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A Population Model to Estimate Recovery Time, Population Size, and Management Impacts on Kemp's Ridley Sea Turtles

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ABSTRACT. – **From 1995–99, the National Marine Fisheries Service Turtle Expert Working Group accumulated census information and life history data for the Kemp's ridley sea turtle (*Lepidochelys kempii*) with the goal of producing population models to address management and viability questions. This is a summary of the preliminary population models produced by the Group. A 37-year time series of nest numbers exists for this species. Because most vital rates (age-specific survival and growth) are uncertain, several sources of data were used in conjunction with model fitting to estimate parameters for the models. A range of parameter estimates was used to test the sensitivity of model results to uncertainty. A range of models had good fits to the observed number of nests; the best fitting model included 10 years to sexual maturity and an increase in benthic feeding turtle survival after 1990 (corresponding with Turtle Excluder Device regulations that are thought to have reduced mortality of those stages). All models predicted rapid population growth (12-16% per year) assuming that current survival rates remain constant. Decreased egg survival with nest density slowed the population growth rate, but not until after the population reached the management target of 10,000 nesting females. While these results were fairly consistent for alternative ages at first reproduction and survival rates, the different models gave a wide range of population size estimates, preventing the Group from setting incidental catch limits. Refinement of vital rates, particularly survival rates, should reduce this uncertainty in the future.**

KEY WORDS. – **Reptilia; Testudines; Cheloniidae; *Lepidochelys kempii*; sea turtle; demography; population model; population dynamics; management; conservation; survival rates; Mexico**

Population models and demographic analyses have been useful tools in sea turtle conservation (see reviews in Chaloupka and Musick, 1997, and Heppell et al., 2002). Models can elucidate patterns and processes that are not apparent from empirical data, thereby guiding research and management efforts. Less often, models are able to provide projections for changes in population size through time. Whether a model serves conservation efforts as a heuristic tool to compare the potential outcomes of a range of management scenarios or as a quantitative tool for predicting population dynamics depends on what questions need to be answered and what data are available. Sea turtle population models have ranged from simple, deterministic stage-based matrix models to detailed statistical models that utilize extensive tagging databases (Chaloupka and Musick, 1997). Important insights gained through these models have included: 1) nesting beach protection efforts alone cannot compensate for at-sea mortality of large juvenile, subadult and adult loggerheads (Crouse et al., 1987); 2) long time delays and variable rates of annual increase are to be expected in sea turtle recovery efforts due to late age at maturity and shifts in the age distribution of the population (Crowder et al., 1994); 3) headstarting is a low-payback management tool when compared to reductions in mortality through effective Turtle Excluder Device (TED) use (Heppell et al., 1996); 4) sea turtle growth dynamics are complex, multi-step functions that probably reflect changes in diet and behavior (Chaloupka and Zug, 1997); and 5) individual variability in growth rates and breeding likelihood can have important implications for population viability (Chaloupka and Limpus, 1996; Chaloupka, 2001).

In general, efforts to understand sea turtle population dynamics through population modeling have suffered from a lack of information on survival and growth rates. Most species nest over wide geographic areas and in-water surveys have been limited to a few populations (Heppell et al., 2002). However, Kemp's ridley turtle (*Lepidochelys kempii*) nesting has been primarily restricted to Rancho Nuevo in

Tamaulipas, Mexico, and nearby beaches, and nest abundance has been intensively monitored for decades (Márquez et al., 2001). Thus, we have a unique, 37-year record of nests and hatchling production for almost the entire species (Fig. 1). Using the known number of hatchlings released as our model input and number of nests as our output (Turtle Expert Working Group, 2000), we constructed age-based population models that matched model nests to observed nests (1978–96) assuming an age at first reproduction of 8, 10, or 12 years. We constructed the models to address the following management questions:

1. Given the current rate of increase, how long will it take the population to reach 10,000 nesting females, the target population size for downlisting from Endangered to Threatened (designations according to the U.S. Endangered Species Act and targets set by U.S. Fish and Wildlife Service and National Marine Fisheries in the 1992 Recovery Plan for the Kemp's Ridley Sea Turtle, *Lepidochelys kempii*).
2. Are recent increases in Kemp's ridley strandings (particularly 1994 and 1995) higher than would be expected from the documented increase in hatchling production?
3. How many individuals can be removed from the population annually without preventing the population from reaching 10,000 nesting females by 2020?

