

Estimating the Annual Size of Hawksbill (*Eretmochelys imbricata*) Nesting Populations from Mark-Recapture Studies: the Use of Long-Term Data to Provide Statistics for Optimizing Survey Effort

RHEMA KERR^{1,2}, JAMES I. RICHARDSON², AND THELMA H. RICHARDSON²

¹Ministry of Agriculture, Kingston, Jamaica;

²Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

[E-mail: rhemaker@hotmail.com]

ABSTRACT.—Certain features of hawksbill (*Eretmochelys imbricata*) nesting biology have constrained survey and monitoring efforts. These are primarily the extended nesting season, the present low nesting densities, and cryptic nest sites. An important objective for conservation and management programs is the design of optimal survey protocols. This paper utilizes previously developed statistical analysis methodology for selecting two key variables of survey design, namely survey length and seasonal timing. We analyzed the frequency and distribution of nesting emergences of an eastern Caribbean population of hawksbills. We investigated the variation in precision of surveys of various durations (8, 12, 18, 21, 30, and 45 days) throughout the nesting season by resampling the nesting activity matrix of one long-term saturation tagging project at Jumby Bay, Antigua. The results show that although a 45-day survey gave the most precise estimates, the results for 18, 21, and 30-day surveys were sufficiently similar that a cost-benefit analysis might indicate the shorter time frame (18 days) as the optimal survey length.

KEY WORDS.—Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; surveys; Monte Carlo simulation; tag-recapture study; conservation; management; Antigua

Nesting beach studies still form the cornerstone of research and monitoring programs to estimate the status and trends in sea turtle populations. Yet the cost effectiveness of such programs, especially the tag-recapture component that many have incorporated, is under serious review (Witzell, 1998) due to the high costs for saturation-tagging projects, recent advances in alternative approaches such as satellite telemetry and DNA studies, and the difficulty in obtaining accurate estimates of demographic parameters.

While pertinent to all sea turtle species, the situation is perhaps most acute in the case of hawksbills (*Eretmochelys imbricata*). Recent proposals for ranching hawksbill populations use demographic parameter estimates that have fueled much debate. This debate stems in large part from the gaps in our understanding of hawksbill population ecology. Typically, few nesting aggregations remain (Meylan, 1989, 1999; Meylan and Donnelly, 1999). Where nesting still exists, it is diffuse both spatially and temporally. In areas as disparate as Australia and the eastern Caribbean, at least some hawksbill nesting activity occurs throughout the entire year (Limpus, 1980; Hoyle and Richardson, 1993). Nesting emergences on small isolated beaches, cryptic nest sites, and ephemeral crawls complete the suite of characteristics that increase the difficulties in estimating hawksbill populations (Meylan, 1989). There are many historic nesting sites in the wider Caribbean, with some record of nesting in 32 of the 35 geopolitical units (Meylan, 1989, 1999). Today only a very few support "significant" nesting activity (by our definition: as many as 5 nesting turtles on a busy night or a cumulative total of at least 20 turtles nesting per year). Most project managers and conservationists are thus faced with the pros-

pect of allocating personnel and other resources for a species with low encounter rates. Reducing survey effort while meeting conservation and management objectives is thus becoming an increasingly important goal for many hawksbill sea turtle recovery and management programs.

There have been several attempts to tackle the problem of optimal survey length and seasonal timing, and depending on the specific objectives, a number of valid approaches exist. In South Carolina, sea turtle surveys are conducted during a narrow 3-day window each month, at which time tidal patterns permit aerial surveys in the morning to distinguish sea turtle crawls made during the previous 24 hours (S. Murphy and T. Murphy, *pers. comm.*). Reynolds (1982) examined the effect of eliminating records from the saturation tagging program at Little Cumberland Island, off the Georgia coast, and estimated the proportion of the population observed against the proportion of the season covered.

