

Decreasing annual nest counts in a globally important loggerhead sea turtle population

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Abstract. The loggerhead sea turtle (*Caretta caretta*) nests on sand beaches, has both oceanic and neritic life stages, and migrates internationally. We analyzed an 18-year time series of Index Nesting Beach Survey (Index) nest-count data to describe spatial and temporal trends in loggerhead nesting on Florida (USA) beaches. The Index data were highly resolved: 368 fixed zones (mean length 0.88 km) were surveyed daily during annual 109-day survey seasons. Spatial and seasonal coverage averaged 69% of estimated total nesting by loggerheads in the state. We carried out trend analyses on both annual survey-region nest-count totals ($N = 18$) and annual zone-level nest densities ($N = 18 \times 368 = 6624$). In both analyses, negative binomial regression models were used to fit restricted cubic spline curves to aggregated nest counts. Between 1989 and 2006, loggerhead nest counts on Florida Index beaches increased and then declined, with a net decrease over the 18-year period. This pattern was evident in both a trend model of annual survey-region nest-count totals and a mixed-effect, “single-region” trend model of annual zone-level nest densities that took into account both spatial and temporal correlation between counts. We also saw this pattern in a zone-level model that allowed trend line shapes to vary between six coastal subregions. Annual mean zone-level nest density declined significantly (–28%; 95% CI: –34% to –21%) between 1989 and 2006 and declined steeply (–43%; 95% CI: –48% to –39%) during 1998–2006. Rates of change in annual mean nest density varied more between coastal subregions during the “mostly increasing” period prior to 1998 than during the “steeply declining” period after 1998. The excellent fits (observed vs. expected count $R^2 > 0.91$) of the mixed-effect zone-level models confirmed the presence of strong, positive, within-zone autocorrelation ($R > 0.93$) between annual counts, indicating a remarkable year-to-year consistency in the longshore spatial distribution of nests over the survey region. We argue that the decline in annual loggerhead nest counts in peninsular Florida can best be explained by a decline in the number of adult female loggerheads in the population. Causes of this decline are explored.

Key words: *Caretta caretta*; endangered species; Florida, USA; loggerhead sea turtle; nesting; population decline; spatiotemporal trends.

INTRODUCTION

The loggerhead sea turtle (*Caretta caretta*) nests on sand beaches (see Plate 1), has both oceanic and neritic life stages, and migrates internationally (species reviews in Dodd [1988], Bolten and Witherington [2003], and Witherington et al. [2006b]). Worldwide, loggerhead sea turtle populations are generally recognized as being depleted, especially in the Pacific (NMFS and USFWS 2007). The species is listed as Endangered on the IUCN Red List and as Threatened under the U.S. Endangered Species Act. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) lists loggerhead sea turtles in CITES Appendix I.

Loggerhead foraging areas are mostly in subtropical and temperate oceans, and the majority of their nesting beaches are located between 19° and 36° latitude in each hemisphere (Dodd 1988). Only two loggerhead nesting assemblages have more than 10 000 females nesting per year: southern Florida, USA) and Masirah, Oman (Baldwin et al. 2003, Ehrhart et al. 2003). Assessments at major nesting beaches worldwide indicate that nesting beaches in Florida and Oman host ~80–90% of the world’s loggerhead nesting activity (Baldwin et al. 2003, Ehrhart et al. 2003, Kamezaki et al. 2003, Limpus and Limpus 2003, Margaritoulis et al. 2003).

Mitochondrial DNA (mtDNA) sequence analyses have revealed that there are significant genetic differences between loggerheads nesting in different geographic regions (Bowen et al. 1994, Pearce 2001, Bowen 2003). In the western Atlantic, populations of females

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nesting on beaches of the southeastern United States (including Florida), Mexico (Yucatan), and Brazil (Bahia) are genetically distinct (Encalada et al. 1998). Based on maternally inherited alleles (from mtDNA), Florida has four distinct subpopulations, including one shared with Atlantic U.S. beaches north of Florida (Encalada et al. 1998, Pearce 2001). These subpopulations are probably maintained by the return of nesting females to their natal beach (Encalada et al. 1998), with genetic separations seen at nesting beaches geographically separated by more than 100 km (Pearce 2001). However, microsatellite assays by Pearce showed no significant population structure in terms of nuclear DNA genotypes. Her conclusions were that male loggerheads had provided significant gene flow between nesting beach locations.

Sea turtles in the water are broadly distributed, genetically mixed, and difficult to count. For these reasons, the most trusted population-size assessments have been made at nesting beaches (Meylan 1982, Schroeder and Murphy 1999). Nesting beaches are easily surveyed, and the females that emerge to nest on a stretch of beach are believed to be of a single genetic stock (Bowen 2003).

On nesting beaches, females crawl above the intertidal zone, deposit a clutch of eggs in the sand, scatter sand over the clutch, and return to the water. This activity leaves conspicuous marks in the sand that can be identified by trained surveyors, who can determine the species of sea turtle responsible for the marks and whether the turtle's activity resulted in eggs being deposited (i.e., whether the mark is a nest). Loggerheads are iteroparous, with a reproductive output that is distributed between periodic nesting forays within each migration to the nesting beach. An individual reproductive loggerhead is likely to make these reproductive migrations once every few years. Loggerheads show nest-site fidelity, with most seasonal nest locations of individual turtles being located within a 5-km range (reviewed by Schroeder et al. 2003). The number of clutches (nests) per loggerhead nesting female per season (clutch frequency) has been estimated to be 3.2–4.2 (reviewed by Schroeder et al. 2003); however, researchers recognize that this number is likely to be an underestimate. A widely accepted estimate for loggerhead clutch frequency is approximately four clutches per female per season (Murphy and Hopkins 1984).

Population-size assessments estimated from seasonal nest counts are conducted annually on Florida beaches for three sea turtle species: loggerheads, green turtles (*Chelonia mydas*), and leatherbacks (*Dermochelys coriacea*). The nest counts are made by hundreds of surveyors in an effort coordinated by the Fish and Wildlife Research Institute of the Florida Fish and Wildlife Conservation Commission (FWC). These nest counts provide the most reliable data from which one might estimate the number of females nesting in any year (assuming annually consistent clutch frequencies

per female). A coordinated program to obtain sea turtle nest counts in Florida began in 1979 and has expanded to include most of Florida's sandy beaches (1300 km). Gaps in nesting surveys occur in the Everglades area and in some of the more remote keys in southernmost Florida. Recognizing the inherent variability in nest-count effort occurring on a broad geographic scale, a consortium of conservation groups in 1989 established a subset of surveyed beaches in Florida to represent a standardized index of sea turtle nesting. An FWC-led program designed to generate nesting indices (the Florida Index Nesting Beach Survey program) has resulted in 18 years of highly resolved spatial and temporal nest counts that are representative of loggerhead nesting in Florida and are suitable for trend assessments. The purpose of this study was to use analyses of these Index data to describe spatial and temporal trends in loggerhead nesting on Florida beaches. In particular, we attempt to characterize a decline in nest counts that appears to have started in the late 1990s and to determine whether this decline has varied geographically or has been consistent over the Index survey region. In a larger context, we present this assessment of nesting trends as a way to assess the efficacy of recovery efforts for loggerhead populations and to measure population effects from threats.

MATERIALS AND METHODS

Nest-count surveys

Since 1989, nest-count surveys in Florida have taken place under two complementary programs: "Statewide" and "Index." Index beaches ($n = 32$) are a subset of Statewide beaches ($n = 190$) (Fig. 1), and the Index survey season is a subset of the complete nesting season. Both Index and Statewide survey programs use trained surveyors who report nest counts and metadata to a centralized database. The two programs differ in their goals. The Statewide program has aimed to be as complete as possible in seasonal and geographic coverage, but has not been highly consistent (stretches of beach have been added, boundaries have fluctuated, and survey dates have varied). The Index program has aimed to be consistent in effort, but has not been complete in seasonal and geographic coverage. The level of data resolution has also differed between the two programs. In comparison to the Statewide program, the Index program collects more highly resolved nest-count data assigned to individual days and discrete beach zones.

Both Statewide and Index loggerhead nest-count data used in this study came from daily surveys that took place during early mornings following the nocturnal nesting activity of loggerheads. Surveyors used visible characteristics of tracks and nest sites to distinguish loggerhead nests from nests of other sea turtle species (green turtles and leatherbacks) and to distinguish nests from abandoned nesting attempts (techniques are described by Schroeder and Murphy 1999).

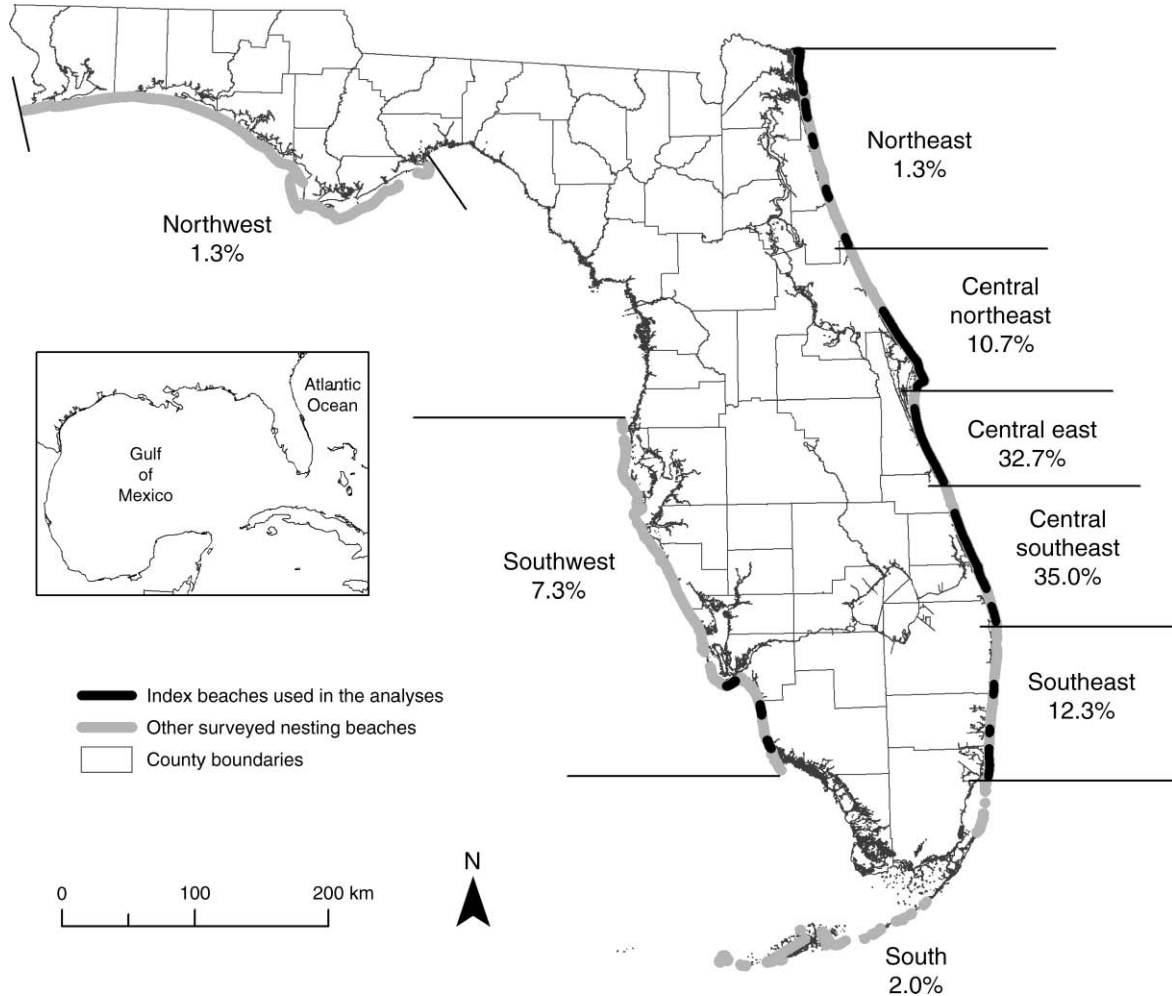


FIG. 1. Sea turtle nesting beaches in Florida, USA, where seasonal nest counts have been made. Gray shoreline shading represents all Statewide beaches surveyed during the period 2001–2006. Dark shading represents Index beaches used in this study; these were surveyed daily from 1989 to 2006 for the Index sampling season (15 May–31 August). The average percentage of total recorded Statewide nesting by loggerheads from 2001 to 2006 is presented for each region.

