

## Development of a Kemp's Ridley Sea Turtle Stock Assessment Model

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We developed a Kemp's ridley (*Lepidochelys kempii*) stock assessment model to evaluate the relative contributions of conservation efforts and other factors toward this critically endangered species' recovery. The Kemp's ridley demographic model developed by the Turtle Expert Working Group (TEWG) in 1998 and 2000 and updated for the binational recovery plan in 2011 was modified for use as our base model. The TEWG model uses indices of the annual reproductive population (number of nests) and hatchling recruitment to predict future annual numbers of nests on the basis of a series of assumptions regarding age and maturity, remigration interval, sex ratios, nests per female, juvenile mortality, and a putative "turtle excluder device effect" multiplier starting in 1990. This multiplier was necessary to fit the number of nests observed in 1990 and later. We added the effects of shrimping effort directly, modified by habitat weightings, as a proxy for all sources of anthropogenic mortality. Additional data included in our model were incremental growth of Kemp's ridleys marked and recaptured in the Gulf of Mexico, and the length frequency of stranded Kemp's ridleys. We also added a 2010 mortality factor that was necessary to fit the number of nests for 2010 and later (2011 and 2012). Last, we used an empirical basis for estimating natural mortality, on the basis of a Lorenzen mortality curve and growth estimates. Although our model generated reasonable estimates of annual total turtle deaths attributable to shrimp trawling, as well as additional deaths due to undetermined anthropogenic causes in 2010, we were unable to provide a clear explanation for the observed increase in the number of stranded Kemp's ridleys in recent years, and subsequent disruption of the species' exponential growth since the 2009 nesting season. Our consensus is that expanded data collection at the nesting beaches is needed and of high priority, and that 2015 be targeted for the next stock assessment to evaluate the 2010 event using more recent nesting and in-water data.

### INTRODUCTION

The Kemp's ridley (*Lepidochelys kempii*) is a critically endangered sea turtle that breeds only in the Gulf of Mexico and spends the majority of its life cycle there. The species declined in the 1960s and 1970s, and by the mid-1980s only a few hundred female Kemp's ridleys came ashore to lay eggs at their primary nesting beach at Rancho Nuevo, Tamaulipas, Mexico (Heppell et al., 2005). As the species began to expand nesting outside of Rancho Nuevo, the surveys expanded too, beginning with the addition of two more survey areas in 1988. Reducing anthropogenic mortality of all life

stages has been the primary objective of Kemp's ridley conservation efforts since 1966 (USFWS and NMFS, 1992; TEWG, 1998; Caillouet, 2010; Crowder and Heppell, 2011; NMFS et al., 2011). Historically, the three greatest anthropogenic sources of mortality were commercial exploitation of eggs in Mexico, incidental capture of neritic life stages (i.e., >age 2) in shrimp trawl fisheries in the Gulf of Mexico and along the U.S. Atlantic Coast (Magnuson et al., 1990; Caillouet, 2006, 2010), and direct take of adults from nesting beaches and adjacent waters in Mexico. Although these sources of mortality have not been completely eliminated, the mortality rates associated with these sources have been

substantially reduced over the years (TEWG, 1998; Caillouet, 2006, 2010, 2011; NMFS et al., 2011). As a result, the number of nesting Kemp's ridleys, extrapolated from the number of nests, increased exponentially from only a few hundred nesting females in 1985 to nearly 10,000 in 2009 (NMFS et al., 2011).

In 2010 and 2011, an elevated number of strandings of Kemp's ridleys in the Gulf of Mexico was observed in Louisiana, Mississippi, Alabama, and northwestern Florida. The Deepwater Horizon (DH) rig explosion and BP-Macondo well blowout on 20 April 2010, ensuing oil spill, remedial responses (e.g., dispersant use, skimming and burning oil, etc.), and the incidental capture of sea turtles in shrimp trawl fisheries in both years were identified as the most likely causes of the increase in turtle strandings by federal and state agencies, conservation organizations, and the media (Caillouet, 2010, 2011; Crowder and Heppell, 2011).

Concurrent with the elevated strandings of Kemp's ridleys, the exponential growth of the adult female population was interrupted in 2010 (Caillouet, 2014), as evidenced by a reduction in the annual number of nests at three adjoining beaches on the coast of Tamaulipas, Mexico used to index nesting trends: Rancho Nuevo, Barra Ostionales-Tepehuajes (North Camp), and Playa Dos-Barra Del Tordo (South Camp) (TEWG, 1998, 2000; Heppell et al., 2005, 2007; NMFS et al., 2011). Demographic model predictions had forecast population growth at an estimated rate of 19% per year during 2010–2020, assuming survival rates within each life stage remained constant and egg-to-hatchling survival rate remained high (NMFS et al., 2011). Instead, as shown by Figure 1, the population's pre-2010 exponential growth was interrupted (Caillouet, 2010, 2011, 2014; Crowder and Heppell, 2011).

The purpose of our study was to develop a Kemp's ridley stock assessment model (KRSAM). Because incidental capture of sea turtles in shrimp trawls was identified in 1990 as the greatest threat to sea turtles at sea (Magnuson et al., 1990), the KRSAM included an objective and quantitative examination and evaluation of Kemp's ridley–shrimp fishery interactions in the northern Gulf of Mexico. Specific objectives were 1) to examine Kemp's ridley status, trends, and spatial distribution within the Gulf of Mexico; 2) to examine status, trends, and spatial distribution of shrimping effort in the northern Gulf of Mexico; 3) to determine relative contributions of declining shrimping effort and turtle excluder

device (TED) regulations toward the exponential increase in the Kemp's ridley population, and 4) to provide baseline outputs from a KRSAM that can be used by future assessments for estimating putative effects of the DH oil spill.

#### MATERIALS AND METHODS

The Turtle Expert Working Group (TEWG) had previously developed a demographic model for the Kemp's ridley population (TEWG, 1998, 2000; Heppell et al. 2005). The model was updated for the revised binational Kemp's ridley recovery plan (NMFS et al., 2011). The updated model used indices of the annual reproductive population (nests, including in situ nests) and hatchling recruitment to predict time-lagged annual numbers of nests on the basis of the assumptions that age at maturity = 12 yr, remigration interval = 2 yr, nests per female = 2.5, female sex ratio = 0.76 for protected nests and 0.64 for in situ nests, and juvenile mortality (ages 2–5 yr) = 0.5, and that large juveniles and adults have the same anthropogenic fishing mortality rate. This predictive model estimated oceanic-stage mortality for ages 0 and 1, late juvenile and adult mortality, and a “TED effect” multiplier beginning in 1990. It assumed density-independent mortality and estimated the number of nests starting from the number of hatchlings 12 yr earlier. The objective function to minimize was the sum of squares of the differences between predicted and observed nests. The TEWG model was based on a “ridley year,” 1 July through 30 June of the following year. The model had major strengths but its limitations included 1) not all available information was used (namely, shrimp trawl effort); 2) the putative TED effect was applied to total mortality, not just anthropogenic mortality; and 3) parameter inference is not possible with least-squares model fitting.

We converted the updated TEWG model to AD Model Builder, and used the same types of input data (hatchlings and nests) and assumptions of the model used by the recovery team (see NMFS et al., 2011), but added additional assumptions and input data. The KRSAM was based on a calendar year, and the ages advance on 1 January. As a result, age 0 persists for only 6 mo. Our estimates of total anthropogenic mortality were assumed all to be attributable to shrimp fishing effort. This results in an overestimate of mortality related to shrimping. However, shrimp fishing mortality has long been

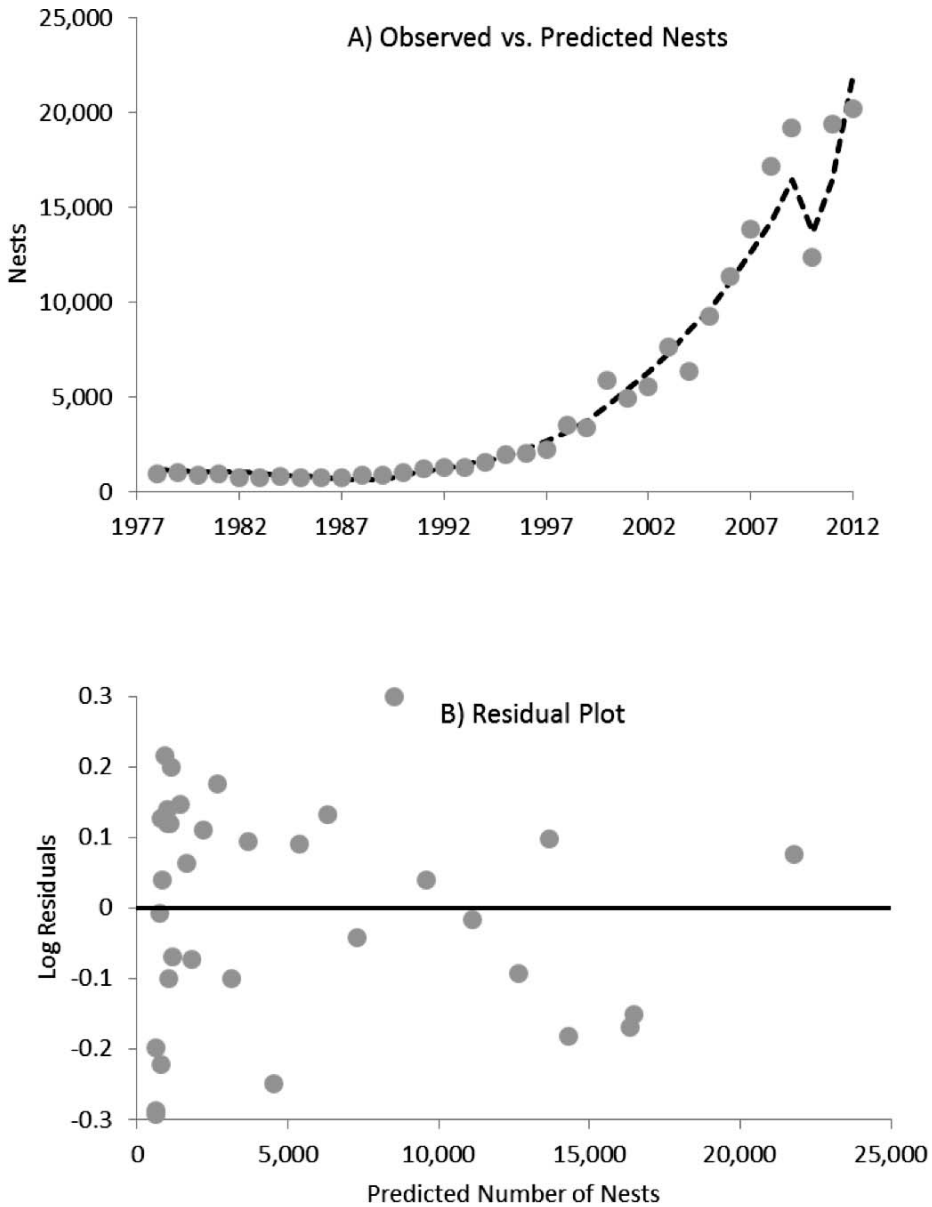


Fig. 1. Observed vs model-predicted nests for 1978–2012 (panel A) and log residuals (observed–predicted) vs predicted nests, 1978–2012 (panel B).

