REPORT

Annual variation in nesting numbers of marine turtles: the effect of sea surface temperature on re-migration intervals

Andrew R. Solow,[1]* Karen A. Bjorndal[2] and Alan B. Bolten[2]

[1]*Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
[2]*Archie Carr Center for Sea Turtle Research and Department of Zoology, University of Florida, Gainesville, FL 32611, USA*
*Correspondence:
E-mail: asolow@whoi.edu*

Abstract

The assessment of marine turtle populations is complicated by large inter-annual variations in nesting numbers. This variability has been attributed to synchrony in the re-migration intervals (i.e., intervals between successive nesting years) of individuals. It has been hypothesized that this synchrony arises from environmental variations that affect the feeding conditions at sea. This paper presents the first direct test of this hypothesis. The analysis identifies a significant effect of sea surface temperature on the re-migration interval in the largest Atlantic population of green turtles.

INTRODUCTION

The fidelity of female sea turtles to specific nesting beaches provides a basis for population assessments. Such assessments are complicated by large year-to-year variations in nesting numbers. These variations have been attributed to the fact that females typically do not nest in consecutive years, but spend 1 or more years feeding at sea between successive nesting years. The time between successive nesting years is called the re-migration interval. Using simulations from two simple models, Hays (2000) – see, also, Solow (2001) – showed that variable re-migration intervals are not sufficient to maintain a high level of variability in nesting numbers. However, this variability can be maintained by even weak synchrony in the re-migration behaviour of individuals.

Carr & Carr (1970), Broderick *et al.* (2001), and others have hypothesized that the re-migration interval is modulated by feeding or other environmental conditions at sea. Because individuals in the same stock tend to experience similar conditions, this can serve to synchronize nesting behaviour. Here, we test for the effect of sea surface temperature (SST) on the re-migration interval in the green turtle (*Chelonia mydas*) nesting stock at Tortuguero, Costa Rica. We focus on SST as a general indicator of oceanographic conditions. Our analysis, which identifies a significant SST effect, appears to be the first direct test for an environmental effect on re-migration interval. In related

work, Limpus & Nicholls (2000) identified a significant relationship between green turtle nesting numbers on Heron Island, Australia and the Southern Oscillation Index. However, the model on which their result was based does not account for re-migration. Chaloupka (2001) analysed time series of green turtle egg production in the South-east Asian region and attributed some of the year-to-year variability to environmental factors, but again did not model re-migration explicitly.

MATERIALS AND METHODS

The green turtle population that nests at Tortuguero is the largest in the Atlantic. The nesting season at Tortuguero runs from early June to mid-November, with peak activity in August and September Annual surveys of the nesting area began in 1971. These surveys are described in Bjorndal *et al.* (1999). Updated estimates of the total number of nests on the northern 18 km of the beach are plotted in Fig. 1 for the period 1971–2000. We will assume that mean clutch frequency has remained constant, so that the number of nests is proportional to the number of females nesting. The time series in Fig. 1 exhibits the large year-to-year variations in nesting numbers typical of green turtles. Following nesting, females from the Tortuguero stock disperse throughout the Greater Caribbean (Carr *et al.* 1978). Tagging studies have shown that re-migration intervals for the Tortuguero stock are predominantly 2 or 3 years (Carr *et al.* 1978).
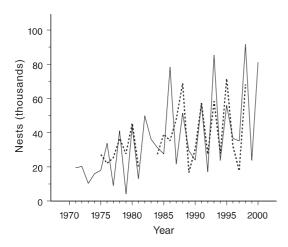
Figure 1 Estimated number of nests on the northern 18 km of the nesting beach at Tortuguero, Costa Rica, 1971–2000 (solid) updated from Bjorndal *et al.* (1999). Also shown are the fitted values, 1975–98 (dashed).

