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Population Ecology and Demographic Implications Drawn From an 11-Year Study of Nesting Hawksbill Turtles, *Eretmochelys imbricata*, at Jumby Bay, Long Island, Antigua, West Indies

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Abstract. – Adult female hawksbill turtles, *Eretmochelys imbricata*, return periodically and with surprising predictability to nest on a single beach in Antigua, West Indies. This consistent behavior has provided a window of opportunity for measuring several elusive parameters such as survival and recruitment, essential for population modeling. A total of 126 females have been identified after 11 seasons of saturation tagging surveys (1987–97). Seasonal nesting cohorts ranged from 22 to 38 individuals. The mean remigration interval for an individual was 2.69 years. The total number of reproductively active females in the population was estimated to be 78 animals, out of which 29 animals (37%) remigrated to nest each season on average. The appearance of 6.9 (range 4–11) new animals each season was considered to be recruitment, representing approximately 9% of the estimated adult female population. The permanent disappearance of 4.8 individuals per year was taken as a best estimate of mortality, representing approximately 6% of the adult female population. An average female laid 5 clutches of 155 eggs per clutch during a nesting season, depositing 775 eggs with roughly 75% emergence success. This equates to an average production of 288 eggs/female per year. Mean survival of adult females was estimated to be 8.1 years of reproductive activity, during which an average female produced 3100 eggs during 4.1 nesting seasons. Recruitment predicted from estimates of fecundity was 5.4 new animals per season, close to the 6.9 new animals observed per season. With a reproductive rate of 288 eggs/year, an adult female must be allowed to reproduce for at least 9 years (4.1 nesting seasons/individual) to replace herself, and some animals must continue to be reproductively active for several decades or more to balance the early mortality of other individuals. The hawksbill's Critically Endangered status is logically the result of adult females not being provided the long term protection they evidently need to maintain population numbers.

Key Words. – Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; population; nesting; annual survival; mortality; fecundity; recruitment; Antigua; West Indies

Sea turtles provide challenging subjects for population analysis. Developmental life stages are difficult to access at sea. Adult females may be observed on nesting beaches, along with their eggs and hatchlings, but sea turtles are long-lived organisms. This fact and the non-annual nesting cycles of the group require many years of intensive surveys before several of the most important population parameters can be measured. Presented here is a preliminary population analysis from a study of hawksbill turtles, *Eretmochelys imbricata*, nesting at Jumby Bay, Long Island, Antigua, West Indies (Corliss et al., 1989; Richardson et al., 1989; Ryder et al., 1989; Hoyle and Richardson, 1993). Annual survival and recruitment represent parameters that are only now becoming evident after a decade of study. Nevertheless, a picture of population ecology is beginning to emerge, even if drawn with broad brush strokes. Demographic implications derived from the study are inevitably speculative at this early stage in the gathering of data, but they provide a point of departure for continuing investigations. Eventually, the parameters measured at Jumby Bay and results from other nesting beach studies will be merged with on-going investigations of juvenile life stages for a more complete life history analysis.

METHODS

The Jumby Bay study site is located at Pasture Bay Beach on Long Island, a small, privately owned island (Jumby Bay Resort) situated several kilometers off the northeast coast of Antigua within the Windward Islands of the Caribbean (Fig. 1). The beach (475 m in length) is of natural origin, a mixture of aragonite sand, exposed outcrops of ancient limestone reef, and accumulations of flint nodules. The beach is windward facing in aspect, historically vegetated with a thick cover of tropical maritime forest, but now largely cleared for resort development. The relatively inaccessible location of this insular nesting site to mainland turtle hunters apparently accounts for the persistent presence of a small population of nesting hawksbills. The Jumby Bay population has survived over the years while most other beaches on mainland Antigua were depleted of their nesting turtles by the early to mid-20th century. The present owners of Jumby

