

**MODELING THE EFFECT OF SEA SURFACE  
TEMPERATURE ON SEA TURTLE NESTING  
ACTIVITIES BY INVESTIGATING  
SEASONAL TRENDS**

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**ABSTRACT.** In the present study, a series of models have been developed in order to investigate the effect of sea water temperature upon the nesting activities of marine turtles. Autoregressive integrated moving average (ARIMA) models, ARIMA models with transfer functions and regression models were developed for forecasting variations in the breeding activity of loggerheads, nesting at the island of Zakynthos, West Greece. Identification and development of the models was determined by the use of several statistical criteria. Weekly data series of sea turtles emerging attempts and number of nests laid were analyzed and compared with sea surface temperature (SST) data series.

Our results indicate that whether SST data were included in the ARIMA models with transfer functions and the regression models that developed to describe both emergence data and

number of nests, tended to improve fitting and forecasting accuracy. Data series of the number of nests laid was further correlated with observation of emergence data. Adding the effect of previous and current year nesting attempts and including SST data resulted to higher forecasting accuracy and fitting performance.

**KEY WORDS:** Time series analysis, sea turtles, ARIMA, forecasting, sea surface temperature.

**1. Introduction.** Understanding the reproductive performance of a species is of great importance for the application of effective protection measures. Sea turtles are long-lived animals spending most of their lifetime in open sea. They come ashore only during nesting periods to lay their eggs. The usual methods for assessing sea turtle population dynamics are based on models developed on long term monitoring data collected during the nesting seasons (Schroeder and Murphy [1999]). However, inter-annual variation in the estimated nesting females (model inputs) caused by temporal variations in several environmental factors (Bjorndal et al. [1999]. Carr and Carr [1970]) could misrepresent actual population status (Hays [2000]). The age of sexual maturation, remigration interval (the interval between two successive nesting seasons) and inter-nesting interval (the interval between two successive nesting attempts during the same nesting season) describe the multiple reproductive pattern of the species, which could lead to variations in the nesting numbers. Hence, understanding how these processes operate and which factors regulate reproductive behaviors is of great importance for assessing sea turtle population dynamics.

Temperature is considered as one of the main forces affecting sea turtle life history (Davenport [1997]). The role of temperature has been identified as one of the basic factors that have various effects on physiological and behavioral processes of the species (Miller [1997], Spotilla et al. [1997]). Sea turtles are among the species that show temperature dependent sex determination with increased ambient temperature controlling the sex of hatchlings (Standora and Spotila [1985], Yntema and Mrosovsky [1980]). Moreover, nest site selection, incubation duration, nesting and hatching success are strongly connected with temperature fluctuations (Davenport [1997], Godley et al. [2001], Miller [1997], Stoneburner and Richardson [1981], Spotila et al. [1997], Wood and Bjorndal [2000]).

Seawater temperature has been recognized as a dynamic stimulus affecting in direct and indirect ways, both external and internal processes associated with reproduction and breeding. Food availability and accumulation (Broderic et al. [2001]), interesting periodicity of the female nesters (Sato et al. [1998], Webster and Cook [2001]) and remigration interval (Solow et al. [2002]) are strongly affected by sea water temperature.

The plasticity in the behavioral strategies of reproduction has also been suggested to be associated with the ectothermic feature of green and loggerhead turtles (Hays et al. [2002]). Behavioral thermoregulation as a characteristic of ectotherm species (Sato et al. [1995]) has been found to affect the intraseasonal nesting activities of sea turtles (Sato et al. [1998]).

The effect of seawater temperature upon nesting intervals has already been examined and recorded in several field studies (Hays et al. [2002], Sato et al. [1998], Webster and Cook [2001]) while recently attention has been given to the development of some theoretical models investigating its importance on reproductive trends (Solow et al. [2002]). In the present study, an effort has been made in order to examine the relationship of sea surface temperature and nesting behavior in a larger data series, by considering sea surface temperature (SST) as a dynamic stimulus affecting reproductive behavior. We develop a series of models based on two standard modeling techniques, in an attempt to examine the importance of sea water temperature upon nesting behavior at a theoretical level. Long term data series have been analyzed and correlated. Two widely used approaches (Box-Jenkins time series approach, and regression model) have been used to evaluate the influence of sea surface temperature (SST) upon the numbers of the emerged turtles and the total number of nests constructed on a nesting beach.

Our basic goal is to examine whether SST has an effect on different model fitting and forecasting by using long term monitoring data. We 'isolated' and used SST as the parameter of interest ignoring all other possible factors that might influence nesting performance. This was done in order to compare and assess the use of the two techniques used here. All individuals in the regression model are subjected to the parameters used in the developed models. In the stochastic time series models different levels of variability introduced by a white noise factor. In this way the effect of SST on long-term data series was evaluated.