assumed to be the major source of anthropogenic mortality at sea (Magnuson et al., 1990). The new model incorporates a shrimp effort time series generated from spatially explicit effort data weighted by adult female habitat utilization. Habitat weighting for each spatial cell in the model was based upon its relative value to Kemp’s ridley, with the focus placed on adult female utilization. The rationale for this focus is that adult females have the highest reproductive

value to the population. Estimates of natural mortality were also a requirement for the new model. Parameter inference is possible with this model, which bases the objective function of the negative log-likelihood of data, plus priors. Additionally, the TED effect is applied to shrimping-related mortality only, not total mortality.

We describe the data available for analysis, expand on requisite growth theory, and develop

a model to predict the data on the basis of fundamental parameters. The statistical likelihoods of observing the data given the predictions are specified and computed. We estimate the fundamental parameters and provide fits to the data and subsequent estimates of key variables (e.g., mortality and population size).

The notation used to describe the model and related objective functions are introduced below and are listed in Table 1. The variables in Table 1 are organized by indices, data, and associated descriptors (any combinations of same), fundamental parameters to be estimated, logged probability density functions, and interim variables (some combination of data and fundamental parameters) that were of interest.

*Available data.*—Annual number of nests: The number of observed nests at the three index beaches combined represented the best available indicator of population trends from 1966 through 2012. Data for 1966–2009 were based on NMFS et al. (2011). The updated nesting and hatchling production data for the index beaches for 2010, 2011, and 2012 were contributed by coauthors who conduct the binational Kemp's ridley beach protection studies. In 2012, 92.6% of all documented Kemp's ridley nests were located at these three beaches. Although additional nesting occurred elsewhere in Mexico and Texas, our estimate reflects a majority, but not all, of the population.

Annual number of hatchlings: The estimated number of hatchlings produced from the three index beaches were available for 1966 through 2012. From 1966 through 2003, most of the hatchlings produced came from nests protected in corrals, and a smaller proportion of the hatchlings came from nests incubated in Styrofoam boxes (nests incubated in corrals and Styrofoam boxes are hereafter referred to as protected nests). Starting in 2004, some hatchlings were also produced from nests left in situ.

Mark–recapture growth increment: The increments in growth from marked–recaptured wild Kemp's ridley turtles in the Gulf of Mexico from 1980 through 2012 were obtained from the Cooperative Marine Turtle Tagging Program (CMTTP). The following mark–recapture data were not used (censored) in our analysis: 1) captive-reared, head-started, or rehabilitated turtles; 2) turtles that transited into or out of the Gulf of Mexico (Mexican and U.S. waters); 3)

turtles with incomplete or missing date marked or recaptured; 4) turtles with missing carapace length measurements (curved or straight) when marked or recaptured; and 5) turtles at large for  $\leq 30$  d. Most turtles had a curved carapace length measurement (CCL) and a straight carapace length (SCL) measurement recorded at release and recapture (204 of 223 records) that enabled the construction of a CCL-to-SCL conversion for the remaining 19 records:

$$\text{SCL} = b_1 + b_2 \cdot \text{CCL} \quad (1)$$

Simple least-squares regression was used to estimate  $b_1$  and  $b_2$  parameters. Equation 1 was used to convert CCL measurements to SCL when a SCL measurement was not provided.

Strandings length frequency: For the years 1980 through 2011, standard SCL measurements of 5,953 stranded Kemp's ridley turtles in the Gulf of Mexico were obtained from the Sea Turtle Strandings and Salvage Network (STSSN). The SCL measurements were summed into 5-cm SCL bins.

Penaeid shrimp trawling effort: Penaeid shrimp effort data (nominal net days fished) in U.S. waters in the Gulf of Mexico were available for the period 1966 through 2012. The U.S. effort was stratified into four areas (statistical reporting areas 1–9, 10–12, 13–17, and 18–21) and four depth zones (inshore, 0–10 fm, 10–30 fm, and >30 fm) (Nance et al. 2008). Shrimp trawling effort by the U.S. fleet fishing in Mexican waters in units of nominal boat days was available for 1966 through 1980 in two spatial areas (James M. Nance, NMFS, pers. comm). We converted the data to nominal net days fished using the mean number of nets per boat per year as used in U.S. waters. Each of Mexican spatial areas was prorated into three depth zones using the adjacent U.S. area (statistical reporting units 18–21) and offshore zones (0–10 fm, 10–30 fm, >30 fm). The 22 area-by-depth strata were assigned a habitat score, on the basis of expert opinion, to reflect susceptibility of Kemp's ridley to shrimping. Each of the effort strata were then weighted by the habitat score and a total directed shrimp effort for the year was calculated. The subsequent effort values were then scaled (mean = 1.0) over the available years.

*Growth theory.*—An important component of the assessment model is the von Bertalanffy growth increment model (i.e., model is an estimate of the

TABLE 1. Notation used in Kemp's ridley stock assessment model organized by indices, data, and assumed known variables, fundamental parameters to be estimated, interim variables, and negative log-likelihoods.

Parameter	Definition
<b>Indices</b>	
$a$	Age in years ( $a = 1, 2, \dots, A$ )
$h$	Subset of ages for catchability coefficient
$i$	Individual observation
$j$	SCL (straight carapace length) frequency Interval ( $j = 1, 2, \dots, J$ )
$y$	Year ( $y = 1, 2, \dots, 47$ ), representing 1966, 1967, ...2012
<b>Data or assumed known variables</b>	
$\Delta \tilde{l}_i$	Years at large for the $i$ th capture–recapture record
$E_y$	Habitat weighted, shrimp trawling effort (net days fished) in year $y$ , scaled by division by its mean over years 1966–2012
$\tilde{f}_{yj}$	Observed proportion of strandings in year $y$ and SCL interval $j$
$G_a$	Proportion of mature females of age $a$
$\tilde{H}_{Cy}$	Number of corral-plus-box hatchlings (both sexes) entering the water in year $y$
$\tilde{H}_{Iy}$	Number of in situ hatchlings (both sexes) entering the water in year $y$
$\tilde{l}_{0,i}$	Observed SCL for the $i$ th individual turtle (either sex) at capture
$\tilde{l}_{r,i}$	Observed SCL for the $i$ th individual turtle (either sex) at recapture
$n_{py}$	Number of SCL measurements of stranded turtles (both sexes) in year $y$
$n_M$	Number of nests per adult female in the population (quotient of annual number of nests per adult female divided by the remigration interval)
$\tilde{P}_y$	Observed conventional index (nests) in year $y$
$r_C$	Proportion of corral-plus-box hatchlings that are female
$r_I$	Proportion of in situ hatchlings that are female
$\sigma_m$	Standard deviation of SCL measurement error $\varepsilon_i$
$v_j$	Midpoint of the $j$ th SCL frequency interval
$w$	Bin width of each SCL frequency interval
<b>Fundamental parameters to be estimated</b>	
$a_c$	Age that partitions catchability coefficient into two subsets ( $1 < a < a_c$ and $a \geq a_c$ )
$a_{50}$	Age at selectivity 0.5 on the ascending limb of the logistic age selectivity function for strandings
$a_{sl}$	Slope of the ascending limb of the logistic age selectivity function for strandings
$b_{50}$	Age at selectivity 0.5 on the descending limb of the logistic age selectivity function for strandings
$b_{sl}$	Slope of the descending limb of the logistic age selectivity function for strandings
$b_1, b_2$	Parameters for the regression of SCL on curved carapace length (CCL), on the basis of capture–recapture records
$K$	von Bertalanffy growth coefficient
$M_\infty$	Instantaneous rate of natural mortality of the accumulation age $A+$
$F_{2010}$	Added 2010-specific instantaneous rate of additional losses affecting turtles ages $a_{2010}$ and older
$\mu_1$	Mean SCL age $t_1$
$\mu_2$	Mean SCL at age $t_2$
$q_h$	Catchability coefficient, where $h = 1$ if $1 < a < a_c$ and $h = 2$ if $a \geq a_c$
$\sigma_L$	Standard deviation of $L_\infty$
$X_{TED}$	Shrimp trawling mortality-reducing multiplier [i.e., turtle excluder device (TED) effect], starting in year $y_{TED}$
$Z_P$	Instantaneous rate of total mortality for ages 0 and 1 turtles (oceanic stage)
<b>Interim and other variables</b>	
$a_0$	Age when SCL = 0 (original von Bertalanffy parameter that was reassigned)
$C_{ya}$	Deaths in year $y$ and at age $a$ , assigned to shrimp trawling by the U.S. fleet
$CV$	Coefficient of variation for growth in SCL
$\Delta l_i$	Expected increment in SCL for the $i$ th turtle
$D_{ya}$	Total deaths at age $a$ in year $y$
$\varepsilon_i$	Deviation of observed SCL from expected SCL for the $i$ th turtle

TABLE 1. Continued.

