Chelonian Conservation and Biology, 1999, 3(2):330–336

Reproductive Biology of the Hawksbill Turtle, *Eretmochelys imbricata*, in Sabah, Malaysia

Nicolas J. Pilcher[1] and Lamri Ali[2]

[1]*Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia [Fax: 60-82-671903; E-mail: nick@tualang.unimas.my];*
[2]*Sabah Parks, P.O. Box 10626, 88806 Kota Kinabalu, Sabah, Malaysia*

Abstract. – Long-term records of nesting by the hawksbill turtle, *Eretmochelys imbricata*, on Pulau Gulisaan, Sabah's most important hawksbill rookery, along with detailed monitoring during 1996 and 1997, provide the basis for the present account. Nearly 2200 hawksbill females have been tagged on P. Gulisaan from 1985 to 1997. Adult females averaged 76.0 cm in straight carapace length and 66.3 cm in width. Average recorded clutch size was 105.3 eggs. Mean nesting frequency was 2.7 times per season with an interval of 18.0 days between clutches. Average individual nesting seasons lasted 130 days, although a significant number of turtles nested for periods lasting up to 24 months without an apparent remigration interval. Remigration interval among most turtles averaged 1.84 years, with curved carapace length growth rates of 0.22 cm/yr. Remigrant turtles were found to nest fewer times laying smaller clutches of eggs than neophytes. Hatchery incubation period averaged 53.7 days with hatching success rates of 41.3% inclusive of nests that did not hatch at all. Eggs weighed an average of 21.1 g and measured an average of 33.8 mm. Hatchlings weighed 11.4 g and measured 37.4 mm in straight carapace length and 25.8 mm in width. The nesting season extended year-round, with a peak from March to August and a drop during October–November. Hawksbills accounted for 23.6% of nesting occurrences with the balance by green turtles, *Chelonia mydas*. Little terrestrial predation threatened developing eggs or emerging hatchlings and no avian predation was observed. Loss of turtles at sea is presently unquantified although it is believed to be significant due to the trawl fishery operating in the vicinity of the islands.

Key Words. – Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; nesting; reproduction; conservation; Sabah; Malaysia

The hawksbill, *Eretmochelys imbricata*, is a circumtropically distributed marine turtle that inhabits and forages on coral reef areas and usually nests on isolated sandy beaches. For centuries the hawksbill has been harvested by man for its shell and meat, and its eggs have been collected for food. It is currently listed as Critically Endangered in the Red Data Book of the World Conservation Union (IUCN).

Nesting in Sabah takes place primarily at the Turtle Islands Park (TIP) lying 40 km north of Sandakan, which encompasses three small islands (Fig. 1), and Pulau Sipadan, an island off the southeastern tip of the State. The highest nesting density in Sabah is found on Pulau Gulisaan in the TIP (> 400 nests/year) accounting for at least 83.3% of total hawksbill nests within the Park (Chan and Liew, 1996; Sabah Parks, unpub. data). The remainder are shared by P. Selingan (10.8%) and P. Bakkungan Kechil (5.9%). At the TIP the beaches are shared by green turtles, *Chelonia mydas*, which account for 92.5 % of nesting on the three islands, and possibly a very few olive ridleys, *Lepidochelys olivacea*. At Sipadan, most nesting is by green turtles and the hawksbill is an uncommon nester (< 50 nests/year). Extensive surveys along the entire coastline of Sabah and many of the hundreds of small islands fringing the coast have revealed evidence of only diffuse hawksbill nesting (*pers. obs.*), a significant drop since Sabah's nesting summary by de Silva (1982), making P. Gulisaan probably the most important hawksbill rookery in the State.

Pulau Gulisaan (6°10'N, 118°2'E) has an area of approximately 1.6 ha and a circumference of about 1000 m, all of which constitutes nesting habitat, and is patrolled by two to three staff who are stationed there full-time. The island is not open to the general public. Nesting takes place year-round with a peak from February to September. The beaches are 5–15 m wide, with the exception of the southwestern tip which is a constantly-shifting sandspit, and are fringed by palms, trees, shrubs, and creeping vegetation. Tidal fluctuation is semi-diurnal, and air temperatures fluctuate from 22 to 38°C. A thorough description of the island is given by UPM et al. (1996).

The TIP, encompassing 1740 ha, recently (May 1996) joined forces with the Philippine Turtle Conservation Project of the Department of Environment and Natural Resources to form the world's first trans-boundary marine park, officially known as the Turtle Islands Heritage Protected Area (TIHPA). Encompassing Sabah's three islands and six from the Philippines and covering an area of 318,000 ha, the TIHPA was gazetted to promote the conservation of marine turtles, coral reefs, and fishing grounds, and to promote ecologically sustainable employment for the people living within the area.

