Hawksbill Turtle, *Eretmochelys imbricata*, Nesting at Milman Island, Northern Great Barrier Reef, Australia

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ABSTRACT. - The nesting patterns, incubation environment, and reproductive biology of hawksbill turtles (Eretmochelys imbricata) are described from data collected during seven surveys on Milman Island, northern Great Barrier Reef, Australia, between 1991 and 1995. Of the 1183 turtles tagged between 1991 and 1995, 83 (7%) returned to Milman Island at 2-yr (6%), 3-yr (46%), and 4-yr (48%) remigration intervals. Nesting activity (range = 0-37 turtles per 24-hr period) peaked in midsummer (late January, early February), coinciding with the onset of the Australian rainy season. Most nesting attempts occurred at night (98%, n = 3676); 76% resulted in eggs being laid. Turtles failing to nest on their first observed nesting attempt returned within the following 6 nights (1.4 \pm 0.07) to try again. Turtle nesting activity was significantly correlated with tide height; more turtles attempted to nest when the night-time high tide occurred before midnight than after midnight, presumably in response to significantly higher tides occurring pre-midnight $(2.73\pm0.5 \text{ m})$ than postmidnight (2.52 \pm 0.43 m). Females laid between 1 and 6 clutches during the monitored portion of a season. Turtles successfully renested every 14.7 days (range = 10-25) at an average distance along the beach of 436.4 \pm 341.3 m from their previous attempt, regardless of the success of that attempt. Nests were between 19 and 91 cm deep (average 39.5 cm), and usually located under trees (71% of 2816 clutches). Incubation environment was characterized by sand grain-size comprised of > 80 % at < 0.85 mm diameter, pH between 8.29 and 9.86, soluble salt content from 17.2-28.3%, and moisture content from 0.21-7.60%. Fine sand had higher water potential (-269.93 J/kg) than did coarser samples (-64.46 J/kg). Average nesting female curved carapace length, width, and weight were 81.6 cm (range = 63.5-91.9), 70.7 cm (range = 53.4-82.5), and 50.5 kg (range = 32.0-72.0), respectively. Females returning for a subsequent nesting season grew an average of 0.14 cm/yr (n =82). Mean clutch size was 122 eggs (range = 18-215); average egg diameter and weight were 3.51 cm (range = 2.83-3.81) and 26.3 g (range = 20.4-31.8), respectively. Clutches incubated an average of 58.5 days (range = 47-71) and had a mean emergence success of 79%. Hatching and emergence success were correlated to the beach section in which eggs were laid as well as the time during the season when the clutch was laid. Hatchlings averaged 3.98 cm straight carapace length (range = 3.20-4.36) and 13.8 g (range = 8.0-17.5). Several linear regression equations were developed for numerous measurements among nesting turtles, their eggs, and hatchlings.

KEY WORDS. - Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; reproductive biology; nesting patterns; incubation environment; Queensland; Great Barrier Reef; Australia

By the end of the 1980s it was apparent that nesting by the hawksbill turtle, *Eretmochelys imbricata*, was globally widespread but that the numbers of nesting females were declining in about half of the known nesting locations around the world (Groombridge and Luxmoore, 1989). At the same time, there was evidence of substantial harvest of hawksbills in many areas around the world (Groombridge and Luxmoore, 1989) and in most countries neighboring the Coral Sea region (Milliken and Tokunaga, 1987). This was occurring in the face of a paucity of biological data (Witzell, 1983) from which a reliable assessment could be made of the survival status and numerical trends of the populations.

Initial surveys on the northern Great Barrier Reef (GBR) and Torres Strait in Queensland, Australia, identified nesting sites that appeared to be significant at a regional and global scale (Limpus, 1980; Limpus et al., 1983a, 1983b). Additional studies, including a review of the species in the southwestern Pacific Ocean region (Miller, 1994), a survey of nesting distribution within the region (Miller et al., 1995), a description of a feeding population in the southern GBR (Limpus, 1992a), and a regional population genetics study (Broderick et al., 1994), were initiated to broaden the data base for conservation management of the species throughout the region.

As a result of the survey work mentioned above, the hawksbill population nesting at Milman Island was identified as the largest in the northern Great Barrier Reef and in January 1991, an annual summer saturation tagging census and associated recording of morphometric and demographic data was initiated (Loop et al., 1995). The present account



Figure 1. Milman Island, northern Great Barrier Reef, Australia. Sections are defined by sector number, vegetation, and beach composition.

describes the reproductive biology (and associated morphometrics of nesting females, their eggs, and hatchlings), nesting patterns, and the nest environment leading to successful incubation and emergence at Milman Island for the first five years of this on-going study.

METHODS

Data presented herein about hawksbill turtles nesting at Milman Island were collected during seven surveys including five in summer (11 January – 27 March 1991, 4–18 February 1992, 15 January – 3 April 1993, 14 January – 22 March 1994, and 25 November 1994 – 14 February 1995) and two in winter (26 June 1993 and 24 June – 7 July 1994). Data from the first survey in 1991 (Loop et al., 1995) and the two limited winter sampling periods (June, July) were included for all parameters to more broadly describe the nesting characteristics of the population. The majority of data presented pertains to the summer nesting season (November to April); seasonal averages were calculated only for summer nesting surveys. Descriptions of Milman Island (Fig. 1) were presented by Loop et al. (1995, 1996) and Dobbs et al. (1997).

Nesting Patterns.—Hawksbill nesting activity patterns (based on the 24-hr time-period from 1200 hrs to 1159 hrs the following day) were characterized during the seven surveys to Milman Island. Monitoring protocol followed Loop et al. (1995). Turtles coming ashore unnoticed were identified to species by their track characteristics (Pritchard et al., 1983). Daytime monitoring documented turtle nesting attempts and turtles still on the beach from the previous night. Tide heights were calculated using Queensland tide tables for Cairneross Island, 8 km south of Milman Island. Individuals were identified by means of titanium tags (Stock Brands Company Pty. Ltd., Perth, Australia) bearing a unique serial number and return address; the tag was attached in the axillary position on the left front flipper (Limpus, 1992b).

Turtles were classified as follows: 1) primary – turtle with no evidence of a tag scar and tagged for the first time; 2) interseason remigrant (ISR) – turtle tagged in a previous nesting season and returning to nest; and 3) interseason recapture retagged (ISR-RTA) – turtle with tag scar (lump of scar tissue) indicating turtle was tagged during a previous season or at another locality; turtle was retagged and included in the total count of tagged turtles each season.

The numbers of hawksbill nesting attempts and clutches laid were counted during nightly patrols. Nesting attempts were classified as: 1) successful – turtle was able to dig an egg chamber and lay an entire clutch of eggs; 2) unsuccessful – turtle was disturbed before laying eggs; or 3) lay/disturbed – turtle was laying eggs but returned to the sea before depositing an entire clutch. Sector number and success of nesting were recorded for most attempts. Number of egg chambers was counted for each nesting attempt by a turtle. Disturbance factors were identified for turtles digging more than one egg chamber during nesting attempts.

Milman Island was partitioned into beach sections based on vegetation, shoreline characteristics, and 50 m sectors (Fig. 1) to quantify nesting attempts and determine nest site fixity (Loop et al., 1995). Sectors were not marked during the two winter surveys (June and July) because of their short duration (1 and 15 days).

Site fixity (distance moved along the beach between successive nesting attempts) for all turtles nesting more than once within a season was calculated by counting the number of sectors separating the two locations and multiplying by the length of each sector (50 m). This value was used to determine whether hawksbills exhibited a preference for nesting in particular areas of Milman Island. Renesting interval was calculated in two ways: 1) the time between a successful nesting and an attempted renesting (*sensu* Limpus, 1985); and 2) the interval between successive successful nestings. Intervals exceeding 25 days were excluded from analysis because it was assumed that the turtle's subsequent nesting attempt was not witnessed.

Incubation Environment. — Incubation environment was described and clutch and hatching success monitored in the sections established around the perimeter of the island (see above) to quantify nesting parameters and evaluate clutch success.

General weather conditions were recorded during the summer surveys. Air temperature was recorded with a mercury minimum/maximum thermometer hung in the shade 346

of a tree. Rainfall (mm) was measured in a plastic rain gauge placed 20 cm above the ground away from overhanging vegetation. Sand temperatures were measured using a mercury glass thermometer placed sideways into the bottom of egg chambers once all the eggs had been removed after oviposition. No sand temperatures were measured in March or April.

