Ecological Applications, 4(3), 1994, pp. 437–445

PREDICTING THE IMPACT OF TURTLE EXCLUDER DEVICES ON LOGGERHEAD SEA TURTLE POPULATIONS[1]

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Abstract. In this paper, we modified and updated a stage-based population model for loggerhead sea turtles (*Caretta caretta*) and used the model to project potential population-level effects of the use of turtle excluder devices (TEDs) in trawl fisheries of the southeastern US. We reduced the seven-stage model of Crouse et al. (1987) to a five-stage model and performed sensitivity analyses on the matrix. The most sensitive matrix parameters were those dealing with survival while remaining in a stage, rather than growth from one stage to the next or reproductive output. Population growth rate was most sensitive to survival in the large juvenile stage, followed by small juvenile survival. Large juveniles are the most common size class among stranded dead turtles found on beaches; 70–80% of strandings are thought to be related to trawl fisheries.

Simulations of our loggerhead model based on estimated effects of TED regulations on stage-specific survivorship suggested that southeastern US loggerhead populations should increase, but rather slowly. If TEDs were required during the shrimping season in offshore areas only (as they were from 1990 to 1992), 70 yr or more would be required for the simulated population to increase by an order of magnitude. Recent estimates of TED effects from South Carolina strandings data suggest a similar recovery rate. Good compliance with regulations requiring TEDs year-round in all waters could allow the population to increase nearly twice as fast as that expected under the "seasonal offshore" regulations. We also used a Leslie matrix version of the model to illustrate the expected transient response in the numbers of females expected on nesting beaches (due to shifting age-size structures with TED use). Rather than a monotonic increase, we expect an initial increase in the number of nesting females, followed by a leveling off or slight decline (perhaps 10–15 yr from now), followed by another increase. The magnitude of the projected population increase will depend upon the actual increases in stage-specific survivorship due to TED regulations. New, or compensatory, sources of mortality could slow or reverse this projected recovery.

Key words: Caretta caretta; *conservation biology; endangered species; loggerhead sea turtles; population modeling; population projection matrix; southeastern US; stage-based modeling; turtle excluder devices.*

INTRODUCTION

All five species of sea turtles found in United States waters are listed as endangered or threatened under the Endangered Species Act of 1973. Of seven sea turtle species recognized worldwide, six are listed pursuant to the Endangered Species Act. All seven are included on the Convention on International Trade in Endangered Species (CITES) appendixes and the World Conservation Union's (IUCN) *Red Data Book* lists. Given limited resources, our conservation efforts need to be focused where they will be most effective.

In 1987, Crouse et al. used a stage-based matrix model for southeastern US loggerhead sea turtles (*Caretta caretta*) to evaluate the strengths and weaknesses in our current knowledge of sea turtle population dynamics as well as the efficacy of several management alternatives on the species' conservation. The authors concluded that, while more studies are needed to strengthen estimates of 1st-yr and small juvenile mortality, growth rates, and age at first reproduction, efforts to improve survivorship of the large juvenile and adult stages appeared far more effective in ensuring population maintenance and growth than did increases in egg survivorship or fecundity. They also noted that the critical large juvenile stage was the most common size

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[1] Manuscript received 12 July 1993; accepted 29 September 1993; final version received 12 November 1993.

class among dead sea turtles stranded on southeastern US beaches.

A National Academy of Sciences panel recently summarized natural and human-caused sources of mortality for sea turtles in US waters (National Research Council 1990). The panel concluded that incidental capture and drowning in shrimp trawls accounted for more deaths than all other human activities combined and may have resulted in >40 000 sea turtle deaths annually in recent years. They affirmed the findings of Crouse et al. (1987) and recommended the use of turtle excluder devices (TEDs—escape hatches that can be inserted into existing trawl nets) in most waters at most times of the year. Turtle excluder devices have been developed to reduce bycatch of sea turtles in trawl fisheries (Seidel and McVea 1982), but their use remains controversial (Rudloe and Rudloe 1989).

Prior to the implementation of TEDs, most sea turtle management in the southeast US consisted of enhancing egg and hatchling survival through protection of nests on beaches or removal of eggs to protected hatcheries. In addition to these egg protection efforts, in 1987 regulations were declared requiring TEDs in shrimp trawls in offshore waters during the primary shrimping season (1 May–31 August) from North Carolina to Texas. Over the next 2 yr, implementation of these regulations was delayed due to challenges in court and in Congress. The regulations were finally implemented and enforced beginning in September 1989. The summers of 1990–1992 saw the first full implementation of federal regulations requiring seasonal use of TEDs in offshore waters. In December 1992, TEDs were required year-round in offshore waters, and current regulations will require all inshore shrimp boats to use TEDs year-round by December 1994. Meanwhile, new potential threats such as a *Sargassum* harvest, which may impact survival of the small juvenile turtles, are under investigation (Coston-Clements et al. 1991).