Parameter	Definition
$F_{ya}$	Instantaneous rate of shrimp trawling mortality in year $y$ and at age $a$
$f_{yj}$	Expected probability of strandings (both sexes) in year $y$ and SCL interval $j$
$l_a$	Expected SCL at age $a$
$l_i$	Expected SCL for the $i$ th individual turtle (theoretical growth development)
$\tilde{l}_i$	Observed SCL for the $i$ th individual turtle (theoretical growth development)
$L_\infty$	Expected mean maximum (asymptotic) SCL at infinity (original von Bertalanffy parameter that was reassigned)
$M_a$	Instantaneous rate of natural mortality at age $a$
$N_{ya}$	Predicted number of female turtles in year $y$ of age $a$
$P_y$	Predicted number of nests in year $y$
$p_{ya}$	Expected proportion of strandings by year $y$ and age $a$
$S^2$	SCL sample variance (theoretical growth development)
$s_a$	Selectivity of strandings (both sexes) at age $a$
$\sigma_a$	Standard deviation of SCL at age $a$
$Z_{ya}$	Instantaneous rate of total mortality in year $y$ of age $a$
Negative log-likelihoods	
$L$	Synthesis model objective function
$L_{\text{prior}}$	Prior information for fundamental parameters
$L_p$	Observed nests
$L_{At}$	SCL growth for a captured–recaptured turtle (both sexes)
$L_f$	SCL frequency of strandings (both sexes)

relationship between SCL and age). Although it is feasible to estimate von Bertalanffy growth using only SCL frequency data, additional growth information is obtainable by incorporating capture–recapture data. As pointed out by Francis (1988) and others, estimates of von Bertalanffy growth-curve parameters based only on capture–recapture data are not consistent with those based on length at age because their error structures differ. Everson et al. (2004) addressed the issue by assuming that the ages of marked animals were a random variable from a parametric distribution that was integrated from the model (i.e., a random effect). We avoid this complex and computationally intensive procedure by deriving von Bertalanffy growth equations with the same parameters and simple error structure.

The traditional three-parameter von Bertalanffy growth equation for length-at-age data (Ricker, 1975), applied to Kemp's ridley growth, is

$$l_a = L_\infty \{1 - \exp[-K(a_i - a_0)]\}, \quad (2)$$

where  $l_a$  is the expected SCL for a turtle of age  $a$ ,  $L_\infty$  is the theoretical maximum (asymptotic) SCL,  $K$  is the von Bertalanffy growth coefficient,  $a_0$  is the theoretical age at SCL of 0, and  $a_i$  is the true age of the  $i$ th turtle. The residual error ( $\varepsilon_i$ ) for the  $i$ th turtle is assumed to be normally distributed; i.e.,

$$\varepsilon_i = \tilde{l}_i - l_a \quad \text{where } \varepsilon_i \sim N(0, \sigma_a^2), \quad (3)$$

$\tilde{l}_i$  is the observed length and  $\sigma_a$  is the standard deviation for a turtle of age  $a$ . Many studies assume that parameters  $L_\infty$ ,  $K$ , and  $a_0$  are common to all individuals in the population and are estimated by minimizing the negative log-likelihood, with the sample variance ( $S^2$ ) of the residuals used to estimate all  $\sigma_a^2$  by a homogeneous error, i.e.,

$$\sigma^2 = S^2 = \sum_{i=1}^n \frac{(\varepsilon_i - \bar{\varepsilon})^2}{n-1} \quad (4)$$

where  $n$  is the number of observations. The coefficient of variation of (CV) is sometimes introduced as an additional parameter to be estimated, assuming it is the same for all individuals (e.g., Cope and Punt, 2007); i.e.,

$$\sigma_a = \text{CV} \cdot l_a. \quad (5)$$

Equation 5 implies that the residual variance of SCL increases with size and age of turtles.

Individual variation of growth parameters has been introduced for application to capture–recapture data to address inconsistent estimators and large biases (e.g., Sainsbury, 1980; James, 1991; Wang and Thomas, 1995; Pilling et al., 2002). We follow their portrayal by assuming that there are two sources of variation among turtles: 1) measurement of SCL, and 2) variation in maximum SCL. If distributions of SCL measurement error and maximum SCL are normal, then

the residual ( $\varepsilon_i$ ) is also normally distributed (Eq. 3 holds) and

$$\text{Var}(\varepsilon_i) = \sigma_a^2 = \sigma_m^2 + \sigma_L^2 \{1 - \exp[-K(a_i - a_0)]\}^2, \quad (6)$$

where  $\sigma_m$  is the standard deviation of measurement error, and  $\sigma_L$  is the standard deviation of maximum SCL for individual turtles. The estimate of  $L_\infty$  using Equation 6 is then the mean maximum (asymptotic) SCL for the sample. Note that if SCL measurement error is small relative to the total residual error (in practice often true), then Equations 5 and 6 are equivalent (to prove set  $\sigma_m = 0$  and note that the standard deviation for the residual is then proportional to  $l_a$  in Eqs. 5 and 6).

The traditional two-parameter ( $L_\infty$ ,  $K$ ) von Bertalanffy growth function (Fabens, 1965), as applied to Kemp's ridley capture-recapture data, is expressed as

$$\Delta l_i = [L_\infty - \tilde{l}_{0i}][1 - \exp(-K \cdot \Delta \tilde{t}_i)], \quad (7)$$

where  $\Delta l_i$  is the expected increment in SCL over the period  $\Delta \tilde{t}_i$ , and  $\tilde{l}_{0i}$  is the measured SCL when the  $i$ th turtle was captured and marked. Using the same SCL-at-age error structure (Eqs. 3 and 6), the counterparts for capture-recapture data become

$$v_i = \tilde{l}_{1i} - \tilde{l}_{0i} - \Delta l_i \quad \text{where } v \sim N(0, \zeta_i^2), \quad (8)$$

and

$$\text{Var}(v) = \zeta_i^2 = \sigma_m^2 [1 + \exp(-2K \cdot \Delta \tilde{t}_i)] + \sigma_L^2 [1 - \exp(-K \cdot \Delta \tilde{t}_i)]^2, \quad (9)$$

where  $v_i$  is the residual error,  $\tilde{l}_{1i}$  is length at recapture, and  $\zeta_i$  is the associated standard deviation. Note that the variance is a function of the observed time at large for the  $i$ th turtle. Equation 9 is equivalent to that provided by James (1991).

Although the error structures are now consistent between the three-parameter and two-parameter von Bertalanffy growth Equations 2 and 7, respectively, the theoretical  $a_0$  parameter (serves to locate the growth curve on the time axis) is not shared by the equations. Reparameterization of the equations can also improve the computational and statistical properties of their parameter estimates (Schnute and Fournier, 1980; Ratkowsky, 1986; Pilling et al., 2002). Following their advice,  $L_\infty$  and  $a_0$  were replaced by less extreme extrapolations of  $\mu_1$  (the expected mean SCL at age  $t_1$ ) and  $\mu_2$  (the expected mean SCL at age  $t_2$ ). After algebraic

manipulations, the corresponding equations for expected SCL ( $l_a$ ) and expected increment in SCL ( $\Delta l_i$ ) are

$$l_a = \mu_1 + (\mu_1 - \mu_2) \frac{1 - \exp[-K(a - t_1)]}{1 - \exp[-K(t_2 - t_1)]}, \quad (10)$$

and

$$\Delta l_i = \left\{ \frac{\mu_2 - \mu_1 \exp[-K(t_2 - t_1)]}{1 - \exp[-K(t_2 - t_1)]} \right\} \times \{1 - \exp(-K \Delta \tilde{t}_i)\}. \quad (11)$$

Note that Equation 11 has three parameters ( $\mu_1$ ,  $\mu_2$ ,  $K$ ), but only  $\mu_2$  and  $K$  can be estimated with capture-recapture data. Parameter  $\mu_1$  (mean SCL at age  $t_1$ ) must be set or given an informative prior, and then  $\mu_2$  can be estimated (i.e.,  $\mu_2$  is conditional on  $\mu_1$ ) and interpreted as the mean SCL  $t_2 - t_1$  years later. The variance estimate for the residual based on SCL-at-age data (Eq. 6) also requires revising (it contains  $a_0$ ) to

$$\begin{aligned} \text{Var}(\varepsilon_i) &= \sigma_i^2 \\ &= \sigma_m^2 + \sigma_L^2 \left\{ 1 - \exp[-K(a_i - t_1)] \right. \\ &\quad \left. \times \frac{\mu_2 - \mu_1}{\mu_2 - \exp[-K(t_2 - t_1)]\mu_1} \right\}^2, \end{aligned} \quad (12)$$

whereas the variance estimate for the residual based on capture-recapture data (Eq. 9) requires no revision. Equation 10 is as given by Schnute and Fournier (1980), whereas Equations 11 and 12 are novel.

*Model definition.*—The following major assumptions dictated the KRSAM structure to predict the expected number of nests as a function of the number of hatchlings, expected increment in growth of a recaptured marked turtle, and the expected probability of a turtle belonging to a SCL interval based on the fundamental parameters to be estimated:

1. The population dynamics of only female Kemp's ridley turtles are modeled.
2. The population consists of  $A + 1$  age classes starting at age 0 (the first year in the water) where the oldest age-class  $A$  represents ages  $A$  and older turtles, which are subject to the same mortality.  $A$  was set to 14 yr.
3. All mortality is density independent.
4. Natural mortality from age 2 forward was assumed age dependent (Lorenzen, 2000).

5. Anthropogenic mortality is proportional to shrimping effort.
6. The trend in growth (age 0+) tracks a von Bertalanffy curve.
7. The age composition of females is similar to males when fitting the stranding data.
8. SCLs of individual turtles belonging to an age class are normally distributed around their mean.
9. Observed strandings are subject to selectivity by age.
10. Other than selectivity by age for strandings, the mark–recapture and strandings data are from the same population.

Other restrictions were placed on the assessment model through the specification of parameter values.