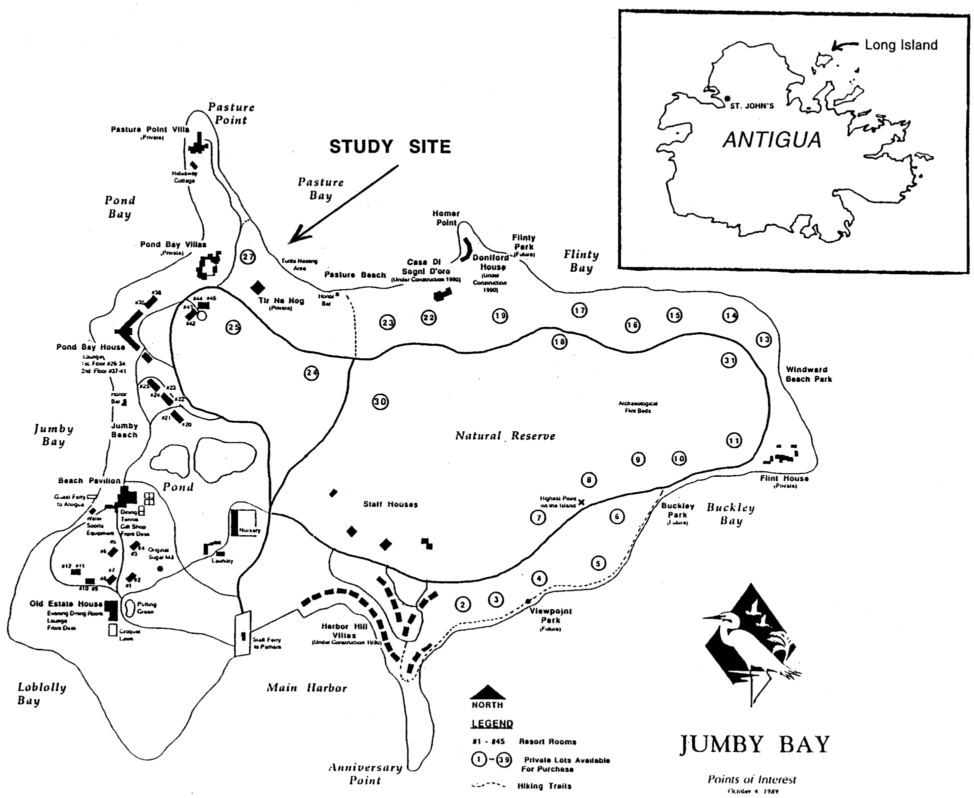

Figure 1. Location of the study site, Pasture Bay Beach, for the Jumby Bay Hawksbill Project, Long Island, Antigua, West Indies.

Bay intend to protect their nesting hawksbills within the constraints of a heavily developed resort island, and herein lies the management challenge facing this relict nesting population.

A preliminary survey at Jumby Bay was conducted in 1986 to confirm the presence of nesting hawksbills and to ascertain that the turtles would be amenable to an intensive long-term study. Saturation tagging was begun in 1987 and has continued each season through 1997, with plans to maintain the study for as long as possible into the future. The study season begins annually on 15 June and ends on 15 November, a period of 153 nights that encompasses nearly all the annual nesting activity, although occasional nesting is known to occur during other months of the year. Since most nesting females deposit multiple clutches over a period of at least eight weeks, the effective survey identifies even those few individuals that have begun nesting a month or so prior to 15 June and those just beginning in early November.

Hourly patrols begin at dusk and end at dawn, such that the beach is covered on a schedule that ensures identification of every nesting female on each of her nesting events during the season. At points along the beach where vegetation reaches the water line, a colonnade of small white dowels (trip sticks) identifies the passage of a turtle where a crawl trace would not be evident. No sea turtle can nest without leaving evidence of its visit, either tracks in the sand or fallen sticks on the ground. Turtles that fail to nest (false crawls) are not subjected to tagging so as to minimize disturbance, although false crawl turtles with existing tags are checked for identification numbers whenever possible. It has always been a concern of the project that a disturbed turtle would move to an unprotected mainland beach, but none has ever been known to do so. To date, false crawl turtles identified by tag number have consistently returned the same evening or within the next several nights until nesting is successfully completed.

Turtles are processed while laying eggs. This includes flipper tagging, drilling of supracaudal scutes, measuring the carapace, photography, etc. Turtles are not handled while approaching and searching for a nest site, while digging a body pit, while covering the eggs, or while departing. Thus, certain measurements such as body weight are not taken because of the harassment factor. Similarly, eggs are left *in situ* whenever possible, and hatchlings emerge and disperse to the water naturally. With the exception of the 1996 and 1997 seasons, when clutch size was counted as part of a relocation feasibility study, hatching success has been estimated from retained nest contents after emergence.

