles that they harvested were nesting in sufficient numbers so that 'at times you could walk a long distance along the beach from turtle to turtle'; most nesting was at night and on the eastern half of the island. Gray did not go on the second trip in February 1959. According to G. E. Rowell (in litt. to Queensland Department of Harbours and Marine, 21 April 1959), once the refrigerated holds were filled with turtle meat, killing ceased and the *Trader Horn's* deck was loaded with live turtle for the return trip to Cairns (Fig. 11C). The live turtles from the first major catching trip were slaughtered at the Smith's Creek Wharf in Cairns. Rowles, as Harbour Master, advised Whittaker that this was not permitted. Whittaker took the live deck cargo turtles from the last trip out to Michelmas Reef where they were butchered and the meat returned to Cairns.

The Whittaker's turtle harvesting enterprise was initiated with a small unquantified harvest from an unstated origin from early in the nesting season in late 1958 (Anon, 1959b). Some of this turtle meat was used to promote sales to Meyer Emporium of Melbourne, Victoria, and to presumably supply the demands of local hotels. The first substantial harvest occurred during a two week trip to Raine Island in January 1959 (Anon, 1959b). The second major expedition to harvest turtles occurred during February 1959. The itinerary of *Trader Horn* for this February trip was: 14th Raine Island, 14-16 Pandora Cay (= Moulter Cay), 17-18 Murray Island Sandbank, 19-22 Pandora Cay, 22 Raine Island. Whittaker met a visiting ornithologist, Dr Warham, on Raine Island by chance and invited him to travel with them for the remainder of the trip (Warham, 1963). On this latter trip, 508 turtles were taken that yielded about 36,000 lb of turtle meat (Anon, 1959c). G. Rowell (in litt. to Qld Dept. of Harbours and Marine, 10 April 1959) provided a summary of the combined summer's turtle harvests by the Whittakers: 'Turtle fishing was commenced in early January, and discontinued during March. During that period approximately 1,200 turtles were taken which produced approximately 80,000 lbs of meat (about 60 to 70lbs of meat per turtle)'.

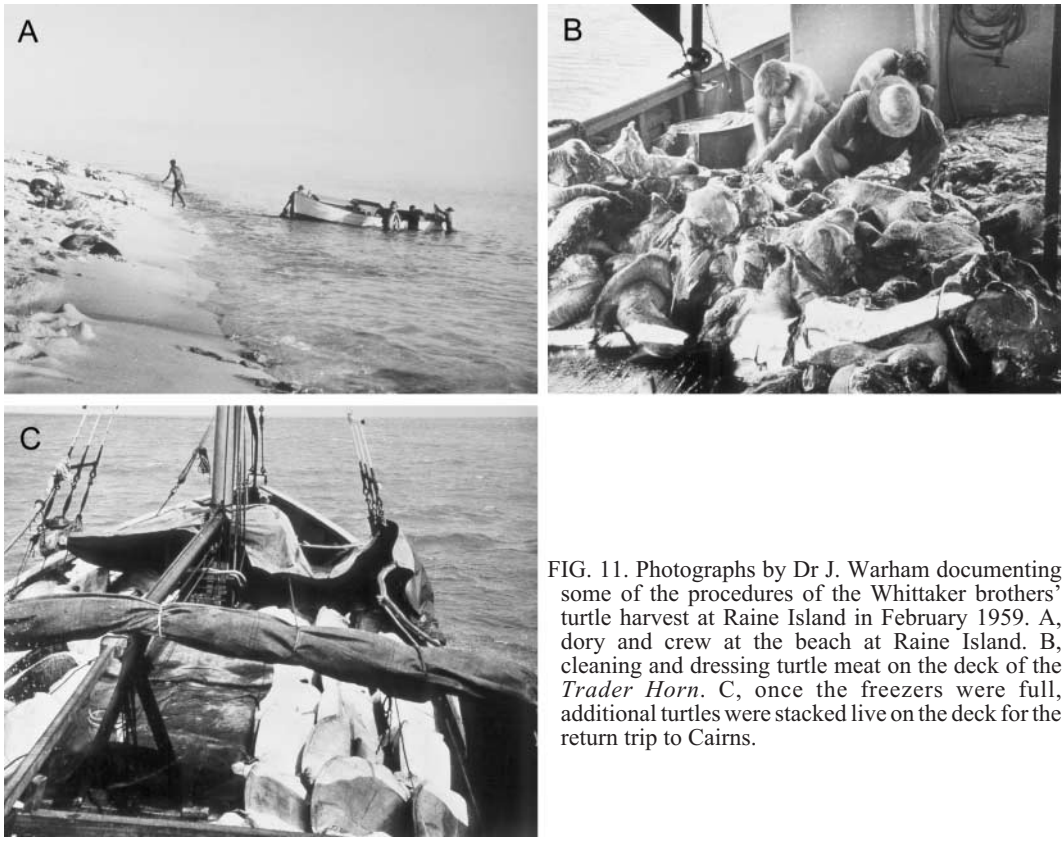

FIG. 11. Photographs by Dr J. Warham documenting some of the procedures of the Whittaker brothers' turtle harvest at Raine Island in February 1959. A, dory and crew at the beach at Raine Island. B, cleaning and dressing turtle meat on the deck of the *Trader Horn*. C, once the freezers were full, additional turtles were stacked live on the deck for the return trip to Cairns.

In preparation for the commencement of turtle harvesting from the Raine Island area, Mr T.A. Hiley was reported in the *Cairns Post* in December 1958 discussing a proposed amendment to the Fish Supply Management Act that would remove turtles from the definition of fish under the Queensland Fisheries Act. The purpose of this was to encourage development of the turtle meat industry north of Cooktown by allowing people engaged in the industry to operate outside the Fish Board and sell direct to the public. This change in regulations did not occur.

Turtle meat was not novel to the Cairns community at this time. The Strand Hotel had been serving turtle steaks at the hotel for six or seven years (Anon, 1959b). The chef, Mr. Leigh Kingston, acknowledged that it was very popular with the southern tourists during the tourist season but the local people did not take to it too well at the beginning (Anon, 1959b). As part of the promotion for sale of turtle meat locally, this hotel staged at least one cooking demonstration for the media and outlined styles of preparation of turtle meat meals prior to the first major consignment of turtle meat arriving in Cairns (Anon, 1959b). A local wholesaler in Cairns, Mr. M. Stock, was organised to distribute the Whittakers' turtle meat at 3/- per lb (Anon, 1959b). Snowy Whittaker promoted it as reasonably priced meat for the 'working man' (Anon, 1959b).

On 15 January 1959, L. Jorgensen, Manager of the Cairns Fish Board, announced (Anon, 1959d) that under the Fish Supply Management Act, because turtles were defined as fish under the Act, it was illegal for the Whittakers to sell their turtle meat in Queensland to anyone except the Fish Board. They were however, entitled to sell their turtle meat direct to buyers outside Queensland. The Fish Board's commission on the sale of turtle meat was 15%. Snowy Whittaker responded that 'the housewife would have to pay at least 4^{d} per lb more for it' (Anon, 1959e). Some of the turtle meat was passed immediately into the local Fish Board coldrooms for local sales. By early February, turtle meat

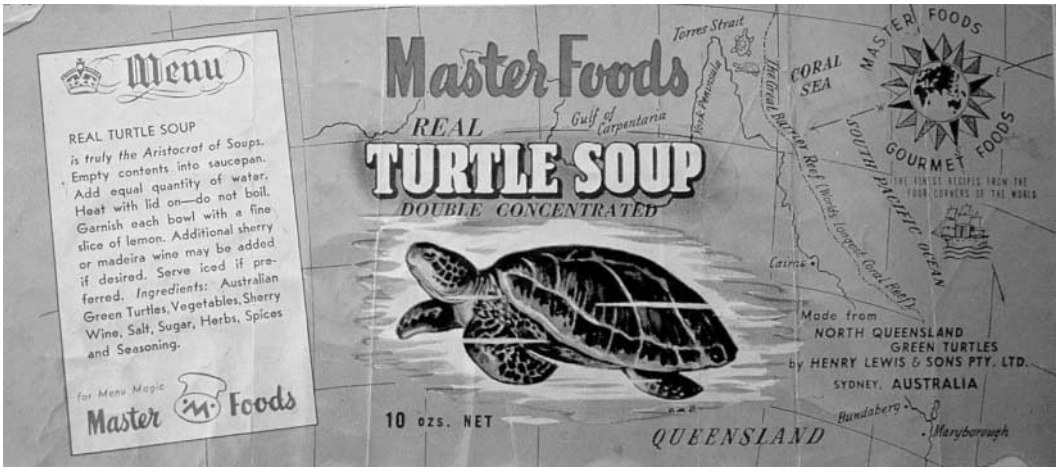

FIG. 12. Label from a can of *Master Foods* turtle soup made from Raine Island *Chelonia mydas* harvested by the Whittaker brothers in January - February 1959. *Master Foods* continued to market turtle soup under this label for approximately another two decades even though their turtles did not originate from the Great Barrier Reef.

from Cairns at 4/6^{d} per lb was selling in Townsville in favour of more expensive beef (Anon, 1959f). The Whittakers canvassed markets interstate in Sydney and Melbourne with the assistance of the Queerah Meatworks providing storage of the majority of the meat without surcharge (Anon, 1959g; N. Whittaker, pers. comm.). Additional markets were also sought internationally in Singapore (Anon, 1959g) and New York (N. Whittaker, pers. comm.). As a result of a Cairns visit by Dr V. Lewis of the Sydney canning company of Lewis and Sons to inspect the Whittakers' catch (Anon, 1959h), most of the turtle meat was to be sold to Lewis and Sons at 1/9^{d} per lb (N. Whittaker, pers. comm.). This meat was processed at their Sydney cannery into turtle soup and marketed under the 'Masterfoods' label (Fig. 12) (N. Whittaker, pers. comm.). This association did not continue as expected because of financial issues (N. Whittaker, pers. comm.).

When sales of turtle meat did not increase as expected, a publicity campaign to counter the conservative eating habits of the north Queensland community provided recipes in the local news paper for cooking turtle meat, including fried turtle steak, crumbed steak, turtle hot pot, turtle rolls, turtle meat sate, turtle saute, turtle roast and curried turtle (Anon, 1959i; N. Whittaker, pers. comm.). Additionally, the Whittakers campaigned for the sale of turtle meat as an alternative to fish. This led to a debate as to whether turtle meat could be eaten by Roman Catholics on Fridays which resulted in Archbishop Duhig ruling that turtle was fish and therefore suitable for Roman Catholics to eat on Fridays (N. Whittaker, pers. comm.). This apparently initiated further discussion between the Fish Board and the Abattoir authority. Because turtles were fish under the Queensland Fisheries Act and under the Abattoir's Act, fish and meat could not be stored in the same coldroom, the turtle meat had to be removed from the meatwork's storage. As of 10 April 1959, of the original estimated harvest of 80,000lb of turtle meat, about 58,000lb remained in Cairns: 23,000lb of the 25,000lb received at the Fish Board, Cairns, remained unsold; and 35,000lb remained in other Cairns cold storage facilities although some of this had been purchased by a Sydney firm (G. Rowell, in litt. to Qld Dept. of Harbours and Marine). The turtle harvest from the Raine Island area did not continue beyond this one season because the Whittaker brothers considered that it was not profitable (N. Whittaker, pers. comm.).

One of the turtles brought back to Cairns by the Whittaker brothers was presented to the Cairns Ambulance Brigade. After preparation by a local taxidermist, this turtle was to be displayed in the first Cairns Ambulance Wildlife Exhibit at the Cairns show in 1959 in conjunction with 'Snakes Alive' (N. Whittaker, pers. comm.).

N. Whittaker (pers. comm.) provided some observations concerning turtle breeding in the 1950's: all the sandbanks of the northern Great

Barrier Reef carried a few nesting turtles, but none with numbers like Raine and Pandora (= Moulter); at Raine Island the turtles dug up lots of eggs while nesting; Raine Island was the only area with lots of frigatebirds and the frigates would prey on hatchling turtles by day off the beach and in the water; and Neil walked the beach one night after turning 100 turtles for killing and counted 'a thousand turtles in one walk of the island'.

Warham (1963) visited Raine Island on 7-14 and 22 February 1959. The crew of the fishing boat *Galeru* that delivered him to the island harvested a nesting turtle for food. Warham identified that many previously laid eggs were dug out by nesting turtles; landrails scavenged on these destroyed eggs; dead turtles were numerous; and some nesting turtles still ashore on the beach after daylight died from over heating. Warham (1961) provided a description of the topography and vegetation of the island, described green turtles as abundant, and identified the rufous night-heron, *Nycticorax caledonicus*, as a predator of turtle hatchlings. Warham (1961) also visited Moulter Cay during 14-16 and 19-22 February 1959. He described the island's topography and vegetation with a 'turtle churned level area surrounding a shrub covered centre. Crested terns, *Sterna bergii*, which were nesting and roosting on the island, patrolled the beaches at daylight and preyed on hatchling turtles on their way to the sea.

Both Neil Whittaker and E. Grey during their above interviews concerning the turtle harvest reported that some hawksbill turtles were seen nesting on Raine Island but not harvested.

Another turtle harvesting business started in Torres Strait at about the same time as the Whittaker brothers began their venture out of Cairns. This Torres Strait based enterprise started in a small way using Islander labour but the Department of Native Affairs disagreed with this and insisted that £15 per week be paid to the Islanders. This and unsuitable weather appear to have stopped the project (Harbour Master, Thursday Island, in litt. 9 June 1959).

There was at least one protest from the conservation lobby against this newly energised turtle harvesting industry. The Townsville and District Natural History Society wrote to the Queensland Government protesting against the slaughter of turtles for their meat (Anon, 1959j). John Warham, the ornithologist who was at Raine Island during one of the Whittaker's harvesting trips, while not critical of the Whittaker's operation, expressed the need for caution with regard to the number of licences operating in the harvest if the turtle resource was not to be substantially reduced (Anon, 1959k).

Another proposal to create industry out of the Raine Island turtles in 1959 does not appear to have progressed to implementation. A Cairns-based mercantile firm, Cairns Coasters, had acquired samples of turtle bones from 'a vast natural grave yard … on the outer reef six or seven hundred miles north of Cairns' to test for their phosphorus content (N. Whittaker, pers. comm.). The plan had been for their vessel, the *West Aussie*, to bring a shipload of bone back to Cairns every time it returned from Thursday Island.

HMAS *Gascoyne* visited Raine Island on 11 November 1961 and her crew carried out some repairs on the tower. There are no records referring to turtles from this visit.

Paul Watson (pers. comm. 18 June 1979) first visited Raine Island with V. Vlassoff in about late November 1965. The area of the island with the densest turtle nesting was at the tower end and south side. Most turtle nesting was by night. On one night Watson had been able to step or jump from turtle to turtle while Vlassoff walked 100 paces beside him. He reported that he subsequently visited Raine Island on a number of occasions in October - December in different years but never saw it again with turtles as thick as on his first visit.

On 18 July 1968 an Order in Council under the Queensland Fisheries Act declared an all year round closed season over all marine turtle species and their eggs through out all of Queensland. This marked the end of a 20yr window of opportunity for commercial harvesting of green turtles in the northern Great Barrier Reef.

In the early 1970s, Dr Robert Bustard, a Scottish herpetologist working out of Canberra who established the Applied Ecology Torres Strait Turtle farms, listed Raine Island as one of the important *C. mydas* rookeries for Queensland (Bustard, 1971) and identified Raine Island as one of the 15 most important green turtle nesting beaches worldwide (Bustard, 1972). In neither publication did he elaborate on how he arrived at these conclusions.

The James Cook University of North Queensland (JCUNQ) 1973 James Kirby Expedition conducted biological studies at Raine Island during 31 October - 4 November (Stoddart et. al. 1981). During this visit, Raine Island had a

measured high tide circumference of 2100m (1600m of sand and discontinuous narrow beach rock; 500m continuous beach rock). They recorded a nightly green turtle track count = 133.8 (SD = 17.8, range = 115-162, n = 4 nights). When corrected for turtles emerging across beach rock that did not result in tracks at the water line, their results indicated that about 200 nesting turtles were coming ashore nightly. Their mean curved carapace length = 109cm (SD = 5.29cm, range = 90-122cm, n = 124). At the time of this early nesting season visit, there was still a substantive *Lepturus* tussock grassland extending out from the cliff to the bare sand beach. In their effort to estimate the size of the total nesting population, they have assumed a 100% nightly nesting success and that the nesting habitat does not include that area of grassland below the cliff. Based on the unquantified observation that some animals 'differed markedly in degree of curvature of carapace', Stoddart et. al. (1981) postulated that some of the nesting turtles may have been flatback turtles, *N. depressus*. It appears that none of the observers had prior experience with the flatback turtle and no photographs were recorded of any of the presumed flatback turtles. We therefore reject this identification in light of prior and subsequent data. CJL examined the skull collected from the dried carcass of an adult sized *E. imbricata* found in central depression of Raine Island by J. Collins during this JCUNQ visit (Limpus, 1980a) and while not reported by Stoddart et. al. (1981), this skull remains the only conclusive evidence that occassional *E. imbricata* come ashore to nest on Raine Island.

Commenting on his first visit to Raine Island in late January 1974, Ben Cropp (pers. comm. 3 March 1975): expressed the opinion that the abundance of track each morning in early 1974 was of the same order of magnitude as he saw on his next trip to the island in February 1975 when he was accompanied by CJL, i.e. tracks from several hundred turtles per night.

Dr G. Goedon of the Queensland Fisheries Service (pers. comm. 1975) counted about 50 recent sets of tracks below the high tide level in one walk of Raine Island in early October 1975. Later in the same breeding season, Dr J. Kowarsky of Applied Ecology Pty Ltd recorded numerous sets of green turtle tracks on Raine Island from the night of 13 January 1976 (Kowarsky, 1978). These tracks were observed during an aerial survey and were not accurately countable. A Torres Strait Islander reportedly counting 160 tracks (? = 80 turtles) freshly made in one night on 29 January 1976 (J. Kowarsky, in litt. 3 March 1976). While Kowarsky was unsure of the accuracy of the count, it is clearly consistent with few turtles nesting on Raine Island that night.

HISTORIC SUMMARY. The authors are unaware of any written records or evidence at the island of use of Raine Island by indigenous people prior to its discovery by Europeans in 1815. However, it is highly likely that at least the inhabitants of Murray, Darnley and Stephen Islands of eastern Torres Strait, with their large dugout sail canoes would have visited these islands prior to European arrival. Similarly there is the possibility that aboriginals from the adjacent mainland may have also ventured out to Raine Island under favourable weather conditions, given that the island is visible from the top of some inshore islands (e.g. Sir Charles Hardy Islands) on a clear day. Since its discovery by Europeans, Raine Island has been inhabited for extended periods on three occasions: during the building of the beacon in 1844, by a beche-de-mer fishery crew in the 1870's and by guano miners for 3 yr from 1890. During the same period, neither Raine Island nor Moulter Cay have been continuously inhabited by indigenous peoples.

From the earliest records of these islands in 1843 until the present times, it is apparent that Raine Island has been a significant *C. mydas* rookery and that large numbers of nesting females may die on the island each year from natural causes.

Since European discovery of these islands, there was only sporadic low intensity harvest of the nesting *C. mydas* at the islands up until January 1959. During January - February 1959 there was a harvest of approximately 1,200 nesting *C. mydas* from Raine Island and Moulter Cay. This large scale harvesting of the nesting turtles was not repeated. Raine Island and Moulter Cay appears to be one of the least disturbed major *Chelonia mydas* rookery regions of the World, having escaped the ravages of intensive turtle harvesting associated with European colonial expansion into tropical seas (Parsons, 1962; Hirth, 1997).

BREEDING DISTRIBUTION IN THE NORTHERN GREAT BARRIER REEF

BREEDING SPECIES. The distribution and abundance of nesting by marine turtles in the

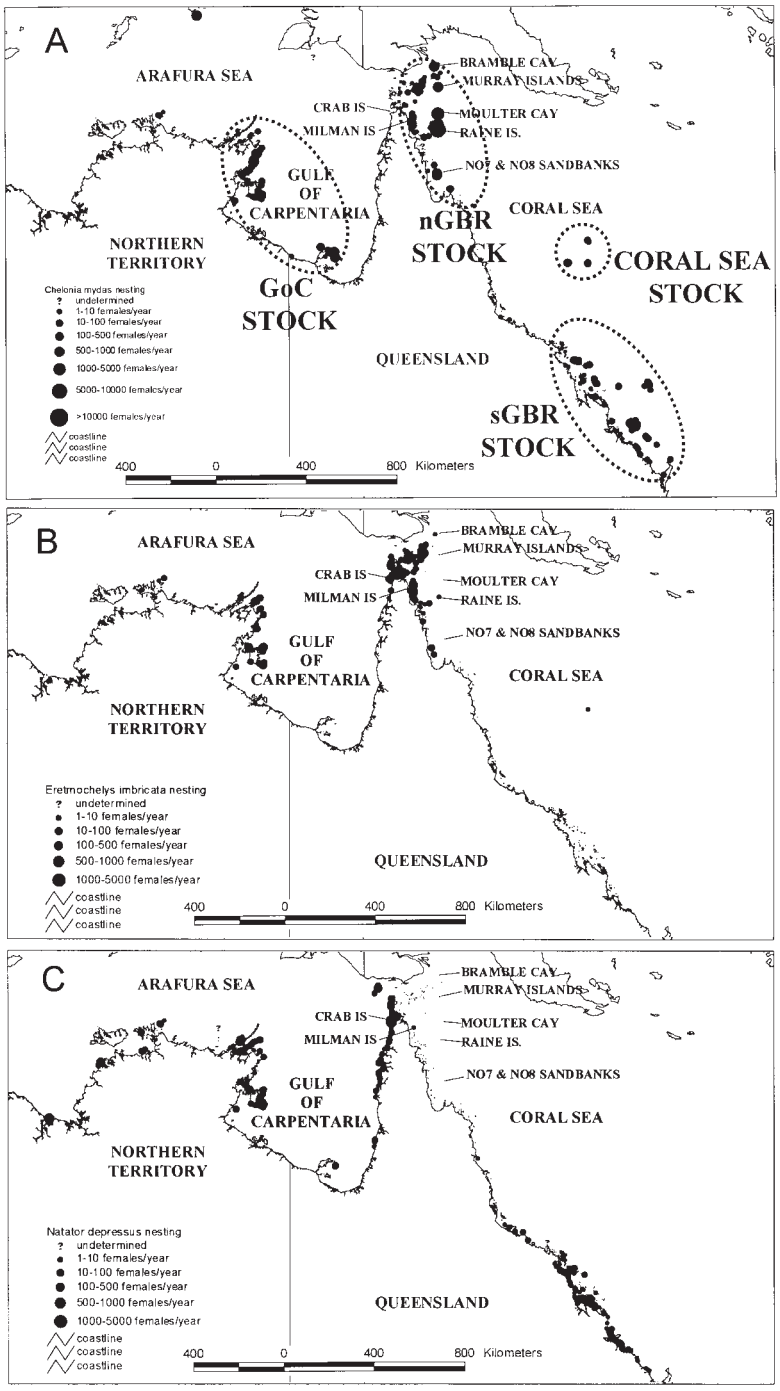

FIG. 13. Maps summarising the distribution and abundance of marine turtle nesting in Queensland. These maps were generated from the QPWS marine turtle nesting database. A, *Chelonia mydas*, green turtle. The groupings of rookeries that represent each of the four genetically separated stocks that breed in northeastern Australia are identified. B, *Eretmochelys imbricata*, hawksbill turtle. C, *Natator depressus*, flatback turtle.

northern GBR and Torres Straight region was undertaken throughout this study by teams landing on beaches and counting turtles or tracks for each species on a nightly basis (Tables 3-6). During the late 1990s, additional data on the temporal and spatial distribution of marine turtle breeding in Queensland was recorded during dedicated aerial survey of nesting beaches (Limpus et al., 2000). Detailed studies of turtle nesting biology from the region have also been published for Bramble Cay (Limpus et al., 2001), Milman Island (Dobbs et al., 1999) and a northern GBR-Torres Strait survey of *E. imbricata* nesting (Miller, et al., 1995). These data have been incorporated into the QPWS Marine Turtle Atlas. This is a relational database that summarises the breeding season, location and estimated size of the annual breeding population by species for marine turtles in Queensland. Analyses of these data have been output as summary maps using GIS software (Fig. 13).

Green turtle, *Chelonia mydas*. There are three concentrations of *C. mydas* rookeries in Queensland: southern GBR; northern GBR and adjacent Torres Strait and southern Gulf of Carpentaria with a fourth adjacent cluster of rookeries on the Coral Sea Platform (Fig. 13A). These data, including the results of the on ground surveys of turtle nesting throughout the northern GBR and Torres Strait region (Tables 3-6), show that *C. mydas* breeding is concentrated onto the cays of the outer barrier reef from Bramble Cay to Princess Charlotte Bay. The main concentration within this outer barrier reef nesting zone occurs on Raine Island (Table 3) and Moulter Cay (Table 4) with subsidiary concentrations on Bramble Cay, Murray Islands (Fig. 13A), No.8 Sandbank and No.7 Sandbank (Table 5). *C. mydas* breeds less frequently on the inner shelf sand cays, continental islands and adjacent mainland (Table 6).

Since 1974 hundreds of thousands of nesting and recently dead adult *C. mydas* and their hatchlings have been observed at Raine Island, Moulter Cay, MacLennan Cay and No.8 and No.7 Sandbanks. A total of 34,361 tagged female *C. mydas* were processed while nesting at Raine Island and 3,015 at the other outer barrier reef islands (Tables 7-9). During the 32 trips on which tagging and census studies were conducted by QPWS and/or Applied Ecology, no adult turtle, turtle track or hatchling of a species other than *C. mydas* was recorded from Raine Island, Moulter Cay, Maclennan Cay, No.8 Sandbank or No.7 Sandbank.

Hawksbill turtle, *Eretmochelys imbricata*. There is one concentration of *E. imbricata* rookeries in Queensland: on coral cays of the inner shelf of the northern GBR from the Piper Islands north to the sand islands and continental islands of central and western Torres Strait (Fig. 13B; Table 10). Low density to sporadic nesting occurs south of the Piper Islands to Princess Charlotte Bay.

British Museum specimen, registration no. 46.7.27.6 is an immature specimen with CCL = 35.5cm collected at Raine Island (A.F. Stimson, in litt., 26 May, 1977) which was presented to the museum by Lieut. Ince in July 1846. This is the Boulenger (1889) specimen 'w'. It was on the basis of this specimen that Stoddard et al. (1981) associated the species with Raine Island. However, the latter study failed to recognise that the turtle was an immature, presumably having been caught on the surrounding reef at the time of the construction of the beacon in 1844. Immature to adult-sized *E. imbricata* were occasionally seen on Raine Island Reef during the present study.

J. Collins (JCUNQ) collected the skull from an adult *E. imbricata* carcass within the central depression of Raine Island in November 1973 (Limpus, 1980a). As only nesting female turtles venture this far inland, this must be accepted as a breeding record for the species from Raine Island. During the January-February 1959 harvest of *C. mydas* from Raine Island by the crew of the *Trader Horn*, 'hawksbill turtles' as well as the abundant green turtles were identified as being ashore nesting (E. Gray, pers. comm., 1983; N. Whittaker, pers. comm., 1983). *E. imbricata* breeding at Raine Island and adjacent outer barrier cays during the present study period may have been unrecorded because very little census work has been conducted during January-March which is the peak of the region's *E. imbricata* nesting season (Dobbs et al., 1999). At Bramble Cay, *E. imbricata* nests at very low density mostly during the January-March period (D. Carter, pers. comm.; C.J. Parmenter, unpubl. data). *E. imbricata* breeds at very low density on Raine Island and probably also on the adjacent outer barrier reef cays.

Flatback turtle, *Natator depressus*. There are three concentrations of *N. depressus* rookeries in Queensland: on continental islands and mainland beaches of the central east coast from Bundaberg to Townsville; sand islands and continental islands of western Torres Strait and the mainland

TABLE 3. List of study trips to Raine Island and other islands of the northern Great Barrier Reef: November 1974 - December 2001, summarising the nightly counts of breeding female turtles and their associated mortality while ashore nesting on the islands. The nightly count of turtles is listed as the tally count or in parenthesis as a tagging census count. The mean nightly count was calculated on half monthly sampling intervals. Nightly mortality includes those turtles found alive but which would have died if left unaided and which resulted from that night's nesting attempt. Accumulated dead turtles were counted at the arrival of the study team for a census period. Only *Chelonia mydas* was recorded. # denotes that the count may include more than one night's nestings. tr = tracks. Key to notes: 1 = JCUNQ, A. Birtles; 2 = C. Limpus & B. Cropp; 3 = G. Goedon (pers. comm.); 4 = Kowarsky, 1978; 5 = QPWS; 6 = B. Cropp (pers. comm.); 7 = QPWS & AE; 8 = QPWS aerial survey; 9 = AIMS, D. Williams; 10 = QPWS/RIC; 11 = D. Williams; 12 = QPWS & GBRMPA; 13 = GBRMPA, J. O'Dyer; 14 = Operation Raleigh; 15 = A. Fleay (in litt.).

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
29/11/74	11565		281	11565	-	1	1
28/2/75	427 tr		>588	447 tr	-	4	2
1//3/75	517 tr						
2//3/75	408 tr						
3//3/75	435 tr						
22/10/75	~50 tr						3
29/1/76	~80 tr						4
2/12/76	-			872	-	2	5
3/12/76	-						
4/12/76	898						
5/12/76	-						
6/12/76	845						
Early/11/77	~40-50						6
3/12/77	(23)	0	0	(32)	-	5	7
4/12/77	(23)	0					
5/12/77	(19)	0					
6/12/77	(41)	1					
7/12/77	(53)	-					
1/12/78	(148)	0	1	(243)	-	5	7
2/12/78	(204)	0					
3/12/78	(240)	1					
4/12/78	(327)	1					
5/12/78	(295)	-					
29/10/79	-	0	18	416	-	2	5
30/10/79	381	0					
31/10/79	451	1					
1/11/79	410	0		427	-	2	
2/11/79	-	0					
3/11/79	-	0					
4/11/79	444	0					
5/11/79	-	0					
6/11/79	-	0					
7/11/79	-	1					
8/11/79	-	1					
9/11/79	-	0					
13/12/79	1211	0	72	1347	-	2	5
14/12/79	1482	3					
8/4/80	1-2 tr						8

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
9-23/6/80	-			0-1	-	14	5
8/12/80	71 (83)	0	0	59	17.5	5	5
9/12/80	68 (81)						
10/12/80	58						
11/12/80	69						
12/12/80	29 (80)						
28/2/81		-	-	(24)	12.7	7	9
1/3/81	(3)						
2/3/81	-	-					
3/3/81	(26)	-					
4/3/81	(36)	-					
5/3/81	(27)	-					
6/3/81	(36)	-					
7/3/81	(30)	-					
8/3/81	-	-					
9/3/81	(10)	-					
7/6/81	0	0	-	(0.4)	0.5	9	10
8/6/81	0	0					
9/6/81	0	0					
10/6/81	(1)	0					
11/6/81	(1)	0					
12/6/81	0	0					
13/6/81	(1)	0					
14/6/81	(1)	0					
15/6/81	0	0					
16/6/81	(1)	0		(0.3)	-	3	
17/6/81	0	0					
18/6/81	0	0					
12/11/81	1019	0	6	1009	-	3	10
13/11/81		0					
14/11/81	1103	2					
15/11/81	906	0					
16/11/81	955	5		2038	446.7	13	
17/11/81		0					
18/11/81	1722	1					
19/11/81	2074	4					
20/11/81	1943	5					

TABLE 3 (*Cont.*)

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
21/11/81	1986	0					
22/11/81	1954	6					
23/11/81	2565	2					
24/11/81	2369	3					
25/11/81	2307	2					
26/11/81	1542	9					
27/11/81	2263	7					
28/11/81	2212	6					
29/11/81		15					
3011/81	2599	10					
1/12/81	2757	6		2094	665.3	12	
2/12/81	2345	13					
3/12/81	1738	15					
4/12/81	1287	8					
5/12/81	1445	2					
6/12/81		2					
7/12/81	1394	2					
8/12/81	1832	2					
9/12/81	1795	8					
10/12/81	2654	5					
11/12/81	1817	8					
12/12/81	2599	8					
13/12/81	3463	8					
21/2/82	350			350		1	11
13/7/82	0	0	189	(0.3)	-	3	10
14/7/82	0	0					
15/7/82	(1)	0					
16/7/82	0	0		(0.5)	0.8	14	
17/7/82	(1)	0					
18/7/82	0	0					
19/7/82	(1)	0					
20/7/82	0	0					
21/7/82	(1)	0					
22/7/82	(2)	0					
23/7/82	(2)	0					
24/7/82	0	0					
25/7/82	0	0					
26/7/82	0	0					
27/7/82	0	0					
28/7/82	0	0					
29/7/82	0	0					
13/11/82	460	0	6	492	-	3	10
14/11/82	525	0					
15/11/82	490	0					
16/11/82	452	1		718	183.4	13	
17/11/82	470	1					
18/11/82	553	0					
19/11/82	670	0					

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
20/11/82	639	1					
21/11/82	716	0					
22/11/82	674	0					
23/11/82	670	1					
24/11/82	822	0					
25/11/82	854	0					
26/11/82	760	0					
27/11/82		0					
28/11/82		0					
29/11/82	1095	1					
30/11/82	959	0					
1/12/82	1000	2		925	112.5	6	
2/12/82		0					
3/12/82	878	0					
4/12/82	810	0					
5/12/82	809	1					
6/12/82	960	2					
7/12/82	1091	2					
8/12/82		2					
25/4/83	2 tr	0	82	3.2 tr	-	5	10
26/4/83	2 tr	0					
27/4/83	8 tr	0					
28/4/83	3 tr	0					
29/4/83	1 tr	0					
15/11/83	Several hundred tracks seen from air						12
3/4/84	8	0	92	9	4.2	13	10
4/4/84	9	0					
5/4/84	6	0					
6/4/84	11	0					
7/4/84	5	0					
8/4/84	3	0					
9/4/84	15	0					
10/4/84	17	0					
11/4/84	8	0					
12/4/84	7	0					
13/4/84	7	0					
14/4/84	6	0					
15/4/84	14	0					
16/4/84	3	0		5	1.9	9	
17/4/84	5	0					
18/4/84	5	0					
19/4/84	4	0					
20/4/84	2	0					
21/4/84	3	0					
22/4/84	7	0					
23/4/84	5	0					
24/4/84	8	0					
25/4/84		0					

TABLE 3 (*cont.*)

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
1/9/84	7 tr			7 tr	-	1	13
21/1184	7739	24	256	6376	-	5	10
22/1184		2					
23/1184	6459	14					
24/1184		15					
25/1184	7074	1					
26/1184		23					
27/1184	5428	33					
28/1184		19					
29/1184	5179	11					
30/1184		12					
1/12/84	7867	8		6493	1683	8	
2/12/84		23					
3/12/84	9301	22					
4/12/84		17					
5/12/84	7070	12					
6/12/84		29					
7/12/84	7099	19					
8/12/84		31					
9/12/84	5633	35					
10/12/84		21					
11/12/84	5764	11					
12/12/84		47					
13/12/84	5295	26					
14/12/84		29					
15/12/84	3916	34					
16/12/84		40		8873	2429	5	
17/12/84	5102	52					
18/12/84		52					
19/12/84	9776	44					
20/12/84	11467	25					
21/12/84	9960						
22/12/84							
23/12/84	8059						
24/11/85			4				10
25/11/85	119	0		196	-	3	
26/11/85		0					
27/11/85	308	0					
28/11/85		0					
29/11/85	162, 202 tr	0					
30/11/85		0					
1/12/85	214	0		227	38	6	
2/12/85		0					
3/12/85	205	0					
4/12/85		0					
5/12/85		0					
6/12/85	227	0					

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
7/12/85		0					
8/12/85	295	0					
9/12/85		1					
10/12/85	236	0					
11/12/84	5764	11					
12/12/84		47					
13/12/84	5295	26					
14/12/84		29					
15/12/84	3916	34					
16/12/84		40		8873	2175	5	
17/12/84	5102	52					
18/12/84		52					
19/12/84	9776	44					
20/12/84	11467	25					
21/12/84	9960						
22/12/84							
23/12/84	8059						
24/11/85			4				10
25/11/85	119	0		196	-	3	
26/11/85		0					
27/11/85	308	0					
28/11/85		0					
29/11/85	162, 202 tr	0					
30/11/85		0					
1/12/85	214	0		227	38	6	
2/12/85		0					
3/12/85	205	0					
4/12/85		0					
5/12/85		0					
6/12/85	227	0					
7/12/85		0					
8/12/85	295	0					
9/12/85		1					
10/12/85	236	0					
11/12/85		0					
12/12/85		0					
13/12/85	183, 323 tr	1					
14/12/85		0					
15/12/85		0					
16/12/85	105, 264 tr	1		151	-	3	
17/12/85		2					
18/12/85	142	0					
19/12/85	205	0					
20/12/85		0					

TABLE 3 (*cont*.)