Mortality: Starting with age 2, following Lorenzen (2000), an age-dependent natural mortality function,  $M_a$ , is based on von Bertalanffy growth such that mortality decreases with age until asymptotic instantaneous rate of natural mortality ( $M_\infty$ ) is reached at age  $A$  and older; i.e.,

$$M_a = \begin{cases} \frac{M_\infty}{K} \ln \left\{ \frac{\exp(K \cdot a) - 1}{\exp[K(a-1)] - 1} \right\} & \text{for } 1 < a < A, \\ M_\infty & \text{for } a \geq A \end{cases} \quad (13)$$

The instantaneous rate of anthropogenic (shrimp trawling) mortality ( $F_{ya}$ ) in year  $y$  and at age  $a$  was assumed proportional to shrimp trawling effort ( $E_y$ ), i.e.,

$$F_{ya} = q_{h(a)} E_y, \quad (14)$$

where  $q_{h(a)}$  is the catchability coefficient for a subset of  $h$  ages. Catchability was partitioned into two subsets ( $q_1$  and  $q_2$ ) with  $a_c$  marking the partition, i.e.,

$$h(a) = \begin{cases} 1, & 1 < a < a_c \\ 2, & a \geq a_c \end{cases} \quad (15)$$

TEDs came into widespread use beginning in 1990 (i.e., post-1989), and reduced Kemp’s ridley mortality associated with incidental capture in shrimp trawls. We applied a TED effect multiplier ( $X_{TED}$ ) to the instantaneous rate of shrimp trawling mortality starting in year  $y_{TED}$ . We also found that additional anthropogenic mortality in 2010 was required to explain reduced nesting in 2010 through 2012. Therefore, we applied an additive instantaneous anthropogenic mortality

rate,  $F_{2010}$ , in 2010 ( $y=45$ ) that included all ages  $\geq a_{2010}$ .

In summary, the instantaneous rate of total mortality ( $Z_{ya}$ ) in year  $y$  and at age  $a$  can be portrayed as

$$Z_{ya} = \begin{cases} Z_P, & a \leq 1 \\ M_a + F_{ay}, & a > 1 \text{ and } y < y_{TED} \\ M_a + F_{ay} X_{TED}, & a > 1 \text{ and } y \neq 45, y \geq y_{TED} \\ M_a + F_{ay} X_{TED} + F_{2010}, & a \geq a_{2010} \text{ and } y = 45 \end{cases} \quad (16)$$

with six fundamental mortality-associated parameters ( $M_\infty$ ,  $Z_P$ ,  $q_1$ ,  $q_2$ ,  $X_{TED}$ , and  $F_{2010}$ ) that require estimation.

Initial population: The synthesis model must be initialized by the number of recruits that enter the female population each year, and by the population size over all ages in the first year ( $y=1$ , representing 1966). The number of age-0 female turtles recruited each year was calculated as the number of female hatchlings that survived their first year in the water; i.e.,

$$N_{y0} = (\tilde{H}_{Cy} \cdot r_C + \tilde{H}_{ly} \cdot r_l) \exp(-Z_{y0}), \quad (17)$$

where  $\tilde{H}_{Cy}$  and  $\tilde{H}_{ly}$  are the annual numbers of protected nests and in situ hatchlings entering the water each year, and  $r_C$  and  $r_l$  are annual proportions of hatchlings that are females, respectively. Note that  $r_C$  and  $r_l$  were assumed to be known parameters (not estimated by the model). For the first year ( $y=1$ ), we assumed that there were no turtles alive older than age 0, except in the accumulated age  $A$ , where the number of adult females was based on the conventional index,  $\tilde{P}_1$ , divided by mean number of nests per adult female in the population [ $n_M$ ; set at 1.25, the quotient of mean number of nests per adult female (2.5) in the population and the remigration interval (2 yr), as adapted from NMFS et al., 2011]; i.e.,

$$N_{1a} = \begin{cases} 0, & \text{for } 0 < a < A \\ \frac{\tilde{P}_1}{n_M}, & \text{for } a = A \end{cases} \quad (18)$$

Update of population: By convention,  $N_{ya}$  refers to the number of age- $a$  female turtles that survive to the end of year  $y$ . With annual recruitment (Eq. 17) and initial year ( $y=1$ ) defined, the populations in the remaining years and ages were updated for mortality:



$$N_{ya} = \begin{cases} N_{y-1,a-1} \cdot \exp(-Z_{ya}) & \text{for } 0 < a < A \\ (N_{y-1,A-1} + N_{y-1,A}) \cdot \exp(-Z_{yA}) & \text{for } a = A \end{cases} \quad \text{and} \quad (19)$$

The annual numbers of total deaths ( $D_{ya}$ ) and shrimping-related deaths ( $C_{ya}$ ) of neritic-stage females were predicted using the Baranov catch equations

$$D_{ya} = \begin{cases} N_{y-1,a-1} [1 - \exp(-Z_{ya})] & \text{for } 1 < a < A \\ (N_{y-1,A-1} + N_{y-1,A}) \cdot [1 - \exp(-Z_{yA})] & \text{for } a = A \end{cases}, \quad (20)$$

and,

$$C_{ya} = \frac{F_{ya}}{Z_{ya}} D_{ya}. \quad (21)$$

Note that total deaths of oceanic-stage (ages 0 and 1) Kemp’s ridleys were not specified (Eqs. 20 and 21) because of likely confounding of oceanic mortality ( $Z_p$ ), hatchling proportions female (protected nests and in situ,  $r_C$  and  $r_b$ , respectively), and mean number of nests per adult female in the population ( $n_M$ ) (see DISCUSSION).

**Predicted nests:** The predicted annual conventional index ( $P_y$ ) was the product of estimated annual number of adult females and mean number of nests per adult female in the population ( $n_M$ ). The annual number of adult females in the population by year was calculated as the sum of products of the neritic-stage female population size ( $N_{ya}$ ) in year  $y$  and at age  $a$ , and the proportion of females mature by age  $a$  ( $G_a$ ); i.e.,

$$P_y = n_M \sum_a N_{ya} G_a. \quad (22)$$

**Predicted length frequency of strandings:** The expected proportion of the strandings ( $p_{ya}$ ) by year  $y$  and age  $a$  was provided by

$$p_{ya} = \frac{s_a N_{ya}}{\sum_a s_a N_{ya}}, \quad (23)$$

where  $s_a$  is selectivity of strandings by age  $a$ . Note that the  $p_{ya}$  sum to 1 over all ages within a year ( $\sum_a p_{ya} = 1$ ). Two alternative selectivity functions were examined: 1) an ascending, logistic-shaped function (Eq. 24), and 2) a dome-shaped function (Eq. 25), which is a double logistic with ascending and descending limbs), i.e.,

$$s_a = \frac{1}{1 + \exp\left(\frac{a_{50}-a}{a_{sl}}\right)} \quad (24)$$

$$s_a = \frac{1}{1 + \exp\left(\frac{a_{50}-a}{a_{sl}}\right)} \cdot \left[ 1 - \frac{1}{1 + \exp\left(\frac{b_{50}-a}{b_{sl}}\right)} \right], \quad (25)$$

where  $a_{50}$  is the age at 50% selectivity (i.e., when  $p_{ya} = 0.5$ ) for the ascending limb,  $a_{sl}$  is the slope for the ascending limb,  $b_{50}$  is the age at 50% selectivity for the descending limb, and  $b_{sl}$  is the slope for the descending limb. Note that the selectivities are symmetrical around the midpoint, 0.5, on a scale of 0 to 1.

Expected SCL ( $l_a$ ) and its associated variance for turtles at age  $a$  were obtained through the application of Equations 10 and 12, respectively. SCLs of individual turtles of the same age ( $a$ ) were assumed to be normally distributed. Following Fournier et al. (1990), the probability ( $f_{yj}$ ) of a turtle measured in year  $y$  belonging to SCL interval  $j$  was approximated by

$$f_{yj} = \frac{w}{\sqrt{2\pi}} \sum_a \frac{p_{ya}}{\sigma_a} \exp\left\{ -\frac{(v_j - l_a)^2}{2\sigma_a^2} \right\}, \quad (26)$$

where  $w$  is the width of each SCL interval (set to 5 cm) and  $v_j$  is the midpoint of length interval  $j$ .

**Assessment model objective function.**—The objective of the analysis was to minimize the sum of the negative log-likelihood density functions ( $L$ ) through the evaluation of alternative fundamental parameter values. In this model we considered four sources of log-likelihood,

$$L = L_{\text{prior}} + L_P + L_{\Delta t} + L_f, \quad (27)$$

where  $L_{\text{prior}}$  is associated with prior information for the fundamental parameters,  $L_P$  with the number of observed nests,  $L_{\Delta t}$  with SCL at release and recapture using the mark-recapture data, and  $L_f$  with length frequency of the strandings data.

**Priors:** A prior normal distribution was assumed for every estimated fundamental parameter to allow any prior information to be included in the objective function. Therefore, its contribution to the objective function (excluding all constant values) was

$$L_{\text{prior}} = \sum_{\theta} \frac{(\hat{\theta} - \theta)^2}{2\sigma_{\theta}^2}, \quad (28)$$

where  $\hat{\theta}$  is the prior value of the estimated parameter,  $\sigma_{\theta}$  is the prior standard deviation of the parameter, and  $\theta$  is the estimate of the

parameter when the KRSAM's objective function was minimized. Note that when a large prior standard deviation for a parameter is assumed, the prior distribution has little influence on the objective function.

Observed nests: Observed annual nests for 1978 through 2012 ( $y = 13, 14 \dots 47$ ) were used to compute the associated contribution ( $L_p$ ) to the objective function. The predicted residuals were assumed to have a log normal distribution. Therefore, the contribution of the observed nests (excluding all constant values) was

$$L_p = \sum_{y=13}^{47} \ln(S) + \sum_{y=13}^{47} \frac{\xi_y^2}{2S_y^2}, \quad (29)$$

where  $\xi_y = \ln(P_y) - \ln(\tilde{P}_y)$ .