Florida Index beaches are spread throughout the principal nesting range of the loggerhead in Florida (Fig. 1). These beaches were surveyed daily from 15 May through 31 August during 1989–2006. On Index beaches (Appendix: Table A1) where surveyors have made complete seasonal nest counts (approximately April–September), we found that ~90% of each year's loggerhead nesting on those beaches took place during the Index survey season (FWC, unpublished data). During 1989–2006, annual nesting recorded by the Index program on these beaches averaged $69\% \pm 5\%$ (mean \pm SD; range 61–79%) of the estimated total nesting by loggerheads in the state. Five additional beaches on the Gulf of Mexico that are currently surveyed according to Index protocols were not used in the analyses because they were added to the program at a later date and have not been monitored for as extensive a time as the other Index beaches. During the years that these five beaches have been monitored

(1999–2006), they have accounted for only a small percentage ($0.70\% \pm 0.05\%$, mean \pm SD) of total annual nesting on Index beaches. Nesting on all Gulf-coast beaches of the state represents less than 10% of Statewide nest-count totals.

Quality assurance and quality control of nest-count data.—Index-beach surveyors received annual training in survey methods and followed a standardized protocol for conducting nest-count surveys. Elements of the protocol included establishment of consistent beach-zone locations (recorded by differentially corrected GPS), fixed seasonal start and end dates, and nest-counting methods. To assure the reliability of daily nest counts, counting effort was restricted to early-morning survey periods, and recorded nests were marked to prevent counting nests more than once. Surveyors also limited daily count bias from changing tidal cycles by counting only nests that were made above the recent tidemark (the beach area that includes the vast majority

of nests). To correctly assign nest counts to the day nests were made, surveys that were conducted after a missed survey day were resumed only after nests from the previous days were marked as not-to-be counted.

We evaluated the diagnostic performance of eight Index-beach survey projects among the 27 that contributed nest counts used in our analysis. This evaluation focused on surveyors' identification of loggerhead sea turtle crawls (tracks from nesting attempts, including completed and abandoned attempts). In our evaluation, we assumed that loggerhead crawls were conspicuous and unlikely to be missed if a beach were completely surveyed. However, we expected that the identification of crawls as either nests or abandoned nesting attempts would have error. With this in mind, we measured Index surveyors' accuracy in identifying crawls during seven separate nesting seasons between 1993 and 1999. Surveyors from one to five randomly selected Index beaches were evaluated each year. During evaluations we encountered a total of 451 loggerheads emerging at night and observed them either nesting (depositing eggs, $n = 344$ females) or abandoning their attempt ($n = 107$ females). A separate group of Index beach surveyors appraised these pre-identified crawls during their regular surveys the following morning. These surveyors recorded 318 loggerhead nests and 133 abandoned attempts by loggerheads. Index surveyors correctly identified true nests as observed nests 91.3% of the time (314/344, 95% CI: 88.1–94.0%), a rate that represented the sensitivity (or true positive rate) for identifying nests in the test population of loggerhead crawls. The false negative rate ($100\% - \text{sensitivity}$) was 8.7% (95% CI: 6.0–11.9%).

Index surveyors correctly recorded true abandoned nesting attempts 96.3% of the time (103/107, 95% CI: 92.0–99.0%), a rate that represented the specificity (or true negative rate) for identifying nests in the test population of crawls. The false positive rate ($100\% - \text{specificity}$) was 3.7% (95% CI: 1.0–8.0%). Given the sensitivity and specificity of Index surveyors for identifying nests in the test population of loggerhead crawls and assuming the prevalence of nests among daily loggerhead crawls in Florida to be ~50% (Florida Fish and Wildlife Conservation Commission [FWC], *unpublished data*), the probability that a nest counted by an Index surveyor was actually a nest was 0.96 (95% CI: 0.92–0.99).

Index nest-count data

Because the goals of our study were to characterize the spatiotemporal pattern of change in annual loggerhead nest counts over the 18 years of Index nesting beach surveys, our trend analyses had to take into account both the key features of the survey design and the inherent properties of the response variable. In its most elemental form, the response variable was a daily count of nests along the shoreline of a survey zone with fixed boundaries and shoreline length. The daily counts were carried out in each zone during an annual survey

season lasting 109 days. Nest counts collected from a total of 368 permanent zones surveyed annually from 1989 to 2006 were used in the analysis. Median shoreline length of these zones was 0.88 km, with an interquartile range of 0.76 to 1.02 km and a complete range of 0.12 to 2.00 km. The great majority of these zones ($n = 345$) covered 300 km of shoreline and were distributed over 600 km of Florida's Atlantic coast. These Atlantic zones were organized into 24 Index beaches (administrative groups of contiguous zones; Fig. 1). An additional 23 zones organized into three Index beaches covered 24 km of shoreline distributed over a 65-km stretch of the southwestern (Gulf of Mexico) coast of Florida (Fig. 1). For the purposes of our analysis, we considered the southernmost survey zones on the Atlantic and those on the southwestern coasts to be separated by a 300-km shoreline distance. Although the Index survey protocol specified that nest counts were to be collected daily in each survey zone during the 109-day survey season, some daily zone-level counts in any year could be missing because of weather, beach closures, or other interruptions in survey effort.

Because a principal purpose of the trend analysis was to characterize annual change in nest counts and because the temporal and spatial features of the Index survey design necessitated the use of computationally intensive statistical models that could account for both temporal and spatial correlation between nest counts, we considered it impractical to model nest counts at the daily level within annual survey seasons: more than 700 000 daily nest counts were collected across all survey zones over the 18-year survey period. We therefore developed a method to appropriately aggregate the large number of daily zone-level nest counts into total annual zone-level counts. Because daily nest counts at the zone level typically increased over the first six to eight weeks of the survey season and then decreased over the last six to eight weeks of the season, daily nest counts could not be simply averaged over the entire 109-day survey season. This seasonal trend in daily counts would have caused the season-long average daily count in a survey zone to be highly dependent upon the temporal pattern of missing daily counts in that zone. To address this problem we averaged daily nest counts within biweekly (once every two weeks) subintervals of the 109-day survey season and then multiplied them by a standard level of biweekly survey effort. These standardized subinterval counts were then summed into an overall standardized annual count for each zone. This ensured fair comparisons between zones and between years, even where some zone-level daily nest counts were missing.

We settled on the appropriateness of two-week subintervals by comparing the average within-interval variance of nest counts for various interval lengths to the variance of daily counts over the entire survey season by zone and year, respectively. The variance of zone-level daily nest counts within three-week, two-week, and one-week subintervals of the 109-day survey season was

lower, on average, across all zones in all years by 13%, 18%, and 19%, respectively, when compared to the variance of zone-level daily nest counts across the entire survey season. Because the variance of daily nest counts improved only slightly for one-week subintervals compared to two-week subintervals, while the proportion of subintervals with completely missing daily counts increased, we considered it reasonable to divide the survey season into two-week intervals (except for a final 11-day interval to fill out the 109-day season). These biweekly intervals aggregate count data within periods encompassing both spring and neap tides in Florida, and they also approximate the loggerhead's inter-nesting interval (the period between successive nests within a season; Schroeder et al. 2003). Each of these factors made biweekly periods a sensible temporal unit for aggregating nest counts.

Considered across all 368 zones and across 18 annual survey seasons, there were 52 992 biweekly zone-level observation intervals in the survey. Complete survey effort (14 daily nest counts or 11 daily counts in the last biweekly interval) was achieved for 90.5% ($n = 47 968$) of these observation intervals. At least 10 daily counts were collected for 97.2% ($n = 51 488$) of all biweekly intervals, and at least seven daily nest counts were collected for 99.1% ($n = 52 616$) of all biweekly intervals.

Only 0.7% of zone-level biweekly observation intervals ($n = 376$) were completely unsurveyed across the 18-year survey period. Almost all of these intervals occurred in either 1989 ($n = 222$) or 1990 ($n = 142$), and were due to limited availability of trained observers in the first two years of the survey. In 1989, 10 zones were not surveyed at all, and the first and last biweekly observation intervals of the 109-day annual survey season were excluded from the survey for 71 zones in 1989 and 1990. The remaining 11 zone-level biweekly intervals with missing nest counts were not surveyed because of bad weather or beach closures and occurred in 1997 ($n = 1$), 1998 ($n = 5$), and 2004 ($n = 6$).

Most of these missing nest counts were within zones with low nesting densities or were at the beginning or end of the annual survey season when nest counts are lowest. Of the 376 biweekly intervals with missing counts, 85.6% ($n = 322$) had mean nest counts of fewer than one per year in corresponding zones and biweekly periods in years with nest counts. Similarly, 94.6% ($n = 356$) had corresponding mean counts of less than three per year in non-missing years, and 5.3% ($n = 20$) had corresponding mean counts ranging from 3 to 158 per year in non-missing years.

For the relatively small number of biweekly, zone-level intervals with completely missing daily counts, daily nest-count rates were imputed using non-missing nest counts in neighboring zones and biweekly intervals. A mixed-effect negative binomial count regression model (McCullagh and Nelder 1989, Wolfinger and O'Connell 1993), as implemented in SAS PROC GLIMMIX (Version 9.1; Littell et al. 2006), was used

to fit separately for each year a two-dimensional radial smoothing spline (Ruppert et al. 2003) to the non-missing nest counts over a two-dimensional response surface. The response surface was defined by zone position along a shoreline axis and the sequence number of biweekly observation intervals along a time axis. The number of knots used for smoothing ($n = 129$) and their location on the radial smoothing-spline surface were based on the recommendations of Ruppert et al. (2003) and were selected using the k-d tree option in PROC GLIMMIX. Daily nest-count rates for the 376 zone-level biweekly intervals with missing counts were estimated using the predicted rates at appropriate locations on the response surface estimated for each of the five years with completely missing daily counts in any biweekly interval.

After daily nest-count rates were imputed for the biweekly intervals with missing counts, daily nest-count rates (averages) were calculated for all other zone-level biweekly intervals in all years, and then all daily rates were multiplied by 14 days (or 11 days for the last interval of the 109-day season). These standardized biweekly counts for each zone in each year were then summed to obtain annual zone-level nest counts standardized to 109 days of survey effort. The 368 standardized zone-level counts for each year were summed to obtain standardized total annual nest counts for the survey region. Because the number of missing nest counts was small, we considered the error introduced by our imputation and standardization procedures to be relatively small, and no attempt was made to adjust for this additional error in our trend analyses of annual nest counts.

Trend analysis of annual nest counts

We conducted trend analyses on both annual survey-region (SR) nest-count totals ($n = 18$) and annual zone-level (ZL) nest counts ($n = 18 \times 368 = 6624$). In both analyses, negative binomial count regression models (McCullagh and Nelder 1989, Wolfinger and O'Connell 1993), as implemented in SAS PROC GLIMMIX (Version 9.1; Littell et al. 2006), were used to fit restricted cubic spline (RCS) curves (Harrell 2001) to annual nest counts. The number of knots, which determines the degree of smoothness of the RCS curves, and the location of the knots along the time scale were chosen based on recommendations by Harrell (2001). Analogous Poisson count-regression models were also considered, but in all cases the residual variability from these Poisson model fits was highly overdispersed as indicated by overdispersion parameters (generalized Pearson χ^2 statistics divided by residual degrees of freedom; Littell et al. 2006) greater than 100. Overdispersion parameters estimated for most of the negative binomial regression model fits were typically ideal, falling between 0.95 and 1.23. Tests based on the t statistic were used to determine if the estimated percentage change in predicted mean annual SR or ZL

nest counts between selected years differed significantly from zero. The method of Kenward and Roger (1997) was used for all ZL nest-count mixed-effect models to calculate standard errors and degrees of freedom for all tests based on *t* statistics and 95% confidence intervals.

Trend analysis of annual survey-region (SR) nest-count totals.—In the trend analysis of annual SR nest-count totals, four separate negative binomial regression models were fitted using one of two different levels of smoothing for the RCS curves (three-knot or four-knot) and one of two different correlation structures for residual errors (independent errors or autocorrelated errors). An autoregressive (AR(1)) covariance structure (Littell et al. 2006) was used to model autocorrelated errors. The AR(1) structure assumed that the correlation between annual nest counts fell off exponentially as a function of the number of years separating any two annual counts. Because of the pseudo-likelihood method used in PROC GLIMMIX to estimate parameters in negative binomial and Poisson regression models with correlated errors (Littell et al. 2006), likelihood-ratio tests or information criteria such as AIC (Akaike information criterion; Burnham and Anderson 2002) could not be used to determine if an autocorrelated error structure adequately improved model fit compared to an independent error structure. Instead, the AR(1) covariance parameter estimates were simply compared to their standard errors. In both the three-knot and four-knot RCS autocorrelated error models, AR(1) covariance parameters were greatly exceeded by their standard errors, indicating no evidence of significant AR(1) autocorrelation among errors in either the three-knot or four-knot RCS models.

To determine which level of smoothing yielded the best model fit for annual SR nest counts in a model with independent errors, we compared model Akaike weights based on the small-sample form of the information criterion, AIC_c (Burnham and Anderson 2002). These weights can be interpreted as the relative likelihoods of the three-knot and four-knot RCS independent-error models, given the data and this set of two regression models. The Akaike weights for the three-knot (three-parameter) and four-knot (four-parameter) models were 0.86 and 0.14, yielding an evidence ratio of 6.1 to 1 in favor of the three-knot model. Consistent with the Akaike weights, there was no improvement in the generalized Pearson χ^2 statistic in the more flexible (less smooth) four-knot RCS model ($\chi^2 = 17.2$) when compared to the less flexible (more smooth) three-knot RCS model ($\chi^2 = 17.2$). For the 18 observed annual SR nest-count totals vs. their predicted expected values, $R^2 = 0.691$ ($P < 0.0001$) for the four-knot RCS independent errors model, only slightly larger than the three-knot model value of 0.675 ($P < 0.0001$). Having established the three-knot model as the most reasonable and parsimonious among the four considered, we used it to estimate percentage change in the predicted expected

value of annual SR nest-count totals between selected years.