Although data sets exist for other hawksbill rookeries (summarized by Witzell, 1983), there is little published

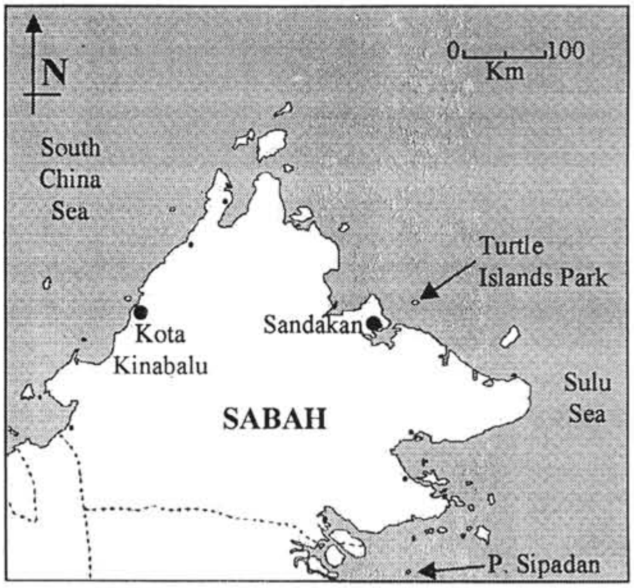

Figure 1. Map of Sabah showing Turtle Islands Park.

information on the reproductive biology of the hawksbill turtle for Sabah, Malaysia. A management strategy was developed in 1996 (Chan and Liew, 1996), and a comprehensive plan published by UPM et al. (1996). Inforrnation on egg production and harvests was presented over a decade ago (de Silva, 1982), but was concerned more with the trade rather than the process. Since that time, the sale of eggs from Sabah's islands has become illegal and practically ceased, due mostly to the efforts of Sabah Parks personnel who have patrolled the beaches every night since 1977. Information on the few eggs that reach market is scarce and guarded.

This paper draws on nesting records collected by Sabah Parks personnel from 1985 to 1997 and detailed nesting and morphometric data collected by one of us (NJP) in 1996 and 1997. Without the long-term records maintained by the Park, trends in the nesting biology would not have been discerned, and the daily data collected by the rangers provide critical insight into nesting changes over the years. The records, along with those reported by Bjorndal et al. (1985) for Tortuguero in Costa Rica and Limpus (1992) for Australia, are among the most important long-term data sets on hawksbill nesting in the world.

METHODS

The current data set examines hawksbill turtle nesting on P. Gulisaan over 13 years from 1985 to 1997. The island's circumference was divided into four quadrants with each beach section measuring about 250 m. Beaches were patrolled almost every night from 1800 to 0600 hrs during the 13-year period and occasionally through the day. Nesting turtles were tagged with monel tags (National Brand and Tag Co., No. 49) on the fourth scale from the axillary position on the front right flipper. At the same time, curved carapace length (CCL) and width (CCW) were measured using a flexible fiberglass tape measure (± 0.1 cm) with measurements following those defined in Limpus (1985), and the nesting location, tide height, and environmental conditions recorded.

Eggs were collected either during oviposition or shortly thereafter and transferred to a central hatchery where they were reburied to a depth of about 75 cm. Each nest was surrounded by a mesh screen to contain emerging hatchlings. Records were kept of tag number, clutch size, nest number, incubation period, and hatching success for each nest. Sample eggs and hatchlings were weighed using a Sartorius electronic balance (± 0.1 g) and measured for straight carapace length (SCL) and width (SCW) using dial scale calipers (± 0.1 mm).

Renesting interval was calculated as the number of days between successful nesting attempts up to and including 60-day periods, as a number of turtles were found to nest repeatedly at > 30 day intervals. Remigration intervals were calculated from the last successful nest of one season to the first successful nest of the following season, after a minimum interval greater than two average nesting seasons. Morphometric measurement accuracy was calculated from repeated measurements of the same individual within the same nesting season. Growth was averaged from measurements of 122 individuals which were recaptured over intervals of up to five years.

RESULTS

Unlike discrete and restricted nesting seasons found with other colonies, turtles utilize the beaches at P. Gulisaan year-round. Most nesting occurs from January to August with peaks in March and July and lowest nesting frequency occurs during October (Fig. 2).

Length of nesting season was calculated individually for 1180 nesting turtles, excluding turtles that nested only once (23.1% of the nesting population). Among these, the nesting season lasted an average of 4.3 months ($\bar{x}$ = 130.3

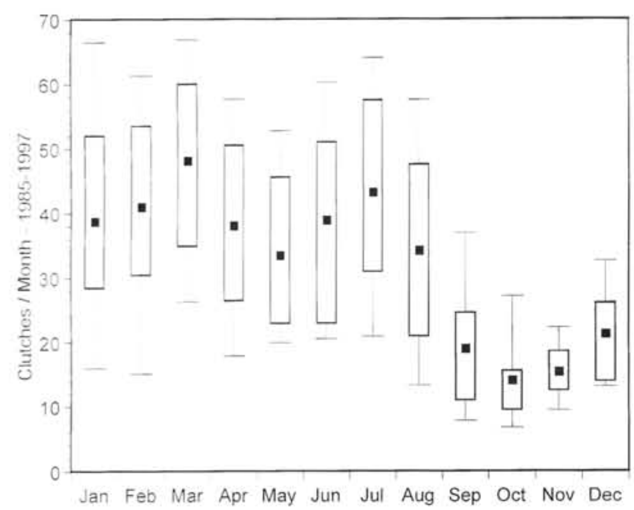

Figure 2. Hawksbill nesting frequency on P. Gulisaan 1985–97. Symbols represent mean values, boxes the standard deviation, and bars the range. Though moderate nesting continues year-round, a clear drop in nesting occurs at year-end, while two nesting peaks occur in March and July.