## 2. Methods.

**2.1 Study area.** Fieldwork was conducted at Laganas Bay, at the southern part of Zakynthos Island, Greece, during the nesting season (May to September) for the years 1984–1995. Zakynthos is a small island (402 km<sup>2</sup>) located in the east part of Greece on the Ionian Sea. The nesting habitat in the Bay of Laganas, comprising of six beaches, is the most important breeding site of the sea turtle *Caretta caretta* in the Mediterranean (Groombridge [1989]). The total number of nests laid each year range from 857 to 2018 (Margaritoulis [2000]). The present study was conducted on one of the six beaches, the 3-km East Laganas beach. In 1999 and after long time efforts, the area was declared a National Marine Park having as a basic goal the protection of sea turtles, their biotopes and their feeding grounds (Dimopoulos [2001]).

**2.2 Data summary.** Data of turtle emergences, and of nestings were collected during night patrols by ARCHELON (the Sea Turtle Protection Society of Greece) project personnel. The beach was patrolled in 1-hour intervals. The total length of the specific beach is about 3 km, and it takes about 45 minutes to walk all over it, so if we suggest that an adult female turtle needs more than 30 minutes to emerge from the sea, construct the nest and return to the sea, it means that all the individual nested have been observed by the patrol team. During morning patrols if there was any unobserved turtle track in the sand, it was noted and after examination it was added to the total amount of emergences or successful nestings. According to the above, the data set includes the total number of sea turtle emergences and number of nests for the period of the study.

Based on previously published information (Hays et al. [2002]) that there was a small change in water temperature at the different depths that sea turtles dive during their nesting activity, we used the average weekly sea surface temperature as a representative parameter of water temperatures. Weekly sea surface temperature data on a one-degree grid were provided by the COADS database (NOAA) (Smith and Reynolds [2003]).

**2.3 Data sets – Data imputation.** Only a small amount (about 3.9%) of the daily data sets was missing. The missing time series values were created from the existing ones. Linear interpolation was used for the estimation replacement and development of a complete time series. Based on the existing values a regression model was developed on an index variable scaled 1 to 1098. The series predicted by this regression was used for the replacement of the missing data.

### 3. Forecasting models.

1. *Univariate models.* Seasonal Autoregressive Integrated Moving Average (ARIMA) models were developed to describe the emergences and the nesting activity of sea turtle *Caretta caretta*. The temporal pattern of sea turtle nesting activities was examined by using the ARIMA modeling procedures discussed in Box and Jenkins [1970]. The models were evaluated and compared with each other in order to detect their efficiency to model weekly sea turtle emergences (WSTE), nestings (WN) and provide accurate forecasts. ARIMA models provide useful information about future values of the time series, describing how any time series value is linearly related to its own past values. ARIMA models can handle seasonality and trend. The general form of seasonal ARIMA model is given by:

$$ARIMA(p, d, q)(P, D, Q),$$

with  $p$  and  $q$  the order of the autoregressive and moving average term respectively,  $d$  the degree of differencing,  $s$  the seasonality and  $P, Q, D$  the seasonal terms corresponding to  $p, q$  and  $d$ , ARIMA general form is described by the equation:

$$(1 - \phi_I B^p)(1 - \Phi_I B^p)(1 - B^d)(1 - B^D)z_t = (1 - \theta_I B^q)(1 - \Theta_I B^q)a_t$$

where  $z_t$  is the value of the variable of interest at time  $t$ ,  $a_t$  the error term at time  $t$ ,  $\phi_I, \Phi_I, \Theta_I$  and  $\theta_I$  are arithmetic coefficients, and  $B$  is the backshift notation with  $B^i z_t = z_{t-i}$ .

Spectral analysis was performed to explore the existence cyclical patterns and evaluate the periodic behavior on both data series. The effect of the SST was then tested by using transfer functions in the

estimated best models. The basic idea of the transfer functions is that the dependent variable is related to its own past values but also represents a linear combination of the past values of the inputs. After the selection of the best ARIMA model for the weekly data we inserted the SST data as a predictor variable in the weekly data models. Cross-correlation functions (CCFs) were used to test the correlation between SST data and WSTE and WN. Based on the analysis of the CCFs significant time-lag correlation we identified and added the appropriate terms into the transfer functions.

No ARIMA models have been built for the monthly data because the total amount of the available data (less than 50) was not sufficient for a useful and reliable forecast (Pankratz [1991]).

2. *Multiple regression models.* Linear multiple regression models including autocorrelation terms were also developed to fit and forecast different treatments. The number of sea turtles emerging from the sea during the previous week were also included as a new variable in the models of sea turtle nesting models. Data from 1984 to 1994 were used for the development of the regression model. Then the utility of the models for forecasting was tested using data from 1994–1995. The general form of the regression model developed applied here is given by:

$$N_t = a_i N_{t-i} + b_q SST_q + c_k E_{t-k}$$

where  $N_t$  is the number of nests laid on the beach in week  $t$ ,  $\alpha_i$  is a constant with  $i = 1 \dots T - 1$ ,  $SST_q$  is the mean weekly sea surface temperature,  $b_q$  is constant with  $q = 1 \dots T - 1$ ,  $E_T$  is the number of emerges at time  $t$  with  $c_k$  constant at time  $k$ ,  $k = 1 \dots T - 1$ .

