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A STAGE-BASED POPULATION MODEL FOR LOGGERHEAD SEA TURTLES AND IMPLICATIONS FOR CONSERVATION[1]

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Abstract. Management of many species is currently based on an inadequate understanding of their population dynamics. Lack of age-specific demographic information, particularly for long-lived iteroparous species, has impeded development of useful models. We use a Lefkovitch stage class matrix model, based on a preliminary life table developed by Frazer (1983*a*), to point to interim management measures and to identify those data most critical to refining our knowledge about the population dynamics of threatened loggerhead sea turtles (*Caretta caretta*). Population projections are used to examine the sensitivity of Frazer's life table to variations in parameter estimates as well as the likely response of the population to various management alternatives. Current management practices appear to be focused on the least responsive life stage, eggs on nesting-beaches. Alternative protection efforts for juvenile loggerheads, such as using turtle excluder devices (TEDs), may be far more effective.

Key words: Caretta caretta; *demography; endangered species; management; (marine) turtles; stage class matrix projection models; southeastern United States.*

INTRODUCTION

Increases in the human population and degradation of habitats have caused many species that were formerly common to decline to near extinction. As a result, we have become increasingly involved in attempting to preserve populations of rare or endangered species. Current management decisions may be critical in preventing their extinction. But to make effective management decisions for any species, we must estimate the population's response to various management alternatives. Unfortunately, many management decisions seem to be based more on ease of implementation or accessibility of particular life stages than a priori clear expectations of population responses to management.

Many marine turtle populations are threatened with extinction (Federal Register 1978, Groombridge 1982), and recently much attention and effort have been focused on their conservation (Bjorndal 1982, Hopkins and Richardson 1985). Nearly all of the conservation efforts have focused on a single life stage: eggs on the nesting-beach. Turtle nests are readily accessible and protectable, and losses and protection successes are easily monitored. But, given our poor understanding of turtle population dynamics, it is not clear whether egg protection efforts will ultimately prevent marine turtle extinction.

Recently some authors have suggested that reductions in juvenile and/or adult mortality may be important to the enhancement of dwindling loggerhead populations (Richardson 1982, Richardson and Richardson 1982, Frazer 1983*a*), but this idea has not been explored systematically and no quantitative predictions have been made. In this paper, we use recent demographic data for threatened loggerhead turtles (*Caretta caretta*) from the southeastern United States to develop a stage class population model. We then test the sensitivity of the model to variations in parameter values and compare the model predictions with what is known about marine turtle population dynamics. We also explore the potential effects of several different management scenarios on the long-term survival of loggerhead turtles.

STAGE CLASS MODELS

Lefkovitch (1965) demonstrated that the Leslie matrix population projection technique (Lewis 1942, Leslie 1945) was actually a special case of the more general matrix A such that

$$\mathrm{A}n_t = n_{t+1}$$

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or

$$\begin{bmatrix} a_{11} & a_{12} \cdots a_{1s} \\ a_{21} & a_{22} \cdots a_{2s} \\ \cdot & \cdot \cdots \cdot \\ a_{s1} & a_{s2} \cdots a_{ss} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ \cdot \\ n_s \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ \cdot \\ n_s \end{bmatrix}_{t+1}$$

where n_t gives the abundance of individuals in a particular life stage at time t.

A is known as the "population projection matrix" and describes the number of offspring born to each stage class that survive a given time period as well as the proportion of individuals in each stage class that survive and remain in that stage vs. those that survive and enter another stage, otherwise known as the "transition probability." Thus the elements of the matrix A incorporate the fecundity, mortality, and growth rates of each stage class. The Leslie matrix divided the population into equal age classes. In the Lefkovitch matrix, there is no necessary relation between stage and age; the fundamental assumption is that all individuals in a given stage are subject to identical mortality, growth, and fecundity schedules. The technique of population projection, postmultiplying this matrix by the population vector, is used to forecast future population states. The dominant eigenvalue λ_m of the Lefkovitch stage class matrix is equal to e^r, where r is the intrinsic rate of increase of the population in the equation

$$N_t = N_0 e^{rt}.$$

Thus, if $\lambda_m = e^r = 1$, then $r = 0$, and the population size remains stable.

In a constant environment, the proportion of individuals in different age classes of a population tends toward a stable age distribution (Lotka 1925). Similarly, each population matrix A has a corresponding right eigenvector $\boldsymbol{w}_m$ that represents the stable stage distribution of the population such that

$$\mathrm{A}\boldsymbol{w}_m = \lambda_m \boldsymbol{w}_m.$$

For the matrices considered here, any initial population stage structure projected forward will approach the stable stage distribution $\boldsymbol{w}_m$, where each stage class increases in size λ_m times each time period. The reproductive value of each stage is given by the elements of the left eigenvector $\boldsymbol{v}$ corresponding to λ_m, defined by

$$\boldsymbol{v}'\mathrm{A} = \lambda_m \boldsymbol{v}'.$$

These reproductive values estimate the expected reproductive contribution of each stage to population growth.

Thus, the primary differences between the Leslie age class matrix and Lefkovitch's stage class matrix are that the stage classes may differ in their duration *and* that individuals may also remain in a stage from one time to the next. Vandermeer (1975, 1978) has clarified the theoretical constraints, resulting from errors due to sample size and the distribution of individuals, on the selection of stage categories when they are not biologically apparent (as with insect instars).

Lefkovitch (1965) originally derived the stage class matrix to model an animal population, the cigarette beetle (*Lasioderma serricorne*). But its more frequent use by botanists, to investigate several plant species with widely diverse life history patterns (Hartshorn 1975, Werner and Caswell 1977, Meagher 1982, Caswell 1986), testifies to the versatility and power of the technique.