Microhabitat was described for most successful and unsuccessful nesting attempts. Egg chamber location was classified by sector number (Loop et al., 1995) and as: 1) below high water if it was below the level of the spring hightide line; 2) in front of and below the slope of the dune; or 3) on top of or behind the dune. Sand above egg chambers was categorized as: 1) unshaded; 2) grass-covered; or 3) shrub/ tree-covered. Egg chamber depth was measured with a flexible fiberglass tape (\pm 0.05 cm) from sand surface to the top egg in the chamber and to the chamber bottom once all eggs had been removed.

Beach height (m) and slope leading from the reef flat to the mean spring high-tide line were characterized between 30 January and 6 February 1993 using a surveyor's theodolite. Beach width was measured using a 50 m flexible measuring tape from the dune/vegetation line to the reef flat. Distance of each clutch from the top of the dune was measured using a 50 m flexible measuring tape. Negative values indicate clutches which were laid below (in front of) the dune.

During the 1993 summer (January–April) survey, sand samples (500 g) were collected from a depth of 45 cm in potential hawksbill nest locations (Loop et al., 1995) to characterize grain size, electrical conductivity ($\sigma \ge 10^4$ dS/ m, EC), pH, and water potential. Grain-size was determined by sorting sand samples through three sieve sizes (2.36 mm, 1.40 mm, 0.85 mm) which yielded four grain-size classes: < 0.85 mm, 0.85–1.39 mm, 1.40–2.36 mm, and > 2.36 mm. Moisture content was determined by weighing each sample when collected on the beach, then drying and reweighing in the laboratory. Weight loss, expressed as a percentage of the original weight, was used as a measure of water content.

Electrical conductivity (EC) and pH were measured by preparing a 1:5 soil/water suspension mixture (Rayment and Higginson, 1992). This was achieved by placing 20 g of oven-dried (35°C) sand into a bottle with 100 ml of deionized water. The mixture was mechanically shaken for 1 h at 25°C then allowed to settle for 20–30 min. Conductivity was measured using a TPS digital conductivity meter LC81. Sand pH was measured using a TPS digital pH meter LC80A (Rayment and Higginson, 1992).

Water potential (J/kg), the energy required to move water from one area to another, was determined using an SC-10A thermocouple psychrometer sample changer attached with an NT-3 nanovoltmeter thermometer (Decagon Devices, Pullman, WA, USA). Sand samples (collected in 1993) were combined to define grain classes based on the following ratio of grain-sizes: *coarsest*: 8.2% > 2.36 mm, 12.5% 1.4– 2.36 mm, 26.9% 0.85–1.39 mm, 52.4% < 0.85 mm; *coarse*: 1.7% > 2.36 mm, 6.8% 1.4–2.36 mm, 45.7% 0.85–1.39 mm, 45.8% < 0.85 mm; *fine*: 1.1% > 2.36 mm, 2.0% 1.4–2.36 mm, 13.1% 0.85–1.39 mm, 83.8% < 0.85 mm; *finest*: 0.04% > 2.36 mm, 0.03% 1.4–2.36 mm, 0.1% 0.85–1.39 mm, 99.8% < 0.85 mm.

Sand (100 g) from the four size-classes listed above was placed into air-tight jars, to which was added 1, 2.5, 5, 7.5, 10, or 20 ml of distilled water, thus simulating a range of moisture contents (1, 2.5, 5, 7.5, 10, and 20%). This sand was then incubated at three temperatures (26, 29, 32°C), representing the range of incubation temperatures occurring around the island. In addition to those unwashed samples, six 100 g sand samples per size-class were washed twice in 500 ml of tap water and a third time in 500 ml of distilled water to remove salts. This sand was then dried. Distilled water (2.5 or 5.0 ml) was added to the samples which were incubated two at each temperature (26, 29, 32°C). All samples (washed and unwashed) were analyzed for water potential three times, at approximately 0.5 hr intervals.

Nesting Females. — Morphological measurements taken on nesting turtles, their eggs, and hatchlings followed the standard measurements for hawksbills recorded within the Queensland Turtle Research program of the Queensland Department of Environment (Limpus, 1980, 1985; Limpus et al., 1983a, 1983b; Miller, 1989; Loop et al., 1995; Loop. 1996).

Curved and straight carapace measurements were taken to allow morphological comparisons with other studies. Flexible fiberglass measuring tapes (\pm 0.1 cm) were used to take curved carapace length (CCL) and width (CCW). plastron length, notch length, and tail length to plastron. vent, and carapace. Negative tail lengths indicate the tail did not extend beyond the edge of the carapace. Straight-line carapace measurements (length [SCL], width [SCW], Carr's length [CSCL, *sensu* Carr and Ogren, 1960]) were taken with wooden calipers, the distance between caliper tips measured with a steel tape measure (\pm 0.1 cm). Barnacles were removed when they interfered with carapace measurements. Head length and width were taken with vernier calipers (\pm 0.1 cm).

Turtles were weighed following oviposition using a Salter dial balance $(\pm 0.5 \text{ kg})$ suspended from a pole. A group of nesting females selected within the first two weeks of each summer survey were weighed each time they nested. Average seasonal weight of nesting females during each survey was calculated using only the first weight recorded for each turtle on each survey.

Injuries to flippers and carapace were documented when present. Scale counts were made on a sample of nesting females and hatchlings during the 1992–93 and 1994–95 summer seasons. Scute patterns were identified using a combination of classifications by Carr (1952) and Pritchard (1979). Growth in CCL was calculated for all interseason remigrants. Nesting mortality rates (probability of dying on the beach) were calculated both as a percentage of the total number of nesting attempts at Milman Island and of the total number of individual turtles encountered.

Eggs. — The number of eggs laid in clutches was counted and 10 eggs per clutch, randomly selected, were

cleaned of sand, measured, weighed, and reburied within 1 hr of oviposition to avoid movement-induced mortality (Limpus et al., 1979). The number of normal-sized eggs laid in a clutch was used as the clutch count. Yolkless eggs (identified as being much smaller than normal-sized eggs [Miller, 1985]) were counted but omitted from the total clutch count. Minimum and maximum egg diameters measured with vernier calipers (\pm 0.1 cm) were averaged to define overall egg diameter (Limpus, 1985). Eggs were placed in a plastic bag and weighed using a Pesola spring balance (\pm 0.5 g).

Nests were marked with surveyor's tape immediately after oviposition. These nests were checked daily for evidence of emergence beginning 45 days after oviposition. Incubation duration (days), from laying to hatchling emergence to the beach surface, was determined and averaged for each summer survey.

The following counts were made when nests were excavated (sensu Limpus, 1985): 1) depredated eggs (e.g., broken by ghost crabs); 2) undeveloped eggs (contained no obvious embryo, i.e., less than stage 11 [Miller, 1985]); 3) unhatched eggs (contained a recognizable embryo, usually between stages 12 and 30 [Miller, 1985]); 4) live hatchlings in chamber (hatchlings alive but not emerged from the nest, stage 31 [Miller, 1985]); 5) dead hatchlings in chamber (hatchling died below beach surface after hatching); and 6) empty egg shells. Clutch success was calculated in two ways. Hatching success was calculated by dividing the number of hatchlings that hatched from their egg shells by the clutch count. This value included emerged hatchlings as well as live and dead hatchlings found hatched from their shells but still in the egg chamber. Emergence success was calculated by dividing the number of hatchlings that successfully emerged from the nest by the clutch count. This value did not include live or dead hatchlings found in the egg chamber.

Hatchlings. — Hatchlings encountered on the beach in the 1990–91, 1992–93, and 1994–95 summer surveys were measured, weighed, and released within 30 min of being found on the beach surface. Straight-line measurements (carapace length and width, plastron length, and head length and width) were taken with vernier calipers (\pm 0.1 cm). Hatchlings were weighed in a plastic bag suspended from a Pesola spring balance (\pm 0.5 g).

Table 1. Number of 24-hr periods (days), primary taggings, interseason remigrants (ISRs), the percentage they represented of the number of individual turtles encountered during the survey, and interseason recaptures (ISR-RTAs), during hawksbill surveys (1991–95) on Milman Island.

Survey Dates	Days	Primary	ISRs	ISRs	ISR- RTAs	No. Turtles
11 Jan - 27 Mar 91	76	365	0	0	0	365
4 Feb - 18 Feb 92	15	106	0	0	0	106
15 Jan - 3 Apr 93	78	312	2	1	0	314
26 Jun 93	< 1	2	0	0	0	3
14 Jan - 22 Mar 94	67	192	31	14	2	225
24 Jun - 7 July 94	14	4	0	0	0	4
25 Nov 94 - 14 Feb 95	82	200	50	20	0	250

Observations of hatchling emergence from egg chambers were made when time allowed, although no attempt was made to quantify this pattern. Incidental observations of hatchling predation on the beach and reef flat were recorded.