For the development of the regression models a stepwise procedure was used. Variables including the previous weeks and year observations as well as the environmental variables were entered to the model if they increased the models'  $r^2$ .

4. **Statistical measures of forecasting accuracy.** The standard statistical method of the sum of squared errors was used in order to choose among the best models developed by the same time series techniques. When using the Box-Jenkins procedure for the identification of the appropriate model we also used to Akaike Information Criterion

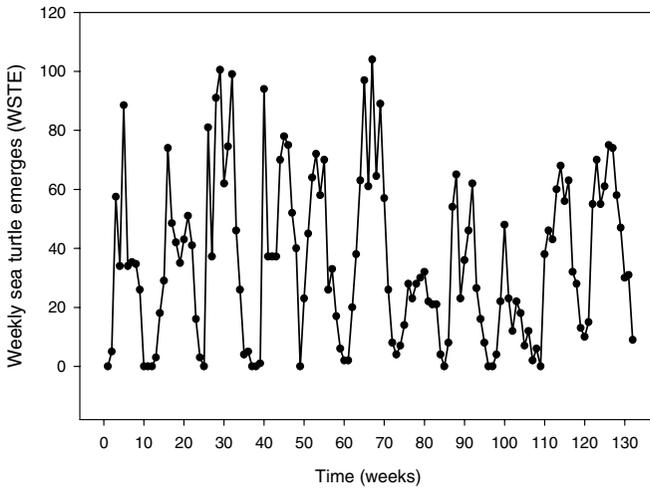
(AIC) and Bayesian Information Criterion (BIC). AIC and BIC statistical tests take into account the number of the estimated parameters and the goodness-of-fit of the model. The minimum value of the two tests yields the selection of the best-fitted model. Besides the AIC and BIC we examine the values of the coefficients to be significant in a 5% level. The Box-Ljung Q statistical test was used to examine whether the errors were autocorrelated. The presence of autocorrelation in the residuals of the regression models was tested using the Durbin-Watson statistic. The accuracy of the developed models was also tested by relative statistical measures (mean absolute error, mean error).

**5. Results.** The models were developed by using the data series produced by the average weekly observations for the years 1984–1994. All models were fitted to the original untransformed data series. Based on the available information for the ten-year period of the original data sets (total 132 observations) we tested all models for their ability to give accurate forecasts for the last year of the available observations, i.e., 1995. The values produced by the forecast techniques were compared with the original values of the observed data using mean error, mean absolute error, and absolute percentage error.

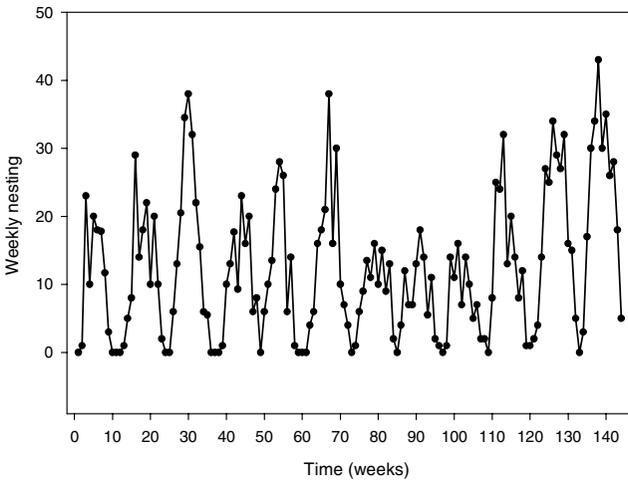
**5.1 Time-series plots.** From Figure 1a, b we can see that there is a strong seasonal pattern, and a cycle is presented every 12 observations. The Periodogram of WSTE data given in Figure 2a shows a peak at a frequency of about 0.083, incorporating a strong seasonal pattern of the weekly data, which can be expressed as the beginning of a new breeding season.

The presence of an annual seasonal cycle is also strongly suggested from Autocorrelation ACF and Partial-Autocorrelation functions PACF. After seasonal differencing ( $D = 1, 12$  months) the seasonal fluctuations has been smoothed from the data, however the ACF and PACF show that the series still retain significant spikes at multiple lags of 12 (Figures 3a, 3b).