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
17/10/86	137			130	-	2	14
18/10/86	123						
13/11/86	1439	0		1549	-	3	
14/11/86	1705	0					
15/11/86	1503	0					
16/11/86	1284	0		3145	-	5	
23/11/86	3142	11	90				10
24/11/86							
25/11/86	3208	23#					
26/11/86		7					
27/11/86	3525	7					
28/11/86		7					
29/11/86	4565	8					
30/11/86		8					
1/12/86	4696	8		3957	686	8	
2/12/86		13					
3/12/86	4547	6					
4/12/86		9					
5/12/86	3991	8					
6/12/86		9					
7/12/86	4838	11					
8/12/86		18					
9/12/86	3648	12					
10/12/86		7					
11/12/86	3643	6					
12/12/86		12					
13/12/86		12					
14/12/86	3382	22					
15/12/86	2910	-					
29/11/87		10	158				10
30/11/87	3296	10		3296		1	
1/12/87	2312	9		4099	-	4	
2/12/87		19					
3/12/87	4489	16					
4/12/87	4585	14					
5/12/87	5011						
29/11/88		1	52				10
30/11/88		2					
1/12/88	516	1		731	-	4	
2/12/88		1					
3/12/88		1					
4/12/88	1088	2					
5/12/88	671	0					
6/12/88		2					
7/12/88	647	0					
28/11/89		24	177				5
29/1189	5919	15		5919	-	1	
30/1189		16					
1/12/89		16		6144	-	3	
2/12/89		18					
3/12/89		19					
4/12/89		14					
5/12/89	5991	14					
6/12/89	5925	14					
7/12/89	6516	14					
29/11/91	2289	20	-	3571	3	6	10
30/11/91	-	6					
1/12/91	3360	8					
2/12/91	-	4					
3/12/91	3483	8					
4/12/91	-	13					
5/12/91	3492	16					
6/12/91	-	6					
7/12/91	3741	33					
8/12/91	-	36					
9/12/91	5062	20					
10/12/91	-	6					
29/11/92	850	3	-	1323	458	6	10
30/11/92	-	3					
1/12/92	874	12					
2/12/92	-	8					
3/12/92	1048	8					
4/12/92	-	7					
5/12/92	1591	6					
6/12/92	-	5					
7/12/92	1936	8					
8/12/92	-	8					
9/12/92	1638	5					
10/12/92	-	8					
29/11/93	9245	11	-	8593	585	6	10
30/11/93	-	33					
1/12/93	9012	27					
2/12/93	-	11					
3/12/93	7596	19					
4/12/93	-	0					
5/12/93	8384	10					
6/12/93	-	20					
7/12/93	8478	5					
8/12/93	-	8					
9/12/93	8841	20					
10/12/93	-	22					
30/11/94	-	0	-				
1/12/94	586	0		645	-	5	10
2/12/94	-	0					
3/12/94	836	0					

TABLE 3 (*Cont.*)

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
4/12/94	-	1					
5/12/94	729	1					
6/12/94	-	1					
7/12//94	404	0					
8/12/94	-	0					
9/12/94	671	0					
5/12/95	4653	5	191	4648	-	5	10
6/12/95	-	8					
7/12/95	4627	9					
8/12/95	5765	15					
9/12/95	4044	14					
10/12/95	-	0					
11/12/95	4150	4					
12/12/95	-	21					
13/12/95	-	6					
30/11/96	11755	67	150	12100	1421	7	10
1/12/96	-	51					
2/12/96	-	52					
3/12/96	11454	75					
4/12/96	11422	29					
5/12/96	10677	58					
6/12/96	-	65					
7/12/96	11209	42					
8/12/96	13667	62					
9/12/96	14519	26					
29/11/97	3184	11	186	4065	905	7	10
30/11/97	3279	6					
1/12/97	3881	4					
2/12/97	3292	10					
3/12/97	4312	10					
4/12/97	-	14					
5/12/97	5284	7					
6/12/97	5223	5					
28/11/98	110	1	35	472	245	7	10
29/11/98	300	0					
30/11/98	-	2					
01/12/98	762	0					
2/12/98	707	1					
3/12/98	-	0					
4/12/98	567	0					
5/12/98	583	0					
6/12/98	-	1					
7/12/98	-	0					
8/12/98	-	0					
9/12/98	273	0					
28/11/99	5806	41	213	5617	-	3	10
29/11/99	5834	18					
30/11/99	5212	13					
1/12/99	-	9		7079	776	8	
2/12/99	7010	14					
3/12/99	-	20					
4/12/99	6282	17					
5/12/99	6848	25					
6/12/99	6745	36					
7/12/99	8101	25					
8/12/99	-	35					
9/12/99	6301	24					
10/12/99	8408	32					
11/12/99	7077	41					
30/11/00	114	1	0	114	-	1	10
1/12/00	82	0		131	31	7	
2/12/00	-	0					
3/12/00	136	0					
4/12/00	136	0					
5/12/00	-	0					
6/12/00	107	0					
7/12/00	171	0					
8/12/00	165	1					
9/12/00	122	0					
1/12/01	4539	20	71	3601	1401	8	10
2/12/01	3194	5					
3/12/01	2462	6					
4/12/01	-	10					
5/12/01	1923	0					
6/12/01	2675	2					
7/12/01	3072	21					
8/12/01	4988	15					
9/12/01	-	15					
10/12/01	5952	4					

coast of north-western Cape York Peninsula and the Wellesley Island of the southeastern Gulf of Carpentaria (Fig. 13C). The on-ground surveys of turtle nesting throughout the northern GBR, recorded only sparse *N. depressus* nesting (Miller et al., 1995; Dobbs et al., 1999) (Table 6).

Stoddart et al. (1981) suggested the possibility that *N.* (=*Chelonia*) *depressus* nested at Raine Island. Their description of the turtles in question is not consistent with that of adult *N. depressus* but fits well within the normal variation in carapace shape of *C. mydas*. In view of the lack of

supporting evidence for the presence of *N. depressus* at Raine Island, the species should not be considered part of the nesting community of Raine Island or the adjacent outer barrier cays.

Loggerhead turtle, *Caretta caretta. C. caretta* has not been recorded breeding in the far northern GBR. An unsuccessful nesting attempt by the species was recorded from Lizard Island prior to this survey (Limpus 1982). This remains the only eastern Australian breeding record for the species from north of Townsville.

Misidentified species. The Leatherback turtle, *Dermochelys coriacea* was recorded ashore at Moulter Cay and Raine Island on 8th and 16 November 1986 among the nesting *C. mydas* (Anon., 1986). The turtles were not described in detail, nor were they measured or photographed. Given that the recorders were naive with respect to marine turtle identification, that during the same breeding season the species was not encountered by experienced observers at these islands, and that the species has not been recorded by any other observers at these islands at any other time, *D. coriacea* will not be considered as part of the marine turtle fauna of the Raine Island area. No records of *D. coriacea* breeding were obtained during the surveys of turtle breeding throughout the remainder of the northern GBR and Torres Strait (Miller et al., 1995; Limpus et al., 2000) (Tables 5-6).

CHELONIA MYDAS BREEDING SEASON. Ellis (1936) in summarising his stay on Raine Island from late 1890 to 1892, identified pedominantly summer nesting by green turtles. The next longest reported habitation of the island was during the construction of the beacon from 29 May until mid September 1844 when MacGillivray (1846) reported only irregular isolated nestings by green turtles with numbers increasing in September. All remaining reports are from trips of about a month or less in duration and at irregular intervals. The nightly density of turtle nesting recorded on all visits to Raine Island and other islands of the northern GBR since November 1974 are summarised in Tables 3-5.

The historical data and that of Tables 3-4 have been combined to produce a summary of the breeding season by months for Raine Island and Moulter Cay (Table 11). While there are marked differences in nesting density from year to year, the general pattern is for sporadic nesting to occur during the dry season (May - August) and breeding turtle numbers to increase from

TABLE 4. Moulter Cay. Only *Chelonia mydas* was recorded nesting at Moulter Cay. See Table 3 for symbols and codes.

Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Mean nightly female count			Notes
				Mean	SD	n	
5/3/75	244 tr	0	142	244 tr	-	1	2
7/12/76	(430+)		7				5
2/12/77	13 tr	0	0	13 tr	-	1	7
24/6/80	0	0	28				10
19/6/81	0						10
30/7/82	0	0					10
10/12/82	402 tr		3	402 tr	-	1	10
14/12/85	148	0	3	157	-	2	10
15/12/85	166	0					
17/10/86	58			76	40	7	14
18/10/86	55						
21/10/86	61						
22/10/86	88						
23/10/86	74						
27/10/86	38						
28/10/86	160						
6/11/86	210			357	108	3	
7/11/86	407						
8/11/86	458						
16/11/86	747			747	-	1	
14/12/86	1669			1807	-	2	10
15/12/86	1945						
4/12/88	627	3	17	627	-	1	10
13/12/92	180 tr	0	0	180 tr	-	1	10
7/12/93	5057	-		5057	-	1	10
7/12/95	2495	0	39	2495	-	1	10
27/11/96	4043	-	-	4043	-	1	10
7/12/97	1671	6	45	1624	-	2	10
8/12/97	1577	2					
10/12/98	-	0	21			2	10
11/12/98	-	0					
12/12/99	3665	31	60	3665	-	1	10
10/12/00	67	1		67	-	1	10
10/12/01	1881	-	42	2022	-	2	10
11/12/01	2163	3					

September and reach a maximum in December and January. Numbers decrease again into the dry season. This also is the pattern for *C. mydas* nesting elsewhere in the northern GBR: at Bramble Cay to the north (Limpus et al., 2001) and at No.7 and No.8 Sandbanks to the south (Table 5). In the southern GBR, *C. mydas* nesting is seasonal, being confined to the mid summer (October - April) period (Bustard, 1972; Limpus,

TABLE 5. Other outer Barrier Reef coral cays of the far northern Great Barrier Reef. Only *Chelonia mydas* was recorded at these islands. See Table 3 for symbols and codes.

Rookery	Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Notes
Bramble Cay	3/1/87	340 tr			5
	4/1/87	290 tr			
	16/1/89	(272)	0	0	5
	17/1/89	(140)	0		
Maclennan Cay	30/11/78	(4)	0	0	7
	25/6/80	0	0	0	10
	19/6/81	0	0		10
	30/7/82	0	0	0	10
	4/12/88	(8)	0	0	10
No.8 Sandbank	28/11/76	~65 tr	0	0	5
	29/11/76	25 tr	0		
	11/12/79	114 tr	0	0	5
	5/6/80	0	0	1	10
	25/6/81	0	0		10
	10/7/82	0	0		10
	11/12/82	(118)			10
	17/12/86	(102)	0		10
	28/11/87	193 tr	0		10
	27/11/88	(30)	0	0	10
	24/11/89	234	0	0	5
	27/11/91	79 tr	0	0	10
	27/11/92	63 tr	0	0	10
	3/12/95	121 tr	0	0	10
	11/12/96	-	0	2	10
	10/12/97	119	0	2	10
No.7 Sandbank	28/11/76	~60 tr	0	0	5
	11/12/79	108# tr	0	4	5
	4/6/80	0	0	3	10
No.7 Sandbank	17/11/81	205# tr	0	0	10
	17/12/86	(79)	0		10
	28/11/87	94 tr	0	0	10
	27/11/88	(26)	0	0	10
	23/11/89	110 tr	0	0	5
	27/11/91	94 tr	1	0	10
	27/11/92	53 tr	0	0	10
	3/12/95	145 tr	0	1	10
	11/12/96	-	0	6	10
	10/12/97	108	0	7	10
No.6 Sandbank	5/6/80	0	0		10
	4/6/81	0	0		10
No.1 Sandbank	14/11/84	13 (tr)	0		10
Ham Cay	12/12/79	61# tr	0		5
	5/6/80	0	0	0	10
	16/11/81	Many tr	0	0	10
	11/12/82	Many tr	0	0	10
	25/11/89	10 tr	0	0	5
Derry Cay	5/6/80	0	0	0	10
	12/12/82	12 tr	0	1	10
	25/11/89	~12 tr	0	0	5
Davie Islet	27/6/81	0	0		10
	12/12/82	14 tr	0	0	10
	23/11/89	22 tr	0	0	5
Tydeman Cay	27/6/81	0	0		10
	12/12/82	29 tr	0	0	10
	18/12/86	11 tr	0		10

1980b). The more tropical location of the Raine Island rookery and the extremely large numbers of breeding females at Raine Island would give a higher chance of a few individuals nesting outside the main breeding season and could be the cause of the expanded breeding season compared to elsewhere in the GBR.

There is considerable variability in the timing of *C. mydas* breeding throughout the Australian continental shelf. Along the eastern and western Australian coasts, *C. mydas* nesting is principally mid-summer. Within the southern Gulf of Carpentaria (Bountiful, Pisonia and Rocky Islands) and Arafura Sea (southern islands of Aru Archipelago), *C. mydas* nesting occurs year round with a midyear peak (Bustard, 1972; Schulz, 1989; C.J. Limpus, unpubl. data). A similar variability in breeding season occurs for *N. depressus* at its various rookeries around northern Australia (Limpus, 1971; Limpus et al., 1983b, 1989).

This variability in timing of the nesting season probably results from the interaction of a number of factors which should include the temperature environment of the rookery (Guinea, 1994), the genetic origin of the breeding population (which, amongst other things, should influence the pivotal temperature for the individual population) and the climate of the feeding grounds providing turtles to the rookeries. The direct cause(s) for this variability in breeding season cannot be explained at present. It is not simply a function of latitude, given the similarity of the breeding seasons in northern and southern GBR and the different breeding season of the southern Gulf of Carpentaria rookeries at an intermediate latitude. The issue is further complicated by turtles from widely scattered

TABLE 6. Coral cays, continental islands and mainland beaches of the inner shelf of the northern Great Barrier Reef. Cm = *Chelonia mydas*; Ei = *Eretmochelys imbricata*; Nd = *Natator depressus*; ? = species unidentified. See Table 3 for other symbols and codes.

Rookery	Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Notes
Sinclair Island	11/12/76	0	0		5
Milman Island	11/12/76	(6) Ei	0		5
	5/12/78	~10 tr Ei	0		7
	31/7/82	~16# tr Ei	0		10
	13/6/84	~5# tr Ei	0		5
Cholmondely Island	1/8/82	3# tr Ei	0		10
Wallace Island	7/12/76	4 tr Ei	0		5
	09/12/76	0	0		
	1/8/82	1# ? 2# tr Ei	0	0	10
Mainland coast south of Usher Point	10/12/76	0	0		5
Little Boydong Island	9/12/76	0	0		5
Boydong Island	9/12/76	(2) Ei	0	0	5
	1/8/82	8# tr Ei	0	0	10
Hannibul Island	6/3/75	1 tr Ei	0		2
Bird Island (north)	5/3/75	(4) Ei	0	0	2
	8/12/76	(1) Cm (3) Ei	0	0	5
	21/6/81	1 tr Ei	0		10
	13/6/84	1# tr Ei			5
Bird Island (south)	21/6/81	1 tr Ei	0		10
Macarthur Island	6/3/75	1 tr Ei	0		2
Saunders Island	5/3/75	2 tr Ei	0	0	2
	21/6/81	1 tr Ei	0		10
	2/8/82	1 tr Ei	0	1 Ei	10
Ellis Island	11/11/79	0	0		5
Magra Island	22/6/81	3# tr Ei	0		10
Ashmore Banks (north western)	1/12/76	2 tr Cm 1 tr Ei	0		5
	7/8/80	1 Ei	0		10
	6/6/81	0	0		10
Ashmore Banks (north eastern)	7/6/81	0	0		10
Ashmore Banks (north eastern)	7/6/80	1 tr/Cm	0	0	10
	7/6/81	0	0		10
Farmer Island	23/4/83	0	0		10
	20/12/85	2 tr Ei	0	0	10
	21/12/85	(6) Ei			
	2/6/86	1 tr Ei	0		10
	28/11/87	2 tr Ei 2# tr Cm	0	0	10
	29/11/87	(5) Ei	0	0	10

Rookery	Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Notes
Sir Charles Hardy Island (northern)	26/10/79	3# tr ?	0		5
	26/6/80	1# tr Ei	0	0	10
	11/11/81	1 tr Cm (1) Ei	0	0	10
	19/12/85	1# tr Cm 4# tr Ei	0	0	10
	5/12/87	9# tr Cm 2# tr Ei	0		10
Sir Charles Hardy Islands (western)	2/12/76	11# tr ?	0		5
	26/10/79	13# tr ?	0		5
	28/7/82	0	0		10
	23/4/83	0	0		10
	19/12/85	1# tr ?	0	0	10
	5/12/87	11# tr ? 2# tr Ei	0		10
Haggerstone Island	10/11/79	0	0		5
	22/6/81	0	0		10
	23/6/81	0	0		
	15/11/81	1 tr Ei	0	0	10
	28/7/82	0	0		10
	30/4/83	0	0		10
	5/12/87	0	0		10
Forbes Island (north)	15/11/81	0	0	0	10
Portland Roads	30/11/76	0	0		5
	30/4/83	0	0		10
Quoin Island	6/6/80	0	0	0	10
	24/6/81	0	0		10
	15/11/81	0	0	0	10
	26/11/89	0	0		5
Chapman Island	17/12/79	0	0		5
	17/11/84	0	0		10
Sherrard Island	17/11/84	1# tr ?	0		10
	6/12/87	1# tr Cm 3# tr Ei	0	0	10
Night Island	25/1/79	0	0		5
	9/11/81	0	0	0	10
	9/11/82	0	0		10
	12/6/84	0	0		5
	16/11/84	0	0		10
Morris Island	6/12/87	13# tr Cm 12# tr Ei	0	0	10
Fife Island	28/11/76	3 tr Ei		0	5
	9/11/82	0	0	0	10
	12/6/84	0	0	0	5
	6/12/87	6# tr Ei	0	0	10
Lowrie Island	9/11/82	0	0	0	10

TABLE 6 (*Cont.*)

Rookery	Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Notes
Hay Island	9/11/82	0	0	0	10
	16/11/84	2# tr Ei	0	0	10
Hannah Island	27/11/76	0	0	0	5
	9/11/82	0	0	0	10
	15/11/84	0	0	0	10
Pelican Island	28/11/76	0	0	0	5
	26/6/81	0	0	0	10
	9/11/81	1 tr Ei 1 Nd hatchling	0	0	10
	16/11/83	1# tr Cm 2# tr Ei		0	12
	7/12/87	2# tr Ei	0	0	10
Stainer Island	11/6/84	0	0	0	5
	15/11/84	3# tr Ei	0	0	10
	7/12/87	0	0	0	10
King Island	14/11/84	0	0		10
Clack Island	19-21/12/86	0	0	0	10
Stanley Island	25/2/75	0	0		2
	18/11/81	0	0	0	10
Flinders Island	24/10/79	0	0		5
	18/11/81	0	0	0	18
	15/11/84	0	0		10
Pipon Island	22/2/75	0	0	0	2
	29/6/81	0	0		10
	14/11/84	0	0		10

Rookery	Date	Nightly count No. ashore	Nightly count Death rate	Accumulated dead turtles	Notes
Cape Melville	12/11/79	0	0		5
	18/11/81	0	0	0	10
	8/12/87	0	0		10
Stapleton Island	29/6/80	0	0		10
	13/11/84	2# tr Cm	0	0	10
Coombes Island	14/11/84	0	0	0	10
Noble Island	18/11/81	0	0	0	10
Rhodda Cay	27/6/81	0	0		10
Wilson Cay	27/6/81	0	0		10
Howick Island	23/10/79	0	0		5
Holm Island	14/11/79	0	0		5
Barnard Island	14/11/79	0	0		5
Eagle Islet	27/6/81	0	0		10
North Direction Island	28/6/81	0	0		10
South Direction Island	28/6/81	0	0		10
Rocky Islet	28/6/81	0	0		10
	14/12/82	0	0	0	10
Three Isles	21/2/75	0	0		2
Low Wooded Isle	3/6/80	0	0		10
Low Island	22/10/79	0	0		5
Michelmas Cay	1/6/80	0	0		10
	30/6/81	0	0		10

rookeries occurring together in feeding grounds in northern Australia and adjacent eastern Indonesia (Limpus et al., 1992). For example, adult female *C. mydas* have been caught off Coburg Peninsula in the Northern Territory that had been tagged while nesting at Raine Island, Lacepede Islands in Western Australia and south eastern Java; others have been caught in the Kei Islands of Indonesia that had been tagged while nesting at Raine Island and at the Turtle Islands of Sabah.

HOW LONG HAS RAINE ISLAND BEEN A *CHELONIA MYDAS* ROOKERY? Prior to the last Holocene transgression of some 10,000 yr ago, a turtle swimming up to the reef on which Raine Island now lies would have been confronted with precipitous cliffs rising to perhaps 45m or more above the then sea level with no beaches suitable for turtle nesting. Indeed, there may have been no suitable beaches for turtle nesting anywhere in the vicinity. The present day Raine Island and the other islands of the northern outer Great Barrier Reef have formed since sea levels stabilised at an upper level approximately 6,000 yr ago and slowly receded about 1m to their current level more than 4,000 yr ago (Hopley, 1983; Chappel, 1983).

Clam shells (*Tridacna* sp. and *Hippopus hippopus*) embedded in the surface of the phosphatic limestone platform of Raine Island have been carbon dated to a calibrated age B.P. of 1130 ± 210yr at the western end of the island and as low as 590 - 630 ± 70yr at the eastern end of the island adjacent to the tower (Limpus, 1987; Polach et al., 1978). Deeper layers of rock are presumed to be older. The other sand cays of the

FIG. 14. Fossil remains of an adult sized *Chelonia mydas* (femur) found at the western end of Raine Island in a bedding plane approximately 60cm below a clam carbon dated to 1130yr B.P.

FIG. 15. Skeletal remains of an adult female *Chelonia mydas* that had been disoriented and died of heat exhaustion in the central depression of Raine Island. This carcass, photographed in December 1987, originated from a turtle that died during the 1984-85 breeding season. Skeletal remains in this central area of the island have the potential for being left undisturbed for years and subsequently buried.

northern outer barrier reef are presumed to be of similar age to Raine Island.

Turtle eggs in nests fossilised in situ were reported during the quarrying of the phosphatic limestone platform at the eastern end of the island for the construction of the beacon (MacGillivray, 1846; Jukes, 1847). This quarry site is adjacent to the beacon and within 50m of the collection site of the clams dated 590-630yr BP. These clutches of turtle eggs must have been laid at least 460 yr before their discovery in 1844.

The weathered fossil remains of an adult-sized *C. mydas* that had died plastron down and whose skeletal remains were relatively undisturbed prior to being covered by sand were found in a horizontal bedding plane approximately 60cm below the clam dated at 1130yr BP. (Limpus, 1987) (Fig. 14). Fragments of turtle bone and bird bone can be found in almost every large phosphatic limestone rock at the margin to the central rock platform of Raine Island.

Death of nesting turtles ashore for nesting attempts has been observed annually on Raine Island during the recent studies and in seasons of high nesting density there may be >1,000 skeletons added to the islands sediments (Table 6). Most of these are scattered as individual bones by subsequent nesting turtles. Only the skeletons of turtles that die in the central depression of the rock platform are likely to be left relatively undisturbed (Fig. 15). It is also only during seasons of high nesting density that numerous turtles enter the central depression and die there of heat exhaustion. Raine Island and Moulter Cay are the only turtle rookeries of the GBR where nesting turtles die in large numbers and where turtle bones are a characteristic of the beach sediments. This turtle mortality is a function of the high density turtle nesting that occurs on these islands. The first accounts of Raine Island from 1843-4 prior to quarrying for construction of the beacon (MacGillivray, 1846; Jukes, 1847) described Raine Island with its turtle bones and dead turtles in a manner consistent with its appearance today. Numerous turtle remains and dead and dying turtles have impressed subsequent visitors to Raine Island in 1845 (Allen & Corris, 1977), 1874 (Moseley, 1879), 1890 (Ellis, 1936), 1913 (MacGillivray, 1917) and c.1953-6 (Fig. 1).

Taken together these observations indicate that Raine Island has supported a high density *C. mydas* rookery with associated frequent adult turtle mortality for long before its discovery by Europeans and indeed, for at least 1190 ± 210 yr B.P. (Limpus, 1987). However turtles could not have been using the island for nesting for more than about 4000 yr (the time that a sand island could have existed on this reef). This is the only marine turtle rookery in Australia with long-term evidence of nesting prior to European colonisation. Because of this fossil evidence for past nesting, Raine Island has the longest continual record of use as a marine turtle rookery anywhere in the world (Groombridge & Luxmore, 1989).

The origin of the turtles that colonised Raine Island after its formation perhaps 4000 yr ago has not been elucidated as yet by genetic studies of

TABLE 7. Numbers of adult female *Chelonia mydas* tagged and recaptured while nesting at Raine Island 1974-2001. AE indicates turtles tagged by Applied Ecology P/L. All other tags applied by QPWS. OR denotes tagged turtles recorded during Operation Raleigh. * denotes migration recaptures of nesting turtles previously tagged at foraging area. In no season was an attempt made to tag the entire nesting population. For remigrant turtles that changed rookeries between breeding seasons, the original rookery was identified: CS = Coral Sea Platform; MC = Moulter Cay; MM = Milman Island; MP = Moore Park; N7 = No. 7 sandbank; N8 = No. 8 Sandbank; RI = Raine Island.

Breeding season	Month	New tags	Within season rookery change	Remigrant			New turtles to rookery	Total turtles with tags
				Same rookery	Rookery change	Retag		
1974-75	Feb-Mar	151					151	151
1975-76								Nil
1976-77	Dec	2420 15 AE	0	0	0	0	2435	2435
1977-78	Dec	53 61 AE	0	0	0	0	114	114
1978-79	Dec	490 398 AE	0	0	0	0	888	888
1979-80	Oct-Dec	1766	0	1	0	0	1766	1767
	June	1	0	0	0	0	1	1
1980-81	Dec	284	0	0	0	0	284	284
	June	1	0	0	0	0	1	1
1981-82	Nov-Dec	2589	0	8 1 AE	1 MC	4	2591	2603
	Jul	2	0	0	0	0	2	2
1982-83	Nov-Dec	1586	0	8	0	7	1586	1601
	April	6	0	0	0	0	6	6
1983-84	Apr	80	0	0	0	0	80	80
1984-85	Nov- Dec	2458 2*	0	59	0	25	2460	2544
1985-86	Nov- Dec	1853 1*	2 MC	31	1 N8	30	1857	1918
1986-87	Nov- Dec	1447	0 12 OR	80	1 N8	177	1460	1717
1987-88	Jul- Aug	4	0	0	0	0	4	4
1988-89	Nov-Dec	1859	0	63	0	29	1859	1951
1989-90	Dec	769	0	264	0	4	769	1037
1990-91	Dec	1210	0	148	1 MC	24	1211	1383
1991-92	Dec	980	0	227	0	17	980	1224
1992-93	Dec	1689	0	129	0	14	1689	1832
1993-94	Dec	1593 6 *	0	152	1 N7	5	1600	1757
1994-95	Dec	991	0	31	1 N7	1	992	1024
1995-96	Dec	1485 1*	0	136	3 MC	43	1489	1668
1996-97	Nov-Dec	1664 9*	0	289	2 MC	28	1675	1992
	Jan-Feb	796 1*	0	91	3 N8	5	800	896
1997-98	Nov-Dec	1022 5*	0	387	1 N8 1 CS	11	1029	1427
1998-99	Nov-Dec	1599	0	156	0	31	1599	1786
1999-00	Nov-Dec	1160 17*	0	847	7 MC 3 MM 3 N7 1 N8	29	1191	2067
2000-01	Nov-Dec	664 1*	0	72	0	19	665	756
2001-02	Dec	1145 4*	0	443	3 N8 2 M 2 N7 1 MM 1 MP	27	1158	1628
Total		33817 474 AE 47*	2MC 12 OR	3622 1 AE	16 MC 10 N8 7 N7 4 MM 1 MP 1 CS	530	34392	38544

TABLE 8. Numbers of adult female *Chelonia mydas* tagged and recaptured while nesting at Moulter Cay, northern GBR, 1974-2001. See Table 7 for definition of codes.

Breeding season	Month	New tags	Within season rookery change	Remigrant			New turtles to rookery	Total turtles with tags
				Same rookery	Rookery change	Retag		
1974-75	Mar	6	0	0	0	0	6	6
1976-77	Dec	425	5 RI	0	0	0	430	430
1977-78	Dec	6 4 AE	0	0	0	0	10	10
1982-83	Dec	2	0	0	0	0	2	2
1984-85	Dec				1 RI		1	1
1985-86	Dec	131	11 RI	0	0	0	142	142
1986-87	Dec	174	8 RI	1	2 RI	11	184	196
1988-89	Dec	98	1 RI	0	2 RI	0	101	101
1989-90	Dec	72	0	1	0	0	72	73
1990-91								Nil
1991-92								Nil
1992-93	Dec	48	0	2	1 RI	2	49	53
1993-94								Nil
1994-95								Nil
1995-96	Dec	94	2 RI	2	1 RI 1 N7	3	98	103
1996-97								Nil
1997-98	Dec	109	13 RI	1	5 RI 1 MM	0	128	129
1998-99	Dec	194	2 RI	0	1 RI	1	197	198
1999-00	Dec	132	3 RI	1	7 RI 1 MM	0	143	144
2000-01	Dec	81	0	0	1 RI	2	82	84
2001-02	Dec	272	5 RI	5	0	2	77	291
Total		1844 4 AE	50 RI	13	21 RI 1 N7 2 MM	21	1922	1956

world wide *C. mydas* populations (Bowen et al., 1989; Norman et al., 1994a,b). Given the precipitous nature of the coastline for that part of Australia in pre Holocene times, the present day rookeries are not the result of a gradual shift of beaches with rising sea levels. Entirely new beaches became available for colonisation following the sea level rise while others, presumably further afield, were submerged. This emphasises the capacity for *C. mydas* to colonise new rookeries that were not natal beaches in response to slow changes in sea level. The process by which turtles locate and/or choose a new rookery site following the elimination of an existing one has not be addressed by present studies.

COURTSHIP. *C. mydas* courtship observed during expeditions to Raine Island is summarised as follows:

1979. 29 October - 9 November: Mating pairs of *C. mydas* were a comon sight in the deep water just outside the reef edge; two pairs of mating *C. mydas* were captured while stranded on the reef flat. 13-14 December: No courting turtles were observed, although the females were still aggregated in large numbers over the reef and beyond the reef edge.

1980. 8-13 December: No turtle courtship observed on or near Raine Island Reef.

1982. 13-31 July: One mounted pair of *C. mydas* observed adjacent to Raine Island Reef. 11 November - 10 December: Courting *C. mydas* were observed adjacent to Raine Island reef on only a few occasions in mid November.

1984. 3-26 April: No courtship observed on or near Raine Island Reef. Vertical aerial photographs of Raine Island from October 1984, commissioned by the Raine Island Corporation, show hundreds of large turtles aggregated in the shallows of the reef flat adjacent to the island. The aggregation in these images resembled of aggregations of mating *C. mydas* observed by the authors at rookeries in the southern Great Barrier Reef and the Wellesley Group in the southern Gulf of Carpentaria.

1985. 9 & 16 December: During underwater observations, adult male turtles were seldom seen (2 males out of 36 *C. mydas* examined). One male had recent courtship damage (Limpus, 1993) to tail and flippers.

TABLE 9. Adult female *Chelonia mydas* tagged and recaptured while nesting at other outer barrier cays in the northern GBR, 1974-2001. See Table 7 for definition of codes.

