

Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua

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Abstract

Hawksbill sea turtle *Eretmochelys imbricata* nesting on Long Island, Antigua, West Indies (also known as Jumby Bay) has been monitored since 1987. Although the numbers of nesting females remained relatively constant for the first 11 survey seasons (1987–1997), inclusion of more recent data (1998–2004) in the analysis reveals a statistically significant upward trend. In particular, neophytes have shown a significant upturn in numbers, whereas the remigrant subpopulation has remained stationary. This indicates that recruitment is driving the upward trend in the total number of nesters. Predictive models based on the Poisson distribution suggest that the neophyte subpopulation will continue to grow in size by an average of 10% per annum. Model-based predictions and their limitations are discussed. The Jumby Bay Hawksbill Project, which has monitored and protected nesting hawksbills and their eggs since the project's onset, is one among several factors that may contribute to the recent increase in nesting females.

Introduction

Hawksbill turtles *Eretmochelys imbricata* are considered critically endangered by the International Union for the Conservation of Nature (IUCN), with Caribbean populations drawing particular concern (Baillie & Groombridge, 1996; Meylan & Donnelly, 1999). Although subsistence take of hawksbill turtles occurs in much of their range, the species' grim survival status is widely owed to overharvesting for their ornate, commercially valuable scutes (Carr, 1972; Parsons, 1972; Nietschmann, 1981; Mortimer, 1984; Cruz & Espinal, 1987; Groombridge & Luxmoore, 1989; Meylan, 1989; Eckert, 1995; Limpus, 1997). Because hawksbills (like other marine turtles) may take decades to reach sexual maturity, are migratory (Bass *et al.*, 1996; Bass, 1999; Meylan, 1999) and make long-term use of distinct developmental habitats during their lives (Nietschmann, 1981; Boulon, 1994; van Dam & Diez, 1998), protection represents an enormous challenge. In 1999, Meylan reported depletion or decline of the species in 22 of the 26 Caribbean geopolitical units for which data were available, whereas populations at Long Island (i.e. Jumby Bay), Antigua and Buck Island, St Croix remained stable and Yucatan Peninsula, Mexico and Mona Island, Puerto Rico showed increases. All of these had a history of protection (Hillis, 1995; Diez, Marshall, & van Dam, 1998; Garduño-Andrade *et al.*, 1999; Richardson, Bell, & Richardson, 1999). The 2002 IUCN

status review added Doce Leguas Cays, Cuba and Barbados to the list of sites with growing populations (IUCN, SSC & MTS, 2002). Here, we identify current trends in the Jumby Bay nesting population.

The Jumby Bay Hawksbill Project was initiated in 1987 on Long Island, a privately owned island located off the north-eastern coast of Antigua (Fig. 1). Surveys of nesting have been precisely repeated annually for the last 18 years and are ongoing. The value of the project lies not only in its longevity but also in its unusually high recapture probability (see Methods). In 1998 we asked whether 11 years of saturation tagging (i.e. tagging all nesting females in the population) would reveal a population trend in the numbers of nesting females. However, the annual variation in these numbers was too great, and a significant trend was not discerned (Richardson *et al.*, 1999). With seven additional seasons of data, we now revisit the question.

Discerning patterns over time (individual females per season) presents a challenge to most sea turtle nesting beach studies (Richardson, 1999). Classical linear regression methods are typically inappropriate for analyzing the results of nesting surveys, as counts of nesting turtles derived from mark–recapture methods violate the assumptions of normality and constant variance required for ordinary least-squares analyses (Skalski & Robson, 1992). In addition, the assumption of independence is often violated when dealing with data collected over time. This is of particular concern in

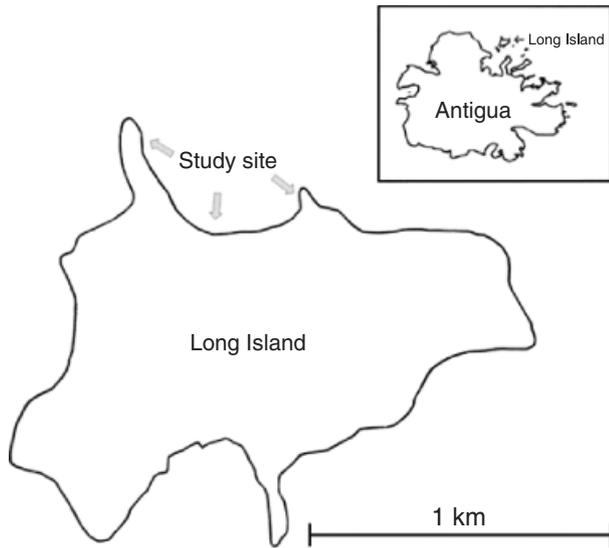


Figure 1 Map of Long Island, Antigua, site of the Jumby Bay Hawksbill Sea Turtle Project (17°8'N, 61°45'W).