WN had also shown the same cyclic pattern (Figure 1b). The ACF function decayed slowly at multiple lags of 12, and the spectral analysis undertaken in order to identify seasonal patterns showed an annual cycle repeated every 12 time lags (Figure 2b). The seasonal first differencing ( $D = 1, 12$  months) applied to remove seasonality



a)



b)

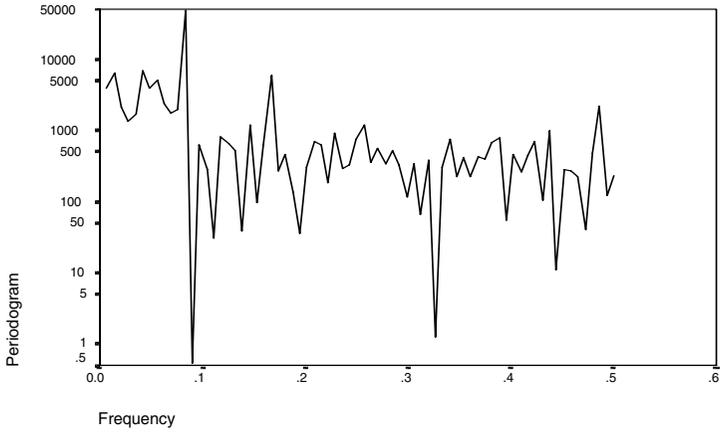
FIGURE 1. a) Original time series of weekly sea turtle emergences and b) original time series of weekly sea turtle nesting, in Laganas nesting beach, Zakynthos Island, Greece, from 1984–1995.

from the original data series. After the differencing ACF all other autocorrelations with lags greater than 16 months were not significant, whether there were some significant autocorrelations at time lags 12 and 16 (Figures 3c, 3d).

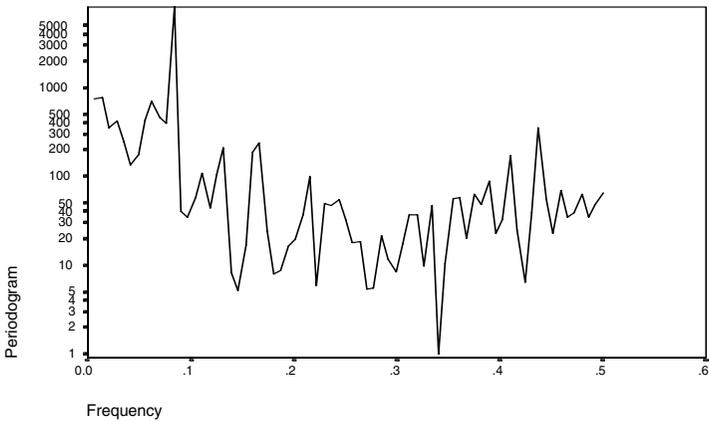
**5.2 ARIMA model for weekly data.** For the development of the ARIMA model we followed step by step the procedure described by Box and Jenkins [1970]. In order to identify the form of the model we formed the Autocorrelation and Partial Autocorrelation Functions. The major assumption in ARIMA models is that time series has to be stationary, which means that mean, variance, and autocorrelation function should be constant through time. For the identification of the appropriate model AIC, BIC were used, all the coefficients were also significant in a  $p = 0.05$  level, and Box-Ljung statistical test applied to examine whether the error were autocorrelated. We should also emphasize here that the choice of the appropriate model except for the statistical test was also based on the principle of parsimony (Box et al. [1994]). The first simple models developed were simple autoregressive, moving average and autoregressive moving average models on which we have just tested the effect of adding MA and AR terms.

An ARIMA  $(2, 0, 0)(0, 1, 1)_{12}$  model was identified as the best model for both weekly data series. The seasonal part of the developed ARIMA model  $(0, 1, 1)_{12}$ , represents an exponentially weighted moving average of the observed series, incorporating the effects of the previous year observations upon data series. The residuals of the model were checked and showed no significant autocorrelation. The ACF and PACF for the residuals series of the estimated ARIMA models are given in Figure 4 (a,b,d,e) and we can see that they are randomly distributed and most of the values are within the 95% confidence limit. Furthermore, Box-Ljung  $Q$  was not significant at any lag ( $P > 0.05$ ). The residuals plot for weekly data is given in Figures 4c and 4f.

In Figures 5a and 5b we have interpolated the observed against the predicted values of the developed ARIMA model for the WSTE and WN data respectively. In these figures we have also plotted the original and predicted values in 95% confidence limits.



a)



b)

FIGURE 2. a) Spectral analysis of sea turtle emergence data and b) sea turtle nesting data, horizontal axis of the Periodogram is referred to frequency and vertical axis is referred to the weight (in log-transformed scale).

