

EVALUATING TRENDS IN ABUNDANCE OF IMMATURE GREEN TURTLES, *CHELONIA MYDAS*, IN THE GREATER CARIBBEAN

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Abstract. Many long-lived marine species exhibit life history traits that make them more vulnerable to overexploitation. Accurate population trend analysis is essential for development and assessment of management plans for these species. However, because many of these species disperse over large geographic areas, have life stages inaccessible to human surveyors, and/or undergo complex developmental migrations, data on trends in abundance are often available for only one stage of the population, usually breeding adults. The green turtle (*Chelonia mydas*) is one of these long-lived species for which population trends are based almost exclusively on either numbers of females that emerge to nest or numbers of nests deposited each year on geographically restricted beaches. In this study, we generated estimates of annual abundance for juvenile green turtles at two foraging grounds in the Bahamas based on long-term capture–mark–recapture (CMR) studies at Union Creek (24 years) and Conception Creek (13 years), using a two-stage approach. First, we estimated recapture probabilities from CMR data using the Cormack-Jolly-Seber models in the software program MARK; second, we estimated annual abundance of green turtles at both study sites using the recapture probabilities in a Horvitz-Thompson type estimation procedure. Green turtle abundance did not change significantly in Conception Creek, but, in Union Creek, green turtle abundance had successive phases of significant increase, significant decrease, and stability. These changes in abundance resulted from changes in immigration, not survival or emigration. The trends in abundance on the foraging grounds did not conform to the significantly increasing trend for the major nesting population at Tortuguero, Costa Rica. This disparity highlights the challenges of assessing population-wide trends of green turtles and other long-lived species. The best approach for monitoring population trends may be a combination of (1) extensive surveys to provide data for large-scale trends in relative population abundance, and (2) intensive surveys, using CMR techniques, to estimate absolute abundance and evaluate the demographic processes driving the trends.

Key words: abundance; Bahamas; capture–mark–recapture; *Chelonia mydas*; Costa Rica; demography; Greater Caribbean; green turtle; long-lived species; population trends; sea turtles; Tortuguero.

INTRODUCTION

Recent studies of life history characteristics and conservation status of long-lived marine species have identified life history traits, including slow growth and delayed sexual maturity, that increase their vulnerability to overexploitation (Musick 1999). Successful management of these vulnerable species depends on knowledge of population trends to assess the risk status of populations and to evaluate the success or failure of management options. Many of these species are also characterized by extensive foraging ranges and relatively restricted breeding areas. Often, monitoring of population abundance focuses on the breeding areas, where abundance can be assessed more easily than on the widely distributed foraging grounds, such as with

Atlantic sturgeon *Acipenser oxyrinchus* (Secor and Waldman 1999), albatrosses *Diomedidae* spp. (Croxall et al. 1990), humpback whales *Megaptera novaeangliae* (Chaloupka et al. 1999), and grey seals *Halichoerus grypus* (Schwarz and Stobo 2000).

For sea turtle populations, most trend analyses have relied on data from nesting beaches based on counts of females, the tracks they leave behind, or nests (e.g., National Research Council 1990, Bjorndal et al. 1999). Assessing population trends at nesting beaches is not without problems. The great fluctuations in nesting numbers from year to year obscure trends and require data collection over many years. Recent studies have improved our understanding of the biological bases of the great annual variation in nesting numbers (Broderrick et al. 2001, Chaloupka 2001, Solow et al. 2002) and have provided improved statistical models to evaluate nesting numbers (Chaloupka 2002, Fujiwara and Caswell 2002, Kendall and Nichols 2002).

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Despite these improvements in our ability to interpret trends in nesting numbers, nesting beach surveys monitor only one life stage (adult females). By not monitoring the juvenile life stages, which extend over decades in most sea turtle species (Chaloupka and Musick 1997), changes in abundance of juvenile stages may be missed. By the time a decline in abundance of juvenile turtles is reflected in a decrease in the number of females appearing at the nesting beach, many years later, opportunities for conservation actions to counteract the declines have been delayed or lost. Monitoring juvenile stages would provide more accurate trends for the entire population and “early warnings” of changes in juvenile survival.

The importance of monitoring life stages of juveniles, in addition to adult females, has been recognized for many years (Bacon et al. 1984, Bjorndal and Bolten 2000). The emphasis on nesting censuses is primarily a result of logistics; relative to nesting beach surveys, in-water surveys are usually more expensive in both funds and time, more technically difficult, and far less rewarding in terms of the number of turtles observed per hour because of the low densities of sea turtles in most in-water habitats. There are a few published estimates of abundance or densities of sea turtles in foraging habitats (see Chaloupka 2000). We are aware of only one study that has evaluated trends in abundance of sea turtle populations on foraging grounds. Chaloupka and Limpus (2001) assessed trends in populations of green turtles (*Chelonia mydas*) and loggerheads (*Caretta caretta*) in the waters of the southern Great Barrier Reef, Australia.