Uncertainty in critical demographic parameters prevented us from answering these questions definitively. But we did document important factors contributing to Kemp's ridley population dynamics and identified a critical need for more information on mortality and growth of juveniles. Complete documentation of our source information, data analysis, model construction, and results can be found in a technical memorandum produced by the Turtle Expert Working Group (2000). Here we briefly summarize the methods and results, compare the model projections to recent nesting beach data, and discuss why our models failed to provide quantitative answers to the questions posed by managers.

METHODS

Model Structure. — Our models were age-based, with age-specific annual survival rates, similar to dynamic pool and virtual population analysis models used in fisheries science (Hilborn and Walters, 1992). The Kemp's life cycle was split into four classes, each with an annual survival rate applied to multiple age classes: pelagic immatures, small benthic immatures, large benthic immatures, and adults (Fig. 2). Hatchlings released from 1966–99 entered the model each year, remained pelagic immatures for 2 years, and entered the benthic feeding population at age 2. This transition age was based on preliminary tag return information and a regression analysis of hatchlings released relative to small ridley strandings 1 through 4 years later, and has been confirmed though wire tag recoveries (Snover, 2002). The small benthic immature stage lasted for 4 years, when the turtles became large benthic immatures with the same annual mortality rate as adults. The length of the benthic immature stage depended on the assumed age at maturity (8, 10, or 12 years). Our choice of the range of age at maturity was based on maturation at 60 cm SCL and growth curves generated from mark-recapture data (Schmid and Witzell, 1997; Schmid, 1998; Turtle Expert Working Group, 2000, Appendix 1) and skeletochronology (Zug et al., 1997). We were unable to achieve model fits with later ages at maturation, although this could be due to model flaws more than biology (Turtle Expert Working Group, 2000). At maturation and for all subsequent years, half of the surviving females nested (assuming a 2-year remigration interval), producing 2.5 nests each (based on a mean of published studies and field data), giving an annual production rate of 1.25 nests per female. We did not invoke a maximum lifespan.

The number of nests each year expected by the model was compared with the observed number of nests at Rancho Nuevo, North and South Camps (Fig. 1) by least-squares. The decision to include North and South Camps was based on the expert opinion that few nests occurred in these areas prior to 1990 and some females from Rancho Nuevo had migrated to these areas following a hurricane (R. Márquez and R. Byles, *pers. comm.*). Model population size was calculated by summing relevant age classes each year and assuming a 1:1 sex ratio (Coyne, 1999). We assumed that nests moved into the protective "corrals" were the only source of viable hatchlings for all years, and started the simulations with a population comprised of only adult females (based on the number of nests) in 1966. The effects of these assumptions on model outputs are shown and discussed in the two assessment reports (Turtle Expert Working Group, 1998, 2000).

Although all available years were used to construct the original models (1966–99), because of uncertainties in the number of nests prior to 1978 and the time lag required to "build-up" the model population's age distribution, we fit the models to minimize sum-of-squares error for 1978–96 (Turtle Expert Working Group, 2000). Nests in years 1997–99 were checked against the model predictions for those years to see how well the models behaved. For this paper, we continued the data set to 2003 and compare the models' expected nest numbers to counts provided by the Gladys Porter Zoo (Fig. 1).

Model Parameters. — The instantaneous mortality rate for small benthic immature turtles (20–50 cm straight carapace length [SCL], age 2–6 yrs) was estimated using a catch curve of stranded turtles, which estimates an instantaneous mortality rate as the slope of a line drawn through the ln-transformed estimate of turtle abundance in each age class (Hilborn and Walters, 1992). We used a von Bertalanffy growth curve estimated by Jeff Schmid and Amy Woodhead (Turtle Expert Working Group, 2000) to translate size to age assuming a birthday of 1 July. Two primary methods were used to determine small benthic immature mortality from pre-1990 strandings data: a cohort-based model that examined reductions in strandings-at-age for each year class, and a year-based model that assumed that the reduction in strandings-at-age within a year reflected a constant annual mortality rate for all cohorts. Both methods required corrections; the cohort model had to be corrected for the relative change in total annual strandings through time, while the yearly model required a correction for cohort strength. In all cases, the relationship between age class and strandings deteriorated markedly after 6 years of age. This may be due to variable growth rates in larger turtles or to a change in capture probability. Because we could not reliably estimate the slope of the mortality function for turtles in older age-classes, we decided to apply our mortality rate estimate only to small benthic immatures age 2–6 yrs.