nesting beach surveys in which marked individuals are not observed with equal probability on an annual basis, such as in this case because hawksbill turtles do not nest annually. Consequently, time-series data from beach surveys may be subject to serial dependence of a form where observations taken in consecutive years may be negatively correlated. In addition, it is reasonable to expect that associations between yearly counts may decrease with the separation between these observations because of time-varying random processes in the environment or in the population dynamics of the species. Therefore, we apply statistical methods appropriate for the analysis of a time series of counts (e.g. Cameron & Trivedi, 1998) to analyze patterns of hawksbill nesting. We investigate trends in the data and use our resultant models to forecast the numbers of nesting females at our study site.

Methods

Survey methodology

Pasture Bay beach on Long Island (475 m) was patrolled by two observers on an hourly basis from dusk until dawn during each night of the nesting season, 15 June through 15 November. When a turtle was encountered, the patrol was always completed by one of the observers. Because it takes at least an hour for a full nesting event to take place, virtually every female was encountered with this protocol. On the basis of the very low numbers of crawls observed during the off season, nearly all females nesting in a calendar year are recorded during the 153-night survey (Hoyle & Richardson, 1993). While laying, each female was fitted with a steel tag (National Band and Tag Co., Newport, KY, USA, Inconel Size 681) on the most proximal pad of each flipper. In addition, a unique pattern of drill holes was made

in the inert portion of the supracaudal scutes as supplemental means of identification in the rare event that both flipper tags were lost. This method of using multiple tags and marks has proved to be extremely effective. We were able to identify the individual in all but one of our 183 remigrant turtle encounters (99.5%). The reliability of this marking system allows us to differentiate between new (neophyte) and previously observed (remigrant) nesting turtles with a high degree of confidence. We define a neophyte as an untagged turtle, assumed to be primiparous (first-time nesters).

Statistical analysis

Each annual cohort of nesting turtles ($n = 18$ years) was divided into remigrant and neophyte categories (Fig. 2). Because the remigration interval between nesting seasons is 2–4 years for most individuals in the population (98%; Fig 3), we chose to differentiate remigrants from neophytes beginning in 1991 following 4 years of saturation tagging. Rather than analyzing each time series (total nesters, remigrants and neophytes) separately, we chose to perform a simultaneous (multivariate) analysis of the series to account for possible correlation between the yearly counts for turtles in each category. Because the total, remigrant and neophyte counts are linearly related, it is sufficient to analyze any two of these three series in a multivariate analysis. Because the remigrant/neophyte distinction could not be made with confidence before 1991, and to avoid limiting the analysis to only post-1990 data, we performed a bivariate analysis of total nesters and neophytes.

The analysis was accomplished through the fitting of a Poisson loglinear model to yearly data on neophytes and total nesters with random year effects to induce and account for a correlation between these series. The model has an analysis of covariance-type structure with separate polynomial effects of time for each nest count category (neophyte or total). Specifically, let y_{it} be the nest count in year t for nest category i ($i = 1$ for neophytes, $i = 2$ for total nesters).

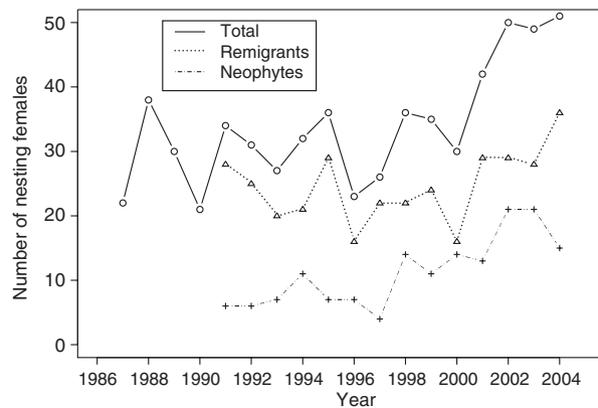


Figure 2 Hawksbill sea turtle *Eretmochelys imbricata* nesting numbers (1987–2004) for total nesters, remigrants and neophytes on Long Island, Antigua.