More recently, Wetherall et al. (in press) looked at green turtle (*Chelonia mydas*) nesting in the French Frigate Shoals in the northwestern Hawaiian Islands. Their objective was to determine the expected numbers of nesters in an entire season from partial-season counts. Five years of saturation tagging throughout the entire nesting season provided the data for determining the nesting emergence patterns. They developed a statistical analysis method that examined the relative precision (as measured by the coefficient of variation) of nesting population estimates by bootstrapping (resampling with replacement) the nesting activity matrix a large number of times. They based optimal survey design on the survey period (10, 20, or 30 days) rendering the greatest precision in the estimated proportion of emerging turtles

caught in a partial-season survey and hence the greatest precision in the population estimate.

Such analyses have not been carried out with hawksbills. There are very few studies of this species that have incorporated saturation tagging for most of the nesting season. Our objective has been to apply comparable goals (maximizing survey precision) and methodology (resampling the frequency and distribution of a nesting activity matrix) to western Atlantic hawksbills. The method provides an estimate of the number of nesters that would have been encountered if the survey period had covered the entire nesting season, as well as sample statistics.

We used data from the Jumby Bay Hawksbill Project, a long-term saturation tagging project at Antigua in the eastern Caribbean, to examine the emergence pattern of nesting hawksbills. Using this information, we formulated a number of strategies that would have represented reduced survey effort and examined the precision of the estimates produced by each. We calculated the proportion of the annual nesting cohort "encountered" by surveys covering only segments of the 175 days actually covered. This approach calculated the sighting probabilities for each of these designated sampling periods and determined when and for which of these periods the relative variation in the sighting probability would be lowest. These results could then be used to support cost-benefit analyses for selecting from a number of alternate sampling strategies.

METHODS

The data set used is from the Jumby Bay Hawksbill Project, Long Island, Antigua, West Indies. These data represent the results of an 11-year saturation-tagging project of a population of nesting hawksbills in this eastern Caribbean country (Richardson et al., 1999). This unique data set is virtually ideal for determining an optimal survey strategy because it is based on a relatively large multi-year data set. With nightly patrols between June and November annually, the Jumby Bay study is one of the most intensively surveyed marine turtle populations in the world. This level of coverage is the result of more than 15,000 dusk-to-dawn patrols by a two-person team tagging and recording all encounters. Despite the length of this reference season, the entire population is not encountered during this period, an important reason why this estimate of number of emerging nesters is not an unbiased estimate of true abundance. In addition to traditional double-tagging (a tag on each front flipper), Jumby Bay animals are given unique drill patterns on the most posterior marginal scutes, reducing the problems of incorrect identification due to tag loss to very low levels (Hoyle and Richardson, 1983). The Jumby Bay population is atypical in two respects. First, the 21–38 animals that have comprised the annual nesting cohorts appear on a very small beach (less than 300 m) and represent a relatively high nesting density. Secondly, the privately owned island provides protection for the nesting turtles and their clutches.

Applying the methodology developed by Wetherall et al. (in press), we used SAS 6.11 (SAS Institute, 1988) to create a nesting activity matrix for the $M_{(j)}$ nesters identified during the n nights covered during each of the J years of M saturation surveys, where $M_{(j)} = 320$, $n = 175$, and $J = 11$. Nesting activity was described during each of the n nights by a 1 (emergence) or a 0 (non-emergence). $M_{(j)}$ is not the number of individual nesters, but the cumulative number of nesters seen in 11 years, with most animals encountered in multiple years. Establishing a starting date of 2 July (the date by which all surveys had started), we used the nesting activity matrix to estimate the proportion of the $M_{(j)}$ nesters sighted at least once during the specified survey period (sighting probability, \hat{p}). Surveys were of varying lengths (8, 12, 18, 21, 30, or 45 sequential days) throughout the season. Our selected survey periods were non-overlapping in all cases, i.e., 18-day periods started on 2 July, 20 July, 7 August, etc. The assumptions here are: 1) the emergence events are independent, and 2) as a nesting turtle is represented by only two possibilities (seen or not seen) then the number of nesters seen during a survey is a binomial random variable.