Loggerhead Demographic Parameters

To construct a stage class population matrix for any species, data on fecundity and survival rates for the individuals in each stage are necessary. In addition, some measure of the probability of remaining in a stage vs. that of moving on to another stage is required. Unfortunately, such demographic parameters are very difficult to measure in long-lived, mobile organisms. In marine turtles only the adult nesting females, eggs and hatchlings, and stranded, dying turtles are ever seen on the beaches. Turtles often travel great distances (Carr 1967), occasionally nesting on more than one beach (Stoneburner and Ehrhart 1981), while a given female may nest only once every several years (=remigration rate: Carr and Carr 1970). Thus long-term monitoring of individual animals, often over a number of beaches, is necessary to obtain accurate estimates of fecundity and survival.

Furthermore, no method has yet been devised to obtain accurate ages of sea turtles. Rapid juvenile growth rates quickly obscure notches cut in the shell margin, so these marks are useful only for short-term studies, and the shells are generally too thin and fragile to hold a reliable tag for long. In various attempts at shell and flipper tagging in the past, the tag return rates have been abysmally low, resulting in inadequate estimates of nesting remigration (and thus fecundity) rates, survival and growth rates, and age at reproductive maturity (Pritchard 1980, Richardson 1982, Frazer 1983*b*).

The lack of reliable information on age-specific rates in marine turtles precludes the use of age-based population models, so stage class models must be employed. A few stages (eggs, hatchlings, and mature, nesting adults) are biologically distinct and easily recognized, and some estimates of survival rates are becoming available for these stages. But the long juvenile period between the hatchling and adult stages presents more difficulties. Most researchers have used size (as measured by carapace length) as an index of age in marine turtles (Uchida 1967, Mendonca 1981), so size-based stage classes seem appropriate.

Only a few studies on particular nesting-beaches (Hughes 1974, Carr et al. 1978, Richardson et al. 1978) have lasted long enough to generate the data necessary to model population dynamics in marine turtles. Estimates for the various components of loggerhead fe-

TABLE 1. Loggerhead fecundity components (ranges based on published literature). Little Cumberland Island (LCI), Georgia, estimates are given in the rightmost column. The source for each datum is given in parentheses.

Component	Low estimate	High estimate	LCI estimate	
			Probability	Year
Remigration rate*	every 5th yr (Frazer 1983)	every year (Hughes 1974, and others)	.0358	1
			.4989	2
			.3221	3
			.1119	4
			.0313	5
			(weighted ave., Frazer 1984)	
Clutch frequency†	1 per season (Richardson 1982)	7 per season (Lenarz et al. 1981)	2.99 per season (Richardson 1982)	
Mean clutch size‡ (eggs/clutch)	100, Florida (Davis and Whiting 1977) 101, Oman (Hirth 1980)	126, South Carolina (Caldwell 1959) 125, Florida (Gallagher et al. 1972)	120 (Richardson 1982)	

* Remigration rate is defined as the interval (yr) between nesting seasons for individual females.
† Clutch frequency is the number of clutches of eggs per female per nesting season.
‡ Mean clutch size is the average number of eggs per clutch for a given nesting-beach.

cundity vary widely (Table 1); estimates of survival are equally variable (Table 2). Recently however, Richardson's 20-yr project on Little Cumberland Island (LCI), Georgia has begun to generate defensible estimates of fecundity (Richardson 1982, Frazer 1984) and survival (Frazer 1983*a*, *b*) for loggerhead turtles in the southeastern United States (see the right-hand columns of Tables 1 and 2).

Frazer recently analyzed the LCI data (Richardson 1982, Frazer 1983*a*, *b*, 1984, 1987) as well as data from other southeastern loggerhead populations and produced a preliminary life table for a natural (=wild) loggerhead population. Frazer's age-specific life table for the LCI loggerhead population (1983*a*) assumes a closed population with a 1:1 sex ratio, first reproduction at 22 yr, a maximum life span of 54 yr, and a population declining at the rate of 3%/yr (Frazer 1983*b*). Frazer's assumptions are subject to debate among sea turtle biologists, but they are well within the published ranges for these values and seem reasonable, at least as a starting point.

Because Frazer's original data derive from survival and fecundity estimates for various size classes rather than from turtles of known ages, a stage-based life table is perhaps easier to defend than Frazer's age-specific life table. Hence we condensed Frazer's life table for the LCI loggerhead population into seven stage classes (Table 3). These classes are: (1) 1st yr (eggs and hatchlings), (2) small juveniles, (3) large juveniles, (4) subadults, (5) novice breeders, (6) 1st-yr remigrants, and (7) mature breeders. Stages 5, 6, and 7 have been considered separately, despite similar survival probabilities, because of large differences in fecundity among these three classes (Frazer 1984). Stage 7 was not subdivided further despite Frazer's carefully calculated age-specific fecundities, because the maximum deviation from 80 of ± 7 eggs in any year was judged to be minor compared with other factors contributing to the population dynamics. In addition to the fact that a stage class approach is better supported by the data, one major advantage over using an age class model based on Frazer's life table is that simulations can be per-

TABLE 2. Loggerhead survivorship estimates for each life stage (from Crouse 1985). Estimates from Little Cumberland Island (LCI), Georgia, are given in the rightmost column. Sources for data are given in parentheses.

Stage	Mortality factors*	Survivorship estimates		LCI estimate (Frazer 1983*a*)
Eggs				
	Predation, erosion, poaching, bacteria, plant roots	6%	(Hopkins et al. 1979)	1st yr = 0.6747
		3 – 90%	(Talbert et al. 1980)	
		77.8%	(Hughes 1974)	
		$\bar{X}$ = 80%	(Hirth 1890)	
Hatchlings	Predation, ORV† ruts, pollution		unknown	
Juveniles	Predation, trawlers		unknown	small juveniles = 0.7857 large juveniles = 0.6758
Adolescents	Trawlers, predation		unknown	subadults = 0.7425
Adults	Trawlers, predation, senescence		unknown	adults = 0.8091

* Major sources of mortality for each stage are given in likely order of importance.
† ORV = off-road vehicles. The 5-cm hatchlings often become trapped in vehicle ruts, which subjects them to increased predation and desiccation.