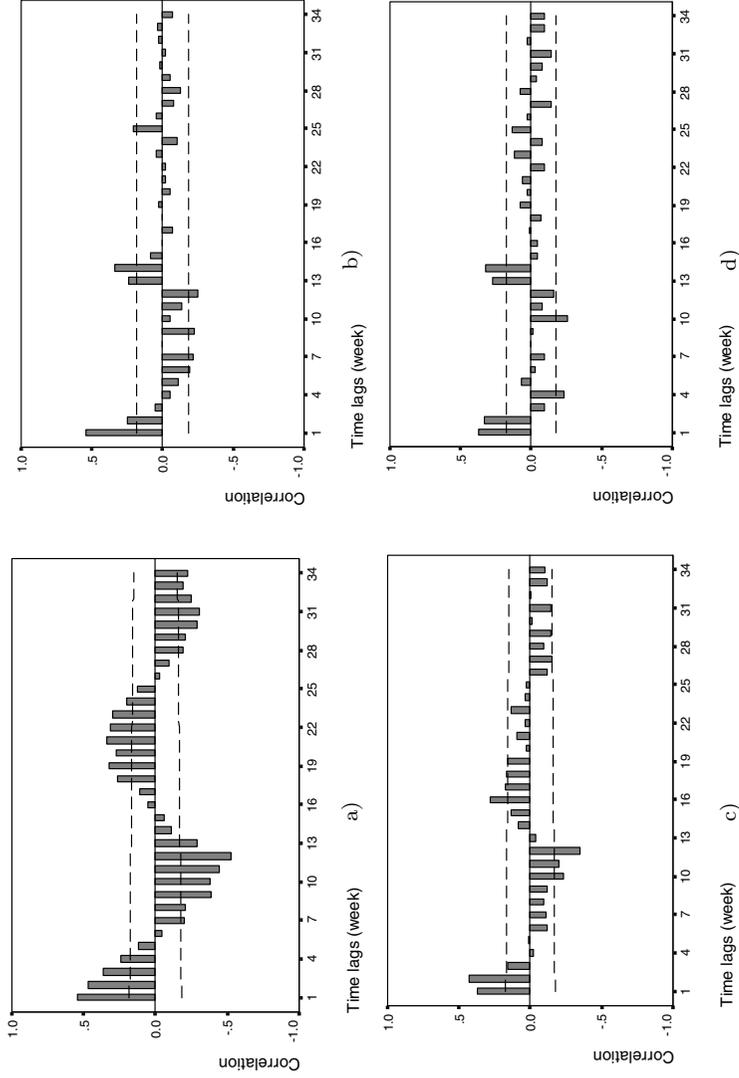


FIGURE 3. After seasonal differencing: a) Autocorrelation function for WSTE series, b) partial autocorrelation function for WSTE series, c) autocorrelation function for WN series, d) partial autocorrelation function for WN series. (Dashed lines indicate 95% confidence limits).