Breeding season	Month	New tags	Within season rookery change	Remigrant			New turtles to rookery	Total turtles with tags
				Same rookery	Rookery change	Retag		
Maclennan Cay								
1978-79	Dec	2 2 AE	0	0	0	0	4	4
1988-89	Dec	8	0	0	0	0	8	8
Subtotal		10 2 AE	0	0	0	0	12	12
No 7. Sandbank								
1976-77	Dec	1	0	0	0	0	1	1
1986-87	Nov	74	0	0	0	0	74	74
1987-1988	Nov	62	0	0	0	0	62	62
1988-89	Nov	26	0	0	0	0	26	26
1990-91	Dec	12	0	0	0	0	12	12
1991-92	Dec	89	0	0	0	0	89	89
1992-93	Dec	53	0	0	0	0	53	53
1995-96	Dec	70	0	1	0	2	70	73
1996-97	Dec	50	0	11	3 N8	0	53	64
1997-98	Dec	45 1*	0	2	0	0	46	48
Subtotal		482 1*	0	14	3 N8	2	486	502
No. 8 Sandbank								
1976-77	Dec	15	0	0	0	0	15	15
1979-80	Dec	34	0	0	0	0	34	34
1981-82	Dec	1	0	0	0	0	1	1
1982-83	Dec	71	0	0	0	0	71	71
1986-87	Nov	102	0	0	0	4	102	106
1987-88	Nov	122	0	0	0	0	122	122
1988-89	Nov	30	0	0	0	0	30	30
1989-90	Dec	10	0	0	0	0	10	10
1990-91	Dec	24	0	2	0	0	24	26
1991-92	Dec	70	0	0	0	1	70	71
1992-93	Dec	60	0	3	0	0	60	63
1995-96	Dec	77	0	1	0	2	77	80
1996-97	Dec	53	0	1	1 N7	0	54	55
1997-98	Dec	67	0	3	0	1	67	71
Subtotal		736	0	10	1 N7	8	737	755
Ham Cay								
1981-82	Dec	1	0	0	0	0	1	1
Bramble Bay Cay								
1989-90	Jan	110	0	0	1 RI	0	111	111
Total		1341 1*	0	24	1 N7 3 N8 1 RI	10	1347	1381

1986. 22 November - 16 December: Several courting pairs of *C. mydas* were observed daily during the early part of the study. No mating pairs were seen after 8 December. During underwater observations on 10 and 14 December, adult male turtles were seldom seen (5 males out of 263 *C. mydas* examined).

1987. 10 July - 19 August: Four mounted pairs of *C. mydas* observed, two pair each with an attendant male. 28 November: One pair of courting *C. mydas* seen on No.7 Sandbank Reef. None seen on No.8 Sandbank Reef. 30 November - 5 December: Only a few isolated pairs of courting *C. mydas* observed adjacent to Raine Island. During underwater observations on 1-5 December, adult male turtles were rarely seen (only 5 males out of 1144 *C. mydas* examined during speedboat transects).

TABLE 10. Adult female *Eretmochelys imbricata* tagged while nesting at coral cays and continental islands along the inner shelf of the northern GBR, 1975- 1989. No *Chelonia mydas* were tagged while nesting on the inner shelf islands during this period.

Breeding season	Month	New tags	Within season rookery change	Remigrant			New turtles to rookery	Total turtles with tags
				Same rookery	Rookery change	Retag		
Farmer Island								
1985-86	Dec	2	0	0	0	0	2	2
1987-88	Nov	2	0	0	0	0	2	2
Sir Charles Hardy Islands								
1981-82	July	1	0	0	0	0	1	1
Bird Island								
1974-75	Mar	3	0	0	0	0	3	3
1976-77	Dec	3	0	0	0	0	3	3
Boydong Island								
1976-77	Dec	1	0	0	0	0	1	1
Milman Island								
1976-77	Dec	6	0	0	0	0	6	6
Combined	18	0	0	0	0	0	18	18

1989. 28 November - 07 December: No courting turtles observed on or near Raine Island Reef.

1991. 29 November - 10 December: 2 courting pairs near Raine Island Reef.

1992. 29 November - 10 December: 3 courting pairs near Raine Island Reef.

1993. 29 November - 10 December: 3 courting pairs near Raine Island Reef.

1994. 30 November - 9 December: 2 courting pairs near Raine Island Reef; 12 males with courtship damage captured during reef survey.

1995. 5 - 13 December: No courting turtles observed on or near Raine Island Reef; 21 males recorded during reef survey.

1997. 29 November - 6 December: 2 courting pairs observed near Raine Island Reef; 2 males recorded during reef survey.

1999. 28 November - 11 December: 1 courting pair observed near Raine Island Reef; 4 males recorded during reef survey.

2000. 28 November - 9 December: 1 courting pairs observed near Raine Island Reef; 2 males recorded during reef survey.

2001. 1 - 10 December: No courting turtles observed on or near Raine Islamnd Reef; 0 males recorded during reef survey.

Courting *C. mydas* were rarely observed at any of the other rookeries of the northern outer barrier reef after mid November. The only time when frequent courtship was observed was in late October - early November. This is consistent with the pattern of courtship relative to nesting observed in the southern GBR where *C. mydas* aggregates for courtship during late September, October and early November, after which courting turtles are rarely seen (Limpus, 1993).

Insufficient courtship was in evidence close to Raine Island and Moulter Cay to account for the large nesting population. No fisherman reported seeing aggregations of hundreds of courting pairs near these islands, which would be expected if the turtles courted adjacent to the rookeries. Reports from fishermen indicated high density courtship occurred in the shallow protected waters north of Cape Grenville in October. The Torres Strait islanders encounter large numbers of courting *C. mydas* during September, October and early November throughout Torres Strait. This favoured turtle hunting time is called 'turtlefast', i.e. the time when the male turtle is fastened onto the female (Johannes & Macfarlane, 1991). The years with a big turtle-fast correspond to the high density nesting seasons and poor turtle fast years are the years in which low density turtle nesting occurs. There is insufficient *C. mydas* nesting within Torres Strait to account for the courtship that occurs there. Therefore it is concluded that the majority of the courtship that occurs within Torres Strait is by turtles that nest at Raine Island and Moulter Cay. If this is the case then significant levels of courtship could be occurring up to 200km from the rookeries. This spatial separation of the courtship area from the immediate vicinity of the female's rookery characterises much of the *C. mydas* courtship in the southern GBR (Limpus, 1993).

TABLE 11. Raine Island. Summary of turtle nesting accounts by month to determine the seasonality of the *Chelonia mydas* nesting. Unless otherwise stated the raw data has been obtained from the recent surveys of nesting density - Tables 2-4.

Month	Year	Day	Observations
July	1843	29	A few turtle tracks (Jukes, 1847)
	1844		Turtles occurred at irregular intervals, generally singularly (MacGillivray, 1914)
	1911	9-15	No reference to turtle nesting or to bird predation on hatchlings (MacGillivray, 1914)
	1957	20-25	Average 5 turtle tracks per night (Attenborough, in Litt. 4 Apr.1981).
	1982	13-28	0-2 turtles per night.
August	1844		Turtles occurred at irregular intervals generally singularly (MacGillivray, 1914)
	1871	31	No reference to turtle nesting (Moseley, 1879)
September	1844		Beginning in September they become more numerous (MacGillivray, 1846)
	1984	1	7 tracks
October	1910	30	Great numbers of turtles are on the beach and in the shallows around the boat (MacGillivray, 1910)
	1975	Early	Approximately 50 females per night
	1979	30-31	381 - 451 tally count
	1986	17-18	123 - 137 tally count
November	1965		Was able to step or jump from turtle to turtle while a companion walked 100 paces beside him (P. Watson, pers. comm. 1979).
	1973	1-3	About 150 - 200 females per night (track count, Stoddart et al. 1981)
	1974	29	11565 female on shore
	1977	early	Approximately 40 - 50 females per night
	1979	1-9	410 - 444 tally count
	1981	12-30	906 - 2757 tally count
	1982	13-30	452 - 1095 tally count
	1984	21-30	5179 - 7739 tally count
	1985	25-30	119 - 308 tally count
	1986	13-30	1284 - 4565 tally count
	1987	30	3296 tally count
	1989	29	5919 tally count
December	1913	4-12	Reference to obvious frequent clutch destruction by nesting turtles. Turtles abundant in the shallows and beach edge and the party 'tormented at night by the nesting turtles who persist in trying to walk over or under our sleeping shelter'. While at Moulter Cay 'thousands of turtles' came ashore for the night (MacGillivray, 1917). Moulter Cay described as a 'turtle- infested sand-bank' (MacGillivray, 1918b).
	1976	2-6	845 - 898 tally count
	1977	3-7	19 - 53 females per night
	1978	1-5	148 - 327 females per night
	1979	13-14	1211 - 1482 tally count
	1980	8-12	80 - 83 females per night
	1981	1-13	1287 - 3463 tally count
	1982	1-7	809 - 1091 tally count
	1984	1-23	3916 - 11467 tally count
	1985	1-20	142 - 323 tally count
	1986	1-15	2910 - 4838 tally count
	1987	1-5	2312 - 4585 tally count
	1988	1-7	516 - 1088 tally count
	1989	5-7	5925 - 6516 tally count
January	1845	28	14 large turtles collected (MacKenzie, 1845).
	1953-6?		(May have been February) Estimated 10000-12000 green turtles ashore in one night (V. Vlassoff, pers. comm.1981)
	1959		Dense turtle nesting sufficient to allow people to 'walk long distances along the beach from turtle to turtle' (E. Gray, pers. comm. 1983). At least 1100 turtles counted in one walk of the island in one night (N. Whittaker, pers. comm. 11 Aug. 1983).
	1974	Late	Several hundred turtle tracks counted by daylight (Ben Cropp, pers. comm. 1975)
	1976	29	Approximately 80 tracks (J. Kowarsky, pers. comm. 1977)
February	1959	7-14,22	'Hundreds were coming ashore after dark' (Warham, 1963)
March	1975	1-3	408 - 517 females per night
	1981	1-9	10 - 36 females per night

TABLE 11 (*Cont.*)

April	1980	8	1 - 2 females per night
	1983	25-29	1 - 8 females per night
	1984	3-26	2-17 females per night
April-May	1845	28-4	Estimated harvesting rate = 2 turtles per night, calculated from Sweatmans account. (Allen & Corris, 1977)
May			No Records
June	1844		Turtles occurred at irregular intervals generally singularly (MacGillivray, 1846)
	1980	9-23	Average < 1 female per night
	1981	7-18	Average < 1 female per night

Only 45 adult male *C. mydas* have been tagged at Raine Island and adjacent islands (Table 12). All of these were breeding males that were captured in courting groups or had recent mating scars on their flippers or tails. Adult males have been recorded only at low density adjacent to these outer barrier rookeries in the northern GBR.

BASKING. *C. mydas* at Raine Island were not observed to haul out onto the beach or onto the reef flat at low tide to bask during any visit. In contrast, vertical aerial photographs of Raine Island from October 1984 show about 100 adult-sized turtles, presumably *C. mydas*, scattered along the tide line of the beach. While most were in the water, tens were above the tide wash. On very calm days during the nesting season large numbers of adult turtles could be seen floating high (with dry carapaces) at the surface for extended periods at the reef edge and over the adjacent deep water. This behaviour is defined as surface basking and is presumed to have a thermoregulatory function. Aggregations of surface basking turtles were only observed adjacent to Raine Island Reef and Moulter Cay Reef.

Beach basking is a prominent behaviour of *C. mydas* at the Wellesley Islands of the south-eastern Gulf of Carpentaria (Limpus et al., 1994a; Bustard, 1972) and on the Capricorn-Bunker

TABLE 12. Summary of non nesting turtles tagged on Raine Island reef and other reefs of the far northern GBR. AE = tagged by Applied Ecology P/L. This table does not include the mid year tagging of turtles at Clack Reef that has been conducted as part of an independent study.

Breeding Season	Month	Size Class				Total for trip
		Adult		Immature		
		male	female	CCL >65cm	CCL <65cm	
Chelonia mydas						
Raine Island Reef						
1977-78	Dec	0	0	1	0	1
1978-79	Dec	12 12 AE	0	0	0 1 AE	25
1979-80	Oct-Dec	3	0	1	0	4
1982-83	Jul	1	0	1	1	3
1986-87	Dec	0	0	0	1	1
1987-88	Jul-Aug	2	0	1	0	3
	Nov-Dec	3	0	5	2	10
1988-89	Dec	0	0	1	0	1
1994-95	Nov-Dec	12	0	0	0	12
Combined	45	0	10	5	60	
Pipon Reef						
1974-75	Feb	0	2	0	0	2
Milman Island Reef						
1978-79	Dec	0	0	4 AE	6 AE	10
Maclennan Cay						
1978-79	Dec	2	0	0	0	2

Breeding Season	Month	Size Class				Total for trip
		Adult		Immature		
		male	female	CCL >65cm	CCL <65cm	
Chelonia mydas						
MacArthur Cay Reef						
1985-86	Jul	0	0	0	1	1
Clack Reef						
1986-87	Dec	0	0	2	3	5
1987-88	Dec	0	1	6	4	11
Corbett Reef						
1988-89	Dec	25	0	0	0	25
Howick Reef						
1988-89	Dec	0	0	0	4	4
Beanley Reef						
1988-89	Dec	0	0	0	2	2
Bewick Reef						
1988-89	Dec	0	0	0	1	1
Combined	27	3	8 4 AE	15 6 AE	63	
Eretmochelys imbricata						
Corbett Reef						
1987-88	Dec	3	0	0	0	3
Bewick Reef						
1988-89	Dec	0	0	0	1	1
Combined	3	0	0	1	4	

Group cays in the southern GBR (Barrett, 1919). Beach basking is also a common behaviour of the Hawaiian *C. mydas* population (Balazs, 1980). This contrasts with its apparent rarity within the northern GBR *C. mydas* population. This is not just a recent phenomenon; beach basking does not feature in any of the historical accounts of *C. mydas* in the northern GBR (see above).

MORTALITY OF BREEDING FEMALES ON THE NESTING BEACHES

MORTALITY RATE. The earliest records show that regular mortality of the female *C. mydas* while ashore attempting to nest has long been a feature of Raine Island (Jukes, 1847; MacGillivray, 1846; Moseley, 1879; Macgillivray, 1917; V. Vlassoff, pers. comm. 1981, fig. 11; Warham, 1963). Tables 3-4 show that this adult female mortality continues in present times. From these tables, a comparison of daily mortality and the number of turtles recorded ashore was made (Fig. 16). Daily adult mortality was dependent on the number of nesting turtles ashore on the previous night. Turtles did not usually die if there were less than 100 females ashore for the night: 95% of nights with no subsequent mortality; 5% with 1 death/day (n=43 days). Daily turtle mortality was still low when the nightly tally counts were in the range of 100-1000 turtles: 71% of nights with no subsequent mortality; 22% with 1 death/day; 7% with 2-12 deaths/day (n=69 days). In contrast when the nightly tally counts exceeded 1,000 there was a substantial increase in daily mortality and there were few days with no turtle mortality: 7% of nights with no subsequent mortality; 2% with 1 death/day; 91% of days with 2-75 deaths/day (n=126 days). Nightly tally counts had to exceed 800 nesting females before the number of dead exceeded 1/day. There was a significant correlation between the daily mortality and the tally count on the preceding night:

daily death rate = 0.003415*tally count - 1.376 (r^2=0.526; d.f.=137. $F_{1,137}$=152; p<0.0005)

Therefore, through the course of a summer breeding season it can be expected that daily mortality rates will increase to a maximum during the mid nesting season and then decline to zero as the season draws to a close. Fig. 17 shows the cumulative mortality during the early part of six breeding seasons representing a wide range of nightly nesting density: 1981/82, 1982/83, 1984/85, 1985/86, 1986/87, 1999/00. With an assumed peak nesting not being completed until mid January then the cumulative 1981/82 adult mortality could have been in the 400-500 range. A count of carcasses in July 1982 was 189 but many carcasses known to have been present earlier in the season had been broken up and/or buried. In April 1983 the 83 carcasses recorded from the preceeding breeding season was also an underestimate because some known carcasses had been lost in the sand, even though the season's nesting density was lower. An end-of-season count of carcasses is thus likely to give a substantial underestimate of annual mortality if the count is not made on a daily basis, especially in years with high density nesting. The large counts of turtle carcasses of 281 in November and 588 in March of the 1974/75 nesting season (Table 3) must be taken as underestimates of the adult mortality during that high density nesting season. The annual mortality of nesting females on Raine Island probably is expected to be negligible in very low density nesting seasons like 1977/78 and 1985/86. It could be approaching 100 in low density nesting seasons like 1982/83 and greater than 2000 in very high density nesting seasons like 1984/85, 1996/97 and 1999/00.

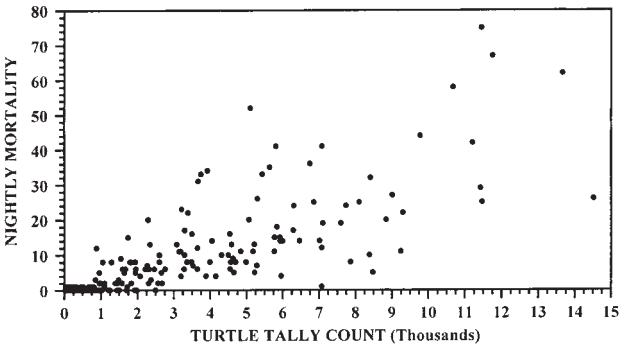

FIG. 16. Nightly mortality rate of adult female *Chelonia mydas* ashore for nesting on Raine Island (Table 3) expressed as a function of the nightly nesting density.

In any one season, far fewer turtles die while ashore nesting at Moulter Cay than at Raine Island (Fig. 17C, Table 4) and negligible numbers die annually at any one of the other outer barrier reef cays (Table 5).

Mortality of adult female *C. mydas* while ashore attempting to nest at Raine Island is clearly density dependent. This natural mortality

accounts for several thousand breeding females in high density nesting years and a few hundred or less in the low density nesting years.

CAUSES OF MORTALITY. Table 13 summarises the causes of mortality of the breeding females ashore on Raine Island. During the first 22yr of the study, 1974/75-1996/97 seasons, death from heat exhaustion of turtles that were still ashore during the first few hours of daylight was the principal cause of death (70-89% of adult turtles dying). Included in these values are those turtles that died of heat exhaustion in the central depression (2-14% of adult turtles dying). The majority of the turtles died of heat exhaustion on the beach platform. The next most prevalent cause of mortality was associated with the cliff line of the central rock platform where 8-20% of adult turtles died, mostly by falling over the cliff onto their backs. Large marine turtles cannot right themselves when they are turned on their backs.

This regular mortality of adult turtles that have come ashore at Raine Island to nest resulted from a variety of natural causes. Some turtles which found their way above the cliff during nesting attempts fell on their backs or became wedged between rocks on their return to the beach while others became trapped in the holes beneath the rock layer. A small (unquantified) proportion of these turtles was killed because their carapaces smashed down onto their heads and fractured their skulls when the fell head-first over the cliff. The remainder, lying on their backs in the sun with their pale coloured plastrons upper most, averaged 3.5 days to die (SD = 1.71, n = 33, Dec 1984). Those trapped in caves and other shaded areas sometimes took weeks to die. The cliff is a natural feature of the island and was not the result of quarrying for limestone to build the beacon or of guano mining as stated by Stannard (1985). The turtle mortality associated with the cliff is the result of natural processes.

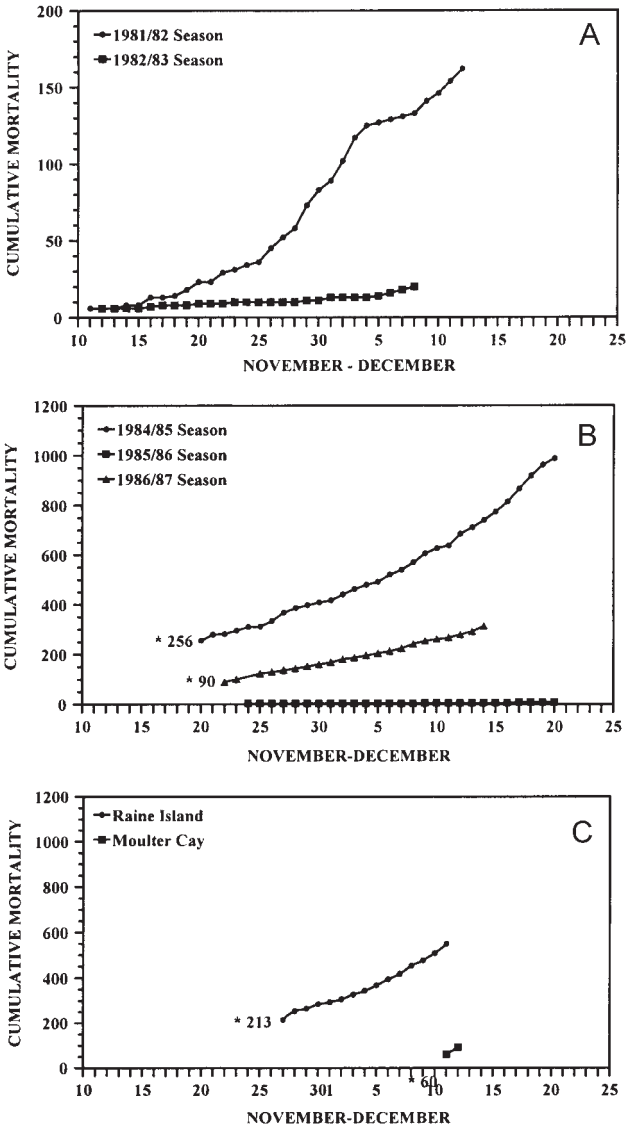

FIG. 17. Cumulative daily mortality of adult female *Chelonia mydas* on Raine Island measured over the early portion of six breeding seasons. * denotes total dead and dying recorded on arrival of the study team at the island.

The number of turtles that died by falling over the cliff was minor compared to those that died from heat exhaustion. Turtles that wandered inland into or beyond the beach depression encountered problems when endeavouring to return to the sea. When in the bottom of this depression, a turtle is exposed to an horizon line at approximately 0° elevation when looking parallel to the beach, but one at 13° when looking seaward. Because marine turtles move towards

TABLE 13. Observed causes of adult *Chelonia mydas* mortality on Raine Island. Percentage of total for observation period are given beneath the raw values. NR = not recorded. + indicates that only a portion of the actual dead turtle for the season could be accurately counted. * denotes turtles buried alive by other nesting turtles. Rescued turtles that would have died without our intervention are shown in brackets with an R prefix and are included in the adjacent count.

Study period	Cause of death							Total
	Heat exhaustion		Fell over		Trapped			
	Central depression	beach	cliff	log	Beneath cliff	In rocks	Under dinghy	
1979: 29 Oct-13 Dec	7 (14%)	33 (67%)	7 (14%)	0	2 (4%)	0	0	49
1981: 11 Nov-12 Dec	3 (19%)	106 (68.4%)	19 (12.3%) (R19)	6 (3.9%) (R3)	12 (7.7%)	8 (5.2%)	1 (0.6%)	155
Whole season count on 27 July	26							
1982: 12 Nov-9 Dec	3 (14%)	15 (71%)	3 (14%)	0	0	0	0	21
Whole season count on 27 July:	5	55+	20	0	4	0	0	84+
1983-84: Whole season count on 22 April:	9	33+	43	0	7	0	0	92+
1984: 22 Nov-23 Dec	17 (2.0%)	654 (78.0%)	135 (16.1%)	1 (0.1%)	14 (1.7%)	12 (1.4%)	5 (0.6%)	838
1985: 24 Nov-20 Dec	0	8 (80%) (R1)	2 (20%)	0	0	0	0	10
1986: 19 Nov-23 Dec	NR	251 + 2* (79.6%)	53 (16.7%)			12 (3.8%)	0	318+
1987: 26 Nov-10 Dec	5 (2.1%)	182 + 1* (77.9%)	32 (13.6%) (R14)	15 (6.4%)	0	0	0	235
1995: 3-13 Dec	1 (0.4%)	201 (73.4%) (R3)	62 (23.0%) (R36)			6 (2.2%) (R1)	0	270
1996: 27 Nov-11 Dec	NR	596 (89.5%)	57 (8.6%)			13 (2.0%)	0	666+
1997: 29 Nov-10 Dec	22 (7.9%)	107 (38.6%)	121 (43.7%)			27 (9.7%)	0	277
1998: 28 Nov-11 Dec	2 (6%)	16 (44%) (R1)	16 (44%) (R2)			2 (6%) (R1)	0	36
1999: 28 Nov-12 Dec	10 (1.8%)	240 (43.1%)	257 (46.1%)			50 (9.0%)	0	557
2000: 30 Nov-10 Dec	0	0	2			2	0	4
2001: Nov-10 Dec	92 (66.2%)		42 (30.2%)			5 (3.6%)	0	139

low elevation, bright areas on their return to the sea (Limpus, 1971), the profile of the Raine Island beach platform causes the females in the beach depression to move approximately parallel to the water line for varying distances. Some may wander the entire length of the island in the beach depression before localised irregularities of topography lead them to the outer crest of the beach and hence to the water. The net result is to increase the time taken to return to the water. Turtles on the beach after daylight heat in the sun, leading to locomotory deterioration as hyperthermia progresses, then ultimately death ensues. Some of the turtles crossing the cliff line entered the central depression and some of these became disoriented and similarly wandered back and forth across the central depression into the daylight hours. These too died of heat exhaustion as the day progressed.

Nesting females remaining on the beach platform have been observed to die as early as 0930hr and all females that had remained on the beach after about 1000hr, carapace uppermost, were dead by approximately 1700hr. During December 1989, six females that remained on the open beach platform towards the middle of the day were selected for study of lethal hyperthermia. Experience had shown that all such turtles died within the current day. Each was fitted with a core body temperature probe and the temperature recorded at approximately half-hourly intervals for several hours (Fig. 17). The core body temperature increased from 35.8°C at 1040hr to as high as 40.4°C in one turtle at 1230hr. All turtles died when their core body temperatures exceeded 39°C. The time of death varied from 1230hr to 1640hr (mode = 1445hr). These temperatures contrast with the core body temperatures of nesting turtles on the beach at night, measured in eggs at the instant of oviposition, that ranged from 26.0°C in early November to 28.4-30.0°C in early December

TABLE 14. Core body temperature of nesting *Chelonia mydas* on Raine Island as indicated by the temperature of a freshly laid egg.

Date	Temperature (°C)			
	Freshly laid egg = core body temp.	Air	Water	Sand
Night time nesting turtles (2000-0200hr)				
5 Dec 77	29.8	27.4	27.0	28.0
6 Dec 77	29.6	27.2		28.0
7 Dec 77	29.2	27.2	27.8	28.0
1 Dec 78	28.4	26.2		27.2
30 Nov 79	26.0			27.0
2 Nov 79	26.0	26.5		26.0
6 Nov 79	26.0			26.00
2 Dec 89	30.0			
Early afternoon nesting turtle (1500hr)				
3 Dec 89	33.0			

(Table 14). A female that came ashore and nested in the heat of the early afternoon had a higher core body temperature of 33°C (Table 14). A turtle on the beach in the heat of the day has a dark carapace surface exposed to the sun and this absorbs solar radiation that can heat the turtle to lethal temperatures. The carcasses continued to heat post mortem as the day progressed. By 1500-1900hr the mean core body temperature, measured during autopsy, of turtles that had died earlier in the day was 41.4°C (SD = 2.77, range = 32.2-54.4, n = 96). For the 1997/98-2000/01 seasons there was a substantial reduction in the proportion of turtles dying from heat exhaustion (0-47%) (Table 13). This change is believed to be a direct consequence of the increased rainfall associated with these latter seasons (Fig. 7). With the overcast conditions and the cooling effect of rain, turtles were less likely to overheat and die.

Thus, those areas of the island that are surrounded by more elevated habitat can become traps that result in the turtles not moving directly seaward but wandering for extended distances. These disoriented turtles are at risk of dying from heat exhaustion if they are still on the island during the heat of the day. Similar disorientation and fatal hyperthermia have been reported for turtles stranded behind a mainland mangrove zone by a cyclone tidal surge (Limpus & Reed, 1985b).

Inverted turtles take longer to attain lethal levels of hyperthermia due to the reduced heat absorption of their pale coloured plastrons. Some turtles that have wandered into partly shaded areas have survived extended periods ashore however exposed parts of their bodies have been extensively sunburned (to the extent that scutes and underlying tissue peeled from their bodies). The turtles trapped in the deeper caves beneath the phosphatic limestone platform are not subjected to heat stress and probably die from dehydration.

NECROPSY RESULTS. All dead turtles examined by necropsy at Raine Island were adult female *C. mydas*. All were gravid females with enlarged mature follicles in their ovaries. All had recently formed corpora lutea in the ovaries consistent with having ovulated in the past 2-3 weeks. Some had oviducal eggs, all of which were of normal ovipositional shell thickness. Four eggs were removed from each of 7 freshly dead turtles, preserved in isotonic formalin within 2 hr of collection and examined for stage of embryonic development. All were at embryonic stage 6, (middle gastrulation) which is the normal ovipositional stage for *C. mydas* (Miller, 1985). It must be concluded that only females ready for oviposition come ashore at Raine Island.

The enlarged vitellogenic follicles of the ovaries of 2 freshly dead females were measured in early December 1988 (Fig. 19). There was a natural grouping of large yolked follicles that were approximately the size of the yolks of post ovipositional eggs. In both females these were distinct from the remaining follicles which were

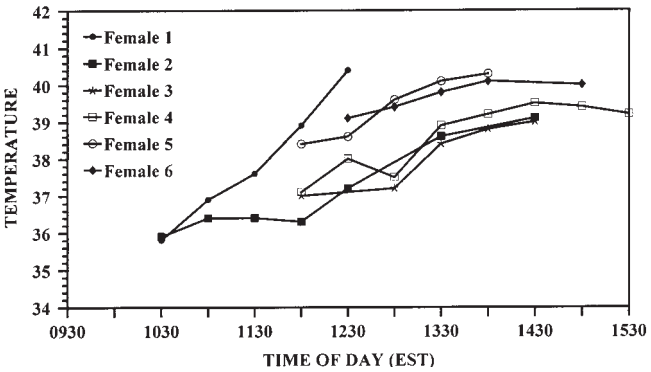

FIG. 18. Core body temperatures of moribund *Chelonia mydas* females that remained on the beach at Raine Island following nesting attempts during the previous night. EST denotes Easter Standard Time.

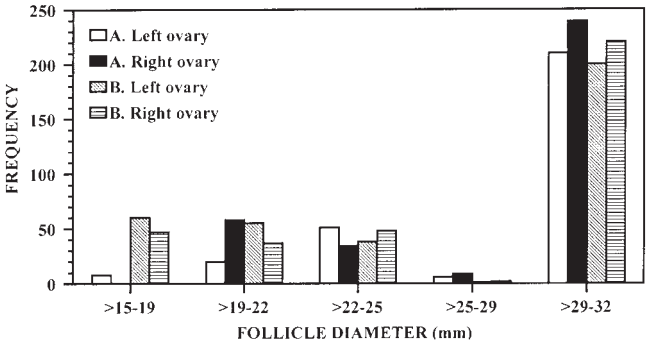

FIG. 19. Size distribution of yolked ovarian follicles in two *Chelonia mydas* females (A & B) that died of heat exhaustion after remaining on the beach at Raine Island following nesting attempts during the previous night.

smaller than normal yolks. This larger size class of yolked follicle is assumed to contain the mature follicles from which the successive clutches were to be produced by each female. Both of these turtles had complete clutches in their oviducts (clutch counts: A = 80, B = 100) from the previous ovulation and sufficient mature follicles in their ovaries for 4 or perhaps 5 additional clutches (mature follicle counts: A = 449, B = 420). These data suggest that by the beginning of the nesting season or very early within it, the female has pre-formed all the mature follicles she will require for the remainder of the season. If the number and/or weight of yolked follicles >25mm in diameter at the commencement of the migration from the feeding grounds, during courtship or as she arrives at the internesting habitat adjacent to the rookery could be quantified, it could provide a measure of the reproductive potential of the turtle without having to monitor it for months through an entire nesting season. The size of mature ovarian follicles and corpora lutea (Table 15) now forms the basis upon which determination of reproductive status of females captured in their feeding grounds are made.

Additional observations of oviducal eggs and ovaries in the necropsied turtles at Raine Island:

1984, 4-23 Dec: Shelled oviducal eggs were present in 66.2% of the dead turtles (SD = 16.21%, n = 12 daily samples totalling 310 turtles), regardless of the cause of death.

1986, 22 Nov-16 Dec: of 27 turtles necropsied, 2 (7%) had laid their entire clutch and 25 (93%) were carrying oviducal eggs.

1988, 29 Nov-8 Dec: All 4 turtles necropsied still retained what appeared to be complete clutches in their oviducts (clutch counts = 80, 100, 104, 113).

1989, 29 Nov-8 Dec: of 99 turtles necropsied, 47 (47%) had laid their entire clutch, 6 (6%) had laid only a portion of their clutch (8-33 eggs remaining in the oviducts), 46 (46%) retained what appeared to be complete clutches in the oviducts (mean clutch = 99.8, SD = 13.85, range = 66 - 127, n = 45). Rain during the first night increased nesting success of turtles for this period. of 8 freshly dead females examined on 8 December, 5 appeared to have begun atresia of almost all remaining mature follicles in the ovaries, even though each had sufficient large follicles for several more clutches. This prompted further examination of this issue in subsequent seasons.

1994, 29 Nov-10 Dec: of 39 females necropsied, mean oviducal egg count = 98.9 eggs (SD = 21.76, range = 34-160, n = 39).

1995, 5-13 Dec: of 22 females necropsied, 6 (27%) had laid their entire clutch while the remainder still contained oviducal eggs. At least 6 (27%) of the 22 sets of ovaries examined contained mature follicles that had begun atresia.

1997, 29 Nov-6 Dec: of 52 females necropsied, 8 (15%) had laid their entire clutch while the remainder still contained oviducal eggs. At least 38 (73%) of the 52 sets of ovaries examined contained mature follicles that had begun atresia.

1998, 1-9 Dec: The single female necropsied had no oviducal eggs and both ovaries had mature sized follicles that had begun atresia.

1999, 30 Nov-11 Dec: of 66 turtles necropsied, 26 (39%) had laid their entire clutch. The remainder carried 41-134 oviducal eggs consistent with having laid no eggs or having been disturbed by other turtles or by unsuitable nesting habitat after laying only part of a clutch. At least 38 (58%) of the sets of ovaries examined contained mature follicles that had begun atresia.