TABLE 3. Stage-based life table for loggerhead sea turtles based on data in Frazer (1983*a*). These values assume a population declining at ≈3%/yr.

Stage number	Class	Size* (cm)	Approximate ages (yr)	Annual survivorship	Fecundity (no. eggs/yr)
1	eggs, hatchlings	<10	<1	0.6747	0
2	small juveniles	10.1–58.0	1–7	0.7857	0
3	large juveniles	58.1–80.0	8–15	0.6758	0
4	subadults	80.1–87.0	16–21	0.7425	0
5	novice breeders	>87.0	22	0.8091	127
6	1st-yr remigrants	>87.0	23	0.8091	4
7	mature breeders	>87.0	24–54	0.8091	80

* Straight carapace length.

formed with a 7 × 7 matrix, instead of an unwieldy 54 × 54 matrix, thereby minimizing error propagation caused by repeated multiplication of parameters.

THEORETICAL POPULATION PROJECTIONS

Model

The stage class matrix we have developed incorporates Frazer's fecundity, survival, and growth rates, and uses yearly iterations to make population projections for loggerhead sea turtles. Frazer (1983*a*) estimated or interpolated the annual survival for each of several size classes of turtles (e.g., large juveniles = 58.1–80 cm straight carapace length [SCL]; adult females = >87.1 cm SCL). He then used previously calculated (Frazer 1983*a*) growth curves for wild loggerheads to assign age ranges to the size classes and divided each class into the corresponding number of age classes. Finally, he assigned each age class the annual survival calculated for that entire size class, assuming that annual survival was constant for all turtles throughout that class, regardless of age. Clearly, the original data better support a stage class approach than a more traditional age-based model.

Our model divides the life cycle into the seven stages shown in Table 3. To create a stage-based projection matrix, we must estimate, for each stage, the reproductive output (F_i), the probability of surviving and growing into the next stage (G_i), and the probability of surviving and remaining in the same stage (P_i). The fecundities F_i are given in Table 3. The transition probabilities G_i and P_i can be estimated from the stage-specific survival probabilities p_i and stage duration d_i. Because we know little about the variability of survival and growth rates within a stage, we will assume that all individuals within a stage are subject to the same survival probability and stage duration. As more precise data on the growth rates and survival of turtles of various sizes become available they can be readily incorporated into the model.

Within each stage there are individuals who have been in that stage for 1, 2, . . . , d_i yr. By setting the proportion of individuals alive in the first cohort of stage class i to 1 and the probability of turtles in that cohort surviving to the next year to p_i (Frazer's annual survival probability for the entire size = stage class), the probability of those individuals surviving d years becomes p_i^d. Assuming that the population is stationary and the age distribution within stages is stable, the relative abundance of these groups of individuals then becomes $1, p_i, p_i^2, \ldots, p_i^{d_i-1}$. In the interval from t to $t + 1$, the oldest individuals in this stage will move to the next stage, if they survive. All the younger individuals will remain in the stage. Thus the proportion remaining, and surviving, is given by

$$P_i = \left(\frac{1 + p_i + p_i^2 + \ldots + p_i^{d_i-2}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}}\right)p_i .$$

Rewriting the geometric series $1 + p + p^2 + \ldots + p^{d-1}$ as $(1 - p^d)/(1 - p)$, we can rewrite (P_i) as

$$P_i = \left(\frac{1 - p_i^{d_i-1}}{1 - p_i^{d_i}}\right)p_i . \tag{1}$$

Thus, the number of individuals in any cohort within a stage class declines through time as a function of the stage-specific annual survival probability and the number of years spent in that stage.

That proportion of the population that grows into the next stage class and survives (G_i) is similarly given by the proportion of individuals in the oldest cohort of the stage times the annual survival for the stage, or

$$G_i = \left(\frac{p_i^{d_i-1}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}}\right)p_i ,$$

which can be rewritten, in the same manner as before, as

$$G_i = \frac{p_i^{d_i}(1 - p_i)}{1 - p_i^{d_i}} . \tag{2}$$

Loggerhead population matrix

The resulting stage class population matrix (Table 4) takes the form

$$\begin{bmatrix} P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix},$$

TABLE 4. Stage-class population matrix for loggerhead sea turtles based on the life table presented in Table 3. For the general form of the matrix and formulae for calculating the matrix elements see Theoretical Population Projections.

0	0	0	0	127	4	80
0.6747	0.7370	0	0	0	0	0
0	0.0486	0.6610	0	0	0	0
0	0	0.0147	0.6907	0	0	0
0	0	0	0.0518	0	0	0
0	0	0	0	0.8091	0	0
0	0	0	0	0	0.8091	0.8089

where F_i is the stage-specific fecundity, and P_i and G_i are the probability of surviving and remaining in the same stage vs. the probability of surviving and growing to the next stage as defined by Eqs. 1 and 2.

Population projections

For each simulation, the power method (Searle 1966, Keyfitz 1977) was used to take successively higher powers of the matrix and postmultiply by the population vectors until the resultant vectors differed from each other by only a scalar factor; this factor is λ_m (the dominant eigenvalue) and the vector is proportional to the right eigenvector $\boldsymbol{w}$. The population vectors at this point represent the right eigenvector or stable stage distribution. The left eigenvector $\boldsymbol{v}$ can be found by applying the same procedure to the transposed matrix. For computing efficiency, an initial population vector was generated (Crouse 1985) based on a stationary population life table proposed by Frazer (1983*a*) and used as the initial vector for all succeeding simulations.