Capture–recapture growth increments: The capture–recapture data applied to growth were the SCL at capture ( $\tilde{l}_{0i}$ ), SCL at recapture ( $\tilde{l}_{1i}$ ), and the time the turtle was at large ( $\Delta\tilde{t}_i$ ). SCL measurement error ( $\sigma_m$ ) was set constant at 0.5 cm on the basis of 82 turtles that exhibited no growth. This sample included turtles with SCL > 63 cm as well as smaller turtles at large less than 10 d; all of these turtles were assumed to have the same SCLs at capture and recapture. Note that a SCL of 60 cm has typically been accepted as minimum size at maturity for Kemp's ridley, although nesters of shorter SCL have been observed. Ages for the mean SCL parameters  $\mu_1$  and  $\mu_2$  were set to age 1 ( $t_2 = 1$ ) and age 10 ( $t_2 = 10$ ), respectively. As pointed out above (see Growth theory), the residuals for the increments in SCL obtained from capture–recapture data were assumed to be normally distributed (see Eq. 8), where the expected increment in SCL ( $\Delta\tilde{l}_i$ ) and its variance ( $\zeta_i^2$ ) were obtained using Equations 9 and 11. The negative log-likelihoods for an individual, variance-weighted, normal distribution of SCL increments ( $\Delta\tilde{l}_i$ ) were then (excluding all constant values)

$$L_{\Delta\tilde{l}} = \sum_i \ln(\zeta_i) + \sum_i \frac{(\tilde{l}_{1i} - \tilde{l}_{0i} - \Delta\tilde{l}_i)^2}{2\zeta_i^2}. \quad (30)$$

This likelihood mainly affects fundamental parameters  $\mu_2$ ,  $K$ , and  $\sigma_L$ .

Length frequency of strandings: The annual SCL frequencies were assumed to exhibit a multinomial distribution. Following Gazey et al. (2008), a robust version of the negative log-likelihood was

used (excluding all constant values), i.e.,

$$L_f = \sum_y \sum_j \tilde{f}_{yj} \sqrt{n_{fy}} \ln\left(\frac{0.01}{J} + f_{yj}\right), \quad (31)$$

where  $n_{fy}$  is the sample size for year  $y$ ,  $\tilde{f}_{yj}$  is the observed proportion of strandings in year  $y$  and SCL interval  $j$ ,  $J$  is the total number of 5-cm SCL bins (class intervals), and  $f_{yj}$  is the predicted proportion of strandings in year  $y$  and interval  $j$ , via Equation 26.

*Parameter estimation.*—Parameter estimation was accomplished by finding the fundamental parameter values that minimize the KRSAM's objective function (Eq. 27). Model definition and minimization of the objective function were implemented through AD Model Builder (Fournier et al., 2012). AD Model Builder allowed restriction or bounding of parameter values, stepwise optimization, and reporting of standard deviations, marginal posterior profiles, and correlations between parameter estimates.

Several parameters were assumed to be known or fixed as specified by NMFS et al. (2011). The female sex ratios ( $r_I$  and  $r_C$ ) in Equation 17 were set to 0.64 and 0.74 for in situ and protected nests, respectively. The number of nests per adult female ( $n_M$ ) in Eqs. 18 and 22) was set to 1.25 (the ratio of 2.5 nests per breeder and a 2-yr migration interval). The maturity schedule ( $G_a$  in equation 22) was assumed to be knife edge 12 yr after hatching, i.e.,

$$G_a = \begin{cases} 0 & \text{for } a < 11 \\ 1 & \text{otherwise} \end{cases} \quad (32)$$

The assessment model was initially run with the prior standard deviations for the fundamental parameters set to very large values (uninformative). If parameter estimation problems were encountered, then prior information was introduced, or some parameters were set constant (i.e., removed from estimation). The model was executed for three alternative ages (5, 6, and 7) used to partition catchability ( $a_c$  in Eq. 15), and three alternative years (1989, 1990, and 1991) to commence the TED effect multiplier ( $y_{TED}$  in Eq. 16). Results are reported only from the run that produced the lowest value for the objective function of the nine trial runs (three alternative  $a_c$  by three alternative  $y_{TED}$  values).

The additional anthropogenic mortality for 2010 was set to start at age 2 ( $a_{2010} = 2$ , Eq. 16) under the rationale that all neritic-stage turtles would be affected equally. Alternatively, a run

TABLE 2. Mortality, growth, and selectivity parameter estimates, and female population size estimates with standard deviations (SD) based on the best model fit of a turtle excluder device (TED) effect beginning in 1990 and a 2010 additional anthropogenic mortality factor in 2010 affecting ages 2+ yr. Population sizes for ages 2–4 represent the size of the population that is not fully recruited to shrimp trawling, ages 2+ reflect the entire neritic population, ages 5+ represent sizes that are fully recruited to the shrimp fishery, and ages 9+ reflect the size of the population that would have been expected to nest during 2010 to 2012.

Parameter	Notation	Estimate	SD
<b>Mortality</b>			
Instantaneous mortality (ages 0 and 1)	$M_p$	1.330	0.117
Instantaneous anthropogenic mortality 2010 event	$F_{2010}$	0.345	0.118
Catchability (ages 2–4)	$q_1$	0.200	0.040
Catchability (ages 5+)	$q_2$	0.155	0.014
TED effect multiplier (starts in 1990)	$X_{TED}$	0.233	0.069
<b>Growth</b>			
SCL (cm) at age 1	$\mu_1$	17.2	0.51
SCL (cm) at age 10	$\mu_2$	58.0	0.63
von Bertalanffy growth coefficient	$K$	0.232	0.013
Individual length variation (SD)	$\sigma_L$	9.37	0.56
<b>Selectivity</b>			
Age when selectivity at 50%	$a_{50}$	1.75	0.22
Slope	$a_{st}$	0.552	0.071
<b>Terminal population size (2012)</b>			
Ages 2–4		78,043	14,683
Ages 2+		152,357	25,015
Ages 5+		74,314	10,460
Ages 9+		28,113	2,987

was made starting at age 9 ( $a_{2010} = 9$ ) such that only age classes of females that would nest in the 2010-to-2012 period were affected.

Goodness-of-fit plots were produced for each of the data types (nest counts, capture–recapture growth increments, and length frequency of strandings). The log of the fitted nest-count residuals was plotted against the predicted annual nest counts. Examination of the growth data properly requires a three-dimensional plot (growth increment, initial SCL, and time-at-large axes) with the data and predicted surface. Because of large variation in individual growth such a plot is very difficult to interpret. Instead, a commonly applied two-dimensional approximation (e.g., Sainsbury, 1980) was used to examine the goodness of fit. Namely, the growth rate was plotted on mean SCL for every recaptured turtle. The predicted growth rate overlaid on this plot is a straight line. To examine the fit to the strandings, the length frequency data were overlaid with the expected length frequency.

RESULTS

The KRSAM was developed during a workshop format to a priori decide on data screening and model implementations. We assigned habitat

weighting factors, set the asymptotic natural mortality ( $M_\infty$ ) to 0.05, and adopted the simple logistic relationship (Eq. 24) to estimate selectivity of strandings by age. A best model fit that produced the lowest value for the objective function of nine trial runs was for a TED effect beginning in 1990 and a 2010 additional mortality factor that affected ages 2+. The remaining fundamental parameter estimates and terminal female population sizes by age are provided in Tables 2 and 3.

The modeling predictions compared with the observed number of nests reflect a reasonable fit (Fig. 1). Note that the residuals were homogeneous and there was no readily apparent trend consistent with the assumed log-normal sampling distribution. The model captured the exponential increase in nesting through 2009, and with the application of the additional mortality or nesting reduction in 2010, reflected reduced nesting in 2010, followed by an increase in nesting in 2011 and 2012 back to 2009 nesting levels.

The model fit to the strandings length-frequency data was reasonably good, especially for recent years, e.g., 2004–2011 (Fig. 2). The predicted frequencies in recent years reflected increased representation of older, larger turtles than were evident in earlier years. This indicates

TABLE 3. Estimated numbers of female Kemp's ridleys by age for 2012 based on the best model fit of a turtle excluder device (TED) effect multiplier beginning in 1990 and a 2010 additional anthropogenic mortality factor in 2010 affecting ages 2+ yr. Annual estimates are based on point estimates of numbers by age from the predictive model.

Age	Age 2+
2	32,060
3	23,057
4	22,918
5	17,034
6	12,524
7	8,532
8	8,105
9	6,164
10	4,578
11	5,178
12	2,670
13	1,895
14+	7,624

that, with recovery, the age classes were filling up over time as more turtles survived and grew.

The growth rate (cm/yr) for every capture–recapture event is plotted as a function of the mean SCL (Fig. 3A). The observed variation is large, but in general the growth rate declined with increase in SCL. The von Bertalanffy growth model predicted a linear decrease in growth rate with size (Fig. 3A). Note that although each point did not provide equal weight to the likelihood (see Eq. 9), the graphical illustration of the variation in growth rate by size enables identification of possible outliers. The two turtles larger than 60 cm with large growth rates had little influence on the model because of a predominance of large turtles with near zero growth rate (Fig. 3A).

The von Bertalanffy somatic growth curve was estimated for both sexes combined (Fig. 3B). Point estimates of size at age can be determined from the growth curve, but note the large variation in SCL for individuals of a given age (especially for older turtles). Variation in size increases with age.

Natural mortality rates for ages 2+ were estimated using the Lorenzen curve and the selectivity curve based on strandings data. On the basis of the Lorenzen curve, natural mortality declined monotonically from about  $M = 0.11$  at age 2, to near the set  $M = 0.05$  at age 12. Kemp's ridleys were not fully recruited to the strandings until about age 5 (Figs. 2, 3). Once recruited at age 5, these large juveniles have the same instantaneous fishing mortality as adults. Instantaneous fishing mortality by year for ages 2–4 and

ages 5+ increased over the period from 1966 through the late 1980s, then plummeted in association with the requirement for TEDs in 1990 (Fig. 4). Fishing mortality then remained relatively consistent through the early 2000s when shrimping effort exhibited a marked decline and leveled out at the present-day low level (post-2004, Fig. 4A).