Conditional on a normally distributed random year effect b_t , we assume that $y_{it} \sim \text{Poisson}(\mu_{it})$ where

$$\log(\mu_{it}) = b_t + \beta_{0i} + \beta_{1i} \text{year}_t + \beta_{2i} \text{year}_t^2 + \dots \quad (1)$$

and where the intercept β_{0i} , linear effect of year β_{1i} , etc. depend on i (are distinct for neophytes and total nesters), and the order of the polynomial in year is estimated from the data and allowed to differ between the two nest categories.

We chose to use Poisson loglinear models here as an alternative to a normal linear regression because the former is appropriate for discrete count data. Note that a loglinear model is not a log transformation of a linear model ($\log Y_t = \beta_0 + \beta_1 t + \varepsilon$) but rather $\log \mu_t = \beta_0 + \beta_1 t$, where μ_t is the mean of a Poisson-distributed count Y_t . Serial correlation was investigated by fitting model (1) assuming independence through time and then testing for autocorrelation among the resulting residuals using Box–Pierce portmanteau tests (Cameron & Trivedi, 1998, section 7.3.2). The final fitted model was used to forecast numbers of nesting turtles for four subsequent seasons (2005–2008).

Results

Model fitting

Models of the form (1) were fitted to the data, revealing a statistically significant quadratic effect of year on total nesters ($t = 2.28$, $P = 0.036$) but not on neophytes ($t = 0.23$,

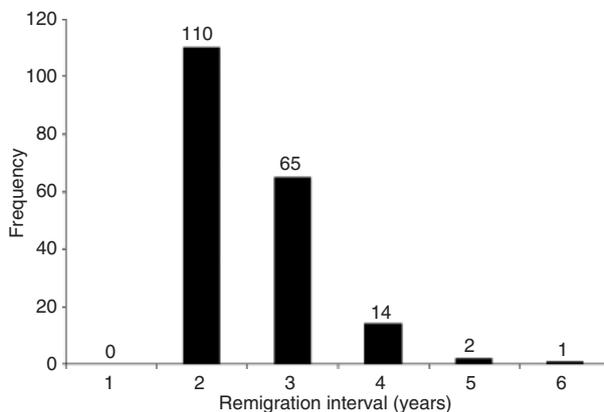


Figure 3 Frequency distribution of remigration intervals observed on Long Island, Antigua from 1987 to 1992 (from Richardson *et al.*, 1999).

$P = 0.818$) which exhibited a significant linear trend ($P < 0.001$). The resulting final model for these data takes the form

$$\log(\mu_{it}) = b_t + \beta_{0i} + \beta_{1i} \text{year}_t + \beta_{2i} (\text{year}_t^2) I(i = 1) = \begin{cases} b_t + \beta_{01} + \beta_{11} \text{year}_t + \beta_{21} \text{year}_t^2 & \text{for total nesters} \\ b_t + \beta_{02} + \beta_{12} \text{year}_t & \text{for neophytes} \end{cases}$$

where b_1, \dots, b_{18} are independent, normally distributed year effects with variance (i.e. variance component) σ_b^2 . Parameter estimates for this model as well as 95% confidence intervals and P -values for the significance of each parameter are given in Table 1. In addition to the significance of the quadratic time effect for total nesters ($P = 0.036$) and linear trend in time for neophytes ($P < 0.001$), note the lack of significance of σ_b^2 . This parameter represents the variance component from year to year (above and beyond the time trend fit in the model) and quantifies the degree of association between the total nesters and neophytes series. Its nonsignificance here indicates that remigrant and neophyte counts are, somewhat surprisingly, not significantly correlated. In addition, Box–Pierce portmanteau tests of serial correlation on the residuals of the fitted model did not detect significant autocorrelation within the total nesters and neophytes series through time ($P = 0.697$ and 0.147 , respectively, for the hypothesis of zero autocorrelation through lag 6).

Trend analysis

The fitted model reveals significant increasing time trends for total nesters and for neophytes (Table 1). The neophyte time series increases by 0.097 per annum (log scale), suggesting that neophytes are entering the Long Island reproductive population at a multiplicative rate of $e^{0.097} = 1.10$ per year. We therefore anticipate that our neophyte subpopulation will continue to grow in size by an average of 10% annually.