The eigenvalue and intrinsic rate of increase for the matrix in Table 4 are $\lambda_m = 0.9450$ and $r = -0.0565$, which are not dissimilar to Frazer's (1983*a*) values of $\lambda_m = 0.9719$ and $r = -0.0285$ for his 54-yr life table. This confirms that our seven-stage matrix adequately describes the population in Frazer's life table.

The stable stage distribution $\boldsymbol{w}$ and reproductive value vector $\boldsymbol{v}$ are given in Table 5. The stable stage distribution is dominated by small juveniles, eggs and hatchlings, and large juveniles; subadults and adults are very rare. The reproductive value is low for the first three stages, jumps dramatically for subadults, and is even higher for the last three stages.

Sensitivity analyses

One benefit of constructing a population matrix is that one may test how sensitive the population growth rate is to variations in fecundity, growth, or survival rates by simulating changes in these parameters and then calculating λ_m and the resultant r of the new matrix. By simulating the same proportional change for each stage successively, one can compare the relative effect on the different stages.

The ranges of population parameters for various loggerhead life history stages (Tables 1 and 2) suggest that it is not unreasonable to expect some loggerhead populations to show reductions of 50% in fecundity or survival of specific stages relative to those in our initial population matrix. Therefore we simulated 50% reductions in these parameters for each life history stage with the remaining matrix components held constant (Fig. 1; Appendix). Changes in stages 2, 3, and 4 were effected by reducing Frazer's overall stage-specific annual survival by 50% and then calculating P_i and G_i for each stage using Eqs. 1 and 2 (see Appendix).

Although 50% reductions in fecundity and 1st-yr (eggs and hatchlings) survival reduce λ_m and cause the population to decline more swiftly (Fig. 1), a similar reduction in survival in any of the immature stages (2, 3, and 4) causes a much larger reduction in λ_m, and a corresponding increase in the rate of population decline. After at least one reproductive season, such a reduction in adult survival results in more moderate reductions in λ_m and r, similar to those seen with reductions in fecundity and 1st-year survival.

What would happen if new management practices eliminated mortality in any of these stages? Of course, no management practice can promise zero mortality for any period of time, but such a simulation should help identify the life stage(s) on which management efforts would be most efficiently spent. The results of elimination of mortality for each stage class respectively are presented in Fig. 1b. Also included is a simulation of a doubling in fecundity, which is within the range of possibilities presented earlier.

Once again, the juvenile and subadult stages are most responsive to such a change. In fact, an increase in survival to 1.0 in any one of stages 2, 3, or 4 (or that of the suddenly immortal mature females) was suffi-

TABLE 5. Stable stage distribution ($\boldsymbol{w}_m$) and reproductive values ($\boldsymbol{v}'$) for the loggerhead population matrix given in Table 4.

Stage class	Stable stage distribution (Dominant eigenvector)	Reproductive values (Left eigenvector)
1 (eggs, hatchlings)	20.65	1.00
2 (small juveniles)	66.975	1.40
3 (large juveniles)	11.46	6.00
4 (subadults)	0.66	115.845
5 (novice breeders)	0.04	568.78
6 (1st-yr remigrants)	0.03	507.37
7 (mature breeders)	0.18	587.67

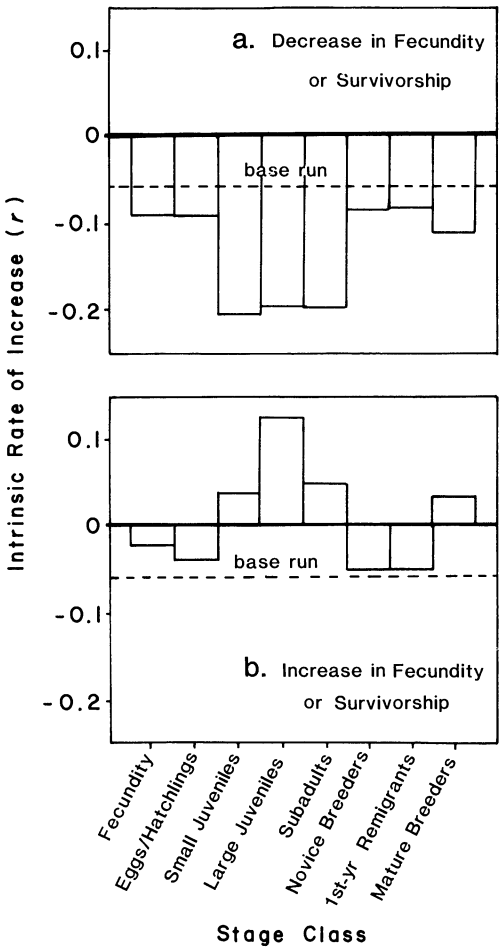

FIG. 1. Changes in rate of increase r resulting from simulated changes in fecundity and survival of individual life history stages in the loggerhead population matrix (remaining components held constant). The dashed line represents the r determined in the baseline run on the initial matrix. (a.) Simulations represent 50% decreases in fecundity or survivorship. (b.) Simulations represent a 50% increase in fecundity or an increase in survivorship to 1.0. Stages 2–4 (juveniles and subadults) show the strongest response to these simulated changes. (Specific calculations are presented in Crouse 1985.)

cient to reverse the decline of the model population. (The tremendous increase in λ_m and r seen in stage 3 [large juveniles] is partly artifact since survival was lowest for this stage initially [see Tables 3 and 4], making the increase to 1 in this stage proportionately larger.) More importantly, the simulation indicates that no matter how much effort was put into protecting eggs on the beach, this alone could not prevent the eventual extinction of the model population. Similarly, the turtles could not reverse their decline via increases in fecundity unless they could more than double egg production, which seems unlikely.