The instantaneous total mortality by year for age 2, age 5, and age-class 14+ closely tracked fishing mortality, except for 2010 when a large increase in apparent anthropogenic mortality was indicated (Fig. 4B). Note that each age has a different mortality profile because natural mortality is monotonically decreasing as a function of age. As described above, adding a significant mortality event in 2010 was required to fit the observed number of nests in 2010, 2011, and 2012.

Shrimp trawling-associated deaths increased from 1966 to 1989, then declined markedly in 1990, but once more began to increase over time as a result of the increasing population (Fig. 5A). The mortality increase that occurred in 2010 dwarfed all previous and subsequent years' estimates of total mortality (Fig. 5B). The major factors that influenced the percentage of total mortality attributable to shrimp trawling were directed shrimp effort, TED use commencing in 1990, and the 2010 mortality event. In the 1980s, fishing (shrimp trawling) mortality accounted for 68 to 74% of total mortality. In 2005 to 2009, fishing mortality had been reduced to about 20 to 25% of the total mortality (Table 4). In 2010, shrimp trawl mortality represented an estimated maximum of 12.5% of the total mortality.

The 2010 estimated total mortality was based on a model where all vulnerable age classes (ages 2+) were assumed to have been affected. Under this scenario, total mortality of female Kemp's ridleys was 65,551, of which only 2,879 (4%) of the deaths were attributable to shrimp trawls (Table 4). In an alternative model, we assumed that the 2010 event only affected large, older turtles (ages 9+), which produced an almost identical fit to the data and yielded very similar parameter estimates. The primary differences were a large reduction in total mortality in 2010 (only 26,626 vs 65,551) and larger estimates of predicted deaths from 2010 through 2012 attributable to shrimp trawling (Table 4).

Terminal 2012 population estimates for 2012 summed over ages 2 to 4, ages 2+, ages 5+, and ages 9+ suggest that the respective female population sizes were 78,043 (SD = 14,683), 152,357 (SD = 25,015), 74,314 (SD = 10,460),

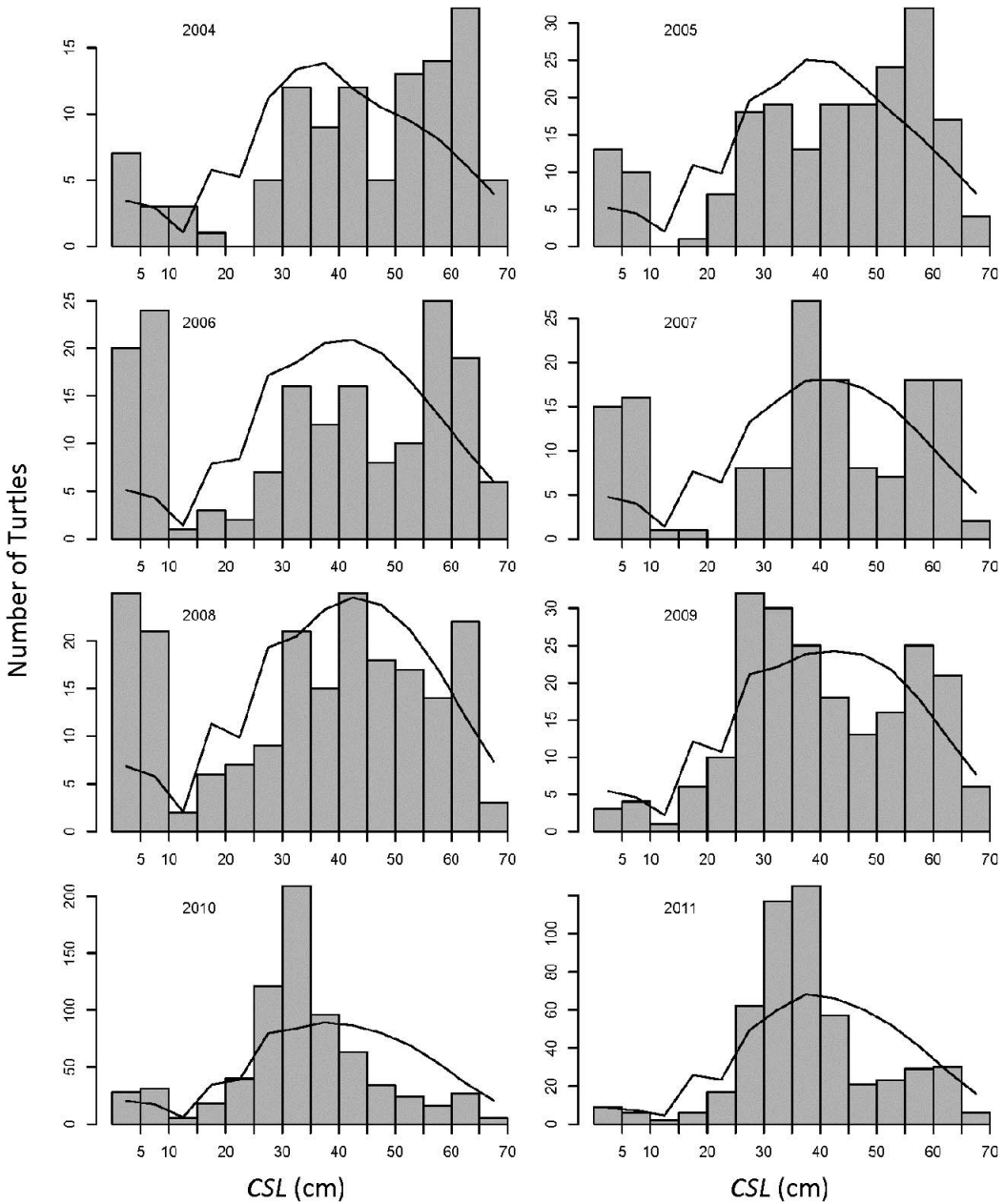


Fig. 2. Observed length frequency of strandings (bars) and model estimates (lines) for 2004–2011.

and 28,113 (SD = 2,987), respectively (see Table 2). These estimates are predicated on the assumptions that the 2010 mortality event affected all ages of neritic turtles (>age 2). Point estimates of female population size by age in 2012 decline from 32,060 at age 2 to 1,895 turtles at age 13 (Table 3). A total of 7,624 females is estimated for ages 14+. Note that slight differences are evident when the point estimates are summed and

compared with the terminal estimates for the same groups. This is attributable to rounding effects and differences in how model error is treated between the two estimators.

#### DISCUSSION

Several model caveats should be recognized or reviewed. First, Kemp’s ridley turtles nest on

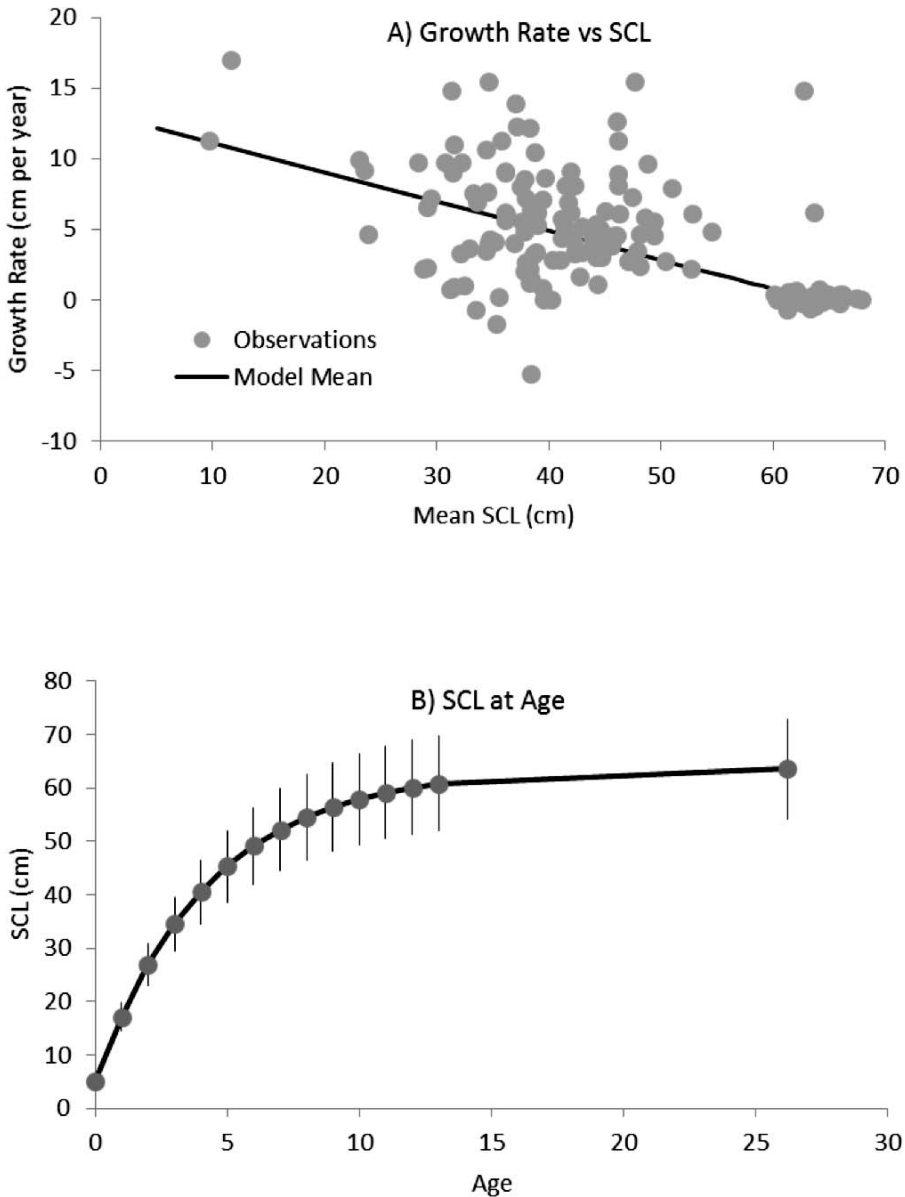


Fig. 3. Growth rate (cm/yr) as a function of the mean straight carapace length (SCL) interval (points) and the predicted model mean (line, panel A) and von Bertalanffy growth with associated error by age ( $\pm 1$  SD). The last point is the mean age of the 14+ age class in 2012 (panel B).

beaches other than the three index beaches (7.4% of registered nests were located at other beaches in 2012). Therefore, our population estimates of female turtles are incomplete and likely lower than the actual population size. However, the level of population underestimation is considered comparatively low.