Trend analysis of annual zone-level (ZL) nest counts.—In the trend analysis of annual zone-level (ZL) nest counts, we first examined the characteristics of temporal and spatial correlation between counts so that appropriate covariance structures could be specified for regression modeling. We assessed temporal correlation by comparing zone-matched counts (standardized by zone shoreline length) between all pairwise combinations of the 18 survey years. We calculated Pearson correlation coefficients (Snedecor and Cochran 1989) for each pairing of annual ZL counts, grouped the correlation coefficients by the lag difference between member years of these pairings, and averaged them by group. Considered in this way, the annual ZL nest counts demonstrated remarkably strong autocorrelation with only very slight decay as the lag difference increased from 1 to 17 years. The ZL counts that were separated by 1, 6, 12, and 17 years had average within-zone correlations of 0.97, 0.96, 0.95, and 0.93. Given such strong autocorrelation, we also expected to see a high degree of consistency from year to year in the pattern of within-year, along-shore spatial variation among ZL counts.

We conceptualized spatial variation in annual ZL nest counts (standardized by zone shoreline length) as occurring in one dimension along a 965-km shoreline axis. This shoreline axis extended south from the northernmost survey zone on Florida's Atlantic coast to its peninsular tip and then back north to the northernmost survey zone on Florida's southwestern (Gulf of Mexico) coast. We used the midpoints of zone-shoreline extents as the spatially explicit locations for ZL counts along this axis. Spatial correlation between ZL counts could then be characterized by using variography (Schabenberger and Gotway 2006) to estimate the correlation between counts as a function of their distance from each other along the shoreline axis.

Empirical semivariograms (Schabenberger and Gotway 2006) estimated separately for the ZL nest counts from each survey year, using between-zone lag-distance increments of 0.5 km, appeared remarkably similar between years, as would be expected given the strong autocorrelation of ZL counts between years already noted. The variance of ZL nest-count pair differences appeared to increase smoothly and exponentially with increasing lag distance between pair members up to ~17–25 km. Count-difference variances beyond 25 km still tended to increase slightly, but much less smoothly. There appeared to be very little evidence of a nugget effect (a nonzero limit for the variance of count-difference pairs as the lag distance approaches zero, possibly due to measurement error or microscale spatial variation; Schabenberger and Gotway 2006). The empirical semivariogram for the ZL nest-count 18-year totals, not surprisingly, appeared to be very similar in

shape and smoothness when compared to the annual semivariograms for ZL nest counts.

To determine the most appropriate spatial covariance structure to use in the trend analysis of ZL nest counts, we considered both 18-year total counts and counts from each year. In each case we compared model-fit statistics from three negative binomial regression model fits. For each fit, ZL counts were modeled on the log-link function scale as a single mean parameter assumed to be constant over the entire range of the shoreline axis, plus spatially correlated errors specified by one of three different spatial covariance structures (exponential, Gaussian, or spherical; Schabenberger and Gotway 2006). Zone shoreline length was included in each of the three models as an offset term (McCullagh and Nelder 1989) to appropriately standardize ZL counts for fair comparison between different-sized zones. In all years, and also for the ZL 18-year totals, spatial covariance parameter estimates greatly exceeded their standard errors, which further confirmed the presence of significant spatial correlation among ZL counts. Pearson χ^2 statistics were smallest for the spherical covariance structure, next smallest for the exponential structure, and largest for the Gaussian structure. However, corresponding overdispersion parameters for the spherical covariance structure ranged from 0.02 to 0.14, indicating severe underdispersion in the residual variability from these model fits. Overdispersion parameters for the exponential covariance structure ranged from 1.02 to 1.37 and from 1.13 to 1.47 for the Gaussian structure. These results confirmed our impressions from the empirical semivariograms and indicated that an exponential spatial covariance structure would be the most reasonable structure to use in the trend analysis of ZL nest counts. In this structure, correlation between ZL counts was assumed to fall off exponentially as a function of the shoreline distance between any two counts.

Although the simultaneous modeling of spatial and temporal correlation between observations can be difficult to implement in practice (Schabenberger and Gotway 2006), the apparent separability and orthogonality of spatial and temporal correlation (Schabenberger and Gotway 2006) among the annual ZL nest counts allowed us to model them in our trend analysis in a relatively straightforward manner using covariance structures available in PROC GLIMMIX. Because the within-zone correlation between ZL nest counts decayed so slowly as the number of years between counts increased from 1 to 17 years ($R = 0.97$ to 0.93), we assumed that within-zone correlation between any two years was effectively constant. The compound symmetry covariance structure (Littell et al. 2006) implied by this assumption is frequently used to analyze responses from repeated-measures study designs in which responses under each of several treatments are collected from each subject in the study (Littell et al. 2006). However, unlike a repeated-measures study in which between-subject

responses under a particular treatment condition are reasonably assumed to be independent of one another, the ZL nest counts in any year are not independent of one another because of their fixed locations along the shoreline axis of the survey region. We therefore reparameterized the compound symmetry covariance structure so that it could be specified in PROC GLIMMIX as a zone ("subject") random effect, and we then imposed a between-zone exponential spatial covariance structure on the levels of the zone random effect. This is equivalent to assuming exponential spatial correlation between the 18-year averages of ZL nest counts. This seemed reasonable, given our earlier assessment of spatial correlation between ZL nest-count 18-year totals. We also imposed a within-year, between-zone exponential spatial covariance structure on the residual error matrix (R-side matrix; Littell et al. 2006), allowing each year to have its own between-zone variance and spatial-correlation parameters.

Having specified a reasonable spatiotemporal covariance structure for our mixed-effect, negative-binomial regression modeling framework, we developed a sequence of trend models that incorporated this structure. Zone shoreline length was again included as an offset term in each model to appropriately standardize ZL nest counts to densities (nest count per shoreline kilometer). We first fit three-knot and four-knot RCS time-curves to the annual ZL nest counts. In these models, we assumed that each ZL count could be modeled on the log-link function scale as a single annual mean value predicted by either of the RCS time curves plus a year-independent between-zone spatially correlated error plus a year-specific between-zone spatially correlated error. We found at least one RCS regression coefficient to be significantly different from zero (t statistic $P < 0.0001$) in both the three-knot and four-knot models, indicating that both trend lines were nonlinear in shape. However, the residual variation from the fitted three-knot model was underdispersed (lower than expected for a negative binomial count model), as indicated by an overdispersion parameter value of 0.82, compared to the more desirable value of 1.02 for the four-knot model. Because the three-knot and four-knot models were not nested, and because the pseudolikelihood method we used to fit all of the mixed-effect, negative-binomial regression models precluded us from using information criteria to compare models, we considered the four-knot model to be a better-fitting model on the basis of the good agreement between observed and expected levels of residual variation for this model. For the 6624 observed ZL nest counts vs. their best least unbiased (BLUP; Littell et al. 2006) predicted expected values from the four-knot model, $R^2 = 0.916$ ($P < 0.0001$).

Trend analysis of annual zone-level (ZL) nest counts by subregion.—To determine whether the shape of the four-knot RCS trend line for annual ZL nest counts depended on location within the survey region, we defined a categorical subregion variable that represented

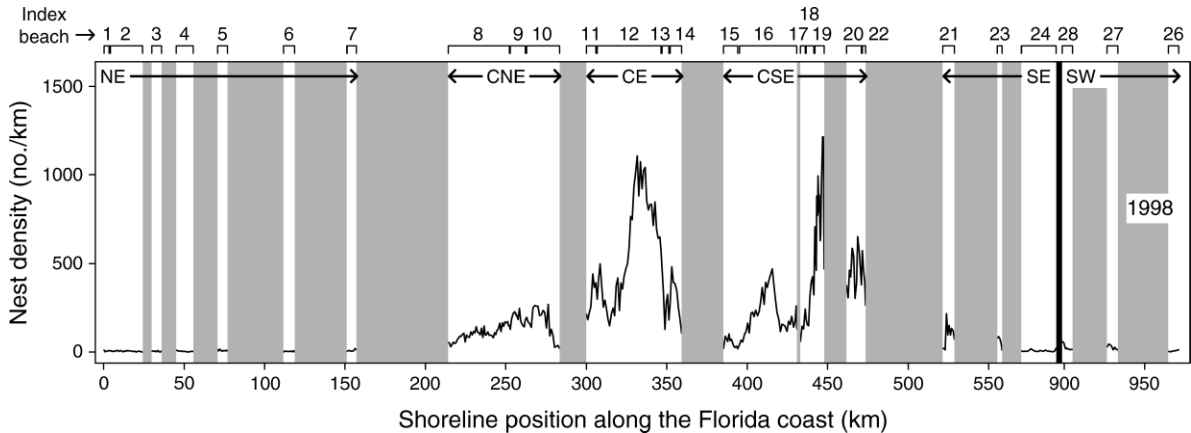


FIG. 2. Shoreline distribution of annual loggerhead nest densities from 368 Florida Index zones surveyed during the 1998 nesting season. Shoreline extents (in km) of numbered Index beaches are indicated by brackets above the plot (Fig. 1, Appendix: Table A1); arrows below the upper edge of the plot indicate the extent of the subregions (Fig. 1, Table 1). Gray bars show beaches not represented in Index counts. The horizontal axis represents approximate shoreline distance from the Florida–Georgia state border (30°6' N, 81°24' W). Abbreviations for Florida subregions are: NE, Northeast; CNE, Central Northeast; CE, Central East; CSE, Central Southeast; SE, Southeast; and SW, Southwest.

six Florida subregions (Fig. 1). We then fit two additional regression models in which the subregions were allowed to have either parallel or nonparallel trend lines. In the “parallel” model, the six subregions shared a common four-knot trend line shape but had different trend-line intercepts. In the “nonparallel” model, each subregion was allowed to have its own uniquely shaped four-knot RCS trend line.

We first compared the parallel subregion trend-lines model fit to the previously fit “single-region” trend-line model. Because the single-region (single-intercept) model could be viewed as nested within the parallel subregion (multi-intercept) model, we used a Pearson-like χ^2 test (Agresti 2002) to determine if the fixed effects in the parallel subregions model explained more of the variability in nest counts. Not surprisingly, significantly more variability was explained by the fixed effects in the larger, parallel-trend-lines model ($\chi^2 = 31.1$, $df = 5$, $P < 0.0001$), because of the great variation in mean annual ZL nest counts among subregions.

Next we compared the parallel-subregion trend-lines model fit to the nonparallel-subregion trend-lines model fit. Because the parallel trend-line (multi-intercept, single-shape) model could be viewed as nested within the nonparallel trend lines (multi-intercept, multishape) model, we again used the Pearson-like χ^2 test to compare them. The test statistic ($\chi^2 = 170.8$, $df = 15$, $P < 0.0001$) indicated that significantly more variability was explained by model fixed effects when each subregion was allowed to have its own uniquely shaped four-knot RCS trend line for annual ZL nest counts. For observed ZL nest counts vs. their BLUP predicted values from the nonparallel trend-lines model, $R^2 = 0.920$ ($P < 0.0001$). Because the R^2 indicator of overall model fit hardly changed in going from a single-region, trend-line model to a subregion model with six uniquely shaped trend

lines (0.916 vs. 0.920), we conclude that the additional variability in ZL nest counts accounted for by fixed effects in the subregion model was being accounted for by random-effects covariance structure in the single-region model.

We used both the single-region and nonparallel subregion trend-line models to estimate percentage change in predicted mean annual ZL nest counts between selected survey years. The 95% confidence intervals and P values for testing whether the percentage change differed significantly from zero were adjusted to compensate for multiple testing of subregions by using a Bonferroni stepdown procedure (Littell et al. 2006). We used a global F test to determine if the percentage change in mean ZL nest densities over a particular survey time interval differed significantly between subregions.