Pelagic immature, large benthic immature, and adult mortality rates were estimated by fitting the model for least squares calculations of expected nests vs. the observed number of nests. We used the Microsoft™ Excel 7.0 Solver Generalized Reduced Gradient (GRG2) nonlinear optimization algorithm to estimate these unknown mortality rates, and assigned the same fitted mortality rate to both large benthic immatures and adults (Fig. 2). We found that an additional parameter was needed to attain the observed rates of population increase: a multiplier (<1.0) that reduced the instantaneous mortality rates for the three benthic stages starting in model years 1990–91. The value of this multiplier was also determined by the model fitting routine.

Model Projections. — We used the three post-1990 models to project the population size over time assuming constant mortality rates. We also calculated the estimated age distributions for 1999. These projections did not include annual variability in mortality or fecundity, but we did examine the effects of a step-wise reduction in egg survival that might occur as nest numbers exceed the capacity of the corrals. The egg survival rates for each nest level were based in part on predicted corral capacity and future protection measures (R. Márquez, *pers. obs.*): 0.65 for the first 5000 nests, 0.5 for the next 1000 nests, which would be screened from predators but left *in-situ*, 0.3 for the next 4000 nests, and 0.2 for nests exceeding the 10,000 nest level. Our goal was not to design a model that could quantitatively forecast population dynamics; our projections served merely to illustrate differences in potential population growth rates for the different models tested and provide a rough estimate of time to 10,000 nesting females, assuming no changes in vital rates over time.

RESULTS

Catch Curve Analysis. — For benthic immatures age 2–6 yrs we estimated a total instantaneous mortality (Z) of 0.3–0.8, depending on the catch curve method and number of years used in the analysis. This translates into an annual proportional survival rate (S) of 0.74–0.45, where $S = \exp^{(-Z)}$. Several catch curve slopes converged on about $Z = 0.5$ ($S = 0.61$), so we used this value to compare model fits for 8, 10, and 12 years to maturity.

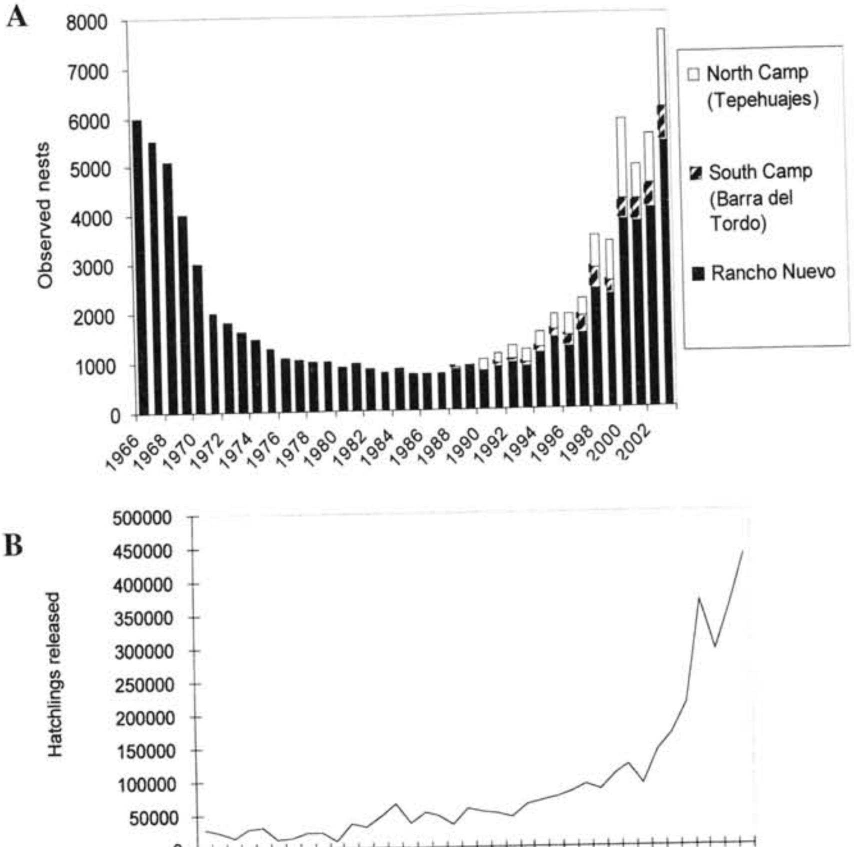

Figure 1. Kemp's ridley nests **(A)** and hatchlings released **(B)** annually at Rancho Nuevo, Tepehuajes, and Barra del Tordo, Tamaulipas, Mexico, 1966–2003.