We used the coefficient of variation around estimates of sighting probability as a measure of the precision of the estimates of annual numbers of nesting females based on the following:

Coefficient of variation (c.v.) = σ/\bar{x} (where σ = standard deviation = $\sqrt{\text{Var}}$; \bar{x} = sample mean);

Let \hat{N} = Expected (E) number of nesters for n nights of a saturation all-season survey; let M = number of individual nesters sighted in a partial-season survey; then

$$\hat{N} = M \cdot \frac{1}{\hat{p}} \quad [1]$$

Ignoring the variability in M (treating M as a constant):

$$E \hat{N} = M \cdot E\left[\frac{1}{\hat{p}}\right]$$

$$\text{Var } \hat{N} = M^2 \cdot \text{Var} \frac{1}{\hat{p}} \quad [2]$$

$$\begin{aligned} \text{c.v. } \hat{N} &= \frac{\sqrt{\text{Var } \hat{N}}}{E[\hat{N}]} \\ &= \frac{\sqrt{M^2 \text{Var} \frac{1}{\hat{p}}}}{M \cdot E\left[\frac{1}{\hat{p}}\right]} \\ &= \frac{\sqrt{\text{Var} \frac{1}{\hat{p}}}}{E\left[\frac{1}{\hat{p}}\right]} \\ &= \text{c.v. } \frac{1}{\hat{p}} \quad [3] \end{aligned}$$

We estimated the c.v. of $1/\hat{p}$ from a Monte Carlo simulation exercise. We chose a simulation because it replaces the uncertain asymptotic error of other methods, with an uncertain Monte Carlo error. This error can be estimated with statistical software such as SAS. For each proposed survey, recording whether each of the $M_{(j)}$ nesters was sighted at least once during the survey period, we created an $M_{(j)} \times 1$ matrix of 1's and 0's and computed an estimate of (proportion sighted at least once) for each survey. We used a computer-generated algorithm to estimate the sampling distribution of $1/\hat{p}$. The sampling distribution of a statistic is the frequency distribution of that statistic calculated from an infinite number of random samples. We used SAS to generate random probabilities from a uniform distribution $U(0,1)$. Through an iterative process, the algorithm generated a cumulative probability ($1/\hat{p}$) from $M_{(j)}$ iterations based on whether the simulated random probability was greater than \hat{p} . The simulation was then repeated 1000 times. The results of the simulation exercise produced an empirical distribution function (EDF), hence an estimate for the relative variation (coefficient of variation) of $1/\hat{p}$. The values of \hat{p} obtained from each survey period were used to define the population randomly generated by the simulation process. This is based on the fundamental assumption that the EDF calculated from the resamples [denoted as $*F(1/\hat{p})$] is a good approximation of the sampling distribution of $1/\hat{p}$. The decision to use only 1000 trials is related to only slight improvement in the estimation of the statistic beyond this number (Efron and Tibshirani, 1986). We did, however, examine the effect of increasing the number of simulations (using 2000 and 5000 trials) on the shape of the distribution.

Table 1. Sighting probabilities for surveys lasting 8, 12, 18, 21, 30, or 45 days.

Survey Period	8-day		12-day		18-day		21-day		30-day		45-day	
	mean	std.	mean	std.	mean	std.	mean	std.	mean	std.	mean	std.
1	0.144	0.351	0.234	0.424	0.334	0.423	0.353	0.479	3.97	0.490	0.522	0.500
2	0.197	0.398	0.263	0.441	0.388	0.488	0.422	0.495	0.575	0.495	0.684	0.465
3	0.172	0.378	0.309	0.463	0.450	0.498	0.509	0.501	0.597	0.491	0.494	0.501
4	0.212	0.410	0.369	0.483	0.531	0.499	0.522	0.500	0.475	0.500		
5	0.206	0.405	0.325	0.469	0.500	0.501	0.466	0.499	0.241	0.428		
6	0.275	0.447	0.403	0.491	0.425	0.495	0.334	0.472				
7	0.200	0.401	0.425	0.495	0.294	0.456	0.294	0.456				
8	0.325	0.469	0.378	0.486	0.181	0.386						
9	0.209	0.408	0.328	0.470								
10	0.297	0.458	0.253	0.435								
11	0.216	0.412	0.206	0.405								
12	0.281	0.450	0.091	0.288								
13	0.203	0.403										
14	0.188	0.391										
15	0.188	0.391										
16	0	0										
17	0.138	0.345										

The c.v.'s obtained from the simulation were plotted against the selected survey start dates.

