Twenty-Six Years of Green Turtle Nesting at Tortuguero, Costa Rica: An Encouraging Trend

KAREN A. BJORNDAL,*§ JERRY A. WETHERALL,† ALAN B. BOLTEN,*
AND JEANNE A. MORTIMER‡

*Archie Carr Center for Sea Turtle Research and Department of Zoology, University of Florida, Gainesville, FL 32611, U.S.A.
†National Marine Fisheries Service, 2570 Dole Street, Honolulu, HI 96822, U.S.A.
‡Caribbean Conservation Corporation, 4424 N.W. 13th Street, Gainesville, FL 32609, U.S.A.

Abstract: *The green turtle (*Chelonia mydas*) population that nests at Tortuguero, Costa Rica, is the largest in the Atlantic by at least an order of magnitude. Surveys to monitor the nesting activity on the northern 18 km of the 36-km beach were initiated in 1971 and extended to the entire beach in 1986. From the survey data, we estimated the total number of nesting emergences on the northern 18 km for each year from 1971 through 1996. Evaluation of the trend in nesting emergences indicated a relatively consistent increase from 1971 to the mid-1980s, constant or perhaps decreasing nesting during the late 1980s, and then resumption of an upward trend in the 1990s. Evaluation of trends in sea turtle nesting populations requires many years of data because of the large degree of annual variation in nesting numbers. The trends reported in this study must be evaluated with caution for several reasons. First, if the mean number of nests deposited by each female each year (clutch frequency) varies significantly among years, changes in the number of nesting emergences among years could reflect changes in the number of nesting females, clutch frequency, or both. Second, we only assessed the trend in one segment of the population (mature females), which may or may not represent the trend of the entire green turtle population and which, because of late maturity, may not reflect changes in juvenile mortality for many years. Third, survey frequency, and thus confidence in annual estimates, varied among years. The upward population trend must be assessed from the perspective of the catastrophic decline that the Caribbean green turtle populations have experienced since the arrival of Europeans. If careful management is continued in Costa Rica and adopted throughout the region, the collapse of the Caribbean green turtle populations—which seemed imminent in the 1950s—can be avoided.*

Veintiséis Años de Nidación de la Tortuga Verde en Tortuguero, Costa Rica: Una Tendencia Alentador

Resumen: *La población de tortuga verde (*Chelonia mydas*) que anida en Tortuguero, Costa Rica, es la más grande del Atlántico en por lo menos un orden de magnitud. Muestreos para monitorear la actividad de nidada en 18 km al norte de un total de 36 km de la playa fueron iniciados en 1971 y extendidos para toda la playa en 1986. De los datos de muestreos estimamos que el número total de salidas para anidar indican un incremento relativamente consistente de 1971 hasta mediados de los 1980s y la reaparición de una tendencia de incremento en los 1990s. Evaluaciones de tendencias en poblaciones de tortugas anidando requieren de muchos años de datos debido al alto grado de variación anual en los números de nidaciones. Las tendencias reportadas en este estudio deben ser evaluadas con precaución por diversas razones. Primero, si el promedio de nidos depositados por cada hembra cada año (frecuencia de nidada) varía significativamente entre años, cambios en el número de salidas para anidar entre años pueden reflejar cambios en el número de hembras anidando, en la frecuencia de nidada o ambos. Segundo, únicamente evaluamos las tendencias en un segmento de la población y la cual, puede o no, representar las tendencias de toda la población de tortuga verde, la cual a su vez, podría no reflejar cambios en la mortalidad de juveniles por muchos años*

---

§*Address for correspondence: Department of Zoology, P.O. Box 118525, University of Florida, Gainesville, FL 32611, U.S.A., email kab@zoo.ufl.edu*

Paper submitted August 11, 1997; revised manuscript accepted March 2, 1998.

Conservation Biology, Pages 126–134
Volume 13, No. 1, February 1999

debido a una madurez tardía. Tercero, los muestreos de frecuencias y por lo tanto la confianza en las estimaciones anuales varían entre años. La tendencia creciente de la población deberá ser evaluada desde la perspectiva de una disminución catastrófica que las tortugas verdes del Caribe han experimentado desde el arribo de los Europeos. Si el manejo cuidadoso continúa en Costa Rica y es adoptado en toda la región, el colapso de las poblaciones de tortuga verde del Caribe—que parecía inminente en los 1950s—puede ser evitado.

Introduction

The population of green turtles (*Chelonia mydas*) that nests at Tortuguero, Costa Rica, is the largest in the Atlantic by at least an order of magnitude (Lahanas et al. 1998). Turtles from this population disperse throughout the Greater Caribbean, as indicated by recaptures of adult females tagged at Tortuguero (Carr et al. 1978) and by evaluation of genetic markers in juvenile green turtle populations (Lahanas et al. 1998). The status of green turtle populations on foraging pastures in many nations throughout the Greater Caribbean depends on the status of the Tortuguero nesting population.