Every adult female is fitted with a size 681 inconel tag (US NMFS issue) through the first, most proximal scale on the trailing edge of each fore flipper. In addition, a unique pattern of holes is drilled through the inert portion of the supracaudal scutes as a backup marker. Only two remigrant turtles in eleven seasons have appeared without tags, and these animals were re-identified by the drill pattern on the supracaudals. There has been no corrosion of flipper tags

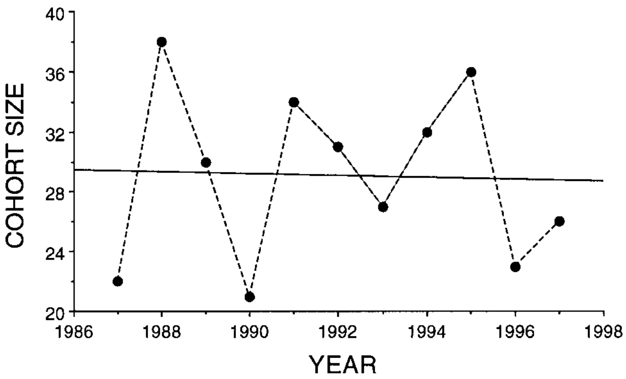

Figure 2. The cohort size (number of turtles observed nesting per season), Jumby Bay, Antigua. Mean = 29.1 turtles, *n* = 320. Linear regression (solid line, $r^2 = 0.001$) indicates the difficulty in identifying trends in the numbers of nesting females over years.

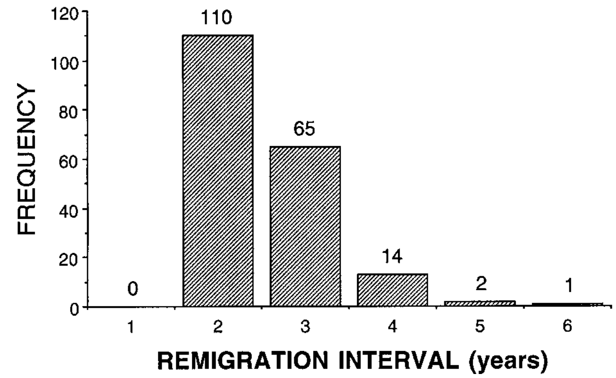

Figure 3. The frequency distribution of remigration intervals observed at Jumby Bay, Antigua. Remigration intervals of 1 year were not observed. Mean = 2.54 years, *n* = 192.

noted. Drill holes "migrate" toward the trailing edge of the scute as a function of scute growth and abrasion; the rate has been measured at approximately 2–3 mm per year. A pattern of holes placed 12–15 mm or more from the trailing edge remains readable for a minimum of 4–5 years. Inconel tag loss has been about 10% after a single 2–4 year remigration interval. Thus, a turtle with two inconel flipper tags applied in the proper location during the previous nesting season has perhaps a 1% chance of losing both tags. A turtle arriving at Jumby Bay without flipper tags or evidence of tag marks or a supracaudal drill pattern is unquestionably a new recruit to the nesting population.

RESULTS

Remigration. — There have been 126 adult female hawksbills tagged at Jumby Bay in eleven seasons (1987–97). Seasonal cohorts have ranged from 21 to 38 animals (Fig. 2). There has been no measurable trend in abundance over the decade of surveying, nor is there any reason to suspect that numbers might be increasing or decreasing over this period of time. Trends in numbers of nesting sea turtles (*Lepidochelys* spp. excepted) are exceedingly difficult to detect reliably because of the characteristically wide variation or variance around the mean from season to season. The Jumby Bay hawksbills remigrate most commonly at 2-yr intervals, although 3-yr intervals are also common, and 4-yr intervals are not uncommon (Fig. 3). Annual remigration has never been observed at Jumby Bay.

There have been sufficient remigration returns to begin assigning individual remigration values to many of the turtles (Fig. 4), given that at least one interval is required for a value to be assigned. For instance, an individual exhibiting remigration intervals of 2, 3, and 3 years would receive a remigration value of 2.67. The population mean is 2.69 years, and it is this value that will be used for further calculations of population fecundity. Note that this measurement represents an underestimate of the true population remigration value, because turtles with short remigration intervals return sooner and, therefore, are seen more often. However, a population remigration value derived from absolute numbers of observed intervals (Fig. 3) is even more biased; compare the mean of 2.54 years by this method to the 2.69 years derived from individual remigration values.