The green turtle is recognized globally as an endangered species (Hilton-Taylor 2000). The massive decline of green turtle populations as a result of hundreds to thousands of years of human overexploitation is well documented (Parsons 1962, Frazier 2003). We know from historic records that, since European contact, several nesting populations in the Greater Caribbean have been destroyed, such as those that once nested on Bermuda, Cayman Islands, and Isle of Savona (Esquemeling 1684, Parsons 1962). Archeological investigations have recently revealed that exploitation by Amerindians in the Caribbean region may well have substantially affected green turtle populations before European contact (Carlson 1999, Pandolfi et al. 2003). Best estimates indicate that current green turtle populations in the Caribbean represent 3–7% of pre-exploitation populations (Jackson et al. 2001).

In the Atlantic, green turtles undergo complex developmental migrations during which they occupy different habitats. It is not known where green turtles spend their first years of life after hatchlings leave the nesting beach. They probably enter an oceanic stage (Bolten 2003), which, in the Greater Caribbean, is estimated to last about three years (Boulon and Frazer 1990, Zug and Glor 1998). Green turtles begin to recruit to neritic foraging grounds at a size of 25 cm

straight carapace length and adopt a largely herbivorous diet (Bjorndal 1997). Green turtles continue to move among neritic foraging grounds as they grow to sexual maturity, a process that requires decades (Bjorndal et al. 2000). The cues that initiate these movements and that determine the selection of successive foraging sites are not known. Once sexually mature, female green turtles migrate from foraging grounds to their natal rookeries (Bowen and Karl 1997) at intervals of two or more years (Carr et al. 1978).

In the present study, we generate estimates of abundance for two sampling populations of immature green turtles in neritic habitats in the Bahamas, based on long-term capture–mark–recapture studies. We use a two-stage approach in which we first estimate recapture probabilities from the capture–mark–recapture data using the Cormack-Jolly-Seber modeling approach advocated by Lebreton et al. (1992), implemented in the software program MARK (White and Burnham 1999). Second, we generate estimates of annual abundance of green turtles at both study sites using the recapture probabilities in a Horvitz-Thompson type estimation procedure. We also use a variance-component approach (Link and Nichols 1994, Gould and Nichols 1998) to partition total variance of the estimates of recapture probabilities into temporal variance and sampling variance. We evaluate trends in abundance over time for the two sampling populations in relation to other demographic parameters of interest: survival and emigration probabilities. We also evaluate those trends in the context of the increasing trend reported for the nesting population at Tortuguero, Costa Rica (Bjorndal et al. 1999) and discuss the challenges of assessing population-wide trends of immature green turtles in the Greater Caribbean. The Tortuguero rookery is the largest in the Greater Caribbean, by at least an order of magnitude (Seminoff 2002), and is the primary rookery source for the two sampling populations, based on mtDNA sequence analyses (Lahanas et al. 1998; K. A. Bjorndal and A. B. Bolten, unpublished data).

METHODS

Study sites and data collection

This study is part of a long-term study of the biology of immature green turtles in the Bahamas. Capture–mark–recapture studies are ongoing at two green turtle (*Chelonia mydas*) foraging grounds: Union Creek and Conception Creek. Union Creek is on the north coast of Great Inagua, the southernmost island in the Bahamas (21.17° N, 73.57° W). Conception Island (23.82° N, 75.10° W) is in the central Bahamas and is a narrow strip of land surrounding the central Conception Creek. In the Bahamas, the term “creek” is applied to salt-water bays, not freshwater streams, as in some other countries. Union Creek Reserve and Conception Island are both within the Bahamas National Park system, and green turtles within their boundaries have legal pro-

tection from exploitation. Protective legislation is well enforced in Union Creek by the wardens of the Bahamas National Trust; enforcement is limited on Conception Island, which is not inhabited by humans. A low level of exploitation may occur in Conception Creek. Union Creek is ~ 20 km² in area, is surrounded by and interspersed with mangroves, and has pastures of the seagrass *Thalassia testudinum*, which is the primary diet plant of green turtles in the Greater Caribbean (Bjorndal 1997). The habitat of Conception Creek is similar to that of Union Creek, except that Conception Creek is smaller in area and its water depth is more shallow.

Immature green turtles enter Union Creek or Conception Creek and then emigrate to other habitats throughout the Greater Caribbean prior to the onset of sexual maturity. Movements away from Union Creek and Conception Creek have been documented by the return of flipper tags from throughout the Caribbean (68 for Union Creek, or 8.9% of green turtles tagged; nine for Conception, or 4.6%). No movement of green turtles between Union Creek and Conception Creek has been observed. Green turtles at both study sites are mixed stocks derived from several green turtle rookeries in the Atlantic, based on analyses of mtDNA sequences (Lahanas et al. 1998; K. A. Bjorndal and A. B. Bolten, unpublished data). Our study of green turtles at Union Creek began in 1975; data presented here were collected each year from 1978 through 2001 except for 1981, 1995, and 1999. In Conception Creek, data collection began in 1989 and continued each year through 2001. In both study areas, green turtles were caught throughout the entire study area by diving on them from the bow of a motorboat following a brief chase. Turtles were tagged with flipper tags bearing an identification number. To maintain individual identification of turtles, 2–4 tags were applied to each turtle and tags were replaced as needed upon recapture, which resulted in very low tag loss. For example, with plastic tags (Jumbo-Roto, Dalton Supplies, Oxfordshire, UK) in Union Creek, only 1.4% of all tags were lost, but all turtles were identified by other tags still attached. Tag loss was not included in our abundance estimates. Straight carapace length (SCL, ± 0.1 cm) was measured from the anterior midpoint of the nuchal scute to the posterior tip of the longer of the pair of posterior marginal scutes. No indication of the disease fibropapillomatosis (Herbst 1994) has been observed in green turtles at either study site. At Union Creek, the annual capture effort was approximately equal among years during a single 7–10 day interval; K. A. Bjorndal and A. B. Bolten collected all data. Data collection at Conception Creek has been conducted in collaboration with the semester-at-sea program of St. George's School (Newport, Rhode Island, USA) aboard the sailing vessel *Gerónimo*. Capture effort was approximately equal among years, with an average of seven days per year. All data

collected in Conception Creek within a calendar year were combined for that year.