2001, 1-11 Dec: of 16 females necropsied, 9 (56%) had laid their entire clutch. The remainder carried oviducal eggs. Thirteen (81%) of the 16 sets of ovaries examined contained mature follicles that had begun atresia. The remaining 3 ovaries contained less than mature-sized follicles that had begun atresia.

These data demonstrate that while considerable variation existed (15-56%), few *C. mydas* that died at Raine Island had successfully laid an entire clutch during the previous night. The majority died while still carrying oviducal eggs: some died carrying reduced numbers of oviducal eggs, consistent with having been disturbed from a nest before a complete clutch was laid; and others appeared to be carrying complete clutches.

TABLE 15. Measurements of mature ovarian follicles and corpora lutea from adult female *Chelonia mydas* that died while ashore for nesting on Raine Island. The corpora lutea were selected from the largest size class, corresponding to the ovulation sites for the follicles represented in the oviducal eggs present in the turtles. The mature follicles were selected from among the largest size class of yolked follicles (Fig. 19). Each structure was measured along its greatest diameter.

Date	Measurement (mm)			
	Mean	SD	Range	n
Mature follicles				
1/12/78	31.1	1.22	29.3-33.5	20
17/12/85	33.2	1.04	31.4-34.9	10
Corpora lutea				
13/12/85	14.7	2.33	10.6-19.6	10
17/12/85	14.1	0.94	12.4-15.6	10

Substantial proportions (27-81%) of the adult female *C. mydas* attempting to breed in early December had already begun resorption of at least some of their mature ovarian follicles. In as much as early December is in the first half of the overall nesting season, these females would clearly not be converting all mature follicles to eggs.

SIZE OF DEAD TURTLES. The size of nesting *C. mydas* females that died on Raine Island is summarised in Table 16.

RESCUING MORIBUND TURTLES. During the research at Raine Island, the primary goal has been to document the functioning of the nesting population with the minimum of interference to it. In this regard it was not a goal to rescue dying turtles. However, in the normal course of the work, when live turtles were encountered that could be rescued easily, this was done. For example in December 1984, over 100 females were rescued. During the 1989-90 trip, 25 females were rescued. However in some years few turtles died, as in the 1985/86 season when only one was able to be rescued while five others died in the 27 nights the team was on the island during 24 November-20 December.

The simplest turtles to rescue were those on their backs that simply required righting. This could be accomplished by one strong person. If the cliff margin was patrolled daily at dawn, all turtles that had fallen on their backs during the previous night could be released before 0830hr. Turtles out on the open sand in daylight needed to be dragged to the beach crest. This normally required several persons working for more than

TABLE 16. Curved carapace length of adult female *Chelonia mydas* that died while ashore for nesting on Raine Island.

Year	Month	Curved carapace length (cm)			
		Mean	SD	Range	n
1976-77	Dec	106.7	4.19	99.5-117.5	23
1979-80	Dec	107.5	6.10	96.5-118.0	36
1981-82	Nov-Dec	106.0	5.12	90.0-122.0	84
1987-88	Nov-Dec	104.4	5.77	94.0-114.5	54
1988-89	Nov-Dec	102.5	4.42	95.0-109.0	13
1989-90	Nov-Dec	104.4	5.32	92.5-119.5	99
1991-92	Dead	104.1	4.618	94.4-110.0	48
1992-93	Dead	101.5		98.0-105.0	2
1993-94	Dead	104.1	4.97	89.0-115.8	53
1995-95	Dead	104.7	5.00	90.9-117.0	93
1996-97	Dec	104.1	4.59	89.6-120.7	379
1996-97	Jan-Feb	103.6	4.59	90.8-117.8	415
1996-97	Dead	103.9	4.59	89.6-120.7	800
1997-98	Dead	104.7	5.39	94.0-130.1	103
1998-99	Dead	103.9	4.17	97.8-113.8	12
1999-00	Nov-Dec	105.0	4.89	91.7-119.7	366
2000-01	Nov-Dec	106.0		96.6-112.9	3
2001-02	Nov-Dec	104.2	5.68	81.6-119.4	90

15 min per turtle, and was very strenuous work. It was debilitating to the research team to attempt to drag turtles across the open sand in the heat of the day. In high density nesting seasons there were often hundreds of turtles (sometimes over a thousand) on the beach as late as 0700hr. Most of these turtles successfully made it back to the water. It was usually after 0900hr before the turtles out on the open sand could be identified as threatened by heat exhaustion. Even at this time many of the turtles present still successfully made their way back to the water without assistance. However, by then it was also stressful for people to be working over this hot sand, so few turtles were rescued after 0900hr or before 1500hr.

If it were considered a priority to rescue moribund turtles at Raine Island the following summary points should be noted: only in high density nesting seasons will there be numerous nesting females dying on the island (most of the mortality will occur from mid November to about mid February); small numbers of moribund turtles can be rescued by righting those turtles which have fallen on their backs; most mortality occurs on the open beach as a result of heat exhaustion, not of turtles falling on their backs around the cliff; to rescue a large proportion of the moribund turtles would require a rescue team's daily presence on the island for months at mid season;

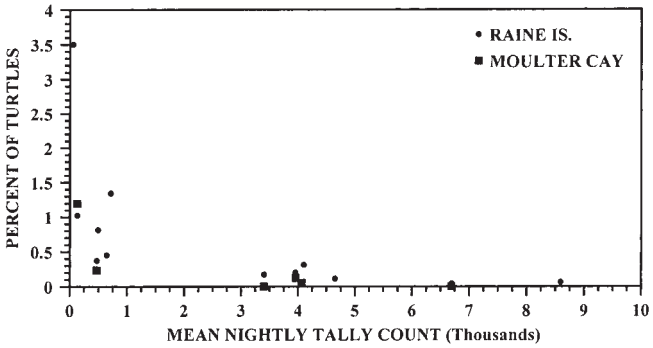

FIG. 20. Proportion of nesting female *Chelonia mydas* at Raine Island and Moulter with recent shark bites. Data sourced from Tables 3 & 17.

it is doubtful if most moribund turtles can be rescued daily in high density nesting seasons without some mechanical assistance.

SHARK PREDATION. During most summer visits large tiger sharks (*Galeocerdo cuvier*) were seen over the shallows of the reef flat and adjacent to the edge of the reef every day. Up to five individuals (judged by size) were seen in the one day at the western end of the island. Tiger sharks regularly were seen scavenging on the carcasses of turtles that had died while ashore at the beacon end of the island and then washed onto the reef flat by high tides. Less frequently they were observed to prey on live adult turtles. For example, in December 1986, a school of 5 tiger sharks attacked and killed an adult female *C. mydas* swimming over the reef flat adjacent to the island. Not all turtles attacked by tiger sharks are immediately killed. One female (X43893) had received a bite which removed a portion of her carapace over the right hind flipper to expose her abdominal cavity. Her intestine was undamaged but exposed. When she was seen nesting on 26 November 1982, the wound was healing and judged to have occurred at about the time of courtship. While she was nesting she had an open hole that permitted sand entry into her abdominal cavity. It did not appear to impede her nesting drive. The broad snout of the attacking shark (identified by tooth scars to the carapace) suggested that she had been attacked by a tiger shark. Observations such as this emphasise the impressive capacity of the large marine turtles to survive extensive injuries through shark attack. It also illustrates the extent to which the female will persist with her nesting drive in spite of debilitation and disturbance.

Each summer a small percentage of the nesting turtles had been recently mauled by sharks and the resulting wounds were still healing when the turtles were examined while nesting (Table 17). The degree of healing of the majority of the wounds indicated that they had probably occurred at, or just prior to, the commencement of nesting, possibly at courtship time. While some of these injuries had been caused by tiger sharks, others may have been caused by the medium to large whaler sharks (*Carcharhinus* spp.) that occur in the area.

Figure 20 illustrates the occurrence of fresh shark bites on the nesting turtles at Raine Island and Moulter Cay (Table 10) with respect to the size of the annual nesting population (December mean nightly tally count for Raine Island has been adopted as an index of population size; Table 3). There was a strong negative correlation between the size of the annual nesting population and the proportion of turtles recently bitten. This is further supported by the one small sample of nesting females examined in mid year 1987 when the nesting density was extremely low with less than 1 turtle/night ashore for nesting: 3 (43%) of the 7 nesting females examined had been recently mauled by sharks (Table 17).

The nesting turtles with fresh shark bite wounds represent the survivors (Table 11) — those that did not sustain a massive bite or a bite to a critical area. The actual mortality rate caused by shark bite of adult female *Chelonia mydas* at these rookeries remains unquantified. If the proportion of turtles surviving bites is positively correlated with the proportion of turtles in the population that are killed by shark attack, then these data suggest that there is a reverse density dependence between the risk of shark attack and the size of the annual nesting population. There is less risk if the turtle breeds in a high density nesting season. However, the risk of being mauled by a shark is highest for turtles that nest out side the main nesting season and for those that nest in low density nesting seasons. In addition it suggests that in the event of a substantial population decline, the remaining turtles would be at increased risk of shark attack when aggregated for breeding, assuming that the shark population remains stable and independent of the size of the nesting turtle population.

TABLE 17. Frequency of occurrence of recent shark bites on nesting *Chelonia mydas* at rookeries in the outer northern Great Barrier Reef.

Rookery & date	No. of turtles examined	Turtles with recent shark bites	
		n	%
Raine Island			
Dec 1980	284	10	3.5%
Nov-Dec 1982	1601	13	0.81%
Nov-Dec 1986	11032	22	0.20%
Jul-Aug 1987	7	3	43%
Nov-Dec 1987	2287	7	0.31%
Nov-Dec 1988	2391	32	1.34%
Nov-Dec 1993	11887	7	0.06%
Dec 1994	1346	6	0.45%
Dec 1995	4615	5	0.11%
Nov-Dec 1997	7122	2	0.03%
Nov-Dec 1998	3284	12	0.37%
Nov-Dec 1999	25283	10	0.04%
Dec 2000	756	8	1.06%
Nov-Dec 2001	9725	17	0.17%
Moulter Cay			
Dec 1986	2581	3	0.12%
Dec 1997	1956	1	0.05%
Dec 1998	427	1	0.23%
Dec 1999	844	0	0%
Dec 2000	84	1	1.19%
Dec 2001	873	0	0%
No.8 Sandbank			
Nov 1988	30	0	0%
Dec 1995	79	4	5%
Dec 1997	183	2	1.09%
No.7 Sandbank			
Dec 1986	74	0	0%
Nov 1988	26	0	0%
Dec 1995	73	0	0%
Dec 1997	108	0	0%

FLUCTUATIONS IN ANNUAL NESTING POPULATIONS

The most accurate method available at present to measure the size of a turtle nesting population requires a whole of season, total tagging census of the rookery (Limpus et al., 2001). At Raine Island this would require a nightly tagging census from early October to about April. In most years it would require numerous staff on the island for more than 3 months to ensure that every turtle ashore was accounted for without adding a major disturbance factor to the turtles. Such an approach has not been logistically or financially feasible to date, and would probably cause significant disturbance to the nesting sea birds. Tagging at Raine Island has been restricted to sampling a small portion of the total number of turtles nesting during any visit.

The *C. mydas* nesting in eastern Australia is confined essentially to a summer breeding season that reaches a peak period of nesting density during December and January (Raine Island: Table 4; Bramble Cay: Limpus et al., 2001; Heron Island: Moorehouse, 1933, Bustard, 1972.). At Raine Island the nesting season is more protracted than in the southern GBR, but it still maintains a mid summer peak of nesting density. It has been demonstrated that the average number of turtles ashore per night at a *C. caretta* rookery within a standard mid season sampling period can be used as an index of the total annual nesting population (Limpus, 1985). Turtle research at Raine Island has been timed to include a common annual sampling period in late November to early December. The mean nightly tally count during the last days of November and the first two weeks of December (Table 3) will be used as the index of the size of the annual nesting population for the purposes of the present study.

C. mydas nesting numbers have fluctuated widely from year to year at Raine Island and adjacent outer barrier reef cays (Tables 3-5). The annual fluctuations in the mean tally count for Raine Island in the two weeks of late November-early December is summarised in Fig. 21. In the mid-season of the very high density nesting years, many thousands of females come ashore nightly at Raine Island and Moulter Cay (Fig. 22). As many as 11565, 11467 and 14519 nesting females have been recorded on Raine Island in single walks of the beach (1974, 1984 and 1996 respectively) (Table 3, Fig. 23). These densities were equivalent to 6.4-8.1 females per metre of waterline for the island. In contrast, in a very low density nesting year, as few as 32 females on average have come ashore nightly (1977) (Table 3). This was equivalent to 1 turtle ashore per 56.3m of water line. The approximate synchrony in annual fluctuations in the size of the *C. mydas* nesting population encompasses the entire GBR. This is illustrated by the high level of synchrony of fluctuations in total annual nesting population at Heron Island in the southern GBR and the early December mean tally count at Raine Island (Fig. 21). These two rookeries have the most comprehensive census data recorded for *C. mydas* in Australia.

The historical records for Raine Island (see above) contain some useful indications of changing nesting population levels in past years.

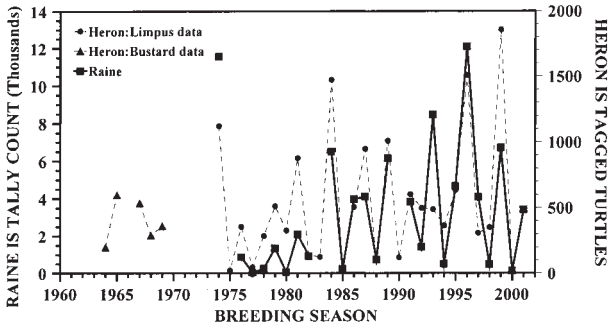

FIG. 21. Annual variation in *Chelonia mydas* nesting density at Raine Island and Heron Island. The mean tally count measured in the first two weeks of December (solid line) is used as an index of the size of the total nesting population. These data are derived from Table 3. The nesting season is denoted by the year it commences. The 1974/75 data were obtained from a single nights visit to the island on 29 November 1974.

The November 1973 estimate by Stoddart et al. (1981) of less than 200 females beaching per night at Raine Island suggests that 1973/74 was a poor nesting season. Whittaker estimated the mid season nesting at 'as many as 1500 turtles ... nightly' (breeding season not specified) when he applied in 1956 for a permit to harvest turtles from Raine Island. This estimate is of a similar magnitude as occurred during the 1979, 1981, 1982 and 1992 breeding seasons. Ellis (1936) described a scene consistent with up to a few thousand, rather than ten thousand, nesting females nightly at Raine Island during the 1890 to 1892 guano mining operation. In addition, there are several records consistent with extremely high turtle nesting density. MacGillivray (1917) described a scene with immense numbers of turtles in the shallows during the late afternoon on 4-11 December 1913 and further he complained of being 'tormented at night by the nesting turtles, who would persist in trying to walk over or under our sleeping shelter'. On 12 December 1913 he recorded on nearby Moulter Cay 'thousands of turtles climbing the sandbank' in the moonlight. Vlassoff (pers. comm.), estimated 10-12 thousand turtles ashore for the night during the 1955/56 season. While the accuracy of this estimate cannot be checked, his measure of about ten new turtles per night falling on their backs along the cliff line is consistent with a huge nesting population as is his photograph showing high density mortality in the central depression (Fig. 11). Similarly Watson's (pers. comm.) account of a breeding season in about 1965 when he stepped or jumped from turtle to turtle while Vlassoff walked 100 paces beside him in late November is consistent with nesting densities greater than those recorded in most recent seasons, except perhaps 1974/75, 1984/85 and 1996-97. In 1987 and 1999, Watson's method of measuring turtle nesting density was repeated at Raine Island and a stepping index recorded for nights with a range of nesting densities (Table 18). No more than 25 paces from turtle to turtle could be made when tally counts of up to 7,010 were recorded. From these considerations it concluded that the 1974/75, 1984/85 and 1996/97 seasons with very high nesting densities were not unique to recent years for Raine Island. Based on the historical data above and the recent quantified data (Tables 3-4) it is concluded that the annual nesting density of *C. mydas* at Raine Island has

FIG. 22. Early morning oblique aerial photographs of Moulter Cay, 7 January 1990, showing high density nesting *Chelonia mydas.*

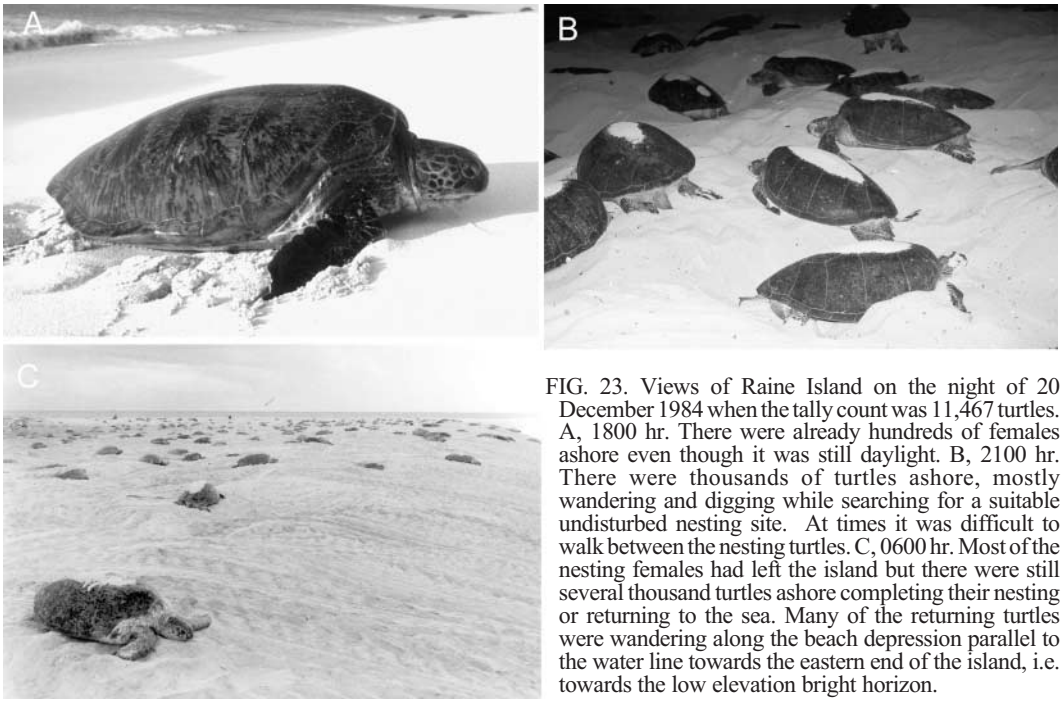

FIG. 23. Views of Raine Island on the night of 20 December 1984 when the tally count was 11,467 turtles. A, 1800 hr. There were already hundreds of females ashore even though it was still daylight. B, 2100 hr. There were thousands of turtles ashore, mostly wandering and digging while searching for a suitable undisturbed nesting site. At times it was difficult to walk between the nesting turtles. C, 0600 hr. Most of the nesting females had left the island but there were still several thousand turtles ashore completing their nesting or returning to the sea. Many of the returning turtles were wandering along the beach depression parallel to the water line towards the eastern end of the island, i.e. towards the low elevation bright horizon.

been fluctuating widely over several orders of magnitude for more than a century.

Limpus & Nicholls (1988, 1994, 2000) demonstrated that the number of *C. mydas* nesting on the eastern Australian rookeries in a given year is a function of the El Nino Southern Oscillation (ENSO) climatic events. The Southern Oscillation Index (SOI), the standardised difference in monthly mean atmospheric pressures between Darwin and Tahiti, is used as a measure of the variability of ENSO climate variation (Bureau of Meteorology Australia, 2002). In testing for the best correlation between breeding numbers and ENSO events, Limpus & Nicholls (2000) identified a significant correlation linked to the mean SOI value approximately 1.5yr before the breeding season commences. This time delay between the climate event and the onset of breeding is determined by the duration of the sequence of physiological processes that culminate in egg production. A female that commences laying eggs in November will have migrated from her distant foraging area approximately two months earlier. Before she commenced her breeding migration, she will have deposited yolk into the hundreds of mature ovarian follicles that she will use for egg production. This vitellogenic process commenced in about February and is completed by about September. Prior to commencement of vitellogenesis, the female will have increased her fat deposits during the previous months. This present study extends the analysis of Limpus & Nicholls (2000) using the more extensive eastern Australian *C. mydas* census data now available from 27 breeding seasons (Table 19). There continues to be a significant linear correlation between the mean May-October SOI approximately 1.5yr before the breeding season (MOSOI) and the natural log of the annual green turtle census data (census) from representative rookeries at each of the eastern Australian breeding aggregations (Fig. 24):

Raine Island:

$\ln(\text{census}) = -0.1178*\text{MOSOI} + 6.8949$ ($F_{1,22} = 19.48$, $p<0.001$; $r^2 = 0.4696$);

Heron Island:

$\ln(\text{census}) = -0.09243*\text{MOSOI} + 5.5755$ ($F_{1,25} = 29.89$ $p<0.001$; $r^2 = 0.5445$).

It is not unreasonalble that a slightly greater proportion of the variability in the number of breeding turtles is explained by the correlation for the Heron Island census. The use of a mid-season index of nesting numbers (Raine Island census) should show more variability than

TABLE 18. A comparison of the stepping index and the nightly tally count measure of *Chelonia mydas* nesting density at Raine Island.

Date	Stepping index (number of paces)			Tally count
	Mean	range	n	
30/11/87	3.5	3-5	4	3296
1/12/87	4.0	2-7	4	2312
2/12/87	4.2	3-6	5	4498
5/12/87	8.2	6-10	5	5011
28/11/99	4.7	4-5	3	5806
29/11/99	7.7	6-8	3	5834
2/12/99	20	15-25	2	7010
6/12/99	15	15	1	6745

a total season tagging census (Heron Island census).

Limpus & Nicholls (2000) have demonstrated that these fluctuations in the size of the annual *C. mydas* nesting populations result from variability in the proportion of adult females present in the distant foraging areas that prepared for breeding in any particular year. Because ENSO is a broad-scale regional climate event for the whole of the Southeast Asia-Western Pacific region, there is synchrony in fluctuations in the annual nesting populations at all *C. mydas* rookeries in the region, not only in eastern Australia but also throughout Southeast Asia (Limpus & Nicholls, 2000; Chaloupka, 2001). Therefore, the long-term census data for Raine Island and Heron Island represent significant baseline measures against which the size of nesting populations at other *C. mydas* rookeries in the Southeast Asia-Western Pacific Region can be compared.

The population census data recorded at Raine Island and Heron Island (Fig. 21) illustrate the difficulty of quantifying the stability of a *C. mydas* nesting population. In the absence of the 1974 data, the annual nesting populations at both these rookeries over a 15 yr period could be interpreted as increasing. However, an inclusion of the 1974 data negates that interpretation. There has been a higher frequency of high density nesting seasons since 1984 than in the ten preceding years. The stability of these *C. mydas* populations cannot be assessed by measuring the size of the annual nesting population over a few years or even over a decade. It will require several decades of detailed monitoring of the size of the nesting population before anything more subtle than catastrophic decline of numbers can be reliably demonstrated.

REPRODUCTIVE DISCRETENESS OF THE NORTHERN GREAT BARRIER REEF *CHELONIA MYDAS* NESTING AGGREGATIONS

Traditionally it has been assumed that marine turtles return to breed at the beach of their birth. However, there are sparse data on marine turtle growth from birth to adulthood to demonstrate the truth of this. There has been one good case history that provides circumstantial evidence that the major *C. mydas* rookery areas support non-interbreeding populations. The once large *C. mydas* population breeding at the Grand Cayman rookery of the Caribbean Sea was overharvested to approximate extinction during the 19th century and almost no *C. mydas* nesting has been recorded there in the 20th Century. However, the large Tortuguero *C. mydas* rookery of Caribbean Costa Rica (approximately 1,000 miles away from Grand Cayman) still functions at high nesting density (Groombridge & Luxmoore, 1989). Turtles born at the Tortuguero rookery have not been recruiting to breed on the Grand Cayman beaches.

Within Australia, Bustard (1972) postulated that the nesting populations of the separate cays of the Capricorn-Bunker Groups, southern GBR, were non-interbreeding groups. The management implications of this were that each island breeding unit could be managed independently of the others. However, movements of breeding turtles demonstrated by tagging-recapture studies of courting and nesting turtles (Limpus et al., 1984a, 1994b; Limpus, 1993) indicate that *C. mydas* cannot maintain non-interbreeding populations among a group of islands as closely spaced as those of the Capricorn-Bunker Groups. In addition, as a result of temperature dependent sex determination among marine turtles and the differences in beach temperatures, different sexes of hatchlings can be produced from different rookeries (Limpus et al., 1983c). This latter study suggested that the warmer rookeries of mainland south Queensland produce mostly female hatchling *Caretta caretta* while the cooler beaches of the adjacent coral cays of the Capricorn-Bunker Groups produced mostly male hatchlings. The entire assemblage of these rookeries probably represented a management unit comprising complementary rookeries for *Caretta caretta*.

PROTEIN ELECTROPHORESIS. Using an electrophoretic survey of presumptive protein loci, Gyuris & Limpus (1988) demonstrated that

TABLE 19. Annual census data for nesting green turtles, *Chelonia mydas*, at Heron Island representing the southern Great Barrier Reef nesting population and Raine Island representing the northern Great Barrier Reef nesting population. MOSOI denotes the mean May to October SOI (Bureau of Meteorology Australia, 2002) from approximately 1.5yr before the breeding season; ln denotes the natural logarithm. The Heron Island census data are derived from a tagging census of the total annual nesting population. The Raine Island census data are derived from the mean nightly tally count (number of nesting females counted in one walk of the island) for the first two weeks of December. These data are an extension of the data summarised in Limpus & Nicholls (2000).

SOI data		Breeding season	Turtle Data			
Year	MOSOI		Heron Island		Raine Island	
			census	ln(census)	census	ln(census)
1972	-13.6	1974	1121	7.02	-	-
1973	9.5	1975	21	3.04	-	-
1974	8.8	1976	355	5.87	872	6.77
1975	17.3	1977	46	3.83	32	3.47
1976	-5.4	1978	285	5.65	243	5.49
1977	-13.0	1979	513	6.24	1347	7.21
1978	4.0	1980	327	5.79	59	4.08
1979	-0.8	1981	878	6.78	2049	7.63
1980	-2.6	1982	139	4.93	925	6.83
1981	6.1	1983	125	4.83	-	-
1982	-18.8	1984	1471	7.29	6493	8.78
1983	1.6	1985	42	3.74	227	5.42
1984	-1.2	1986	505	6.22	3956	8.28
1985	-1.0	1987	947	6.85	4102	8.32
1986	-0.1	1988	111	4.71	731	6.59
1987	-15.2	1989	1009	6.92	6144	8.72
1988	11.2	1990	120	4.79	-	-
1989	6.4	1991	602	6.40	3828	8.25
1990	1.5	1992	498	6.21	1417	7.26
1991	-10.6	1993	488	6.19	8462	9.04
1992	-5.7	1994	370	5.91	500	6.21
1993	-11.7	1995	632	6.45	4647	8.44
1994	-15.0	1996	1509	7.32	12100	9.40
1995	-0.6	1997	289	5.67	4067	8.31
1996	6.28	1998	351	5.86	471	6.15
1997	-18.1	1999	1801	7.50	6693	8.81
1998	9.47	2000	26	3.26	129	4.86
1999	2.98	2001			3402	8.13

if reproductive isolation occurred among the *Caretta caretta* rookeries of the southern Great Barrier Reef then the isolation was between the rookeries of the Swain Reefs and those of the remainder of south Queensland. A similar study of eastern Australian *C. mydas* was attempted. Non-sibling *C. mydas* hatchlings from Raine Island and other eastern Australian rookeries were collected during the 1979/80 breeding season for a collaborative study of the population genetics of eastern Australian *C. mydas* with Commonwealth Scientific and Industrial Research Organisation staff (Cleveland Laboratory). The specimens were inadvertently destroyed at the laboratory before the study was completed and no results are available. During the 1982/83 breeding season 21 non-sibling *C. mydas* hatchlings were collected at Raine Island. Another sample of >50 non-sibling hatchlings collected from Raine Island in April 1984 was lost before analysis as the result of a freezer power failure. An electrophoretic survey of 27 presumptive protein loci was made of the available *C. mydas* hatchlings from Raine Island and a similar series collected from Heron Island (Gyuris, 1984). This study identified low genetic variability within the species but the results were insufficiently differing to reject the nul hypothesis of there being a single breeding population of *C. mydas* within the GBR. The low

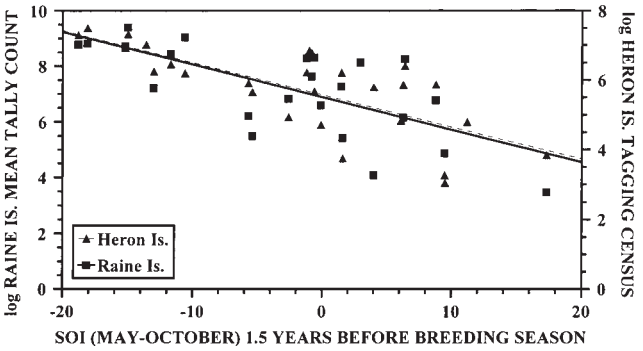

FIG. 24. Correlation of the natural logarithm of the annual census data recorded for northern and southern Great Barrier Reef *Chelonia mydas* populations and the mean May-October Southern Oscillation Index (SOI) approximately 1.5 years before the breeding season. Census data (Table 19): for Raine Island, annual mean tally count during the first two weeks of December; for Heron Island, annual total tagged nesting population. See text for regression equations and goodness of fit statistics.

levels of electrophoretic variability in sea turtles is such that it is not sensitive enough to deliniate reproductively isolated populations.

DNA ANALYSES. The application of mitochondrial DNA restriction analysis to Australian *C. mydas* nesting populations at Raine Island, Heron Island and Western Australia (Norman et al., 1994a) reinforced the studies of Bowen et al. (1989, 1992) and Meylan et al. (1990) that demonstrated that the nesting female returns to breed in the region of her birth. Norman et al. (1994a) further demonstrated that, while widely separated female breeding aggregations were genetically different, the nesting populations on nearby islands could not be discriminated. These results were subsequently corroborated by mtDNA sequencing studies and microsatellite nuclear DNA analysis by Norman et al. (1994b), FitzSimmons et al. (1995, 1997a) and Moritz et al. (2002). In particular, these studies have identified that there are three separate genetic stocks that breed in eastern Australia in the northern (nGBR), the southern GBR (sGBR) and the Coral Sea Platform (Fig. 13). Each of these stocks is also genetically separate from each of the other breeding aggregations tested from within the Indian Ocean and Pacific Ocean basins. Torres Strait is identified as a stock boundary with 100% genetic isolation occurring between *C. mydas* breeding at GBR rookeries and those of the Gulf of Carpentaria. The nGBR stock encompasses rookeries from Bramble Cay in northeast Torres Strait south to at least No.8 Sandbank which lies north of Princess Charlotte Bay, with the largest nesting aggregations centred at Raine Island and Moulter Cay. Each stock is characterised by a dominant haplotype and all show very low levels of within population variation. The dominant haplotypes of the nGBR and sGBR stocks are shared at low frequency by the other respective stock. This overlap in the distribution of the dominant nGBR and sGBR haplotypes indicates that a very low level of interbreeding by females could be occurring between the two stocks. In contrast there is no detectable female mediated gene flow between the east Australian and Gulf of Carpentaria-Western Australian stocks.

FitzSimmons et al. (1997b) compared the mtDNA haplotypes of breeding male *C. mydas* at three courtship areas (Raine Island Reef, nGBR; Heron Island Reef, sGBR; Bountiful Island, Gulf of Carpentaria) with mtDNA haplotypes from nesting females at the rookeries adjacent to each of these courtship areas. They found that breeding males were displaying comparable philopatry to the courtship area as the nesting females were to their nesting beaches. A comparison of rates of nuclear DNA gene flow (male and female mediated gene flow) and mtDNA gene flow (female mediated) among *C. mydas* rookeries located around the Australian coast (FitzSimmons et al., 1997a) identified that the estimated rates of gene flow between stocks were generally higher than expected for nuclear DNA relative to mtDNA. The difference was most pronounced between turtles from the nGBR and sGBR stocks. It was proposed that the atypical nuclear DNA difference between the nGBR and sGBR stocks was most likely the result of the geography of Torres Strait that caused a bottleneck for turtles migrating from the west. Some breeding females from the sGBR stock migrate from foraging areas in Arnhem Land and Gulf of Carpentaria through Torres Strait towards their traditional nesting area in the southern GBR. These sGBR females could be mated by males from the nGBR stock in the Torres Strait courtship area as the sGBR females pass through. Nuclear DNA gene flow could thus occur between the stocks even though both the males and females display comparable high

TABLE 20. The geographical distribution of foraging areas identified via tag recoveries of adult female *Chelonia mydas* recorded nesting at northern Great Barrier Reef rookeries. * Tag recoveries from Torres Strait could also include migrant turtles captured at courtship or turtles captured while migrating through the area.

Foraging area (Recapture location)	Rookery area					
	Northern GBR Stock					Southern GBR
	Eastern Torres Strait	Raine Is + Moulter Cay	No.7 & No.8 Sandbanks	Inner shelf, nth GBR	Total	
Indonesia	2	17			19	0
Arnhem Land & Gulf of Carpentaria	2	40	4		46	11
Torres Strait* (PNG+Qld)	17	215	6	1	239	15
Eastern & northern PNG	3	14	2	1	20	3
Vanuatu		1			1	0
Fiji					0	2
New Caledonia		2			2	31
GBR: Cape York to 14°S	3	60	1		64	24
GBR: 14-24°S	1	7	1		9	298
Qld >24°S		3			3	109
New South Wales					0	1
Total	28	359	14	2	403	494

levels of philopatry to their respective breeding areas (FitzSimmons et al., 1997b).

In summary, the assemblage of *C. mydas* that breeds at the rookeries and courtship areas of the northern GBR centred on Raine Island and Moulter Cay and the dispersed assemblage of these same turtles in their respective foraging areas represents a globally significant, single, independent management unit.

MIGRATION

Limpus et al. (1992) reported on breeding migrations from the eastern Australian *C. mydas* stocks. The sample size of migration recaptures of adult females from the northern GBR rookeries (n=403) has approximately doubled since that study. The current dataset is summarised in Table 20 & Fig. 25. Conclusions from this larger dataset are summarised.