One can use population models to estimate future population trends and responses to management regimes, but this approach is somewhat constrained by the available data. Because of limitations in tagging technologies, many details of the loggerhead life history are still poorly known; thus growth rates and age at first reproduction as well as survivorship in some stages are based on preliminary estimates (Frazer 1983*a*, *b*, 1984, 1987), and several assumptions have been made (cf. Crouse et al. 1987). But the estimates seem reasonable as first approximations, and one of the benefits of the matrix projection technique is the ability to identify, via sensitivity analysis, those parameter estimates which are most important to verify.

Our primary goal was to develop and modify the loggerhead population model (Crouse et al. 1987) and to use this model to simulate recovery rates of loggerhead populations in response to "seasonal offshore" TED requirements (1990–1992). We also examined the potential impact of expanded requirements for the use of turtle excluder devices (TEDs) in trawl fisheries of the southeastern United States. The purpose of the model simulations is primarily heuristic—to clarify the importance of our limited knowledge of particular life history parameters as a guide to research and management. But we have also used the model to examine population-level implications of particular management strategies that intervene at different life stages.

MODEL DEVELOPMENT AND IMPLEMENTATION

As suggested in the National Academy of Sciences report on the decline of sea turtles (National Research Council 1990), we reduced the original seven-stage model proposed by Crouse et al. (1987) to a five-stage model, combining the three adult stage classes (novice breeders, 1st-yr remigrants, and adult breeders) into a single group. Because all three of the original adult stages had the same estimate for annual survivorship, only a minor modification in the annual fecundity estimate had to be made for the new five-stage model. This fecundity estimate characterizes average annual egg contribution based on fecundity of each age class weighted for the proportion of the female population in each class. The stages, stage durations, survivorships, and fecundity values used in the new matrix are given in Table 1. All caveats and assumptions outlined by Crouse et al. (1987) for the seven-stage model still apply.

Another minor change from the parameters in Crouse et al. (1987) is a reduction of small juvenile survivorship. The value of 0.8144 was estimated by Frazer (1983*a*) for the Little Cumberland Island loggerhead life table. This value may be too high; it was calculated assuming an annual population decline of 3%/yr. The true value for small juvenile survivorship is unknown, as these small turtles are highly pelagic and rarely seen. In recent years, Frazer, Dr. James Richardson, and others at Little Cumberland Island have seen a more rapid rate of population decline, ≈5%/yr. Therefore, we have reduced small juvenile survivorship to 0.75 in the new model, which results in a calculated decline of 4.96%/yr.

A new method for calculating matrix elements in a stage-classified model was introduced by Caswell (1989). It uses stage duration and an initial estimate of the rate of population change to calculate the annual probability of growing into the next stage class (see Appendix 1). The matrix transition parameters are then defined and calculated (Appendix 1). The form of the stage class population matrix is as follows:

$$A = \begin{matrix} P_1 & F_2 & F_3 & F_4 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5, \end{matrix}$$

where P_i is the probability of surviving and remaining in the same stage, G_i is the probability of surviving and

TABLE 1. Five-stage life history parameters for loggerhead sea turtles based on the model in Crouse et al. (1987), modified to reflect ≈5% annual decline in Little Cumberland Island loggerheads.

Stage	Description	Stage duration (yr)	Annual survivorship (σ)	Annual fecundity
1	Eggs/hatchlings	1	0.6747	0
2	Small juveniles	7	0.75	0
3	Large juveniles	8	0.6758	0
4	Subadults	6	0.7425	0
5	Adults	>32	0.8091	76.5

growing into the next stage, and F_i is the stage-specific reproductive output.

Each year of a simulation (i.e., each time the matrix is multiplied by a population vector) a proportion of the individuals in a stage class makes a transition into the next stage according to the estimated probabilities (Table 2). The timing of the "census," or the time during the simulated year when the multiplication takes place, plays a critical role in determining values of F_i. For our model, we assume the census takes place right after nesting (a post-breeding census). Thus reproductive output for adults is dependent on their survival through the previous year (0.8091), as well as the predicted remigration interval, number of clutches, and number of eggs per clutch. Because the census takes place only once per year, those subadults that will grow into the adult stage must also contribute to reproduction. Thus, the final matrix includes a small value, F_4, for subadults (Table 2).

Each population matrix $\mathcal{A}$ has a corresponding right eigenvector that represents the stable stage distribution w (Table 3). Any initial population stage structure projected forward will tend to converge on the new stable stage distribution where each stage class increases at the same rate, λ. At the stable stage distribution, this population is dominated by small juveniles; the adult stage accounts for only 0.3% of the total population.