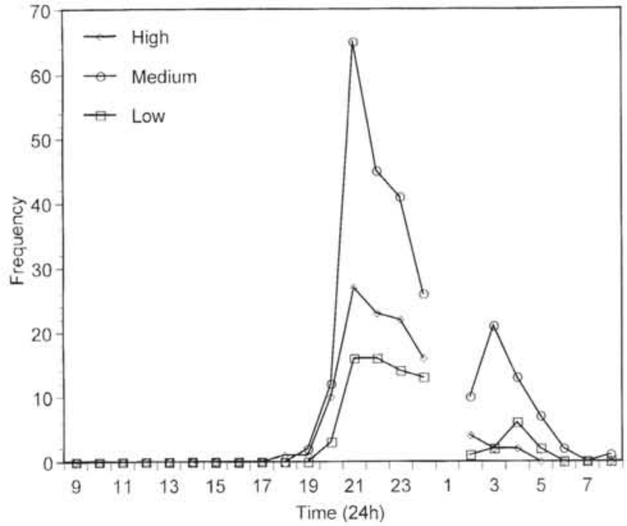

Figure 3. Nesting occurrence in relation to time and tidal height. Most nesting occurs between 1900 and 2300 hrs, with little of this occurring at high tide. The gap at 0100 hrs represents a personnel shift change, when workers temporarily leave the beaches.

days, SD = 106.54, range = 6–793 days). Over 65% of nesting took place within one- to five-month nesting seasons.

Out of the 253 remigrant turtles, 68 (25.7%) appeared to return after intervals of less than 12 months, even after an interval of at least two nesting seasons (262 days). These remigration intervals averaged 310.3 days (SD = 28.73, range 264–363). Although tag loss or erroneous reading of tag numbers could introduce a degree of error into the above findings, it is believed that the number of cases for which this phenomenon was found demonstrate actual remigration intervals of less than 12 months for some turtles at P. Gulisaan. After the remigration intervals, 66 turtles nested on more than one occasion (subsequent nesting records), supporting the accuracy of nesting records. In further support of this, of the 5069 nests laid by the 2181 turtles first encountered on P. Gulisaan, only 15 (0.3%) were laid on other islands (4 on P. Bakkungan and 11 on P. Selingan). This suggests that little nesting by these turtles occurs elsewhere, and combined with nightly patrols during the entire 13-year period and the lack of records of these hawksbills nesting on the nearby Philippines islands (UPM et al., 1996), may virtually eliminate the possibility of missed nesting attempts.

Nesting was infrequent during daylight hours (< 1.5%) and generally began at around 1900 hrs, peaking between 2100 and 2300 hrs, and gradually decreasing until 0700 hrs. Nearly 65% of turtles nested between 2100 hrs and midnight. While P. Gulisaan is surrounded by fringing coral reef, only a small portion at the northeast corner is exposed during low tide, allowing turtles to emerge and nest at virtually any tide height. Only 17.4% of turtles chose to nest at high tide, when the land distance to suitable nesting sites is shortest, with the majority (57.7%) nesting during mid-(receding or advancing) tides (Fig. 3).

Of 311 turtles monitored during 1996 and 1997 only 7 (0.22%) displayed true nest site fixity, returning to the same beach on all successive attempts. The remainder were found to nest at more than one of the island's four beach sections, and no significant preference for beach sectors was found ($\chi^2 = 3.27^{-28}$, $n = 311$, $p < 0.005$).

The internesting intervals (within season) were calculated for all turtles nesting within 60 days of the first recorded attempt (Fig. 4). When intervals > 30 days were