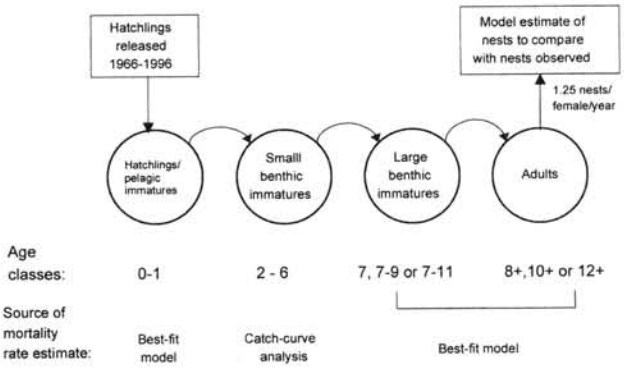

Figure 2. Schematic of the population models used by the Turtle Expert Working Group (1998, 2000).

Model Fitting for Age to Maturity. — The best-fit parameter estimates and residual sums-of squares for model nests vs. observed nests (1978–96) and small benthic immature $Z = 0.5$ are shown in Table 1. Of the three models (8, 10, and 12 yrs), 10 years to maturity gave the best fit with observed nests (Fig. 3), but only if a post-1990 multiplier of 56% was included (total instantaneous mortality Z multiplied by 0.56 for benthic immature and adult turtles) (Table 2). All three models showed very poor fits if mortality was not decreased in recent years. Changing the small benthic immature mortality rate had little effect on model sums-of-squares or residual patterns of model vs. observed nests because the best-fit estimate for pelagic immature mortality simply compensated for those changes to achieve the same number of nests.

Population Rates of Increase. — The observed mean annual rate of increase for nests, calculated for the years 1988–99, was 12.9% ($r^2 = 0.95$); the addition of nesting data through 2003 gave a growth rate of 14.9% per year ($r^2 = 0.96$). Hatchling production over the same time interval increased by 10.3% per year ($r^2 = 0.95$), but with more rapid increases in recent years. The addition of nesting data through 2003 gave a growth rate of 14.9% per year ($r^2 = 0.96$) for nests and 13.15% per year ($r^2 = 0.91$) for hatchlings. All three of our models predicted a 12-14% per year increase in benthic immature turtles for years 1988–97. Strandings of benthic immature turtles on U.S. beaches increased by 11.5% over the same time period, but with larger increases in the Gulf of Mexico (Turtle Expert Working Group, 2000).

Assuming no changes in annual mortality and constant 65% egg survival each year, the future rates of increase for the 8, 10, and 12 years to maturity models were 13.9%, 15.1%, and 14.8% per year, respectively, calculated for the years 2015–25. The model rates of increase depended on constant high egg survival and constant mortality rates through time. When we simulated a reduction in egg survival with increasing nest density, the rates of increase dropped dramatically to 7.9%, 9.2%, and 10.1% per year for years 2015–25. However, there was a lag in this decrease in the population growth rate due to age at maturity, and in all model projections the rate of nest increase did not drop substantially until after the 10,000 nesting females goal had been reached.

Estimates of Population Size. — We estimated population size as a function of its sensitivity to the small benthic immature mortality rate. We added the total number of small benthic immature, large benthic immature, and adult turtles expected by each model in 2000, using small benthic immature $Z = 0.5$ and assuming a 1:1 sex ratio (Table 2). The number of adults expected did not vary much as this was directly related to the number of nests. But population sizes for the remaining stages differed dramatically for each model because of differences in the estimated mortality rates and the number of age classes in the large benthic immature stage. We analyzed the sensitivity of our 2000 population size estimate to changes in the small benthic immature survival rates with the 10 years to maturity model (Fig. 4). While the expected number of adults remains relatively constant, the size of the small immature stage varies by 5-fold and the large immature stage by over 150%. This results in an estimate of 25,000 – 93,000 benthic turtles (adults and juveniles) for the year 2000, simply due to our uncertainty in parameter estimates.