RESULTS

Spatiotemporal variation in nest counts

An important result of this trend assessment can be seen in the detailed spatiotemporal picture of Florida loggerhead nesting (Figs. 2 and 3). Within-year variation in ZL loggerhead nest density was high for the Index zones used in this study (Fig. 2), spanning a minimum range of 0–573 nests·km⁻¹·yr⁻¹ in 2004 to a maximum range of 0–1576 nests·km⁻¹·yr⁻¹ in 1990. However, there was a remarkable consistency in the pattern of longshore spatial variation in ZL nest density between years. Through the 18-year time series, peaks in nesting density remained centered on the same clusters of Index zones, with no obvious shifts in later years between high- and low-density zones from earlier years (Fig. 3). This year-to-year consistency in the relative along-shore distribution of annual ZL nest counts was evidenced in our analysis by strong within-zone temporal autocorrelation

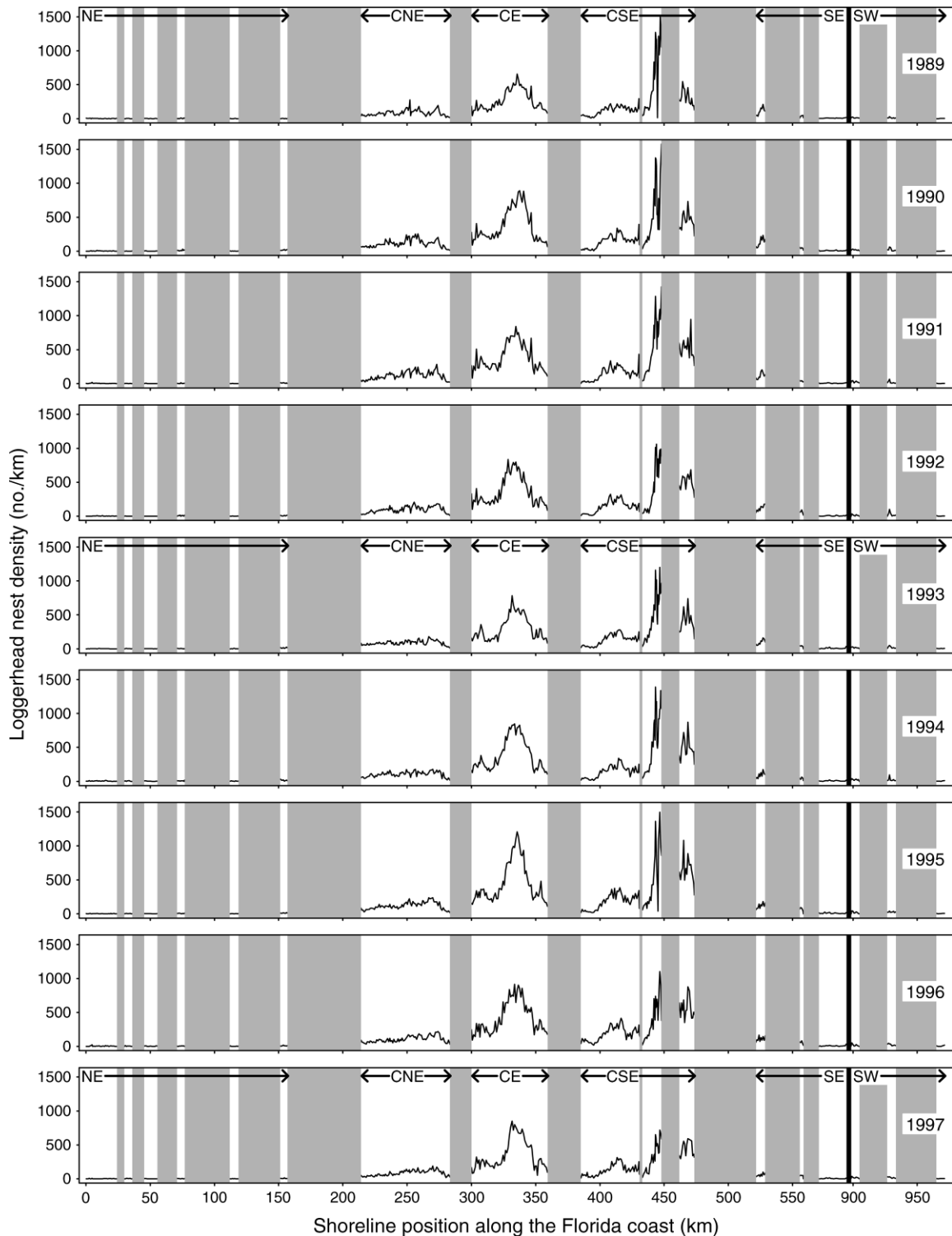


FIG. 3. Shoreline distribution of annual loggerhead nest densities from 368 Florida Index zones surveyed during each nesting season from 1989 to 2006. Shoreline extents of subregions (Fig. 1, Table 1) are indicated along the upper edge of the plot. Gray bars show beaches not represented in Index counts. The horizontal axis represents approximate shoreline distance from the Florida-Georgia state border ($30^{\circ}6' N, 81^{\circ}24' W$).

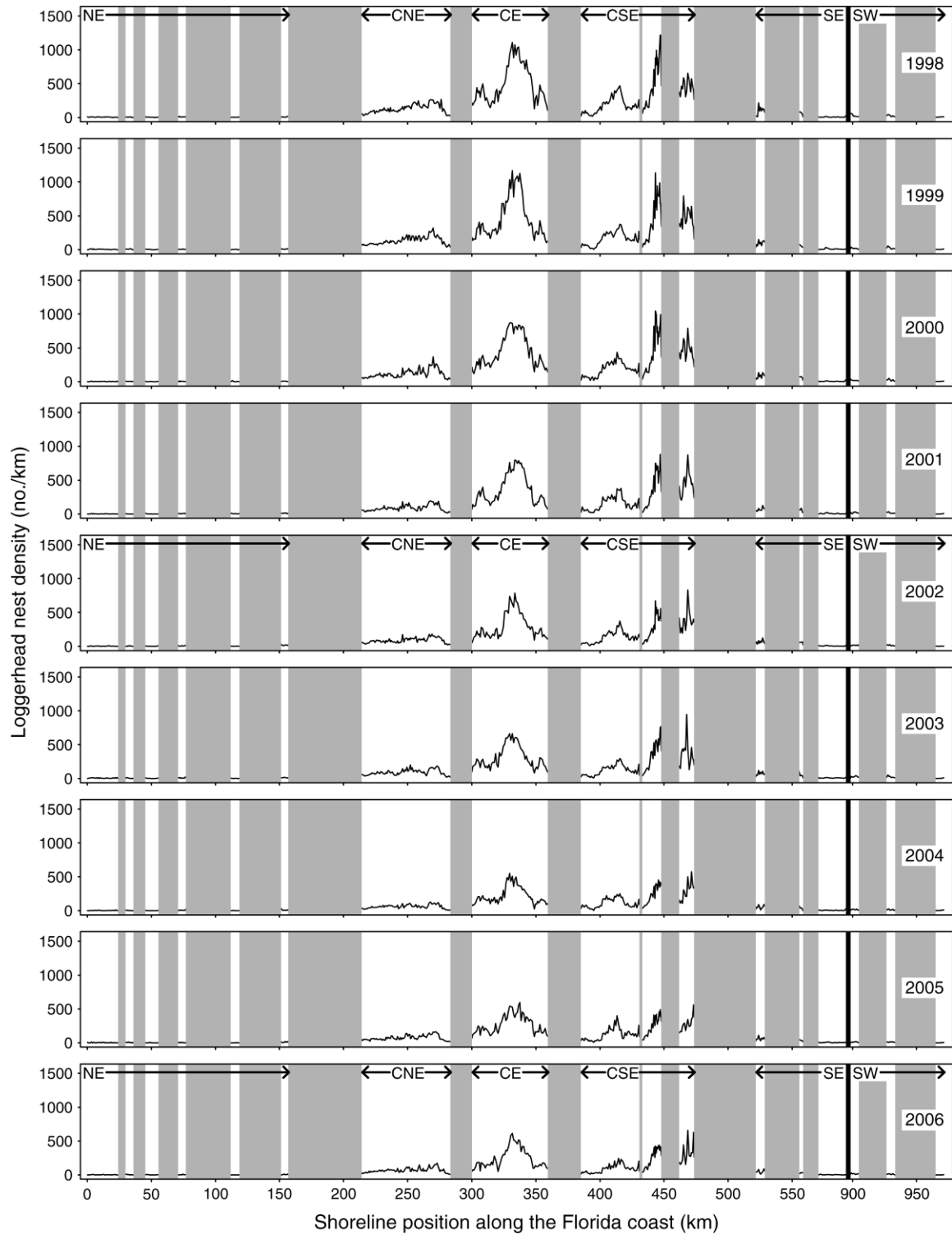


FIG. 3. Continued.

that decayed only slightly over the time series; average within-zone correlations between annual counts fell from 0.97 to only 0.93 as the lagged time interval increased from 1 to 17 years. This spatial consistency is

further supported by the exceptionally good ZL trend-model fits that we obtained (observed vs. expected count $R^2 > 0.91$) using a spatiotemporal covariance structure that presumed an extremely high degree of consistency

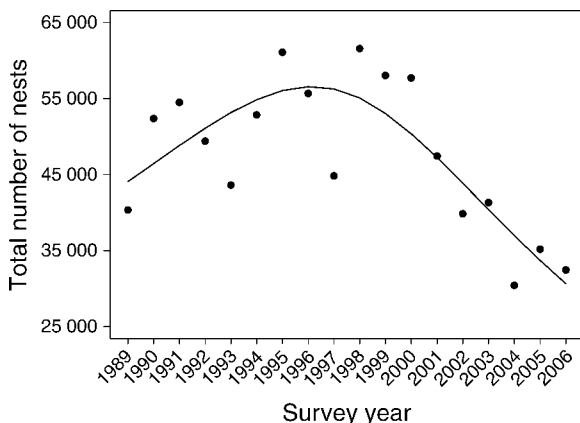


FIG. 4. Annual total nest counts for loggerhead sea turtles on Florida Index beaches, 1989–2006. The trend line was estimated by fitting a three-knot restricted cubic spline curve to the total counts via negative binomial regression (survey-region [SR] model; see *Materials and methods*).

in within-year spatial covariance among nest counts from year to year.

Trend analysis of annual nest counts

Each of the negative binomial count regression models that we used described a similar large-scale trend in annual loggerhead nest counts. During the 18-year period between 1989 and 2006, loggerhead nest counts on Florida Index beaches initially increased but then declined, with an overall net decrease for the period. This pattern was evident in the most reasonable and parsimonious among four trend models of annual survey-region (SR) nest-count totals (Fig. 4). A similar pattern was seen in the most reasonable “single-region” zone-level (ZL) nest-count trend model that took into account both spatial and temporal correlation between counts (Fig. 5). We also saw this pattern in a ZL model that allowed RCS trend-line shapes to vary among the six Florida coastal subregions (Fig. 6). Although the shapes of these trend lines varied slightly between subregions (Fig. 6), they all showed a pronounced decline after 1998, similar to the “single-region” models describing expected SR and ZL nest-count trends for peninsular Florida Index beaches (Figs. 4 and 5). In the ZL subregion model, one standout was southeastern Florida. In this subregion, there seemed to be no indication of the loggerhead nest-count increase seen in other subregions between 1989 and 1998 (Fig. 6, Table 1).

We used the models just described to estimate percentage change in predicted mean annual nest counts between selected years, along with 95% confidence intervals (Table 1). “Single-region” estimates comprising all Florida Index zones used in this study indicated that loggerhead nesting increased by 25–27% between 1989 and 1998 ($P \leq 0.025$), but then declined by 43–44% between 1998 and 2006 ($P < 0.0001$). Because the

decline after 1998 was larger than the increase prior to 1998, the nesting trend for the entire 18-year period represented a decline of 28–31% ($P \leq 0.001$; Table 1).

Estimates of percentage change in annual mean nest density from the subregion trend model indicated statistically significant increases ($P \leq 0.007$) between 1989 and 1998 in five of the six subregions (Table 1). Increases in these five subregions ranged from 22% to 85%, with the highest increase occurring in the Southwest subregion (SW). There was no significant change ($P = 0.934$) in the Southeast subregion (SE) during this period (Table 1). For the period 1998–2006, estimates of percentage change indicated nesting declines in all subregions ($P \leq 0.0001$). Declines ranged from 29% to 51%, with the steepest decline occurring in the SW subregion. The magnitude of percentage change in annual mean nest density differed significantly between subregions for the period 1989–1998 ($F = 5.45$, $df = 5$, 960.6 [denominator df adjusted by Kenward-Roger method], $P < 0.0001$). The magnitude of percentage change also differed significantly between subregions for the period 1998–2006 ($F = 4.00$, $df = 5$, 683.2, $P = 0.001$). Consistent with the difference in F statistics, the variance of the six subregion percentage-change estimates for the period 1989–1998 was twice that for 1998–2006.