Abundance estimation

We used a Horvitz-Thompson type estimation procedure to generate estimates of annual abundance of green turtles at both study sites, in which

$$N_i = (n_i/\rho_i) \quad (1)$$

where N_i is the number of turtles in the sampling population, n_i is the number of turtles captured in the i th year, and ρ_i is the recapture probability in the i th year. We estimated approximate 95% confidence intervals for N_i following Loery et al. (1997) by first calculating the standard error of N_i as

$$SE(N_i) = \{(n_i/\rho_i)^2[\text{var}(\rho_i)/(\rho_i)^2]\}^{0.5} \quad (2)$$

where $\text{var}(\rho_i)$ is the variance of the recapture probability in the i th year. Then 95% confidence limits of N_i were calculated as $N_i \pm 1.96SE(N_i)$. Advantages of Horvitz-Thompson estimators for sea turtle populations are discussed in Chaloupka (2000) and Chaloupka and Limpus (2001).

Recapture probabilities (ρ_i) were generated by models developed for a study of survival and emigration probabilities (Bjorndal et al. 2003), which gives details of model evaluation. Briefly, we used the Cormack-Jolly-Seber modeling approach advocated by Lebreton et al. (1992). All modeling was implemented using Program MARK (version 2.1) with logit link function to constrain estimates between 0 and 1 (White and Burnham 1999, Cooch and White 2001). We assessed live-recaptures-only models and combined live-recaptures and dead-recoveries models (Burnham models; Burnham 1993). Live-recaptures-only models generate estimates of apparent survival probability (Φ), which is the probability that a turtle has not died or emigrated from the study population, and recapture probability (ρ), which is the probability that a turtle that is available for capture in the study population is caught. Combined live-recaptures and dead-recoveries models generate estimates for true survival probability (S), which is the probability that a turtle has not died; recapture probability (ρ); fidelity probability (F), which is the probability that a turtle remains in the study area; and recovery probability (r), which is the probability that a tagged turtle that dies is found and the tag is returned to us.

Goodness of fit (GoF) of the models was evaluated in a series of tests. First, we tested the full-parameter Cormack-Jolly-Seber model (time-dependent Φ and time-dependent ρ) using RELEASE TEST2+3 within Program MARK (White and Burnham 1999) to evaluate assumptions that marked turtles had the same recapture probability and survival probability (Burnham et al. 1987, Lebreton et al. 1992). We next used UCARE (Choquet et al. 2001), which implements the extended form of TEST2+3 derived originally by Burnham et

al. (1987), to evaluate capture heterogeneity with TEST2.Ct (Pradel 1993). Selection of the best model from a series of models was based on the quasi-likelihood corrected form of the Akaike Information Criterion (QAIC_c) (Burnham et al. 1995, Anderson et al. 1998). The GoF of the best-fit model selected by QAIC_c was then assessed in absolute terms using a parametric bootstrap approach implemented in MARK.

Based on this selection procedure, the best model for Union Creek green turtles was a Burnham model with four tag-cohort-age-classes, age-class-dependent survival and fidelity probabilities, and time-dependent recapture and recovery probabilities. Because we do not know the ages of green turtles in Union Creek, we used tag-cohort-age, for which 0 was set as the year in which the turtle was first tagged in Union Creek. There was no evidence of transience or capture heterogeneity (= trap dependence). The best model for Conception Creek green turtles was a reduced Cormack-Jolly-Seber model with constant apparent survival probability and time-dependent recapture probabilities. Burnham models gave unrealistically high estimates of S (approaching 1.0). We believe that the failure of Burnham models resulted from the low number of dead recoveries. Although there was no evidence of transience, there was strong evidence of heterogeneity of recapture probabilities (UCARE TEST2.Ct, trap-dependence statistic = -2.94 , $P = 0.003$). The negative value of the trap-dependence statistic indicates that the turtles are "trap happy;" that is, previously captured turtles have a higher recapture probability. Trap-dependent effects can be difficult to interpret (Pradel 1993); Lebreton et al. (1992) found "trap dependence" in their case study involving Greater Flamingos (*Phoenicopterus ruber*), although the flamingos were not physically recaptured, just resighted. The only explanation for trap-happy green turtles that we can propose is that the data structure mimics trap-happiness because of the very high recapture probability in Conception Creek resulting from its small area and shallow waters. We concluded that we could proceed with the model, but that results should be interpreted with caution because trap dependence could result in positively biased estimates of recapture probabilities (Pradel 1993). The variance of the recapture probability estimates was partitioned into temporal and sampling variance following Gould and Nichols (1998).