DISCUSSION

Since the completion of the second assessment report (Turtle Expert Working Group, 2000), the number of Kemp's ridley nests at Rancho Nuevo and neighboring camps has continued to increase rapidly, with over 6000 nests protected in 2000 (Márquez et al., 2001) and over 8000 nests protected in 2003 (U.S.-Mexican Project, 2003; Márquez et al., 2004).

Table 1. Parameter estimates and sums-of-squares for 4 different population models fit to observed nests, assuming a small benthic immature instantaneous mortality rate (Z) of 0.5 (annual survival $S = 0.61$, where $S = \exp^{-Z}$) prior to 1991. The post-1990 multiplier (x) represents a proportion multiplied by the instantaneous mortality rates of small benthic immature, large benthic immature, and adult turtles, giving a post-1990 $S = \exp^{(-Z*x)}$. Projections of time to reach 10,000 nesting females are based on constant mortality rates and egg survival = 65%.

	Pelagic immature annual survival		Large benthic immature and adult annual survival (age 7+)		Post-1990 instantaneous mortality multiplier	Sums-of-squares, 1978–96	Year to reach 10,000 nesting females
Age at maturity	pre-1990	post-1990	pre-1990	post-1990			
8	0.25	0.25	0.84	0.90	0.62	209,838	2016
10	0.31	0.31	0.85	0.91	0.56	86,669	2013
12	0.37	0.37	0.85	0.92	0.55	165,800	2014
10 – without post-1990 multiplier	0.38	0.38	0.83	0.83	1.00	606,936	2044

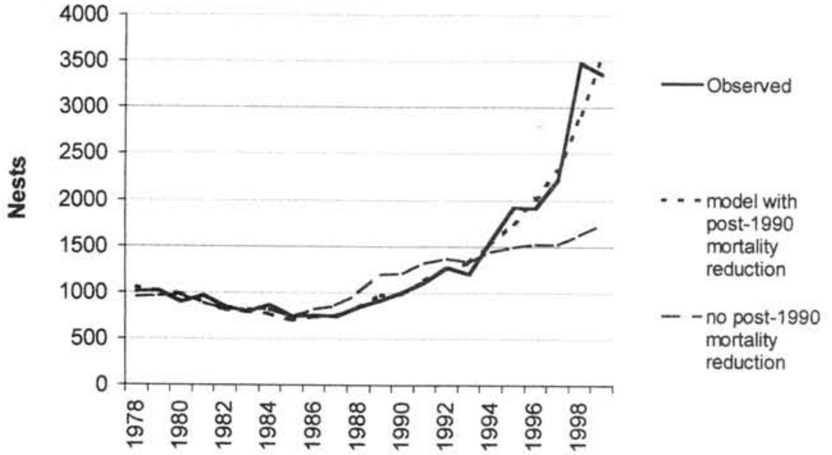

Figure 3. Model predicted nests vs. nests observed for the 10 years-to-maturity model, with and without the post-1990 mortality multiplier which increases the annual survival rate of benthic immature and adult turtles after 1990.

Although our models did not produce a reliable estimate of population size, we did learn some important things that may aid future management efforts.

1. An increase in annual survival of benthic immatures and/or adults has occurred over the past 7–8 years. This is evident from an increase in the number of nests per hatchling released and the need for a mortality reduction in the model to match the recent observed rate of increase in nests. We did not conduct a sensitivity analysis to determine the exact year that this mortality decrease took place; undoubtedly it was not a step-wise change from one constant rate to another. But it is possible that management efforts by Mexico and the U.S. directed at reducing at-sea mortality of benthic-feeding juveniles and adults are responsible. It seems unlikely that the current rate of increase is due to nest protection efforts alone, but rather to a combination of increased cohort size through the hatchery program and reduced fishing mortality. Our model estimates of the post-1990 decrease in instantaneous mortality are strongly dependent on the age at maturity (Table 1).