In 1954 Archie Carr wrote about the "passing of the fleet" and reported his fears for the future of the Caribbean green turtle (Carr 1954). In those years nearly every female green turtle that came ashore to nest on Tortuguero Beach was intercepted by *veladores* ("stayers awake") and shipped to market. The conservation outlook for the Caribbean green turtle appeared so bleak that from 1959 to 1968 Carr conducted "Operation Green Turtle" in which, with the help of the U.S. Navy, he distributed green turtle hatchlings from Tortuguero to other, diminished green turtle rookeries throughout the Caribbean in the hope of forestalling the collapse of the Caribbean green turtle populations (Eliazar et al., in press).

The Tortuguero green turtle population survived this period of intense exploitation, probably in large part because the large number of age classes in the subadult portion of the population continued to supply recruits to the breeding population, even after years of complete harvest on the nesting beach (Bjorndal 1985). Although it buffers the population against extinction during periods of heavy harvest, the long interval to sexual maturity also slows the rate of recovery. Thus, positive responses to management actions on the nesting beach—in the form of increased numbers of nesting females—may take many years to appear.

This lag time in response to changes in management, either increasing or decreasing population productivity, is characteristic of long-lived species (Congdon et al. 1993, 1994; Heppell et al. 1996*a*). The difficulty of assessing the effects of management actions is compounded in species that are difficult to census, such as wide-ranging marine organisms. These obstacles to assessing population change are among the major challenges in the conservation of long-lived marine species (Norse 1993; Dayton et al. 1995).

In 1971 Archie Carr initiated surveys of the numbers of nesting emergences at Tortuguero. We estimated the total number of nesting emergences at Tortuguero Beach each year from 1971 through 1996 in the northern 18 km of beach and assessed trends in annual nesting emergences over those 26 years. Also, to evaluate survey methods, we examined the relationship between survey frequency and the precision of the total emergence estimate.

Methods

Surveys

Green turtles emerge from the ocean at night to nest, and evidence of their emergences persists in the form of tracks and body pits—craters about 0.5 m deep that the turtles create during the nesting process. These emergences do not always result in a nest; for a variety of reasons, green turtles will return to the ocean without depositing a clutch. Surveys were conducted on foot, early in the morning, by an individual experienced in distinguishing between nesting emergences and non-nesting emergences. Almost all surveys were conducted by four members of the Rankin family, long-time residents of Tortuguero village. During each survey, the number of nesting emergences from the previous night were recorded for each 0.2-km interval. Attempts were made to survey the beach weekly during the nesting season, but logistical problems sometimes interfered (Table 1). In our analyses of nesting emergences on the northern 18 km, we used data from 18-km surveys and the northern half of the 36-km surveys. Beginning in 1986, 36-km surveys were sufficiently frequent to allow comparison of nesting estimates for the southern 18 km with those of the northern 18 km. In 1994 and 1995 the beach south of km 30 became inaccessible when the river behind the beach washed over the beach. Because this southernmost area supports very low levels of nesting (the three surveys in 1994 and 1995 that did include the area south of km 30 reported no nesting emergences, and less than 1% of all nesting emergences occurred in that area in

Table 1. Number of nesting surveys and dates on which they were conducted at Tortuguero, Costa Rica.

	Survey[a]		*Survey date*[b]					
Year	*18-km*	*36-km*	*June*	*July*	*August*	*September*	*October*	*November*
1971	8	0	—	—	23,28*	3,9,18,25	2,9	—
1972	18	0	29	9,15,22,30	5,14,19,27	2*,10,16,24	7,15,22,29	5
1973	14	0	30	4,7,22,29	19*	16,23,30	7,14,21,28	4
1974	10	0	—	11,13	3,11,18,25	6*,28	12,31	—
1975	12	0	28	5,12,21,27	4,11,18,25	1,8*	11	—
1976	14	0	—	5,11,17	7*,15,22,31	8,12,19	1,7,16,25	—
1977	13	5	22	3,9,16,23,30	7,13,20,27	3*,10,17,24	2,8,29	5
1978	12	4	—	1,8,15,22,29	8,19,29*	2,11,20,30	6,15,22,29	—
1979	8	7	25,30	7,14,21,28	4,12,18,25	2,9*,16,24	7	—
1980	7	4	—	3,10,18,24	1,7,15*,21,28	6,11	—	—
1981	6	5	—	1,16,23,28	6*,13,20,27	3,10,17	—	—
1982	10	0	—	14,20,28*	6,13,18,25	1,9,15	—	—
1983	9	3	—	1,7,25	2*,8,15,19,27	2,12,19	2	—
1984	6	7	—	9,16,23,30	6,14*,20	1,7,13,25,29	16	—
1985	5	5	—	13,20,27	3,10,18,24*,31	7,14	—	—
1986	0	12	—	23,30	7,14,22*,29	6,11,17,25	2,10	—
1987	0	12	—	3,11,17,25	2,8,14,23,28	4*,11,20	—	—
1988	0	19	24	2,8,16,23,30	5,13,19,27*	3,10,17,24,30	9,15,25	6
1989	0	11	—	7,15,21,30	5,12,20,27	2,10,15*	—	—
1990	0	12	—	9,17,21,28	5,11,21,27*	1,8,22,29	—	—
1991	1	16	—	10,16,24,31	7,14,21,29*	7,12,30	10,17,25,30	7,14
1992	0	15	—	8,13,20,29	5,11,18,25	3,13*,21,26	1,19,24	—
1993	0	18	—	2,9,16,23	4,11,16,21,27*	3,10,17,24	1,8,15,22,29	—
1994[c]	0	19	—	4,10,20,24	1,7,19,24,31*	14,25	2,9,15,20,27	23,30
1995	0	10	24,28	7,12,20,28	4,15,24*,28	—	—	—
1996	0	11	8,22	2	7,13,20	4*	5,12,17,26	—