During the entire 18-year survey period, 1989–2006, nesting declined significantly ($P \leq 0.002$) within each of the four subregions on the central and southern Atlantic coast of Florida (CNE, CE, CSE, and SE), where ~88% of Florida’s loggerhead nesting takes place (Fig. 1, Table 1). Overall declines in these four subregions ranged from 29% to 37%, with the steepest decline occurring in the Central Northeast subregion (CNE) (Table 1). No significant change ($P \geq 0.579$) in annual mean nest

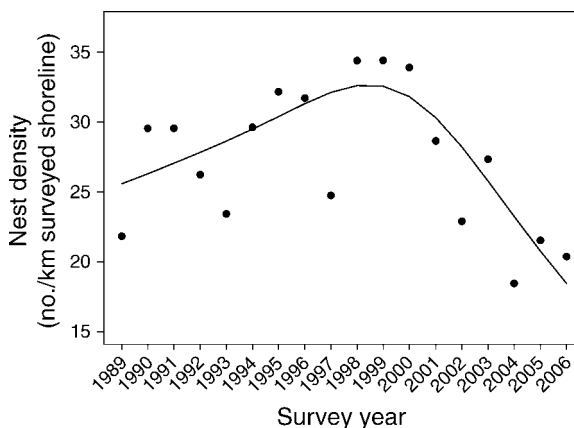


FIG. 5. Annual mean zone-level nest densities for loggerhead sea turtles on Florida Index beaches, 1989–2006. The trend line was estimated by fitting a four-knot restricted cubic spline curve to Index-zone nest counts via mixed-effect negative binomial regression (single-region ZL model; see *Materials and methods*). An 18-intercept “year-means” form of the regression model was used to generate point estimates of marginal mean nest densities.

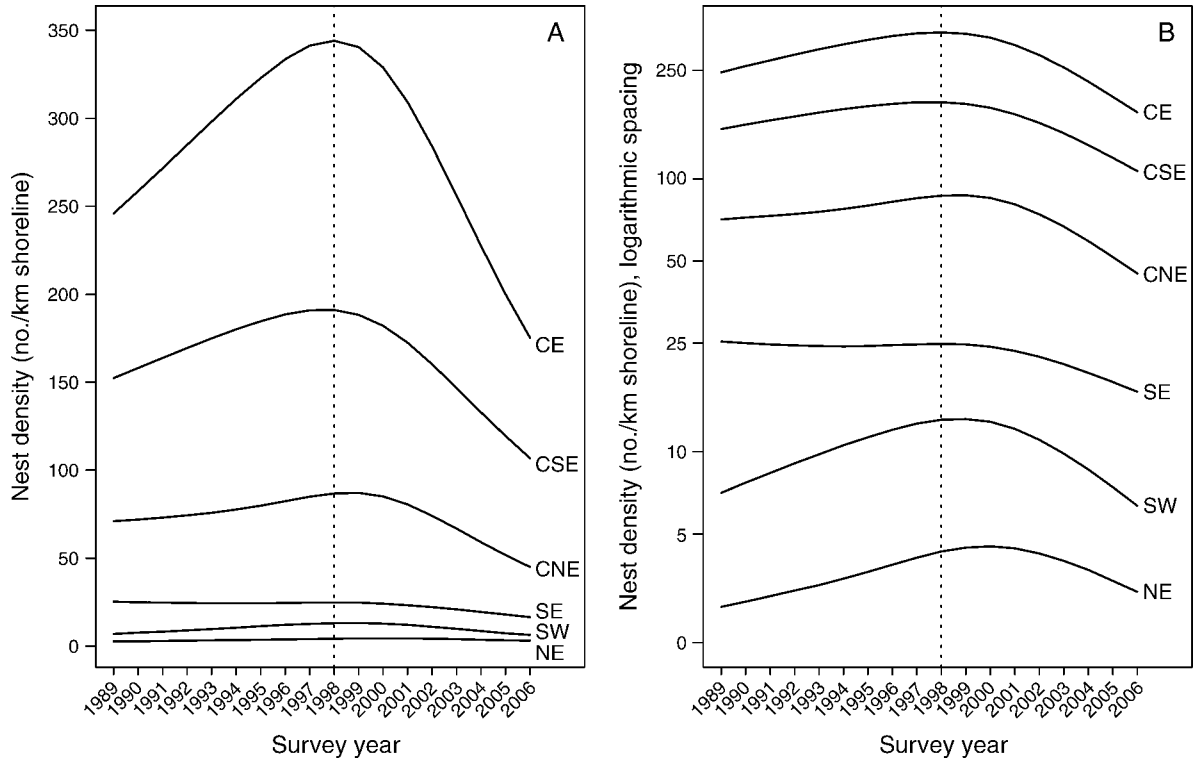


FIG. 6. Annual mean zone-level nest densities for loggerhead sea turtles on Florida Index beaches by subregion, 1989–2006. Shoreline extents of subregions are shown in Fig. 2. Subregion trend lines were estimated by fitting four-knot restricted cubic spline curves to Index-zone nest counts via mixed-effect negative binomial regression (subregion ZL model; see *Materials and methods*). Nest densities are linearly spaced in Plot A, and logarithmically spaced in Plot B. Abbreviations for Florida subregions (Fig. 1) are: NE, Northeast; CNE, Central Northeast; CE, Central East; CSE, Central Southeast; SE, Southeast; and SW, Southwest.

density was detected in either the Northeast (NE) or Southwest (SW) subregions (Table 1).

DISCUSSION

Spatiotemporal aspects of Florida loggerhead nesting

In our analysis of annual zone-level nest counts, we found a unique tool to study spatiotemporal nesting trends in the set of Florida Index zones. Although within-year spatial variability was high (Fig. 2), the spatial covariance structure that we used to generate percentage-change estimates effectively partitioned error variability into between-zone and within-zone components. The strong, positive, within-zone temporal correlation of annual nest counts that we observed between survey years ($R = 0.93\text{--}0.97$; Fig. 3) translated directly into relatively low between-zone variability of within-zone changes, resulting in good precision of mean percentage change estimates by the ZL models. A related small-scale spatiotemporal analysis of loggerhead nesting conducted by Weishampel et al. (2006) showed a similar consistency in along-shore loggerhead nest distribution.

We attribute some of the strong, positive, within-zone correlation of annual nest counts to a high level of site fidelity (site fixity) in loggerhead nesting. This nest-site

fidelity is well known in loggerheads (LeBuff 1974, Richardson 1982, Bjørndal et al. 1983, Gyuris and Limpus 1988, Hays and Sutherland 1991, Katselidis et al. 2004). Most loggerhead sea turtles tagged and reobserved on beaches have had nest sites within a few kilometers, both within and between nesting seasons (Webster and Cook 2001, Schroeder et al. 2003). At this scale, it seems clear that over the 18 years of Florida loggerhead nesting, the locations of “peaks” and “valleys” in nesting density have remained relatively constant (Fig. 3). We find that a mountain range metaphor is useful to describe the appearance of this spatial variation. Each year shows a similar mountain profile, although nesting magnitude changes (an increase, then a decline) give the appearance of profiles viewed from various distances.

Although sea turtles as a taxonomic group are often characterized as being faithful in their nesting to particular stretches of beach, there are exceptions to this generalization. For instance, Pritchard (2004) reported large shifts in the spatial nesting distribution of three species of sea turtles following large-scale geomorphological changes at beaches in the region of the Guianas (northern central South America). There have not been any similarly profound beach changes that could have affected loggerhead nesting in Florida

TABLE 1. Percentage change in annual loggerhead nest-count indices (mean and confidence limits) for various survey periods and Florida subregions.

Survey period and region	Nests counted (%)	Shoreline surveyed (%)	Change in annual mean density (%)		<i>P</i> (% change = 0)
			Mean change (%)	95% CL	
1989 to 1998					
SR-All	100.0	100.0	24.9	3.3, 51.0	0.025
ZL-All	100.0	100.0	27.4	18.9, 36.5	<0.0001
ZL-NE	0.5	19.8	59.2	26.2, 100.9	<0.0001
ZL-CNE	14.2	21.6	22.2	0.9, 48.1	0.007
ZL-CE	44.1	18.5	39.9	13.6, 72.3	<0.0001
ZL-CSE	38.5	22.8	25.4	4.3, 50.7	0.001
ZL-SE	2.2	10.3	-1.9	-25.9, 29.9	0.934
ZL-SW	0.6	7.0	85.2	30.7, 162.2	<0.0001
1998 to 2006					
SR-All	100.0	100.0	-44.3	-53.8, -33.0	<0.0001
ZL-All	100.0	100.0	-43.3	-47.5, -38.9	<0.0001
ZL-NE	0.6	19.8	-28.7	-42.7, -11.3	<0.0001
ZL-CNE	14.9	21.6	-48.1	-56.8, -37.8	<0.0001
ZL-CE	46.0	18.5	-49.1	-58.2, -37.9	<0.0001
ZL-CSE	35.8	22.8	-44.0	-53.0, -33.3	<0.0001
ZL-SE	1.9	10.3	-33.1	-49.1, -12.1	0.0001
ZL-SW	0.7	7.0	-51.4	-65.4, -32.0	<0.0001
1989 to 2006					
SR-All	100.0	100.0	-30.5	-42.1, -16.1	0.001
ZL-All	100.0	100.0	-27.8	-34.2, -20.8	<0.0001
ZL-NE	0.5	19.8	13.5	-15.2, 52.1	0.579
ZL-CNE	14.5	21.6	-36.6	-50.2, -19.3	<0.0001
ZL-CE	44.7	18.5	-28.7	-45.1, -7.5	0.001
ZL-CSE	37.5	22.8	-29.8	-44.3, -11.6	<0.0001
ZL-SE	2.1	10.3	-34.4	-54.0, -6.4	0.002
ZL-SW	0.7	7.0	-10.1	-42.2, 39.8	0.940

Notes: Nest-count data came from annual surveys of 368 Index Beach zones. "SR" indicates that estimates were obtained from a "survey region" model of annual nest-count totals; "ZL" indicates that estimates were obtained from a "zone-level" model of annual nest densities (see *Methods and materials*). Abbreviations for Florida subregions (see Fig. 1) are: NE, Northeast; CNE, Central Northeast; CE, Central East; CSE, Central Southeast; SE, Southeast; and SW, Southwest.

during the 18 years of our analysis. However, we do know of numerous, localized, artificial changes in Florida beaches that have occurred as a result of beach nourishment (artificial beach-widening) projects. These projects have been observed to lower sea turtle nesting success during 1–2 years (Crain et al. 1995, Steinitz et al. 1998, Rumbold et al. 2001) over the extent of project areas (commonly several kilometers).

Because the peaks and valleys in Fig. 3 are similar in consecutive years, this strong, positive, within-zone temporal autocorrelation of annual nest counts must be, in part, the result of agreement between loggerhead cohorts that share few members. Individual loggerheads seldom nest in consecutive years; the number of years between reproductive migrations (remigration interval) is typically between two and four (reviewed by Schroeder et al. 2003). Thus, beach attributes that have been relatively constant throughout the study period are likely to have shaped the loggerhead nesting distribution.

Detection of small-scale spatiotemporal shifts, such as those resulting from scattered beach nourishment projects, was not a goal of our analysis. Our current ZL model did not make use of covariates that described

attributes of Florida beaches that might matter to nesting loggerheads. However, we did notice some coincidence of loggerhead nesting peaks with reflective and intermediate beaches (beaches having coarse-grained sands and steep beach profiles; Benedet et al. 2003) and with centers of barrier islands (beach locations distant from inlets). A preference of nesting loggerheads for steep beaches has also been reported by Provanca and Ehrhart (1987), and an aversion to inlets has been reported by Witherington et al. (2004). Although the predicted values from our current ZL model accounted for a large proportion of the variability of observed annual nest counts ($R^2 > 0.91$), we believe that this model can still serve as a foundation for generating more biologically relevant models of loggerhead spatiotemporal nesting distributions. This would be accomplished by shifting nest-count variability from the error-structure side of the model to the fixed-effect side of the model through the inclusion of relevant beach-characteristic covariates.

Declining loggerhead nest counts on Florida beaches

Our SR and ZL model estimates of percentage change agree regarding the general trends that have occurred in

loggerhead nesting within Florida's Index beach zones. These trends indicate that Florida's loggerhead nest counts have declined significantly between 1989 and 2006 and have shown a steep decline within the most recent period, 1998–2006 (Table 1). With the shape of the estimated RCS trend lines as a guide, we believe that Florida loggerhead nesting increased before 1998, but then declined steeply (Figs. 4 and 5).

Possible effects from local spatial shifts.—Adverse beach and nearshore conditions, present in Florida and thought to locally affect nesting activity include: chronic erosion; acute erosion from tropical storms and hurricanes; coastal armoring; artificial lighting; human beach activity; and periodic, coastal upwelling of cold water (Lutcavage et al. 1997, Witherington 2003; B. E. Witherington, *personal observation*). Each of these phenomena is relatively localized or brief and would be expected to show effects within the spatiotemporal scale of Fig. 3. Although some combination of these effects may be influencing subtle subregional differences in nesting trends (Fig. 6), we do not believe that region-wide effects near beaches have produced the observed nesting decline. If adverse beach conditions have caused loggerhead nesting declines in Florida, then these same conditions would be expected to have similar effects on other species of sea turtles nesting on Florida beaches. In Florida, green turtles have similar nesting habitat requirements, a similar nesting season (late-May–September), and have peaks in their spatial distribution that match peaks in loggerhead nesting (Witherington et al. 2006a, b; Florida Fish and Wildlife Conservation Commission [FWC], *unpublished data*). Unlike loggerhead nesting, green turtle nesting in Florida has been increasing significantly (Witherington et al. 2006a; *data available online*).⁵

An important indicator of adverse beach conditions is sea turtle nesting success (the proportion of nesting attempts that result in a nest). Many beach conditions that discourage or prevent nesting (e.g., effects from beach nourishment; Rumbold et al. 2001) result in low nesting success and a high number of abandoned nesting attempts. Nesting success of loggerheads on the 27 Index beaches used in our analyses averaged 0.51 nests per attempt (95% CI: 0.50–0.53), with no significant linear pattern in temporal variation ($R^2 = 0.17$, $P = 0.084$). One low outlier in the annual time series, with a nesting success ratio of 0.41, occurred in 2005, a year in which many anthropogenic changes to Florida's beaches (artificial sand placement) occurred following erosion from hurricanes in 2004. Nesting success rose to 0.49 nests per attempt in 2006. We find no indication from variation in nesting success that would signal increasing effects from adverse beach conditions large enough to have resulted in the decline in nest counts that we present here.