Since the estimates of growth and of age at first reproduction in the literature (Crouse 1985) show considerable uncertainty, another reasonable question is: What if age at first reproduction is really only 16? or 28? These conditions, a 6-yr decrease or increase in the age of reproductive maturity, were simulated (Fig. 2) by subtracting and adding 2 yr to the calculations of P_i and G_i for each of the three immature stages. In fact, a mere 3-yr reduction in the age of first reproduction, well within the bounds of the growth estimates available, comes very close to halting the decline in this population. How flexible loggerheads might be in age at first reproduction is unknown, but clearly it would be profitable to have better estimates of age at reproductive maturity in order to forecast population changes.

One disadvantage of simulation experiments of this sort is that the results are dependent on the chosen perturbations of the original matrix. Analytical methods (reviewed by Caswell 1986) avoid this difficulty by calculating the sensitivity of λ to changes in life cycle parameters. Here we are interested in the proportional sensitivity (or "elasticity") of λ_m; that is, the proportional change in λ_m caused by proportional change in one of the life cycle parameters. These proportional sensitivities can be calculated, given the stable stage distribution $\boldsymbol{w}$ and reproductive value $\boldsymbol{v}$. The proportional sensitivity of λ_m to a change in each matrix element a_{ij} is given by

$$\frac{\partial \ln \lambda}{\partial \ln a_{ij}} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda}\left(\frac{v_i w_j}{\langle \boldsymbol{v}, \boldsymbol{w} \rangle}\right),$$

where $\langle\rangle$ denotes the scalar product.

The elasticities of λ_m with respect to F_i, P_i, and G_i are shown in Fig. 3. Because these elasticities sum to 1 (DeKroon et al. 1986), the relative contribution of the matrix elements (F_i, P_i, and G_i) to λ_m can be compared. This supports the conclusions of our previous

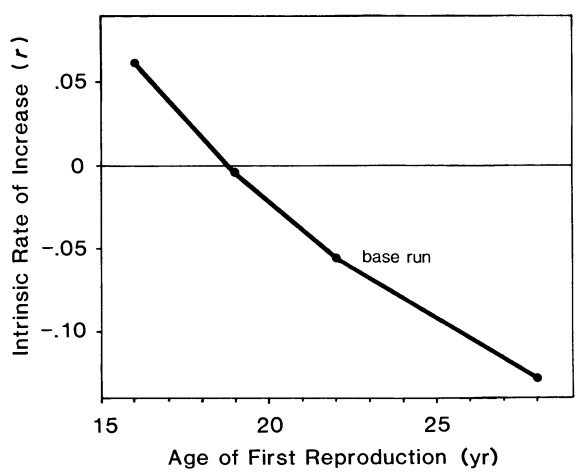

FIG. 2. Resultant r for model loggerhead population with different growth rates (represented by age of first reproduction). The baseline run assumed age at first reproduction of 22 yr. Increasing age at first reproduction decreases r. Age of first reproduction near 19 yr would lead to r nearly equal to 0.

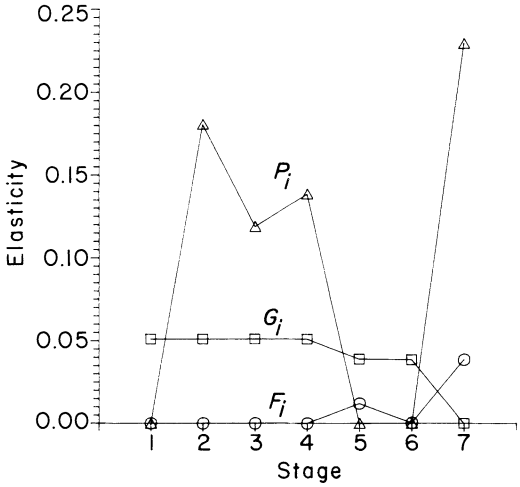

FIG. 3. The elasticity, or proportional sensitivity, of λ_m to changes in fecundity F_i (○), survival while remaining in the same stage P_i (△), and survival with growth G_i (□). Because the elasticities of these matrix elements sum to 1, they can be compared directly in terms of their contribution to the population growth rate r.

simulations: increases in fecundity have only a small effect on λ_m. Changes in the probability of survival with growth G_i are more important, while changes in the probability of survival in the same stage P_i contribute the most to λ_m. By the same token, changes in the juvenile, subadult, and mature adult stages have a greater impact on λ_m than changes in the 1st yr, novice breeders, and 1st-yr remigrants.

In this model, P_i and G_i are derived parameters; they depend on both stage-specific annual survival probability p_i and stage duration d_i. We have also calculated the elasticities of λ_m with respect to these parameters (Fig. 4). The population dynamics are very sensitive to variations in the survival probability of juveniles and subadults (Fig. 4a). The results of changes in stage duration are relatively small (Fig. 4b), and are generally negative (since increases in stage duration usually cause decreases in λ_m).

Hence, it would appear that survival, particularly in the juvenile and subadult stages, has the largest effect on population growth. Conveniently, survival is also the parameter that is most amenable to human alteration. With this in mind, we simulated several possible management scenarios.

Management scenarios

While it would be impossible to increase survival of any stage to 1.0, the National Marine Fisheries Service has recently devised a technology, the Trawl Efficiency or Turtle Excluder Device (TED), that virtually eliminates turtle mortality due to incidental capture and drowning in shrimp and fish trawls (Seidel and McVea 1982, Anonymous 1983). Such incidental capture is believed to be the major source of mortality in juvenile and adult turtles in the southeastern United States (Anonymous 1983, Mager 1985). Since use of this technology would presumably affect all of the turtles feeding in estuaries and nearshore marine habitats, an increase in survival of all three immature stages was simulated (Table 6). Simply increasing immature survival to 0.80 would allow this population to increase.