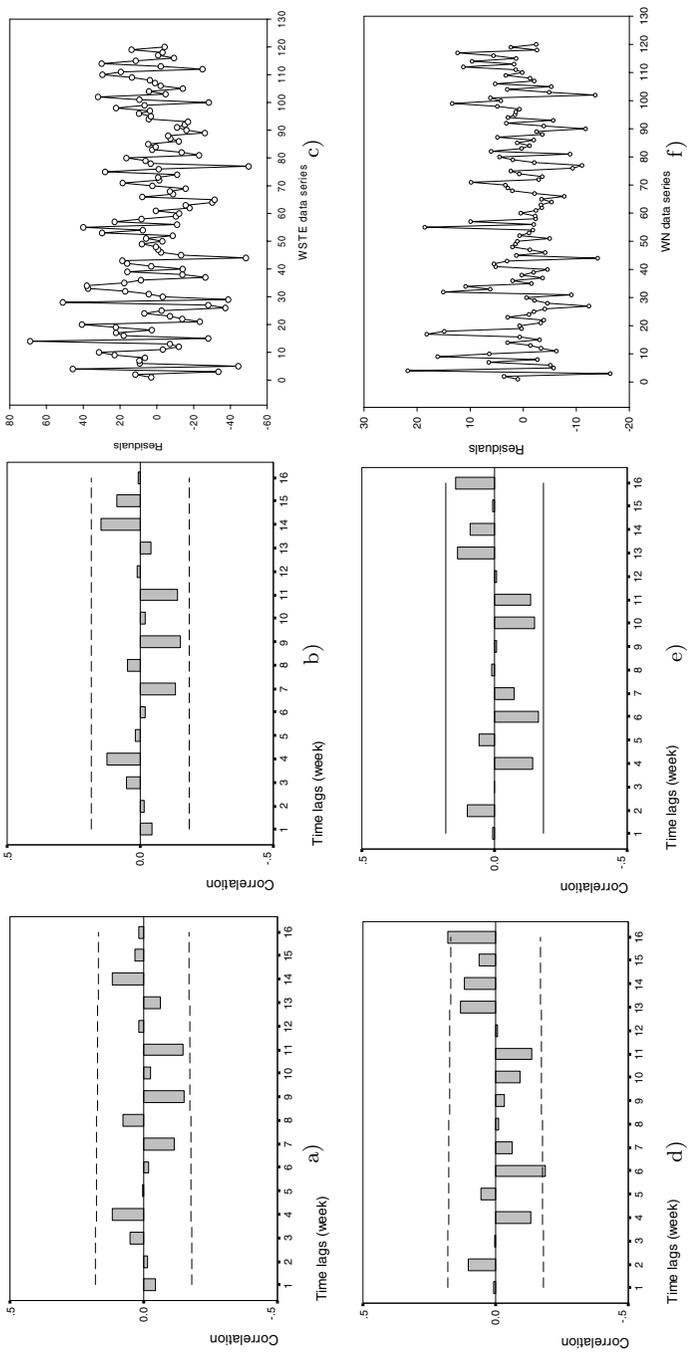


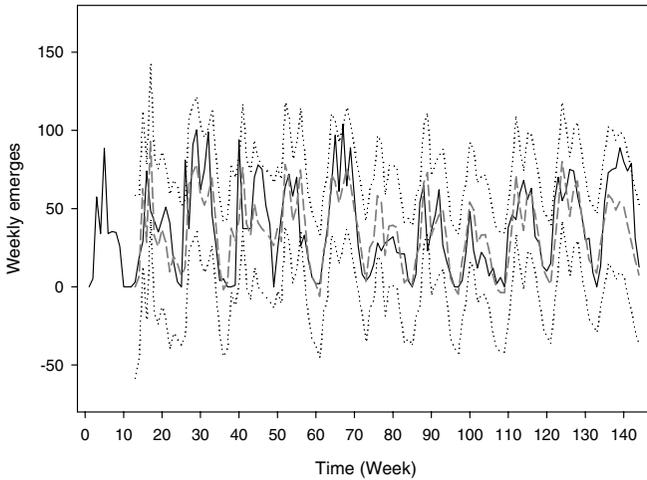
FIGURE 4. a) Autocorrelation function for the residuals of WSTE series, b) partial-autocorrelation function for residuals of WSTE series, c) residual plot for WSTE data series, d) autocorrelation function for residuals of WN series, e) partial-autocorrelation function for residuals of WN series, f) residual plot for WN data series. (Dashed lines indicate 95% confidence limits).

**5.3 ARIMA models with transfer function.** After the estimation of the parameters of the ARIMA model we added the environmental effect of the available weekly variable WSST. Based on the cross-correlation analysis we added to the seasonal ARIMA  $(2, 0, 0)(1, 0, 1)_{12}$  model the terms that have been recognized to have the strongest correlation. The result shows an improvement in models fit in terms of the ACI and BIC statistic tests. Moreover, all new models outperformed simple ARIMA models, in both terms of fitting and forecasting performance, Table 1. The forecasts against produced by ARIMA models with the transfer functions are plotted against the observed values within 95% confidence limits are given in Figures 6a, b.

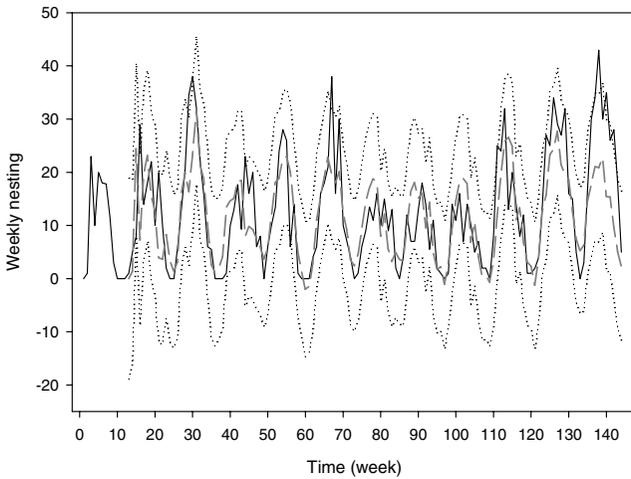
TABLE 1. Comparison of mean errors (ME) and mean absolute errors (MAE) between model fits and forecasts of the ARIMA models and the ARIMA model with the transfer functions, developed for sea turtle emerges (WSTE) and successful nesting (WN) data series.

| Data | Model  | Fit     |         | Forecast |         |
|------|--|---------|---------|----------|---------|
|      |  | ME      | MAE     | ME       | MAE     |
| WSTE | ARIMA(2,0,0)(0,1,1) <sub>12</sub>                            | 0.7879  | 15.4989 | 17.9225  | 21.8121 |
|      | ARIMA(2,0,0)(0,1,1) <sub>12</sub><br>with transfer functions | -1.0988 | 13.3645 | 17.1034  | 19.8949 |
| WN   | ARIMA(2,0,0)(0,1,1) <sub>12</sub>                            | 0.4245  | 4.8083  | 9.4277   | 10.8307 |
|      | ARIMA(2,0,0)(0,1,1) <sub>12</sub><br>with transfer functions | 0.2096  | 4.660   | 8.1571   | 10.1217 |

**5.4 Regression models for weekly data.** The first regression model developed for both weekly data sets included only the variable of WSST and explained only about 0.629 and 0.583 of the values for the WSTE and WN data respectively. For all simple linear regression models (developed for all different data series) including only environmental parameters as independent variables produced the poorest fit. By increasing the number of environmental variables and including past values of the inputs, multiple regression models developed that were characterized by higher accuracy.



a)



b)

FIGURE 5. Comparison between predicted (obtained from ARIMA model) and observed (real data from loggerhead nesting population) values a) of sea turtle emergences, and b) of sea turtle nestings. The black solid line indicates the observed values, the gray dashed line indicates the predicted values and the dotted lines indicate the 95% confidence interval.