Given the between-year spatial consistency in loggerhead nest counts at Index zones, we consider it unlikely that spatial shifts occurred that would have changed the representative nature of Florida Index zones over the 18 years of our analysis. Evidence to support this contention comes from our ZL modeling exercise, in which within-zone autocorrelation diminished only slightly even after a 17-year lag. We also see no evidence of spatial shifts in the within-year spatial nest-count distributions, which are recognizable as the same along-shore “mountain range” in each survey year (Fig. 3).

Additional evidence of a loggerhead nesting decline comes from nest counts made at non-Index beach areas (included in the Statewide Nesting Beach Survey program). These Statewide nest counts indicate a declining trend (Fig. 7) similar to the one described by the models using Index counts (Figs. 4–6). The Statewide counts differ from the Index counts in not having a constant level of survey effort. To partially account for changes in effort, we plotted effort as measured by kilometer-days (Fig. 7). Although this counting effort increased on non-Index beaches over the 18-year period of 1989–2006, the increased effort did not seem to dampen a post-1998 decline in nest counts similar to that indicated by our models of Index counts. Similarity in the temporal nest-count trends in Index and Statewide data support the argument that any shift between Index beach zones and adjacent beaches has been too small to affect how Index zones represent Florida loggerhead nesting.

Possible effects from regional spatial shifts.—Similarity between Index and Statewide nest-count trends indicates that loggerhead nesting declines cannot be explained by large-scale spatial shifts from Index beaches to non-Index beaches in Florida (Fig. 7). Non-Index Florida beaches include the Panhandle region, where three stretches of beach (62 km in Walton, Bay, and Gulf counties) have been surveyed under Index Beach protocol between 1997 and 2006. Rather than showing increases in nest counts that might have resulted from spatial shifts in nesting, these Panhandle beaches have shown declining nest counts in recent years (FWC, *unpublished data*).

We next searched for evidence of a major shift in loggerhead nesting from Florida beaches to beaches outside Florida. In this search, we reasoned that only nearby regional beaches could potentially harbor loggerheads that formerly nested on Florida beaches. Genetic (mtDNA lineage) evidence has shown significant genetic separations between loggerheads nesting in different geographic regions (Bowen 2003) and has indicated that large-scale movement between regional nesting beaches has been rare. The regional nesting beaches closest to Florida, where one would look for nesting increases corresponding to Florida's nesting declines, are in the state of Georgia to the north and in the Mexican state of Yucatan to the southwest.

⁵ http://research.myfwc.com/features/view_article.asp?id=10690

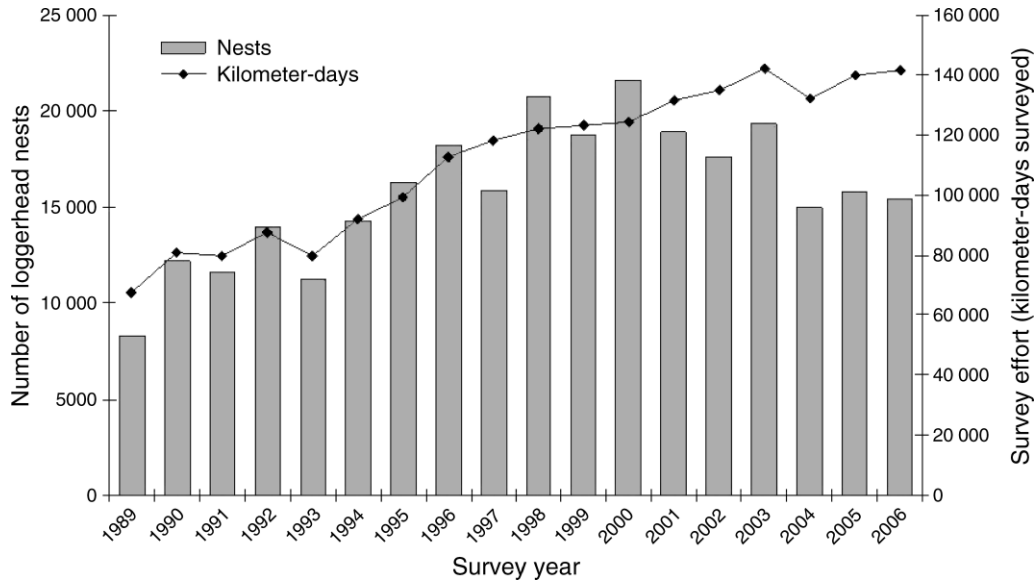


FIG. 7. Loggerhead nest counts and nest-survey effort at non-Index Statewide beaches in Florida, 1989–2006. These beaches (73–147 survey areas, 543–870 km), are surveyed as part of the Statewide Nesting Beach Survey and were not included in the trend analysis. Annual survey effort is estimated by the total number of kilometer-days expended. Cases in which kilometer-days could not be calculated from submitted survey data accounted for 0.2–2.23% (mean = 0.68%, SD = 0.86%) of total annual nests on these beaches.

Standardized surveys at 11 beaches in North Carolina, South Carolina, and Georgia indicate a 1.9% annual decline from 1983 to 2005 (NMFS and USFWS 2007), and in Yucatan, loggerhead nesting between 1987 and 2006 increased and then declined in a pattern similar to that seen in our analysis of Florida Index nest counts (Zurita et al. 2003, Arenas-Martinez 2005; J. Zurita, *personal communication*). We note that increases in loggerhead nesting outside Florida would have had to be profoundly steep in order to explain Florida nesting declines; Florida hosts ~90% of regional loggerhead nesting (including Mexico, the wider Caribbean, and the eastern United States; Ehrhart et al. 2003).

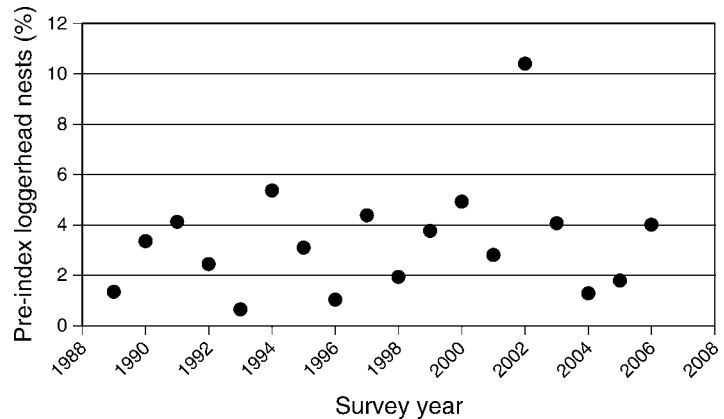
Possible effects from temporal shifts in nesting activity.—Because Florida's Index nest-count period (survey season) is constant from year to year (15 May–31 August), it is possible that temporal shifts in loggerhead nesting could have influenced the Index counts made over the 18-year time series. Weishampel et al. (2004) suggested such a temporal shift following observations that the median nesting date of loggerheads nesting on a Florida beach advanced 10 days over a 15-year period. Working at a nearby loggerhead nesting beach, Pike et al. (2006) found changes in season length that may explain the shift in median date. These changes in season length occurred because fewer nests were made in September, following the end of the Index season surveyed in our analysis. Such a shift would be expected to dampen apparent nesting declines in Index nest counts.

The Florida beach for which Weishampel et al. (2004) measured a shift in median date (southern Brevard

County, within the Central East subregion; Fig. 1) is the most densely nested stretch within the subset of Index beaches used in our trend analysis. To examine how closely the Index nest-count period represented the loggerhead nesting season at this beach, we used the nest counts made 1 May–31 August (Fig. 8; data provided by L. Ehrhart, University of Central Florida). This period captures nearly all seasonal loggerhead nesting and includes the only significant seasonal gap in the Index period, which is the onset of nesting in May. Loggerhead nesting after 31 August averaged only 0.16% of the annual total at the southern Brevard County beach (L. Ehrhart, *unpublished data*). At this beach, the average annual percentage of total nests recorded before Index counts began was small: only 3.4%. We believe that this is too small a percentage for within-season temporal shifts to account for declines in Index nest counts. In addition, there was no significant relationship between the percentage of pre-Index nests and year ($R^2 = 0.11$, $P = 0.180$). If declines in Index nest counts had been influenced by seasonal shifts, there would have been a strong increase in the proportion of pre-Index loggerhead nests.

Attributes of the nesting decline.—One important attribute of the post-1998 nesting decline was its consistency between subregions (coherence) in comparison to the pre-1998 nesting increase. As evidenced by our subregional trend analysis (Fig. 6) and subregional estimates of percentage change (Table 1), increases in annual ZL nest density prior to 1998 were more variable between subregions (by a factor of 2) than were decreases after 1998. This may be a result of an

FIG. 8. Annual percentage of loggerhead nests recorded before the start date of surveys on 21 (21 km) Index beach zones in south Brevard County, Florida. In this analysis, the pre-Index period was 1–14 May, and the Index nesting season was 15 May–31 August. Annual loggerhead nests recorded after 31 August on these beaches averaged only 0.16% between 1989 and 2006. Data are from L. Ehrhart, University of Central Florida.



abundance of recruits during the (mostly) increasing period and fewer recruits during the declining period. Loggerhead recruits (neophytes) have been shown to have a higher variability in nest-site choice (greater distances between successive nests) in comparison to remigrant turtles (those identified during previous nesting seasons) (Hays and Sutherland 1991, Katselidis et al. 2004). It is possible that the high degree of consistency in the rate of decline among beaches and subregions after 1998 was related to a lowered recruitment rate (fewer immature loggerheads surviving to adulthood) over the entire survey region.

Does a Florida nesting decline indicate population decline?

Although nest counts are widely used as a proxy for adult sea turtle population size (Meylan 1982, Schroeder and Murphy 1999), variation in reproductive rates among individuals has the potential to change nest numbers even when the population of adult females is stable (Hays 2000). The two most important reproductive rates influencing nest numbers are clutch frequency (nests per female per seasonal migration) and remigration interval (years between seasonal migrations).

Clutch frequency has been measured by repeatedly observing nesting turtles identified by flipper tags. Considerable errors in these measures come from turtles that nest unobserved. Because of this, extensive research projects that tag nearly every nesting turtle (e.g., Hughes 1974, Frazer and Richardson 1985) provide the most reliable estimates. Frazer and Richardson (1985) estimated mean annual clutch frequencies for loggerheads nesting on Little Cumberland Island, Georgia, USA, and found this rate to range between 2.81 and 4.18 nests per female per season over a 10-year period during the 1970s and 1980s. Within this range, years with high nesting levels tended to have the highest mean clutch frequencies. However, Frazer and Richardson did not find any temporal pattern in clutch frequency, such as a steady decline, which could explain a multiyear decline in nest counts. These clutch frequencies for Georgia loggerheads varied ~20% around a median rate over 10 years. Annual variation in mean clutch frequency for

loggerheads nesting in Natal, South Africa, ranged between 3.65 and 4.21 nests per female per season over a four-year period (Hughes 1974), which is ~7% around a central rate. This variation has been far lower than the change that we measured in Florida loggerhead nest counts (43–44% in eight years). Additional long-term studies are needed to fully describe the role of loggerhead clutch frequency in annual nesting variation.

Remigration intervals for loggerheads have been reported from many locations and time periods. Research projects in which extensive tagging of loggerheads allows the most reliable remigration interval estimates include projects at Little Cumberland Island, Georgia (mean = 2.54 years, $n = 242$; Richardson et al. 1978); Brevard County, Florida (mean = 2.71 years, $n = 161$; Bjorndal et al. 1983); Natal, South Africa (mean = 2.58 years, $n = 740$; Hughes 1982); and Queensland, Australia (mean = 2.98 years, $n = 1112$; Limpus 1985). These rates vary ~7% around a central value. Green turtles nesting in Australia have shown some nesting peaks that lag two years behind recurrence of the El Niño Southern Oscillation (Limpus and Nicholls 2000). However, this cycle was superimposed over a shorter (2–3 year) and more pronounced cycle that is probably driven by a similar period in remigration interval. In an examination of remigration intervals of Atlantic green turtles, Solow et al. (2002) showed that cycles correlated with winter (non-nesting season) sea-surface temperature, but there was no indication that interruption in the turtle's typical two-year reproductive cycle was more than temporary (one or two years). Saba et al. (2007) demonstrated a similar correlation between leatherback turtle remigration interval and the Pacific El Niño Southern Oscillation. This correlation suggested cycles set over approximately five years, but gave no indication of longer trends in changing remigration intervals. There is no evidence for periodicity in loggerhead remigration intervals approaching the length of the decline that we describe here.