Data were analyzed using Zar (1974) and Microsoft Excel (1992). Mean values \pm one standard deviation (s.d.) are presented for various parameters. Statistical significance levels were set at p < 0.05. A time period common to four of the five summer monitoring seasons. 15 January to 14 February, was used in assessing population trends by comparing the number of nesting attempts and clutches laid each season. The number of turtles available was calculated as the total number of turtles encountered each season minus the number of turtles recorded at their last nesting attempt for the season. Hawksbills nest year-round at Milman Island, so values assigned to weights of nesting females and clutch counts may not accurately reflect their stage within the nesting cycle. Some turtles may have already nested previously in the season, and although the weights or clutch counts were considered to be the first of the season, they may not have been. General linear model (GLM) and least squares difference (LSD) analyses of grain size, temperature, and percent moisture content of sand were performed using SAS (SAS Institute Inc., 1988). A multiple linear regression analysis of factors influencing hatching and emergence success rates was performed using SigmaStat (Jandel Scientific Corporation, 1994).

RESULTS

Nesting Patterns. — Between 1991 and 1995, 1183 hawksbills were tagged on Milman Island, with 31% (n =365) of these during the initial summer season (Table 1). Eighty-three ISRs (7.0% of 1183) identified from three summer seasons (1991, 1992, 1993) were encountered nesting at intervals of 2 (n = 5), 3 (n = 38), and 4 (n = 40) years: the average remigration interval was 3.40 ± 0.62 yrs, but because these data cover only 5 seasons (up to a maximum remigration interval of 4 years), this average is preliminary and not necessarily indicative of the population. The proportion of ISRs in relation to the total number of turtles encountered in a nesting season increased from 0 (1991, 1992) to 20% (1995) (Table 1).

A total of 3750 hawksbill nesting attempts were recorded, comprising 3137 (84%) direct observations and 613 determined from track characteristics. Over 94% of 2846 clutches laid during the surveys were observed. Almost all turtles (98%, n = 3676) attempted to nest at night. Turtles attempting to nest at night did so in greater numbers when the night-time high tide occurred before midnight (13.0 ± 7.1 turtles, range = 2–37, n = 231 nights) than after midnight (8.2 ± 5.3 turtles, range = 0–27, n = 89 nights) (Fig. 2a). Peak nesting activity (Fig. 2b) occurred during night-time high tides between 2000 and 2200 hrs (11.1 ± 6.3 turtles, range = 2–27, n = 82 nights). The two summer nights with no hawksbill nesting attempts occurred when the night-time high tide was between midnight and 0200 hrs. Height of the



Figure 2. Number of hawksbill nesting attempts (*a*) and clutches laid (*b*) per 24-hr period, and tide height (*c*) as a function of the time of the night-time high tide at Milman Island during the 1991–95 nesting surveys.

night-time high tide was significantly higher before midnight (2.73 ± 0.5 m, range = 1.07–3.78) than after midnight (2.52 ± 0.43 m, range = 1.24–3.48) (t-test: t_{320} = 12.47, *p* < 0.0005) (Fig. 2c). Turtle nesting activity was significantly correlated with tide height (t-test: t_{320} = 32.5, *p* < 0.0005).

The number of turtles available for study at Milman Island peaked in January and early February (Fig. 3). At no time was the entire nesting population present at the island in any survey period. The decrease in the number of turtles counted during the last two weeks of each study is a result of the research team leaving the island; turtles attempting to nest in the last fortnight were not available to the research team after that nesting. The actual number of turtles remaining at Milman Island after the research team left was unknown.

Nesting activity per day (24-hr period) was greatest in summer months, averaging from 7 to 15 turtles/day among the summer surveys (range = 0–37). The winter 1994 survey had the lowest average nesting activity (0.6 ± 0.8 turtles/day, range = 0–3) of all surveys at the island. Only twice (0.6% of 333 days) during the five summer seasons did no hawksbills attempt to nest. Conversely, half of the days in winter surveys (June and July) recorded no hawksbill nesting attempts.

During summer surveys, the number of nesting attempts and clutches laid per day peaked in January and gradually declined as the summer progressed (Fig. 4). The numbers of turtles attempting to nest and clutches laid in the 15 January to 14 February interval were greatest in 1991 (Fig. 5). Data for the 1992 season were not available for the entire interval because of that survey's short duration (4–18 February).

Seventy-six percent of the 3750 nesting attempts were successful while only 0.4% resulted in partial clutches from lay/disturbed nesting attempts. Turtles failing to nest returned to attempt another nesting either the same night or within the following 6 nights (mean = 1.4 ± 0.07 , n = 264).

The average number of egg chambers dug by a turtle on a successful nesting attempt was lower $(1.4 \pm 0.96$ chambers, range = 1–11, n = 1912) than when there was no oviposition $(1.6 \pm 2.1$ chambers, range = 0–12, n = 244). Top nest depth of successful egg chambers ranged from 0– 53 cm $(17.8 \pm 8.76, n$ = 1245 nests) and bottom nest depth from 19–91 cm $(39.5 \pm 7.21, n$ = 1249 nests). Nesting



Figure 3. Number of hawksbills available for study at Milman Island during the summer survey periods (1991–95). The 1991–92 survey was not included because of its short duration (15 days). \blacktriangle = 1990–91 survey, \blacksquare = 1992–93 survey, \blacklozenge = 1993–94 survey, \blacklozenge = 1994–95 survey. Arrows represent the start of the last 2-week interval for each survey, during which turtles would not have been encountered again before the end of the survey.



Figure 4. Average number (\pm one standard deviation) of hawksbill nesting attempts (shaded bars) and clutches laid (open bars) per 24-hr period each summer month on Milman Island, 1991–95.



Figure 5. Number of hawksbill nesting attempts (shaded bars) and clutches laid (open bars) from 15 January – 14 February each summer nesting season on Milman Island, 1991–95. * Data from the 1991–92 season is only for 4–14 February.

failures frequently coincided with roots in the egg chamber or dry sand collapsing egg chamber walls, human interference (tagging, reading tag number, checking on nesting activity), injured flipper(s) resulting in non-uniform egg chamber walls, nesting activity of a nearby turtle, lightning, shadows on the beach (humans, tree branches swaying in the wind), daylight (morning sunrise, midday sun), beachrock preventing access to suitable nesting sites, and beach obstructions (tree stumps, roots, branches, or steep sand dunes).

Hawksbills laid between 1 and 6 clutches (mean = 2.5) during the summer. However, because nesting was in progress at the start of each survey, the total number of clutches laid per

Table 2. Distance (m) along the beach between nesting attempts by hawksbills laying 2 or more clutches at Milman Island. Distance travelled by a turtle attempting to nest in the same 50 m sector as the previous nesting attempt was counted as 0 m because further delineation of the sector was not available. The total circumference of Milman Island is 2400 m, the greatest possible distance between nesting attempts is 1150 m.

		D	m)	
Nesting Attempt Result	П	Mean	s.d.	Range
Unsuccessful after successful	180	403.9	325.2	0-1150
Successful after successful	1547	435.9	344.1	0-1150
Successful after unsuccessful	230	454.2	333.6	0-1150
Unsuccessful after unsuccessful	46	497.8	340.1	50-1150
Successful after disturbed laying	6	375.0	358.8	0-950
Overall	2009	436.4	341.3	0-1150

turtle within a 12-month period could not be determined. The average interval between a successful nesting and the subsequent attempt (regardless of success) was 14.5 ± 1.7 days (range = 10-21, n = 1363) (Fig. 6). The average time between successful nestings was 14.7 ± 2.0 days (range = 10-25, n = 1329).

The distance along the beach between successive nesting attempts averaged 436.4 \pm 343.3 m (maximum possible distance = 1150 m) regardless of the success of the previous attempt (F_{4,204} = 0.99, *p* > 0.25) (Table 2). Over 50% of all renesting attempts were within 350 m of the previous attempt (Fig. 7).

Incubation Environment. — All data represent average values by section around Milman Island unless otherwise stated. Air temperature ranged from 24 to 49°C. Average air temperatures were highest in December (32.6°C, range = 25.9–49.2) and coolest in March (30.1°C, range = 25.8–34.7). Differences in daily maximum and minimum air temperatures fluctuated between 1 and 23°C. Rainfall ranged from 0–83 mm/day and precipitation occurred on 45–75% of the days of each summer survey. Monthly average rainfall increased from 4 mm/month in November to 169 mm/month in January, before decreasing to 9 mm/month at the end of the summer season in April. Sand temperatures ranged from 25–31.5°C and were highest in January (29.0°C), then decreased when the summer monsoon period began in late



Figure 6. Renesting intervals recorded for hawksbills nesting on Milman Island during summer nesting surveys (1991-95).