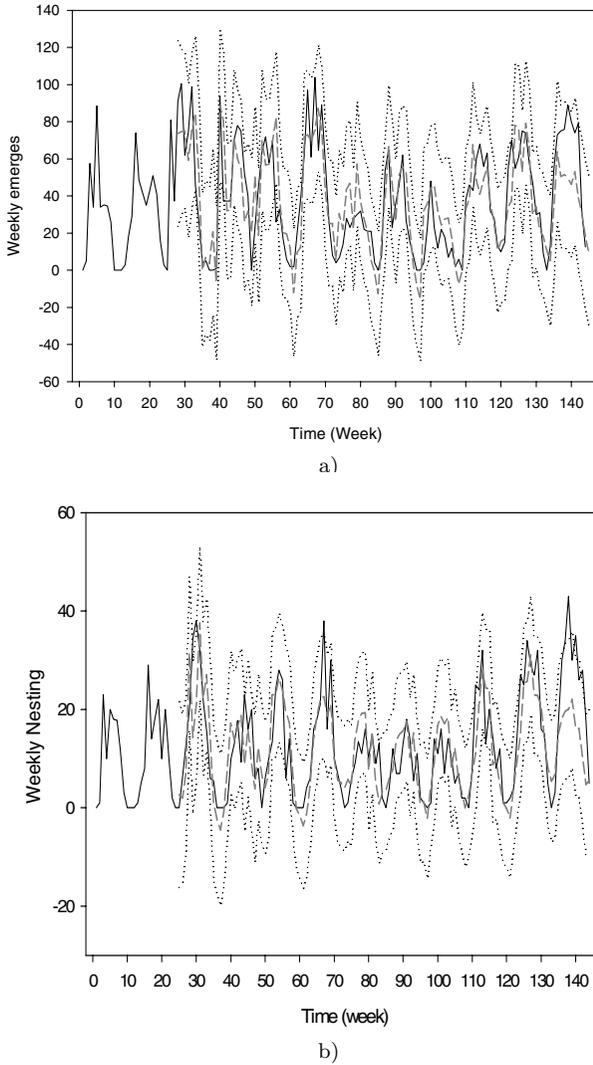


FIGURE 6. Comparison between predicted values (obtained from ARIMA model with transfer functions) and observed (real data from loggerhead nesting population) values a) of sea turtle emergences and b) of sea turtle nestings. The black solid line indicates the observed values, the gray dashed line indicates the predicted values and the dotted lines indicate the 95% confidence interval.

For the development of these models we used cross correlation analysis and the identification of the important time lags. In the regression models including the environment variables in significant lags an improvement in models fitting and forecasting was observed. For WSTE data a significant improvement was also noted by adding to the above models the previous year observation, Table 2. In all models the residuals were checked by using Durbin-Watson statistic and showed no significant autocorrelation.

For the WN data the best model ( $r^2 = 0.841$ ) included values of the successful nesting attempts of the previous week ( $t-1$ ,  $t-2$  and  $t-12$ ), sea surface temperature variables at multiple lags, and also the number of emerges from the sea at one, three and twelve weeks (previous year) periods before ( $t-1$ ,  $t-2$  and  $t-12$ ), Table 3. Durbin-Watson statistical also indicated a small positive autocorrelation (1.962).

**6. Discussion.** This study was motivated by the suggestion that water temperature could be an important cue in sea turtles breeding behavior (Hays et al. [2002], Hughes and Brend [1972], Mrosovsky [1980], Lebuff [1990], Solow et al. [2002]). In view of a global change in climatic conditions worldwide, the above inquiry could be of high importance in explaining population trends and designing protection measures. In an attempt to examine its effect on long-term data series we used a theoretical approach coupled with long term field data. A series of simple models was developed in order to investigate the effect of SST upon model accuracy and fitting, assuming and considering a dynamic factor, and environmental indicator, which might regulate the general nesting trends.

Among the factors that influence nesting attempts, successful nesting and hatching are considered the slope of the beach, sand particle size, vegetation cover, salinity of surface sand, air moisture and sand temperature (Garmestani et al. [2000], Mrosovsky and Yntema [1980], Wood and Bjordnal [2000]). The former parameters can be easily divided into topographic and climatic parameters. The high fidelity that sea turtles show during nesting area selection could be an intrinsic mechanism to save energy by choosing each time the same "tested" favorable nesting habitats. Considering the group of factors characterized as climatic, we assume that turtles should also have a way to be informed about the conditions in order to save energy for the next process and

TABLE 2. Regression model for WSTE series. The table indicates model structure (variables induced) and the comparison of mean errors (ME) and mean absolute errors (MAE) between model fits and forecasts.