The stage-specific reproductive values are given by the left eigenvector v (Table 3). These reproductive values estimate the expected per capita contribution of individuals in each stage to population growth. Note the pattern in reproductive values. The transition from eggs/hatchlings to small juveniles confers a 40% increase in reproductive value. The transition from small juveniles to large juveniles increases reproductive value 4.4×. As they grow from large juveniles to subadults, individuals increase their reproductive value more than 14.3×. Finally, the transition from subadult to adult confers an additional 2.8-fold increase in reproductive value. Reproductive value increases most rapidly during the large juvenile stage.

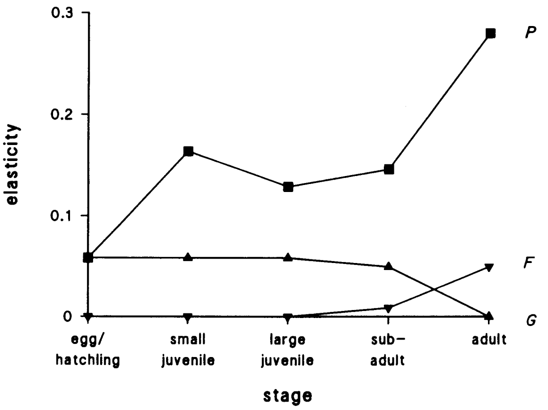

FIG. 1. The elasticity, or proportional sensitivity, of λ to changes in reproductive output (F), survival while remaining in the same stage (P), and survival with growth into the next stage (G). Because the elasticities sum to one (Caswell 1989), they can be compared directly in terms of their contribution to population growth rate, r.

SENSITIVITY ANALYSES

We performed three types of sensitivity analysis on the new model, similar to those given in Crouse et al. (1987, see Appendix 2). The proportional sensitivity (or "elasticity") of the dominant eigenvector λ to changes in any of the matrix elements (P, G, or F) is given in Fig. 1. The elasticity values sum to one over all matrix elements (Caswell 1989); so Fig. 1 shows the relative contribution of each matrix element to λ. The graph indicates that changes in P values (the probability of surviving but remaining in the same class) will have a greater effect on the population than changes in stage-specific reproductive output (F) or growth (G).

Because P and G sum to the survival probability σ and cannot be altered independently, it may be more useful to calculate the overall elasticity of λ to changes in σ for each stage class (for equations see Appendix 2). This analysis suggests that large juveniles are the most critical stage (Fig. 2), followed by small juveniles. Estimates of survival in the juvenile stages, particularly for small juveniles, still need a stronger empirical basis (Crouse et al. 1987). Egg and hatchling survival contributes little to population growth because this stage is short compared to the life-span of a turtle and the reproductive value of these individuals is low.

One topic of considerable debate among sea turtle biologists is the estimated length of each life history stage. The stage lengths used in this model were originally estimated based on growth curves derived by Frazer and Ehrhart (1985). The elasticity to changes in stage duration suggests that uncertainty in the duration of the large juvenile stage has the greatest effect

TABLE 2. Five-stage population matrix $\mathcal{A}$ for loggerhead sea turtles.

0	0	0	4.665	61.896
.675	.703	0	0	0
0	.047	.657	0	0
0	0	.019	0.682	0
0	0	0	0.061	0.8091

TABLE 3. Stable stage distribution (w) and reproductive values (v) for the loggerhead population matrix given in Table 2.

Stage	Stable stage distribution	Reproductive value
1	0.2385	1
2	0.6478	1.4
3	0.1033	7.5
4	0.0073	115.0
5	0.0031	432.2

on λ (Fig. 3). Note that elasticities to duration are negative because duration and population growth rate are inversely correlated. But elasticities for duration are much lower in absolute value than those for survivorship and so have a small overall effect.

Finally, we performed a series of simulations to calculate changes in the rate of population growth with decreases in annual mortality (mortality = 1 − survival) during a particular stage (Fig. 4). Recall that the intrinsic rate of increase of the population is equal to ln(λ). A 10% reduction from current mortality rates in any one stage still leads to an overall population decline. A 50% reduction in mortality in the large juvenile stage would allow the simulated loggerhead population to recover; a 50% reduction in mortality in any other stage would merely slow the rate of population decline. A 90% decline in mortality in any one stage (except eggs and hatchlings) would allow the population to increase.

As in the Crouse et al. (1987) model, even perfect survival in the egg and hatchling stage would not allow a population increase unless mortality can also be reduced at some later stage. Changes in large juvenile mortality have the greatest effect on the population growth rate. Reasonable increases in reproductive output alone could not lead to a population increase given the current survival schedules (Fig. 4).