Figure 7. Distances (m) along the beach between hawksbill nesting attempts on Milman Island (maximum possible distance = 1150 m).

January to early February. The average nest depth at which sand temperatures were measured was 35.5 ± 6.65 cm (range = 19–65; *n* = 308 egg chambers).

Hawksbills attempted to nest in every sector on Milman Island and were successful in all but sector 40 in the W section (Fig. 8). Overall, 20% of nesting attempts (n = 751) and 19% of clutches (n = 531) occurred in the NW section.



Figure 8. Number of hawksbill nesting attempts (shaded bars) and clutches laid (open bars) per sector on Milman Island during 1991–95 summer seasons.

More nesting attempts occurred in this NW section than in the other sections in 1990–91 (31%), 1991–92 (24%) and 1994–95 (21%) but shifted to the SW section in 1992–93 (18%) and 1993–94 (18%). The fewest clutches (6%) were laid along the W section with only 56% of the 306 attempts resulting in eggs being laid. The W section consisted of a 500 m length of beachrock which often prevented access for nesting turtles to the forest beyond. Nesting attempts were most successful (> 80% of all attempts were successful) at the SW, E1, and E2 sections.

Most clutches (n = 2657, 94%) were laid on or behind the top of the dune (Table 3). Turtles nested an average of 8.04 ± 5.35 m (range = -2.0-23.98, n = 92) from the top of the dune, although this varied with habitat type. Nests in grass (11.09 ± 5.88 m, range = 5.72-18.27, n = 4) or under shrubs or trees (8.79 ± 5.17 m, range = 0.50-23.98, n = 72) were laid significantly farther from the edge of the dune ($F_{3.88}$ = 4.73, p < 0.005) than were nests laid in unshaded sand (5.60 ± 4.22 m, range = -2.00-14.00, n = 12) or below the slope of the dune (0.76 ± 1.58 m, range = -0.70-2.95, n = 4).

Beach width (distance from reef flat to mean spring high tide line) ranged from 16.9 to 100.4 m (Fig. 9a), although averaged between 20.6 and 44.5 m by section. The approach to nesting sites included 750 m along the beach where sand extended from the vegetation line to the reef flat, 1350 m

 Table 3. Distribution of hawksbill nests by vegetation cover and dune location on Milman Island from 1991 to 1995.

Vegetation Cover	On or Behind Slope	On Dune Slope	Below High Water Mark	Total	Percent
Tree/Shrub	1973	18	0	1991	70.7
Grass	315	2	0	317	11.3
Unshaded	369	51	88	508	18.0
Total	2657	71	88	2816	
Percent	94.4	2.5	3.1		



Figure 9. Incubation environment parameters by section of Milman Island: (*a*) beach width (m); (*b*) beach height (m); (*c*) sand grainsize (mm); (*d*) soluble salt and moisture content (%); (*e*) pH: and (*f*) emergence and hatching success (%).

where a combination of sand and beachrock had to be crossed, and 300 m where beachrock covered the areas from the reef flat to the vegetation line.

Beach height above the mean spring high tide line ranged from 0 to 1.69 m. The SW section was the lowest (mean = 0.17 m) (Fig. 9b). In contrast, the W section consisted of a beachrock approach to the vegetation line and a steep incline turtles had to traverse to reach potential nesting sites, with an average height of 1.0 m above the high tide line.

Sand composition at nest depth was uniform in most sections (Fig. 9c); most sand was comprised of > 80% of the smallest size-class, < 0.85 mm. Coarsest sand was in the NW section (67% of sample < 0.85 mm), finest sand at the S section (98% < 0.85 mm). By habitat, the finest sand at nest depth was from grass-covered habitats (91% of sample < 0.85 mm), while that from unshaded and shrub or tree-covered areas had similar coarser compositions (82 and 83% < 0.85 mm, respectively).

Electrical conductivity (EC), expressed as percent total soluble salts when multiplied by 0.34 (Rayment and Higginson 1992), differed significantly among sections ($F_{7.74} = 2.93, p < 0.01$). Highest EC was along the W section where the highest percentage of total soluble salts occurred (28.3%). The SE section sand had the lowest EC and corresponding lowest soluble salt content (17.2%) (Fig. 9d). Sand from shrub or tree-covered habitats had a higher percent soluble salt content (24.1%) than unshaded (20.3%) or grass-covered (18.6%) habitats. Positive but weak correlations were found among sections between EC and the three largest sand grain size-classes (> 2.36 mm, r² = 0.045; 1.4–2.36 mm, r² = 0.18; and 0.85–1.39 mm, r² = 0.27). EC was negatively correlated with the finest grain size-class (< 0.85 mm, r² = -0.24) when compared by section.

Sand pH ranged from 8.29–9.68 across all habitat types at 45 cm nest depth. The NW section was significantly more alkaline than other sections (Fig. 9e). Unshaded sand was most basic (9.1); grass- (8.9) and shrub- or tree-covered (8.8) sand were slightly more acidic. Sand pH was positively correlated with the three largest grain size-classes (> 2.36 mm, $r^2 = 0.72$; 1.4–2.36 mm, $r^2 = 0.74$; 0.85–1.39 mm, $r^2 =$ 0.74), but negatively correlated with the < 0.85 mm sizeclass ($r^2 = -0.75$). EC correlated weakly with pH ($r^2 = 0.13$).

Moisture content averaged $3.45 \pm 1.55\%$ (range = 0.21– 7.60, n = 57) and did not differ significantly among habitats or sections (Fig. 9d). Weak correlations existed between moisture content and pH ($r^2 = -0.04$), and the percentage of sand sample at each grain-size class: < 0.85 mm ($r^2 = -0.18$), 0.85–1.39 mm ($r^2 = 0.26$), 1.4–2.36 mm ($r^2 = -0.002$), and > 2.36 mm ($r^2 = -0.12$). Moisture content and EC were strongly correlated ($r^2 = 0.80$).

The finest sand class (99% < 0.85 mm) exhibited consistently higher water potential (J/kg) for all temperatures and moisture contents (Fig. 10), indicating more energy was needed to extract water from the sand. Water potential (J/kg) was significantly lower in sand washed to remove salts than in unwashed samples under every experimental condition ($F_{1.46} = 8.89$, p < 0.005). Water potential decreased with



Figure 10. Water potential (J/kg) recorded for four sand grain-size classes incubated at 29°C: \diamond 99% < 0.85 mm (finest) • 86% < 0.85 mm (finest) • 86% < 0.85 mm (finest) • 86% < 0.85 mm (coarse), and \blacksquare 52% < 0.85 mm (coarsest).

increasing moisture content, the greatest decline occurred when moisture content increased from 1 to 2.5%. Water potential was highest at the 1% moisture content and lowest at 20% ($F_{5.66}$ = 26.51, *p* < 0.0005).

Significant interactions existed between moisture content and grain size ($F_{10} = 2.91, p < 0.05$) and moisture content and temperature ($F_{15} = 13.70$, p < 0.0001); but no significant interaction occurred between temperature and grain size (F₆ = 0.74, p > 0.5) when a GLM was executed on moisture content, temperature, and grain size-class. An LSD performed on the same parameters revealed significant differences (LSD = 46.101, df = 30) between 1% and 2.5% moisture contents, in that they exhibited the highest water potentials of those measured (means of -557.19 and -144.95 J/kg, respectively), and were significantly different from each other and all other moisture levels. The 7.5% and 10.0% moisture contents (-45.51 and -33.87 J/kg, respectively) did not differ from either 5.0% (-69.15 J/kg) or 20.0% levels (-19.74 J/kg) although the 5.0% and 20% moisture contents were significantly different from each other. Sand incubated at 26°C had significantly higher water potential (-173.75 J/kg) than that at 29°C (-133.23 J/kg) and 32°C (-128.23 J/kg). Water potential from sand incubated at 29°C and 32°C did not differ significantly. Lowest and highest water potential were detected in the 52% (-64.36 J/kg) and 99% (-269.63 J/kg) grain-size classes, respectively. These size classes were significantly different from all others.

Nesting Turtles. — CCL and CCW of nesting turtles (n = 1236) ranged from 63.5–91.9 cm and 53.4–82.5 cm, respectively (Table 4, Fig. 11). Most (80.6%) CCL measurements were between 75.0 and 85.0 cm, while most (79.6%) CCW measurements were between 65.0 and 75.0 cm (Fig. 11).