[a] *The 18-km surveys were conducted on the northern half of the 36-km beach.*
[b] *Dates with an asterisk (*) are surveys with the highest count for the year.*
[c] *Last survey on 4 December.*

1996), surveys of the 30 km were used as 36-km surveys for 1994 and 1995.

Estimating Annual Nesting Emergences and Assessing the Trend

Scatterplot smoothing (Härdle 1990; Hastie & Tibshirani 1990; Simonoff 1996) was used to estimate each year's pattern of nesting emergences. Annual survey data were regarded as a sample time series drawn from a stochastic process of nightly emergence activity. The relationship between the nightly number of nesting emergences and Julian date was then approximated by fitting a cubic smoothing spline ("smooth") to each time series using the generalized additive model function, *gam()*, of S-plus software (Mathsoft, Inc., Seattle, Washington). Predicted nightly nesting emergences derived from the smooth were integrated over the nesting season to estimate total nesting emergences in the northern section (1971–1996) and southern section (1986–1996).

Each time series of survey counts was incomplete. Not only were many nights skipped between surveys, but nesting activity occurred outside the range of survey dates at the beginning and end of each nesting season. Accordingly, prior to the spline fitting, artificial endpoints were added to each time series and given a value of zero emergences. The selected endpoints were 30 May and 15 November; these dates bracketed the months of substantial nesting (Carr et al. 1978) and all survey dates during 1971–1996, except for three survey dates in late November and early December 1994 on which a negligible number of emergences were observed. To account for uncertainty about the start and finish dates, endpoints were downweighted relative to observed emergence counts during the spline fitting. Arbitrary weights of 1.0 were assigned to each observed survey count, and weights of 0.10 were given to endpoints. A uniform weighting scheme was also tried. After smooths were generated, emergence counts for nights between survey dates were estimated by interpolating between knots of the fitted spline.

The spline integration covered predicted nesting activity both inside and outside the observed range of survey dates. Negative predicted counts were trimmed from tails of the smooths and remaining predicted counts were summed to estimate total annual nesting emergences.

The *gam()* procedure estimated the standard error of the predicted count for observed survey dates and endpoints only. A separate S-plus routine was written to interpolate the standard errors for dates not surveyed. Daily variances were integrated to yield a measure of precision for the annual estimate of total nesting emergences.

The cubic spline procedure was also used to smooth the 26-year time series of annual nesting emergence estimates in the northern section. In this application of *gam()* no interpolation was required (there were no data missing). The annual estimates of total nesting emergences were weighted uniformly, and pointwise error bands of ±2 SE were generated for the smooth.

Monte Carlo Analysis of Survey Frequency

The effect of survey frequency on estimates of total nesting emergences was assessed by applying smoothing splines to samples of output from a simulation model of nesting activity and survey coverage. The simulation model was constructed to mimic four stochastic processes that determine a nester's emergence history: arrival date (nights after first emergence); clutch frequency (number of nesting episodes); duration of a nesting episode; and internesting interval. Each process was characterized by a probability distribution (Fig. 1) estimated from information in Carr et al. (1978) and used to generate a typical time series of nesting counts.

A Monte Carlo sampling algorithm was applied to the four process distributions to generate a season's composite nesting history for 10,000 nesters. Independence between nesters and between processes was assumed because there are no data to support a more elaborate model with some pattern of dependency among the processes. Also, the assumption of independence is not critical to judging the applicability of the *gam()* smoothing procedure. Artificial survey data were produced from each simulated time series of nesting emergences by sampling the series at intervals of 1 to 65 nights and applying a random survey coverage rate (termed "efficiency" by Carr et al. [1978]). Due to the length of the nesting season, 65 nights was the maximum survey interval because the *gam()* smoothing requires a minimum of four data points (including endpoints). True endpoints of nesting activity were always included in the set of survey observations. The *gam()* procedure was used to fit a cubic smoothing spline to each set of artificial survey data (with uniform weighting), and the smooth was interpolated and integrated to estimate the season's total nesting emergences. The foregoing steps were repeated 100 times, yielding 100 replicate estimates of total nesting emergences for each survey frequency. The effect of survey frequency was judged by comparing bias and coefficients of variation of total nesting emergence estimates. Bias is the percent difference between the mean estimate of total emergences for the given survey interval and the true number of emergences derived from complete coverage.