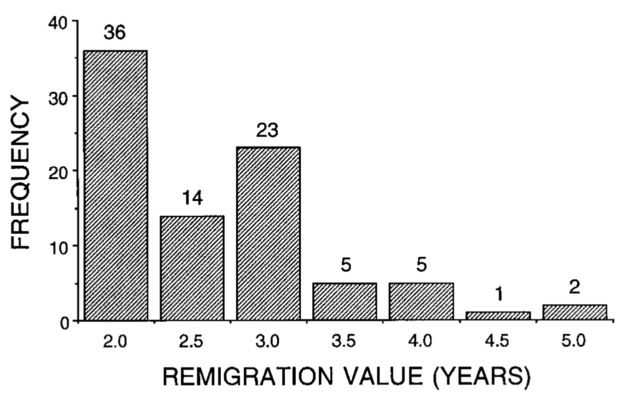

Figure 4. The frequency distribution of the mean remigration interval of individual hawksbill turtles nesting at Jumby Bay, Antigua. Each remigration category includes values up to the next category level (i.e., the value of 2.0 on the *y*-axis represents a range from 2.0 to < 2.5). Mean = 2.69 years, *n* = 86.

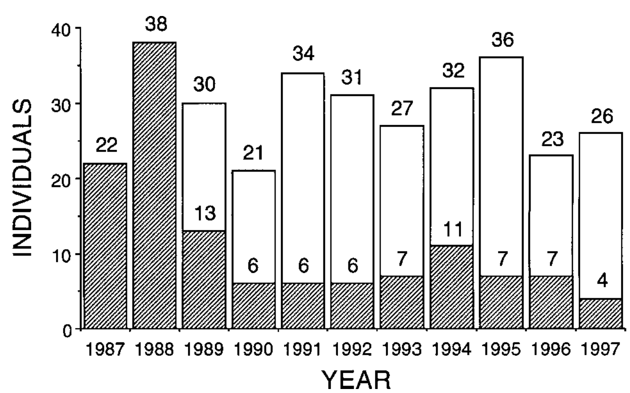

Figure 5. Total turtles and the number of unmarked turtles or neophytes (hatched bars) observed per season, Jumby Bay, Antigua, as an indication of recruitment (1991–97) to the population. Early years (1987–90) were not used to estimate recruitment, as these years were required to tag the original nesting population with remigration intervals of 2–4 years.

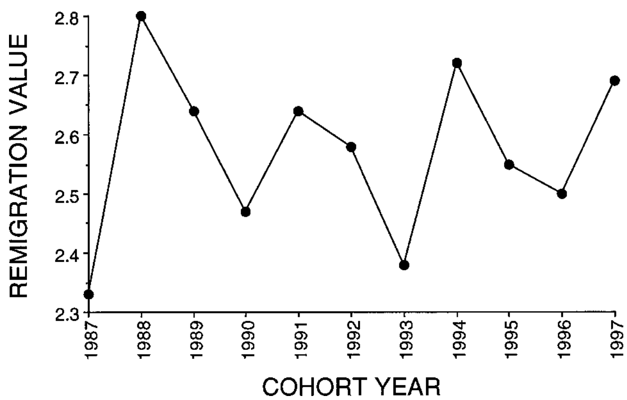

Figure 6. The mean remigration value of 11 seasonal cohorts of unmarked turtles (1987–97) observed nesting for the first time at Jumby Bay, Antigua. Numbers for 1991–97 are assumed to represent true recruits to the nesting population. Mean = 2.57 years.