RESULTS

Sighting probabilities (\hat{p}) for the six different partial-season survey periods are shown in Table 1. Comparing start-of-the-season values (the first survey period), these values ranged from 0.144 in the 8-day surveys to 0.522 for one 45-day survey. Values of $\hat{p} > 0.5$ (at least 50% of the expected nesters sighted) were obtained by 2 of 8 survey periods for surveys lasting 18 days, and 6 of 15 survey periods for surveys lasting 21 days or longer. Figs. 1 and 2 show yearly variation in sighting probabilities with selected survey start dates for 18-day and 30-day surveys.

We conducted a chi-squared test of homogeneity to test whether inter-annual variation in \hat{p} was significant. If the variability was significant it would preclude the use of the

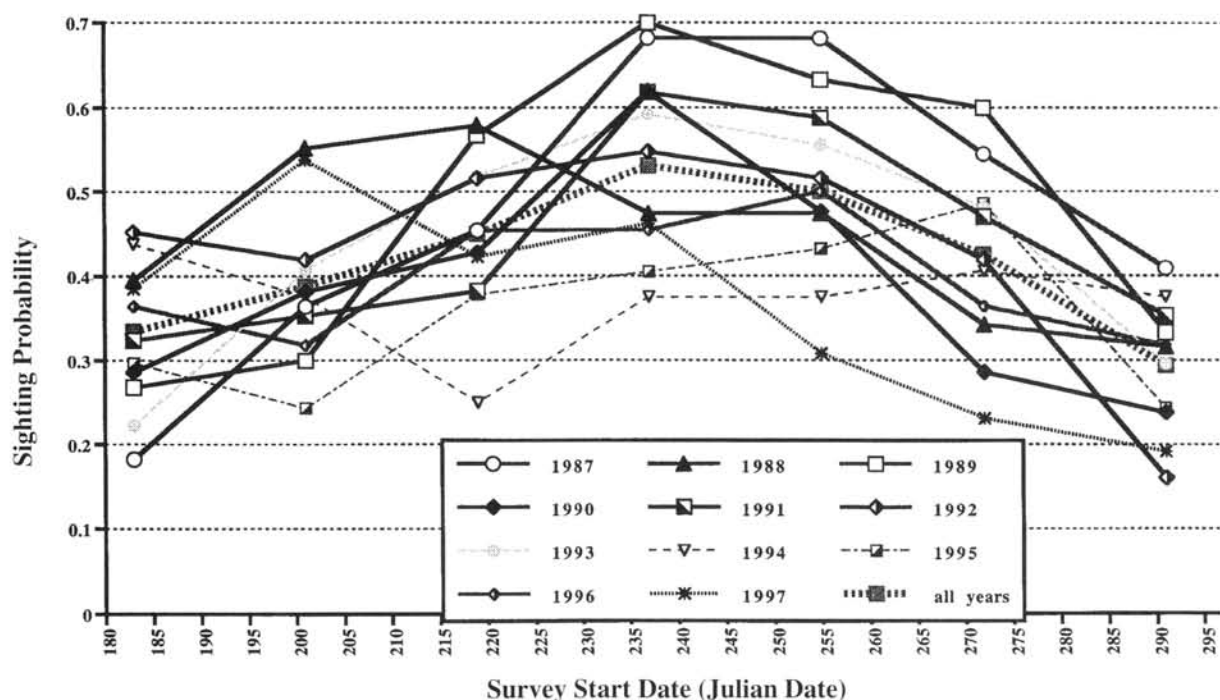


Figure 1. Estimates of the proportion of the annual nesting cohort (sighting probability, \hat{p}) "encountered" by surveys lasting 18 days. Jumby Bay hawksbills, 1987–97.