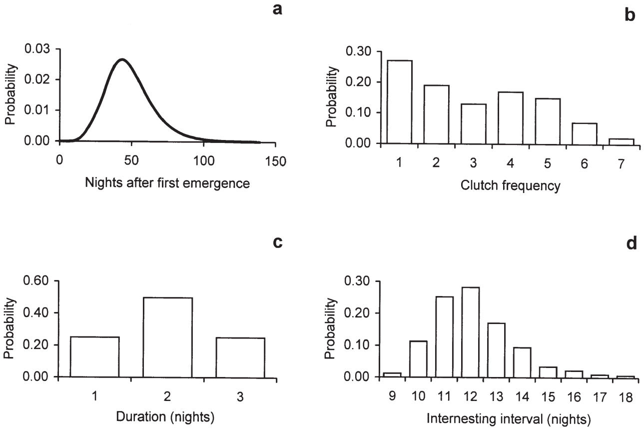

Figure 1. Probability distributions for green turtles nesting at Tortuguero Beach for four processes used in the Monte Carlo sampling algorithm: arrival date (nights after first emergence) (a), clutch frequency (b), duration of a nesting episode (c), and internesting interval (d).

Results

Annual Nesting Emergences and Trends

The smooths appeared to capture the expected nesting emergence pattern (Fig. 2a); most were unimodal with a slight rightward skew, as described for the population (Carr et al. 1978). The standard errors of predicted nesting emergence counts varied with the magnitude of daily variation in counts, but even more so with the frequency of observations. Consequently, standard errors of the predicted counts tended to be smallest in the middle of the nesting season and higher toward the endpoints. Moreover, because the endpoints were artificial, standard errors of predicted counts were underestimated outside the range of survey dates under a uniform weighting scheme.

The shapes of the smooths and estimates of total nesting emergences were virtually unaffected by the weighting scheme used. Standard error estimates, however, were greatly increased by downweighting the endpoints. Downweighting was particularly influential in a few years during which surveys began or ended midway through the nesting season (e.g., 1971 and 1995; Table 1; Fig. 2b & 2c) or emergence variability was high (e.g., 1985; Fig. 2d). Because of uncertainties associated with endpoint selection, weighting, and interpolation of smooths outside the range of survey dates, it is doubtful that the integrated variances reflect the true statistical variation in the spline estimation procedure. Still, they are useful measures of the relative precision of annual nesting emergence estimates.

The estimates of total nesting emergences for the northern section displayed a high degree of interannual variation (Fig. 3). This variation resulted largely from natural

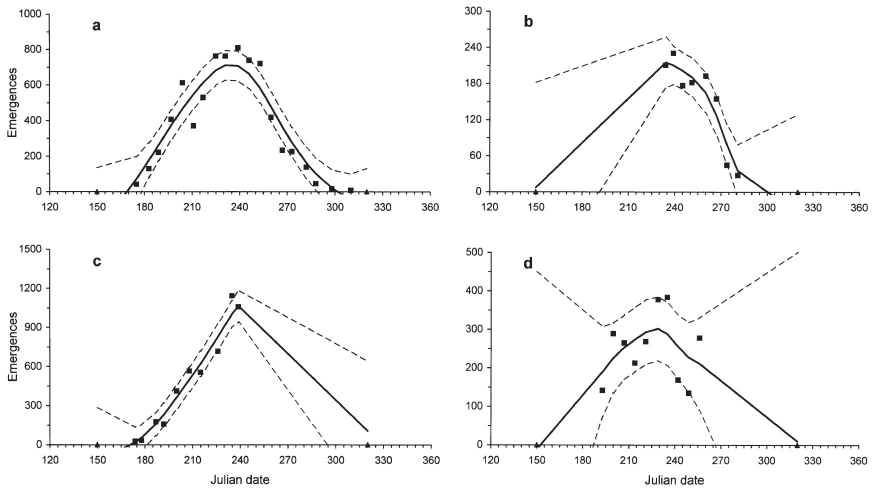

Figure 2. Four examples of individual year curves of nesting emergences of green turtles in the northern 18 km of Tortuguero Beach. In each graph, the solid line is the fitted smooth (cubic smoothing spline procedure) of the predicted number of nesting emergences; dashed lines are error bands (±2 SE); squares are observed counts; triangles are designated endpoints: 1988, a year with good distribution of surveys (a); 1971, a year in which surveys began mid-season (b); 1995, a year in which surveys ended mid-season (c); and 1985, a year in which nesting emergence variability was high (d).

causes (variation in recruitment and remigration processes), but survey sampling error and estimation error also contributed to the variation. To parse out sources of variation, one would have to analyze data from saturation surveys conducted over many years in succession.

Despite the high interannual variation in nesting emergence estimates, a visual inspection of these estimates suggests an increase in the average nesting activity in the northern section from the beginning of the time series through the mid-1980s, followed by a brief leveling off or slight decline and then a resumption of the increase in recent years. Spline smooths of the complete 26-year time series confirmed this pattern. Results varied slightly depending on the choice of statistical weights. When uniform weights were used, the estimated smooth was essentially flat during the late 1980s (Fig. 3).