Tail length from tip to carapace was a highly variable characteristic (range = -10.2-7.5 cm, Table 4), although

most (85.5%) of the adult females measured had tails that extended beyond the edge of the post-central scales.

Post-ovipositional weight of nesting females ranged from 32.0–72.0 kg (mean = 50.4 kg, Table 4, Fig. 12). Turtles laying a minimum of 3, 4, or 5 clutches within a survey showed no significant within-season weight loss

Table 4.	Morphometrics	of nesting	hawksbills,	their egg	s, and
hatchling	s at Milman Islar	nd from 199	1-95. * Incl	udes inters	eason
remigran	ts, s.d. = one star	ndard devia	tion.		

	n	Mean	± s.d.	Range
Adult Females	8			
Curved carapace length (cm)	1236*	81.6	3.67	63.5-91.9
Curved carapace width (cm)	1123*	70.7	3.88	53.4-82.5
Straight carapace length (cm)	280	75.0	3.48	60.1-83.5
Straight carapace width (cm)	285	56.7	3.49	49.4-70.5
Carr's straight carapace length (cm) 275	75.5	3.86	61.5-92.2
Head length (cm)	118	19.1	1.15	16.3-24.3
Head width (cm)	124	10.6	0.55	9.4-12.4
Plastron length (cm)	421	60.8	2.94	50.3-69.6
Tail length to plastron (cm)	471	16.3	1.80	12.5-21.5
Tail length to carapace (cm)	740*	2.3	2.23	-10.2-7.5
Tail length to vent (cm)	471	4.8	0.77	2.3-9.5
Length from plastron to vent (cr	n) 471	11.6	1.66	6.4-16.6
Notch length (cm)	1249*	0.8	1.27	0.0-9.0
Weight after laying (kg)	582*	50.4	6.45	32.0-72.0
Eggs $(n = \text{No. Clutches})$				
Clutch size (no. normal eggs)	1296	122	23.8	18-215
Egg diameter (cm)	346	3.51	0.16	2.83-3.81
Egg weight (g)	280	26.80	2.15	20.4-31.8
Yolkless eggs/clutch	1296	0.11	0.43	0-5
Multiyolked eggs/clutch	1296	0.12	0.34	0-5
Hatchlings (n = No. Clutches	[No. Hate	hlings])		
Straight carapace length (cm)	34 [339]	3.98	0.16	3.20-4.36
Straight carapace width (cm)	34 [339]	2.96	0.13	2.07-3.31
Weight (g)	34 [339]	13.80	1.50	8.0-17.5
Plastron length (cm)	34 [339]	3.23	0.17	2.68-3.88
Head length (cm)	7 [202]	1.92	0.07	1.77-2.15
Head width (cm)	33 [329]	1.37	0.07	1.0-1.98
Tail length to carapace (cm)	5 [103]	0.42	0.06	0.28-0.60



Figure 11. Curved carapace length (black bars) and width (open bars) frequencies for nesting hawksbills on Milman Island. CCL, n = 1236; CCW, n = 1123.

 $(F_{2.108} = 0.53, p > 0.25, F_{3.64} = 0.42, p > 0.25, F_{4.20} = 0.44, p > 0.25$, respectively).

Growth rates of ISRs were calculated by remigration interval (number of years between nestings). Two-year interval ISRs grew -0.55 ± 1.32 cm/yr (range = -2.8-0.8, n=6). Turtles renesting after three years grew an average of 0.17 ± 1.01 cm/yr (range = -2.4-2.1, n = 36), while those renesting after four years grew an average of 0.18 ± 0.74 cm/yr (range = -1.8-1.5, n = 39). Overall average growth rate, regardless of remigration interval, was 0.14 cm/yr.

Irregularities in scute patterns were present on 10% (6 of 59) of the nesting females examined. These aberrations included a reduced number of marginal (n = 3) and prefrontal scutes (n = 2) and the addition of two smaller prefrontals in the middle of the two pairs normally found in hawksbills (n = 1).

About 2% (14 of 670) of summer nesting females exhibited mating damage (*sensu* Limpus [1993], wounds on the dorsal and lateral surfaces of the neck and shoulder). Summer seasonal proportions for this parameter ranged from 0% in 1991–92 (0 of 106 turtles) and 1992–93 (0 of 314 turtles) to 6% (14 of 250 turtles) in 1994–95. None of the 6 turtles nesting in winter were recorded with mating damage. Mating at the water's surface was observed twice on an opportunistic basis, once in early February 1991 (Loop et al., 1995) and again in early February 1995.

Nearly 30% of all nesting females (n = 1183) exhibited some form of visible injury. Carapace damage, consisting of minor cuts (where burrowing barnacles, *Tubicinella cheloniae*, were found) to large sections of the rear of the carapace missing, was found on 261 (22%) nesting turtles. Injuries to left (n = 91, 8%) and right (n = 88, 7%) rear







Figure 13. Sequential measurements of all eggs laid by a 76.7 cm CCL hawksbill at Milman Island on 19 January 1995: (*a*) diameter (cm) and (*b*) weight (g). Diameter is average of minimum and maximum diameter.

flippers and left (n = 23, 2%) and right (n = 21, 2%) front flippers ranged from ragged edges to complete flipper loss.

Recent shark bites were noted only twice and only during the 1992-93 summer survey. One turtle exhibited no evidence of physical injury on her first two nesting attempts (25 January and 8 February 1993), however, she received a significant wound to her left front flipper prior to her subsequent nesting attempt on 26 February 1993. The flipper was used in a normal manner during the nesting process, but was bleeding during this nesting attempt. Another turtle, missing one half of its left front flipper, had exposed bone and swollen, necrotic tissue around the wound, indicating a recent attack. Wounds consistent with those caused by cookie-cutter sharks (Isistius brasiliensis) were observed infrequently on nesting turtles (0.6%). These circular wounds were noticed on the ventral side of the neck and front flippers and ranged in diameter from 2 to 4 cm. One turtle's esophagus was visible through the neck injury and although necrotic tissue was present, swelling was slight. Most wounds were healed, but leeches (Ozobranchus sp.) were attached to some edges.

Only four nesting females (0.10% of 3750 nesting attempts, 0.34% of 1183 turtles encountered) would have died as a result of natural nesting hazards (disorientation behind a large grass dune, n = 2; entanglement in tree roots, n = 2). These turtles were rescued by the research team during daylight patrols.

Eggs. — Almost half (45%) of the 2846 clutches laid during the seven surveys were counted (n = 1296). Clutches contained from 18 to 215 eggs per nest. The average count was 122 ± 24 eggs (Table 4) and this did not differ significantly among surveys ($F_{4,1291} = 0.798$, p > 0.25).

Table 5. Fate of 26,940 hawksbill eggs from 226 clutches excavatedon Milman Island from 1991 to 1995.

Fate of Eggs	No. No. eggs clutches		% Total clutches	% Total eggs	
Empty Shells	22,377	225	99	83.1	
Live Hatchlings	753	78	35	2.8	
Dead Hatchlings	138	59	26	0.5	
Unhatched	2297	176	78	8.5	
Undeveloped	1260	182	81	4.7	
Depredated	892	105	46	3.3	

X	У	b	r^2	F-statistic	p	n
CCL	SCL	0,920	0.75	832.99	< 0.0001	277
CCL	CSCL	0.926	0.66	519.92	< 0.0001	273
CCL	CCW	0.866	0.59	1626.80	< 0.0001	1121
CCL	Weight	0.619	0.44	454.78	< 0.0001	571
log ₁₀ CCL	log _m Weight	0.889	0.41	398.11	< 0.0001	571
SČL	Weight	0.676	0.42	159.93	< 0.0001	220
log _{in} SCL	log ₁₀ Weight	0.908	0.40	145.17	< 0.0001	220
CČW	SCW	0.804	0.35	149.41	< 0.0001	279
CCL	SCW	0.695	0.29	114.06	< 0.0001	278
SCL	CSCL	1.007	0.73	748.79	< 0.0001	275
CCL	Head length	0.235	0.14	18.87	< 0.0001	116
CCL	Head width	0.130	0.23	36.60	< 0.0001	122
CCL	Plastron length	0.745	0.61	635.84	< 0.0001	412
SCL	Plastron length	0.809	0.48	186.43	< 0.0001	200
CCL	Notch length	0.009	0.00	1.92	< 0.2500	1236
SCL	Notch length	0.011	0.02	4.93	< 0.0250	280
CCL	Clutch size	1.505	0.13	192.58	< 0.0001	1298
Weight	Clutch size	1.630	0.20	207.90	< 0.0001	843
Hatchling SCL	Hatchling Weight	3.474	0.45	26.60	< 0.0001	34
log ₁₀ Weight	Egg weight	15.570	0.04	6.31	< 0.0100	151
Egg diameter	Egg weight	7.494	0.13	42.90	< 0.0001	278

Table 6. Linear regression analyses of hawksbill morphometrics from Milman Island, using adult females, eggs, and hatchlings.