The scaled directed shrimping effort profile was, in general, insensitive to alternative habitat scores (the weighted and unweighted profiles of

shrimping effort were very similar). Offshore shrimping effort in the U.S. Gulf of Mexico is highest in the nearshore zone (0–10-fm depths), intermediate in the mid-shelf zone (0–30-fm depths), and lowest in the outer shelf area (>30-fm depths) (James M. Nance, NMFS, pers.com). The ranking of habitat value for Kemp's ridley females exhibited a similar gradient of value by depth. Large weights (high habitat scores) were given to the 0–10-fm areas,

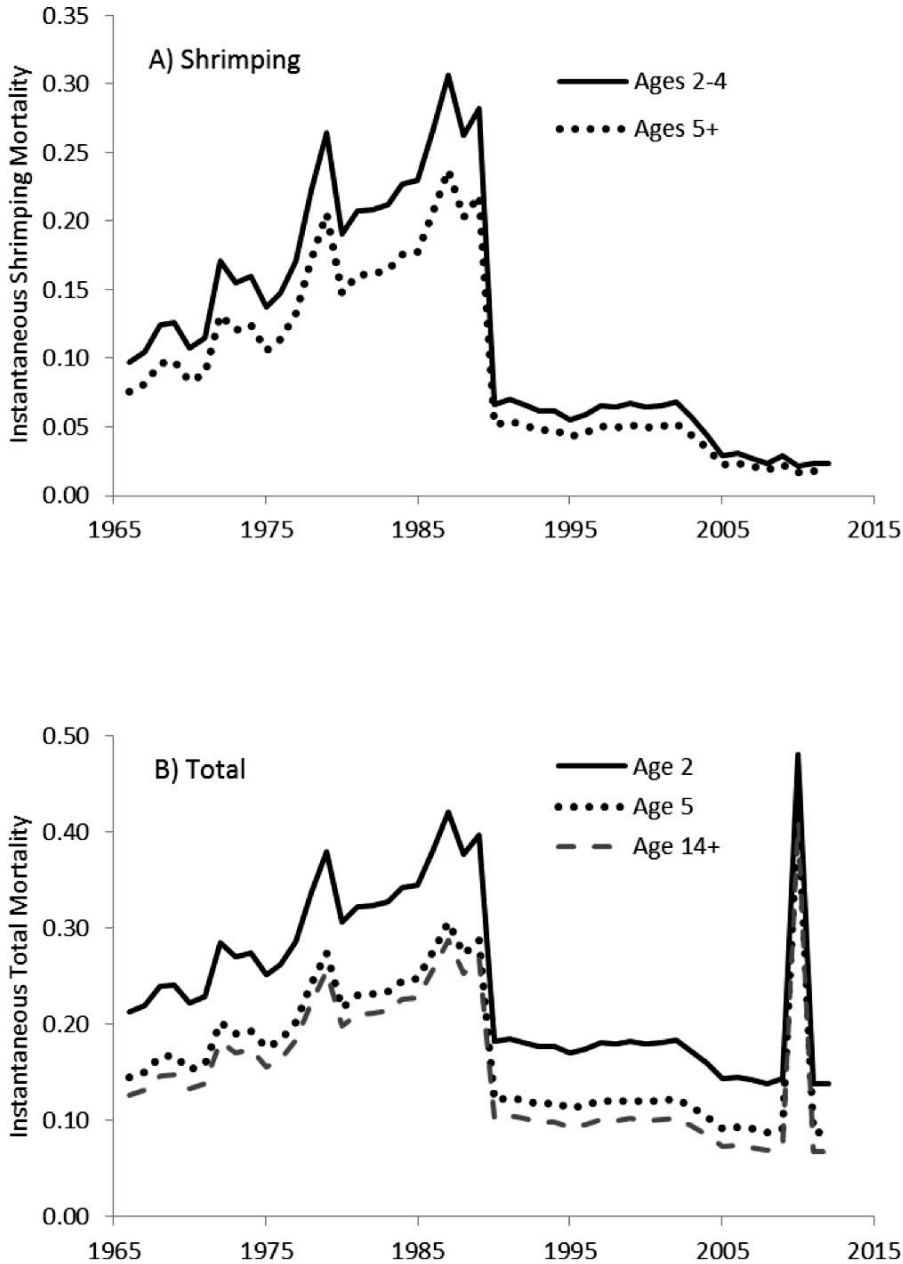


Fig. 4. Instantaneous fishing and total mortality by year. Constant instantaneous fishing mortality rates are assigned within each of the two age-class groups shown in panel A. Note that each age has a different total mortality profile because natural mortality is monotonically decreasing as a function of age (panel B).

intermediate habitat scores were given to mid-shelf areas, and low scores were assigned to deep areas. The rationale for the high weight given to the 0–10-fm depth category was that it incorporated important foraging areas and migration corridors used by Kemp’s ridleys (Magnuson et al., 1990; Musick and Limpus, 1997; Morreale

and Standora, 2005; Morreale et al., 2007; Witherington et al., 2012; Shaver et al., 2013). Thus the scaled shrimping effort trend by year was almost identical to the unweighted effort trend by year. In terms of model fit to the nesting data, the effective U.S. shrimp effort worked well for the 1981–2012 period. We believe that

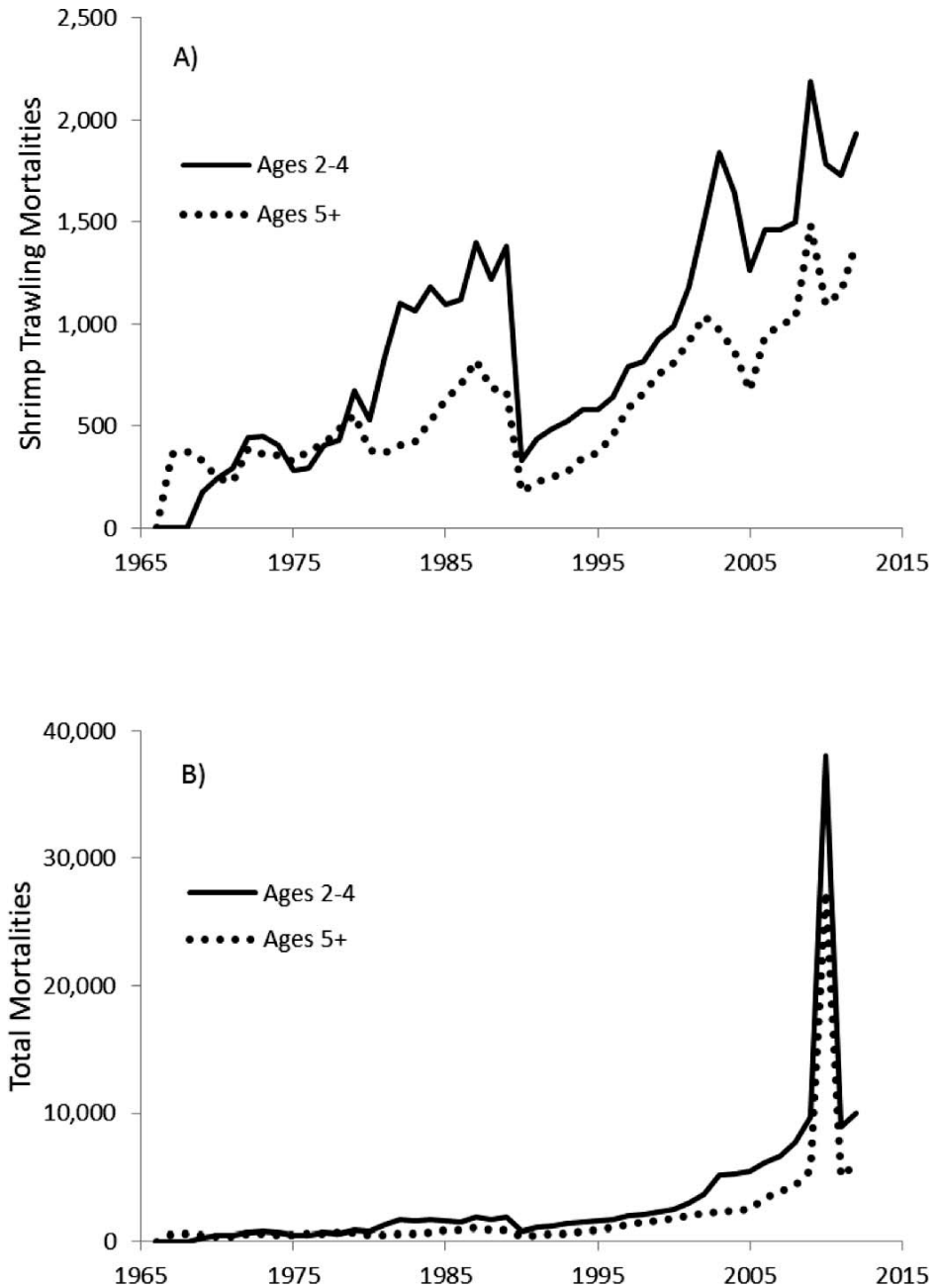


Fig. 5. Model estimates of the number of Kemp's ridley deaths by year. Panel A shows mortalities assigned to shrimp trawls and panel B shows total deaths. Note the scale of the 2010 mortality event.

shrimp fishing effort in 1966 to 1980 was underestimated and that better estimates could be achieved by obtaining estimates of shrimping effort by Mexico's shrimping fleet in the Gulf of Mexico during years 1966–2012, calculated on the same basis as for the U.S. shrimping fleet.