Nesting emergences in the northern section appeared to be a reliable basis for evaluating trends in nesting emergences for the entire nesting beach. There was a strong correlation between the number of nesting emergences observed nightly on the northern 18-km section and nesting emergences on the total 36-km beach (Pearson's correlation, $r = 0.983$, $n = 195$, $p < 0.001$). The northern section consistently accounted for over half of total nesting emergences during 1986–1996. The ratio of total nesting emergences to nesting emergences in the northern section was between 1.6 and 1.7 in 9 of the 11 years and has been relatively constant since 1991 (Fig. 4).

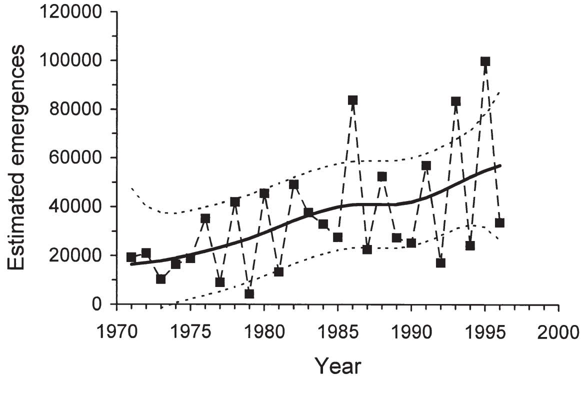

Figure 3. Estimated annual nesting emergences of green turtles in the northern 18 km of Tortuguero Beach. Solid line is the fitted smooth (cubic smoothing spline procedure), dashed lines are error bands (±2 SE), and squares are annual estimates. Annual estimates of total nesting emergences were weighted uniformly for gam() *fitting.*

Survey Frequency

Simulated nesting emergence patterns (Fig. 5 is an example) resembled those seen in nature (Fig. 2a), at least in general characteristics. The analysis of sampled output from the simulation model showed that the procedure of fitting spline smooths to survey counts and then inte-

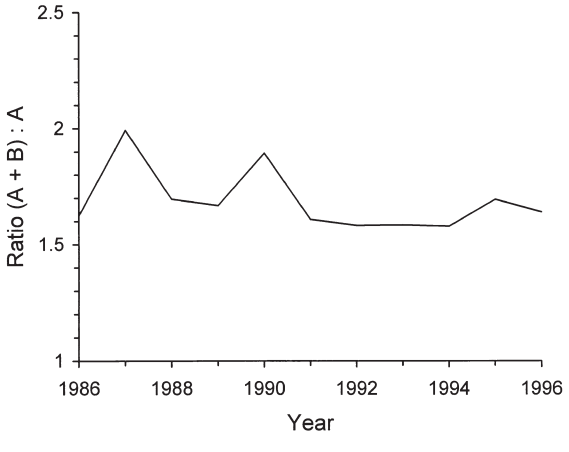

Figure 4. Ratio of nesting emergences on the entire 36 km of Tortuguero Beach (A + B) to the nesting emergences on the northern 18 km of beach (A).

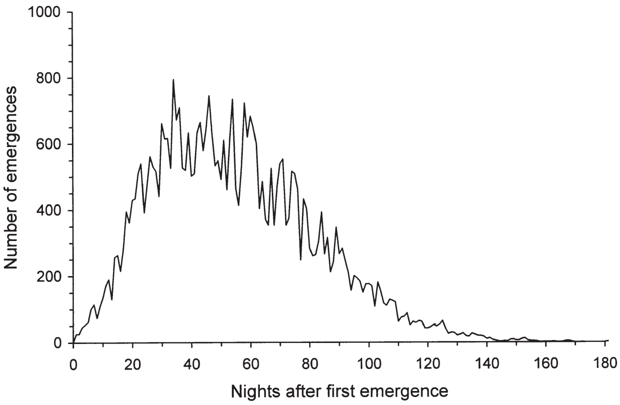

Figure 5. Sample output from the simulation model of nesting emergences of green turtles at Tortuguero Beach.

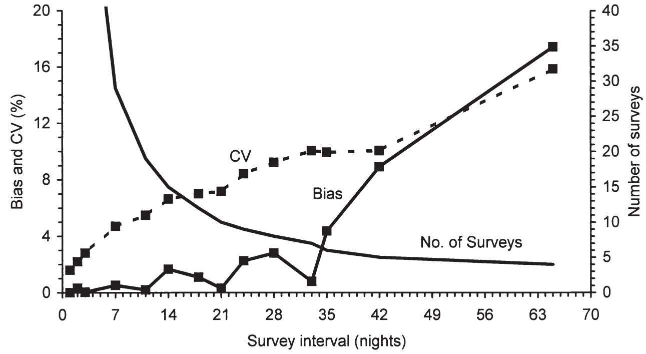

Figure 6. Effect of survey interval on the bias and coefficient of variation for the estimate of total nesting emergences from the simulated time series of green turtles at Tortuguero Beach. The relationship between number of surveys and survey interval is also plotted.

grating the smooths produces estimates of total nesting emergences with low bias for survey intervals of up to 5 weeks (Fig. 6). Coefficients of variation of the estimates, as expected, are inversely related to survey frequency. The results indicate that a survey interval of 3 weeks may yield results nearly as precise as a 2-week interval. But given other considerations (e.g., other survey objectives, unanticipated problems with the survey, and uncertainties in the simulation model), it would seem prudent to conduct surveys at least once every 2 weeks, preferably weekly. The weekly survey frequency used during 1971-1996 would yield a 5% coefficient of variation for the estimate of total annual nesting emergences (under the assumptions of the simulation model). These results assume that surveys commence with the earliest nesting arrival and continue until emergences are negligible. Under these conditions, endpoints are known and much more reliable estimates are possible than if the endpoints are estimated.