The number of eggs per clutch did not differ significantly within a nesting survey for turtles laying a recorded minimum of 3 clutches ($F_{2,162} = 1.20, p > 0.25$), 4 clutches ($F_{3,132} = 0.18, p > 0.25$), or 5 clutches ($F_{4,35} = 0.87, p > 0.25$). Egg diameter ranged from 2.83 to 3.81 cm, egg weight from 20.4 to 31.8 g (Table 4).

Every egg in one clutch was measured and weighed in the order in which it was laid (Fig. 13). Average egg diameter was 3.54 ± 0.059 cm, average egg weight was 27.99 ± 0.892 g. Groups of 10 eggs (grouped in sequential order from first to last laid) were significantly different in egg diameter (F_{12,116} = 28.138, *p* < .0005) and weight (F_{12,116} = 15.641, *p* < 0.0005). Eggs laid first tended to be larger and heavier than those laid last. However, the mean size and weight of five randomly selected groups of 10 eggs were not significantly different from those of the entire clutch (*p* > 0.5).

Small, yolkless eggs (up to 5 per clutch) occurred in 27 of 1296 clutches (2%) (Table 4). Diameters of these eggs ranged from 0.54 to 2.30 cm (n = 27) and weight varied between 1.0 and 15.0 g (n = 17). Less than 1% (n = 11) of 1296 clutches contained multi-yolked eggs (up to 5 per clutch, Table 4). The number of yolkless ($F_{4,1291} = 1.51$, p > 0.10) and multi-yolked ($F_{4,1291} = 0.71$, p > 0.25) eggs per clutch did not differ significantly among summer surveys.

Clutches remained relatively undisturbed throughout their incubation period. Eggs exposed as the result of dune erosion were observed being preyed upon by ruddy turnstones (*Arenaria interpres*). Nesting hawksbills disturbed between 0 and 4.8% of the hawksbill clutches laid during a survey. Number of eggs recorded as displaced ranged from 1 to 94 per clutch, although field notes reported entire clutches (no counts recorded) being disturbed.

Duration of incubation to emergence ranged from 47 to 71 days (58.5 \pm 5.46 days, n = 113 nests). The incubation period recorded during summer surveys fluctuated from year to year between 56.3 \pm 4.82 days (1994–95) and 63.8 \pm

4.65 days (1993–94); these differed significantly ($F_{3,109} = 18.44$, p < 0.0005). Nests laid below the dune slope and in unshaded sand yielded the shortest incubation duration (52.9 ± 2.1 days), while those on top of dunes under trees exhibited the longest (60.1 ± 5.3 days). Incubation times among habitats differed significantly ($F_{3,108} = 9.80$, p < 0.0005) despite the fact that incubation durations in unshaded sand (55.1 ± 4.1 days) and grass-covered (56.0 ± 2.4 days) nest locations were statistically similar ($t_{21} = 0.15$, p > 0.25).

Hatching success averaged $82.4 \pm 20.3\%$ (range = 0–100, n = 226 clutches) and emergence success averaged 79.2 $\pm 24.2\%$ (range = 0–100, n = 226 clutches). Only 2 clutches (0.9%) had zero hatching success; one clutch produced only a single live hatchling which failed to emerge from the egg chamber.

Hatching and emergence success rates did not vary significantly with habitat type ($F_{3,204}$ = 0.763, p > 0.25, $F_{3,204}$ = 2.263, p > 0.05, respectively); however, there was a significant difference in both hatching ($F_{7,278}$ = 3.26, p < 0.0025) and emergence ($F_{7,278}$ = 4.51, p < 0.0005) success by beach section (Fig. 9f), with success being lower in the S and SE sections.

Using a multiple linear regression analysis, hatching and emergence success rates were analyzed using two models; biotic factors (CCL, clutch count, nest bottom depth) and abiotic factors (beach width, electrical conductivity, pH, sand grain-size classes [coarsest, coarse, fine, finest], moisture content, and beach height above high tide line). Neither model was able to predict hatching (biotic: $F_{3,125} = 0.457$, p> 0.5; abiotic ($F_{8,107} = 1.53$, p > 0.1) or emergence (biotic: $F_{3,125} = 0.685$, p > 0.5; abiotic: $F_{8,107} = 1.51$, p > 0.1) success in a significant manner.

Hatchlings.—Hatchling straight carapace length (SCL) ranged from 3.20 to 3.46 cm and weight from 8.0 to 17.5 g (Table 4). Of 180 hatchlings examined for scute irregularities from 12 clutches, 41 individuals (23%) had an aggregate total of 66 carapace abnormalities (n = 6 clutches) and another had an extra left inframarginal on the plastron (n =1 clutch). Carapace aberrations included extra marginal (n =14), costal (n = 18), and vertebral (n = 32) scutes, and costals overlapping into the vertebrals (n = 2). Two albino hatchlings remaining in their egg chambers had eye, jaw, and flipper deformities.

Hatchlings emerged by both day and night, but no attempt was made to quantify this aspect of the emergence process. Most hatchlings from a clutch emerged as a group; however, small numbers of hatchlings emerged from unshaded- or grass-covered clutches over a period of a few days instead of *en masse* during the 1994–95 survey. Some hatchlings (up to 100 from a single clutch) emerging during daylight hours became dehydrated on their way to the sea and died. This was observed twice during the seven surveys.

There were 753 hatchlings found alive in the egg chamber and 138 dead hatchlings in 226 excavated clutches (Table 5). This represented 2.8 and 0.5%, respectively, of the total number of eggs laid (26,940) in those nests. Live hatchlings remaining in egg chambers were more prevalent in 1995 (62% of excavated clutches) than in previous seasons, while depredated clutches were more prevalent in 1993 (71%) and 1994 (77%).

Birds were the major predator of hatchlings on Milman Island. At night hatchlings were eaten by rufous night herons (Nycticorax caledonicus). Daylight predation by beach thicknees (Esacus magnirostris), silver gulls (Larus novaehollandiae), crested terns (Sterna bergii) and lesser crested terns (Sterna bengalensis) was also noticed. Ghost crabs (Ocypode sp.) preyed on hatchlings crossing the beach at night and would occasionally be found in egg chambers after a clutch had emerged. There are no mammals on Milman Island, hence no mammalian predation occurred. Black-tipped (Carcharhinus melanopterus) and whitetipped reef sharks (Triaenodon obesus) ate hatchlings swimming across the reef flat. An entire clutch of hatchlings was eaten by a mixed school of trevally (Carangidae) and black-tipped reef sharks. Gulls and terns also took hatchlings from the sea.

A few hatchlings became disoriented while making their way to the sea. Some became confused when leaving nests constructed behind the dune or behind thick vegetation blocking a view of the sea. Moonlight, sunset, and sunrise caused some hatchlings to veer in the direction of light, increasing their time on the beach.

Statistical Regressions. — Numerous significant linear regressions were found among measurements taken on nesting females, their eggs, and hatchlings (Table 6). Nesting female SCL and CCL were significantly related (r^2 =0.75) as were SCL and Carr's SCL (r^2 =0.73). CCL usually had higher correlation coefficients than SCL when compared with similar measurements. Carapace notch length of nesting females was not significantly correlated with CCL (r^2 =0.001) but was correlated weakly with SCL (r^2 =0.001) and

weight ($F_{1.98} = 68.86$, p < 0.0001) were not significantly correlated with nesting female weight, nor was there a significant correlation between hatchling SCL ($F_{1.114} = 37.26$, p < 0.0001) and weight ($F_{1.120} = 7.68$, p < 0.0001) with nesting female SCL.

DISCUSSION

Hawksbill turtles, like other sea turtles, exhibit iteroparous reproduction, a patterned set of nesting behaviors, fidelity to a particular nesting site, and lay multiple clutches, each containing a large number of eggs, per season (Miller, 1997). In contrast to some other species, hawksbills tend to nest in widespread, low density throughout the tropics (Witzell, 1983; Groombridge and Luxmoore, 1989) with few dense nesting colonies. In eastern Australia, hawksbills generally nest in low density (0-5 turtles per island per day, [Miller et al., 1995]); however, Milman Island, northern Great Barrier Reef, hosts high density nesting (> 10 turtles per day). Nesting data presented herein expand those previously available for hawksbills at Milman Island (Loop et al., 1995) and in the southern Pacific Ocean region (Miller, 1994) and support many generalities (Witzell, 1983) concerning the biology of this species (e.g., peak nesting occurring at high tides, at night, and during the summer monsoon season).