Because the small juveniles occur less frequently in nearshore marine systems, it might be difficult to increase their survival using TEDs. Thus a simulation was performed where the survival of stage 2 was left unchanged but survival of stages 3 and 4 was increased to 0.80, and the survival of adults was increased to 0.85 (presuming that adults also would benefit from

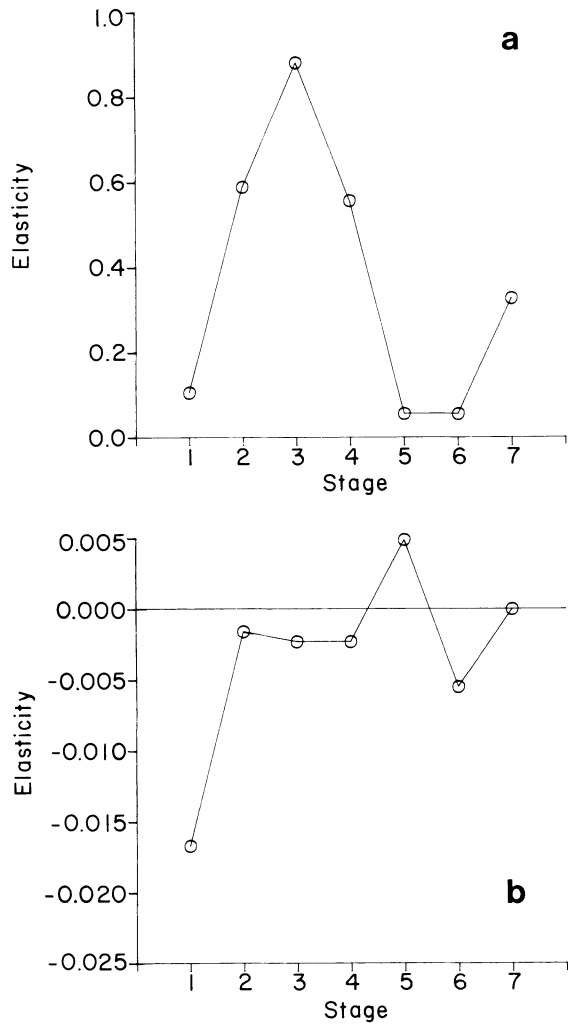

FIG. 4. (a) The elasticity, or proportional sensitivity, of λ_m to changes in annual stage-specific survival probability p_i. (b) The elasticity of λ_m to changes in stage duration d_i. Elasticity in stage duration is negative because stage duration and population growth rates r are inversely related. Overall, proportional sensitivity is much higher to survival than to stage duration.

the TED). Once again, the simulated population started to grow (Table 6).

Hatch success on specific beaches frequently falls below the 0.80 that Frazer used for his life table calculations. Therefore a simulation was performed with 1st-yr survival decreased by 50% (corresponding to a hatch success of 40%), while for stages 3 and 4 survival was increased to 0.80 and adult survival was increased to 0.85. Even with little active egg protection, these small increases in immature and adult survival caused the simulated loggerhead population to grow (Table 6).

Finally, if protection efforts were to focus on one stage over the others, perhaps because of the availability of appropriate technology or ease of access to a particular life stage, how much of an increase in the survival of any *single* stage would be necessary to produce a stable population? As noted earlier, even 100% survival in stages 1 (eggs and hatchlings), 5 (novice breeders), and 6 (1st-yr remigrants) alone would be insufficient to achieve stability. In fact, increasing stage 1 survival to 1.0 increases r to only -0.0357 (Fig. 1b), and the population continues to decline, suggesting that achieving zero mortality of eggs on nesting-beaches would likely be ineffective as a management tool if no concurrent action were taken in the juvenile stage. However, increasing stage 2, 3, 4, and 7 survival one at a time revealed that stability ($\lambda_m = 1$, $r = 0$) could be achieved by increasing stage 3 survival by just 14% (from 67.6 to 77%), whereas an increase of 16% would be necessary for stage 2, 18.5% for stage 4, or 17% for stage 7. In other words, the increase in survival necessary to achieve population stability was smallest for stage 3 (large juveniles).

TABLE 6. Three management scenarios involving changes in mortality in various life stages of loggerhead sea turtles. For each scenario, the stages are listed along with the old and the new matrix elements* (P_i, G_i) and the resulting λ_m and r.

Change in initial matrix				Result	
Stage	Coefficient	Old	New	λ_m	r
Immature survivorship increased to 0.80					
2	P_2	0.7370	0.74695		
	G_2	0.0486	0.0531		
3	P_3	0.6610	0.7597		
	G_3	0.0147	0.0403	1.06	+0.06
4	P_4	0.6907	0.7289		
	G_4	0.0518	0.0710		
Large juveniles and subadults = 0.80; adults = 0.85					
3	P_3	0.6610	0.7597		
	G_3	0.0147	0.0403		
4	P_4	0.6907	0.7289		
	G_4	0.0518	0.0710	1.06	+0.06
5	G_5	0.8091	0.8500		
6	G_6	0.8091	0.8500		
7	P_7	0.8089	0.8500		
First-year = 0.33735; large juveniles, subadults = 0.80; adults = 0.85					
1	G_1	0.6747	0.33735		
3	P_3	0.6610	0.7597		
	G_3	0.0147	0.0403		
4	P_4	0.6907	0.7289		
	G_4	0.0518	0.0710	1.02	+0.02
5	G_5	0.8091	0.8500		
6	G_6	0.8091	0.8500		
7	P_7	0.8089	0.8500		

* P_i = the probability of survival while remaining in the same stage. G_i = the probability of surviving while growing to the next stage.