| Variables Used                                 |                | Fit   |        |          | Forecast |         |
|--|----------------|-------|--------|----------|----------|---------|
|  |                | $r^2$ | ME     | MAE      | ME       | MAE     |
| WSST <sub><math>t-1</math></sub>               |                | 0.629 | 0.0332 | 22.97712 | 36.0092  | 36.0092 |
| WSST <sub><math>t-1,t-3,t-12,t-15</math></sub> | $E_{t-1}$      | 0.792 | 0.4009 | 16.69214 | 9.0767   | 18.9767 |
| WSST <sub><math>t-1,t-3,t-12,t-15</math></sub> | $E_{t-1,t-12}$ | 0.811 | 0.1981 | 15.84907 | 5.6242   | 10.5291 |

TABLE 3. Regression model for WN series. The table indicates model structure (variables induced) and the comparison of mean errors (ME) and mean absolute errors (MAE) between model fits and forecasts.

| Variables                                      |                        | Fit            |         |         | Forecast |         |
|--|------------------------|----------------|---------|---------|----------|---------|
|  |                        | $r^2$          | ME      | MAE     | ME       | MAE     |
| WSST <sub><math>t-1</math></sub>               |                        | 0.583          | 11.7154 | 11.7155 | 11.85    | 11.85   |
| WSST <sub><math>t-1,t-3,t-10,t-12</math></sub> |                        | 0.730          | 0.0137  | 6.9661  | 10.47    | 12.2733 |
| WSST <sub><math>t-1,t-3,t-12</math></sub>      | $E_{t-1,t-2,t-3,t-12}$ | 0.824          | -0.4917 | 4.9225  | 5.1158   | 7.0608  |
| WSST <sub><math>t-1,t-3,t-12</math></sub>      | $E_{t-1,t-2,t-3,t-12}$ | $N_{t-1}$      | 0.839   | 0.0818  | 4.6441   | 3.9583  |
| WSST <sub><math>t-1,t-3,t-12</math></sub>      | $E_{t-1,t-2,t-3,t-12}$ | $N_{t-1,t-12}$ | 0.841   | 0.0288  | 4.5907   | 3.2292  |
|  |                        |                |         |         |          | 5.8358  |

migration trip. By concentrating our interest and focus our analysis on data series collected during the short breeding period, we assume that all individuals that have been observed to participate in breeding processes have already successfully reached a threshold body condition (Broderic et al. [2001], Hays [2000]) by storing and accumulating all the energy required for reproduction. Under these circumstances we suggest that species emergences occur under a response to external stimuli. These stimuli could be an environmental parameter, which acts like indicator of the condition of the terrestrial environment.

From Tables 1, 2 and 3 we can clearly see the effect of SST when it is introduced to the model; in all case mean error and mean absolute errors in terms of fitting and forecasting performances are decreasing significantly. The results of the comparison of two series of models developed for WSTE and WN support the former assumptions. SST is more closely correlated with WSTE than WN, suggesting that can be the determinant stimuli that lead turtles to go out of the water, however their nesting success depends on many other factors. The correlation of WN and SST can be easily explained as the result of the increased number of individuals emergences from the water. Moreover in most of the models we can see that SST at time lags of 1 and 3 weeks is used. The biological explanation to this can be derived by field observations that record interesting interval between 10 and 15 days (Hays et al. [2002], Margaritoulis [1983]).

Our results indicate that introducing SST components in different time series models always improve model fitting and forecasting accuracy. Introduced SST components at different time lags, representing information for the same nesting season ( $t - 1$ ,  $t - 2$ ,  $t - 3$ ), have a clear biological explanation. However, fitting and improving models by adding SST at larger temporal scales ( $t - 12$ ) remains questionable. A possible explanation of this remarkable pattern could arise by assuming that sea water temperature is a factor of unknown magnitude, that may mask species responses to environmental variations. In this manner we would expect that behavioral and biological processes of species life history would be influenced by varying weather conditions. The former hypothesis is further supported by recent findings on the effect of sea surface temperature on the re-nesting interval of green turtles (Solow et al. [2002]). However, in our analysis previous years' data of SST could have a significant biological explanation, only in the case of

a stable population, expressing interannual variations and forecasting the remaining nesting cohorts.

Since the decision at the individual level of a female to nest at the designated site or not is based on a number of factors (environmental and behavioral) we isolated the sea water temperature and tried to investigate its role explaining female turtle emergences. The finding that our data can be best fitted by SST of previous years is in accordance with the fact of the emergences of a remigrating portion of the female turtles. That means that even if a small portion of the population is returning on the same beach during successive years the effect of this factor could be observed. A more detailed experimental scheme, e.g., tagging frequency, could be used in order to re-examine our hypothesis.

Concluding we would like to mention that as empirical studies have shown (Hays et al. [2002], Sato et al. [1998], Webster and Cook [2001]), our model predicted that SST is an important factor on sea turtle reproductive behavior. The need for the development of more sophisticated models in order to assess sea turtle population size and dynamics is obvious. Moreover, the examination and analysis of biotic and abiotic external stimuli as well as the internal processes that dominate population dynamics should be continued, while further field observation efforts are also needed.

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