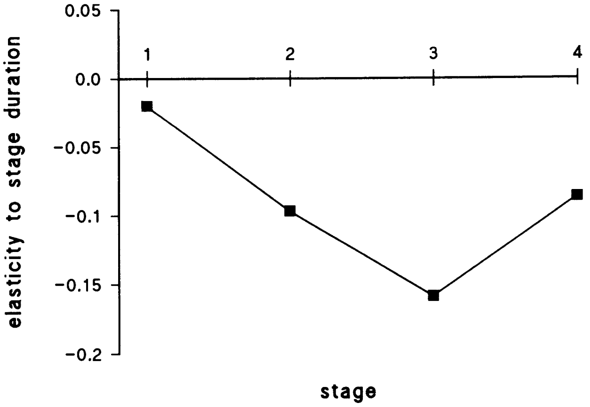

FIG. 3. The elasticity, or proportional sensitivity, of λ to changes in stage duration.

SIMULATIONS OF VARIOUS MANAGEMENT SCENARIOS

We used the model to forecast changes in loggerhead population size due to implementation of turtle excluder devices (TEDs). First, we calculated predicted responses in population growth rates (λ) due to decreases in large juvenile, subadult, and adult mortality. For this initial prediction we assumed that TEDs will have the same effect on each of these three stages. Small juveniles strand less frequently and may be less available to trawls because these juveniles are more common offshore. The response surface (Fig. 5) shows a family of lines indicating simulated population trajectories as mortality is decreased by 10% intervals over the range 0–80% for large juveniles, subadults, and adults. Because the model is deterministic and predicts an exponential growth rate, the trajectories appear as straight lines on a log plot. We acknowledge the considerable uncertainty in making quantitative population projections using a simple deterministic model.

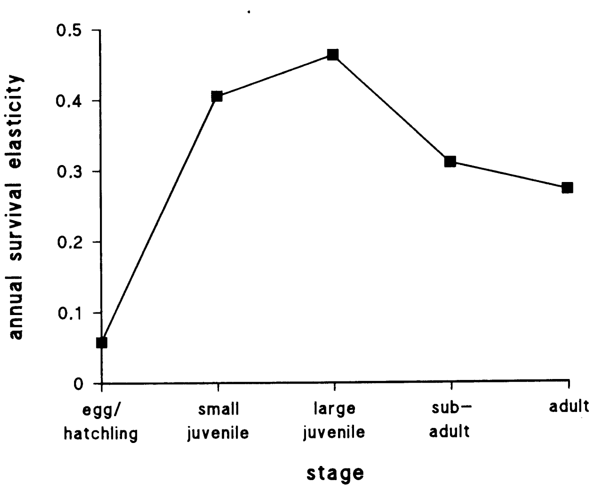

FIG. 2. The elasticity, or proportional sensitivity, of λ to changes in annual stage-specific survival probability.

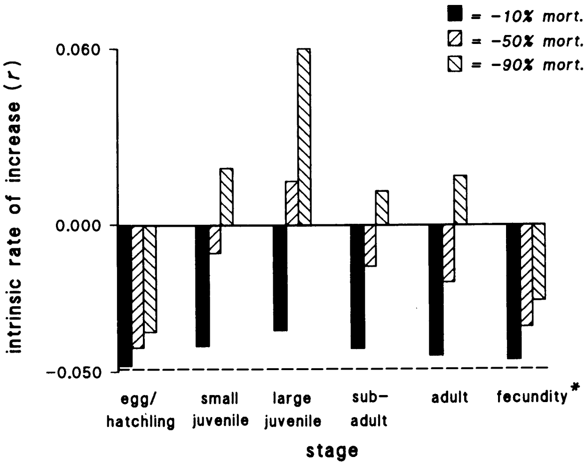

FIG. 4. Effect of stage-specific mortality rate reductions of 10, 50, and 90% on loggerhead population growth rate, r. *Fecundity values reflect an increase of 10, 50, or 90%.

But our interest is primarily in determining our qualitative position on the population response surface.

Assuming that growth and survivorship rates in the model population approximate those of southeastern US loggerheads, and that TEDs can reduce mortality in large juveniles, subadults, and adults by 20% or more, the loggerhead population could recover eventually. If mortality is reduced by 40% or more we may see an order-of-magnitude increase in loggerheads in 50 yr or less. But the response surface (Fig. 5) is based on the turtles reaching their new stable stage distribution (which takes 20–30 yr, based on simulations). In fact, we expect the current stage distribution to reflect non-TED years, which induces a time lag into the transient response of the population. We address the possible effects of this transient response after we discuss various management scenarios.