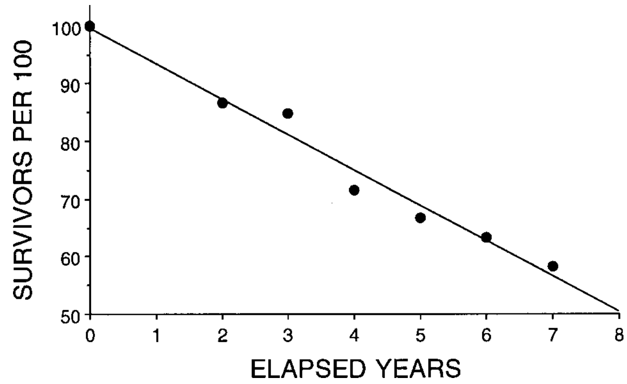

Figure 7. Survivorship of adult nesting females from the combined cohorts of the 1987 and 1988 seasons (n = 60) plotted for 7 nesting seasons, Jumby Bay, Antigua. Linear regression model: $y = 99.63 - 6.14x$, $r^2 = 0.974$.

Recruitment. — Recruitment represents a parameter of crucial importance to understanding population dynamics, yet this parameter is also one of the most elusive. Untagged turtles appearing for the first time in the Jumby Bay population are classified as "neophytes." A neophyte may be a true recruit to the population, appearing as a first-time nesting female, or she could be a wandering turtle with an unknown history of nesting prior to her first appearance. Following the first four years of surveys (1987–90) during which the established nesting population was being tagged for the first time, the number of neophytes in subsequent seasons has averaged 6.9 per season (Fig. 5), with a range of 4 to 11 individuals.

Whereas laparoscopy would provide a guaranteed procedure for determining the status of recent Jumby Bay neophytes, it shall be assumed in the absence of this examination that these animals are, in fact, first-time nesters and true recruits based on their remigration behavior being not noticeably dissimilar from established remigrants. In other words, wandering turtles would be expected to visit Jumby Bay perhaps once and then depart, whereas true recruits would be expected to join the resident population as typical remigrants. Since Jumby Bay neophytes remigrate at a rate not different from established remigrants (Fig. 6), they have been used to approximate recruitment at this preliminary stage of population analysis. We do not know if these recruits derive from Jumby Bay hatchlings or from other beaches in the Antigua region.

Survivorship. — The combined 1987 and 1988 cohorts (n = 60) represent a pool of animals whose remigration behavior has been analyzed for 6 years (7 nesting seasons), with at least 3 additional nesting seasons available to determine if individuals not seen during the fourth through sixth year of analysis still survived. These animals have failed to return to Jumby Bay at a rate of roughly 6% per year (Fig. 7), although their failure to return is not absolute evidence of mortality. Despite such uncertainty, this characteristic of the Jumby Bay population has been used to calculate a minimum estimate of annual survival of 0.94 from the linear approximation of the regression.

As annual survival approaches 1.00, small changes in this population parameter have an increasingly dramatic effect on model predictions such as years of reproductive activity and lifetime fecundity. Thus, it is important to note that annual survival expressed by the separate 1987 and 1988 cohorts is divergent (H: $B_1 = B_2$; $F_{1,10} = 12.65$; $Pr > F = 0.0052$) (Fig. 8), with values of 0.96 and 0.93, respectively. Given that these cohorts represent two groups of animals handled in precisely replicate manner from the same nesting location, the phenomenon is puzzling. However, the cohort remigration values also differ, with the 1988 cohort with the lower survival rate having a longer mean remigration value (2.80 years) and the 1987 cohort with the greater survival rate having a shorter mean remigration value (2.33 years) (Fig. 6), which may be related to the difference in survival rates. The two cohorts have been followed for sufficient years to rule out experimental error in coverage.

Fecundity. — The mean number of clutches per turtle during a nesting season is 4.5, with a pronounced mode of 5 (Fig. 9). Individuals chosen for this analysis initiated their nesting activity at least three weeks after the June 15 start of the patrol season and completed their nesting activity at least three weeks prior to the November 15 close of the patrol season. A small part of the sample (6%; n = 12) is represented by individuals observed nesting only once. If a few wander-

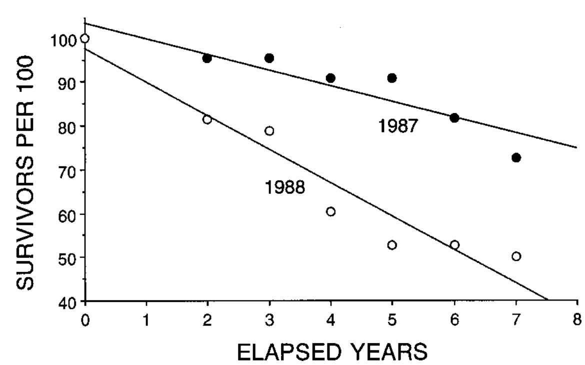

Figure 8. Comparison of survivorship of the individual 1987 (n = 22) and 1988 (n = 38) cohorts of adult nesting females plotted for 7 nesting seasons, Jumby Bay, Antigua. Linear regression models: 1987: $y = 103.31 - 3.56x$, $r^2 = 0.840$; 1988: $y = 97.49 - 7.64x$, $r^2 = 0.932$.