We estimated "apparent immigration" by calculating the percentage of turtles captured each year in Union Creek (n_t) that had not been tagged in previous years. The percentage of untagged turtles is a reasonable approximation for comparing relative immigration rates among years because annual sampling effort is consistent, recapture probability is high, and the number of turtles captured is a large proportion of the abundance estimate each year in Union Creek. Estimates of apparent immigration are not used in our analyses of population abundance or trends; they are used only to

facilitate interpretation of the causes of changes in abundance in Union Creek.

Assessment of trends in abundance

We evaluated trends in green turtle abundance on foraging grounds with variance-weighted linear regression models with log link and autocorrelation error to account for any temporal correlation. For Conception Creek, we used an autoregression (order 1) error structure because partial autocorrelation analysis of the detrended data revealed a significant one-year lag ($P < 0.05$). Partial autocorrelation analysis of the detrended Union Creek data revealed no significant lags; we employed a moving-average (order 1) correlation structure because there was substantial overlap of individual turtles between successive years and, thus, biologically significant temporal correlation between successive years. The response variable (Horvitz-Thompson annual abundance estimates) was transformed to natural log form so that the slope of the regression (b) is an estimate of the instantaneous rate of population change, assuming constant rate of change over the time interval; e^b is an estimate of the finite annual rate of population change; and $e^b - 1$ is the annual percentage population change. The models were variance-weighted with natural-log-transformed abundance variance estimates ($SE(N_i)$ values squared) to account for measurement uncertainty. For the trend at Tortuguero, Costa Rica, previously published estimates of the number of nests deposited annually from 1976 to 1998 on the northern 18 km of the 36-km beach were used as a proxy for numbers of nesting females (Bjorndal et al. 1999, Solow et al. 2002) and were transformed to natural log form. Partial autocorrelation analysis of the detrended data revealed a significant one-year lag ($P < 0.05$), so we used an autoregression (order 1) error structure. The models for Union Creek, Conception Creek, and Tortuguero were fitted using generalized least squares by restricted maximum likelihood estimation to account for nonstandard error covariance structure due to variance weighting and the autocorrelated error. Autocorrelation and regression analyses were conducted using S-PLUS software (version 6.1, 2002, Insightful Corporation, Seattle, Washington, USA).

RESULTS

Turtle captures and estimates of abundance

In Union Creek from 1978 through 2001, 764 individual green turtles were captured for a total of 1579 captures. Individual turtles were captured between one and 10 times (only one capture each year), with individual turtles captured over a range of 1–15 years. Straight carapace length (SCL) ranged from 25 to 84 cm (Fig. 1a); many turtles emigrated before reaching 60 cm and most emigrated at sizes <70 cm. All turtles in Union Creek were immature; the size of nesting female green turtles at Tortuguero is 100.2 ± 5.0 cm

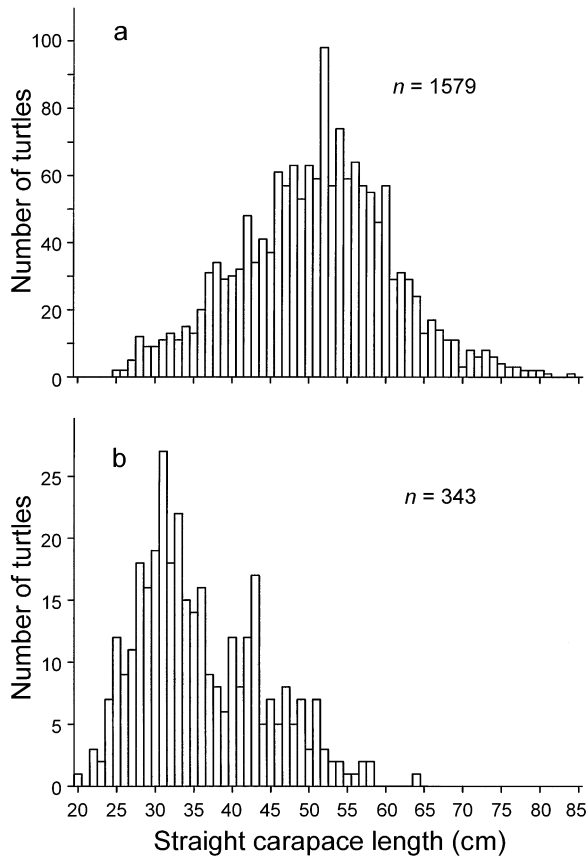


FIG. 1. Size distribution of green turtles captured in (a) Union Creek, Great Inagua, Bahamas, and (b) Conception Creek, Conception Island, Bahamas. Measurements of individual turtles caught in successive years were included. The sample size for Conception Creek is less than the number of captures reported in the text because not every turtle was measured at each capture.