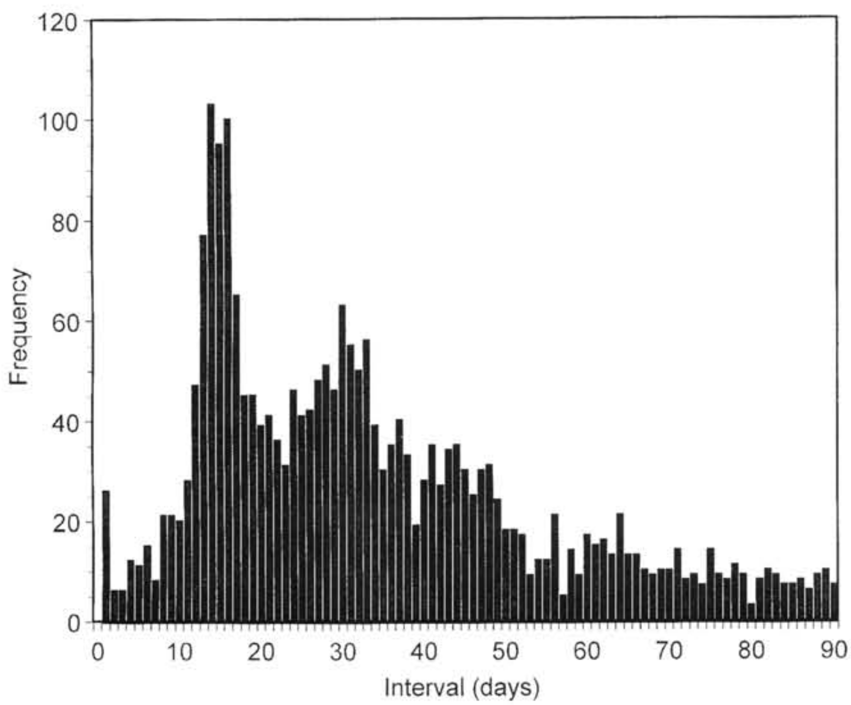

Figure 4. Renesting intervals for hawksbills on P. Gulisaan. Though there is a peak indicating a third renesting interval after 45 days, actual data suggest this is uncommon. The second peak around 30 days represents turtles renesting for the second time and possibly turtles renesting for the first time on a 30-day interval.

excluded, turtles were found to return after 18.0 days (SD = 7.13, n = 1235), comparable to that reported for Tortuguero ($\bar{x}$ = 16.4 days, Bjorndal et al., 1985) and Milman Isl. ($\bar{x}$ = 14.2 days, Loop et al., 1995). However, it is suggested that this is not the case for the entire population, as a significant number of turtles (> 10%) was found to nest consistently at approximately one-month intervals.

Remigration (between seasons) was calculated from 256 individuals that returned to nest after a period greater than two average nesting seasons. The average remigration period was 1.84 years (SD = 1.231, range = 0.7–10.2). Remigration intervals spanned from nine months to seven years (Fig. 5).

Less than 50% of the turtles that nested at P. Gulisaan over the 13-year period have been recaptured, even though a tagging program has been in effect since 1970. The general trend in recapture rates, which indicates a general increase in recaptures over the 13-year period, is described by the formula: $y = 1.92x + 7.593$ (Fig. 6). However, it is believed that a significant number of tagged turtles are not recorded due to tag loss or incorrect tag recording, and the actual percentage of the population that has been tagged may be higher.

Adult curved carapace length and width were recorded for 431 females nesting during 1996 and 1997. The average CCL was 76.0 cm (SD = 6.01, range = 59.7–98.0). Average CCW was 66.3 cm (SD = 6.31, range = 50.2–92.0). The correlation between CCL and CCW (r^2 = 0.71) was weaker than that reported for other rookeries: Western Samoa, r^2 = 0.99 (Witzell, 1980), Indonesia, r^2 = 0.97 (Uchida, 1980). No data are currently available on weight or other morphological measurements for this population. Data accuracy was considered to be reliable with an average error of 2 mm among repeated measurements of the same individuals within a season ($\bar{x}$ = 2.0 mm, SD = 2.39, n = 122 errors between different readings).

Growth was calculated for 122 individuals, several of which were recaptured twice during the 13-year period. Of these, 77 turtles (63.1%) were found to not grow at all, common to most sexually mature adults (Limpus, 1992b ; Boulon, 1994). The size distribution for the no-growth turtles was: 60–70 cm (n = 15), 70–80 cm (n = 48), and 80–90 cm (n = 16). CCL increment across all size classes averaged 0.22 cm/yr (SD = 0.737, range = 0–6.37), while CCW increment across all size classes averaged 0.22 cm/yr (SD = 0.680, range = 0–5.63). Only four of these turtles (all within the 70–80 cm size class) were found to grow in excess of 1 cm/yr, with the majority (68.8%) growing less than 0.5 cm/yr. These growth rates are significantly slower than those reported by Limpus (1992b) for nearby Australian rookeries.

Egg morphometrics were recorded from 179 eggs from 19 different nests. Average diameter was 33.8 mm (SD = 0.718, range = 32.0–35.8), while average weight was 21.1 g (SD = 0.718, range = 17.3–23.9). These average figures are lower than any others reported worldwide, although the ranges overlap those reported for the nearby Philippines (Alcala, 1980), and Indonesia (Nuitja, 1979).