To our knowledge, the only long-term SST time series in the Caribbean region is the monthly record for La Parguera in south-western Puerto Rico (Winter *et al.* 1998). In Fig. 2, the winter SST anomaly used in the analysis described below is plotted for the period 1973–97. In each year, the winter SST anomaly was formed by averaging all available SST measurements during the period December – February and subtracting the average winter SST over the period 1973–97. As a result of missing monthly values, some winter SST values are based on fewer than three monthly anomalies. Our convention is that the year associated with a winter SST anomaly is the year of the corresponding December value (whether or not it was available). No values were available between December 1980 and February 1981, so it was not possible to form a winter SST anomaly for 1980.
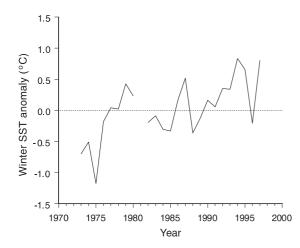

Figure 2 Winter SST anomaly at La Parguera, 1973–97.

In qualitative terms, the model adopted here operates in the following way. Consider an adult female that nests in the summer of calendar year t. After nesting, she returns to sea to feed. While at sea, she faces an annual mortality probability of $1-s$, where s is the annual survival probability. Provided this individual survives to the summer of year $t+2$, she nests again with probability p_t, so that p_t is the 2-year re-migration probability for individuals nesting in year t. If she does not nest in the summer of year $t+2$, then she remains at sea for an additional year and, provided she survives, nests in the summer of year $t+3$. Under this model, only 2- and 3-year re-migration intervals are possible, which is a reasonable approximation for this population, so that $q_t = 1-p_t$ is the 3-year re-migration probability for individuals nesting in year t. In addition to re-migrants, some of the females nesting each year represent new recruits to the nesting stock.

Let the random variable N_t be the nesting number in year t. Under the model outlined above

$$N_t = N_{t-2}(2) + N_{t-3}(3) + \mu + \varepsilon_t \qquad (1)$$

where $N_{t-2}(2)$ is the number of females nesting in year $t-2$ that also nest in year t, $N_{t-3}(3)$ is the number of females nesting in year $t-3$ that also nest in year t, μ is the mean number of recruits in each year, and ϵ_t is a normal error with mean 0 and unknown variance σ^2 reflecting unmodelled variations in recruitment. Conditional on the observed value n_{t-2} of nesting number N_{t-2} in year $t-2$, assuming that individuals behave independently, and recalling that s denotes the annual survival probability, $N_{t-2}(2)$ has a binomial distribution with mean

$$E(N_{t-2}(2) \mid n_{t-2}) = n_{t-2}\, s^2 p_{t-2} \qquad (2)$$

and variance

$$\mathrm{Var}(N_{t-2}(2) \mid n_{t-2}) = n_{t-2}\, s^2 p_{t-2}(1 - s^2 p_{t-2}) \qquad (3)$$

For computational convenience, we will adopt a normal approximation to this binomial distribution. Similarly, conditional on the observed value n_{t-3} of N_{t-3}, $N_{t-3}(2)$ has an approximate normal distribution with mean $n_{t-3}\, s^3 q_{t-3}$ and variance

$$n_{t-3}\, s^3 q_{t-3}(1 - s^3 q_{t-3}).$$

Interest here centres on testing the null hypothesis H_0 that the 2-year re-migration probability p_t does not depend on SST. Towards this end, we adopt the linear logistic model:

$$p_t = \frac{\exp(\beta_0 + \beta_1 x_{t+1})}{1 + \exp(\beta_0 + \beta_1 x_{t+1})} \qquad (4)$$

where x_{t+1} is the winter SST anomaly in year $t+1$. At first glance, this expression appears to involve a logical difficulty, in that p_t depends on x_{t+1}. This difficulty arises from the notation in which p_t is the 2-year re-migration probability for individuals nesting in year t. Unfortunately,

other choices of notation give rise to similar difficulties. Under this model, the 2-year re-migration probability depends on SST in the *second* winter following nesting. This timing is consistent with our understanding of vitellogenesis in green turtles (Miller 1997). A female can nest after a 2-year re-migration interval only if her nutritional status in the previous winter can sustain vitellogenesis. However, if feeding conditions are unfavourable, follicle development will be postponed to the following year. It is important to emphasize that the specification of this model was based solely on biological considerations and not on an analysis of the data. Although it would be possible to use the data to optimize the model specification, this would cause complications in using the same data to assess significance.