(mean \pm 1 SD; $n = 2107$; Bjorndal and Carr 1989). Numbers of green turtles captured each year (n_i) varied from 22 to 155 (Table 1). Annual estimates of recapture probability (ρ_i) were generated for all years except 1978, 1981, 1995, and 1999 from the Burnham model with four tag-cohort-age-classes, age-class-dependent survival and fidelity probabilities, and time-dependent recapture and recovery probabilities (Table 1). Estimates could not be derived for 1978 because, as the first year, no recaptures were possible; for the other three years, there was no capture effort. Estimates of annual recapture probabilities, which ranged from 0.262 to 0.884 with a geometric mean of 0.549, are high for capture-mark-recapture studies (see Pollock et al. 1990). Horvitz-Thompson annual estimates of abundance (N_i) ranged from 41 to 257 (Table 1; Fig. 2a). Apparent immigration (percentage of untagged turtles captured each year) varied from 23.2% to 89.8% (geometric mean = 42.4%).

In Conception Creek from 1989 to 2001, 196 individual green turtles were captured 1–7 times for a total

of 401 turtle captures (counting only the first capture each year), with individual turtles being captured over a range of 1–7 years. SCL of green turtles in Conception Creek ranged from 20 to 64 cm (Fig. 1b). All green turtles in Conception Creek were immature; most turtles emigrated before reaching 50 cm and all but one turtle emigrated at sizes <60 cm. Numbers of green turtles captured each year (n_i) varied from 20 to 45 (Table 1). From the reduced Cormack-Jolly-Seber model with constant apparent survival probability and time-dependent recapture probabilities, annual estimates of recapture probability (ρ_i) were generated for all years except the first year (Table 1). The estimates of recapture probability for each year ranged from 0.328 to 0.940 (geometric mean = 0.590), which are high for capture-mark-recapture studies, as also reported for Union Creek. Horvitz-Thompson annual estimates of abundance (N_i) ranged from 41 to 65 (Table 1; Fig. 2b). If recapture probabilities are positively biased as a result of trap dependence in the Conception Creek green turtles, abundance estimates will be low (see Eq. 1). If we assume that any trap dependence was consistent over the course of the study (a reasonable assumption) then the trend in abundance would not be affected.

Trends in abundance

Trend analyses revealed no significant overall trend from 1979 to 2001 for Union Creek green turtles (Table 2). This lack of significant trend, however, was not constant over the time interval (Fig. 2a). From 1979 to 1985, green turtle abundance increased significantly at an annual rate of 38.8%, followed by a period of significant decrease in abundance from 1985 to 1994 at an annual rate of -13.1% . Then, from 1994 to 2001, abundance in Union Creek did not change significantly. The upward shift in 2001, which has been followed by a higher year in 2002 (data not included here) suggests that green turtles in Union Creek may be entering another period of increasing abundance.

From 1990 to 2001, green turtle abundance in Conception Creek was relatively constant (Fig. 2b), and the trend was not significantly different from 0 (Table 2). For comparison, the trend in Union Creek was also analyzed for the years 1990 to 2001; there was no significant change in abundance.

To evaluate the relationship of trends in nesting numbers at Tortuguero with the trends on the foraging grounds, we assumed a three-year lag from hatching to recruitment at the foraging grounds at 25-cm carapace length (Boulon and Frazer 1990, Zug and Glor 1998). Therefore, we analyzed the Tortuguero rookery data for 1976–1998 and for 1987–1998 (Table 2). These are the years that would have produced hatchlings that could recruit to Union Creek and Conception Creek, respectively, during the years of our study.

Partitioning variance into the two components of temporal and sampling variance revealed a relatively low proportion of sampling variance (see Link and

TABLE 1. The number of green turtles captured (n_i), Horvitz-Thompson type estimate of abundance (N_i), standard error of N_i (SE (N_i)), recapture probability (ρ_i), and standard error of ρ_i (SE (ρ_i)) each year at Union Creek and Conception Creek, Bahamas.

Year	n_i	N_i	SE (N_i)	ρ_i	SE (ρ_i)
Union Creek					
1978	22
1979	23	41	9	0.559	0.117
1980	22	54	14	0.407	0.108
1981
1982	49	187	76	0.262	0.107
1983	74	178	32	0.417	0.076
1984	144	224	21	0.642	0.061
1985	155	257	23	0.604	0.053
1986	149	248	21	0.600	0.051
1987	64	229	32	0.279	0.039
1988	125	194	16	0.644	0.055
1989	82	233	32	0.353	0.048
1990	69	150	17	0.460	0.053
1991	47	121	18	0.389	0.056
1992	80	104	10	0.771	0.072
1993	57	90	12	0.631	0.081
1994	57	80	8	0.709	0.074
1995
1996	65	74	4	0.884	0.053
1997	62	82	8	0.753	0.072
1998	69	85	7	0.815	0.065
1999
2000	64	91	11	0.706	0.083
2001	100	138	16	0.723	0.081
Conception Creek					
1989	25
1990	20	61	24	0.328	0.129
1991	28	46	8	0.611	0.112
1992	32	65	15	0.492	0.112
1993	21	43	9	0.490	0.099
1994	27	59	13	0.460	0.104
1995	45	48	3	0.940	0.057
1996	39	51	7	0.763	0.099
1997	25	43	7	0.576	0.090
1998	44	54	6	0.811	0.090
1999	31	52	9	0.602	0.099
2000	36	41	4	0.883	0.094
2001	28	63	16	0.447	0.113

Note: Ellipses indicate that data are not available.

Nichols 1994, Gould and Nichols 1998) in the estimates of recapture probabilities: 0.158 of total variance for Union Creek and 0.272 for Conception.