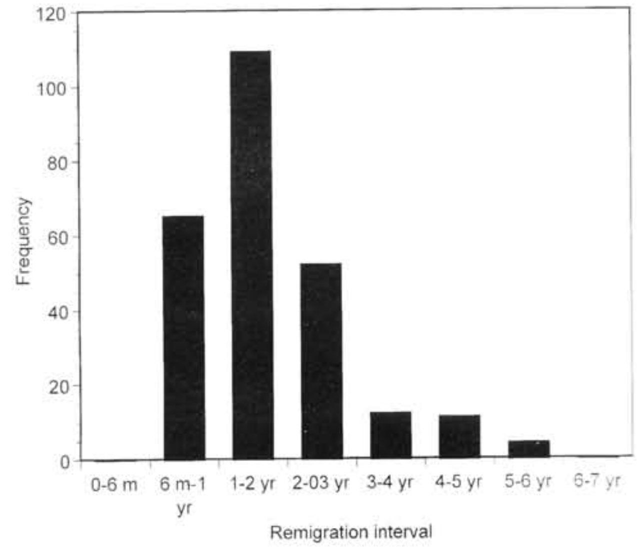

Figure 5. Remigration intervals between nesting seasons. Intervals of less than two average nesting seasons were not considered separate seasons and although unlikely, this may have been the case. Just over 25% of remigrants return after less than 12 months and it is believed the lack of returns after 6 years is partially a result of tag loss.

Clutch size recorded from 5016 nests averaged 105.3 (SD = 27.65, range = 10–220). Average clutch size was relatively small, particularly as compared to other southeast Asian populations (115–151), but comparable to average clutch sizes in the Middle East (Ross and Barwani, 1982; Witzell, 1983). Although rangers were previously allowed to take some eggs for personal consumption (recording only the number of remaining eggs actually transferred to the hatchery), this practice has been gradually phased out and was never observed during detailed monitoring in 1996–97. With the caveat that this practice may have occasionally affected recorded clutch size, it is, however, believed that the large sample size provides a relatively accurate estimate of

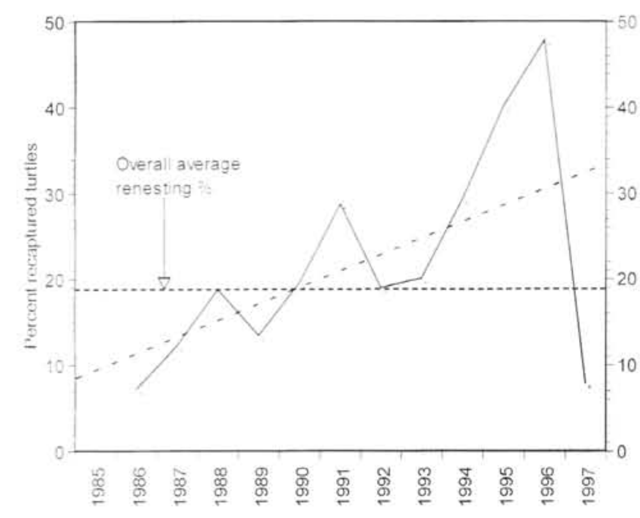

Figure 6. Long-term recapture of tagged hawksbills. Approximately 40% of turtles tagged since 1985 have been recaptured by 1997, though the average recapture incidence in each year averages only 20%. These figures are believed to be low due primarily to tag loss.

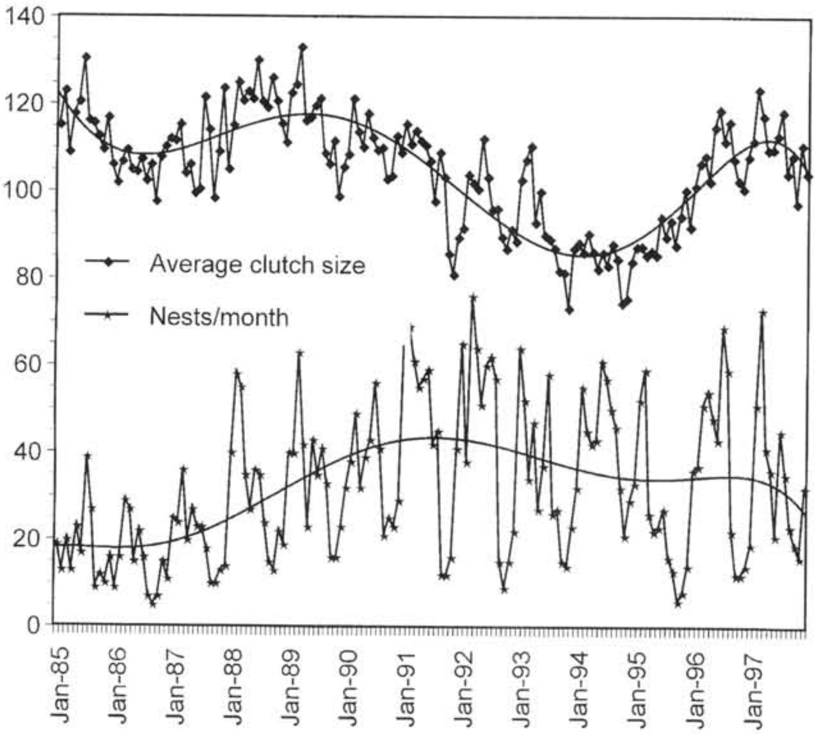

Figure 7. Seasonal fluctuation of average clutch size (calculated monthly). No clear relationship was found between clutch size and nesting occurrence, though the data represent total and not individual nesting patterns.

average clutch size. A certain amount of cyclical seasonal reproductive variation was found per month over the 13 years, with no apparent link between clutch size and number of clutches per month, but these figures represent the performance of the population as a whole and not of individual turtles (Fig. 7).