Under this model, the null hypothesis that p_t does not depend on SST corresponds to H_0: $\beta_1 = 0$. This hypothesis can be tested against the general alternative hypothesis H_1: $\beta_1 \neq 0$ through a likelihood ratio (LR) test (Silvey 1975). The LR statistic is given by $\Lambda = -2(L_0 - L_1)$ where L_0 and L_1 are the log likelihood maximized under H_0 and H_1, respectively. For this model, the maximization of the log likelihood, which is given in the Appendix, under both H_0 and H_1 must be done numerically. Under H_0, Λ has an approximately chi-squared distribution with 1 degree of freedom so that H_0 can be rejected at significance level α if the observed value of Λ exceeds the upper α-quantile of this distribution.

RESULTS

The model outlined in the previous section was fitted by maximum likelihood (ML) to the data in Figs 1 and 2 both with and without the restriction that $\beta_1 = 0$. For the unrestricted model, the ML estimate $\hat{\beta}_1$ of β_1 was 14.8 and the ML estimates of the other parameters were $\hat{\beta}_0 = -0.6$, $\hat{s} = 0.80$, $\hat{\mu} = 16\,756$ and $\hat{\sigma} = 16\,867$. When the model was fitted under the restriction that $\beta_1 = 0$, the ML estimates of these parameters were 0.8 (corresponding to a constant 2-year re-migration probability of 0.69), 0.97, 5696, and 19 344. The value of the LR statistic Λ was 12.0. The corresponding significance level is around 0.0005, so that the null hypothesis of no SST effect can be decisively rejected. It is notable that the estimate of β_1 under the unrestricted model is positive, as would be expected from biological considerations. In Fig. 3, the fitted linear logistic model of the 2-year re-migration probability is shown. As discussed below, it is also notable that the estimates of s and μ under the unrestricted model seem more reasonable than the corresponding estimates under the restricted model. If $\hat{\sigma}$ is taken as representing year-to-year variations in recruitment alone, then it is somewhat large in comparison to $\hat{\mu}$. However, as $\hat{\sigma}$ also

includes the effects of unmodelled variations in s, β_0, and β_1, its magnitude does not seem unreasonable given the simplicity of the model.

The fitted values

$$\hat{N}_t = n_{t-2}\hat{s}^2\hat{p}_{t-2} + n_{t-3}\hat{s}^3\hat{q}_{t-3} + \hat{\mu} \qquad (5)$$

under the unrestricted model are also plotted in Fig. 1, where $\hat{p}_{t-2}$ and $\hat{q}_{t-3}$ are based on the fitted probability model in Fig. 3. The gaps in this series are due to missing values of SST. The fitted values appear to capture the behaviour of the data reasonably well. The main exception is the failure to capture the large number of nests observed in 1986. The model does capture the interruptions in the regular year-to-year seesaw pattern in nest numbers that occurred in 1990 and 1997. This seesaw pattern is consistent with large 2-year re-migration probabilities related to warm winter SST. The interruptions appear to be related to relatively cold winter SST in 1988, 1989, and 1996.

DISCUSSION

The analysis presented here is the first direct test for the effect of an environmental variable on the re-migration interval in marine turtles. The dependence of the re-migration interval on SST provides the synchrony necessary to maintain the substantial variation in annual nesting numbers of green turtles at Tortuguero. Understanding the source of this variation should contribute to the assessment of population trends. Such an assessment is critical to the management of this endangered species.