Nesting Patterns. — The remigration intervals observed (2–4 yrs) were within previously reported ranges for the Caribbean (1–6 years, Carr and Stancyk, 1975; Pritchard and Trebbau, 1984; Hillis, 1994) and the Indian Ocean (2–3 years, Ross, 1981; Brooke and Garnett, 1983). Geographic differences in remigration intervals could result from the short duration of the present study (5 summer seasons) or might signify a disparity in the nutritional quality or availability of food in each region, possibly as a result of stochastic events such as El Niño/Southern Oscillation (ENSO).

The lack of ISRs in 1991–92 was expected because the previously reported average remigration interval for hawksbills was 2 or more years (Witzell, 1983). ISRs did not exhibit a regular pattern of remigration — 6% returned after 2 years, 46% after 3 years, and 48% after 4 years. One exception was a turtle recorded renesting during three seasons, each at 2-year intervals. Continued monitoring of hawksbill nesting at Milman Island will further describe the typical remigration pattern exhibited by ISRs.

More turtles attempted to nest when rising tides occurred before midnight. Hawksbills nesting in the Solomon Islands (McKeown, 1977), on Cousin Island, Seychelles (Garnett, 1978), and Masirah Island, Oman (Ross, 1981) follow a similar pattern. Reef flats and shallow lagoons surrounding portions of Milman, Cousin, and Masirah islands must be submerged by high tides to allow turtles access to potential nesting sites. Mid-evening peak-nesting times also occurred at Jumby Bay, Antigua, even though turtles have unrestricted access to potential nest sites 24 hrs a day (Hoyle and Richardson, 1993). The reef flat around Milman Island drains during low tides associated with the full- and newmoon phases (Loop et al., 1995), making certain regions around the island more inaccessible to nesting turtles. During nights when high tide occurred between 0100 and 0500 hrs, sectors in the SE section of the island were not accessible to turtles attempting to nest, causing them to come ashore in the NW, W, SW, E1, and E2 sections.

The number of hawksbills attempting to nest peaked in late January and early February, coinciding with the beginning of the Australian rainy season (Bureau of Meteorology, 1988). Peak nesting season in the tropics often coincides with the onset of summer monsoon rains (Witzell, 1983, and included references). Nesting activity at other times of the year is greatly reduced (Limpus, 1980, Miller, 1994).

Initiation of nesting is staggered throughout the year; a proportion of hawksbills begin nesting only after the summer peak nesting period. This makes assessment of the true size of the nesting population difficult because some turtles are beginning their own nesting seasons at this time of the year. Tagging every turtle emerging to nest on Milman Island would require continuous monitoring of the island over the entire 3- to 4-year remigration interval. However, the non-peak nesting period could be quantified if accurate track counts were conducted during all months. Data collected during the peak nesting period needs to be compared with that collected during non-peak nesting months to determine if there are differences in the proportion of ISRs encountered and their remigration interval.

The apparent decline over the survey years in the number of nesting attempts and clutches laid per season at Milman Island within the 15 January – 14 February interval may be a reflection of natural fluctuation in population abundance or environmental influences. The number of green turtles nesting annually on the Great Barrier Reef is influenced by the ENSO event (Limpus and Nicholls, 1988). Green turtles are primarily herbivores; therefore, their food supply is directly affected by the ENSO (Limpus and Nicholls, 1988). Adult hawksbills consume primarily sponges in the Caribbean (Meylan, 1988); therefore, their food supply may be indirectly affected by ENSOtype environmental events.

Most hawksbills at Milman Island nest at night, as do populations in the Red Sea (Hirth and Abdel Latif, 1980), Torres Strait (Bustard, 1979), Antigua (Hoyle and Richardson, 1993), Costa Rica (Carr et al., 1966), the Solomon Islands (McKeown, 1977), Samoa (Witzell and Banner, 1980), and Oman (Ross, 1981). Daytime nesting attempts were more common in the Seychelles (Diamond, 1976) where most nesting occurred between 1500 and 1800 hrs.

Most (76%) hawksbills attempting to nest at Milman Island were successful in digging an egg chamber and laying eggs. This was higher than that of hawksbills nesting at Buck Island National Monument (65%, Hillis, 1994), where vegetation prevented turtles access to much of the island, and at Antigua (63%, Hoyle and Richardson, 1993). Beachrock cliffs along the W section of Milman Island prevented turtles from reaching potential nest locations and lowered the success rates of nesting attempts in this area, though few nesting attempts (8% of 3690) occurred there.

Nesting activity may have been influenced by location of the research camp (Loop, 1996). The majority of nesting activity shifted from the NW section in 1990–91 and 1991– 92 to the SW section in 1992–93 and 1993–94, and back to the NW section in 1994–95. This shift may have been in response to moving the research camp from behind southwestern sectors 3 and 4 (1990–91) to behind northwestern sectors 34 and 35 (1991–92 to 1994–95). A large accreted sand spit in the NW section during the 1994– 95 survey (Loop, 1996) may have shielded the camp from turtles attempting to nest, resulting in greater nesting activity in that section.

The recorded average number of clutches laid per hawksbill per season at Milman Island (2.5), where censusing was incomplete because of year-round nesting occurring in the region, was lower than that noted for other studies: 3.94 in Antigua (Hoyle and Richardson, 1993), 3.0 in Buck Island National Monument (Hillis, 1994), and 3.0 and 3.1 in Seychelles (Garnett, 1978; Wood, 1986). Most turtles observed laying a single clutch per survey at Milman Island were those encountered either at the beginning or end of a survey. The majority of the nesting attempts of such turtles were probably unobserved because they occurred before or after the monitored period. One turtle tagged on 2 April 1993 nested 82 days later on 26 June. This turtle and four others known to have laid at least six clutches per season imply a high reproductive output for at least some turtles in the Milman Island nesting population. Peak recorded clutch production in 1994-95 may have resulted from the timing of the research team's arrival (November) and extended stay (82 days) that season.

Renesting intervals reported in this study (mean = 14.5 days) were shorter than those observed in Caribbean Nicaragua (18.5 days, Nietschmann, 1981), Caribbean Costa Rica (19 days, Carr and Stancyk, 1975), the Seychelles (15–18 days, Diamond, 1976; Garnett, 1978) and the Solomon Islands (18 and 24.5 days, McKeown, 1977; Vaughan, 1981). However, intervals recorded at Antigua (14.1–15.0 days, Hoyle and Richardson, 1993) and Buck Island National Monument (15.5 days, Hillis, 1994) were similar to those at Milman Island.

Incubation Environment. — Sea turtles nest in a broad array of habitats and localities (Stancyk and Ross, 1978; Mortimer. 1982, 1990) ranging from temperate mainland beaches to tropical coral cays. Although all sea turtle species follow the same general nesting pattern, factors influencing nest site selection and incubation success are not fully understood. Numerous ecological factors, including sand temperature, particle size, water content, and salinity (Miller, 1985; Packard and Packard, 1988) affect hatching and emergence success. Survival of green turtle clutches on Ascension Island has been positively correlated with nest depth and sand particle diameter, and negatively correlated with electrical conductivity (Mortimer, 1990). Larger grain sizes (= larger pore spaces) and less uniformity in composition allow sand to hold more water (Folk, 1966; Buckman and Brady, 1969; Hesse, 1971), as long as the pore spaces are not too large (Mortimer, 1990). Beach and sand characteristics at a hawksbill nesting site were described by Horrocks and Scott (1991), but other hawksbill nesting beaches have not been adequately described.

The generalized weather patterns at Milman Island reflect the onset of the monsoonal activity common to tropical locations. Air and sand temperatures tended to decrease with the beginning of rainfall in late January to early February. The rainy season in the southern hemisphere occurs during the latter half of summer (January – March); little rain falls prior to that time period (Bureau of Meteorology, 1988). The influence of the rainy season (air and sand temperatures, rainfall) on clutch success and hatchling sex ratio are to lower sand temperatures by a few degrees one to two days after heavy rain, and to alter sex ratio if the change occurs during the middle third of incubation (Loop et al., 1995).