Nesting frequency averaged 2.7 nests within a season (SD = 1.69, $n = 1161$), ranging from 1 to 8 nests per season, irrespective of the turtle's status as a neophyte (possible first time nester) or remigrant. Clutch sizes from remigrant turtles ($\bar{x} = 97.7$) were smaller ($z = 4.17$, $p < 0.001$) than clutches from neophytes ($\bar{x} = 104.7$), and remigrant turtles nested less often in a season ($\bar{x} = 1.2$, SD = 0.56, range = 1–4) than neophytes ($\bar{x} = 3.0$, SD = 1.68, range = 1–8) ($z = 33.21$, $p = 0$), possibly indicating a decrease in reproductive output with time and/or age. This is in contrast to that found by Brooke and Garnett (1983) in the Seychelles.

Incubation period was recorded for 747 hatchery clutches and averaged 53.7 days (SD = 5.06, range = 43–80), and was generally shorter than that of other studied populations. As with elsewhere, the correlation between carapace length and clutch size ($r^2 = 0.16$) was weak, suggesting that carapace length is a poor indicator of egg-laying capacity. Average emergence success for clutches from which one or more hatchlings emerged ($n = 754$) was 46.6% (SD = 27.60, range = 0.6–100). This figure is comparable to previous reports in the region: Sabah, 47.3% (de Silva, 1969) and peninsular Malaysia, 47.9% (Heang, 1975). However, out of the available records ($n = 849$) a significant fraction (11.2%) did not hatch at all. The inclusion of these failed nests results in an overall hatchery hatching success of 41.3%, the lowest reported anywhere and less than half of that reported for Pacific Ocean colonies. It is possible that the depth to which the eggs were reburied in the hatchery may negatively affect hatching success. While incubation period was found to vary significantly with time of year ($\chi^2 = 8.259$, $p < 0.005$, $n = 754$), becoming approximately 10 days longer during December to February, there was no significant correlation between incubation period and incubation success ($r^2 = -0.0048$, $n = 24$), which was evenly distributed over time ($\chi^2 = 40.548$, $p < 0.025$, $n = 24$).

Hatchlings were collected from 20 nests from which 186 individuals were weighed and measured. Average weight was 11.4 g (SD = 0.91, range = 9.4–12.8). Average SCL was 37.4 mm (SD = 1.31, range = 35.4–39.5), and average SCW was 28.8 mm (SD = 1.42, range = 25.8–31.8). The small average hatchling size and weight match the small average egg size and rank lowest on the world scale (Witzell, 1983), although the ranges overlap those of other southeast Asian rookeries. These smaller hatchlings represent yet another stepwise loss in the reproductive output energy budget, where increasingly fewer and smaller offspring result from each nesting attempt. Due to the relatively recent reduction of terrestrial predation through the use of the hatchery, the decreased hatching success is likely the result of hatchery operations rather than any adaptive mechanism

The island's hatchery, built in the early 1970s, has been successful in minimizing egg collection by neighboring villagers, but hatch rates are the lowest found among nesting colonies. Possible contributing factors are the lack of consistency in hatchery nest depths, which although reported to be 75 cm, are often as shallow as 25 to 54 cm at the deepest point, and temperature, which was found to range from 28.3 to 32.9°C (UPM et al., 1996).

Predation on eggs and hatchlings by mice *(Mus* sp.), rats *(Rattus* sp.), and monitor lizards *(Varanus salvator)* has been mostly eliminated through the use of the hatchery, although nests that are not collected are occasionally dug up by monitor lizards. Little or no avian predation exists, the islands and surrounding waters being particularly devoid of avifauna, possibly as a result of the presence of egg predators such as the monitor lizard (many seabirds nest on the beach rather than off the ground) and distance from the mainland.

A number of emerging adult female turtles carried scars of encounters with marine predators, with rear flippers or portions of the front flippers missing. In several cases the turtle's carapace was split, either from an encounter with a large predator or with a fast-moving vessel. Up to 30% of hatchlings released from the hatchery are lost to marine predators within the 10 m depth contour (Pilcher et.al., unpub. data). These predators have not been identified, but are believed to include groupers (Serranidae), snappers (Lutjanidae), and various sharks that inhabit the fringing reef.

By far the most serious threat derives from the dense trawler fishery that operates in the vicinity of the island. During the six-month northwest monsoon period (March–October), up to three hundred small to medium trawlers operate in the shallow waters surrounding the turtle nesting islands, and a significant number of adult turtles are believed to be caught every day. Although there is no systematic harvest of hawksbills by the fishery or artisanal fishermen, it is believed that incidental take accounts for much of the adult mortality in the region.