Because variation in loggerhead clutch frequency and remigration interval are known to exist, it is clear that these rates affect nest counts on beaches and add

uncertainty to estimations of adult females from nest counts. If changes in loggerhead reproductive parameters are occurring because of environmental factors affecting Florida sea turtles, these factors do not seem to have affected nesting by green turtles and leatherbacks, which have had their respective Florida nest counts increase by a factor of 6 and 10 during the period 1989–2007 (Chaloupka et al. 2008; FWC, unpublished data). One could postulate that the declines in Florida loggerhead nesting that we have shown are largely the result of declining clutch frequencies and lengthening remigration intervals. However, given that there are no studies to support declines in reproductive rates of loggerheads anywhere in the world, it is also possible that these rates have increased and that decline in adult female loggerheads has been more severe than nest counts indicate. In our assessment of coherence in the nesting decline (Fig. 6, Table 1), we suggested that loss of adult recruitment might explain the post-1998 decline. One important effect of reduced recruitment could have been an increase in clutch frequency among turtles in the nesting population. Neophyte loggerheads are observed to have lower clutch frequencies than remigrants (Frazer and Richardson 1985, Hawkes et al. 2005). Thus, we expect that, for a given level of population decline, decreased recruitment would reduce nest counts less than an increase in adult mortality. If, as we suspect, Florida's nesting decline has predominantly involved lower recruitment, the rates of decline that we report here would underestimate the corresponding decline in nesting females.

Another scenario in which nest counts could decline without a simultaneous decline in population numbers would be if some surviving females failed to reproduce, as might occur if mates were not available. Because primary sex ratios of sea turtles are determined by nest incubation temperature (Mrosovsky 1980), it is possible that global climate changes that took place ~50 years ago (one generation prior to the nesting decline) significantly skewed operational sex ratios. However, there are no data suggesting that there are insufficient loggerhead males to fertilize females in the population. Such a decrease in mate availability might affect clutch viability rates far more than it might affect clutch frequency or remigration interval. We are not aware of evidence for any change in the proportion of infertile eggs, or in the degree of multiple paternity in loggerhead clutches.

Although nest counts are likely to be a reliable index of the number of adult females in the population, and are also an index of hatchling recruitment, they do not immediately reflect the number of loggerheads in intermediate, juvenile, life stages. This is an important consideration regarding the forecasting of population trends. No regionally indexed count of immature loggerheads exists, largely because of the difficulty in observing these turtles in the marine environment.

Potential causes of the Florida loggerhead decline

For the reasons just outlined, we believe that the observed decline in the annual counts of loggerhead nests on Index and Statewide beaches in peninsular Florida can best be explained by a decline in the number of adult female loggerheads in the population. Identifying the potential causes of a decline in nesting females is not a straightforward task because individuals from this population may traverse the Atlantic Ocean basin and even enter the Mediterranean Sea in their lifetimes, which may span a half-century or more. Each life stage (egg, hatchling, juvenile, and adult) has its own array of threats (reviewed by Lutcavage et al. 1997, NMFS and USFWS 2007). A further complication in understanding population declines is the late age of sexual maturation of most sea turtles, estimated to be 20–35 yrs in Atlantic loggerheads (Parham and Zug 1997, Bjorndal et al. 2001, Snover 2002). A consequence of this life history characteristic is that the effects from threats acting on the earliest life stages may not manifest themselves at the nesting beach for 30 years or more, making it difficult to link cause and effect and to assess the efficacy of management efforts.

The decline in the number of loggerheads nesting on Florida beaches might be attributed to reduced female hatchling production at Florida nesting beaches (beginning ~30–45 years ago), to increased mortality of immature females (occurring ~10–30 years ago), or to increased mortality of mature females (occurring through the last decade or more). Under the scenarios of reduced hatchling production and increased mortality of immature turtles, nesting females that die would not be replaced because the supply in the “pipeline” would dwindle. This loss might not be apparent until there was a drop in nesting activity, as is the case now.

In comparing effects from mortality during various loggerhead life stages, one should consider stage reproductive values (age-specific expectation of future offspring; Pianka 1994) in addition to death rates. Mortality among older-juvenile and young-adult loggerheads, which have high reproductive values, has a much greater effect on population growth than does mortality in eggs and hatchlings, stages that have relatively low reproductive values (Crouse et al. 1987).

Reduced female hatchling production at nesting beaches.—Given the influence of temperature on loggerhead hatchling sex ratios (Yntema and Mrosovsky 1982), it is possible that low incubation temperatures a generation ago brought about a male-biased primary sex ratio on Florida beaches that has resulted in male-biased operational sex ratios over the past decade. However, there are no empirical data to suggest that changes in hatchling sex ratios have resulted in fewer nesting females today. Given current patterns of global warming, and given sex ratios skewed toward female for hatchlings on Florida beaches (Mrosovsky and Provan-cha 1992, Blair et al. 2006), the Florida population may be in a long-term cycle favoring production of females.



PLATE 1. A female loggerhead sea turtle camouflaging her nest on a Florida beach, USA. Photo credit: B. Witherington.

A thorough examination of climatological records may reveal the extent to which changes in incubation temperature may have affected current female loggerhead abundance.

Conservation programs directed at nesting loggerheads in Florida began in the early 1970s. Although Statewide hatchling production estimates from that era are not available, we believe that hatchling production is likely to have improved steadily during the last 35 years. Managers of several large, high-density nesting beaches (e.g., Cape Canaveral National Seashore, Merritt Island National Wildlife Refuge, Hutchinson Island) have reduced nest predation rates by implementing predator control and nest protection programs and thus have increased hatchling production (FWC, *unpublished data*). Reliable, decades-old estimates of predation by raccoons (*Procyon lotor*, which are known to be a leading cause of nest failure in Florida) come from the Hutchinson Island Index nesting beach (Index beach 16; Fig. 2). These published accounts describe depredation rates of 50–75% in 1967 (Routa 1968), 28% in 1971 (Gallagher et al. 1972), and 44% in 1973 (Worth and Smith 1976). In comparison, recent mammalian predation rates at Hutchinson Island ranged from 1% to 4% between 2001 and 2004 (Brost et al. 2008).

Numerous conservation activities have taken place in recent decades that would be expected to have enhanced sea turtle hatchling production in Florida. Land acquisition efforts have resulted in the establishment of new wildlife refuges, such as the Archie Carr National Wildlife Refuge (comprising Index beaches 12, 13, and 14; Fig. 2), as well as new state and county parks that offer enhanced protection to sea turtles. During the past 35 years, human take of eggs on Florida beaches has

been minimal and has probably been decreasing with enhanced enforcement and education efforts (FWC, *unpublished data*). Community-based conservation efforts on behalf of sea turtles exist statewide and are increasing. Nesting habitats have deteriorated because of coastal development and associated efforts to artificially stabilize beaches, but we are not aware of large-scale changes in the linear extent of suitable nesting beaches during this period. Florida has recently experienced several seasons with high levels of hurricane activity. However, loss of turtle nests to heavy beach erosion and inundation during such events has tended to be localized and relatively small (Brost et al. 2008). For loggerheads, significant storms generally occur late in the summer after hatchlings have left most loggerhead nests (Brost et al. 2008). Storms appear to affect nesting females negligibly, with no obvious mortality and only a brief (1–2 days) effect on nesting activity (FWC, *unpublished data*). If recent hurricanes and other storms have had significant effects on hatchling production, we would not expect to see this reduced recruitment affect numbers of nesting females for 20–35 years. We do not believe that recent storms have contributed significantly to the loggerhead nesting decline.

Mortality of immature and mature life stages.—

1. *Direct take.*—Direct take of loggerhead turtles on Florida beaches or in adjacent waters has been minimal over the past 35 years. Nesting sea turtles and their nests have been protected by Florida statute since 1953, and sea turtles in Florida waters have been protected since 1974. Loggerheads were federally protected in 1978 by the U.S. Endangered Species Act of 1973 and were similarly listed under the Florida Endangered and Threatened Species Act of 1977. Both nesting females

and large subadult loggerheads observed in Florida waters are known to forage along the Atlantic states of the United States and Canada (Ehrhart et al. 2003), and they also travel south to the waters of the Bahamas, Cuba, and Mexico (Meylan et al. 1983, Schroeder et al. 2003). Hunting of loggerheads is legally permissible in the Bahamas and Cuba, but the majority (68%) of countries in the northwestern Atlantic have laws that give complete protection to loggerheads in their waters (NMFS and USFWS 2007). Some direct take is likely to be occurring even in countries with protective legislation. We are not aware of any estimates of total direct take in the northwestern Atlantic basin. However, we predict that this number is likely to have decreased over the past 35 years, with an increasing number of countries adopting protective legislation or joining international conventions for the protection of living marine resources (see review in NMFS and USFWS 2007).

2. *Fisheries bycatch*.—The incidental capture of sea turtles in commercial and artisanal fisheries is considered to be the most significant factor affecting the conservation and recovery of the loggerhead turtle (NMFS and USFWS 2007). It has been implicated in the huge decline of loggerhead nesting populations in the Pacific: 50–90% declines in Japan (Kamezaki et al. 2003) and 86% declines in eastern Australia (Limpus and Limpus 2003). Loggerheads are captured in a variety of gear types in the Atlantic and Mediterranean basins, the most important of which (in terms of mortality) are gillnets, trawls, and longlines.

Shrimp trawling increased dramatically in the southeastern United States between the 1940s and the 1960s. By the late 1970s, there were sufficient data to show that thousands of loggerheads were being killed annually in this region (Henwood and Stuntz 1987). A subsequent analysis that broadened these estimates and corrected for post-catch mortality gave approximations of 5000 to 50 000 loggerheads per year killed in U.S. waters (NRC [National Research Council] 1990). NRC (1990) concluded that shrimp trawling was the most significant anthropogenic source of sea turtle mortality in U.S. waters, in part due to the high reproductive value of turtles taken in the fishery. This level of annual loggerhead mortality is believed to have occurred up to 1992–1994, when U.S. law required all shrimp trawlers in the Atlantic and Gulf of Mexico to use Turtle Excluder Devices (TEDs, which allowed some captured turtles to escape nets before drowning) (NMFS [National Marine Fisheries Service] 2002). Analyses of sea turtle strandings concluded that TEDs reduced sea turtle mortality by ~20–40% (Crowder et al. 1995, Lewison et al. 2003). Although poor regulatory compliance was cited as limiting TED effectiveness in reducing mortality (Lewison et al. 2003), it was also clear that ~40% of stranded loggerheads (large immatures and adults) were too large to fit through TED openings and escape from TED-equipped trawl nets (Epperly and Teas 2002). Larger TED openings were required on

most shrimp trawls in 2004; the current Biological Opinion from NMFS (2002) forecasts ~4000 loggerhead deaths annually in U.S. waters from trawling under these new regulations.

Trawling for species other than shrimp has caused additional mortality to loggerheads with high reproductive value. Murray (2006) estimated that loggerhead mortality in fisheries using bottom otter trawl gear in the U.S. Mid-Atlantic between 1996 and 2004 was ~400–900 turtles per year. Scallop trawls and dredges operating in the same region are believed to kill ~100–200 loggerheads annually (Murray 2007).

Pelagic longline fisheries in the Atlantic Ocean and Mediterranean Sea hooked approximately 210 000 to 280 000 loggerheads in the year 2000, with mortality rates for captured loggerheads estimated to be 17–42% (Lewison et al. 2004). Florida has by far the largest loggerhead nesting aggregation contributing to populations in these basins, and the feeding grounds of juveniles and subadults of this population are known to overlap with longline fishing areas. Thus it is likely that a large percentage of Atlantic longline captures are turtles that were hatched on Florida nesting beaches. On the basis of mtDNA sequence analysis of loggerheads caught in longline fisheries in the Azores and Madeira, Bolten et al. (1998) demonstrated that pelagic juveniles found in eastern Atlantic waters were derived from rookeries in the southeastern United States and the Yucatan Peninsula of Mexico. Similarly, Laurent et al. (1993, 1998) provided genetic evidence that a portion of the loggerheads in the western Mediterranean originated from beaches in the United States, and they suggested that American loggerheads were subject to capture in the Spanish swordfish longline fishery. The average size of loggerheads captured in longlines ranged from 37 to 74 cm curved carapace length in the Atlantic and Mediterranean (Lewison and Crowder 2007, López-Mendilaharsu et al. 2007).