Adult females from the nGBR stock migrate from foraging areas in eastern Indonesia, Papua New Guinea, Vanuatu, New Caledonia, Northern Territory and from throughout coastal Queensland to breed at rookeries within the northern GBR and Torres Strait. These foraging areas span a region 25° in latitude from southern Irian Jaya in Indonesia to Moreton Bay in south Queensland and 37° in longitude from Melville Island in western Northern Territory to southeastern New Caledonia. While the majority of recaptures have occurred within a few hundred kilometres of the rookery, the longest distance between rookery and capture site was 2,773km from Raine Island to Vanuatu.

The majority of the nGBR stock tag recoveries have been from north and west of the nesting beaches, from foraging areas in Torres Strait, Gulf of Carpentaria and coastal areas of the Arafura Sea in Irian Jaya and Northern Territory. The north-south distribution of foraging area tag recoveries from eastern Australia of adult females from each of the nGBR and sGBR stocks are summarised in Fig. 26. While there has not been equal sampling effort at each latitude, the nGBR stock is the dominant component of the foraging populations within eastern Australia to as far south as approximately latitude 13°S. South of this, the sGBR stock is dominant. These data indicate that adult females from stocks breeding at opposite ends of the GBR do not occupy identical feeding distributions.

Migration data are available for only one adult male. This resident from Shoalwater Bay (~22°20'S, 150°12'E) in Central Queensland was trawl captured in Torres Strait at courtship time.

Most (76.7%, n=310) of the reported nGBR *C. mydas* stock migration recaptures were of turtles hunted for food, 3.2% (n=13) were from incidental captures in commercial fisheries, mostly trawling, 15.8% (n=64) were captured during systematic sampling of feeding populations during Queensland Turtle Research projects and 2.2% (n=9) were from stranded dead or rescued turtles. The remaining 2.0% (n=8) of reports did not identify the capture method.

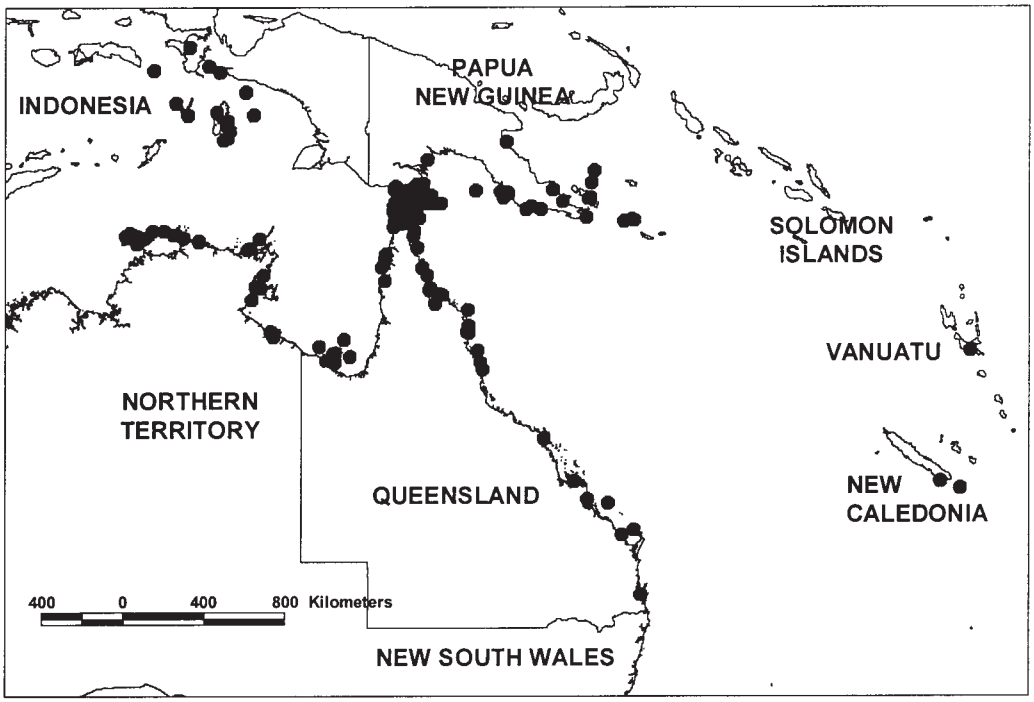

FIG. 25. Distribution of non-nesting recaptures of adult female *Chelonia mydas* that had been tagged at rookeries of the northern Great Barrier Reef stock: No.7 and No.8 Sandbanks, Raine Island, Moulter Cay and Bramble Cay.

In addition to these tag recoveries there have been other reports of tagged turtles for which the tags and/or the data were not returned. This is particularly so in neighbouring countries where there may be low levels of literacy or a poor capacity to read the English text of the tags. In remote areas, hunters may not be able to afford the postage to return tags. In some parts of northern Australia groups of tags have been found in homes of hunters, the tags having been retained as souvenirs of the hunting. In contrast, there is a belief among many of the turtle hunting communities of eastern Indonesia, PNG and some parts of northern Australia that the tag represents ownership of the turtle and that the hunter will 'get into trouble' for killing someone else's turtle if he reports the capturing of a tagged turtle. In the same area there also has been negative publicity concerning turtle hunting and tags are associated with bureaucratic interference in the hunting practices. In these latter cases the tags are apparently often discarded. These reasons may account for the recent paucity of tag returns from Indonesia even though there was a substantial increase in *C. mydas* hunting for the Bali market in the Aru and Irian Jaya areas since about 1988 (J. Schulz and I. Suwelo, pers. comm., Nov. 1990) until the 2001 closure of the Bali turtle trade (W. Adnyana, pers. comm., May 2002). This shift in hunting effort probably was in response to the substantial decreases in *C. mydas* populations in other parts of Indonesia (Groombridge & Luxmoore, 1989).

There are some general principles for *C. mydas* breeding migrations that can be drawn from these data.

1) The individual adult female has a strong site fidelity to her traditional nesting beach (Table 7). However, the present study has not demonstrated clearly the corresponding fidelity of the female to her particular feeding area as has been demonstrated for the females migrating to breed at the southern GBR *C. mydas* rookeries (Limpus et al., 1992). With most post-nesting migration recaptures from the northern GBR rookeries having been derived from turtles hunted for food, there was a reduced potential for recording turtles over successive legs of their migration between foraging and nesting areas to establish foraging area fidelity.

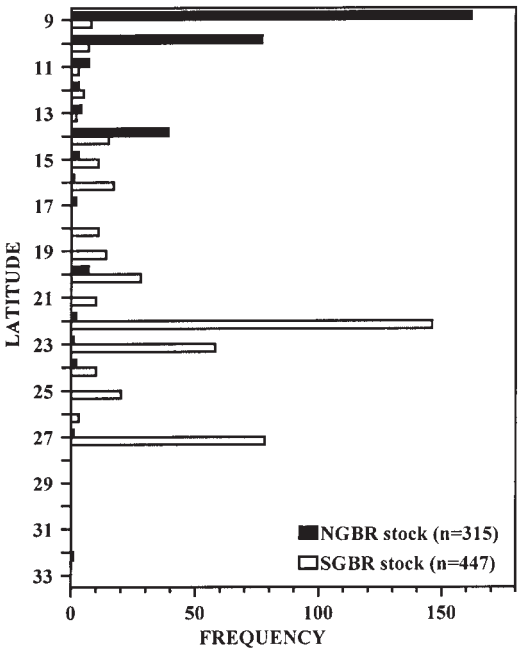

FIG. 26. Comparison of frequency distributions of captures in eastern Australian foraging areas south from the Papua New Guinea coast of Torres Strait of adult female *Chelonia mydas* recorded on nesting beaches of the northern and southern GBR stocks. Recaptures grouped by 1° latitudinal blocks.

2) Adult females that breed at the same rookery do not all migrate from the same foraging area (Table 20).

3) Breeding females did not necessarily nest at the closest rookery to their respective foraging areas. For example, X10925 was tagged at Raine Island, stranded 1,057km away by cyclone Kathy in the MacArthur River delta 3 yr later was rescued, then again recorded nesting at Raine Island after a 4yr remigration interval (Limpus & Reed, 1985b). She did not go to the Wellesley Group rookeries of the southern Gulf of Carpentaria or the eastern Arnhem Land rookeries that were closer to her feeding area. This also applies for all recaptured turtles from the Northern Territory. Similarly, not all the females that lived on the reefs of the far northern GBR migrated to the adjacent Raine Island and Moulter Cay rookeries. Some migrated past Raine Island to breed in the southern GBR.

4) Females living in the same foraging area do not all nest at the same rookery (Table 20).

5) Turtles in foraging areas represent populations of mixed genetic stocks. For example, in addition to those that breed at nGBR rookeries, female *C. mydas* foraging in the Princess Charlotte Bay area in the northern GBR have been recorded breeding at rookeries in the Coral Sea Platform, the southern GBR and internationally in eastern Papua New Guinea, eastern Solomon Islands, and northern New Caledonia. In an extreme case, adult female *C. mydas* captured off Coburg in the Northern Territory, have been recorded nesting at Raine Island, at Western Australian rookeries and in southeastern Java, Indonesia.

REMIGRATION

Remigration, the interval between breeding seasons, varies between species and has posed a problem for measurement because of the long remigration intervals. The main problems have resulted from tag loss and the logistics of systematically monitoring a rookery for many years. Early research on marine turtle reproductive ecology did not rigorously address tag loss. In 1974 the Queensland Turtle Research Project was requested to take over the *C. mydas* field studies at Heron Island that had lapsed following the departure of Dr H.R. Bustard from Australia. The methodologies of the original project were initially retained, in particular the tagging methodology of applying a monel tag to the L1 tagging position (Bustard, 1966). Within a few years it was apparent that there was a significant tag loss problem within this study. In 1978 systematic studies were commenced to identify the optimal position for tag application and to find a tag that had low rates of loss over a 10 yr development. These studies identified the need for a new design of turtle tag that used a metal with very low corrosion rates, and that was at a reasonable cost. Titanium and inconel 625 were identified as the preferred metal types. Within the Queensland Turtle Research Project, we were able to locate a tag manufacturer prepared to produce turtle tags from titanium. In a parallel study in Hawaii, G. Balazs worked with an American manufacturer to produce a turtle tag from inconel 625. The tag trial studies (Limpus, 1992a) demonstrated that the optimal tagging position is in the axillary area on the trailing edge of the front flipper (L3 or R3 tagging positions). The more distally the tag is applied, the more likely it is to be lost. Monel tags have a high probability of tag loss, approaching 100% in 10 yr. Plastic tags did not perform better than the monel tags in the long term. Titanium tags were

TABLE 21. Frequency distribution of remigration recaptures of nesting female *Chelonia mydas* recorded by tagging year cohorts at Raine Island since the commencement of Raine Island Corporation funded research and monitoring. The summer breeding season is defined by the year at the commencement of the breeding season. Tag type definitions follow the tag design definitions of Limpus (1992a): M, monel tags; T, titanium tags. Slight variations in design of the titanium tags are denoted by T1, T2, T3 and T4. However, the variation in the design of the titanium tag is not included in the analysis of this study.

Census for recovery of tags		Breeding season for commencement of cohorts originally tagged while nesting at Raine island																				
Year		1981	1982	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
	No. tagged turtles	2605	1094	504	80	2545	1919	1717	1559	1952	1037	1208	1368	1999	1593	1034	1668	2997	1434	1982	2210	840	1417
	Tag type	M2	M2	T1	T2	T2	T2	T2	T2	T2	T2	T2	T2	T2	T3	T3	T4	T4	T4	T4	T4	T4	T4
1981																							
1982		0																					
1983	No RIC survey	22	1	0																			
1984		16	8	1	0																		
1985		43	22	5	1	0																	
1986		9	5	14	2	2	0																
1987		1	2	17	2	9	0	1															
1988		0	0	1	1	34	23	1	0														
1989		40	0	2	0	138	92	29	0	0													
1990	No RIC survey	2	7	0	0	27	25	51	40	3	0												
1991		2	0	0	2	37	11	29	39	86	0	0											
1992		0	1	2	0	12	13	5	27	72	2	0	0										
1993		0	3	3	0	38	12	12	40	53	22	6	0	0									
1994	No RIC survey	0	0	0	0	8	1	1	7	3	1	6	2	0	0								
1995		1	0	1	0	18	2	6	12	23	16	31	23	4	0	0							
1996	2 (Dec+Feb) surveys	0	0	2	1	42	13	18	33	42	42	40	56	74	23	0	0						
1997		0	0	5	0	33	13	9	26	45	22	44	39	84	57	13	0	0					
1998		0	0	1	0	14	2	2	7	24	6	17	9	31	28	13	3	0	0				
1999		0	0	0	0	57	7	21	46	56	43	61	67	114	176	74	115	32	1	0			
2000		0	0	0	0	2	5	0	2	7	2	2	5	11	5	12	3	11	6	0	0		
2001		0	0	3	3	23	3	8	17	17	16	18	25	41	31	21	59	108	53	12	0	0	
Remigrant : Cumulative total		136	49	57	12	494	222	193	296	431	172	225	226	359	320	133	180	151	60	12	0	0	

found to have at least a 50% lower rate of tag loss within the 6 yr period that titanium tags had been under trial. The experimental studies on tag retention were conducted in the southern GBR where it was logistically easier and less expensive to make repetitive captures of the same turtles over many years. As improvements in tagging methodology have been developed they have been applied to the nGBR studies.

REMIGRATION TAG RECOVERIES. The number of remigration recaptures during each study trip are summarised in Tables 7-9. There have been 3,727 remigrant recaptures of turtles still wearing a tag up until the end of the 2001-2002 breeding season at Raine Island and adjacent rookeries. These are not all of the tagged remigrants that have returned to these islands as there has been no examination of the entire nesting population in any one season, nor has the entire nesting population been tagged in any one season. The vast majority (98%, n=3,659) of remigrant recaptures were recorded at the same rookery at which each turtle was originally tagged (Tables 7-9). Of the 33,234 females originally tagged at Raine Island prior to 2001, one has been recaptured nesting at Bramble Cay and 21 at Moulter Cay. This very low rate of interseason change of rookery will be partly the result of the low sampling rate at nGBR rookeries other than Raine Island. However, of the 2,992 females tagged on the other outer cays of the northern Great Barrier Reef prior to 2001, only 1.2% (n=37) have been recaptured nesting at Raine Island in a later season: 16 from Moulter Cay, 10 from No.8 Sandbank, 7 from No.7 Sandbank and 4 from Milman Island. In addition, one from No.7 Sandbank and two from Milman Island changed rookeries between breeding seasons to nest at Moulter Cay; three from No.8 Sandbank changed to No.7 Sandbank and one from No.7 Sandbank changed to No.8 Sandbank.

There has been considerable tagging of *C. mydas* at other Australian rookeries in the southern GBR, Coral Sea region and the Wellesley Group in southeastern Gulf of Carpentaria since 1974. Only one of the approximately 40,000 female *C. mydas*, tagged while nesting in the southern GBR prior to the 2001/2002 season, was recaptured nesting at any northern GBR rookery (Tables 7-9), although there have been many thousands of remigration recaptures of southern GBR nesting females returning to nest in the southern GBR rookeries in later seasons (C. Limpus, unpubl. data). Similarly, only one nesting female from the QPWS and Environment Australia Studies at the Coral Sea Platform rookeries has been recaptured

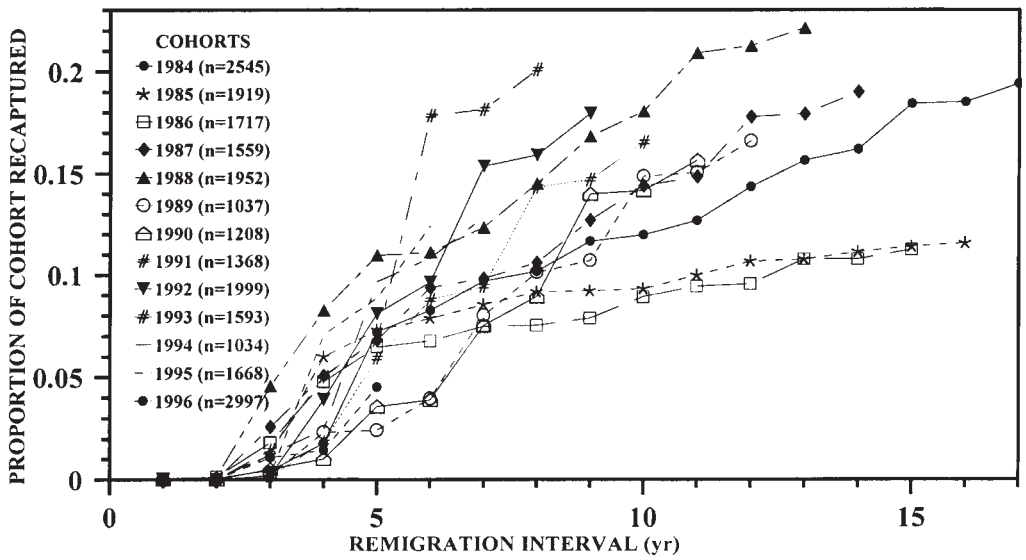

FIG. 27. Cumulative recapture rate of remigrant adult female *Chelonia mydas* at northern GBR rookeries recorded by the yearly tagging cohorts at Raine Island. Data are presented for the yearly tagging cohorts for which titanium tags were applied from 1984 until 1996.

breeding at Raine Island. None of the females tagged while nesting at the northern GBR rookeries have been recaptured nesting at the more intensively studied southern GBR rookeries. None of the more than 1,000 nesting *C. mydas* tagged nesting at Bramble Cay by Applied Ecology Pty Ltd in 1974 to 1980 has been recaptured nesting at Raine Island. No female *C. mydas* tagged nesting at an eastern Australian rookery has been recaptured nesting at a rookery outside of eastern Australia or vice versa.

Collectively, these data demonstrate that an adult female *C. mydas* exhibits a high level of fidelity to a particular nesting beach and can return to that same nesting beach even after migrating large distances to home feeding areas in the intervening years (Limpus et al., 1992). These observed rates of movements of breeding females among rookeries are reinforced by the results of DNA genetic analyses of *C. mydas* breeding populations of the Indo-Pacific Region (Moritz et al., 2002) that demonstrate a genetic interchange among adjacent rookeries such as those of the northern GBR and Torres Strait. At the same time, there is very little genetic interchange between the rookery regions of the north and south of the GBR (Norman et al., 1994a) or between rookeries of the nGBR stock and those much further away (Norman et al., 1994a; Moritz et al., 2002). The remigration tag recovery data are consistent with the genetic data in identifying groupings of *C. mydas* rookeries that support an interbreeding population separated from more distant breeding aggregations with which they do not interbreed.

RECAPTURE RATE OF REMIGRANTS. The remigration recaptures at Raine Island, uncorrected for tag loss, are summarised according to the breeding season in which they were tagged in Table 21 along with a summary of the tagging methodology used with each tagging year class. Less than 1% recapture rates resulted from tagging with monel tags applied in the L1 or R1 positions. The change to tagging in the L3 position improved the recovery of monel tagged turtles by a factor of approximately 5 to 10 times. The change to L3 applied titanium tags has more than doubled the rate of recovery over that of L3 applied monel tags (Table 22). Currently, the sampling of the Raine Island nesting population for approximately 2 weeks in early December each year is yielding a recovery of titanium tagged remigrants equivalent to 12-22% of the turtles originally tagged in the cohort (Fig. 27). These recovery rates continue to improve as additional sampling continues. In 2001 there were still recoveries being made from all year classes of titanium tagged turtles including 23 remigrants from the 1984/1985 season (17 yr since first tagged) (Table 21). There were even

TABLE 22. Frequency distribution of remigration from various year classes pooled by tag design. M1 and M2 denote different designs of monel tags (National Band and Tag Co. #49 and #19 respectively); T1 and T2 denote titanium tag designs as described by Limpus (1992a).

	Breeding season		
	1979/1980 + 1980/1981	1981/1982 + 1982/1983	1982/1983 + 1983/1984
No. tagged in cohort	2053	3696	584
Tag design	M1	M2	T1 & T2
Tag position	L3	L3	L3
Remigration interval	Frequency	Frequency	Frequency
1 yr	0	0	0
2 yr	0	1	2
3 yr	4	30	7
4 yr	9	38	16
5yr	23	48	18
6 yr	2	10	3
7 yr	5	3	3
8 yr	2	3	
9 yr	1		
Total	46	133	49
Proportion recaptured	2.2%	3.6%	8.4%

TABLE 23. Regression equations (in the form y = ax + b) for transformation from curved carapace length (CCL. cm) to other carapace measurements (cm) for breeding *Chelonia mydas* at Raine Island. * = not significant.

x	Y	a	b	r^2	n	P
Female						
CCL	Curved carapace width	0.776	14.469	0.769	504	<0.001
CCL	Straight carapace length (SCL)	0.983	3.356	0.997	54	<0.001
CCL	Carr's straight carapace length (CSCL)	0.787	16.243	0.963	29	<0.001
SCL	Straight carapace width (SCW)	0.494	26.733	0.575	54	0.02>p >0.01
Male						
CCL	Curved carapace width	0.735	16.272	0.703	25	0.01>p >0.005
CCL	Straight carapace length	0.771	17.613	0.967	25	<0.001
CCL	Carr's straight carapace length	0.799	15.516	0.937	14	<0.001
SCL	Straight carapace width	0.540	20.681	0.569	24	0.2>p >0.1*

three turtles recorded for the first time since they were tagged in 1982/1983 when titanium tags were first deployed. These extremely long intervals between captures probably represent multiple remigration intervals, given incomplete annual censusing. The tag recovery rate would improve if the sampling period at the island each summer was increased in duration.

In the December 1986 sample there were 2.2 times as many tag-scarred remigrants as there were remigrants with tags. During the December 1988 sampling period (6 yr after introduction of titanium tags) when many hundreds of nesting females were examined for tags each night, tagged remigrants were recorded at the rate of 2.0% of the nesting females examined (SD = 0.888, range = 0-2.55%, n = 9 nights). Remigrants that had lost their tags were recognised at an equal rate (mean = 2.0%, SD = 1.49, range = 0-3.95%, n = 9 nights). Most of these tag-scarred turtles are probably from the monel tagging years. By the December 2001 sampling (19 yr after introduction of titanium tags), tagged remigrants were recorded at the rate of 5.07% of the nesting females examined (SD = 1.996, range = 3.012-10.030%, n = 10 nights). Remigrants with lost tags were recorded at a rate that was an order of magnitude lower (mean = 0.79%, SD = 0.419, range = 0.149-1.399%, n = 10 nights). Large numbers of nesting turtles at Raine Island need to be examined on a nightly basis to ensure good sample sizes for remigration tag recoveries.

REMIGRATION INTERVAL. The frequency distribution of recaptures, uncorrected for tag loss, of remigrant *C. mydas* at Raine Island by tagging cohort and year of recapture are summarised for all years since the commencement of the Raine Island Corporation funded research in 1981 (Table 21). The usual method for presenting remigration data summarises the remigration interval recorded at a rookery within the year of recapture (Limpus et al., 1994b). While this method has value when considering events associated with the immediate breeding season, it confounds nesting season and tagging cohort effects. To enhance understanding of population dynamics, an analysis of remigration interval by tagging cohorts is more appropriate. Because the consecutive annual tagging cohorts have differing durations over which remigrants are recorded, an analysis of the raw data from each cohort (Table 21) would introduce a bias from the longer studied cohorts. The following considerations have been taken into account in choosing an interval for comparison

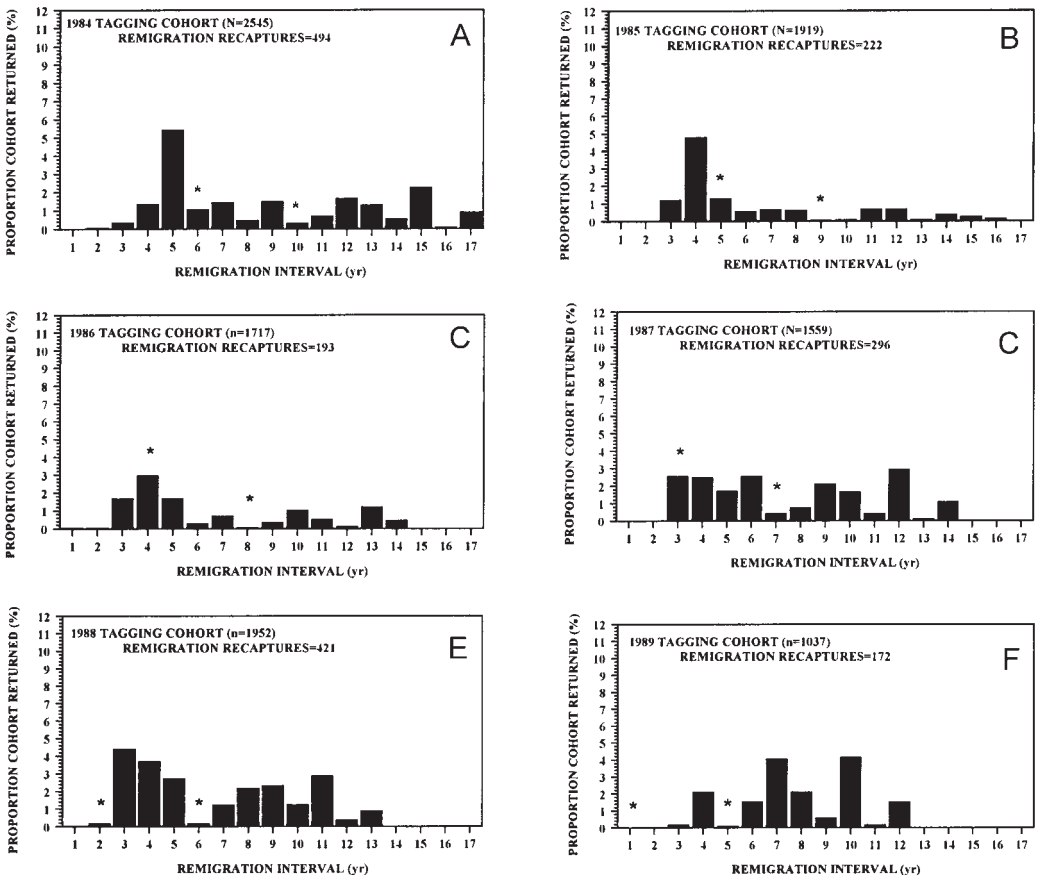

FIG. 28. Frequency distribution for remigration interval recorded from yearly cohorts of adult female *Chelonia mydas* tagged nesting at Raine Island since the introduction of large scale use of titanium tags, 1984-1997 (Table 21). * denotes an incomplete sampling year when no Raine Island Corporation survey trip occurred.

between cohorts. Bustard (1976) recorded no 2yr or 3yr remigration intervals during a major part of his nine consecutive years of total tagging census, commencing in 1964/1965, of the Heron Island *C. mydas* population (single monel tagging in L1 position). The Applied Ecology project at Bramble Cay recorded no remigration recaptures from four consecutive years of total tagging census of the *C. mydas* population during 1976/1977-1979/1980 (double monel tagging in L1 and R1 positions. Limpus et al., 2001). Based on long term titanium tagging, Limpus et al. (1994a) recorded that the majority of the *C. mydas* remigrants at Heron Island returned after 5-8 yr intervals. These studies indicate that the eastern Australian *C. mydas* stocks may not be breeding on the usually hypothesised 2-3 yr remigration interval for the species (Hirth, 1997). Because of the incomplete annual sampling of the nesting population at Raine Island, the longer recorded remigration intervals may be confounded by recaptures of turtles that had actually remigrated in intervening years but had not been recorded. The majority of the remigration intervals for the Raine Island *C. mydas* population were within 4-6yr (Table 21). Most tagging cohorts show a reduction in remigration recapture rate at about eight years (Fig. 27). Therefore the results from the 10 consecutive years of large scale titanium tagging at Raine Island during 1984-1993 will be analysed for remigration interval using only recaptures at less than nine years following first tagging or the last recorded breeding for a recaptured turtle. It is expected that restricting the analysis of the first eight years of remigration data for each cohort will minimise the number of multiple cycles that are mistakenly

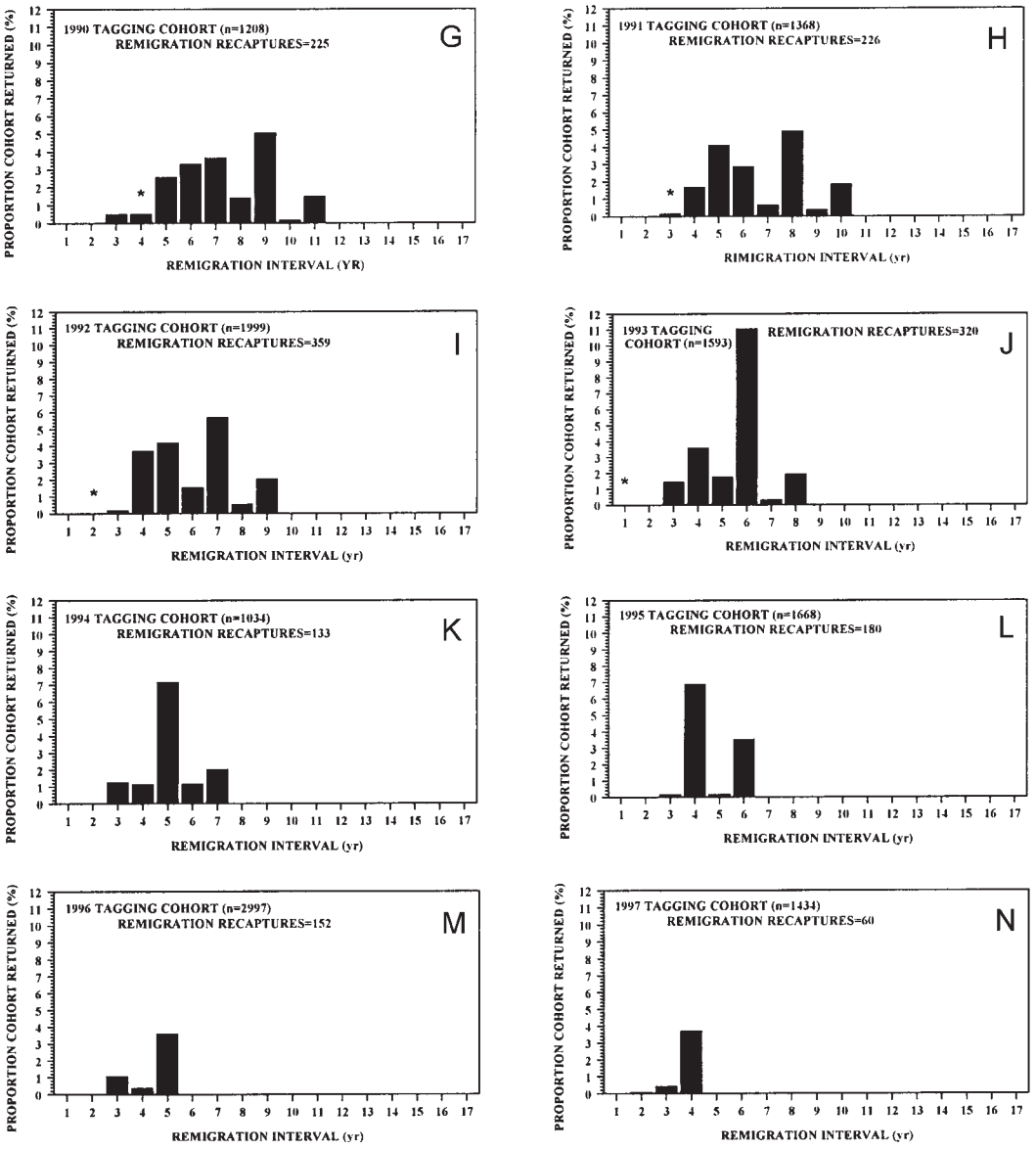

FIG. 28 (*Cont.*)

included in the analysis, while capturing the majority of the remigrations for the cohort.

It should be noted that the quantification of remigration interval at Raine Island has been partly compromised by the lack of continuity of sampling effort. The standard December sampling trips were not run in some years: 1983, 1990, 1994. The impact of reduced numbers of recaptures resulting from not checking large numbers of turtles for tags in these years can be tracked through the sequential remigration frequencies for each cohort (Fig. 28). Each cohort was impacted at a different remigration interval. For the combined 10 years of data from 1984 to 1993, some of these resulting between-year differences are expected to be smoothed.

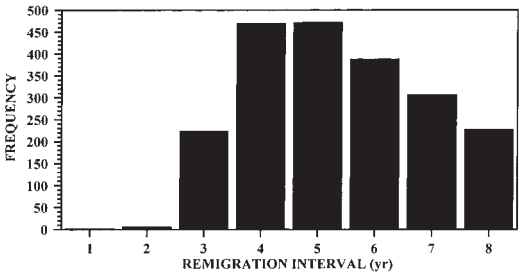

FIG. 29. Frequency distribution of remigration interval for adult female *Chelonia mydas* recorded at northern GBR rookeries pooled for ten annual tagging cohorts, 1984-1993. To minimise the confounding effect of varying durations of study period for the cohorts, only remigration recaptures spanning <9 yr have been considered. To minimise the confounding effect of tag design, only titanium tagged cohorts have been included.

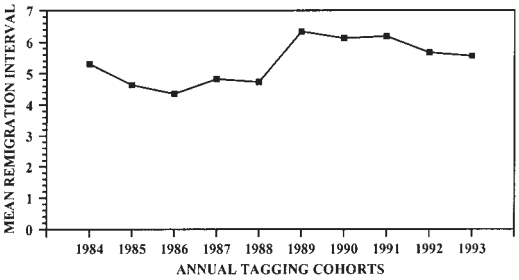

FIG. 30. Variability in mean remigration interval measured for 10 consecutive annual tagging cohorts of adult female *Chelonia mydas* nesting at Raine Island: 1984 - 1993.