The significant quadratic effect of time on total nesters suggests a time-dependent rate of increase by a multiplicative factor of $\exp\{\hat{\beta}_{11} + \hat{\beta}_{21}(2t + 1)\} = \exp\{-0.0413 + 0.00388(2t + 1)\}$ from year t to year $t + 1$, where t is the number of years since the beginning of the study ($t = 1, 2, \dots$ corresponding to 1987, 1988, \dots). Thus, not only is the total number of nesting females increasing annually, but also the rate of increase appears to be accelerating. We provide a graphical presentation of predicted values for total nesters (Fig. 4) and for neophytes (Fig. 5) using the

Table 1 Regression parameter estimates describing time trend for total nesters and neophytes

Parameter	Interpretation	Estimate	SE	95% CI	P -value
β_{01}	Intercept, total nesters	3.45	0.146	(3.14, 3.74)	<0.001
β_{11}	Linear year effect, total nesters	-0.0413	0.0343	(-0.114, 0.0310)	0.245
β_{21}	Quadratic year effect, total nesters	0.00388	0.00170	(0.000296, 0.00747)	0.036
β_{02}	Intercept, neophytes	1.23	0.283	(0.631, 1.83)	<0.001
β_{12}	Linear year effect, neophytes	0.0968	0.0209	(0.0528, 0.141)	<0.001
σ_b	Variance component due to year	0.0374	0.117	(-0.210, 0.285)	0.754

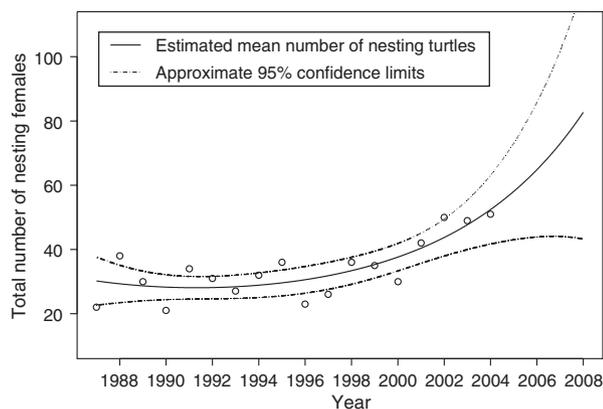


Figure 4 A loglinear model with quadratic time effects (95% confidence limits) fit to total numbers of nesting hawksbills (1987–2004) and forecast to subsequent seasons (2005–2008), Long Island, Antigua.

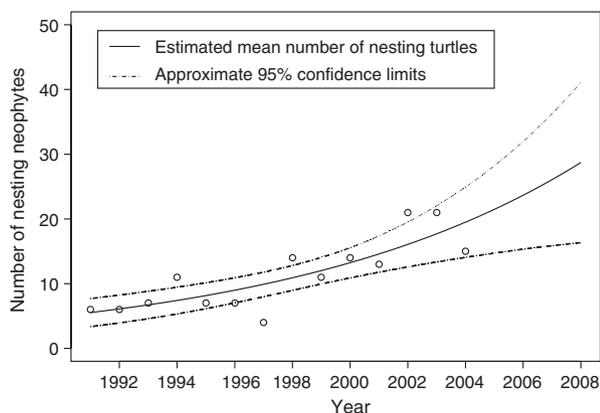


Figure 5 A loglinear model with linear time effects (95% confidence limits) fit to neophyte numbers of nesting hawksbills (1987–2004) and forecast to subsequent seasons (2005–2008), Long Island, Antigua.

fitted loglinear model. Forecasted numbers of individuals for 2005–2008 are provided for total nesters and for neophytes (Table 2). All predictions beyond the range of these data must be treated with caution because they are extrapolations based on an assumption that the fitted model will continue to hold moving forward through time. Of course, future predictions are increasingly speculative the further they are extended in time, so we have chosen to present forecasts only for the next 4 years.