DISCUSSION

Trends on foraging grounds

The abundance of green turtles in Union Creek varied substantially over the 24-year study period from 1979 to 2001. The trend over the total duration of the Union Creek study indicates an overall stable abundance, but shorter intervals of monitoring would have yielded very different conclusions of rapidly increasing or rapidly decreasing trends. The importance of long-term studies in assessing trends in sea turtle abundance is clear. A recent symposium on conservation of sea turtles in the Greater Caribbean produced a recommendation (Eckert and Abreu-Grobois 2001:138) that trends in abundance of sea turtles on foraging grounds should be continued "until a statistically significant

change in abundance is detected (or until population stability is demonstrated with statistical precision)." Given that green turtles in Union Creek exhibited successive statistically significant trends with very different slopes, this recommendation should be reconsidered; monitoring should be continued as long as there are management issues.

The shorter 13-year study at Conception Creek indicates that abundance of green turtles is stable, consistent with the 12-year period of stability in Union Creek (1990–2001; Table 2, Fig. 2). The shorter monitoring interval for Conception Creek precludes comparing the overall relative stability of the two sampling populations.

An advantage of the modeling approach used in this study (Cormack-Jolly-Seber models followed by Horvitz-Thompson type estimation) to estimate population abundance is that trends in abundance can be interpreted in relation to other demographic parameters,

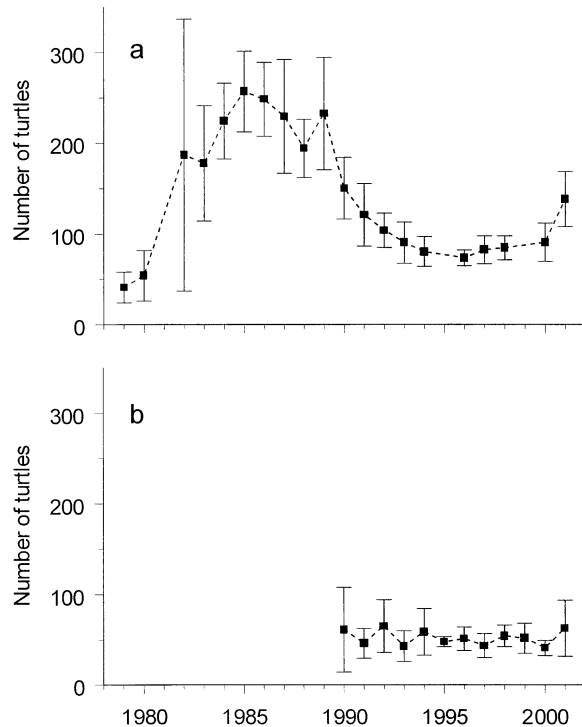


FIG. 2. Annual estimates of abundance (N_t) for green turtles in (a) Union Creek, Great Inagua, Bahamas, and (b) Conception Creek, Conception Island, Bahamas. Error bars represent 95% confidence limits; the same axis scales are used in both graphs to facilitate comparison.

such as survival and emigration. For example, Chaloupka and Limpus (2001) employed this modeling approach in a study of trends in abundance of loggerhead turtles (*Caretta caretta*) in waters of the southern Great Barrier Reef and found that adult female loggerheads declined at $\sim 8\%$ annually from 1985 to 1992. Based

on estimates for survival probabilities, they were able to conclude that the decline in adult females was not a result of decreased survival of subadult and adult loggerheads (which was high and constant over that time), but rather a result of low recruitment due to either high predation on loggerhead eggs by introduced foxes or high juvenile mortality in oceanic habitats.

Changes in population abundance in Union Creek can result from changes in immigration, emigration, or survival. We conclude that changes in immigration have been largely responsible for changes in abundance because, throughout the course of this study, green turtles had a consistently high annual survival probability (0.891) and low annual emigration probability (0.122) for three years after entering Union Creek, based on the Burnham model with the best fit (Bjorndal et al. 2003). After three years, emigration probability increased to 0.330 and survival probability decreased to 0.761 as the turtles left the protection of the Union Creek Reserve. The decrease in survival probability is well supported by returns of flipper tags from fishers throughout the Caribbean (Bahamas, Colombia, Costa Rica, Cuba, Dominican Republic, Haiti, Honduras, Nicaragua, Panama, and Venezuela; Bjorndal et al. 2003). The conclusion from the Burnham model that immigration has been the driving factor in changes of abundance is supported by the pattern of "apparent immigration" into Union Creek. Those years in which abundance increased (1980–1985, 1989, and 2000–2001) had apparent immigration values above the geometric mean (42.4%). All other years had apparent immigration values below the geometric mean. Interpreting the trend in light of demographic parameters indicates that the major decline in Union Creek between 1985 and 1994 did not result from increased mortality (Bjorndal et al. 2003) and thus did not require

TABLE 2. Summary of trend regression analyses for green turtles in the Bahamas.