Discussion

Population Trend

Analysis of population trends in sea turtles requires many years of data (National Research Council 1990), largely because trends are obscured by the great variation in the annual number of nesting females that is characteristic of many sea turtle populations (Limpus 1995). This variation (Fig. 3) has intrigued sea turtle biologists for many years (Carr et al. 1978), but a possible explanation has been developed only for green turtles in Australia. A significant correlation exists between indices of the El Niño Southern Oscillation and the numbers of green turtles nesting approximately two years later at Heron Island and Raine Island (Limpus & Nicholls 1988, 1994). The mechanism is not known, but is believed to have a nutritional basis (Bjorndal 1997). Analyses are underway to evaluate the relationships between the estimates of annual nesting emergences presented here for the Tortuguero green turtle population and various environmental parameters that may reflect the regulating mechanism (K.A.B. and A.B.B., unpublished data).

Green turtles at Tortuguero usually deposit more than one egg clutch per year. If the mean number of egg clutches deposited each year—clutch frequency—were known, the number of nesting emergences could be converted to the number of nesting females. An estimate of 2.8 clutches per year has been presented (Carr et al. 1978), but is not reliable because of tag loss (Bjorndal et al. 1996) and incomplete beach coverage. Mean clutch frequency could be as high as 6 clutches per year.

Three caveats should be considered in the evaluation of the upward trend reported here for the Tortuguero green turtle population. First, number of nests is used to reflect population numbers, but clutch frequency may vary among years. If it does, in years with high clutch frequencies population levels would be overestimated relative to years with low clutch frequencies. Data on annual variation in clutch frequencies are not available for the Tortuguero green turtle population. Clutch frequency is difficult to monitor (Miller 1997), but there is no evidence of great interannual fluctuations—certainly not in the range required to significantly affect the trend analysis reported here.

Second, and more important, these trends represent only one portion of the population: adult females. As David Ehrenfeld so eloquently expressed it, "Looking at green turtle [nesting] population data is like looking at the light from a star 25 light years away. It appears to be shining now, but, in fact, you are looking at history, and there is no way of telling whether, during the past 25 light years, that star has increased in brightness or perhaps has gone out altogether" (Bacon et al. 1984: page 148). Caribbean green turtles take at least several decades to reach sexual maturity (Bjorndal & Zug 1995). By monitoring only the number of nesting females or the number of nests deposited, drastic changes in the survival of early life stages—and thus in the trend for the population as a whole—would not be apparent on the nesting beach for many years. For example, number of nests does not necessarily reflect number of hatchlings produced. Hatchling emergence success can be low and varies among years. At Tortuguero, hatchling emergence success has been measured during only 4 years. In 1977 hatchling emergence success was 35% (Fowler 1979), and in 1986, 1988, and 1989 it was 57%, 46%, and 67%, respectively (Horikoshi 1992). One cause of concern was Horikoshi's finding that a substantial source of mortality was drowning of eggs by ground water. Horikoshi hypothesized that changes in land-use patterns and watersheds in the upper reaches of the Tortuguero River have raised the water level of the river and the groundwater table under Tortuguero Beach. Because hatching success is not monitored at Tortuguero, we do not know how many hatchlings emerge from the thousands of nests deposited each year.

Third, 1995 was the year with the greatest number of nesting emergences (Fig. 3) but it was also the year with the poorest coverage in the latter half of the nesting season (Table 1; Fig. 2c). Therefore, the estimate for 1995 should be viewed with caution.

The upward trend of the Tortuguero green turtle population must be placed in the proper perspective to avoid the pitfalls of the "shifting baseline syndrome" (Pauly 1995; Sheppard 1995; Jackson 1997)—the use of inappropriate baselines to assess population change or stability. Referring to fisheries management, Pauly (1995) described the syndrome as the tendency of scientists to use population levels at the beginning of their careers as the baseline against which to measure population change. Historical data for nest density at Tortuguero are lacking, but Caribbean green turtle populations have declined substantially since the arrival of Europeans, perhaps by 99% (Bowen & Avise 1995; Jackson 1997). Therefore, although the upward trend for the Tortuguero population is encouraging, the population is probably far below its natural level.

Alternative Trend Analysis

Can the nesting survey data be analyzed by a simpler method to evaluate population trends? To address this question, we used values from the highest survey each year and the mean of the three highest surveys each year in the same cubic spline procedure used to smooth the 26-year time series of annual nesting emergence estimates. Although both the highest survey and the mean of the three highest surveys yielded an overall increasing trend over the 26-year period, similar to the trend based on annual nesting emergences, the three smooth lines differed substantially during various phases. These differences resulted primarily from those years in which there was considerable variation in the number of nesting emergences on a nightly basis (e.g., in 1985; Fig. 2d). We do not know why the degree of night-to-night variation in the number of nesting emergences varies among years. But in years with high variation among nights, the highest survey and the mean of the three highest surveys overestimate—sometimes substantially—the relative index of nesting emergences.