We have applied the same approach to a time series of green turtle nest numbers on a 21-km stretch of beach in the Archie Carr National Wildlife Refuge on the east coast
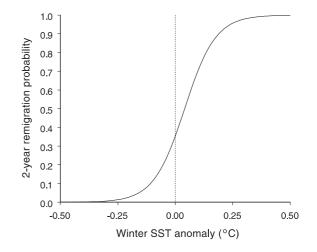

Figure 3 Fitted relationship between the 2-year re-migration probability and SST anomaly in the second winter following nesting.

of Florida for the period 1982–97 (Bagley *et al.* 2000). Although we again found a significant positive relationship between the 2-year re-migration probability and SST, this result was due to a single interruption of a strict 2-year periodicity in nesting numbers associated with the coldest winter during this period. For this reason, we do not present detailed results here. However, it is interesting to note that the variations in nest numbers at this site are out of phase with those at Tortuguero. Although this is not at all inconsistent with our model, it would lead to contradictory results in simply correlating nest numbers with lagged SST. This underlines the importance of explicitly incorporating re-migration in a model of nesting numbers.

Although the goal of the analysis presented here was to identify an environmental effect on the re-migration interval, our model also provides estimates of two important demographic parameters – recruitment and survival. The estimate of percentage annual recruitment, defined as the ratio of the estimate $\hat{\mu}$ of mean recruitment to the average of the fitted nesting numbers $\hat{N}_t$, is 0.44. The only previous estimate for the Tortuguero stock, based on tagging data for the northern quarter of the nesting beach reported by Carr (1980) for the period 1971–79, was around 0.80. However, this earlier estimate is inflated by tag loss and also by unreported nesting of tagged individuals in the southern part of the beach. Estimates of annual percentage recruitment of green turtles on Heron Island, Australia, based on laparoscopy, range from 0.24 to 0.32 (C. J. Limpus, personal communication).

The estimate of annual survival probability of adult females based on our model is 0.80 with an approximate 0.95 confidence interval of 0.63–0.98. The only earlier estimate for the Tortuguero stock of 0.60 was found by Bjorndal (1980) by following annual cohorts (1959–72) over time. This underestimates survival because, as with the estimate of percentage recruitment, the patrol area did not cover the entire nesting beach. The annual survival probability of adult green turtles in the southern Great Barrier Reef, Australia, has been estimated at around 0.95 (Chaloupka 2002) by mark–recapture methods. We speculate that the higher percentage recruitment and lower survival probability in the Tortuguero stock compared to this Australian stock reflect, in part, the extensive harvest of Tortuguero turtles on their foraging grounds throughout the Caribbean and particularly in Nicaragua (Lagueux 1998).

ACKNOWLEDGEMENTS

REFERENCES

Bagley, D.A., Uong, L.T., Danner, A.B., Hirama, S., Wick, L.A. & Ehrhart, L.M. (2000). Marine turtle nesting at the Archie Carr National Wildlife Refuge in 1997. In: *Proceedings of the Eighteenth International Sea Turtle Symposium* (eds Abreu-Grobois, F.A., Briseno-Duenas, R., Marquez, R. & Sarti, L.). NOAA Technical Memorandum NMFS-SEFSC-436, Washington, DC, pp. 175–177.

Bjorndal, K.A. (1980). Demography of the breeding population of the green turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. *Copeia*, 2002, 525–530.

Bjorndal, K.A., Wetherall, J.A., Bolten, A.B. & Mortimer, J.A. (1999). Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: An encouraging trend. *Cons. Biol.*, 13, 126–134.

Broderick, A.C., Godley, B.J. & Hays, G.C. (2001). Trophic status drives interannual variability in nesting numbers of marine turtles. *Proc. Roy. Soc. Lond.*, B268, 1481–1487.

Carr, A.F. (1980). Some problems of sea turtle ecology. *Am. Zoo.*, 20, 489–498.

Carr, A.F. & Carr, M.H. (1970). Modulated reproductive periodicity in *Chelonia*. *Ecology*, 51, 335–337.