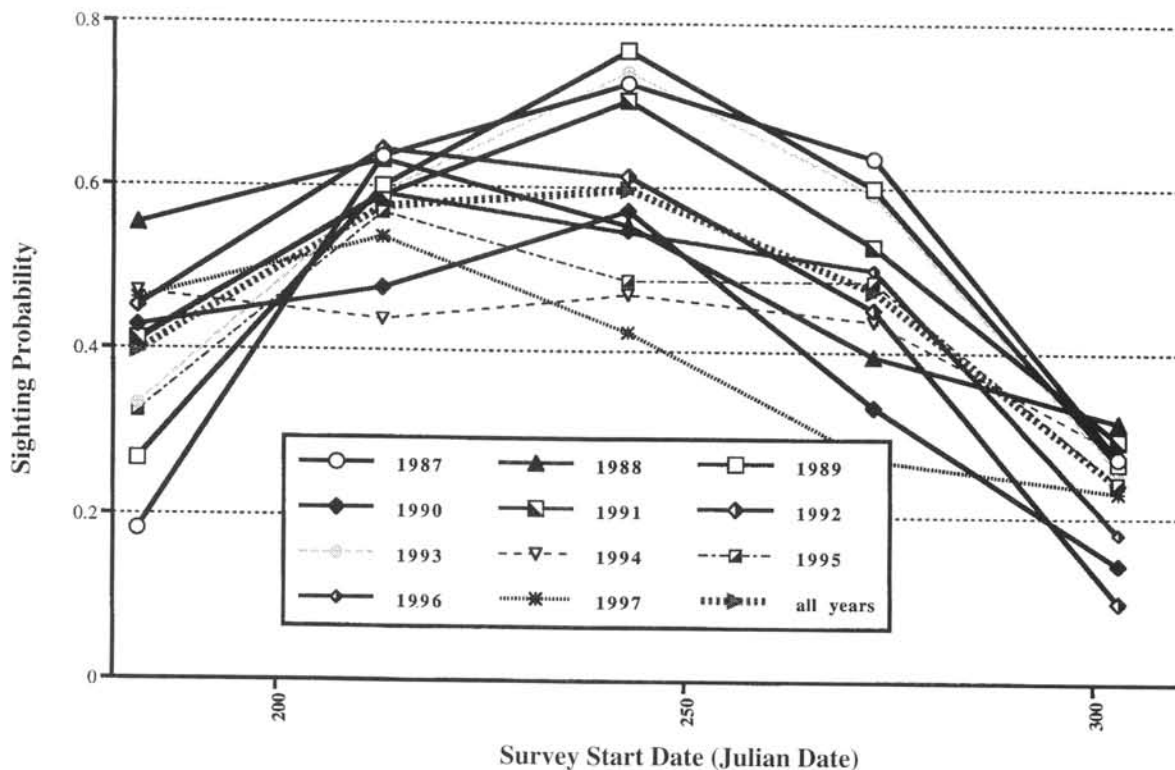


Figure 2. Estimates of the proportion of the annual nesting cohort (sighting probability, \hat{p}) "encountered" by surveys lasting 30 days. Jumby Bay hawksbills, 1987–97.

combined multi-year data set. We performed this test on both 18-day and 30-day surveys and it was not significant for either survey time frame (18-day surveys, $\chi^2 = 13.14$, $p = 0.216$; 30-day surveys, $\chi^2 = 17.11$, $p = 0.07$). We therefore performed the simulation using the combined data set of all nesters over the 11 years, as a larger sample size would provide a better approximation of the sampling distribution $F(1/\hat{p})$.

The frequency distribution of $1/\hat{p}$ derived from the simulation is shown in Fig. 3, and has approximately normal distribution. The simulation shows only moderate improvement with increasing number of trials. Fig. 4 illustrates the effect of survey start date and length on the