At Raine Island, short remigration intervals of one and two years were extremely rare (0.33% from a sample of 2,094 turtles) (Fig. 29). Three year remigration intervals accounted for only 10.7% of recaptures. The modal remigration interval for the Raine Island *C. mydas* population was 4-5yr (Fig. 29). There are significant differences in annual remigration intervals among the annual tagged cohort from 1984 to1993 (one way ANOVA: F9,2084 = 42.02; $p<0.001$). No explanation is offered for the abrupt increase in mean remigration interval between the 1988 and 1989 cohorts (Fig. 30). While some of the differences may be attributable to the lack of continuity of sampling (Fig. 28), many of the differences appear to result from stochastic variability in the modal return interval among cohorts. When a strong positive SOI results in very depressed nesting numbers in a particular season, it limits the number of remigrants available for capture in that season. For example, during the extremely low density 2000/2001 nesting season, the remigration group corresponding to that in 2000 was very depleted within each cohort's recaptures (Fig. 28). However, a different remigration interval was impacted for each tagging cohort. In contrast, with high density nesting seasons such as 1999/2000, the remigration groups corresponding to those in 1999 were atypically high for their respective tagging cohorts (Fig. 28). It is apparent that there is no fixed remigration interval that applies for this stock. Remigration interval is variable in a complex response to regional climate fluctuations.

To further investigate remigration variability from the perspective of the breeding season of recapture, the remigration data (Table 21) was reanalysed with respect to the year of recapture (breeding season) within the 11 seasons 1991-2001 (Fig. 31). Again, the analysis was restricted to the remigration intervals <9 yr. Remigration intervals analysed from this period encompass returns from the years since the introduction of titanium tagging of the Raine Island nesting population in 1983. A reasonable comparison cannot be easily made with data originating from the earlier years when turtles were tagged with monel tags, given the high rate of tag loss for monel tags (Limpus, 1992a). There were significant differences in remigration interval by nesting season of recapture for the years 1991-2001 (1 way ANOVA: $F_{10,2146} = 15.65$; $p<0.001$). In addition there was a significant linear correlation between the mean remigration interval and the year:

Remigration interval = 0.08364*year – 161.5452
($F_{1,9} = 8.30$, $0.01<p<0.025$. $r^2 = 0.48$, DF = 9).

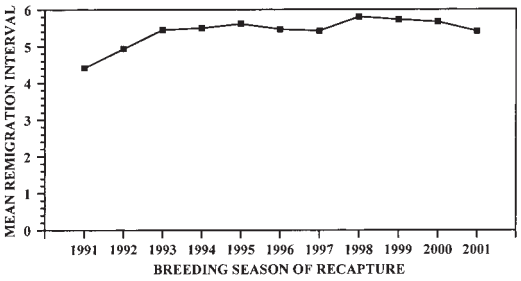

FIG. 31. Variability in mean remigration interval measured within 11 consecutive breeding seasons for adult female *Chelonia mydas* nesting at Raine Island: 1991 - 2001.

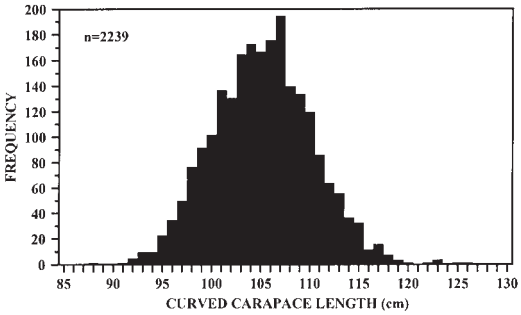

FIG. 32. Frequency distribution of size of nesting female *Chelonia mydas* recorded at Raine Island and Moulter Cay during the 1999-2000 breeding season.

Mean remigration interval has increased over at least the past decade (Fig. 31).

No significant linear correlation was found between the mean annual remigration interval measured within the breeding season of recapture and the mean May-October SOI measured 1.5 yr before the breeding season ($F_{1,9} = 0.007$, $p > 0.25$).

SIZE OF BREEDING ADULTS

FEMALES. A comparison of several methods of measuring turtle size is shown (Table 23). Because CCL has been the standard length measurement of marine turtles used in Australia (Bustard, 1972; Limpus & Walters, 1980; Limpus, 1980b; Limpus et al., 1983a,b) and South Africa (Hughes, 1974a,b) and because of the high correlation between CCL and the two other length measurements in common use (Carr's straight carapace length: Carr & Ogren, 1960; Straight Carapace length: Hughes, 1974a,b), CCL will continue as the standard length measurement for this study. Should the need arise for comparison with overseas studies, CCL can be transformed to other required lengths using the equations of Table 23.

The carapace measurements of nesting females are summarised in Tables 24-26 and Fig. 32. Averaged over the 25 seasons of sampling in November - December at Raine Island, the mean female CCL = 105.97cm (SD = 5.142, range = 86.0 - 130.1, n = 20947. Table 24). Averaged over 6 of these seasons, mean female CCW = 98.1cm (SD = 5.04, range = 82.3 - 115.5, n = 2237, Table 28). Mean straight carapace measurements are summarised for comparison with other studies in Table 28.

There were significant differences in mean CCL among annual November-December samples (Table 24, Fig. 33). There has been a significant downward trend in mean carapace length of the nesting female *C. mydas* at Raine Island and Moulter Cay during mid summer over 26 breeding seasons, 1976-2001 ($F_{1,23} = 28.66$, $p < 0.0005$; $r^2 = 0.555$, df = 23, $0.001 < P < 0.0025$). Within this trend, whenever there were very high density nesting seasons proximal to low density nesting seasons, there were fluctuations in mean CCL. On average smaller turtles bred in the high density nesting seasons and larger ones in the low density seasons. Parmenter (1980b) recorded significant differences in mean CCL between nesting seasons (1976-1979) for Bramble Cay *C. mydas* and attributed the differences to only the larger size turtles being able to complete physiological preparation for nesting in the low density years. We have shown the size of the annual nesting *C. mydas* population is a function of the mean May-October Southern Oscillation Index ~1.5yr before the commencement of the breeding season. Therefore we tested for a

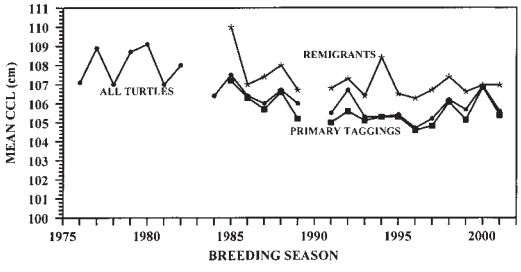

FIG. 33. Changing size (CCL) of nesting female *Chelonia mydas* recorded nesting at Raine Island and adjacent rookeries in the northern GBR during 26 years of monitoring. * = remigrants; square = primary taggings; dot = all turtles.

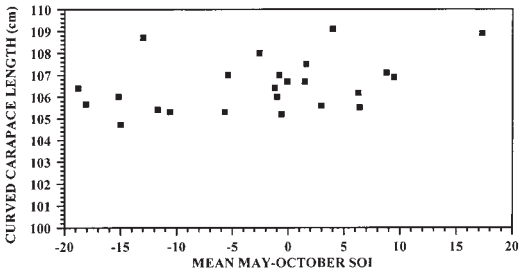

FIG. 34. Examination of a possible regional climatic regulation of the size of adult female *Chelonia mydas* nesting at Raine Island. The mean May-October SOI measured ~1.5yr before the breeding season (Table 19) was used as the measure of climate variability. Turtle size = mean carapace length measured in December (Table 24).

TABLE 24. Annual variation in curved carapace length (CCL) of nesting female *Chelonia mydas* at Raine Island and adjacent Moulter Cay ##MC) during the mid summer nesting season. Primary denotes turtles tagged for the first time in that season. Remigrant denotes turtles recorded breeding in a previous season.

Year	Rookery	All Turtles			Primary			Remigrant		
		Curved carapace length (cm)			Curved carapace length (cm)			Curved carapace length (cm)		
		Mean (Range)	SD	n	Mean (Range)	SD	n	Mean (Range)	SD	n
1976 (Dec)	RI	107.1 (93.5-124.0)	5.24	266						
1977 (Dec)	RI	108.9 (99.5-120.5)	4.39	125						
1978 (Dec)	RI	107.0 (90.5-125.0)	5.62	331						
1979 (Dec)	RI	108.7 (96.5-125.5)	4.86	390						
1980 (Dec)	RI	109.1 (96.0-124.0)	5.18	201						
1981 (Dec)	RI	107.0 (95.0-121.5)	4.96	538						
1982 (Dec)	RI	108.0 (91.0-123.0)	5.11	504						
1983-										
1984 (Dec)	RI	106.4 (93.0-119.0)	4.81	489						
1985 (Dec)	RI	107.5 (92.0-124.0)	5.41	400	107.2 (92.0-124.0)	5.47	303	110.0 (100.0-117.0)	4.07	30
1986 (Dec)	RI	106.4 (93.0-125.0)	4.82	771	106.3 (93.5-125.0)	4.83	445	107.0 (95.0-121.5)	5.17	75
1987 (Dec)	RI	106.0 (87.0-123.5)	5.34	494	105.7 (87.0-118.5)	5.36	403	107.4 (98.5-116.5)	4.43	40
1988 (Dec)	RI	106.7 (93.0-122.0)	4.85	534	106.6 (93.0-122.0)	4.73	476	108.0 (95.5-120.0)	5.09	54
1989 (Dec)	RI	106.00 (89.0-120.0)	4.92	488	105.2 (89.0-120.0)	5.30	227	106.7 (97.0-120.0)	4.48	261
1990 (Dec)	RI	106.72 (90.0-126.0)	5.23	526	106.32 (90.0-126.0)	5.37	380	107.76 (98.5-118.5)	4.72	146
1990 (Dec)	MC	107.61 (95.4-120.5)	5.49	46						
1991 (Dec)	RI	105.5 (90.9-119.4)	4.86	660	105.0 (90.9-119.4)	5.00	450	106.8 (91.2-117.3)	4.31	210
1992 (Dec)	RI	105.91 (89.5-123.0)	5.14	673	105.65 (89.5-123.0)	5.24	565	107.31 (98.5-118.0)	4.39	108
1992 (Dec)	MC	105.66 (93.0-118.5)	5.62	48						
1993 (Dec)	RI	105.31 (87.8-122.0)	5.36	1360	105.14 (87.8-122.0)	5.37	1172	106.36 (92.8-119.4)	5.13	188
1994 (Dec)	RI	105.30 (86.0-123.5)	5.49	520	105.30 (86.0-123.5)	5.56	423	108.4 (97.5-120.5)	5.48	20
1995 (Dec)	RI	105.41 (88.8-123.7)	5.28	1733	105.30 (88.8-123.7)	5.26	1468	106.49 (94.6-120.5)	5.14	141
1995 (Dec)	MC	105.40 (86.6-123.7)	5.21	109						
1996 (Dec)	RI	104.70 (86.5-127.5)	4.88	1945	104.47 (86.5-127.5)	4.90	1466	106.34 (92.5-118.4)	4.90	287
1996 (Jan)	RI	104.12 (90.2-121.0)	4.65	1180	104.15 (90.2-121.0)	4.73	822	105.61 (94.3-117.5)	4.44	88
1996 (Pooled)	RI	104.48 (86.5-127.5)	4.80	3125	104.36 (86.5-127.5)	4.84	2288	106.17 (92.5-118.4)	4.80	375
1997 (Dec)	RI	105.35 (87.2-130.1)	4.99	1861	104.82 (87.2-130.1)	4.99	1487	106.70 (90.6-121.3)	4.83	374
1997 (Dec)	MC	104.43 (92.0-119.1)	4.97	164						

TABLE 24 (*Cont.*)

Year	Rookery	All Turtles			Primary			Remigrant		
		Curved carapace length (cm)			Curved carapace length (cm)			Curved carapace length (cm)		
		Mean (Range)	SD	n	Mean (Range)	SD	n	Mean (Range)	SD	N
1998 (Dec)	RI	106.22 (91.0-126.5)	4.85	1715	106.08 (91.9-126.5)	4.80	1521	107.38 (91.0-119.7)	5.01	154
1998 (Dec)	MC	105.86 (94.2-117.4)	4.55	193	105.87 (94.2-117.4)	4.57	191			
1999 (Dec)	RI	105.59 (88.4-126.1)	5.01	2071	105.13 (88.4-126.1)	5.04	1160	106.6 (92.3-125.5)	4.87	766
1999 (Dec)	MC	105.27 (92.3-118.4)	4.79	168	105.12 (95.7-118.4)	4.84	131			
2000 (Dec)	RI	106.93 (91.5-121.3)	5.39	735	106.87 (91.5-121.3)	5.43	661	106.95 (99.0-118.8)	5.02	57
2000 (Dec)	MC	106.50 (96.6-116.1)	3.99	85	106.59 (97.3-116.1)	3.81	81			
2001 (Dec)	RI	105.58 (88.6-121.7)	4.92	1617	105.46 (91.6-120.7)	4.89	1145	106.00 (88.6-121.7)	4.98	361
2001 (Dec)	MC	105.00 (86.0-123.3)	5.04	281	105.02 (86.0-123.3)	4.97	270			

relationship between the mean May-October SOI (Table 19) measured ~1.5 yr before the *C. mydas* nesting season and mean summer CCL measured in December (Table 24). However, the mean summer CCL of the nesting females did not show a significant correlation with the mean SOI from ~1.5 yr before the breeding season ($r^2 = 0.144$, DF = 22; $F_{1,22} = 3.71$; $0.1>p>0.05$) (Fig. 34).

In contrast with the Raine Island results, Limpus et al. (1984a) found no between-season variation in the size of nesting *C. mydas* at Heron Island over eight breeding seasons, 1974-1981. Similarly there was no significant difference in CCL among annual samples from No.7 and No.8 Sandbanks (Table 26), possibly because of the small annual samples relative to the variance within the samples. No significant difference in CCL was found between the Raine Island sample and the various northern GBR island samples within any one year.

For all years except 2000 during the 17 yr period, 1985 to 2001, remigrant nesting females were significantly larger on average than females that were tagged for the first time (Table 24). The first-time-tagged group of turtles included new recruits to the nesting population as well as turtles that had nested in previous seasons but which had not been tagged. *Caretta caretta* (Limpus, 1991) and *N. depressus* (Parmenter & Limpus, 1995) nesting in the southern GBR and *E. imbricata* (Miller et al., 2000) nesting in the northern GBR display a similar characteristic of new recruits to the breeding population being smaller on average than remigrant females.

There were significant differences in mean CCL among annual November-December samples for both remigrant and primary tagged females at Raine Island across the 17 yr period, 1985-2001 (Fig. 33; Table 24) (Primary tagged turtles: $F_{16,13,735} = 15.71$, $p<0.0001$. Remigrant turtles: $F_{16,3,255} = 2.75$, $p<0.001$). There was no significant downward trend in the annual mean size of the primary tagged females across this period ($F_{1,15} = 2.36$, $0.1<p<0.25$; $r^2 = 0.136$, df = 15, $p>0.25$). Although the correlation was poor, there was a significant downward trend in the annual mean size of the remigrant turtles within the same period (Remigrant turtles: F1,15 = 7.08, $0.01<p<0.025$; r2 = 0.321 df = 15, $0.1<p<0.25$).

There was no significant log-log correlation between adult female *C. mydas* CCL and weight for the small sample weighed after completion of

TABLE 25. Annual variation in curved carapace length (CCL) of nesting female *Chelonia mydas* at Raine Island outside the mid summer nesting season.

Year, month	Curved carapace length (cm)		
	Mean (Range)	SD	n
1975 Feb	106.3 (98.0-117.0)	4.66	64
1980 Jun	110.0 (110.0)	-	1
1981 Jun	100.0 (100.0)	-	1
1982 Jul	104.3 (100.0-108.5)	-	2
1983 Apr	99.9 (94.5-104.5)	3.90	4
1984 Apr	106.1 (97.0-118.0)	4.59	77
1987 Jul	108.5 (97.5-114.5)	6.55	4
2001 Feb	104.9 (92.9-114.4)	4.09	99
combined	105.6 (92.9-118.0)	4.55	252

TABLE 26. Annual variation in curved carapace length of nesting female *Chelonia mydas* at No.7 and No.8 Sandbanks during the mid summer nesting season.

Year	Rookery	Curved carapace length (cm)		
		Mean (Range)	SD	n
1976	N8	105.6 (98.0-112.0)	4.15	14
1979	N8	107.1 (101.0-118.0)	4.69	16
1986	N7&N8	105.1 (93.0-121.0)	4.42	119
1987	N7&N8	106.3 (93.0-121.0)	5.30	169
1988	N8	107.6 (95.0-117.0)	5.07	47
1989	N8	105.9 (99.5-119.0)	5.45	10
1990	N7	106.8 (91.6-113.5)	6.14	12
1990	N8	107.5 (99.5-118.0)	4.61	25
1991	N7	104.9 (94.0-114.7)	4.63	85
1991	N8	104.6 (93.0-118.0)	6.03	56
1992	N7	106.9 (98.5-118.5)	4.16	53
1992	N8	106.6 (94.5-115.5)	4.91	63
1995	N7	106.4 (91.8-121.6)	5.32	72
1995	N8	105.6 (97.1-117.4)	4.71	80
1996	N7	105.1 (92.2-117.9)	5.75	70
1996	N8	103.8 (92.7-116.3)	4.65	54
1997	N7	105.3 (87.2-114.0)	5.29	52
1997	N8	104.7 (91.2-119.5)	5.11	185
combined	N7&N8	105.6 (87.2-121.6)	5.11	1194

laying: $\log_{10}$wt = 1.28 × $\log_{10}$CCL - 0.491 (n = 24, r = 0.606, 0.1>p>0.05. wt in kg and CCL inc m). The average female weighed 126.15kg (SD = 13.913, range = 101-154, n = 24; CCL of weighed sample ranged 95-114cm).

MALES. A series of male *C. mydas* captured while courting, or in association with courting groups on Raine Island reef (Table 28) had a pooled mean CCL = 99.4cm (SD = 4.89; range = 90.5-114.5cm; n = 37). A set of various carapace measurements using the same methodologies as used for the females is summarised in Table 28. The breeding males, on average, were very much smaller than the nesting females.

There was a significant log-log correlation between CCL and weight of breeding males at courtship: $\log_{10}$wt = 1.65 x $\log_{10}$CCL - 1.273 (n = 24, r^2 = 0.756, 0.002<p<0.005. Wt in kg and CCL in cm). The average male weighed 97.63kg (SD = 9.528, range = 83-122.5, n = 24; CCL of weighed sample ranged 90.5 - 112cm).

SIZE COMPARISONS. The size of the nesting female *C. mydas* is relatively uniform throughout the GBR rookeries with a CCL = 107cm (Heron Island: Limpus et al. 1984a; Bramble Cay: Parmenter 1979, Limpus et al., 2001). The Raine Island female *C. mydas* are of intermediate size

TABLE 27. Annual variation in curved carapace width of nesting female *Chelonia mydas* at Raine Island and Moulter Cay during the mid summer breeding season. One way ANOVA: $F_{7,2229}$ = 4.35; P<0.001, significant.

Year	Curved carapace width (cm)		
	Mean (Range)	SD	n
1974/75	98.1 (86.0-111.0)	4.92	64
1976/77	97.5 (83.0-113.0)	5.26	263
1977/78	98.9 (88.5-111.5)	4.48	125
1979/80	98.7 (86.0-115.5)	5.09	390
1980/81	98.8 (86.5-115.0)	5.37	201
1981/82	97.3 (84.0-108.5)	4.81	538
1982/83	98.2 (82.5-114.0)	5.07	504

for the species world wide, being approximately the same size as the females from the Tortuguero rookery in Caribbean Costa Rica and Aldabra Island in the Indian Ocean (Hirth, 1980). Much smaller sized females nest in Hawaii, the Arabian Peninsula and the eastern Pacific Ocean while considerably larger sized nesting females occur at Europa Island, Surinam and Ascension Island (Hirth, 1980; Miller, 1989).

The mean CCL of the dead females recorded on Raine Island over 18 breeding seasons (Table 16) was smaller than the mean CCL of the nesting female sample recorded in the respective breeding seasons (Table 24). Why the death of the nesting female should be size related is not clear. To address this question, detailed autopsies of turtles dying from a variety of causes are needed to identify the extent to which the mortality is related to the turtle being small, irrespective of its past breeding history, or to newly recruited turtles to the breeding population. This bias in the death of smaller turtles is contrary to the bias that would be needed for the death of nesting turtles on these islands to be the primary cause of the long term reduction in CCL of turtles breeding at Raine Island and Moulter Cay.

Size is not a reliable measure of maturity or age in adult marine turtles (Limpus & Reed, 1985a,b; Limpus et al., 1994c; Limpus & Chaloupka, 1997) and not all turtles reach sexual maturity at the same size (Limpus, 1991). Therefore the question of why there are inter-rookery and inter-seasonal differences in CCL of nesting females probably cannot be resolved by studies at the rookeries. The size of the breeding female should be a function of a number of factors, including its genetic stock, the climate of its particular feeding area, its diet and its breeding age. Potentially all these factors can now be

TABLE 28. Carapace measurements of adult male and female *Chelonia mydas* breeding at Raine Island and adjacent islands.

	Measurement (cm)		
	Mean (Range)	SD	n
Female			
Straight carapace length: 1978/79	100.3 (89.0-107.6)	4.37	54
Straight carapace width: 1978/79	76.3 (68.6-90.0)	3.76	54
Carr's straight carapace length: 1978/79	99.7 (93.0-109.3)	3.69	29
Male			
CCL: 1978/79	98.5 (90.5-112.0)	4.36	28
CCL: 1979/80	103.7 (103.0-104.5)	0.76	3
CCL: 1982/83	96.0 (-)	-	1
CCL: 1987/88	102.4 (90.5-114.5)	6.51	5
Curved carapace width: 1978/79	88.8 (82.5-97.0)	4.50	28
Straight carapace length: 1978/79	93.1 (86.9-102.5)	3.37	25
Straight carapace width: 1978/79	71.0 (66.1-78.2)	3.34	24
Carr's straight carapace length: 1978/79	93.0 (88.4-98.4)	2.74	14

addressed in studies of *C. mydas* in its feeding areas. The north-south distribution of the eastern Australian feeding areas and the capacity to identify the genetic stock of individual turtles make the eastern Australian turtles ideally located for further studies on what determines the size composition of the nesting population.

EGG PRODUCTION

NESTING SUCCESS. Observations of individual turtles ashore through the night have shown that a female does not always successfully lay her eggs on each nesting crawl. During 22 November - 16 December 1986, 26 nesting females were followed for their entire time ashore. Of these, only four were observed to lay eggs (nesting success = 0.15).

It was concluded from the results of autopsies of turtles dying while ashore at Raine Island that only females attempting to nest come ashore. When a turtle comes ashore and fails to lay her eggs it should result primarily from negative impacts on the turtle while it is ashore. Two principal sets of factors that contribute to whether or not a turtle will successfully lay during a nesting crawl on these remote northern GBR beaches are identified.

FIG. 35. Adult female *Chelonia mydas* wandering into each other as they searched for nesting sites at Raine Island, 19 December 1984. The nett result of these interactions is that turtles spread more widely across the beach and spend more time ashore for nesting than would occur in a low density nesting situation.

1) Environmental disturbance. The sand of Raine Island beach was very dry, and without grass/tree roots to bind it together. The coralline sand particles did not adhere readily. The dryness and looseness of the sand generally resulted in the digging of very deep body pits with the associated likelihood of collapse of the body pit wall into the egg chamber. Egg chambers were repeatedly collapsing as the females attempted to dig their nests. Turtles with damaged hind flippers had even more problems in digging if this hampered their ability to lift sand from the egg chamber. Bustard & Greenham (1968) discussed this problem for the Heron Island *C. mydas* nesting population. Another potential cause of disturbance to the nesting turtle on these islands was buried rocks, timber and turtle bone. Large obstructions could prevent the turtle digging an egg chamber, but this type of problem occurred less frequently. It mostly confronted those turtles that attempted to nest on top of the phosphatic limestone platform.

2) Turtle interactions. Most turtles, when undisturbed, made their first nesting attempt for the night near the crest of the outer beach rim. When turtles were beaching at a density that resulted in approximately overlapping turtles around the perimeter of the beach in the early part of the night, i.e. 1 turtle per 2m of beach line, there was a high probability of a turtle encountering another turtle already ashore (Fig. 34). Therefore, with higher density nesting (mean nightly tally count exceeding ~900), turtles that beached early in the night and become established in nest digging were often disturbed

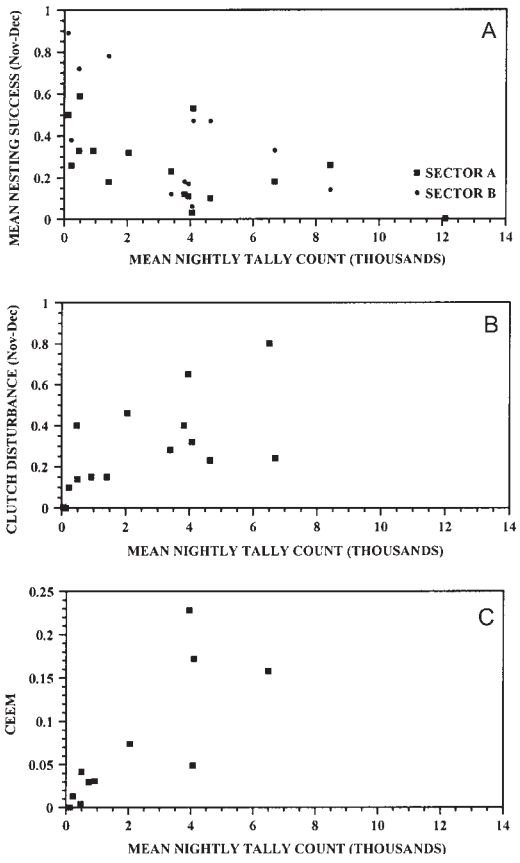

FIG. 36. Variation in annual nesting success (A), rate of clutch disturbance by nesting turtles (B) and clutch equivalent egg mortality (CEEM) (C) for *Chelonia mydas* breeding at Raine Island with respect to nesting density. See Table 29 for seasonal data.

by later arrivals. This usually resulted in the one or both turtles moving on to seek an alternative nest site further in from the water line. Disturbance that caused a turtle to abandon a site ranged from one turtle bumping another to a turtle that was digging a nest throwing sand into the face of another. A person walking near or gently touching a turtle wandering on the beach platform on a high density turtle night appeared to make no additional impact on the nesting success of the turtle which was already reacting to regular 'disturbance'.

It was not uncommon for turtles to be ashore for over 6hr, alternately wandering and digging without successfully constructing a nest before returning to the sea. Without a completed nest, the turtle would not lay. Difficulties in preparing a nest and completing a laying will increase the time a turtle spends on the beach and hence increase the probability of still being ashore after daylight. This in turn increases the probability of heat induced mortality. Hence at Raine Island, death on the nesting beach is density dependent on the size of the nightly nesting numbers.

The nesting success recorded in 1986 above contrasted with the nesting success recorded for individual turtles during low density nesting in April 1984 at Raine Island. Of 165 recorded beachings, 109 (66%) resulted in laying, 41 (25%) resulted in the turtle leaving the beach without laying and 15 (14%) were not assessed for nesting success. During this visit, it rained on 7 of the 23 days/nights and the sand was noticeably moist and egg chambers appeared to be dug easily without the walls collapsing. The combination of low nesting density (daily number of beachings = 3 - 17) (Table 3) and moist sand appears to have contributed to the high nesting success (= 0.73 for the 150 beachings assessed for nesting success) at this time. These data illustrate the variability that can occur in nesting success for turtles attempting to nest in coralline sand. Similar intra-seasonal variability in nightly nesting success has been described *C. mydas* attempting to nest in similar coralline sand at from Bramble Cay (Limpus et al., 2001).

For a more rapid assessment of nesting success, sampling sites A to E (Fig. 2) were selected and where possible, nesting success was quantified on opposite sides of Raine Island on the same night. Nightly nesting success recorded in these sectors for the November-December sampling periods is summarised in Table 29. The mean nightly nesting success data showed a significant correlation with the mean tally count (MTC) for the respective sampling period (Fig. 35A): nesting success = $-0.000042 \times MTC + 0.4411$ ($F_{1,15} = 19.69$; $p<0.001$; significant. $r^2 = 0.565$, DF = 15.). Nesting success, measured at a standard sampling period across several breeding seasons, is therefore negatively correlated with the density of the nesting turtles on the island. However, factors such as how recently it rained and the amount of rainfall can vary on a daily basis within and between seasons and will influence nesting success by changing the adhesion of the sand particles.

When a turtle does not lay her eggs on one night she attempts to nest again on the same or on one of the following nights (Miller, 1985). This can be repeated a number of times until the turtle

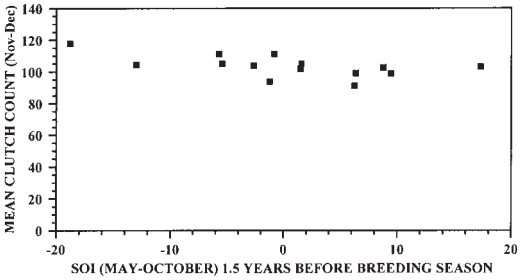

FIG. 37. Comparison of the mean November-December clutch count for adult female *Chelonia mydas* nesting at Raine Island (Table 29) with the mean May-October Southern Oscillation Index (SOI) approximately 1.5 yr before the breeding season (Table 19).

eventually lays her clutch. When a factor such as nesting density contributes to lowered nesting success, it results in the female having to make more nesting crawls per clutch.

Within the one nesting season, because nesting density will be low at the beginning and end of the season and maximal in December and January, nesting success must vary throughout the season. In the absence of rain, the trend should be for nesting success to be minimal in December and January.

RENESTING INTERVAL. Renesting interval is measured as the time from successfully laying a clutch to the return of the turtle to the beach to attempt to lay her next clutch. During most visits to Raine Island, the high density nesting precluded spending the time with each turtle to establish its nesting success for the night. High nesting density also made it difficult to examine every turtle ashore for the night to check it for tags and hence establish its identity. Therefore, on most visits it was not possible to reliably measure renesting interval at Raine Island and Moulter Cay.

During the April 1984 visit to Raine Island, nesting density was low enough for the nesting success of almost every turtle for the night to be assessed. Because of this, it was possible to record the timing of subsequent returns of females following a successful nesting. The mean renesting interval was 12.4 d (SD = 1.02, range = 10-14, n = 16). This is very similar to the mean renesting interval of 12.0 d (SE = 0.04, range = 9 - 21, n = 979) and 12.4 d (SD = 1.67, range = 9-19 d, n = 2781) measured over an entire nesting season at Bramble Cay during the 1978/79 and 1979/80 breeding seasons, respectively (Parmenter, 1979; Limpus et al., 2001). These values recorded within the nGBR *C. mydas* stock are considerably shorter than the renesting interval for the species at Heron Island in the southern GBR (renesting interval: 13.52 d in 1974/75; 14.08 d in 1980/81. Limpus, 1980b; Limpus et al., 1984a). These differences are more likely to be the result of different water temperatures in the interesting habitat during the oviducal phase of embryogenesis and egg shell formation (Miller, 1985) rather than a genetic difference between the stocks.

NESTING BEACH FIDELITY. Once nightly tagging of nesting turtles at Raine Island commenced on each sampling trip there were numerous recaptures of these tagged turtles on subsequent nights at Raine Island. For example in November 1984, 77 recaptures of recently tagged turtles were made over the 2nd to 10th night of tagging on the island. These were of turtles that had not completed a successful nesting on the previous beaching. When Moulter Cay was visited after a period of intense tagging at Raine Island there were small numbers of recaptures of nesting females that had been tagged while attempting to nest at Raine Island within the previous few nights (50 recaptures) (Table 8). Two similar recaptures of turtles changing islands have been made on Raine Island when intense tagging on Moulter Cay was followed by work on Raine Island (Table 7). There have been no within season changes of rookery recorded from the studies at MacLennan Cay, No.7 and No.8 Sandbanks. There has been no record of intra-seasonal *C. mydas* interchange between the northern and southern GBR rookery areas.

These observations are consistent with those from more detailed long term recapture studies of *C. mydas* at other rookeries (Heron Island: Bustard, 1972, Limpus et al., 1984a; Sarawak Turtle Islands: Hendrickson, 1958; Hawaii: Balazs, 1980; Tortuguero: Carr et al., 1978). *C. mydas* displays a high level of fidelity to the individual nesting beach with only a small percentage of the females interchanging between nearby rookeries within the same nesting season.

EGGS. *C. mydas* of the nGBR stock lay the typical white, approximately spherical, soft shelled eggs for the species. The mean clutch counts recorded across the breeding seasons at Raine Island and No. 7 and No. 8 Sandbanks are summarised in Table 30. There was a significant difference among the annual samples of clutch counts. The combined seasons mean clutch count

TABLE 29. Nesting success and clutch disturbance measurements for *Chelonia mydas* at Raine Island. Measurements made in sampling sites A and B (Fig. 2).