Carr, A.F., Carr, M.H. & Meylan, A.B. (1978). The ecology and migrations of sea turtles, 7. The West Caribbean green turtle colony. *Bull. Am. Mus. Nat. Hist.*, 162, 1–146.

Chaloupka, M. (2001). Historical trends, seasonality and spatial synchrony in green sea turtle egg production. *Biol. Cons.*, 101, 263–279.

Chaloupka, M. (2002). Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecol. Modelling*, 148, 79–109.

Hays, G.C. (2000). The implications of variable remigration intervals for the assessment of population size in marine turtles. *J. Theor. Biol.*, 206, 221–227.

Lagueux, C.J. (1998). *Marine turtle fishery of Caribbean Nicaragua: human use patterns and harvest trends*. PhD Dissertation, University of Florida, Gainesville.

Limpus, C. & Nicholls, N. (2000). ENSO regulation of Indo-Pacific green turtle populations. In: *The Australian Experience* (eds Hammer, G.L., Nicholls, N. & Mitchell, C.). Kluwer Academic Publishers, Dordrecht, pp. 399–408.

Miller, J.D. (1997). Reproduction in sea turtles. In: *The Biology of Sea Turtles* (eds Lutz, P.L. & Musick, J.A.). CRC Press, Boca Raton, FL, pp. 51–81.

Silvey, S.D. (1975). *Statistical Inference*. Chapman & Hall, London.

Solow, A.R. (2001). A comment on two models of the remigration interval in marine turtles. *J. Theor. Biol.*, 209, 371–372.

Winter, A., Appeldoorn, R.S., Bruckner, A., Williams, E.H. & Goenaga, C. (1998). Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs*, 17, 377–382.

APPENDIX

This appendix outlines the derivation of the log likelihood for the model of nesting numbers described in the second

section of the paper. Consider a time series $N_1, N_2,..., N_m$ of nesting numbers of length m with observed values $n_1, n_2,..., n_m$. The likelihood is defined as the joint probability density of the observed time series regarded as a function of the unknown parameters. Conditional on n_1, n_2 and n_3, the log likelihood for the model is:

$$L = \sum_{t=4}^{m} f(n_t | n_{t-2}, n_{t-3}) \qquad (A1)$$

where $f(n_t | n_{t-2}, n_{t-3})$ is the probability density of n_t given n_{t-2} and n_{t-3}. In constructing this log likelihood, we have used the property of the model by which N_t is conditionally independent of $N_1, N_2,..., N_{t-4}$, and N_{t-1} given the values of N_{t-2} and N_{t-3}. Although it is suppressed in the notation, $f(n_t | n_{t-2}, n_{t-3})$ depends on the unknown parameters β_0, β_1, s, μ, and σ^2. Also suppressed in the notation is the conditioning on the initial values n_1, n_2, and n_3.

Under the basic model given in eqn 1, $f(n_t | n_{t-2}, n_{t-3})$ is the normal density with mean equal to

$$E(N_t | n_{t-2}, n_{t-3}) = n_{t-2}s^2 p_{t-2} + n_{t-3}s^3 q_{t-3} + \mu \qquad (A2)$$

and variance

$$Var(N_t | n_{t-2}, n_{t-3}) = n_{t-2}s^2 p_{t-2}(1 - s^2 p_{t-2}) \\ + n_{t-3}s^3 q_{t-3}(1 - s^3 q_{t-3}) + \sigma^2 \qquad (A3)$$

where both p_{t-2} and q_{t-3} depend on the unknown parameters β_0 and β_1 through eqn 4. The corresponding normal density is substituted in eqn A1 to form the log likelihood, which can then be maximized over the unknown parameters with and without the constraint $\beta_1 = 0$ to find L_0 and L_1 and to form the LR statistic Λ. In both cases, the maximization must be done numerically. Here, the MATLAB optimization routine fmins was used.