Loggerhead mortality from each of these fisheries is believed to be underestimated because of difficulties with observer coverage and reduced compliance in unobserved fishing vessels (Lewison et al. 2003, Cox et al. 2007). Total fisheries mortality estimates are also limited principally to federally regulated fisheries, which do not include many trawl, trap, gillnet, and hook-and-line fisheries operating within state waters of the United States. Additional loggerhead mortality is likely to occur in U.S. state-regulated fisheries and to go unrecorded due to the presence of few observers.

Although loggerhead mortality is high in trawl and longline fisheries, green turtle mortality from these fisheries is much lower, probably due to the limited exposure of green turtles to these fisheries. Young juvenile green turtles spend a shorter time in oceanic habitats than do juvenile loggerheads, and older juvenile green turtles prefer shallow seagrass pastures where trawling is rare (Witherington et al. 2006a).

3. *Disease*.—Florida's Sea Turtle Stranding and Salvage Network's (STSSN) documentation of more frequent epizootic events in recent years suggests that the incidence of disease in sea turtles may be rising. The Florida network documented an average of 25 emaciated loggerheads per year from 1986 to 1990 (2.4% of total annual loggerhead strandings) and 193 emaciated loggerheads per year from 2002 to 2006 (15% of total annual loggerhead strandings; A. Foley, *personal communication*). In the absence of practical means to screen for disease in all stranded turtles, an emaciated body condition is used as an indicator of potential disease; relatively few dead turtles are professionally necropsied because of limited resources. The actual extent of disease in the population is not well known because health information on live turtles is collected in few studies. Baseline data on turtle health are also scarce, making it difficult to detect and diagnose diseases or to assign causes of death. Brevetoxicosis, a disease caused by exposure to harmful algal blooms (especially "red tide," associated with the dinoflagellate *Karenia brevis*), is suspected to be a mortality factor for loggerheads (Redlow et al. 2003). In several recent years, toxic algal blooms have been chronic in some areas, such as southwestern Florida, that are known to be important foraging areas for loggerheads. Large-scale loggerhead die-offs associated with red-tide exposure have occurred in Florida in almost every year since 1995 (Florida STSSN database; A. Foley, *personal communication*). However, as with loggerhead mortality from other diseases, rates of mortality caused by red tide and other harmful algal blooms have not been measured for the population at large.

4. *Boat-related mortality*.—Loggerheads in Florida face an increasing threat from strikes by boat propellers. The occurrence of propeller wounds in loggerheads recovered by the stranding network in Florida has increased from an annual average of 9.7% ($N = 92$ turtles) between 1986 and 1990 to 20.3% ($N = 305$) between 2002 and 2006 (Florida STSSN database; A. Foley, *personal communication*). Total loggerhead strandings have also increased over the same period. Although approximately one-third of all examined boat-strike injuries have had characteristics definitively indicating that they occurred antemortem, some of the remaining fraction of injuries may have occurred post mortem (A. Foley, *personal communication*). This uncertainty makes it difficult to accurately assign mortality figures to this cause.

5. *Pollution*.—This factor includes entanglement in, or ingestion of, marine debris (including abandoned fishing gear), fouling with petroleum products, exposure to heavy metals and other anthropogenic toxins, and eutrophication. In samples of neonate (weeks-old) loggerheads from Atlantic waters off Florida, percentages of turtles that have ingested plastics or tar range between 20% (from esophageal lavage of 66 extant turtles; Witherington 2002) and 90% (from necropsy of

134 storm-stranded turtles; Witherington and Hiram 2006; B. Witherington and S. Hiram, *unpublished data*). Mortality from this debris ingestion is probably high, but has yet to be quantified. Although we are not able to find trends in mortality from these sources, we reason that multiple effects of pollution have increased during the period of loggerhead nesting decline. Long-term studies are needed to fully describe the role of this threat in the decline of Florida's loggerhead population.

6. *Global warming*.—Although not a direct mortality factor, global warming could be expected to have indirect effects on the Florida loggerhead population by changing sex ratios, reproductive periodicity, marine habitats, or prey resources. It is likely that decades will pass before we understand the consequences of global climate change on loggerhead populations.

7. *Decline of food resources*.—Food resources in the Chesapeake Bay and coastal waters of Virginia, an area known to be important to Florida loggerheads (Musick and Limpus 1997), have changed significantly in recent decades. A substantial reduction in the spawning stock, recruitment, larval abundance, and female size of the blue crab (*Callinectes sapidus*), an important loggerhead prey item, was documented in studies spanning the period 1979–2000 (Lipcius and Stockhausen 2002). Gut content analyses of loggerheads in Virginia waters by Seney and Musick (2007) documented a shift in loggerhead prey items from predominantly horseshoe crabs (*Limulus polyphemus*) during the early to mid-1980s, to predominantly blue crabs during the 1980s, to finfish discarded by fisheries in the mid-1990s and in 2000–2002.

Comparison of threats and concordance with nesting data.—Multiple factors are likely to be involved in the decline in loggerhead nesting in Florida, but the temporal and spatial patterns of the decline suggest that one or more factors are new or are having significantly greater effects on the loggerhead nesting population following a time lag (consequences just now apparent due to reduced recruitment to the nesting beach).

The following temporal and spatial characteristics of the decline in loggerhead nesting may hold clues to the causes of this trend: (1) the decline in nesting in Florida began in approximately 1998; (2) the magnitude of the decline has been large, ~44% in eight years; (3) prior to 1998, the number of loggerhead nests in Florida was increasing significantly in five of six subregions (Table 1, Fig. 6); (4) since 1998, all six subregions have decreased significantly (Table 1, Fig. 6); (5) the decline began at approximately the same time in all subregions (Fig. 6); (6) green turtle and leatherback nesting has increased on the same Florida beaches where loggerhead nesting has declined (1989–2006; data *available online*; see footnote 5).

Table 2 summarizes the concordance of possible mortality factors with these temporal and spatial characteristics of the nesting data. Although better data are needed on all of the mortality factors (particularly

TABLE 2. Concordance of loggerhead threat factors with attributes of the loggerhead nesting decline.

Concordance	Hatchling decline	Direct take	Fisheries bycatch	Disease	Boat-related mortality	Pollution	Global warming	Food resource decline
Consistent with time frame of nesting decline?	no	no	yes	possibly	yes	yes	possibly	yes
Consistent with magnitude of nesting decline?	no	no	yes	possibly	no	possibly	no	possibly
Consistent with temporal pattern of nesting decline?	no	no	yes	possibly	no	possibly	unknown	unknown
Similar effects on nesting between subregions?	no	yes	yes	yes	no	yes	yes	yes
Different expected effects on green turtle and leatherback nesting?	no	no	yes†	no	no	no	no	yes
Score	0	1	5	2.5	1	3	1.5	3.5

Notes: Decreased production of hatchlings may result from predation, hurricane effects, or habitat deterioration. Disease may include harmful algal blooms. Pollutants include oil, plastics, and discarded fishing nets. Score is the sum of categories in which the effect of the factor is concordant with the patterns observed in the nesting data; possible concordance was scored as 0.5.

† Longlines principally affect loggerheads and leatherbacks; trawling principally affects loggerheads.

pollution, disease, and the decline of food resources), it is clear that several factors are inconsistent in many respects with the patterns observed in the nesting data. Decreased hatchling production is the least concordant. One would expect large subregional differences in nesting if factors such as habitat deterioration or increased predation were a principal cause. Instead, the data show all six subregions behaving similarly (declining significantly; Table 1, Fig. 7). Another line of evidence that decreased hatchling production is not the primary reason for the nesting decline is that other species of sea turtles nesting on the same beaches at the same time have experienced an increase in nest numbers over the same time period.

The causal factor that best fits the nesting decline is fisheries bycatch (Table 2). The North Atlantic longline fishery began to expand in the early 1980s with the growing use of monofilament nylon gear and the expansion of the Spanish fishing fleet (FAO 2005). Since this time, longline mortality to oceanic-stage loggerheads has increased to tens of thousands of turtles annually (Lewison and Crowder 2007). Loggerheads from this period that survived their oceanic stage recruited to U.S. coastal waters at a time when mortality from trawling was estimated to be as high as 50,000 loggerhead deaths per year (NRC 1990). Shrimp-trawling mortality of maturing and adult loggerheads was extensive for decades up to 2004. Following additional federal TED regulations enacted in 2004, loggerhead mortality has continued at levels (thousands per year) that may have impeded population recovery. The estimated magnitude, timing, and ongoing nature of these fisheries threats are consistent with the steep decline in nesting following 1998. We believe that the only other factors that approach this level of concordance with the loggerhead decline are disease and the decline of food resources. Regarding both of these factors, our knowledge is too incomplete to rule out their importance.

The differential susceptibility of loggerheads and green turtles to coastal trawl and oceanic longline fisheries may explain the dramatic differences in Florida nesting trends for these species. However, an increasing nesting trend in Florida by leatherbacks appears to be inconsistent with strong effects from oceanic longline fisheries because these turtles are oceanic for most of their lives (data *available online*; see footnote 5). One would expect that leatherback nesting would also be in decline in Florida because this species is also subject to incidental capture in fisheries. One possible explanation is that loggerheads and leatherbacks are differentially affected by various fisheries (trawls, gillnets, longlines). In the case of the longline fishery, far fewer (only a quarter) leatherbacks are captured than loggerheads (although the capture rates proportional to population sizes are unknown), and there is lower mortality (8–27% of leatherbacks vs. 17–42% of loggerheads) (Lewison and Crowder 2007). In the case of trawl fisheries, loggerhead mortality was estimated to be eight times that of green turtles and 50 times that of leatherbacks (NMFS 2002), probably because of the diet differences (and thus habitat use) between the three species (NRC 1990).

One further pattern in the nesting data is worthy of mention. The rate of decline in the subregions (Fig. 6) was less variable after 1998 than the rate of increase prior to that time (Table 1). One interpretation is that multiple factors were operating during the nesting-increase period, including some with subregional effects, and that these accounted for the observed variability. After 1998, these factors continued to affect the population, but a new factor emerged that affected all subregions and was of sufficient magnitude that it dampened the variability of existing effects. The only factors in Table 2 that we think could be considered new (within 35 years) are fisheries bycatch (principally commercial longlines), pollution (plastics), boat-related mortality, and the decline of food resources.

Predictions for the 2007 loggerhead nesting season.— We predicted a loggerhead nest count for Florida Index beaches using the trend line estimated by a three-knot restricted cubic spline curve to the annual survey-region nest-count totals via negative binomial regression (SR model; Fig. 4). This prediction was 27 432 nests in 2007, which was close to the actual nest-count total of 28 880 nests. This nest count for 2007 represents the lowest loggerhead nest count in 19 years. Although we did not have a spatially detailed data set available for our zone-level (ZL) models at the time of manuscript submission, we were able to use the survey-region (SR) RCS model (previously described) to estimate percentage change in predicted mean annual nest counts between selected years, along with 95% confidence intervals ($R^2 = 0.85$). Estimates comprising all Florida Index zones used in this study indicated that Florida loggerhead nesting declined by 37% (25–47% CI) between 1989 and 2007 and declined by 49% (39–57% CI) between 1998 and 2007.

Management recommendations

We believe that the decline in loggerhead nesting on Florida beaches warrants heightened attention from resource managers. An extrapolation of declining loggerhead nest counts reveals that numbers of nests in 2017 will have declined 80% from the number counted in 1998 if conditions do not change. This 19-year period would be less than half of the loggerhead's ~45-year generation time. An 80% decline over an even more prolonged period (three generations) is sufficient to warrant the IUCN status of Critically Endangered (IUCN 2001). Our extrapolation of nesting data does not result in an unreasonable forecast, given loggerhead nesting declines of 50–90% observed in the Pacific (Kamezaki et al. 2003, Limpus and Limpus 2003). We feel that these nesting declines reveal adult population declines, which are particularly alarming considering that loggerheads have been listed for three decades under the U.S. Endangered Species Act. These circumstances suggest that loggerheads would benefit from broader protection and more comprehensive management across state, federal, and international waters that has been achieved in recent decades. We recommend that such broadening include elevated monitoring and regulation of the wide variety of coastal and oceanic fisheries that intersect with loggerhead distribution. These actions will need to include international collaborative fisheries management efforts throughout the Atlantic range of the loggerhead sea turtle.

Research should continue to further our understanding of the effects of fisheries capture (including mortality from repeated trawl captures and longline hooking), disease, harmful algal blooms, toxins, entanglement, debris ingestion, decline in food resources, and global climate change on loggerhead populations. Even threats without immediate tenable solutions need to be sufficiently understood so that managers might predict the

level of success needed in solving other conservation problems.

Although we find no evidence that nesting-beach conditions are principally responsible for the loggerhead nesting decline, nesting beaches in Florida remain the most accessible places where conservation activity and habitat protection efforts can benefit loggerheads. We point to the consistent portrait of loggerhead spatial nesting patterns as a guide for directing protection, such as refuge-land acquisition, to the most critical nesting areas.

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APPENDIX

A table showing attributes of Index beaches used in the analysis of trends in Florida loggerhead nesting (*Ecological Archives* A019-003-A1).