Date	Sector	Turtles entering sector		Number of clutches laid	Number of existing clutches disturbed	Nesting success	Clutch disturbance rate
		From beach	From sides				
		X	Y	Z	C	Z/X	C/Z
12/12/81	A	222	-	75	25	0.34	0.33
13/12/81	A	170-200	-	57	35	~0.31	0.61
1981					Combined values	~0.32	0.46
29/12/82	A	52	-	20	2	0.38	0.10
3/12/82	A	93	-	34	5	0.37	0.15
6/12/82	A	93	-	25	5	0.27	0.20
1982					Combined values	~0.33	0.15
28/11/85	A	20	0	3	0	0.15	0
1/12/85	A	16	1	2	0	0.13	0
9/12/85	A	27	4	8	1	0.30	0.13
16/12/85							
1985	A				Combined values	0.26	0.12
28/11/85	B	9	4	4	0	0.44	0
3/12/85	B	20	2	7	1	0.35	0.14
13/12/85	B	13	3	2	1	0.15	0.50
16/12/85	B	22	3	11	0	0.50	0
1985	B	Combined values			Combined values	0.38	0.08
28/12/86	A	313	-	37	20	0.12	0.54
4/12/86	A	449	-	50	17	0.11	0.34
8/12/86	A	520	-	47	28	0.11	0.60
12/12/86	A	369	-	47	21	0.13	0.45
1986	A	Combined values			Combined values	0.11	0.48
26/11/86	B	216	-	24	23	0.11	0.11
2/12/86	B	275	-	35	37	0.13	1.06
6/12/86	B	334	-	58	44	0.17	0.80
10/12/86	B	241	-	34	20	0.14	0.59
1986	B	Combined values			Combined values	0.17	0.82
3/12/87	A	330	-	35	30	0.11	0.86
1/12/87	B	73	-	24	7	0.33	0.29
6/12/88	A	78	10	39	5	0.50	0.13
7/12/88	A	74	17	31	0	0.42	0
8/12/88	A	76	21	50	9	0.66	0.18
1988	A	Combined values			Combined values	0.53	0.12
6/12/88	B	33	8	24	5	0.73	0.21
7/12/88	B	33	10	15	6	0.46	0.40
8/12/88	B	80	10	29	5	0.36	0.17
1988	B	Combined values				0.47	0.24
6/12/91	A	157	65	11	9	0.07	0.82
8/12/91	A	117	63	22	10	0.19	0.45
1991	A	Combined values				0.12	0.58
6/12/91	B	125	74	23	2	0.18	0.09
8/12/91	B	77	65	14	6	0.18	0.43
1991	B	Combined values				0.18	0.22
6/12/92	A	122	12	24	3	0.20	0.13
8/12/92	A	134	38	21	5	0.16	0.24
1992	A	Combined values				0.18	0.18
6/12/92	B	35	27	20	5	0.57	0.19
8/12/92	B	44	32	42		0.95	0.06

TABLE 29 (*Cont.*)

Date	Sector	Turtles entering sector		Number of clutches laid	Number of existing clutches disturbed	Nesting success	Clutch disturbance rate
		From beach	From sides				
		X	Y	Z	C	Z/X	C/Z
1992	B	Combined values				0.78	0.11
4/12/93	A	131	43	25	9	0.19	0.36
6/12/93	A	87	124	31	10	0.36	0.32
1993	A	Combined values				0.26	0.34
4/12/93	B	77	30	14	2	0.18	0.1
6/12/93	B	119	37	14	11	0.12	0.79
1993	B	Combined values				0.14	0.46
6/12/94	A	13	3	9	0	0.69	0
8/12/94	A	36	3	20	1	0.56	0.05
1994	A	Combined values				0.59	0.03
6/12/94	B	86	16	32	8	0.37	0.25
8/12/94	B	27	14	5	1	0.19	0.2
1994	B	Combined values				0.33	0.24
6/12/95	A	413	100	57	12	0.13	0.21
12/12/95	A	323	126	18	5	0.06	0.29
1995	A	Combined values				0.10	0.23
6/12/95	B	99	113	52	12	0.53	0.23
12/12/95	B	88	64	35	8	0.40	0.13
1995	B	Combined values				0.47	0.23
2/12/96	A	259	146	1	11	0.004	11.0
4/12/97	A	495	86	20	7	0.03	0.35
4/12/97	B	465	34	28	8	0.06	0.29
30/11/98	A	29	7	11	0	0.38	0
6/12/98	A	26	4	8	0	0.31	0
1998	A	Combined values				0.33	0
6/12/98	B	60	5	47	5	0.72	0.11
30/11/98	C	29	7	11	0	0.31	0
7/12/98	D	30	5	11	1	0.31	0.09
7/12/98	E	47	2	28	0	0.57	0
1/12/99	B	212	59	53	17	0.22	0.32
8/12/99	B	272	117	90	10	0.34	0.11
1999	B	Combined values				0.30	0.19
1/12/99	D	589	34	93	6	Incomplete sampling	0.06
8/12/99	D	328	183	59	7	0.18	0.12
1999	D	Combined values				0.18	0.09
1/12/00	A	11	0	6	0	0.55	0
4/12/00	A	5	1	2	0	0.40	0
2000	A	Combined values				0.50	0
1/12/00	B	12	1	10	0	0.83	0
4/12/00	B	6	1	6	0	1.00	0
2000	B	Combined values				0.89	0
4/12/01	A	115	34	34	6	0.23	0.18
4/12/01	C	199	49	29	11	0.12	0.38

of 104.3 for the November- December nesting period at Raine Island was very similar to the mean clutch count of 103.8 measured for the two samples from No. 7 and No. 8 Sandbanks. There was no significant correlation between annual November-December clutch count and the southern oscillation index measured approximately 1.5 yr before the nesting season

TABLE 30. Comparison of annual clutch counts of *Chelonia mydas* from Raine Island and No. 7 and No. 8 Sandbanks.

Year	Clutch count			
	Mean	SD	Range	N
Raine Island: November-December				
1976/77	102.7	19.02	63-147	48
1977/78	103.1	21.34	65-166	38
1978/79	105.1	19.31	69-143	59
1979/80	104.3	24.85	59-158	24
1981/82	111.3	17.25	79-152	20
1982/83	103.9	12.32	79-123	22
1984/85	117.8	22.13	62-175	36
1985/86	106.2	19.51	76-163	38
1986/87	93.9	14.50	66-130	39
1991/92	99.1	21.37	62-142	45
1992/93	101.8	14.0	73-130	54
1994/95	111.2	19.65	75-139	40
1995/96	100.7	23.6	47-124	9
1997/98	118	-	118	1
1998/99	91.1	18.92	65-142	20
2000/01	99.0	18	72-126	8
Combined	103.88	19.83	47-175	501
One way ANOVA: $F_{15,485} = 3.60$; $p<0.001$; significant				
Raine Island: April				
1983/84 (Apr)	83.3	17.82	62-111	7
No.7 and No. 8 Sandbanks: December				
1988/89	116.0	26.55	88-147	4
1991/92	97.4	19.19	68-118	6
Combined	104.84	25.52	68-147	10

($F_{1,14} = 3.43$; $0.2>p>0.1$. $r^2 = 0.196$, DF = 14) (Fig. 36). However, the clutch count from the extreme El Nino and La Nina years are very poorly represented in the samples (Fig. 36). This relationship warrants further investigation.

No attempt has been made to record successive clutches from the same turtle within a breeding season at Raine Island. The smaller clutches laid in April (Table 30) are consistent with the decline in clutch count that Parmenter (1979) recorded with the last clutch for the season with each turtle at Bramble Cay. The mid season clutch count (Table 30) and egg diameters from Raine Island (Table 32) is very similar to the December clutch counts and egg diameters from Bramble Cay (Parmenter, 1979) and the mean clutch count of 102.2 measured across the entire breeding season at Bramble Cay in 1979/80 (Limpus et al., 2001). Clutch counts from Heron Island (Bustard, 1972; Limpus, 1980b; Limpus et al., 1984a) are higher than the clutch counts recorded in most years at Bramble Cay and Raine Island. When compared

FIG. 38. Portion of an ovary from an breeding female *Chelonia mydas* that died while ashore for nesting on Raine Island, 9 December 2002. In addition to the normal 25-32mm diameter mature follicles (MF), this turtle had many large 25-32mm diameter atretic follicles (AF).

worldwide, *C. mydas* clutch counts and egg diameters from the various rookeries scattered within the GBR are relatively uniform and occur close to the middle of the range for the species (Hirth, 1980; Miller, 1989).

Counting the number of eggs in a clutch at Raine Island is complicated by the disturbance of nesting turtles by other turtles. A turtle that has been disturbed before she has laid any eggs from the current clutch can be expected to return to lay those eggs later on the same night or on a subsequent night without reducing the number of eggs in her clutch (Miller, 1985; Limpus, 1985). However, if a turtle has laid part of her clutch and is disturbed while laying, she can be expected to cease laying the remainder of the clutch and move off the nest with the following consequences (Miller, 1985; Limpus, 1985). If she has laid less than approximately half a clutch, she can be expected to return to lay the remainder of the clutch either on the same night or within the next few nights. In this case she will have deposited two 'clutches', each with less than less than the actual clutch count. Should she have laid more than half a clutch before she was disturbed, she is unlikely to return to lay the remainder of that clutch on the beach. She will normally return in about two weeks to lay a complete clutch. Some turtles can be seen laying small numbers eggs as they return across the beach to the sea at Raine Island. On occasions, turtles can be seen underwater and resting under ledges along the edge of Raine Island Reef with small clusters of

TABLE 31. Frequency of occurrence of yolkless and multiyolked eggs in *Chelonia mydas* clutches at Raine Island. Unless otherwise stated, measurements were recorded in November - December.

Year	Yolkless eggs per clutch				Multiyolked eggs per clutch			
	Mean	SD	Range	n	Mean	SD	Range	n
1976/77	0.05	0.224	0-1	20	0		0	20
1977/78	0.13	0.404	0-2	40	-			
1978/79	0.10	0.399	0-2	60	0		0	60
1979/80	0.04	0.204	0-1	24	0		0	24
1981/82	0.18	0.529	0-2	62	-			
1982/83	0.09	0.288	0-1	23	-			
1983/84 Apr	0.14	0.350	0-1	7	0		0	7
1984/85	0.11	0.393	0-2	36	0.17	0.697	0-4	36
1985/86	0.11	0.383	0-2	39	0.03	0.160	0-1	39
Combined	0.12	0.399	0-2	349	0.03	0.290	0-4	224
One way ANOVA	$F_{9,339} = 0.37$; $p>0.25$; not significant				$F_{6,217} = 1.69$; $0.1>p>0.25$; not significant			

eggs under the tail. In both these cases, it is presumed that these are females that have been disturbed after they have laid more than half a clutch and were voiding the remainder of that clutch. For these turtles, the 'clutch' laid on the beach is less than a complete clutch and the voided eggs represent a loss of eggs to the rookery. Thus in high density nesting seasons, there will be a number of apparent clutches counted that will be less than a complete clutch. The impact of this turtle-turtle disturbance in altering the average number of eggs in a clutch remains unquantified. Of greater consequence in high density nesting seasons should be the depletion of the stored fat reserves if the turtle makes numerous unsuccessful nesting crawls over an extended series of nights. The turtles seen at necropsy that have large numbers of mature sized, atretic follicles are believed to be turtles from this latter category that have commenced mobilisation of the nutrient and energy reserves of some mature follicles to maintain their nesting activity and possibly support their homeward migration. For these turtles, the consequence of repetitive disturbance would include a reduction in the number of clutches she can lay for the season. While the impact also remains unquantified, there is a density dependent effect in high density nesting seasons that should result in a reduction in clutch count and a reduction in the number of clutches laid for the season.

TABLE 32. Seasonal variation in *Chelonia mydas* egg diameters at Raine Island and No.8 Sandbank. 10 eggs measured per clutch during November - December.

Year	Egg diameter			
	Mean	SD	Range	N
Raine Island				
1976/77	4.38	0.081	4.15-4.56	160
1977/78	4.44	0.163	4.10-5.38	400
1978/79	4.39	0.138	4.01-4.70	460
1981/82	4.37	0.129	3.93-4.67	200
1982/83	4.42	0.114	4.18-4.60	200
1983/84 (Apr)	4.33	0.179	3.86-4.61	70
1984/85	4.40	0.132	3.93-4.85	390
1985/86	4.36	0.119	4.03-4.58	240
1986/87	4.34	0.127	3.86-4.78	390
1988/89	4.33	0.126	4.11-4.58	540
1991/92	4.34	0.117	4.02-4.59	450
1993/94	4.25	1.87	3.66-5.09	950
1994/95	4.30	0.131	3.84-4.67	44
No. 7 and No. 8 Sandbanks				
1988/89	4.31	0.161	4.11-4.50	40
1991/92	4.31	0.105	4.19-4.42	60
All combined	4.34	0.860	3.66-5.38	4594
One way ANOVA: $F_{14,4579} = 1.56$; $0.1>p>0.05$; not significant				

Yolkless eggs and multiyolked eggs were uncommon and there was no significant difference in the occurrence of yolkless eggs or multiyolked eggs per clutch among the seasons (Table 31). The low frequency of yolkless eggs per clutch is typical of the species from the non Arabian Peninsula rookeries (Miller, 1989).

There were significant differences in the mean egg diameter between clutches laid by different females within the one breeding season (one way ANOVA, $p<0.001$ in each season). The seasonal samples of clutch counts are summarised in Table 32. There were no significant differences in egg diameters among nesting seasons or between

TABLE 33. Depth from beach surface to top and bottom of *Chelonia mydas* clutches at Raine Island, measured from the beach surface at the completion of laying.

Year	Nest depth to top of eggs (cm)				Nest depth to bottom of eggs (cm)			
	Mean	SD	Range	N	Mean	SD	Range	N
1977/78	70.0	-	70	1	85.7	9.81	74-98	3
1978/79	52.0	11.40	36-77	20	75.7	12.36	60-100	17
1979/80	51.8	13.53	33-88	24	91.1	19.73	64-152	16
1981/82	-				82.5	15.73	55-96	60
1982/83	-				78.2	7.78	60-95	26
1992/93	-				79.5	9.64	66-90	11
1994/95	-				81.0	18.12	65-109	5
Combined	52.3	12.61	33-88	45	81.63	14.73	55-152	138
One way ANOVA	$F_{2,42} = 1.01; p>0.25$; not significant				$F_{6,131} = 1.99; 0.1>p>0.05$; not significant			

Raine Island and No. 8 Sandbank. The mean size of the eggs laid by nGBR stock *C. mydas* (Table 32) are very similar is size to those laid by sGBR stock females (Limpus et al., 1984a). However, in the extremes, the smallest nGBR *C. mydas* eggs were smaller than eastern Australian *Caretta caretta* eggs (Limpus et al., 1984a) and the largest eggs were comparable in size to eastern Australian *N. depressus* eggs (Limpus, 1971).

Given the similarity of the recorded data from Raine Island with that from Bramble Cay and the difficulty of repetitively sampling the same female at Raine Island to determine valid whole season values for most clutch related parameters and for renesting interval, it is proposed that the Bramble Cay clutch data and renesting interval should be used to describe these parameters for Raine Island turtles.

NEST DEPTH. Depths of eggs within the sand at the completion of laying are summarised in Table 33. No significant inter-seasonal difference in nest depth was detected (Table 33). The mean depth to the top of a clutch was 52.3cm and the mean depth to the bottom of a clutch was 81.6cm. These nest depths are considerably deeper than nests constructed by sGBR stock females (Limpus et al., 1984a).

EGG MORTALITY CAUSED BY NESTING TURTLES. Some nesting turtles dig into existing clutches (Fig. 37) as they prepare their own nests. It is unusual for the entire existing clutch to be disturbed, either by being dug out or rolling down into the new egg chamber. When incubating turtle eggs are moved there is a high probability of mortality unless care is taken in their handling (Limpus et al., 1979; Parmenter, 1980b). Eggs dug up by nesting turtles are jarred violently and even if they are not broken in the process, they are most likely killed as they are thrown out. In addition, eggs thrown to the surface and surviving the jarring are most likely to desiccate in the hot dry sand by day and die. Thus the eggs thrown out of existing clutches by nesting turtles are regarded as totally killed. When these eggs are eaten by birds it will be treated as scavenging rather than predation, since birds are not the primary cause of the mortality. At Raine Island and Moulter Cay, buff-breasted landrails, rufous night herons, silver gulls and all the species of terrestrial crabs regularly scavenged on turtle eggs brought to the surface by nesting turtles. Egg mortality caused by nesting turtles was measured in a two step process that quantified the rate of disturbance of clutches by nesting turtles and quantified egg mortality per disturbed clutch.

Clutch Disturbance by Nesting Turtles. Two counts of clutch disturbance by nesting turtles have been measured over the entire beach at Raine Island during periods of low density nesting. 1980/81, 8-12 December: In this very low density nesting season only 1 clutch was

FIG. 39. Loss of eggs as a nesting turtle digs into an existing clutch at Raine Island, 19 December 1984.

TABLE 34. Number of eggs destroyed per clutch when nesting *Chelonia mydas* dug into existing clutches at Raine Island. Samples were taken from throughout the nesting habitat of the island.

Sampling period	Egg mortality per disturbed clutch			
	Mean	SD	Range	N
Raine Island				
1981: 12 Nov-15 Dec	18.0	13.69	2-54	33
1982: 11 Nov-10 Dec	21.6	15.53	6-62	21
1984: 21 Nov-23 Dec	23.3	13.15	5-61	49
1985: 29 Nov-19 Dec	14.0	13.24	1-71	44
1986: 22 Nov-16 Dec	32.9	26.62	4-125	70
1987: 29 Nov-5 Dec	28.0	12.78	12-59	11
1988: 29 Nov-8 Dec	16.9	5.65	2-59	48
1994: 30 Nov-10 Dec	33.5	18.2	1-82	4
1996: 1-12 Dec	10.8	8.8	2-40	80
1997: 29 Nov-19 Dec	18.2	12.95	1-62	74
1998: 30 Nov-7 Dec	8.18	7.15	1-25	11
1999: 28 Nov-11 Dec	15.3	11.11	1-50	241
2001: 1-10 Dec	19.77	13.81	2-77	128
Combined	18.28	14.881	1-125	814
One way ANOVA: $F_{12,801} = 11.94$; $p<0.001$; significant				

disturbed by nesting turtles in 5 successive nights of observation. With approximately 81 nesting females ashore per night on the whole island, if nesting success is assumed to be at least 50% then this would give an estimated nightly clutch disturbance by nesting turtles for the entire island = 0.005 (Table 35). 1982/83, April: In five nights, a total of 16 beachings occurred (Table 3) but no incubating clutches were disturbed by the nesting turtles. This is the only measure of clutch disturbance from late in a nesting season.

For a more rapid assessment during higher density nesting seasons, clutch disturbance was quantified in the same sampling sites, A to E (Fig. 2), on Raine Island as were used for measuring nesting success. Nightly clutch disturbance by the nesting turtles during November-December within these sites is summarised in Table 29. These clutch disturbance data, combined with those from following individual females, showed a significant correlation with the mean tally count (MTC) for the respective sampling period (Fig. 35B): clutch disturbance = 0.000548 × MTC + 0.9118 ($F_{1,16} = 15.90$; $p<0.001$; significant. $r^2 = 0.4984$, DF = 16.). Clutch disturbance by nesting turtles, measured in a standard sampling period across several breeding seasons, is therefore positively correlated with the density of the nesting turtles on the island. Since the density of clutches in the beach will increase through the nesting season until substantial numbers begin hatching, clutch disturbance should also be a function of when in the nesting season it is measured. Thus the above mid season measurements cannot provide a total seasonal summary of clutch disturbance by nesting turtles.

TABLE 35. Turtle induced egg mortality - a summary of the annual egg mortality per disturbed clutch (EMpDC), rate of clutch disturbance (CD) and clutch count recorded for *Chelonia mydas* at Raine Island (From Tables 34, 29, 30 respectively.). The clutch equivalent egg mortality per clutch laid (CEEM) was calculated as: CEEM = (EmpDC × CD)/clutch. * denotes an estimated value.

Sampling period	EMpDC	CD	Clutch count	Clutch equivalent of eggs killed per clutch laid
November-December				
1980	-	0.005	-	0.001*
1981	18.0	0.46	111.3	0.074
1982	21.6	0.15	103.9	0.031
1984	23.3	0.80*	117.8	0.158*
1985	14.0	0.10	106.2	0.013
1986	32.9	0.65	93.9	0.228
1987	28.0	0.58	94.6	0.172
1988	16.9	0.18	102.2	0.030
1991	-	0.40	99.1	-
1992	-	0.15	101.8	-
1993	-	0.40	-	-
1994	33.5	0.14	111.2	0.042
1995	-	0.23	100.7	-
1996	10.80	11.0	-	-
1997	18.2	0.32	118.0	0.049
1998	8.18	0.04	91.1	0.040
1999	15.30	0.14	-	-
2000	-	0	99.0	0
2001	19.77	0.28	-	-
April				
1983	-	0	-	0

Egg Mortality Per Disturbed Clutch. The number of eggs dug from existing clutches when a nesting turtle disturbed them was counted for a series of clutches in most breeding seasons (Table 34). There were significant inter-seasonal differences in egg mortality per disturbed clutch (one way ANOVA: $F_{12,801} = 11.94$; $p<0.001$; significant) but there was no significant correlation detected between egg mortality per disturbed clutch and the mean tally count of the sampling period ($F_{1,11} = 0.305$; $p>0.25$. $r^2 = 0.027$, DF = 11). The mean egg mortality per disturbed clutch, pooled across the nesting seasons was = 18.3 (Table 34).

The rate of egg loss per clutch laid during each sampling period is expressed as a clutch

TABLE 36. Straight carapace length and weight of hatchling *Chelonia mydas* from Raine Island. h denotes hatchlings, c denotes clutches.

Breeding Season	Straight carapace length (cm)			Weight (g)			Sample
	Mean	SD	range	Mean	SD	range	
1974/75: Feb	4.91	0.191	4.17-5.22	23.9	1.92	17.5-27.5	69 h, 7 c
1978/79: Dec	4.80	0.099	4.70-5.00	22.9	0.88	21.5-24.5	8 h, 1 cl
1979/80: Jun	4.83	1.978	3.84-5.17	22.6	1.6	18.0-25.0	57 h, 6 c
1982/83: Apr	4.83	0.160	4.31-5.14	24.5	1.95	20.0-28.5	100 h, 10 c
1983/84: Apr	4.87	0.183	4.25-5.43	23.8	1.91	18.5-29.5	460 h, 46 c
Combined	4.86	0.588	3.84-5.43	23.8	1.92	17.5-29.5	694 h, 70 c

equivalent egg mortality (CEEM) and is tabulated in Table 35. When the annual CEEM values for the December sampling period are correlated against the respective mean tally counts (MTC. Table 35), there was a very obvious positive correlation of egg mortality with nesting density (Fig. 35A): CEEM = 0.000036MTC × 0.002125 ($F_{1,8}$ = 14.88; 0.0025>p>0.001. r^2 =0.6504; DF = 8). The clutch equivalent egg mortality varied from a low value of approximately zero in December 2000 and 0.005 in December 1980 to 0.23 during dense nesting in December 1986. There is also the potential for substantial intra-seasonal variability, particularly in the early and late breeding seasons relative to mid season. For example, CEEM was approached towards the end of the 1982/83 nesting season. The data (Fig. 32) suggest that there will be a definable mathematical relationship between CEEM and the mean tally count that should have potential in modelling the seasonal egg mortality caused by nesting turtles. However, to achieve this it will be necessary to systematically sample from additional medium to very high density nesting seasons to establish the relationship with any precision. Additionally it will be necessary to determine the variability of CEEM throughout several breeding seasons with differing nesting densities and relate the within season model to the standard sampling period data that can be gathered over a larger series on breeding seasons.

Bustard & Tognetti (1969) proposed that *C. mydas* clutch destruction at Heron Island was density dependent on the size of the nesting population. However, they did not precisely define their methodology. Bustard & Mathers (1975, unpubl., reported in Bustard, 1976) indicated that there was substantial destruction of *Caretta caretta* clutches by nesting *C. mydas* at Heron Island. Studies at Heron Island (Limpus unpubl. data) have been unable to reproduce comparable data sets to those in the above studies. The data as presented by Bustard & Tognetti (1969) suggests that nesting densities such as those at Raine Island and Moulter Cay are unsustainable. It would be appropriate at this time to investigate new models to describe the possible role density dependent egg destruction by nesting turtles in regulating the population size.

While egg destruction is an obvious feature observed on nights of dense turtle nesting at Raine Island, it represents an egg loss equivalent to only a small portion of the nightly egg production — certainly in the early to middle part of the nesting season. There is a large net gain in eggs to the beach each night during the nesting season. This turtle induced egg mortality in low to medium nesting density years at Raine Island is smaller than the 33-44% mortality of Bramble Cay *C. mydas* eggs which are lost through erosion each summer (Parmenter, 1980b; Limpus et al., 2001). In Surinam, Schulz (1975) estimated that *C. mydas* egg mortality from flooding and erosion of nests was 30%, 38% and 44% in each of the 1971, 1972 and 1973 breeding seasons respectively. High egg mortality would appear to be a natural feature of at least several widely scattered *C. mydas* rookeries which are functioning at very different nesting densities.

HATCHLINGS

Hatchling *C. mydas* were only examined in detail from Raine Island. These hatchlings were typical for the species with dark brown to black dorsal colours and white ventrally. Dorsally the trailing margin of the flippers and the carapace margin were edged in white.

HATCHLING SIZE. There was no significant difference in hatchling straight carapace length (SCL) among the annual samples of freshly emerged hatchlings (Mean hatchling SCL = 4.86cm) (Table 36). There were significant differences in hatchling weight among the annual

TABLE 37. Frequency distribution scute pattern on hatchling *Chelonia mydas* from Raine Island. * All costal and vertebral variability and most of the remaining variability occurred in one clutch. # 3 hatchlings from one clutch sample each with 2 small scutes between the pair of prefrontals = inter-prefrontal scutes. One hatchling from another clutch with an intervertebral scute between 1st and 2nd vertebral scutes. ** preoccular scales were not counted with all clutches.

		1978 Dec	1979/ 80	1983 April	1984 April	Total
Clutches examined		1	6	10*	46	63
Scute	Scute count	Frequency				
Nuchal	1	8	57	100	457	622
	2				3	3
Vertebral	5	8	52	97	441	598
	6		3	3	14	20
	7		2		4	6
	8				1	1
Post-vertebral	1/1	8	57	98	450	613
	1/2			2	4	6
	2/2				6	6
Costal	4/4	8	53	97	450	608
	4/5		1		2	3
	5/4			2	4	6
	5/5		2	1	4	7
	5/6		1			1
Marginal	10/11			1		1
	11/10				1	1
	11/11	8	57	99	453	617
	12/12				5	5
	13/13				1	1
Postoccular	1/1				1	1
	3/3		5	1	14	20
	3/4	1	3	2	6	12
	4/3		2	1	10	13
	4/4	6	35	80	336	457
	4/5		3	4	40	47
	5/4		4	9	35	48
	5/5	1	5	2	18	26
	6/5			1		1
Preocular**	0/0	-	57	100		157
Prefrontal	2	8	57	100#	459	624
	1				1	1
Post-parietal	1				2	2
	2	8	54	14	372	448
	3		3	16	71	90
	4			69	14	83
	5			1	1	2
Infra-marginal	3/3				2	2
	3/4		1		3	4
	3/5		1			1
	4/3			2	5	7
	4/4	8	54	97	435	594
	4/5			1	1	2
	5/4		1		9	10
	5/5				5	5

samples (Mean hatchling weight = 23.80g) (Table 36). The size of the hatchlings varied significantly between clutches within each breeding season (Table 36). The inter clutch differences in hatchling weights may reflect varying degrees of desiccation of the hatchlings as they dig their way from the nest to the beach surface.

For a sample of 100 hatchlings from ten clutches, there was a significant log-log correlation between straight carapace length and weight: $\log_{10}wt = 1.446 \log_{10}CCL - 1.046$ (wt in g, CCL in cm; $r^2 = 0.607$, n = 100 hatchling, $p<0.001$).

These hatchlings were very similar in size to emerged *C. mydas* hatchlings from Bramble Cay in 1978/79 (mean SCL = 4.85cm; mean wt = 23.23g; Parmenter, 1979) and from Heron Island in 1974/75 (mean SCL = 4.97cm, mean wt = 24.83g; Limpus, 1980b) and in 1980/81 (mean SCL = 4.89cm, mean wt = 24.93g; Limpus et al., 1984a). *C. mydas* hatchlings from both the northern and southern GBR are similar in size and collectively are near the middle of the size range for hatchlings worldwide (Hirth, 1980).

HATCHLING SCALATION. The variability in hatchling scute pattern is summarised in Table 37. The modal scute pattern of the Raine Island *C. mydas* hatchlings was typical of the species: 1 nuchal, 5 vertebrals, 1/1 post vertebrals, 4/4 costals, 11/11 marginals, 4/4 postocculars, 0/0 preocculars, 2 prefrontals, 2 post parietal, 4/4 inframarginals (Pritchard, 1979).

INCUBATION AND EMERGENCE SUCCESS. In assessing hatching and emergence success at Raine Island, no attempt was made to quantify the proportion of clutches that produced zero emergence of hatchlings to the beach surface. There is, therefore, no measure of total clutch failure for this rookery. Total clutch failure can result from erosion and flooding by high tides, from problems within the egg that are derived from the female herself and possibly from microbial infections. At Raine Island there is an additional problem of flooding by a rise in the water table below the island following rain, with very high tides or from storm wash over of the beach. For example: in April 1984, following heavy rain, the water table on the beach was above the sand surface in the lower parts of the beach depression (between the beach crest and the cliff) with pools of water lying scattered in the lower areas of the beach. Nests along this depression that contained eggs yet to hatch would have been flooded for several days. When turtle eggs are immersed in water for more than a few

TABLE 38. Hatching and emergence success of *Chelonia mydas* clutches that produced hatchlings to the beach surface at Raine Island.

	1979 June		1983 April		1984 April	
No. of clutches	37		16		162	
Hatchlings						
Emerged from nest	2814	74.37%	1278	82.77%	13115	78.35%
Live in nest	7	0.18%	16	1.04%	78	0.47%
Dead in nest	13	0.34%	11	0.71%	81	0.48%
Eggs						
Unhatched	256	6.77%	142	9.20%	1328	7.93%
Undevel-oped	669	17.68%	94	6.09%	1942	11.60%
Predated by crabs	25	0.66%	3	0.19%	195	1.16%
Total	3784		1544		16739	

minutes they drown. Fig. 40 illustrates the flooding of eggs by an elevated water table in February 1997. That February visit to Raine Island followed one of the largest recorded December nesting populations, so it was expected that vast numbers of hatchlings would be crossing the beach daily. Instead, only tens to low hundreds of *C. mydas* hatchlings were crossing the beach nightly. In response to this unexpected low hatchling production, 93 holes were dug to nest depth at random locations within each habitat type and each 100m sector around the beach platform. Dead turtle eggs in situ in nests were encountered in every hole. No live eggs were found in any hole. It is highly likely that only a trivial proportion of the eggs laid on Raine Island during the massed nesting season of 1996/97 produced hatchlings.

Since 1996, flooding of much of the nesting habitat during the mid nesting season has been a regular event. Subsequent extensive flooding of the nesting habitat, as evidenced by the water table being visible in the bottom of body pits, occurred through at least early to mid December of 1998, 1999 (Figs 9, 10), 2000 and 2001. Eggs that were laid up to 8 weeks prior to these flooding events are expected to have drowned and failed to hatch. Only 1997 had a relatively dry early nesting season (Fig. 7) and should not have had the clutches subjected to this broad scale flooding.

Hatchling emergence in February-March which should originate from the peak period of nesting has only been evaluated in February 1997. Most hatching and emergence success data

FIG. 40. *Chelonia mydas* laying eggs into a water-filled egg chamber on the cliff top at the western end of Raine Island, early February 1997.

have been recorded from four samples of nestings from the latter part of nesting seasons. The hatching and emergence success are summarised in Table 39. There was a low proportion of eggs that showed no obvious embryonic development (6-18% of eggs laid) and a high proportion of hatchlings successfully emerged onto the beach surface (74-83% of eggs laid). Predation of eggs within the nests was low (0.19-1.16%) and could be attributed to predation by the ghost crab *Ceratophthalmus cordimana*, the only ghost crab, living in the supratidal habitats. These values apply only to clutches that produced hatchlings to the beach surface.

On four occasions, emerged clutches were dug to determine the proportion of clutches that had been laid into an existing clutch:

1979, 13-14 December: of 38 emerged clutches dug, 1 was a clutch on top of another and both these clutches had a high hatching success. Only one of the 38 clutches contained yolkless eggs.

1980, 8-24 June: of 78 emerged clutches dug, 3 were clutches that had been laid into an existing clutch and in each case both the clutches had a high hatching success.

1983, 24-29 April: of 18 emerged clutches dug, 2 were clutches that had been laid into an existing clutch and in each case both the clutches had a high hatching success.

1984, 3-25 April: of 162 emerged clutches dug, no clutch had been laid into an existing clutch.

These observations indicate that the eggs remaining in disturbed clutches can have a comparable hatching success to those in undisturbed clutches.

Emerging hatchlings dug to the surface from nests that had a mean depth of 80.6cm (SD = 9.073, range = 44-102, n = 200). This nest depth

TABLE 39. Hatching and emergence success data (Table 38) from *Chelonia mydas* clutches at Raine Island reanalysed on a clutch by clutch basis.

	Mean	SD	Range	n
1979: June (37 clutches)				
Clutch (counted at emergence)	102.27	22.345	68-168	37
Emerged hatchlings per clutch	76.05	30.305	1-149	37
Live hatchlings in nest	0.19	0.462	0-2	37
Dead hatchlings per nest	0.35	0.538	0-2	37
Unhatched eggs per clutch	6.92	9.867	0-41	37
Undeveloped eggs per clutch	18.08	15.004	1-55	37
Crab predated eggs per clutch	0.68	2.028	0-10	37
Hatching success (%)	74.45	23.137	1.17-99.0	37
Hatchling emergence success (%)	73.90	23.184	1.17-99.0	37
Nest depth (cm), bottom	76.64	7.407	65-96	33
1983: April (16 clutches)				
Clutch (counted at emergence)	96.50	25.458	46-139	16
Emerged hatchlings per clutch	79.88	25.458	46-139	16
Live hatchlings in nest	1.00	1.317	0-3	16
Dead hatchlings per nest	0.69	1.352	0-5	16
Unhatched eggs per clutch	8.88	8.484	0-31	16
Undeveloped eggs per clutch	5.88	7.822	0-32	16
Crab predated eggs per clutch	0.19	0.544	0-2	16
Hatching success (%)	85.52	13.139	45.68-100.0	16
Hatchling emergence success (%)	83.92	13.352	44.82-100.0	16
Nest depth (cm), bottom	79.73	6.638	65-90	15
1984: April (167 clutches)				
Clutch (counted at emergence)	103.33	19.568	37-155	162
Emerged hatchlings per clutch	80.96	21.600	18-139	162
Live hatchlings in nest	0.48	1.035	0-8	162
Dead hatchlings per nest	0.50	2.622	0-31	162
Unhatched eggs per clutch	8.20	7.846	0-53	162
Undeveloped eggs per clutch	11.99	12.882	0-91	162
Crab predated eggs per clutch	1.20	2.735	0-18	162
Hatching success (%)	79.58	14.958	20.43-100.0	162
Hatchling emergence success (%)	78.62	15.205	19.35-100.0	162
Nest depth (cm), bottom	81.55	9.400	44-102	152

was not significantly different to the nest depth recorded at laying (t>0.2) (Table 33).

The high emergence success of non disturbed and non inundated *C. mydas* eggs incubate at Raine Island (Table 39) indicate that they do not suffer from the very high level of microbial induced mortality associated with the high density *Lepidochelys olivacea* rookeries of Pacific Costa Rica (Cornelius 1986). The limited data suggest that the hatchling emergence from undisturbed nests will be very similar to that of the low density *C. mydas* rookeries elsewhere in the GBR, at Bramble Cay in 1978/79 (72.1%, n =31; Parmenter, 1979) and at Heron Island in 1966/67 and 1967/68 (87.9%, n = 26; 84.9%, n = 40 respectively; Bustard, 1976). Similarly the hatching success of the undisturbed Raine Island clutches was comparable to the hatching success recorded for Heron Island *C. mydas* clutches in 1980/81 (mean = 90.2%, n = 60; Limpus et al., 1983c).