DISCUSSION

Loggerhead model

Our simulations strongly suggest that if the fecundity, survival, and growth rates of loggerhead turtle populations in the southeastern United States are at all similar to those proposed by Frazer, then the key to improving the outlook for these populations lies in reducing mortality in the later stages, particularly the large juveniles.

Yet Pritchard (1980) noted that many sea turtle biologists are unclear whether to focus their conservation efforts on eggs, immatures, or breeding adults; Pritchard himself opted for saving mature females over juveniles, noting that the adults had already survived the hazards of the long juvenile stages and were ready to lay their valuable eggs. While it is true that reproductive value is highest in the adults, very few turtles actually make it to these stages to reproduce (Table 5). By increasing survival of large juveniles (who have already survived some of the worst years) a much larger number of turtles are likely to reach maturity, thereby greatly magnifying the input of the increased reproductive value of the adult stages.

Frazer (1983*a*) acknowledged his parameter estimates are somewhat uncertain, particularly survival in the earlier stages. First-year survival was interpolated based on literature estimates for undisturbed natural nests. Young juvenile survival was also interpolated, based on gross survival from eggs to adults, and assuming a closed population with a stable age distribution. And Frazer noted that the LCI population clearly has been "exploited," albeit unintentionally, by trawlers in recent years and is not likely at a stable age distribution. However, although Frazer's assumption of a closed population has yet to be proven, evidence of morphological differentiation, heavy metal concentration, and genetic polymorphisms (Smith et al. 1977, Stoneburner 1980, Stoneburner et al. 1980) supports the idea of closed populations, at least on a regional basis. And Frazer's estimate of older juvenile survival seems more reliable because it was based on a catch curve analysis of data for stranded and live-caught turtles. Finally, Frazer's calculations were made on one of the longest, most complete data bases available, in which quality control has been excellent.

In fact, the results of our sensitivity analyses indicate that uncertainty in 1st-yr survival estimates, leading to a fairly large change in those estimates would have

relatively little effect on λ_{m}, though a similar error in estimation of small juvenile survival would have a larger effect. Because the highly sensitive large juvenile stage (stage 3) is one where Frazer's estimate is stronger, the inferences we have drawn with respect to parameter variations in this stage are both more valid and more important. The most serious problem for our projections is the possibility of compounded errors, i.e., errors in the same direction in two or more stages (Wilbur 1975, Tinkle et al. 1981). While an endless variety of scenarios could be simulated using this model, we feel it is better to explore the sensitivity of the various assumptions and parameters of the model. In this way, the importance of our ignorance of the natural history or rate functions of various life stages can be evaluated.

The simulations do indicate that the model is sensitive to changes in age at reproductive maturity, suggesting that weak estimates and/or regional shifts in growth rate might be important. Balazs (1982) has reported wide variance in growth rates for green turtles feeding in different habitats. Indeed, more recently Frazer and Ehrhart (1985) have suggested that maturity in loggerheads may come as late as 30 yr, i.e., the population might actually be declining faster than 3%, and require even more attention to halting juvenile mortality. The sensitivity of the model to growth rate combined with the strong possibility of different growth rates in various estuarine habitats points to an important gap in our understanding of loggerhead natural history.

Another important lesson brought home by the population projection technique is that population strength or longevity does not come from sheer numbers alone, but rather from the integrative result of survival, fecundity, and individual growth throughout the life cycle. For example, if an initial population of 500 000 animals (including 1277 adult females) is subjected to a 50% reduction in large juvenile survival, the population will have no (<1) adult females in just 40 yr, and is clearly headed for rapid extinction. However, the same starting population retains >52 adult females (≈ 60 times as many), and thus some potential for recovery, after 40 yr when the same 50% reduction is induced in the egg/hatchling stage. Thus the presence of large numbers of animals can be deceptive, implying robustness, when in reality such a population might be highly susceptible to perturbations in particular life stages.

Life history strategies

Loggerheads probably evolved under conditions of high environmental uncertainty on the nesting-beaches, leading to highly variable survival in the eggs and hatchlings. Relatively low mortality in the larger stages allowed delayed maturity and iteroparity, thereby facilitating high fecundity rates to offset the egg and hatchling mortality. Unfortunately, as Wilbur (1975) noted when he published the first life table for any species of turtle, "One of the most serious gaps in the study of life histories is the analysis of long-lived, iteroparous species."

A recent attempt to develop a unified model for patterns of covariation in the life history traits of reptiles (Stearns 1984) was based entirely on snakes and lizards because of the paucity of accurate demographic information for turtles. Average adult female length was most influential on covariation in reptilian life history traits, with some additional influence attributed to phylogenetic relationships (Stearns 1984). Stearns further suggested that microevolutionary explanations are not sufficient to account for the patterns in the data.

More recently, Wilbur and Morin (1987) analyzed the life history evolution of 80 species of turtles with respect to a number of traits in addition to those that Stearns (1984) examined, concluding that female size and habitat are the most important factors determining reproductive characteristics. They also compared data from three widely scattered populations of green turtles (*Chelonia mydas*), where differing predation rates on various life stages have occurred for hundreds of years, and concluded, in contrast to Stearns, that "these different selective regimes could well have resulted in genetic differences in the life histories of isolated *Chelonia* populations."

Long-lived iteroparous animals probably adjust short-term reproductive effort to maximize lifetime reproductive success rather than short-term gains (Wilbur and Morin 1987). Thus females may become reproductive only when they have been able to store sufficient energy. The frequency of reproduction may not be the result of selection for any particular reproductive cycle, but instead the result of phenotypic plasticity, such that reproductive frequency would be expected to change in the face of environmental fluctuations (Frazer 1983*a*).