DISCUSSION

Since the establishment of the Turtle Islands Park and with gradual changes in natural law, the turtles nesting on the islands have become progressively better protected since de Silva (1982) reported on the collection and sale of turtle eggs from these islands and tabulated egg production. After 1977 the sale of turtle eggs from the Park practically ceased, and the decline in nesting and hatchling release was reversed. Today, P. Gulisaan is one of the few protected hawksbill nesting sites in the region, and produces over 15,000 hatchlings annually. The long-trend data sets collected by Sabah Parks staff, collected each night for over 13 years, allow an assessment of trends in nesting and reproductive output over the years, along with details of individual nesting behavior and dynamics.

Predictions of renesting and remigration occurrence are hampered by drawbacks in the current tagging program, such as poor tag placement (applying the tag closer to the body would reduce the chances of it being lost), use of monel tags (with which there is a likely tag loss of 50% in less than three years), and use of only one tag on each turtle. However, by assuming an equal chance of tag loss and/or unrecorded nesting events for both tagged and untagged turtles, the present records are assumed to be indicative of general trends. It is estimated that turtles nesting at P. Gulisaan may lose up to 95% of their tags within six to seven years, using the most conservative estimates suggested by Limpus (1992a) in his study of the probability of tag loss for green and loggerhead turtles *(Caretta caretta)*. Hawksbills may have a higher chance of losing tags while foraging on coral reefs compared with green turtles on seagrass pastures, resulting in a higher incidence of tag loss, particularly under the present tagging regime. Compounding this, whereas obvious evidence of previous tagging might be noted, the less-obvious healed scars, in particular when covered in sand and under cover of night, might easily be overlooked.

With these factors in mind in mind, the actual incidence of remigration is probably higher than that reported here (< 20%), but obscured by the high rate of tag loss, and current data are only reliable for population modeling within 2–3 years of tag placement. Additionally, current practices are to tag new turtles only after they have laid eggs, as opposed to when they are first seen. Thus, unlike renesting interval reports from elsewhere, turtles at P. Gulisaan lack prominent returns recorded at 0, 1, 2, or 3 days, usually attributed to unsuccessful first nesting attempts.

All untagged nesting attempts are counted by Park personnel (as it was possible a number of these turtles might only nest once), introducing an error into estimates of total annual nesting. As tag-loss is not believed to be significant during the first season (based on findings by Limpus, 1992a), and monitoring during the 13-year period was carried out every night, it is believed the probability of missing tagged turtles was low. Monitoring on the other islands in the Park is as intensive as on P. Gulisaan, and the low incidence of migration among islands and across international boundaries suggests that these hawksbills only infrequently nest elsewhere.

Although hawksbills usually nest after a greater than 12-month remigration period (Ross, 1981; Brooke & Garnett, 1983; Limpus et al., 1983; Bjorndal et al., 1985), a number of turtles at P. Gulisaan appear to have shorter interseason breaks. It is unknown whether they leave the area during this time, although three tag recoveries from the Philippines and one from southern Sabah (UPM et al., 1996) indicate migrations do occur.

The historical nesting records from P. Gulisaan are considered accurate in view of the small degree of error over multiple measurements of the same individuals (2 mm only), providing a reliable assessment of growth rates. The slow growth rate (CCL 0.22 cm/yr) encountered among females nesting at P. Gulisaan corroborates the limited studies on growth in wild mature populations, with increments approaching 0 cm/yr in the larger adult size classes. The distribution of the large proportion of no-growth turtles (63.1%) among size classes (with > 80% being smaller than 80 cm CCL) suggests that size alone is not a reliable indicator of growth rate, which is probably linked to other factors such as recruitment size, size at sexual maturity, food availability, nesting and foraging energy expenditure, and remigration distance.

Tag loss within a season may result in underestimating nesting frequency, and it is possible that tags that have been attached for a long time (such as those on remigrant turtles) may have a higher chance of being lost during the nesting process than those recently applied. Additionally, mistaking some remigrant turtles for neophytes (due to tag loss) might account for underestimating nesting frequency of remigrants. However, most of the interseason periods of remigrants were shorter than the 2–3 year period for expected tag retention, and it is believed that older turtles do in fact lay fewer and smaller clutches of eggs.

Overall, hawksbills in Sabah lay smaller clutches than other populations, which also contain eggs which are among the smallest compared with other rookeries. The low reproductive output may possibly be the result of stresses to wild foraging populations in the form of unavailable food supplies. With the continuing destruction of the region's coral reefs (see Pilcher and Oakley, 1997), the turtles face a formidable challenge in finding food material as many of the region's sponges and reef invertebrates are extirpated by dynamite and cyanide fishing. Coupled with this, hawksbill eggs in the hatchery on P. Gulisaan have the lowest hatching success rate worldwide (41.3%), further reducing the population's reproductive output, in addition to producing some of the world's smallest hatchlings. While the fact that the nesting population has continued to return to the island may be heartening, its long-term fate remains to be seen. Low numbers of small eggs with a > 50% loss in the nest alone and a high degree of mortality once the hatchlings leave the island's shores, along with a low remigration rates among adults, suggest that all may not be well with Sabah's hawksbills, and may be reflective of the long lasting exploitation of these turtles for their shell and eggs in past years. Though nesting trends show a slight and promising rise in numbers of adults reaching the beaches, the cyclic nature of turtle nesting patterns precludes any conclusive argument in this respect.