HATCHLING PREDATION. 1975, 28 February-4 March: A typical day's observation of hatchling emergence and predation was as follows:

4 March. 1500hr almost no hatchlings were crossing beach. 1515hr, immediately following the mid afternoon heavy rain shower, large numbers of hatchlings were observed crossing the beach and entering the flat calm sea. Bird predation was intense at this time. Sharks and large fish were very obvious as they broke the smooth sea surface while feeding on the hatchlings streaming away from the island. The sharks were mostly *Carcharhinus* spp. (black-tipped whalers and grey whalers) the largest of which were in excess of 2m in length. The fish were mostly trevally, *Caranx* sp. By 1630hr there was again intense sunlight and few hatchlings were crossing the beach. From 1730hr onwards, even though there was only scattered cloud, abundant hatchlings were crossing the beach. Vast numbers of hatchlings were crossing the beach throughout the night into the hours approaching dawn. Approximately no hatchlings were crossing the beach during the mid morning hours the following day.

Predation by birds: Rufous night herons were scattered around the beach late in each afternoon and were observed regularly to pick up *C. mydas* hatchlings. Some were eaten on the beach but others were carried away. Regurgitated *C. mydas* hatchlings were seen at rufous night heron nests containing unfledged chicks. Crested terns were observed on four instances to pick *C. mydas* hatchlings from the water and on three instances to take hatchlings from the beach. In each case the hatchling was subsequently dropped and no further attempt to recover the hatchling was made by the bird. The regurgitated remains of *C. mydas* hatchlings were adjacent to numerous crested tern nests on Moulter Cay (5 February). None of the other species of birds (King, 1986) that were numerous around the island during these mass daylight emergences of

TABLE 40. Observed predation of *Chelonia mydas* hatchlings during emergence from the nest and the beach crossing phase at Raine Island during 4-7 April 1984. * denotes avian predators did not approach the nest, probably because of its close proximity to the bird hide and most hatchlings reached sea. The numbers of hatchlings that successfully reached the water are shown in parenthesis.

Date	Clutches examined				
	No. of clutches	Predation on hatchlings crossing beach			Not quantified
		100%	0%	Part of clutch	
4th	15	10	1 (104)	3 (87)	1*
5th	10	10	0	0	
6th	25	21	0	3 (75)	1*
7th	19	8	0	9 (84)	2
Total	69	49	1 (104)	15 (246)	4

hatchlings were observed to show any interest in the hatchlings. Even the larger species of sea birds present (brown, red- footed and masked boobies, lesser and greater frigatebirds, red-tailed tropicbirds) were not predators of the hatchlings.

Attraction of hatchlings to lights: When the deck lights of boat anchored adjacent to the western end of Raine Island reef were left on after dark, there was a dense carpet of hatchlings across the smooth water surface in the illuminated area within minutes. The hatchlings did not swim from the illuminated area but swam back and forth within it. Large numbers of fish and shark could be seen preying on the hatchlings. The light acted as a trap, holding the hatchlings in a dense concentration, and made them easy prey for the fish. When the lights were switched off the hatchlings dispersed away from the island out into the open sea. A *Carcharhinus* sp. (~150cm long) caught on the western reef edge at 2100hr had a stomach content of 17 *C. mydas* hatchlings, ranging from well digested to still alive.

1978, December: A small crocodile, *Crocodylus porosus*, was captured on the reef flat (Limpus, 1980c). This crocodile was using the island as a basking site by day and appeared to be foraging along the beach margin at night. Its stomach contained no food.

1980, 8-13 December: Ghost crabs, *Ocypode ceratopthalmus* and *O. cordimana* were abundant along the water line at night. Both were observed preying on the hatchling *Chelonia mydas*. Several of the small grey terrestrial hermit crab, *Coenobita* sp., were present but they were not observed to prey on turtle hatchlings.

1984, April: Rufous night herons were observed daily and nightly on the beach throughout the visit.

These were observed aggregating around nests and preying on the hatchlings as they emerged from the nests (Fig. 41). Example predation case histories:

1) At 1745hr on 7 April, 113 rufous night herons were observed in the vicinity of one nest with 58 of them

FIG. 41. Rufous night heron, *Nycticorax caledonicus*, preying on a *Chelonia mydas* hatchling at Raine Island, April 1983.

crowded at the nest site. These birds were observed to eat 67 *C. mydas* hatchlings from this nest. The hatchlings were taken as they emerged from the nest to the beach surface or, for hatchling just below the sand surface and wriggling to disturb the beach surface, the herons stabbed down to grasp and pull the hatchling from the nest. The herons carried the turtle hatchlings from the nest site and away from other birds before swallowing them whole.

2) On 11 April, observations over the southeastern beach commenced at 1600hr. A group of 15 rufous night herons was present . Other birds in the vicinity included common noddy, lesser frigatebird, silver gull, ruddy turnstone, Australian ibis, crested tern. 1620hr 25 rufous night herons present; 1650hr 9 rufous night heron present. 1710-1715hr, *C. mydas* clutch emerged with 50 hatchlings taken by rufous night herons and 1 by a crested tern. Herons were coming and going during the hatchling emergence and 39 were still present after the hatchlings ceased emerging.

HATCHLING PREDATION RATES DURING THE BEACH CROSSING. Hatchling predation was quantified at two periods of different densities of rufous night heron at Raine Island.

During April 1984, thousands of rufous night herons were breeding at the island with chicks in the nests. The number of clutches of *C. mydas* hatchlings emerging per 24hr period was counted on 13 days during 3-25 April 1984. The mean daily number of clutches of hatchlings emerging was 20.5 (SD = 5.18, range = 14-32, n = 13). Over four days and nights, 4-7 April, predation of *C. mydas* hatchlings during the beach crossing up to their entry to the sea was quantified for as many clutches as possible. The results are summarised in Table 40. From this sample, 350 hatchlings reached the sea from 69 clutches (assuming clutch count = 102, emergence success = 78.4%) (Table 39). This is equivalent to a hatchling survivorship while crossing the beach to the point of entry to the sea = 6.7%. Almost all of the associated predation was by rufous night herons.

During June 1980 there were only hundreds of rufous night herons on Raine Island and none were breeding. Few birds aggregated on the beach to prey on the hatchling turtles. Estimates of predation rates were made by direct observation and by examination of tracks on the beach for hatchlings emerged from 11 clutches: no predation for 5 clutches; crabs took 1 hatchling per clutch from each of 5 clutches (*Ocypode cordimana* identified at two of the hatchlings); an unidentified bird took 1 hatchling from 1 clutch. From these 11 clutches (assuming clutch count = 102, emergence success = 74%) (Table 39), the 6 hatchlings preyed upon during the beach crossing represent a hatchling survivorship during the beach crossing = 99.3%.

TABLE 41. Field data based on flipper tag recognition of female turtles within the internesting habitat tagged while nesting at Raine Island. These data were used to calculate Petersen estimates with Bailey's correction of the number of breeding *Chelonia mydas* present (N) in the internesting habitat of Raine Island Reef during December in successive breeding seasons. M = total number of marked turtles in the population; m = number of marked turtles recaptured in the adjacent waters out of a sample of n turtles examined for marks.

Date	Transect type	Marking	Days since marked	M	m	n	Estimate N ± SE
4/12/77	snorkel	Monel tag, L1	1	37	1	12	241 ± 128
6/12/77	snorkel	Monel tag, L1	1-2	49	1	16	417 ± 226
4/12/78	speedboat	Monel tag. L1	1-3	496	8	79	4,409 ± 1,313
4/12/81	speedboat	Monel tag, L3	1-27	2,421	34	197	13,696 ± 2,071
2/12/84	snorkel	Titanium tag, L3	1-11	1,765	1	83	74,130 ± 42,286
3/12/84	snorkel	Titanium tag, L3	1-12	2,034	7	127	32,544 ± 12,732
8/12/84	speedboat	Titanium tag, L3	1-17	2,104	7	91	24,196 ± 7,665
17/12/84	snorkel	Titanium tag, L3	1-26	2,362	2	44	35,430 ± 17,114
19/12/84	snorkel	Titanium tag, L3	1-28	2,475	6	97	34,650 ± 11,805
9/12/85	snorkel	Titanium tag, L3		1,385	4	10	3,047 ± 919
16/12/85	SCUBA	Titanium tag, L3		1,765	4	10	3,883 ± 1,171

The rufous night heron breeds on Raine Island in large numbers during the main period of hatchling emergence. It may require some 20-30 clutches of hatchlings to satiate these birds each evening/night. When there are hundreds or thousands of turtle clutches emerging nightly, the birds will make little impact on the hatchling numbers. However, when there are few clutches emerging, most of the hatchlings may be eaten before they reach the water. Outside the rufous night heron breeding season these birds are minor predators of the turtle hatchlings. This seasonality of intense predation by this nocturnal bird species on turtle hatchlings is a similar to that observed with the rufous night heron predation on *N. depressus* hatchlings on the beach at Crab Island (Limpus et al., 1983b).

These observations suggest that the most productive seasons with respect to hatchling survival during the beach crossing to the sea will be the dense nesting seasons. No attempt has been made to quantify predation of hatchlings after they entered the sea or to determine where they swim after they disperse from Raine Island Reef.

ESTIMATION OF THE ANNUAL RAINE ISLAND NESTING POPULATION SIZE

At present, the only precise method for measuring the total annual nesting population at a turtle rookery is via a total tagging census. This requires every female using the rookery to be tagged or checked for existing tags on every night of the five months or more of the nesting season. The remoteness of Raine Island makes it logistically and financially difficult to monitor an entire breeding season. In addition, the usually large size of the nesting population also makes it very difficult to tag every turtle present on any one night at mid season.

From repetitive total tagging censuses of the Heron Island *Chelonia mydas* rookery (Limpus, unpubl. data) and the Mon Repos *Caretta caretta* rookery (Limpus, 1985) it can be established that the nesting density at a standard sampling time within the mid nesting season can be used as an index of the size of the annual nesting population. However, it would be an advantage if the absolute size of the nesting population could be estimated from population sample data recorded at the island.

PETERSEN ESTIMATE. To reduce the problem of widening confidence limits that result from multiplying several factors, each with their own 95% confidence limits, a tagging - recapture method was used to relate the number of nesting turtles ashore on the island directly to the number of turtles swimming in the internesting habitat surrounding the island (see Methods). This method provides a single step calculation for estimating the number of female turtles within the nesting habitat.

The flipper tagging and transect data used to calculate the Petersen estimates with Bailey's

TABLE 42. Data recorded during estimation of the size of the annual Raine Island *Chelonia mydas* nesting population. The turtles were marked with paint on the carapace. Different colours or markings were applied on different nights within a breeding season. The number of adult female *Chelonia mydas* in the waters adjacent to Raine Island was estimated using a Petersen estimate, with Bailey's correction.

Painting on beach			Counts by speedboat transects							*C. mydas* Population estimate
			Counts of adult female *C. mydas*				Counts of non 'adult females'			
							C. mydas			
Date	No. painted (M)	Paint code	Date	Paint code	Total Short-tailed Adult-sized (n)	Painted (m)	Long-tailed adult	Immature sized	*E. imbricata*	
1987: coloured oil-based paint			Speedboat transects							
30/11/87	441	Yellow	1/12/87	Yellow	217	10	0	0	0	8,740 ± 2,458
1/12/87	241	Blue	2/12/87	Yellow	55	1	0	1	0	12,348 ± 7,001
2/12/87	838	Red	2/12/87	Blue		2				4,499 ± 2,188
3/12/87	542	Blue-green	3/12/87	Yellow	184	3	2	1	0	20,396 ± 9,022
			3/12/87	Blue		0				-
			3/12/87	Red		5				25,838 ± 9,606
			4/12/87	Yellow	327	3	3	2	0	36,162 ± 16,073
			4/12/87	Blue		0				-
			4/12/87	Red		5				45,811 ± 17,156
			4/12/87	Blue-green		0				-
			5/12/87	Yellow	356	3	3	1	0	39,359 ± 17,503
			5/12/87	Blue		0				-
			5/12/87	Red		12				23,013 ± 6,037
			5/12/87	Blue-green		0				-
			SCUBA							
			1/12/87	Yellow	376	7	0	0	0	20,782 ± 6,853
			2/12/87	Yellow	56	2	0	0	0	8,379 ± 4,078
			2/12/87	Blue		0				-
			3/12/87	Yellow	239	2	0	6	0	35,280 ± 17529
			3/12/87	blue		0				-
			3/12/87	red		6				28,731 ± 10,009
1988: white oil-based paint			Speedboat transects							
30/11/88	402	Stripe	1/12/88	Stripe	402	19	9	1	0	1,970 ± 384
1/12/88	237	Cross	2/12/88	Stripe	147	8	8	1		6,611 ± 2,026
6/12/88	289	V	2/12/88	Cross		0				-
			3/12/88	Stripe	161	8	0	0	0	7,236 ± 2,224
			3/12/88	Cross		2				12,798 ± 6,339
			7/12/88	Stripe	130	7	0	0	0	6,582 ± 2,126
			7/12/88	Cross		3				7,762 ± 3,418
			7/12/88	V		5				6,310 ± 2,330
			SCUBA							
			1/12/88	Stripe	19	4	0	0	0	1,608 ±569
			3/12/88	Stripe	46	3	0	0	0	4,724 ± 2,021
			3/12/88	Cross		2				3,713 ± 1,796
			7/12/88	Stripe	23	1	0	6	0	4,824 ± 2,667
			7/12/88	Cross		1				2,844 ± 1,572
			7/12/88	V		0				-
1991-2002: Transects standardised to boat transects										
6/12/91	950	Stripe	7/12/91	Stripe	435	30	0	0	0	13,361 ± 2,276
8/12/91	600	V	9/12/91	Stripe	543	18	0	2	0	27,200 ± 5,975
			9/12/91	V		2				108,800 ± 54,250

TABLE 42 (*Cont.*)

Painting on beach			Counts by speedboat transects							*C. mydas* Population estimate
			Counts of adult female *C. mydas*				Counts of non 'adult females'			
							C. mydas			
Date	No. painted (M)	Paint code	Date	Paint code	Total Short-tailed Adult-sized (n)	Painted (m)	Long-tailed adult	Immature sized	*E. imbricata*	
1991-2002: Transects standardised to boat transects (cont.)										
1992/93	Sea too rough to make counts									
1993/94	Sea too rough to make counts									
1994/95	Sea too rough to make counts									
1995-2002: Paint standardised to Airpave™										
6/12/95	1,010	Lengthwise	7/12/95	Lengthwise	1,039	24	21	0	1	42,016 ± 8,140
1/12/96	1,033	Lengthwise	2/12/96	Lengthwise	194	6	-	-	-	28,776 ± 9,990
7/12/96	1,526	Crosswise	8/12/96	Crosswise	489	28	-	-	-	25,784 ± 4,566
1/12/97	553	Lengthwise	2/12/97	Lengthwise	145	3	2	3	0	21,290 ± 9,397
1998/99	Sea too rough to make counts									
8/12/99	1,239	Lengthwise	9/12/99	Lengthwise	3,261	50	4	13	0	79,247 ± 10,903
10/12/99	1,147	Crosswise	11/12/99	crosswise	3,812	55	0	8	0	78,098 ± 10,268
4/12/00	86	Lengthwise	5/12/00	Lengthwise	39	2	2	0	0	1,147 ± 551
7/12/00	96	Crosswise	6/12/00	Lengthwise	30	2	1	0	0	889 ± 422
			7/12/00	Lengthwise	54	5	0	1	0	788 ± 281
			8/12/00	Lengthwise	40	3	0	0	0	882 ± 374
			8/12/00	Crosswise		0				-
6/12/01	1,188	Lengthwise	7/12/01	Lengthise	1,024	8	1	3	0	135,300 ± 42,597
8/12/01	1,163	Crosswise	9/12/01	Crosswise	1,024	16	1	3	0	70,122 ± 16,390

correction of the number of adult female *C. mydas* in the waters surrounding Raine Island during early December, 1977-1985, are summarised in Table 41. While there is some variability in the results from within a single nesting season, the 95% confidence limits usually overlapped.

When the method was first used, it relied on the turtles being tagged distally on the trailing edge of the front flipper (L1 tagging position) with monel tags. These distally applied tags were highly visible (flashing in the sun light) on the swimming turtle in the clear shallow waters surrounding Raine Island. When the tagging position was changed from L1 to L3, the tag became more difficult to distinguish. The tag became even more difficult to detect on a swimming turtle when the tag design changed, to improve tag retention, from the highly polished monel tag to the more dull lustred titanium tag. Under the latter circumstances many more turtles were being excluded from the underwater counts of tagged/untagged females because of uncertainty of recognising the presence/absence of a tag, especially during speedboat transects. This resulted in more time having to be spent counting turtles with divers/snorkelers in the water rather than using speedboat transects. With the former came the increased frequency of encountering big tiger sharks.

In 1987 a system of paint tagging the nesting females was introduced (Figs 42-43) to increase the visibility of a tagged turtle in the water. The paint marks on the turtle carapaces held well for about 4 days following application. Some turtles were encountered back on the island after more than 4 days with most of the paint mark obliterated. Within the internesting habitat, most of the paint loss was caused by abrasion as turtles pushed into crevices under coral. The paint peeled off more readily if the carapace was not dry when painted or if there was an algal coat on the carapace. The different paint colours (Table 42) were not equally recognisable in the water. For example, no green painted turtles were 'recaptured' swimming over the reef while all other colours were recognisable. This lack of recaptures was not because the green paint marks had been shed by the turtles. Green painted turtles were frequently encountered ashore on the island on subsequent nights. Blue paint was only marginally more visible than the green paint. From 1998 onward, the paint tagging has been standardised to white paint. White paint was very

FIG. 42. Paint tagging a nesting turtle at Raine Island, December 2000 as part of the Petersen Estimate of the size of the total nesting population.

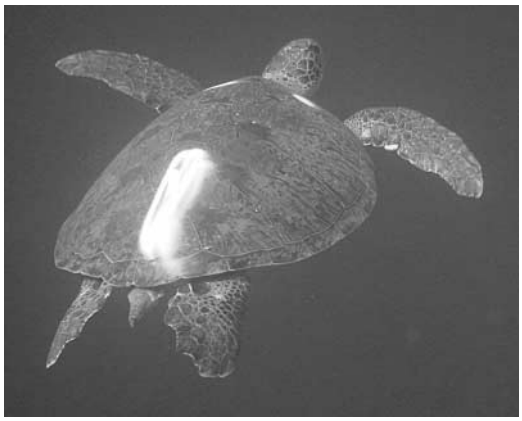

FIG. 43. A paint tagged female (longitudinal stripe) in the internesting habitat of the reef margin to Raine Island Reef, December 2002. (Photo W. MacPharlane)

visible on the backs of the turtles in the water and contrasting paint mark designs were easily distinguished up to 30m underwater, even when the turtle was barely distinguishable at that distance. Since 1995, the paint tag has been the more durable outdoor paint designed for road marking. As it became apparent that very large sample sizes had to be marked and examined to provide estimates with tight confidence limits, the underwater transects swum with snorkel or SCUBA were phased out in favour of the speed boat transects. This also provided for reduced risk to the team given that large tiger sharks were regularly encountered during swim transects at Raine Island Reef.

A search of Raine Island Reef waters and the water of adjacent reefs during December 1988 demonstrated that turtles nesting at Raine Island were mostly concentrated in the waters immediately surrounding Raine Island and were not scattered widely throughout the region during the internesting intervals (Table 43).

Within any one sampling period, the population estimates obtained using carapacial painting to tag the nesting females were variable. When large numbers of nesting females were painted ashore at Raine Island and a very large sample (thousands) of the turtles examined in the internesting habitat on Raine Island Reef, there was usually reasonable agreement among the estimates of the internesting population size (Table 42). However, the results are probably influenced by sea surface conditions. Unfortunately, the weather is not always compatible with these types of studies and in at least 4 years the counts on the reef flat could not be undertaken because of the weather.

The relationship between the mean nightly tally count and the estimated size of the internesting population in the adjacent waters is illustrated in Fig. 44. For most years, the Petersen estimate has correlated well with the mean tally count. This has been particularly so for mean tally counts up to about 4,000 females per walk of the beach. At this mean tally count level, there is an estimated internesting population adjacent to the Raine Island rookery of approximately 25,000 breeding female *C. mydas*. The relationship is poor when there are very dense nesting populations. In particular, in the 1999

TABLE 43. Numbers of turtles recorded during speedboat transects over reefs adjacent to Raine Island, 4-6 December 1988. Only *Chelonia mydas* were identified during these transects. No painted turtles from Raine Island or from Moulter Cay were observed during these transects.

Date	Short-tailed		Long-tailed	Reef location (transect time)
	Adult sized	immature		
4/12/88	76	0	0	Moulter Cay (30 min)
5/12/88	1	0	0	11-093
	0	5	0	11-095
	1	0	0	11-096
	0	0	0	11-097
	0	0	0	McGillivray Cay (20 min)
6/12/88	2	0	0	Jukes Reef

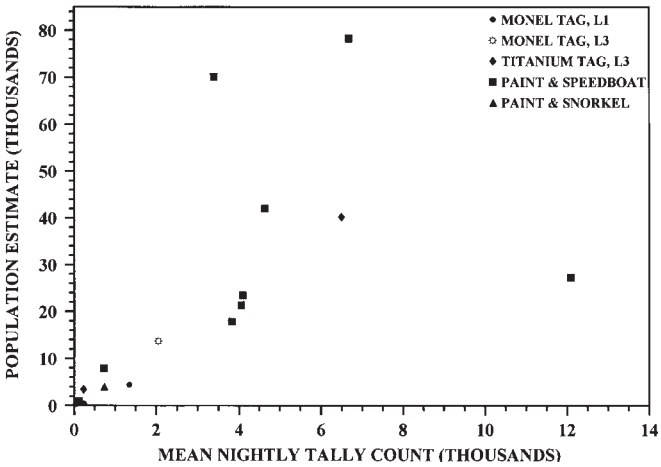

FIG. 44. Comparison of the Mean nightly tally count with the estimated number of adult females in the interesting habitat of Raine Island. The Petersen estimate was used to estimate the size of the interesting population. See text for description of the tagging and transect count methods.

season, the estimate of 78,672 ± 10,586 was not expected from the mean tally count of 6,693. However, this estimate would appear to be consistent with the exceptionally dense population of *C. mydas* photographed in the Raine Island internesting habitat in late 1999 (Chadwick & Doubilet, 2000). In the exceptionally dense nesting seasons, there could be approximately 80,000 females in the Raine Island internesting habitat in early December.

Estimating the size of the total annual nesting population for Raine Island via a single Petersen estimate calculation using data derived from marking on the nesting beach and 'recapture' in the internesting habitat in the days immediately following tagging is cost effective. The method warrants further investigation to improve its rigor in the very high density nesting seasons. Carapacial painting is a workable method for tagging the turtles, provided the paint marks are prominent and of a suitable colour. Selected colours and/or paint marks can be used to distinguish different tagging cohorts. To maximise the precision of the estimate, it is essential to maximise the proportion of the total population of internesting turtles tagged in any one nesting sample and to maximise the number of turtles examined in the aquatic recapture phase. In this regard, further investigation of the painting technique would be appropriate to develop a method for paint tagging many thousands of nesting females in a single night. At the same time the paint-retention time needs investigation to improve the capacity for pooling painted cohorts from different nights.

Within any one nesting season there will be different numbers of active nesting females present at different times of the season, with small numbers present in early and late season and maximum numbers present in mid season. From total tagging census studies at Bramble Cay in 1979/80, approximately 85% of the total annual nesting population visited the island during the last two weeks of December (Limpus et al., 2001). This should equate to the total population in the internesting habitat in early December. In addition, there is a strong correlation between the nightly number of nesting *C. mydas* using Moulter Cay (MCTALLY) (Table 4) with the nightly tally count Raine Island (RITALLY) (Table 3) on the same or adjacent night: MCTALLY = 0.3928 × RITALLY + 95 ($F_{1,14} = 47.6$; $p<0.005$. $r^2 = 0.773$, DF = 14.). By combining these two values it is possible to obtain an estimate of the size of the total annual nesting *C. mydas* at Raine Island, Moulter Cay and immediately adjacent islands:

= (Raine Is December estimate + Moulter Cay December estimate) / 0.85

= (RI December estimate + 0.3928 × Raine Is December estimate + 95) / 0.85

= 1.6386 × Raine Is December estimate + 112

Thus the estimated total annual nesting population for Raine Island and Moulter Cay in the very high nesting density seasons would approximate 131,000 females. The total nesting population in the extremely dense nesting seasons for the entire nGBR stock will be slightly higher if a few thousand additional females nesting at Bramble Cay, Murray Islands, No. 7 and No. 8 Sandbanks, Milman Island and the other *C. mydas* rookeries of the northern GBR and Torres Strait are added. A more typical dense nesting population with a mean tally count of about 4,000 females at Raine Island, may be in the order of 41,000 females breeding annually.

The nGBR stock, for which Raine Island - Moulter Cay are the primary breeding sites, supports the largest nesting aggregation of *C. mydas* remaining anywhere in the world (King, 1982; Groombridge & Luxmoore, 1989).

TABLE 44. Frequency distribution of the presence and absence of corpora albicantia on the ovaries of breeding adult female *Chelonia mydas* examined at Raine Island. The proportion of females with no corpora albicantia provides an estimate of the rate of recruit of new females into the breeding population (± 95% confidence limits).

Breeding season	Method of assessment	Nesting females examined			Recruitment	
		Total	With albicantia	Without albicantia	Estimated value	95% confidence limits
1989, Dec	Necropsy	98	85	13	13.3%	7.2-21.6%
1990, Dec	Necropsy Laparoscopy	8 52	59	1	1.7%	0.04-8.9%
1991, Dec	Necropsy Laparoscopy	29 50	77	2	2.5%	0.3-8.8%
1992, Dec	Necropsy Laparoscopy	2 97	93	6	6.1%	2.3-12.7%
1993, Dec	Necropsy	33	33	0	0%	-
1994, Dec	Laparoscopy	51	44	7	13.7%	5.7-26.2%
1995, Dec	Gonads sampled by non-standard method. Data deleted from analysis.					
1996, Dec	Necropsy	35	34	1	2.9%	9.9-14.8%
1997, Feb	Necropsy	100	100	0	0%	0.0-3.6%
1997, Dec	Necropsy	52	48	4	7.7%	2.1-18.5%
1998, Dec	Necropsy	1	1	0	-	-
1999, Dec	Necropsy	65	53	12	18.5%	9.9-30.0%
2000, Dec	No freshly dead turtles available during study.					
2001, Dec	Necropsy	16	14	2	12.5%	1.6-38.8%

ESTIMATION OF ADULT RECRUITMENT RATE

Ovaries of samples of breeding female *C. mydas* at Raine Island were examined for the presence or absence of corpora albicantia (Fig. 45). Corpora albicantia are ovarian scars from ovulations in previous years. Hence, females without corpora albicantia are in their first breeding season i.e. new recruits to the breeding population. The proportion of breeding females without corpora albicantia provides a measure of the recruitment rate of new adult females into the breeding population (Table 44). Commencing in 1989, an attempt was made to quantify the annual recruitment of new turtles into the Raine Island breeding population.

The annual recruitment rate of new adults into breeding population is low: mean = 7.17% (SD = 6.41, range = 0 – 18.5%, n = 11) (Table 44, Fig. 46).

These measurements are based on two underlying assumptions. 1) the rate measured on dead females at Raine Island is similar to the rate for the entire population, i.e. the nesting turtles that died on the island were a random sample of the entire nesting population with respect to recruitment. 2) that the recruitment rate measured in early December is representative of the entire breeding season. This assumption needs testing with *C. mydas* given that new recruit *C. caretta* and *N. depressus* tend to arrive later in the nesting season at south Queensland rookeries (C.J. Limpus and C.J. Parmenter, respectively, unpubl. data). This assumption was tested during the 1996 breeding season only and similar results were obtained in early December and early February (Table 44). Although the results from laparoscopy and necropsy provide no indication of a bias from the dead turtles (Table 44), this assumption warrants further testing.

There are few studies of marine turtles against which to judge the significance of these recruitment values. This recruitment rate for the Raine Island *C. mydas* is considerably lower than that estimated from tagging studies with *Caretta caretta* (30-50%, Natal, South Africa, Hughes, 1989; 30-40%, Georgia, USA, Richardson & Richardson, 1982; 44.2% ± 5.7%, Queensland, Australia, Limpus, 1985). However, all of these values for *C. caretta* have been measured in depleted populations. In contrast, the annual recruitment rate estimated from tagging

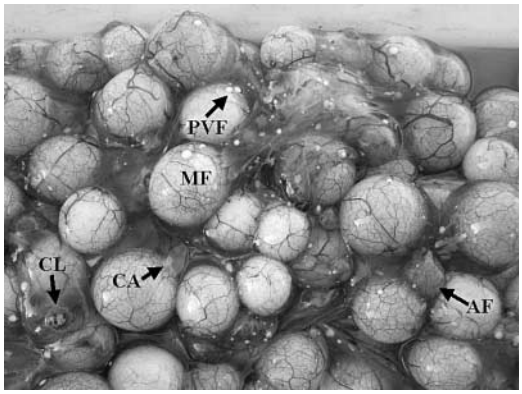

FIG. 45. An ovary with corpora albicantia. This ovary was from an adult female *Chelonia mydas* that died while ashore attempting to nest at Raine Island, December 2002. MF = mature ovarian follicle; AF = atretic follicle; PVF = pre-vitellogenic follicle; CA = corpus albicantium; CL = corpus luteum.

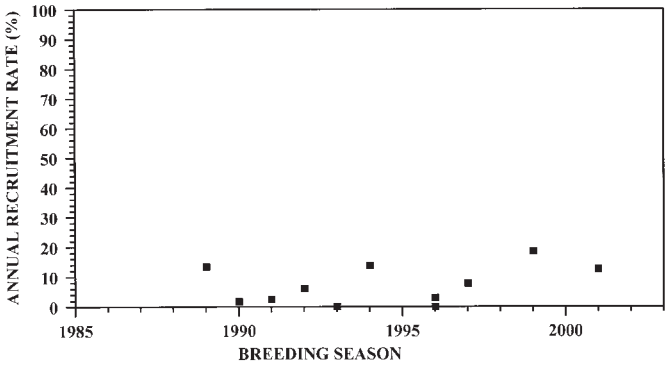

FIG. 46. Annual variability in recruitment rate of new females into the *Chelonia mydas* breeding population at Raine Island.

studies with the stable population of the eastern Australian *N. depressus* stockbreeding at Mon Repos, Peak Island and Wild Duck Island was in the range of 10-20% (Parmenter & Limpus, 1995; Limpus et al., 2002). The mean annual recruitment rate estimated from gonad examination using laparoscopy with the declining *E. imbricata* population the breeds in the northern GBR during 1991-2000 was 15.5% (SD = 6.65, range = 8.3 – 27.3%, n = 8) (Miller et al., 2000). Thus, the recruitment rate of new adults into the nGBR *C. mydas* stock is only slightly lower than the recruitment rate estimated for the stable population of *N. depressus* and the declining *E. imbricata* population that breed in eastern Australia.

ACKNOWLEDGEMENTS

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Annette Fleay, Valonna Baker, David Butler, Margaret Card, Michael Cassematy, Robyn Delaney, Carl, French, Matt Freher, Emma Gyuris, Mark Hamann, Brad Jones, Steven Neil, Mark Read, Darryl Reimer, Linda Rhineholdt and numerous volunteers collected data under the primitive field conditions on the islands. Brian King provided valuable team coordination for many study trips to Raine Island and worked in collaboration with us in documenting the significance of turtle nesting on the islands of the northern Great Barrier Reef.

Ken and Betty Butler, through their personal commitment to conservation in Queensland which led to the establishment of the Raine Island Corporation, have made a lasting contribution conservation within the Great Barrier Reef and to marine turtle conservation within the Australasian region. This assistance and support is gratefully acknowledged.

CONCLUSION

Raine Island has been a nesting site for green turtles for over 1,000 years. The nesting population of green turtles has been known to Europeans for approximately 175 years during which a navigation beacon tower was built, guano was mined and turtles were harvested. Green turtles nesting at Raine Island are part of a larger genetic stock that utilizes many islands in the northern Great Barrier Reef (nGBR) and eastern Torres Strait. This population is one of the largest remaining stocks for the species on a global scale. The nesting green turtles of the nGBR are morphologically similar to other genetic stocks of eastern Australia and the Gulf of Carpentaria, as well as elsewhere in the world. The population is chatacterised by a very long remigration interval with a mean of 4-5 years. The number of turtles using Raine Island varies by orders of magnitude among seasons. Fluctuations in numbers of nesting turtles are correlated with alterations in the ENSO measured 18 months preceding. Intra-annual variation also occurs; the highest density nesting occurs during the mid summer months and the lowest density nesting occurs during the winter months.

Adult mortality on the nesting beach and egg mortality were positively correlated, while predation by sharks on the nesting turtles and

nesting success were negatively correlated with an index of the size of the annual nesting population. In high density nesting seasons following repetitive disturbance females reduce the clutch production as a result of resorption of ovarian follicles. Death of nesting turtles is a natural phenomenon and occurs primarily from heat exhaustion on the beach by day following extended unsuccessful nesting attempts.

There has been a progressive decline in the size of nesting females over the decades of the study. This decline was associated with a decline in size of remigrant turtles. There was no decline in the size of turtles being tagged for the first time. The decrease in size of the females occurred in conjunction with a progressive increase in remigration interval. In recent times, the nesting population is also characterised by a very low recruitment rate. These demographic characteristics may indicate that this large population is in the early stages of decline as a result of loss of adult turtles. There is wide spread hunting of turtles from this population that preferentially targets the adult and near adult size (Schulz, 1984; Kwan, 1991; Johannes & MacFarlane, 1991) that could account for these changes. In addition, if the recent phenomenon of very low hatchling production resulting from flooding of the Raine Island nesting habitat continues, then significant declines can be expected in the numbers of young *C. mydas* in the dispersed foraging areas. Taken together, there is a high probability that this population will decline in the foreseeable future. It is recommended, that monitoring of the impact of human induced mortality on the population throughout it dispersed foraging areas be increased and that steps be taken to reduce human mortality to a sustainable level.

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