Most hawksbills nested under trees or shrubs at Milman Island, a pattern similar to that in the West Indies (Horrocks and Scott, 1991), Yemen (Hirth and Carr, 1970), Seychelles (Diamond, 1976), Sudan (Hirth and Abdel Latif, 1980), and Torres Strait (Bustard, 1972). However, the preponderance of nesting in vegetation does not necessarily indicate a preference for this type of habitat, which happens to be the dominant type at Milman Island (Loop et al., 1995). Numerous unvegetated sand cays in the northern Great Barrier Reef, Torres Strait, and the Arabian Gulf support low-density (4 or less turtles per day in summer) nesting by hawksbills (Bustard, 1972; Carr and Main, 1973; Miller, 1989; Miller et al., 1995).

Average beach height above the high tide line at Milman Island was less than double the 45 cm depth at which hawksbills lay their eggs (Witzell, 1983; Loop et al., 1995). This beach feature becomes significant when assessing the impact of flooding upon incubating eggs (Miller, 1985). The same fate may await eggs laid in the SE section and may have contributed to the lower hatching and emergence success detected there.

Sand composition at Milman Island was within ranges previously reported for other hawksbill nesting beaches fine siliceous sand to coarse shell and coral fragments (Mortimer, 1982, and included references). The coarsest sand and highest pH and EC were detected in the NW section, where dynamic conditions changed with prevailing wind pattern and tidal cycle (Loop, 1996). This area was exposed to high winds during January and February, causing sand to be blown offshore onto the reef flat. When the prevailing wind direction changed to southwesterly in March (Loop, 1996), sand was pushed back to this end of the island, where 20% of all turtle nesting attempts recorded in the 1991–95 summer surveys occurred. The coarseness of sand in this section may have made it easier for turtles to excavate nests. Wind- and wave-driven sand movement would prevent finer grain sizes from settling and accumulating at nest depth.

Beach topography and sand characteristics presented here fell within those previously reported for the species (Witzell, 1983). The role of these parameters in clutch success needs to be considered when beach renourishment programs become necessary because of degradation of the nesting environment. Utilizing new techniques such as nest casting (Carthy, 1994), which allows for examination of fine-scale effects in nest chamber construction between natural and renourished beaches, will help determine optimal substrates to be used at renourished beaches. Baseline data for other hawksbill nesting beaches need to be collected so geographic patterns can be incorporated into worldwide conservation plans.

Reproductive Biology. — The morphometric data on adult females, their eggs, and hatchlings at Milman Island place this population within the middle range for most known hawksbill nesting populations (Hendrickson, 1980; Witzell, 1983; Miller, 1989; Van Buskirk and Crowder, 1994). On average, Milman Island females were of a medium size and laid a moderate number of eggs, but their hatchlings tended to be small and their eggs were some of the smallest recorded for the species.

Tail lengths were similar to those reported by Miller (1989) for Arabian Gulf hawksbills (tail length to carapace: 3.3 ± 1.17 cm, range = 2.0-7.0; tail length to vent: 3.9 ± 0.44 cm, range = 3.0-5.0; vent to plastron: 11.8 ± 1.20 cm, range = 10.0-14.5). Adult tail lengths, especially the longer tail of males, have been used as a sexing technique for sea turtles (e.g., Limpus, 1985; Limpus and Reed, 1985; Limpus et al., 1994). The paucity of published data on the length of adult female hawksbill tails indicates caution must be used when determining sex of short-tailed immature and adult hawksbills using tail length, because females may have tail lengths up to 7.0 cm beyond the edge of the carapace.

Regression lines developed for various morphological characteristics of hawksbills were valuable in allowing a comparison among studies where data collection methods differ. Limpus et al. (1983a) reported that carapace length could be converted from straight to curved with a high degree of accuracy, and recommended midline curved carapace length be the standard measurement taken for studies of Australian populations. Regardless of what measurement is taken, it should be defined when presenting data.

Growth rates of interseason remigrants (CCL: 0.14 cm/ yr) were half of that reported for hawksbills nesting at Tortuguero, Costa Rica (SCL: 0.3 cm/yr, n = 4, Bjorndal et al., 1985). Negative growth values recorded for hawksbill interseason remigrants at Milman Island were included in the analysis because no viable reason could be established for not including the values. As the study continues at Milman Island, more growth increments will enable a more accurate picture of this parameter. The growth rates recorded here were somewhat lower than those reported for other nesting sea turtle species: green turtles (*Chelonia mydas*) at Tortuguero, Costa Rica (0.4 cm/yr, n = 179, Carr and Goodman, 1970), and Hawaii (0.5 cm/yr, n = 18, Balazs, 1980), loggerhead turtles (*Caretta caretta*) in the southeastern United States (0.6 cm/yr, n = 70, Bjorndal et al., 1983) and eastern Australia (0.1–0.3 cm/yr, Limpus, 1985).

Few scute variations were found on adult and hatchling hawksbills at Milman Island, which was similar to those reported in other studies (Witzell, 1983; Miller, 1989). Hatchling scute abnormalities were common in turtles from the Solomon Islands (Vaughan, 1981) and also have been found in other sea turtle species (Carr, 1952; Pritchard, 1969). Goodwin (1981) noted that the presence of hatchling morphological abnormalities was greater in transplanted nests than in natural nests.

Eggs laid within a single hawksbill clutch at Milman Island tended to decrease in size and weight from first to last laid. Limpus (1985) noted this pattern in six sequentially measured and weighed loggerhead clutches at Mon Repos, Queensland, Australia. Statistical analysis of these clutches indicated that a randomly selected sample of 10 eggs/clutch was sufficient to describe average diameter and weight of eggs within the respective clutches. Hawksbill clutches appear to follow a similar pattern at Milman Island, but measuring additional clutches would yield a more robust data set to describe this trend.

Hatching (82%) and emergence (79%) success of hawksbill clutches laid on Milman Island were within ranges previously summarized by Witzell (1983) and reported for Tortuguero, Costa Rica (58.3%, Bjorndal et al., 1985), Antigua (82%, Hoyle and Richardson, 1993) and Barbados (85%, Horrocks and Scott, 1991). Hawksbill clutch success rates are fairly uniform around the world (Witzell, 1983), indicating this species is able to nest successfully in a wide variety of substrates and habitats. However, higher clutch success at the start of the nesting season, with proportionately more unhatched embryos in later nests, was noticed on Cousin Island, Seychelles (Wood, 1986). Clutch success should be evaluated at other times of the year to test if a similar trend exists at Milman Island.

Lower incubation success in the S and SE sections corresponded to finer-grained sand, lower soluble salt content, and lower average beach height. Although moisture content in these sections was similar to other sections around Milman Island, the finer-grained sand had a higher water potential. Eggs incubating under those conditions would be less able to extract water from the sand, causing a lower hatching success. Mortimer (1982) determined that sea turtle nests fail in sand that is either too fine or too coarse. She suggested that hatchlings that did emerge from their egg shells might not be able to climb out of their chamber because the coarse, dry sand could collapse the air pocket typically found above incubating eggs (Mortimer, 1990). However, Mortimer (1982) did not detect any correlation between hatchling emergence success and nesting density at Ascension Island.

Birds were the primary, non-aquatic predators on hatchlings at Milman Island. The small size of the hatchlings allows them to be eaten by gulls and other birds which might have problems consuming larger prey. Low hatchling predation has been reported for populations along the Red Sea (Hirth and Abdel Latif, 1980), Samoa (Witzell and Banner, 1980) and Oman (Ross, 1981). Ghost crabs (*Ocypode* spp.) did not have a major effect on egg survival on Milman Island, but depredate up to 3% of clutches laid in the Solomon Islands (Vaughan, 1981) and 21% of those on Cousin Island, where entire clutches were sometimes destroyed (Diamond, 1976; Garnett, 1978; Wood, 1986).

Morphological characteristics of hawksbills were highly variable within the Milman Island population. For example, an average female would produce 122 eggs per clutch, but the large range (18–215) and its corresponding weak correlation ($r^2 = 0.13$) with CCL (range = 63.5–91.9 cm) indicated the size of the female was not a good prediction of the clutch size.

Data gathered in this study of hawksbills only accurately describe activities during the peak nesting months for a population nesting year-round (Limpus, 1980; Loop, 1993; Miller, 1994). Nesting patterns and success rates remain unquantified during non-peak months. Off-peak seasons ideally should be monitored also to determine population trends, and compared with those in summer. Surveys of longer duration at Milman Island, beyond those already conducted (82 days maximum), are needed to accurately assess whether turtles exhibit significant changes in the number of clutches laid per season or if the number of eggs in clutches varies significantly within a nesting season.

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