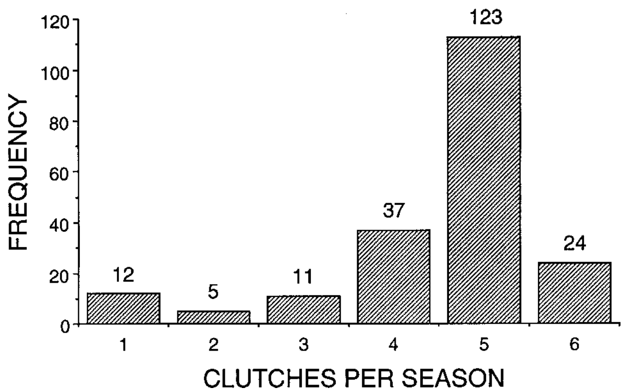

Figure 9. Frequency distribution of the number of clutches recorded per turtle during the nesting season, Jumby Bay, Antigua.

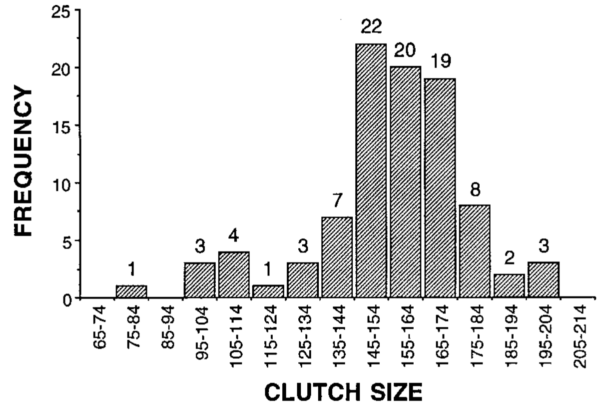

Figure 10. Frequency distribution of clutches by size class (increments of 10 eggs per class). Clutches were counted at time of laying, Jumby Bay, Antigua, 1996–97. Mean = 155 eggs/clutch, n = 93 nests.

ing turtles visit the study site at Jumby Bay only occasionally, this subset would appear to fit such an explanation. In fact, there exists a small pocket beach within 0.5 km of the study site which is inaccessible to the patrol because of its private ownership. This 20 m beach was carved from a limestone cliff by the property owner and provided with a supply of sand imported to the island. Perhaps a half dozen nests are believed to be placed at this location per year, which could explain the occasional appearance of a single-visit animal in the study population. The anomaly of one-time nesters is not great, and the difference between 5 and 4.5 clutches per turtle does not seem to affect the conclusions drawn. Since 4.5 is clearly a minimum estimate, a mean of 5 clutches per turtle has been chosen for population analysis purposes.

Clutch size was estimated from a stratified sample of nests counted during 1996 and 1997 in association with experiments testing the efficacy of relocation. A sample of 93 nests provided a mean of 155 eggs per clutch counted at the time of laying (Fig. 10). Post-emergent estimates of clutch size were not used in the calculation, in that egg shells at this time are frequently shredded by the activity of the hatchlings, introducing error into the estimate.