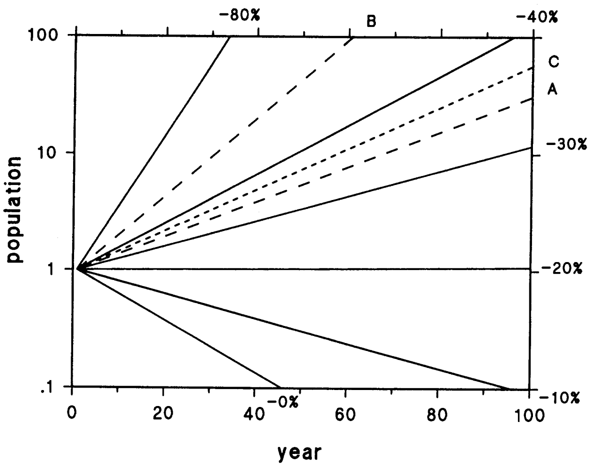

FIG. 5. Projected loggerhead population response to reductions in mortality in large juveniles, subadults, and adults. Lines indicate reductions in mortality rates at 0% (population vital rates without TEDs), 10, 20, 30, 40, and 80%. Line A shows the projected population response to reductions in trawling-related mortality commensurate with "seasonal offshore" TED regulations. Line B shows the projected population response to expanded (all waters, all seasons) TED regulations. Line C is based on reductions in the numbers of stranded turtles in South Carolina, which is assumed to be proportional to trawling-related mortality.

TED EFFECTS ON LOGGERHEADS

The proportion of the total mortality of particular stages of loggerhead sea turtles caused by shrimp trawls is not yet known (National Research Council 1990), which makes it difficult to predict if or how rapidly loggerhead populations might increase with TED regulations in place. The National Academy of Sciences Panel (National Research Council 1990) estimated that 70–80% of stranded turtles may have been caught and killed in shrimp trawls; if TEDs are 97% effective (as required for certification) they could reduce trawling-related mortality substantially. But it remains unclear what proportion of total mortality in particular stage classes is trawling related.

Although all of the US loggerhead populations have been subject to trawling pressure, a well-studied loggerhead population in Australia, that is relatively isolated from trawling activity, may provide reasonable survivorship estimates for a relatively unexploited population (C. Limpus, *unpublished data*). Loggerhead turtles on Heron Island, Queensland, show annual survivorships of 0.91 for adults and 0.83 for large juveniles and 0.885 for subadults (based on preliminary calculations). In addition, Henwood et al. (1992) examined the impact of TEDs on sea turtles based on extensive TED testing and predicted that trawling-related mortality may be reduced by about two-thirds under the "seasonal offshore" TED regulations which were in effect in 1990–1992.

To predict the population response for US turtles with TEDs in place, we took the difference between Australian and US survivorships for large juveniles, subadults, and adults, then multiplied those differences by 0.67. The result for each stage was then added to the current survivorship estimate. This assumes that sources of mortality are additive and that upon reducing trawling-related mortality, mortality from other causes would remain unchanged. If there is compensatory mortality, our projected times for the population to reach a particular size would increase. We also simulated the effect of the expansion of TED regulations to all waters at all times by assuming a trawling-related mortality reduction of 0.99 (cf. Henwood et al. 1992). We recognize that using vital rates from Australian loggerheads to simulate southeastern US populations is risky, but we simply have no data on unexploited populations in the US.

The population projection for the 0.67 reduction in trawling-related mortality due to "seasonal offshore" TED regulations suggests a reduction of total mortality of loggerhead sea turtles in vulnerable stages of ≈35%. In terms of population dynamics, this implies that under these regulations ≈70 yr would be required for an order-of-magnitude increase in simulated loggerhead abundance (Fig. 5, line A). This line corresponds to a rate of population increase of 3.6%/yr. A 0.99 reduction in trawling-related mortality due to expanded TED regulations would lead to a nearly 50% reduction in overall mortality (Fig. 5, line B). This implies that an order-of-magnitude increase in loggerhead population size could be achieved in about half the time if TED regulations were expanded and good compliance with the regulations was achieved.

Another way of estimating the reduction in mortality due to TEDs is to examine recent reductions in sea turtle strandings. Stranded turtles are found dead on beaches; strandings are closely correlated with the onset of shrimping activity. Sally Hopkins-Murphy of the South Carolina Department of Wildlife and Marine Resources has accumulated 12 yr of reliable data on strandings throughout South Carolina. The number of

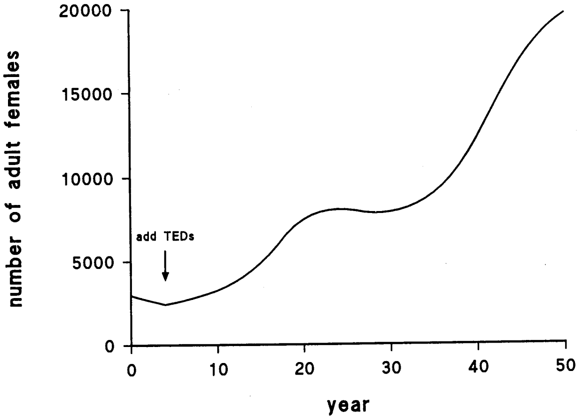

FIG. 6. Transient response in numbers of nesting loggerheads assuming 10^6 turtles distributed according to a stable age distribution in year 0 (≈1983). Mortality decreased to estimated levels under current TED regulations (Fig. 5) beginning in year 6 (Arrow: ≈1989) simulating the effects of TEDs. Note initial expected increases in the numbers of nesting females may be followed by leveling off or slight declines 10–15 yr after TEDs are introduced.