Discussion

We have shown a significant increase in total nesters (1987–2004), which we equate with the positive recruitment of primiparous individuals to the Long Island population. Although we cannot be certain that neophytes have not bred previously because we do not perform laparoscopic examinations on our study animals (Limpus, 1990), the assumption is circumstantially supported in several ways. Firstly, we observe that neophytes return to nest at Pasture Bay

Table 2 Forecast numbers for total nesters and neophytes with 95% confidence limits

Year	Lower limit	Prediction	Upper limit
<i>Total nesters</i>			
2005	43.0	58.1	73.1
2006	43.9	64.8	85.8
2007	44.1	72.9	101.8
2008	43.3	82.7	122.1
<i>Neophytes</i>			
2005	14.7	21.5	28.2
2006	15.3	23.7	32.0
2007	15.9	26.1	36.3
2008	16.3	28.7	41.1

beach in subsequent seasons with approximately the same predictability as remigrants (Richardson *et al.*, 1999), indicating that they become integrated within the Jumby Bay population and do not represent a subset of wandering turtles passing through the region. Second, we have never in the history of the project found a tagged turtle from another nesting beach, nor have any of our tags been reported on nesting beaches elsewhere in the region. Whether new individuals in our nesting population represent first-time nesters, individuals who have previously bred elsewhere or some combination thereof, the conclusion that neophyte numbers are driving the increase in total nesters remains logical and crucial. A meaningful increase in population size should reflect a recruitment rate that exceeds mortality, as appears to be the case with this population. Our population of reproductive adults exhibits an annual survivorship of 94% (Richardson *et al.*, 1999; Kendall & Bjorkland, 2001). Thus, an increase in total nesters by this long-lived species should be the result of recruitment. Because neophytes provide the first indication of population growth, assuming regional recruitment and philopatry (Bowen & Karl, 1997), we chose neophytes as the population subset best suited to forecasting, in addition to total nesters.

Our model for the total number of nesting females predicts 58.1, 64.8, 72.9 and 82.7 over the same 4 years. Our model for neophyte nesting predicts an annual increase of 10%, leading to forecasts of 21.5, 23.7, 26.1 and 28.7 for 2005–2008, respectively. Forecasting nesting trends using our model involves extrapolation of a fitted pattern over time, which is inherently risky. The 95% CI for our 2005 forecast for neophytes (14.7–28.2 neophyte units) illustrates the considerable degree of uncertainty associated with forecasting numbers of nesting hawksbill sea turtles. However, we do not question that increasing recruitment and increasing total numbers of nesting hawksbills are real phenomena occurring at Jumby Bay.

Finally, we must note that incipient population recovery at Long Island cannot yet be causally related to the Jumby Bay conservation program that has been protecting adult turtles and eggs on Pasture Bay beach since 1987. However much we may wish to bask in the success of our conservation track record, the measure of our success must await

additional information on nesting trends at both Long Island and nearby beaches. It is known that low-level nesting occurs on most of the mainland Antigua beaches, although we have no information at this time on whether their nesting numbers have been increasing in recent years. If the Long Island output of hatchlings is seeding mainland beaches with adult recruits, as we presume it must (natal philopatry is not proven at this small a scale; see Bowen & Karl, 1997), then the numbers of neophyte nesters on those beaches would be increasing as well. There is plenty of available nesting habitat on Antigua, so there is no reason for us to believe that turtles are fleeing mainland nesting habitat in favor of Jumby Bay. It would be useful to establish monitoring on mainland Antigua beaches and on adjacent islands such as Barbuda to elucidate potential dynamics among local populations. Causes other than protection by the Jumby Bay Hawksbill Project may be driving the trends we have observed, such as the drastic reduction of hawksbill take in Cuban waters since 1990 (Carrillo, Webb & Manolis, 1999), the establishment of Organisation of Eastern Caribbean States (OECS) guidelines on the taking of hawksbills within the Eastern Caribbean region, efforts by CITES to reduce international trade in tortoiseshell, and the fact that blue water sharks, an important predator of sea turtles, have been dramatically reduced in numbers from overfishing (Baum *et al.*, 2003).

It is important to recognize that population recovery reported herein is at a local scale, and is not necessarily reflective of the regional status of hawksbills. Because so few nesting colonies have been afforded long-term protection, we cannot conclude that hawksbills are increasing proportionally throughout the Caribbean. We do not believe that decreased prey availability (reef-associated invertebrates) is a regulatory factor at current hawksbill densities. Chicken-liver sponges, a primary prey item of young hawksbills, have been shown to proliferate in areas of dying coral (e.g. Aronson *et al.*, 2002; Peckol *et al.*, 2003), and it is generally accepted that adults feed on deeper reefs which have not exhibited coral declines. Instead, we predict that density-dependent population regulation will occur on the nesting beach, because of intraspecific competition for nest sites (but see Girondot *et al.*, 2002). We have already begun to observe nesting turtles dig up incubating eggs at Jumby Bay.

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