Some parameters in the model were fixed (assumed). The number of nests per adult female

(1.25, calculated from the ratio of nests per breeder and the breeding interval as provided by NMFS et al., 2011) was scaled to the number of adult females in the population (given the observed number of nests). Moreover, this direct scaling allowed total oceanic-stage mortality to be estimated from the number of juvenile females (age 2) entering the neritic population.



TABLE 4. Mortalities assigned to shrimp trawls in comparison with total mortalities with the 2010 mortality event affecting ages 2+ or ages 9+ yr, and a turtle excluder device (TED) effect multiplier beginning in 1990.

Year	$a_{2010} = 2+$			$a_{2010} = 9+$		
	Shrimp trawl	Total	%	Shrimp trawl	Total	%
1980	906	1,339	67.7	916	1,349	67.9
1981	1,201	1,742	68.9	1,217	1,759	69.2
1982	1,492	2,178	68.5	1,513	2,201	68.7
1983	1,478	2,113	70.0	1,497	2,133	70.2
1984	1,691	2,381	71.0	1,711	2,403	71.2
1985	1,716	2,410	71.2	1,735	2,429	71.4
1986	1,818	2,428	74.8	1,835	2,446	75.0
1987	2,210	2,885	76.6	2,233	2,907	76.8
1988	1,895	2,569	73.8	1,914	2,589	74.0
1989	2,040	2,705	75.4	2,061	2,726	75.6
1990	512	1,212	42.3	513	1,213	42.3
1991	660	1,532	43.0	662	1,537	43.1
1992	741	1,766	42.0	745	1,773	42.0
1993	802	1,988	40.3	806	1,998	40.4
1994	920	2,263	40.6	925	2,275	40.7
1995	946	2,487	38.1	952	2,500	38.1
1996	1,097	2,748	39.9	1,103	2,764	39.9
1997	1,379	3,249	42.4	1,387	3,268	42.4
1998	1,511	3,612	41.8	1,520	3,634	41.8
1999	1,710	3,958	43.2	1,721	3,981	43.2
2000	1,825	4,347	42.0	1,837	4,374	42.0
2001	2,111	4,981	42.4	2,125	5,013	42.4
2002	2,558	5,931	43.1	2,576	5,970	43.2
2003	2,819	7,440	37.9	2,842	7,492	37.9
2004	2,512	7,646	32.9	2,533	7,699	32.9
2005	1,939	7,951	24.4	1,955	8,006	24.4
2006	2,406	9,574	25.1	2,424	9,639	25.2
2007	2,461	10,465	23.5	2,479	10,535	23.5
2008	2,525	12,099	20.9	2,544	12,180	20.9
2009	3,678	15,268	24.1	3,705	15,371	24.1
2010	2,879	65,551	4.4	3,339	26,626	12.5
2011	3,069	14,109	21.8	4,204	19,454	21.6
2012	3,779	16,497	22.9	5,214	22,890	22.8

Similarly, the asymptotic instantaneous natural mortality ( $M_\infty$ ) had to be set to allow estimation of the TED effect multiplier. Setting  $M_\infty$  at 0.05 implied a TED efficiency of 77% for the exclusion of Kemp’s ridley turtles. This level of efficiency is lower than would be expected and may reflect lower compliance than expected. Compliance was likely a factor but was unmeasured. The TED efficiency estimate was sensitive to estimates of asymptotic natural mortality. For example,  $M_\infty$  set to 0.06 would yield an 88% TED efficiency. In contrast,  $M_\infty$  set to 0.05 implies that many Kemp’s ridley turtles could live to a very old age. Our model suggests that values beyond

$0.04 < M_\infty < 0.06$  result in unreasonable estimates for other parameters.

Knife edge maturity (12 yr from hatching at a mean length of 59 cm) was also set following NMFS et al. (2011). This parameter dictated the age distribution of adults and affected the generation time of the population. Reasonable parameter estimates were obtained only when maturity was set at 11, 12, or 13 yr from hatching. Variable maturity schedule by age (i.e., not knife edge) had little impact on model behavior if the mean age of maturity did not change. A current size distribution of breeders would greatly enhance our ability to quantify a maturity schedule by age.

The female sex ratios were also set from NMFS et al. (2011). However, if applied as stationary values as in Equation 17, there was little influence on the female population size because of complete confounding with oceanic-stage mortality (i.e., estimates of oceanic mortality were directly related to the sex ratio such that population size did not change). However, any inference with respect to the male population size is dependent on the sex ratios.

As noted above, oceanic-stage mortality served to scale the number of hatchlings to the number of turtles entering the population as age-2 neritic juveniles. Our model subjected the oceanic stage to 2 yr of estimated equal mortality. However, age-0 turtles are actually only exposed for about 6 mo. Therefore, our partitioning of the population between ages 0 and 1 is suspect. Moreover, oceanic-stage mortality is confounded with the assumed (fixed) parameters of the sex ratios, nests per female, asymptotic natural mortality, and the maturity schedule. Consequently, we do not present estimates of age-0 and age-1 population size.

The analysis of the mark-recapture growth increment data is preliminary. A concern is that the time-at-large criteria of 30 d was too short and introduced bias in the  $K$  and  $\sigma_L$  parameters because of seasonal growth. Unfortunately, using only turtles that had been at large more than a year resulted in a 40% loss in observations and an inability to estimate the lower size parameter  $\mu_1$  (size at age 1). Setting  $\mu_1$  to 17.2 cm (the value obtained using the 30 d-at-large criteria) and carrying through with the parameter estimation with capture-recapture events of more than a year resulted in slightly smaller  $K$  and  $\sigma_L$ , which in turn led to somewhat higher estimates of natural mortality and lower estimates of shrimping-related mortality. Sample size could have been

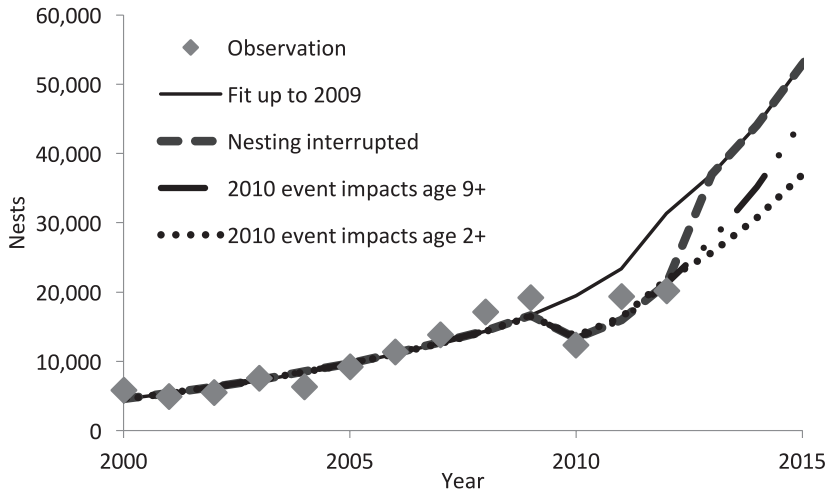


Fig. 6. Predicted number of nests for some alternative models to account for the 2010 event with projections to 2015. The “Fit up to 2009” used 2009 terminal mortalities and population by age estimates to make the 2010-through-2015 projections. Similarly, the remaining alternatives used 2012 terminal mortalities and population by age estimates to make the 2013-through-2015 projections.

increased by including captured–recaptured turtles that transited between Gulf of Mexico and Atlantic waters. However, additional variability would have been introduced by differences in growth rates of Kemp’s ridleys in Atlantic and Gulf waters (Snover et al., 2007; Caillouet et al., 2011). Also, additional data on the mean size and variation in sizes of individual turtle hatchlings (e.g., Marquez-M., 1994) and 1-yr-olds (if available) could and should be included as prior information for the  $\mu_1$  parameter.

The numbers of nests observed for the period 2010 through 2012 were significantly lower ( $P < 0.001$ ) than expected on the basis of projections using data before 2010 (Fig. 6, see also NMFS et al., 2011). If some event on the foraging grounds (e.g., cold winter/spring temperatures) caused some turtles not to migrate and nest in 2010, they should eventually return to the nesting beaches and the former trajectory should be resumed. If a mortality event did occur (and this seems likely), the trend of increase should be resumed in relatively short order (depending on what ages were affected) because of population momentum. Most of the scenarios we had examined at the time of this assessment suggested that nesting should once more exhibit an increasing trend in the next few years. In short, the model lacks any density-dependent mechanisms that would impede exponential growth. However, recent data for 2013 and 2014 indicate that nest numbers in 2013 were less than in 2012 and in 2014 were comparable with 2010 numbers (Laura Sarti

Martinez, CONANP, pers. comm; Shaver et al., unpubl. data). Continued monitoring of the nesting beaches is critical for evaluating the status of the population in future years and determining the magnitude and consequences of the 2010 mortality event. Updating of the KRSAM with alternative density-dependent mechanisms for the 2015 stock assessment will provide a timely evaluation of stock status and trend and allow for exploration of hypotheses relative to the 2010 mortality event.

#### ACKNOWLEDGMENTS

This project was funded by the Gulf States Marine Fisheries Commission. We extend special thanks to Selina Heppell, who provided her model; state coordinators of the National Marine Fisheries Service (NMFS) STSSN, who granted permission to use stranding data; to the NMFS Southeast Fisheries Science Center for estimated annual nominal shrimp trawling effort data; and to participants in the CMTTP for permission to use mark-recapture data. STSSN participants who were not authors were Jackie Issacs, Alabama and Alan Foley, Florida. CMTTP participants who were not authors were Mike Anderson, Clearwater Marine Aquarium, Clearwater, FL; Benjamin Higgins, NMFS Galveston Laboratory, Galveston, TX; Jaime Peña, Gladys Porter Zoo, Brownsville, TX; Rebecca Brudek-Wells, Gulfarium Marine Adventure Park, Fort Walton Beach, FL; Jeff George, Sea Turtle Inc., South

Padre Island, TX; and André Landry, Texas A&M University at Galveston, Galveston, TX. Any use of trade, product or firm names is for descriptive purposes only, and does not imply endorsement by the U.S. Government.

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