2. The population could reach 10,000 nesting females by 2015 if our fitted mortality rates are reasonably correct and remain constant. All three models predict rapid population increase with the best-fit mortality estimates. However, extrapolations of the models should be interpreted cautiously because model fits do not reflect potential changes in mortality rates. Nest counts from 1997–2003 suggest that the population may be growing even faster than the models predict. Continued monitoring over the next few years may reveal whether this rate of increase is likely to be maintained and how our models should be updated.

Table 2. Estimates of population size (benthic feeding turtles only, males + females, rounded to nearest hundred) for the year 2001 from 3 population models with varying age to maturity. Small benthic immature $Z = 0.5$ (annual survival = 0.61) for all models. Assumes 1:1 sex ratio. The number of age classes included in the large benthic immature stage depends on age at maturity. The actual number of nests recorded at Rancho Nuevo, Tepehuajes, and Barra el Tordo in 2003 was 7600 (J. Peña, *pers. comm.*).

Age at maturity (yrs)	Small benthic immatures (20-50 cm, age 2-6)	Large benthic immatures (age 7 to age at maturity-1)	Adults	Nesting females	Nests
8	42,300	1,850	8,600	2150	5380
10	81,400	9,000	10,100	2530	6320
12	101,000	18,500	10,000	2510	6280

3. Time lags are important. Population monitoring that is based on nest counts alone results in assessments that are strongly influenced by the time lag to maturity. The realization of changes in population trends due to management efforts that affect juvenile life stages will be delayed and, potentially, swamped by environmental variance or concomitant management actions. The 10 years-to-maturity model provided the best fit, although this should not be taken as strong evidence that Kemp's ridleys mature in 10 years. Recent skeletochronology and growth curve estimation puts age at maturity closer to 12 years (Snover, 2002). A polyphasic growth curve fit to age-length data obtained from growth rings on the humerus bones of dead turtles placed age at 60 cm SCL (minimum size at maturation) around 12–14 years and suggested that mean age at maturity could be greater, between 15 and 20 years (Chaloupka and Zug, 1997). This study also indicated that Kemp's ridley growth rates can be highly variable through life and likely highly variable among individuals. We were unable to fit our models to age at first reproduction of greater than 14 years because annual survival rates in the pelagic stage had to be greater than 1.0 to achieve a fit (Turtle Expert Working Group, 1998). This does not preclude the possibility that some Kemp's ridleys mature at a later age, only that we were not able to generate a simple model (constant age at maturity and survival rates) with a late age at maturity that would fit the observed number of nests.

4. Future reductions in nest survival will dramatically slow the population growth rate, although potentially not before the population reaches 10,000 nesters. Various functions could be used to model the impact of reduced nest survival. Our current model suggests that these effects will not be manifested as a reduction in nests for several years because these reductions have not yet occurred (although egg survival in 1998 was lower than normal due to extreme weather conditions). It is important to be realistic about the

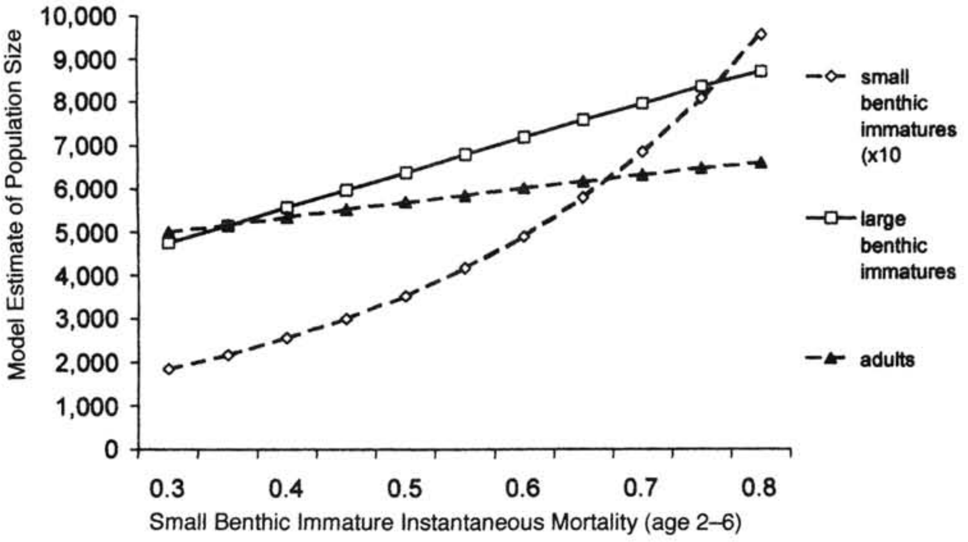

Figure 4. Changes in the 1999 population size estimates for each life stage from best-fit models using different small benthic immature mortality rates. Example shown is from the 10 years-to-maturity model.