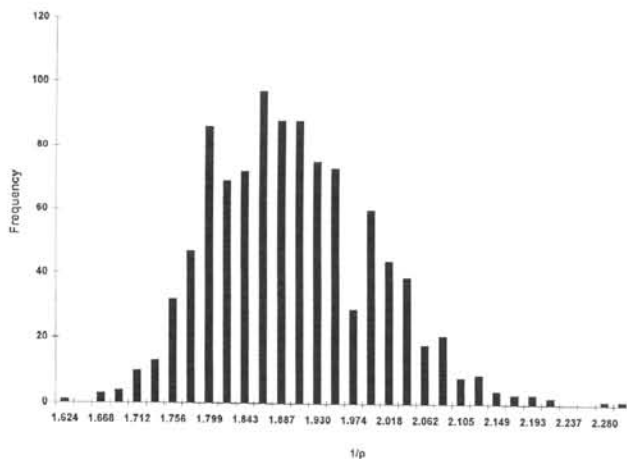


Figure 3. Frequency distribution of $1/\hat{p}$ derived by Monte Carlo simulation, 1000 trials.

precision of the estimates for the Jumby Bay data set. The values generated by the simulation exercise are plotted against the survey start dates (Julian date). The general shape of the curve is similar for all 6 survey periods, showing an increase in precision (decrease in variation) toward a maximum as the season progresses, followed by a decline in precision towards the end of the season. Surveys of 8 days had the lowest precision and greatest variability in the estimates, suggesting that this is too short a period for reliable estimates. Of the alternatives studied, the most precise estimates could be achieved by conducting 45-day surveys or longer. However, the gain in precision compared to 18-day and 30-day surveys (approximately 5.2% to 3.5%) may not be worth the additional cost. Thus 18-day surveys started within the period 25 August to 11 September (Julian dates 237 to 254) have c.v.'s ranging from 5 to 5.5%, an acceptable level of precision under most circumstances.

DISCUSSION

Our analysis of the impact of the timing and duration of partial-season surveys on survey precision indicates that there is only moderate gain in extending surveys beyond 18 days. In the case of Jumby Bay hawksbills, satisfactory precision can be gained by conducting 18-day surveys between late August and early September.

We believe the method can be applied to extrapolate from a partial-season survey to an estimate of total seasonal nesting, as per the following example:

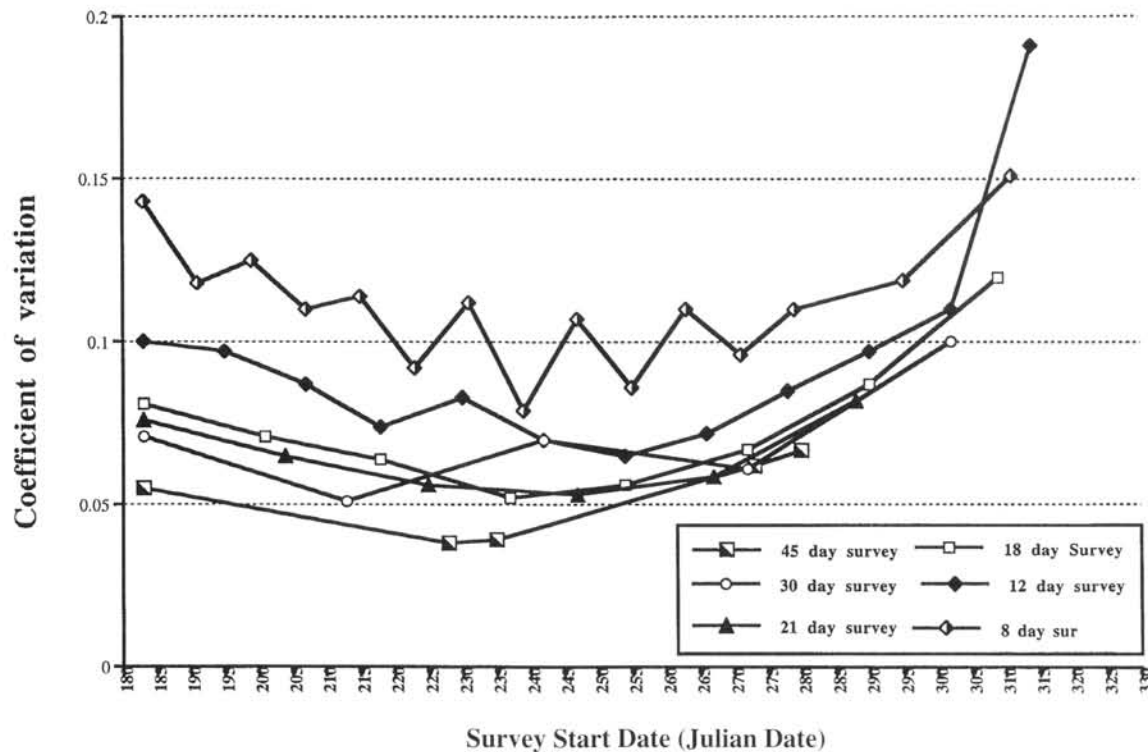


Figure 4. Relative precision of nesting beach surveys lasting 8, 12, 21, 30, or 45 days based on the simulated variation in sighting probability.