Emergence Success. — Seasonal emergence success can vary greatly. During the early years of this study (1987–92) when resort development was not a serious disturbance and the weather was peaceful, 55 randomly selected nests yielded an average emergence of 79% per clutch (Fig. 11). Emergence is defined here as the proportion of a clutch represented by hatchlings reaching the surface of the sand and dispersing to the water's edge. In 1989, Hurricane Hugo battered Antigua, but the sustained winds struck from the back of the beach, and virtually no damage occurred to the incubating clutches. In 1995, Hurricane Luis destroyed about 6000 eggs at the study site in a single night, along with a substantial portion of the unprotected remnant patches of beach vegetation within which the turtles nest. If the original maritime forest had been intact, the severity of the damage would have been far less. In 1996, construction activity was a problem on the beach, poaching was occurring, and Hurricane Bertha paid a glancing visit. A sample of 42 nests from 1996 produced an average emergence of 64% per clutch (Fig. 11), including three clutches destroyed by the storm, six clutches taken by poachers, and a single nest destroyed by another nesting turtle. This suggests that emergence success may become less in the future as a result of beach development. In the absence of mongoose predation and with adequate maritime shrub forest for protection from storms of average intensity, Jumby Bay hawksbills should have been capable of achieving 75% or greater emergence success per season in the decades leading up to this study, and human take was apparently not serious because of the insular location of the study site. Several direct hits per decade from hurricanes at mid-season could drop long-term emergence success at Jumby Bay by 10–20% in the future, but this is not a predictable trend. Thus, it is the historically logical 75% emergence value that has been chosen for additional calculations.

Sex Ratio. — Sex ratios of hatchlings from naturally incubating clutches have not been determined at Jumby Bay. *In situ* sand temperatures were taken in 1989 and 1990 at

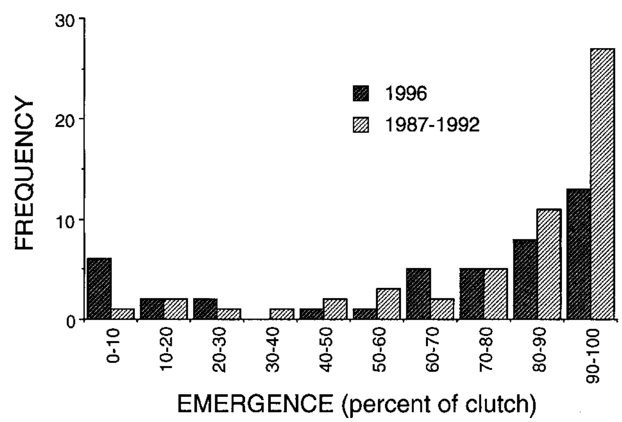

Figure 11. Frequency distribution of emergence success, defined as the proportion of a clutch represented by hatchlings reaching the surface of the sand and dispersing to the water's edge. Dark columns indicate clutches from 1996 (mean = 64.4% emergence, n = 43). Light columns indicate clutches from 1987–92 (mean = 79.2% emergence, n = 55). Jumby Bay, Antigua.

incubation depths and compared to the pivotal temperature (29.2ºC) calculated from two clutches of Jumby Bay eggs incubated in the laboratory (Mrosovsky et al., 1992). Sand temperatures were usually but not always lower than the pivotal temperature, suggesting that hatchling hawksbill turtles at Jumby Bay should not be female-biased. In lieu of additional data on the subject, a sex ratio of 1:1 has been chosen for calculations in this paper.

Population Size. — The average total adult female population using Jumby Bay, including those animals not nesting on any given year, may be approximated at 78 females by multiplying the mean annual cohort size (29.1 females) by the mean remigration value for the population (2.69 yrs). This estimate should not assume a population closed to immigration and emigration, although these parameters appear to be relatively minor, based on the nesting records of the turtles.

Population Recruitment and Mortality. — Annual mortality is estimated to be 6%, derived from the permanent disappearance of 4.8 individuals per year from the nesting population of 78 reproductively active females. Recruitment is estimated at 9%, derived from the ratio of the average number of neophytes observed per season (6.86 females) to the estimated population size (78 females). The uncertainty of these estimates and the annual variation in numbers of nesting females (Fig. 2) preclude the optimistic view that the Jumby Bay nesting population may be increasing at a rate of 2 females per season.

Annual Production of Eggs and Hatchlings. — An average of 29.1 actively nesting females each deposit 5 clutches of 155 eggs/clutch per season. This represents an individual seasonal fecundity of 775 eggs/female and an individual annual fecundity of 288 eggs/female per year based on a mean remigration interval of 2.69 years. The mean seasonal fecundity for the population is 22,550 eggs, the product of 29.1 females/season times 775 eggs/female. A 75% emergence success would produce 16,900 hatchlings annually for dispersal offshore, including 8450 female hatchlings if the population has a 1:1 sex ratio at emergence.