The use of the highest survey or the mean of the three highest surveys would not decrease significantly the required field work because the peak of nesting shifts among years. From 1971 through 1996, the survey night with the highest count ranged from 28 July in 1982 to 15 September in 1989 (Table 1). Therefore, to capture the peak nesting and obtain good estimates of the highest nesting counts, the beach must be surveyed for the majority of the nesting season. These alternative indices would be worth considering only if the survey schedule is constant among years. This is a serious constraint. The "integrated smooth" approach that we present performs well even with interannual variation in the survey schedule.

The major disadvantage of this simpler approach, in comparison with the integrated smooth approach, is that it does not yield an estimate of total number of nests. This value is of immediate significance in evaluating hatchling production, estimating numbers of adult females if mean clutch frequency and mean remigration interval are known, and developing a model of population dynamics.

Therefore, the "simpler" method requires nearly equal survey effort and a more rigid survey schedule, yields less reliable relative nesting indices, and does not generate estimates of number of nests. We see little value in pursuing these alternative analyses.

Conservation Outlook

The upward trend of the population gives encouragement that the stewardship of the Tortuguero green turtle nesting population by the people of Costa Rica has been successful. The management program has included limitations on harvest of eggs and adult turtles begun in the late 1950s and early 1960s and continued with the establishment of Tortuguero National Park in 1976 with its protection of the nesting population and habitat. The continued legal harvest of breeding green turtles in waters off Tortuguero must be carefully controlled, however, and the effect of the harvest on population trends must be monitored to ensure that the recovery of the population is not impeded.

The Caribbean green turtle populations continue under threat from a series of sources (National Research Council 1990; Eckert 1995; Lutcavage et al. 1997): other, smaller rookeries are in decline; directed take of sea turtles is high in many areas of the Caribbean, exacerbated by increasing coastal human populations throughout the region; incidental capture in fisheries is a substantial source of mortality; nesting beaches are being developed for human use, often in ways incompatible with turtle nesting; and foraging habitats are being degraded by destructive fishing practices, anchor scars, pollutants, and inappropriate construction practices that result in siltation. Recent studies have underscored the difficulty of sustainably harvesting species, such as green turtles, with slow growth rates, late sexual maturity, and complex migratory life histories (Congdon et al. 1993, 1994; Crouse & Frazer 1995; Chaloupka & Limpus 1996; Heppell & Crowder 1996; Heppell et al. 1996*a*, 1996*b*). These difficulties are illustrated by the Tortuguero hawksbill (*Eretmochelys imbricata*) population, which has declined significantly from 1956 to 1991 despite being afforded the same regulatory protection on the nesting beach as the Tortuguero green turtle population (Bjorndal et al. 1993), and its decline has not reversed in recent years. The trend in the Tortuguero green turtle nesting emergences, however, offers a glimmer of hope that, with continued careful management of this regional resource, the Caribbean green turtle fleet will not, as Archie Carr feared, pass from existence.

Acknowledgments

This study would not have been possible if the late Archie Carr had not had the foresight and continuity of purpose to establish and maintain the Tortuguero program; the authors are grateful for his inspiration. We are also grateful to those surveyors who walked the long, hot, black sand beach of Tortuguero, especially the late Durham Rankin and his sons Alonzo, Eddie, and Thomas. The surveys were conducted from 1971 to 1996 under the auspices of the Caribbean Conservation Corporation and were supported from 1971 to 1979 by grants from the National Science Foundation to A. Carr. We thank P. Eliazar, C. Taft, S. Bouchard, S. McCauley, K. Moran, M. Tiwari, and D. Wood for assistance with data compilation. The manuscript was improved by comments from M. Chaloupka and S. Heppell.

Literature Cited

Bacon, P., F. Berry, K. Bjorndal, H. Hirth, L. Ogren, and M. Weber, editors. 1984. Proceedings of the Western Atlantic Turtle Symposium. Center for Environmental Education, Washington, D.C.

Bjorndal, K. A. 1985. Nutritional ecology of sea turtles. Copeia **1985:** 736–751.

Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. Pages 199–231 in P. L. Lutz and J. A. Musick, editors. The biology of sea turtles. CRC Press, Boca Raton, Florida.

Bjorndal, K. A., and G. R. Zug. 1995. Growth and age of sea turtles. Pages 599–600 in K. A. Bjorndal, editor. Biology and conservation of sea turtles. Revised edition. Smithsonian Institution Press, Washington, D.C.

Bjorndal, K. A., A. B. Bolten, and C. J. Lagueux. 1993. Decline of the nesting population of hawksbill turtles at Tortuguero, Costa Rica. Conservation Biology **7:**925–927.

Bjorndal, K. A., A. B. Bolten, C. J. Lagueux, and A. Chaves. 1996. Probability of tag loss in green turtles nesting at Tortuguero, Costa Rica. Journal of Herpetology **30:**566–571.