A survey of an insular Caribbean hawksbill population starting on August 25 and extending for 18 days yields a count of 20 nesters encountered during that period. Using the Jumby Bay estimate, \hat{p} for that period is 0.5312. The c.v. ($1/\hat{p}$) for the estimate, equal to the c.v. of \hat{N} for that survey period and length, is 0.05.

Using Equation [1]:

$$\begin{aligned}\hat{N} &= M \cdot \frac{1}{\hat{p}} \\ &= \frac{20}{0.5312} \\ &= 37.65 \text{ (total seasonal nesters predicted).}\end{aligned}$$

Confidence intervals for \hat{N} can be non-parametrically estimated by determining the values of $1/\hat{p}$ within the desired confidence interval and relating this to Equations [1] and [2].

The method uses straightforward SAS programming. The technique for analyzing the frequency and distribution of mark-recapture data offers a method for estimating the size of the annual nesting cohort. The assumptions made under this method are tenable and include: 1) a lack of "trap response" and 2) independence of nesting events. The Jumby Bay data suggest neither trap-wary nor trap-happy responses from the tagged nesters (Hoyle and Richardson, 1993). Independence of nesting events means that the timing of the emergence of a nesting female is independent of the emergence of other nesters. This would not be the case for ridley turtles (*Lepidochelys* spp.), but no evidence exists for any

similar non-independent nesting behavior for current hawksbill populations.

The method allows us to estimate the number of animals that would have been sighted in a season as defined by the period of the saturation survey, but it is not an unbiased estimate of abundance \hat{N} . An unbiased estimate would require assumptions of 1) population closure over 11 years and 2) complete enumeration of the population. As the 175 days covered by the saturation survey each season is not the entire period during which nesting animals will emerge, this is not a tenable assumption.

There are four categories of error in estimating population parameters: error due to demographic and environmental fluctuations, systematic error, random error, and error due to sampling (Conroy and Smith, 1994). The research design of the Jumby Bay hawksbill project (consistent all-night patrols, saturation tagging, and double marking system) minimizes sampling error. The opportunities for systematic error are relatively few, but do include less-than-expected philopatry and nesting activity outside of the survey hours. A gross estimation of this error would be the number of expected emergences (based on the expected number of clutches per turtle and the mean interval between nesting episodes) that were missed by the patrol team. The estimate on the number of these missed events suggests a very small error (Hoyle and Richardson, 1993). There is also no evidence that western Atlantic hawksbills nest in any great degree during the daytime. The estimates of \hat{p} are thus an approximate measure of the variability due to demographic and environmental fluctuations and random errors.

A further assumption is that the empirical distribution function (EDF) generated by the simulation is a good estimator of the population distribution function (PDF). Underlying this is the general assumption that the sample is a good approximation of the population. Using the 11 years of data provides a large sample ($n = 320$). The high capture probabilities suggest that all females nesting between June and November from 1987 to 1997 have been sampled. While $*F(1/\hat{p})$ does not estimate $F(1/\hat{p})$ perfectly, we can expect EDF under these circumstances to approach the population mass function (Mooney and Duval, 1993).