Lifetime Fecundity. — The linear model of survivorship (Fig. 7) predicts that 50% of the adults identified in a cohort will still be present in 8.1 years, just past the ninth nesting season. Thus, an average female might be expected to produce 775 eggs during her first season and then the equivalent of 288 eggs/year for 8.1 years of non-annual remigrations, for a lifetime total of 3108 eggs (1554 female eggs, assuming a 1:1 sex ratio). Based on these calculations and assumption, Jumby Bay beach has been producing an average of 8450 female hatchlings per year. Thus, if the Jumby Bay nesting population is considered to be stationary (not increasing or decreasing significantly in numbers) and each female is replacing herself, then the number of recruits should be 8450/1554 or 5.4 nesting females per season. This estimate approximates the 6.9 neophytes/season actually observed from 1991 to 1997.

Additional Predictions. — The value of this exercise is to explore the range of possible reproductive output requirements for an average individual hawksbill under various estimates of adult annual survival. Using the linear approximations to measured annual survival (Figs. 7 and 8), the following predictions can be offered, with $\boldsymbol{y}$ = turtles and $\boldsymbol{x}$ = years:

Combined 1987 and 1988 cohorts: [$y = 99.63 - 6.14x$]

- 50% of the females recruiting to the nesting population would be expected to survive for at least 8.1 years and produce 3100 or more eggs during 4.1 nesting seasons (as calculated above).
- 10% of these individuals would be expected to survive for at least 14.6 years and produce 4980 or more eggs during 6.4 nesting seasons.

1987 cohort: [$y = 103.31 - 3.56x$]

- 50%: 15.0 years; 5100 eggs in 6.6 nesting seasons.
- 10%: 26.2 years; 7550 eggs in 10.7 nesting seasons.

1988 cohort: [$y = 97.49 - 7.64x$]

- 50%: 6.2 years; 2560 eggs in 3.3 nesting seasons.
- 10%: 11.5 years; 4088 eggs in 5.3 nesting seasons.

DISCUSSION

The results in this paper are presented as an exploration of possible population dynamics. Few of the parameters have been definitively measured. Most will require at least an additional decade of intensive surveys for further clarification. Annual survival has been calculated only for the 1987 and 1988 season cohorts. With another decade of surveys, at least 10 additional season cohorts will become available for estimating annual survival. Annual survival of the combined 1987 and 1988 cohorts apparently fits a linear model over the 7-yr period investigated. Accepting such a model implies that an adult female has an equal probability of surviving from one year to the next, regardless of age. With an additional decade of surveys, survivorship could prove to be curvilinear, indicating increased survival potential with age or, conversely, possible senescence, but there is no evidence of this at the present time.

The number of years that a certain proportion of turtles might be expected to survive and the predicted egg production during this period are broad estimates. However, there is nothing contradictory in the results measured to date. The estimates of mortality and recruitment are comparatively close, supportive of a population that appears to be stationary or changing slowly in numbers. In addition, estimates of fecundity provide a prediction for recruitment that is close to measured recruitment. From this, it is apparent that less than one egg per thousand is surviving to adulthood under the conditions encountered by Jumby Bay hawksbills during their life cycle.

The estimates and predictions presented in this paper may not yet be robust, but they provide a starting point for discourse and present a challenge to other investigators who may arrive at different conclusions. For instance, at a fecundity of 288 eggs/yr, the average female must be allowed to survive and reproduce for at least 8 years (9 nesting seasons) to replace herself. Some individuals must be allowed to reproduce for multiple decades to balance the early mortality of other individuals. Turtles do not live forever, but if age to reproductive maturity in hawksbills proves to be 15–25 years (Boulon, 1994; van Dam, 1997), it would be commonplace for many hawksbills to live for half a century, and a centenarian would be a distinct possibility.

The next step for this work, in addition to firming estimates with statistical confidence, is perhaps to investigate those parameters that will never be conclusively measured during the lifetime of a single researcher and his/her team. Sex ratios, egg survival measured over decades, the potential for immigration and emigration, remigrant behavior, and survivorship of recent neophyte arrivals are such examples. Sensitivity analysis to a range of estimates for a single parameter is a logical direction to take. There was no attempt in this paper to provide a comparative analysis of results from other important hawksbill nesting studies. Merging beach data with in-water investigations is another important step to take. One only hopes that with time, our image of the population will take on a progressively sharper focus.

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