Bowen, B. W., and J. C. Avise. 1995. Conservation genetics of marine turtles. Pages 190–237 in J. C. Avise and J. L. Hamrick, editors. Conservation genetics: case histories from nature. Chapman and Hall, New York.

Carr, A.F. 1954. The passing of the fleet. AIBS (American Institute of Biological Sciences) Bulletin. **4:**17–19.

Carr, A., M. H. Carr, and A. B. Meylan. 1978. The ecology and migrations of sea turtles, 7. The West Caribbean green turtle colony. Bulletin of the American Museum of Natural History. **162:**1–46.

Chaloupka, M., and C. J. Limpus. 1996. Heuristic modeling of *Chelonia mydas* population dynamics: Southern Great Barrier Reef. Pages 66–69 in J. A. Keinath, D. E. Barnard, J. A. Musick, and B. A. Bell, compilers. Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. Technical memorandum NMFS-SEFSC-387. National Oceanographic and Atmospheric Administration, Miami, Florida.

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology **7:**826–833.

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist **34:**397–408.

Crouse, D. T., and N. B. Frazer. 1995. Population models and structure. Pages 601–603 in K. A. Bjorndal, editor. Biology and conservation of sea turtles. Revised edition. Smithsonian Institution Press, Washington, D.C.

Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems **5:**205–232.

Eckert, K. L. 1995. Anthropogenic threats to sea turtles. Pages 611–612 in K. A. Bjorndal, editor. Biology and conservation of sea turtles. Revised edition. Smithsonian Institution Press, Washington, D.C.

Eliazar, P. J., K. A. Bjorndal, and A. B. Bolten. In press. Operation green turtle revisited. In Proceedings of the Sixteenth Annual Symposium on Sea Turtle Biology and Conservation, Hilton Head, South Carolina. National Oceanographic and Atmospheric Administration Technical Memorandum, Miami, Florida.

Fowler, L. E. 1979. Hatching success and nest predation in the green sea turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. Ecology **60:** 946–955.

Härdle, W. 1990. Applied nonparametric regression. Cambridge University Press, New York.

Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. Chapman and Hall, London.

Heppell, S. S., and L. B. Crowder. 1996. Analysis of a fisheries model for harvest of hawksbill turtles (*Eretmochelys imbricata*). Conservation Biology **10:**874–880.

Heppell, S. S., L. B. Crowder, and D. T. Crouse. 1996*a*. Models to evaluate headstarting as a management tool for long-lived species. Ecological Applications **6:**556–565.

Heppell, S. S., C. J. Limpus, D. T. Crouse, N. B. Frazer, and L. B. Crowder. 1996*b*. Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. Wildlife Research **23:**143–159.

Horikoshi, K. 1992. Egg survivorship and primary sex ratio of green turtles, *Chelonia mydas*, at Tortuguero, Costa Rica. Ph.D. dissertation. University of Florida, Gainesville.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs **16(suppl):** S23–S33.

Lahanas, P. N., K. A. Bjorndal, A. B. Bolten, S. Encalada, M. M. Miyamoto, R. A. Valverde, and B. W. Bowen. 1998. Genetic composition of a green turtle (*Chelonia mydas*) feeding ground population: evidence for multiple origins. Marine Biology **130:**345–352.

Limpus, C. J. 1995. Global overview of the status of marine turtles: a 1995 viewpoint. Pages 605–609 in K. A. Bjorndal, editor. Biology and conservation of sea turtles. Revised edition. Smithsonian Institution Press, Washington, D.C.

Limpus, C. J., and N. Nicholls. 1988. The southern oscillation regulates the annual numbers of green turtles (*Chelonia mydas*) breeding around northern Australia. Australian Journal of Wildlife Research **15:**157–161.

Limpus, C. J., and N. Nicholls. 1994. Progress report on the study of the interaction of the El Niño Southern Oscillation on annual *Chelonia mydas* numbers at the southern Great Barrier Reef rookeries. Pages 73–78 in Proceedings of the Australian Marine Turtle Conservation Workshop. Queensland Department of Environment and Heritage, and Australian Nature Conservation Agency, Brisbane.

Lutcavage, M. E., P. Plotkin, B. Witherington, and P. L. Lutz. 1997. Human impacts on sea turtle survival. Pages 387–409 in P. L. Lutz and J. A. Musick, editors. The biology of sea turtles. CRC Press, Boca Raton, Florida.

Miller, J. D. 1997. Reproduction in sea turtles. Pages 51–81 in P. L. Lutz and J. A. Musick, editors. The biology of sea turtles. CRC Press, Boca Raton, Florida.

National Research Council. 1990. Decline of the sea turtles: causes and prevention. National Academy Press, Washington, D.C.

Norse, E. A., editor. 1993. Global marine biological diversity. Island Press, Washington, D.C.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution **10:**430.

Sheppard, C. 1995. The shifting baseline syndrome. Marine Pollution Bulletin **30:**766–767.

Simonoff, J. S. 1996. Smoothing methods in statistics. Springer-Verlag, New York.