annual strandings may reflect shrimp trawling effects as well as a declining population (≈5%/yr, Murphy and Murphy 1989). But a strong negative correlation between the use of TEDs and strandings occurred in 1990 (S. Hopkins-Murphy, *unpublished data*), suggesting clear TED effects. TEDs were required from 1 May to 31 August, but the regulations went off on 1 September. A major increase in strandings never before observed in fall months occurred immediately after TEDs were no longer required (S. Hopkins-Murphy, *unpublished data*).

To estimate the reduced mortality due to TEDs from Hopkins-Murphy's strandings data, we calculated the mean biweekly strandings from the beginning of the shrimping season for each year to 31 August during the period when TEDs were not in use (1980–1987). The data were $\ln(X + 1)$ transformed to normalize variances and the means fit via least squares regression. Strandings for TED years (in 1988–1989 TEDs were required intermittently based on challenges to state and federal regulations; in 1990–1992 TEDs were required throughout shrimping season) were then compared with expectations based on the non-TED years. A mean reduction in strandings of 37% was estimated between that expected, based on the non-TED years, and 1990 and 1991 when TEDs were required through most of the shrimping season in state and federal waters.

When applied to large juveniles, subadults, and adults, the reduction in mortality estimated from the South Carolina strandings data suggests a very similar rate of population recovery (Fig. 5, line C) to that estimated from comparison of survival in exploited (Little Cumberland Island) vs. relatively unexploited (Heron Island, Australia) loggerhead populations (Fig. 5, line A). Additional data should help clarify possible loggerhead responses, but generally, the prognosis suggests that TEDs will have a significant impact on reversing the current decline in loggerhead populations. The population recovery, however, may be rather slow. Recovery rates should be enhanced substantially when TED regulations are expanded to include all waters in all seasons, if good compliance can be achieved (Fig. 5, line B).

TRANSIENT RESPONSE OF LOGGERHEADS TO TEDS

Trawling-related mortality has affected loggerheads on the Atlantic coast for several decades (Henwood and Stuntz 1987, National Research Council 1990). Shrimp harvest and shrimping effort both have increased over the past 20 yr. Because loggerheads take >20 yr to mature, current population age and size structures reflect this period of increasing trawling-related mortality. The use of TEDs should lead to a shift in population age/size structure as well as to changes in population numbers.

To illustrate the possible transient responses in loggerhead populations subject to intensive trawling bycatch, followed by an elimination of that mortality source by TEDs, we expanded our stage-based model to an age-based Leslie matrix. The Leslie model is a 54 × 54 matrix with each row and column representing a single year in a turtle's life. Unlike the stage-based model, the Leslie matrix incorporates time lags that affect turtle abundance. We began the simulation with 10^6 loggerheads distributed according to a stable age distribution in year 0 (similar to 1983) using mortality rates used in our stage-based model (see *Model development and implementation*). In year 6 (similar to 1989), we reduced mortality in large juveniles, subadults, and adults by 37% (line C, Fig. 5), simulating a "step function" effect of TEDs similar to that estimated for the "seasonal offshore" regulations. We ran the simulated transient responses in the number of adult females for the next 50 yr.

Our Leslie matrix simulations suggest that the transient response of the loggerhead population may be expected to show "waves" in abundance of nesting females (Fig. 6). Because the number of nesting females declined over the first 6 yr of the simulation, the number of eggs laid also declined, potentially resulting in a "hole" in the age/size distribution of the population that may be evident only when those reduced cohorts reach maturity. Depending upon variation in growth rates and how much TEDs actually reduce mortality for vulnerable stages, it is possible that we may see an initial increase in the numbers of nesting loggerheads, followed by a leveling off or slight decline 10–15 yr after TEDs are required. This should be followed by yet another increase beginning in 25–30 yr. Assuming all other effects equal over time, the wave will dissipate as the total number and average age of females increases and the population approaches its new stable stage distribution. However, this expected transient response will prolong the period required for the population to increase to any particular value relative to the equilibrium trajectories in Fig. 5.