ACKNOWLEDGMENTS

We would like to acknowledge the numerous Park Rangers and Assistant Rangers who collected the long-term data. The present work would not have been possible without the assistance of Asdari Belout, Karim Kassim, and Joe Micheal, whose help is gratefully acknowledged. This work was partially funded by UNIMAS Grant No. 90/96, the Shell Chair in Environmental Science, and MacArthur Foundation Grant No. 44416-0. This financial assistance is gratefully acknowledged.

LITERATURE CITED

ALCALA, A.C. 1980. Observations on the ecology of the Pacific hawksbill turtle in the central Visayas, Philippines. Fish. Res. J. Philipp. 5:42.

BJORNDAL, K.A., CARR, A., MEYLAN, A.B., AND MORTIMER, J.A. 1985. Reproductive biology of the hawksbill *Eretmochelys imbricata* at Tortuguero, Costa Rica, with notes on the ecology of the species in the Caribbean. Biological Conserv. 34:353-368.

BOULON, R.H., JR. 1994. Growth rates of wild juvenile hawksbill turtles, *Eretmochelys imbricata*, in St. Thomas, United States Virgin Islands. Copeia 1994:811-814.

BROOKE, M.D.L., AND GARNETT, M.C. 1983. Survival and reproductive performance of hawksbill turtles *Eretmochelys imbricata* L. on Cousin Island, Seychelles. Biological Conserv. 25:161-170.

CHAN, E.H., AND LIEW, H.C. 1996. A management plan for the green and hawksbill turtle populations of the Sabah Turtle Islands. A report to Sabah Parks. SEATRU (Sea Turtle Research Unit), Faculty of Fisheries and Marine Science, Universiti Pertanian Malaysia, 102 pp.

DE SILVA, G.S. 1969. Turtle conservation in Sabah. Sabah Soc. J. 5:6-26.

DE SILVA, G.S. 1982. The status of sea turtle populations in East Malaysia and the South China Sea. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithson. Inst. Press, pp. 327-337.

HEANG, K.W. 1975. Report on the turtle beach of Tanjong Kling, Malaysia. Malay Nat. J. 29:59-69.

LIMPUS, C.J. 1985. A study of the loggerhead sea turtle, *Caretta caretta*, in eastern Australia. Ph.D. Thesis, Univ. of Queensland.

LIMPUS, C.J. 1992a. Estimation of tag loss in marine turtle research. Wildl. Res. 19:457-469.

LIMPUS, C.J. 1992b. The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground. Wildl. Res. 19:489-506.

LIMPUS, C.J., MILLER, J.D., BAKER, V., AND MCLACHLAN, E. 1983. The hawsbill turtle, *Eretmochelys imbricata* (L.), in north-eastern Australia: the Campbell Island rookery. Austral. Wildl. Res. 10:185-197.

LOOP, K.A., MILLER, J.D., AND LIMPUS, C.J. 1995. Nesting by the hawksbill turtle (*Eretmochelys imbricata*) on Milman Island, Great Barrier Reef, Australia. Austral. Wildl. Res. 22:241-252.

NUITJA, I.N.S. 1979. Penyu sisik (*Eretmochelys imbricata*) dan masala perdacancannya. Bogor: Bogor Agricultural University, 11 pp.

PILCHER, N.J., AND OAKLEY, S.G. 1997. Unsustainable fishing practices: crisis in coral reef ecosystems of Southeast Asia. In: Proc. Oceanology International 97 Pacific Rim, Singapore, 12-14 May 1997, pp. 77-87.

ROSS, J.P. 1981. Hawksbill turtle *Eretmochelys imbricata* in the Sultanate of Oman. Biological Conserv. 19:99-106.

ROSS, J.P., AND BARWANI, M.A. 1982. Review of sea turtles in the Arabian area. In: Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithson. Inst. Press, pp. 373-383.

UCHIDA, I. 1980. The report of a feasible research on artificial hatchery and cultivation of hawksbill turtle *Eretmochelys imbricata* in waters adjacent to Malaysia, Singapore and Indonesia. Tokyo: Japan Tortoise Shell Assoc., 63 pp.

UPM, UMS, AND PERHILITAN, J. 1996. Development and management plan: Turtle Islands Park. Sabah, Malaysia: Sabah Parks.

WITZELL, W.N. 1980. Growth of captive hawksbill turtles, *Eretmochelys imbricata*, in Western Samoa. Bull. Mar. Sci. 30:909-912.

WITZELL, W.N. 1983. Synopsis of biological data on the hawksbill turtle *Eretmochelys imbricata* (Linnaeus, 1766). FAO Fisheries Synopsis 137:1-78.

Received: 17 June 1998
Reviewed: 29 November 1998
Revised and Accepted: 16 January 1999