Applying this method requires the assumption that the timing and distribution of the nesting emergences of the Jumby Bay nesting population and another population being surveyed are the same. Data from projects in Barbados, St. Croix, and Puerto Rico suggest similar patterns of nesting activity, however, Yucatán hawksbills appear to be very different (M. Garduño, *pers. comm.*). Why Mexican hawksbills should show a difference in nesting patterns is unclear. It is conceivable that human exploitation and harvesting might provide selective pressures favoring those animals that nest outside of the expected season, and hence alter the nesting emergence patterns. Such a shift in the nesting distribution of exploited populations might limit the usefulness of the non-harvested Jumby Bay population as a comparable model. Comparative analyses to test this hypothesis will be difficult, as the statistical tests will probably have low power due to the limited number of hawksbill tagging projects in the western Atlantic and the differing levels of sampling effort.

Nesting beach studies should and will continue to have a variety of research aims and objects. Many of these may be more important in determining the form and timing of research projects and survey effort than considerations of optimal sighting probabilities. While many more challenges remain in estimating hawksbill demographic parameters, we hope that this analysis will facilitate an increase in hawksbill survey and monitoring programs in the wider Caribbean.

ACKNOWLEDGMENTS

The authors wish to thank Jerry Wetherall (National Marine Fisheries Service, Honolulu Lab), Phillip Dixon (Savannah River Ecology Laboratory, University of Georgia), Clint Moore (Warnell School of Forest Resources, University of Georgia), Michael Pryce (Ministry of Agriculture, Jamaica), and the many persons and organizations that have supported the project since 1987. Last, but by no means

least, to all the survey teams whose dedication and hard work made the data collection and subsequent analysis possible, we extend our appreciation.

LITERATURE CITED

- CONROY, M.J., AND SMITH, D.R. 1994. Designing large scale surveys of wildlife abundance and diversity using statistical sampling principles. Trans. 59th North American Wildlife and Natural Resources Conference.
- EFRON, B., AND TIBSHIRANI, R. 1986. Bootstrap methods for standard errors, confidence intervals and other measures of statistical accuracy. *Statistical Science* 1:54-77.
- HOYLE, M., AND RICHARDSON, J.I. 1993. The Jumby Bay hawksbill project: survivorship, mortality, recruitment and reproductive biology and behavior of adult female hawksbill sea turtles (*Eretmochelys imbricata*) nesting at Pasture Bay, Long Island, Antigua, W.I. Athens, GA: Unpublished Technical Report, Georgia Sea Turtle Cooperative, Institute of Ecology, University of Georgia, 76 pp.
- LIMPUS, C.J. 1980. Observations on the hawksbill turtle (*Eretmochelys imbricata*) nesting along the Great Barrier Reef. *Herpetologica* 36:265-271.
- MEYLAN, A.B. 1989. Status report of the hawksbill turtle (*Eretmochelys imbricata*). In: Ogren, L., Berry, F., Bjørndal, K., Kumpf, H., Mast, R., Medina, G., Reichart, H., and Witham, R. (Eds.). Proceedings of the Second Western Atlantic Turtle Symposium. NOAA Tech. Memor. NMFS-SEFC-226, pp. 101-115.
- MEYLAN, A.B. 1999. Status of the hawksbill turtle (*Eretmochelys imbricata*) in the Caribbean region. *Chelonian Conservation and Biology* 3(2):177-184.
- MEYLAN, A.B., AND DONNELLY, M. 1999. Status justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as Critically Endangered on the 1996 IUCN Red List of Threatened Animals. *Chelonian Conservation and Biology* 3(2):200-224.
- MOONEY, C.Z. 1997. Monte Carlo Simulation. Newbury Park, CA: Sage.
- RICHARDSON, J.I., BELL, R., AND RICHARDSON, T.H. 1999. 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. *Chelonian Conservation and Biology* 3(2):244-250.
- SAS. 1988. SAS Introductory Guide for Personal Computers. Release 6.03 Edition. Cary, NC: SAS Institute.
- WETHERALL, J.A., BALAZS, G.H., AND YONG, M.Y.Y. In press. Statistical methods for green turtle nesting surveys in the Hawaiian Islands. Proc. 17th Symp. Sea Turtle Conserv. Biol., 4-8 March 1997, Orlando, Florida.
- WITZELL, W.N. 1998. Messages in bottles. *Marine Turtle Newsletter* 80:3-5.

Received: 1 August 1998

Reviewed: 31 January 1999

Revised and Accepted: 7 March 1999