DISCUSSION

The recent report of the National Academy of Sciences panel, *Decline of the Sea Turtles: Causes and Prevention* (National Research Council 1990) has argued strongly that shrimp trawling is *the* major source of mortality for sea turtles in US waters. Henwood and Stuntz (1987) estimated that 11 000 loggerheads and Kemp's ridleys (*Lepidochelys kempi*) experienced shrimping-related mortality annually. The National Academy panel judged this to be an underestimate, perhaps by a factor of 4. The panel also estimated that as many as 70–80% of the stranded turtles on southeastern US beaches were related to shrimp trawling. Crouse et al. (1987) noted that these stranded turtles are precisely the size class that is most sensitive in the loggerhead model (large juveniles), and, if conserved, could contribute most to a population recovery.

We know turtle excluder devices (TEDs) can protect these vulnerable and valuable stages. But the extent to which requiring TEDs in the shrimp fishery will be translated into changes in the trajectory of the loggerhead population is still to be learned. In our simulations, we estimate the response of the loggerhead population to various management scenarios including "seasonal offshore" TED regulations that were required from 1990–1992 and expanded TED regulations. Given the limitations in the available demographic data and the many assumptions one must employ when developing a population model, quantitative predictions such as we have made are risky. However, our expectations regarding the outcome of various management scenarios must be clearly stated so that we can determine whether we have obtained our management objectives (Taubes 1992).

In addition to the limitations in the basic demographic data (cf. Crouse et al. 1987), we also must estimate shrimping-related mortality. Henwood et al. (1992) argued that "seasonal offshore" TED regulations and enforcement can reduce shrimping-related mortality by two-thirds. But what proportion of total mortality is shrimping related? Fortunately, the Heron Island, Queensland, loggerhead population has been extensively monitored by Colin Limpus and provides reasonable survivorship estimates for a relatively unexploited loggerhead population. Recent reductions in strandings in South Carolina during the periods when TEDs have been required also suggest that shrimping-related mortality could be reduced sufficiently to allow the loggerhead populations to recover. The agreement between these two independent estimates of the mortality reduction based on current TED regulations is remarkable. Our estimates assume that shrimping-related mortality is noncompensatory (i.e., it is additive), and that if it is reduced, natural or other human-induced mortality rates will not increase. While our best estimates of TED effects suggest they can reverse the rapid rates of decline in loggerhead populations, how fast loggerheads will increase under current TED regulations remains to be determined.

We argue that the general form of the model is robust (cf. National Research Council 1990) and that while making quantitative forecasts is risky, the risks associated with *not* making forecasts of endangered species' responses to various management scenarios are also high (Taubes 1992). The Crouse et al. (1987) model focused our attention on the relative importance of the juvenile stages to loggerhead populations and provided support for the TED regulations. The simulations presented here suggest that TED regulations should allow the recovery of loggerheads, but that this recovery will be slow. Any compensatory mortality factors could slow or reverse this recovery. Expanded TED regulations could counter such compensatory mortality, speed the population recovery, and more quickly resolve uncertainty regarding the outcome of management decisions. Our simulations also suggest that the transient response of the population, due to shifting age-size structure, should lead to a short-term increase in the numbers of nesting females, followed by a leveling off or slight decline 10–15 yr after TEDs are required. This should be followed by another increase in nesting females. This expected transient response should be taken into account by researchers conducting beach survey programs. Finally, new or additional sources of mortality (e.g., related to *Sargassum* harvest or long-line fisheries) on sensitive life stages could reverse or retard this projected recovery.

We urge caution in extending our quantitative results directly to other sea turtle species (e.g., to Kemp's ridley as suggested in the National Research Council [1990] report). Each species has different life history parameters, and loggerhead population parameters are *much* better known than for any of the other sea turtles (Van Buskirk and Crowder 1994). Furthermore, these differences, particularly in stage-specific survivorship and age at first reproduction, can have strong effects on our predictive capability (Crouse et al. 1987). While we suspect the qualitative predictions of other sea turtle population models would be similar, quantitative predictions might differ dramatically.

We agree with Walters' (1991) recent assessment, "effective conservation of endangered species requires insightful research that incorporates theory, and that judicious use of research findings can result in designing successful management techniques." There is no substitute for a clear understanding of the basic natural history of an endangered species, including the basics of its life history evolution and population parameters. However, theoretical insights and models can assist in understanding the population-level implications of particular observations. Frequently, there are reasonably well-defined relationships between, for example, environmental variation and a particular life history parameter (e.g., predator numbers and egg survival), but we have only a limited understanding of the *population-level implications* of this relationship.

Population models, such as the loggerhead model, are probably most valuable from the perspective of identifying the importance of parameter sensitivity and so directing additional research efforts. The models also can help us to synthesize the available information on these stage-specific relationships and to address population-level questions. Because we are interested in the long-term viability of populations, we will frequently need to conduct this synthesis. Developing models for endangered species is risky in the sense that data are often limited, but if modeling is viewed as a process of synthesis and identifying sensitive parameters in the data and not as a product in itself, it can prove useful in conservation biology of endangered species.