Study site and year	Estimate of slope	SE	t	P	RSE	Population growth (%)		
						Mean	LCL	UCL
Union Creek								
1979–2001	-0.0029	0.0202	-0.142	0.889	0.205	0		
1979–1985	0.3276	0.0501	6.543	0.003	0.101	38.8	25.8	53.1
1985–1994	-0.1404	0.0159	-8.851	<0.0001	0.053	-13.1	-15.8	-10.3
1994–2001	0.0591	0.0425	1.392	0.236	0.100	0		
1990–2001	-0.0216	0.0269	-0.804	0.445	0.113	0		
Conception Creek								
1990–2001	-0.0104	0.0047	-2.215	0.511	0.078	0		
Tortuguero								
1976–1998	0.0465	0.0098	4.764	0.0001	0.640	4.8	2.8	6.8
1987–1998	0.0423	0.0167	2.536	0.030	0.498	4.3	1.0	7.8

Notes: Estimate of slope is instantaneous growth rate; SE is standard error of slope estimate; RSE is model residual standard error; population growth is mean annual population growth, $[(e^{\text{slope}}) - 1] \times 100$. LCL and UCL are lower and upper 95% confidence limits for population growth, calculated as $(e^{\text{slope} \pm 1.96\text{SE}} - 1) \times 100$. Five intervals are presented for Union Creek, representing all years of the study; three phases of increasing, decreasing, and stable trends (see Fig. 2a), and years that coincide with the Conception Creek study. Two intervals are presented for the Tortuguero, Costa Rica rookery, representing the years over which hatchling production could affect recruitment to Union Creek (1976–1998) and Conception Creek (1987–1998).

a management intervention. This conclusion could not have been reached based on trends in relative abundance alone.

The Burnham model allowed us to distinguish between mortality and permanent emigration for Union Creek green turtles. This distinction is important for interpreting the population dynamics responsible for changes in abundance at sites, like Union Creek, where permanent emigration is necessarily high because the habitat does not support adult turtles. However, Burnham models cannot always be used successfully because of low numbers of dead recaptures (e.g., Conception Creek). We therefore evaluated a live-recaptures-only model (in which mortality and emigration are confounded in the estimate of apparent survival probabilities) for Union Creek to compare estimates of abundance with those from the Burnham model. The live-recaptures-only model that had the best fit (four-tag-cohort-age-class survival and time-dependent recapture probabilities) yielded estimates almost identical to those of the Burnham model. Mean absolute difference between annual recapture probabilities was 0.0032 (range 0.000019–0.0118), and the mean absolute difference between annual abundance estimates was 0.7 (range 0–2.2). Direction of difference (one model estimates greater than the other) was 50:50.

When evaluating temporal trends in population abundance or demographic parameters, it is important to distinguish between the two components of total variance: temporal variance (the variance of ecological interest) and sampling variance (a measure of precision). If the proportion of sampling variance is high, removing sampling uncertainty from analyses of trends can significantly change the conclusions (Link and Nichols 1994, Gould and Nichols 1998). We could not directly estimate the proportions of temporal and sampling variance in the estimates of annual abundance because the two-stage Horvitz-Thompson estimation procedure that we used to derive the abundance estimates using recapture probabilities precluded calculating a covariance matrix. However, the proportion of sampling variance is probably small due to the following. For both Union Creek and Conception Creek, sampling variance was a relatively low proportion of total variance in the estimates of recapture probabilities, recapture probabilities were high, and the annual samples were a large proportion of the estimated abundance. In addition, coefficients of variation for the abundance estimates ($SE(N_i)/(N_i)$) suggested good precision (geometric mean $CV = 12.3\%$ for Union Creek and 16.6% for Conception Creek). All of these factors tend to yield low sampling variance (Burnham et al. 1987, Link and Nichols 1994).

Studies of trends at individual foraging sites can be of great value for local management decisions. Our results indicate that numbers of green turtles in protected sites in the central and southern Bahamas have been stable over the course of the studies. Whether the

same trend has occurred in areas in the Bahamas not protected from exploitation is not known, but it is unlikely given the high levels of exploitation and the low recapture rates in capture–mark–recapture studies at other sites in the archipelago (K. A. Bjorndal and A. B. Bolten, *unpublished data*).

Comparisons of trends in abundance of neritic juveniles and nesting females

As illustrated by the trends in abundance at Union Creek and Conception Creek compared with Tortuguero, trends in foraging-ground aggregations of immature turtles will not always track trends of the abundance of nesting females. Over the years that the Tortuguero nesting numbers were increasing, the numbers of turtles in Conception Creek were stable and the numbers of turtles in Union Creek did not change significantly (although there were successive periods of increase, decrease, and stability). Understanding the causes of the lack of concordance between trends in abundance of adult females at nesting beaches and of immature turtles on neritic foraging grounds is essential for evaluation of population trends and for correct interpretation of the “early warning” messages from trends of immature turtles.

Why was there not an overall significant increase in abundance of green turtles in Union Creek and Conception Creek resulting from the significant increase in numbers of nesting females at Tortuguero? We could conclude that the increase in nesting females did not result in an increase in immature turtles at neritic foraging grounds because mortality of eggs and/or oceanic juveniles was elevated, resulting in lowered recruitment to neritic foraging grounds. That is, this would be an example of an “early warning” revealing that survival in immature life stages had been lowered, a decline that would not be reflected in trends in nesting numbers for decades.