level of egg survival achievable with continued nest protection efforts. The rapid population growth rates calculated by our best-fit models can only be maintained by a high level of egg survival (65%). As corral capacity becomes limiting and as the population expands into unprotected areas the proportion of nests laid that produce surviving hatchlings will undoubtedly decrease, even though the absolute number of hatchlings should continue to increase for many years with continued management.

5. The model estimate of population size is very sensitive to our estimate of benthic immature mortality and growth rate estimates. This is not surprising, given that in our deterministic models the size of an individual cohort is dependent on its initial size (hatchlings released) and survivorship to a given age. If mortality is high early in life, cohort size will be smaller in the benthic stages and vice-versa. To get the correct output (i.e., number of nests from neophytes), mortality rates must balance each other through the immature phase. Thus, when our mortality estimate for small benthic immatures was high, the pelagic immature and large benthic immature mortality rates were necessarily low. If better mortality estimates for benthic immature stages can be obtained, our range of possible population size will decrease. But without an estimate of the proportion of a cohort lost in the pelagic phase we will continue to have this compensation problem in the model fits.

This model fell short of our original goals because we did not have enough information about juvenile mortality to calculate a reliable estimate of population size. Nor was it possible to eliminate one or more of the models by comparing model output to empirical data. Management recommendations such as allowable take limits cannot be adequately answered without a population size estimate, whether it comes from a population model or empirical observation. Establishing the number or proportion of a population that can be removed without adversely affecting its recovery rate depends on procuring defensible estimates of natural and fishing mortality rates, size of the population (all or most life stages), and recruitment to the nesting population. It is likely that many of these parameters can be obtained through continued field work and further analysis of existing data. Until that time, management efforts should continue to minimize at-sea mortality and increase cohort size through nest protection.

We could improve the existing models by adding stochastic variability in the survival rates, variable growth rates and reproductive rates (remigration interval and nests/female), and catastrophes. Relying on a deterministic model to estimate future population size would be rash, and we strongly advise that our results be used to guide future research and modeling efforts and not as a basis for making specific management decisions. However, without reliable estimates of mean mortality rates we feel it is premature to add additional unknowns in the form of variance parameters. At this point, the ranges of mortality and growth rates are primarily a result of uncertainty, not environmental variability. This distinction should be made prior to constructing models for forecasting population size (Beissinger and Westphal, 1998).

The Turtle Expert Working Group (2000) advised that future research effort should be focused on improving our estimates of growth and mortality and ways to empirically estimate population distribution and abundance. Important existing field projects include in-water mark-recapture surveys and tagging and monitoring efforts at Rancho Nuevo. Trends in abundance of at-sea life stages may also be useful, although they are difficult to detect if capture rates are highly variable (Taylor and Gerrodette, 1993). We anticipate that improved models can be constructed as better data are accumulated, and after verification with field data, such models could be used to formulate more specific management plans.

Currently, the Kemp's Ridley Recovery Team is using an updated version of the model to reformulate the federal recovery plan. New information on age at maturity from skeletochronology (Chaloupka and Zug, 1998; Snover, 2002) has suggested that 12 years to maturity is most plausible, and sex ratio estimates from work at Rancho Nuevo suggests a primary sex ratio of 70% female (T. Wibbels, *pers. comm.*). Unfortunately, there are no updates available for survival rates. The new parameters give qualitatively similar results: pelagic juvenile survival = 0.35, adult/large benthic juvenile survival = 0.845 prior to 1990, and a post-1990 multiplier of 0.55. The model's population growth rate is 16% per year, with an estimate of 2012 as the year to reach 10,000 nesting females if survival rates remain constant. Corral capacity scenarios with this model suggest that population growth will gradually decrease, due to a reduction in mean egg survival rate. However, unless growth or survival of juvenile and adult turtles is reduced by environmental factors or human interactions, positive population growth is expected to continue for some time.

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