ACKNOWLEDGMENTS

This research was supported by NOAA/NMFS and UNC Sea Grant (R/MER-21 and NOAA/NMFS NA90AA-D-S6847). We thank Nat Frazer, Jim Richardson, Col Limpus, and Sally Hopkins-Murphy for sharing data and insights. Hal Caswell and Libby Marschall helped with modeling questions and Andy Royle assisted with analysis of the strandings data. Nat Frazer, Hal Caswell, and Steve Carpenter commented on a previous version of the manuscript. Nancy Thompson, Bud Cross, and Brad Brown have provided institutional as well as personal support for this project.

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APPENDIX 1

MATRIX ELEMENT CALCULATIONS

The transition probabilities used in the loggerhead matrix model are calculated using fixed stage durations (per Caswell 1989). The distribution of individuals within a stage, and their subsequent probability of growing into the next stage, is determined by the stage length in years and the annual survivorship probability for that stage. This method assumes a stable age distribution within a stage. The annual probability of an individual growing into the next stage (γ) is calculated by:

$$\gamma = (\sigma_i/\lambda)^{Ti} - (\sigma_i/\lambda)^{Ti-1}/[(\sigma_i/\lambda)^{T_i}] - 1, \qquad (1)$$

where i is the stage number (1–5), σ is survivorship, and T is stage duration in years. λ is an initial estimate of the overall population increase or decline. For the loggerhead model and all matrix calculations used for simulations, λ is iterated using the dominant eigenvalue obtained from the matrix until the initial λ and the final λ used to calculate the intrinsic rate of increase are equal to the fourth decimal place. Since the lifespan of adult turtles is unknown, we did not truncate the final stage ($P_5 = 0.8091$).

TABLE A1. Definitions and equations for matrix transition parameters used in the loggerhead model

Parameter	Definition	Calculation
P	Probability of surviving and remaining in stage i	$P_i = \sigma_i \times (1 - \gamma_i)$
G	Probability of surviving and growing to stage $i + 1$	$G_i = \sigma_i \times \gamma_i$
F	Reproductive output	$F_i = (\text{fecundity}_i \times P_i) + (\text{fecundity}_{i+1} \times G_i)$

APPENDIX 2

ELASTICITY ANALYSIS

Elasticities, or proportional sensitivities, are values used to determine which elements of a projection matrix have the greatest effect on λ, or the intrinsic rate of increase for the population. The elasticity of λ to any parameter $a_{i,j}$ within the projection matrix may be calculated as:

$$e_{i,j} = \frac{a_{i,j}}{\lambda}\frac{\partial\lambda}{\partial a_{i,j}} = \frac{a_{i,j}}{\lambda} \times \left(v_i \times \frac{w_j}{|w \times v|}\right)$$

(Caswell 1989), where v is the left eigenvector of the matrix, representing the stage-specific reproductive values, and w is the right eigenvector of the matrix, representing the stable stage distribution. $|w \times v|$ is the inner-product of the two eigenvectors. The elasticity of λ to lower level parameters, such as survivorship (σ) or stage duration (T) may be calculated as:

$$\frac{x}{\lambda}\frac{\partial\lambda}{\partial x} = \frac{x}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial x}$$

(Caswell 1989).

Since the P and G values of our projection matrix are calculated as functions of λ (see Appendix 1), we used the following derivation to obtain elasticity values for changes in survivorship:

$$\frac{\sigma_i}{\lambda}\frac{\partial\lambda}{\partial\sigma_i} = \frac{\sigma_i}{\lambda} \times \left[\frac{\partial\lambda}{\partial P_i}\frac{\partial P_i}{\partial\sigma_i} + \frac{\partial\lambda}{\partial G_i}\frac{\partial G_i}{\partial\sigma_i}\right]$$

$$\frac{\partial G_i}{\partial\sigma_i} = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{\left[\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1\right]^2} \times \left[T_i\left(1 - \frac{\sigma_i}{\lambda}\right) + \left(\frac{\sigma_i}{\lambda}\right)^{T_i+1} - \left(\frac{\sigma_i}{\lambda}\right)\right]$$

$$\frac{\partial P_i}{\partial\sigma_i} = 1 - \frac{\partial G_i}{\partial\sigma_i}.$$

A more time-consuming, though less menacing, way to calculate elasticities is to change each parameter by plus or minus a small percentage, then divide the difference of the new λ's calculated with the parameter changes by a fraction of the original λ. For instance, for changes in parameter x, the elasticity of λ may be calculated as:

$$E = \frac{\lambda_{(x+0.01x)} - \lambda_{(x-0.01x)}}{0.02 \times \lambda}.$$

The multiplier in the denominator is always equal to twice the percentage multiplied by x. We used this method to calculate the elasticities for stage duration.