Thus, while more life history information for turtles has become available in recent years, it is clear that major gaps still exist and that the implications for marine turtle protection are as yet unclear. Even if adult female size is the primary determinant of reproductive strategies, differential selection histories and very recent environmental conditions may result in differential expression of reproductive traits.

Loggerhead management

These gaps in our knowledge become especially important when managers must decide where to focus protection efforts. While most marine turtle conservation projects in the southeastern United States have concentrated on reducing egg mortality on beaches, several researchers have noted recently that after 20 and even 30 yr of nest protection on some beaches we have not yet seen the increase in nesting turtles expected as a result of nest protection (Carr et al. 1978 and J. I. Richardson 1982 and *personal communication*). This may, in part, be an artifact resulting from

the ever increasing estimates of age at first reproduction for several species. It may also be a consequence of less rigid "beach imprinting" than previously believed. Even so, a general increase in regional nesting populations would be expected.

Obviously, based on the uncertainties in Frazer's estimates of survival in the youngest stages and the variability possible in age at maturity, we should maintain current efforts to reduce egg mortality, particularly on beaches with consistently low egg survival. However, the low elasticity of stage 1 survival indicates that the model can tolerate considerable uncertainty in this parameter. As more data are amassed on other aspects of the sea turtle life cycle, managers need to address the uncomfortable possibility that their current conservation efforts may be focusing on the part of the turtle's life history least likely to produce noticeable, long-term results. If, as the results of this investigation imply, mortality must be reduced at other life stages, what can be done?

This analysis indicates that a 14% increase in survival of large juveniles would allow the simulated loggerhead population to grow ($\lambda_m > 1$, $r > 0$). As noted, incidental capture and drowning in shrimp trawls is believed to be the largest single source of mortality in juvenile and adult marine turtles in the southeastern United States (Anonymous 1983, Mager 1985). Data for 3 yr from North Carolina (Fig. 5; Crouse 1985) indicate that the majority of the turtles that "strand" (wash up on the beach, dead or dying) fall in the 50–80 cm SCL size range. This finding is similar to those seen in the Chesapeake Bay and Georgia (Ruckdeschel and Zug 1982, Lutcavage and Musick 1985). This range closely overlaps the large juvenile stage class, which proved most sensitive to simulated reductions in mortality.

The Trawl Efficiency Device (or Turtle Excluder Device, TED) mentioned earlier can be installed in existing trawls and virtually eliminates the capture and drowning of marine turtles (Siedel and McVea 1982 and C. Oravetz, *personal communication*). The TED has the added advantage of eliminating other large objects (bycatch) from the trawl, thereby improving the hydrodynamics of the trawl and improving fuel efficiency (Anonymous 1983). Easley (1982) found that a small but significant increase in the shrimp caught in paired tests resulted in an economic advantage to larger vessels installing the device. Smaller and lighter versions of the TED are currently being tested for performance and durability (C. Oravetz 1985 and *personal communication*). Increased use of TEDs in the trawl fishery might provide advantages to both the fishery *and* threatened loggerhead populations.

It seems clear that more information should be collected on the distribution of immature turtles in the nearshore waters, incidence of trawl-related juvenile mortality, and the potential for the TED to reduce mortality in specific size classes. Additional studies clearly are needed to strengthen the parameter estimates in Frazer's life table, particularly in the areas of 1st-yr and small juvenile mortality, growth rates, and age at first reproduction. However the model's responses to increases in survival in the large juvenile and adult stages imply that we should not wait for these results before implementing measures, such as the TED, to reduce mortality in the larger size classes.

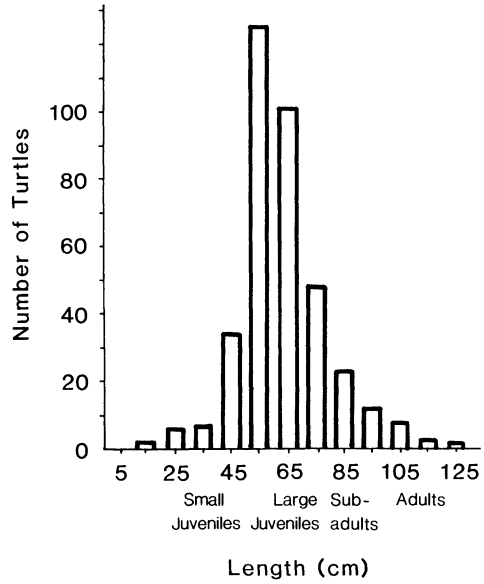

FIG. 5. Size-frequency distribution of stranded turtles in North Carolina, 1981–1983. Total number of stranded turtles reported by 10 cm (straight carapace length) size classes, June 1981–December 1983 (from Crouse 1985). The stage classes used in this analysis are named below their respective size categories.

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APPENDIX

TABLE A1. Sensitivity analysis. Resultant eigenvalue (λ_m) and r after simulated 50% decreases in fecundity and survival probabilities for loggerhead sea turtles.

Change in initial matrix				Result	
Stage	Coefficient	Old	New	λ_m	r
None	Baseline run			0.945	−0.06
Fecundity	F_5	127	64	0.91	−0.09
	F_6	4	2		
	F_7	80	40		
1	G_1	0.6747	0.33735	0.91	−0.09
2	P_2	0.7370	0.3919	0.81	−0.21
	G_2	0.0486	0.00085		
3	P_3	0.6610	0.3378	0.82	−0.20
	G_3	0.0147	0.0001		
4	P_4	0.6907	0.3696	0.82	−0.20
	G_4	0.0518	0.0016		
5	G_5	0.8091	0.4045	0.92	−0.08
6	G_6	0.8091	0.40455	0.92	−0.08
7	P_7	0.8089	0.4045	0.90	−0.11