However, differences in trends observed at neritic foraging grounds and at source rookeries must be interpreted with caution. These differences in abundance trends may result from several factors. First, green turtles that nest at a rookery are drawn from many widely dispersed foraging grounds. For example, turtles at the Tortuguero rookery come from foraging grounds throughout the Greater Caribbean (Carr et al. 1978, Lahanas et al. 1998, Bass and Witzell 2000, Luke et al. 2004). Trends in abundance of immature turtles from one or a few neritic foraging grounds will not necessarily reflect that of the entire neritic immature life stage of the population. The foraging grounds will be differentially influenced by local conditions, including different levels of human-induced mortality and habitat degradation, and stochastic environmental conditions that vary temporally and spatially over the range of foraging grounds. The effects of local conditions are exacerbated by the fact that green turtle foraging grounds currently being monitored are small in area

relative to the total foraging area for a rookery and are low in number of turtles compared with the number of nesting turtles at a rookery. The trend in the annual number of female green turtles arriving to nest at a rookery is an integration of the trends at all of the contributing foraging areas over the preceding years. This integration of trends is superimposed on the conditions at the rookery that affect female survival and hatchling production. Because nesting populations are an integration of many foraging-ground aggregations, trends in numbers of nesting turtles should exhibit less short-term temporal variation than trends at foraging grounds. (We are not referring here to the annual differences in nesting numbers, but to the overall trends in nesting numbers.) That is, we would not expect the relatively short-term, abrupt changes in trends at Tortuguero that we see at Union Creek.

Second, mixed-stock analyses of foraging aggregations of immature Atlantic green turtles have revealed that they are mixed stocks with several source rookeries (Lahanas et al. 1998, Bass and Witzell 2000, Luke et al. 2004). If the different source rookeries experience different population trends, trends on foraging grounds and at rookeries will, of necessity, be different. We do not believe that this explains the differences in trends in our study because Tortuguero provides the great majority of turtles on the foraging grounds (~80% at Union Creek; Lahanas et al. 1998) and the annual number of nesting turtles at Tortuguero, in the tens of thousands, is so much greater than that of the other rookeries in the Greater Caribbean, each with fewer than 2000 nesting turtles annually (Seminoff 2002).

Third, caution must be used in selecting the correct time series over which to compare rookeries and foraging grounds. The time lags that elapse between trends in one life stage being reflected in other life stages vary among life stages. A change in numbers of nesting females will be reflected immediately in the number of eggs, after a few months in the oceanic juvenile stage, and after approximately three years in the neritic juvenile stage. In contrast, changes in the numbers of green turtles that leave nearshore foraging grounds, such as Union Creek at ~60 cm carapace length or Conception Creek at ~50 cm, will not be reflected in the number of nesting females for perhaps a decade or more (Bjorndal et al. 2000). Again, we do not think that this explains the differences in trends in our study because we accounted for the three-year lag for recruitment to neritic foraging grounds in our comparison.

Fourth, abundance trends may vary among foraging grounds and their contributing rookeries if the turtle densities represent different proportions of the carrying capacity (K) of the habitat and thus have different potential for change. We believe that this accounts for the differences between Union Creek and Tortuguero. The number of nests deposited each year at Tortuguero is still well below K (M. Tiwari, K. A. Bjorndal, and A.

B. Bolten, *unpublished data*). As discussed in an earlier paper (Bjorndal et al. 2000), the changes in trends at Union Creek probably resulted from the abundance of green turtles overshooting K in the early years of the study, followed by a decrease in abundance as a result of resource depletion, followed by a stable period at or near K .

This last point is particularly important because of the bias in the selection of study sites for ongoing long-term studies on sea turtle foraging grounds. Most of these studies were not established with the purpose of monitoring trends in population abundance. Rather, studies were initiated with other objectives, such as evaluation of nutritional ecology and somatic growth; therefore, sites with high turtle densities were selected. If the overall numbers of green turtles increase in the Greater Caribbean, these current study sites may yield underestimates of the increasing trend because, like Union Creek and Conception Creek, the monitoring period began at high densities relative to those throughout the region.

CONCLUSIONS

How can we ensure that trends in abundance of sea turtles measured on foraging grounds will accurately represent the trends in the entire neritic immature life stage? The best approach may be a combination of extensive and intensive surveys in a series of monitoring sites, carefully selected to represent the range of habitats and turtle densities. Extensive surveys, such as aerial or vessel surveys, yield measures of relative abundance over large areas and are more logistically feasible than intensive techniques in some areas. Intensive techniques that employ capture-mark-recapture are usually more restricted in geographic area, but can provide estimates of absolute abundance and demographic parameters. A combination would provide trends in relative abundance on a large scale and the ability to interpret the demographic processes behind those trends. Understanding the demographic basis for changes in abundance allows for more informed and effective management. This monitoring approach would apply equally well to other long-lived species with widespread foraging areas and discrete reproductive areas, such as other species of sea turtles, albatrosses, and many marine mammals.

For accurate assessment of population trends in long-lived organisms, trends in the different life stages should be evaluated. However, interpretation of these trends will be complex in those species, such as sea turtles, that undergo extensive developmental migrations among different and widely dispersed foraging habitats. Monitoring programs should be continued as long as there are management issues and should be conducted at sites that represent the range of habitat types and population densities. Therefore, metapopulation models that incorporate long-term studies from a wide range of foraging grounds as well as breeding

areas would be a valuable approach for the analysis of population trends (see Chaloupka 2004).

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