

Abstract.—Sandbar sharks (*Carcharhinus plumbeus*) support an important commercial fishery. They are managed as a component of a multispecies group, termed large coastal sharks, by the National Marine Fisheries Service (NMFS) under the Fishery Management Plan (FMP) for Atlantic sharks. Currently, large coastal sharks, generally, and sandbar sharks, specifically, are considered overfished. Several management options, including nursery ground closures and size limits, are being considered to conserve the fishery. We explored the implications of management options for large coastal sharks within the framework of a stage-based model. Based on biological criteria, the life cycle of the sandbar shark was represented as five stages: neonate, juvenile, subadult, pregnant adults, and resting adults. The model followed only females. From a fishing mortality rate (F) of 0.20, estimated in the 1996 stock evaluation workshop (SEW), the model projects a population decline to 13% of its current abundance within 20 years. The population is not stabilized until F is reduced to 0.07. In one run of the model, we assumed that F on neonates and pregnant adults was zero in order to assess the impact of a “perfect” nursery ground closure. Under this scenario, the population continued to decline unless F on the remaining stages was reduced to 0.097. Even with the closure of nursery grounds or the introduction of size limits to protect neonates and juveniles, F has to be reduced substantially. The model is highly sensitive to the dynamics of juveniles and subadults, which implies that management should protect these immature sharks to rebuild the stock.

Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model*

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The sandbar shark (*Carcharhinus plumbeus*) is a species of primary importance in the Atlantic and Gulf of Mexico shark fishery (NMFS, 1993; NMFS¹; Branstetter and Burgess²). It is managed as a part of the large coastal shark group defined under the Atlantic shark Fishery Management Plan (FMP; NMFS, 1993). Since the mid 1980s, the demand for shark has increased (NMFS, 1993). The fishery peaked in 1989 with landings of approximately 4600 metric tons (t) dressed weight (dw; NMFS³). Catch per unit of effort of large coastal sharks declined rapidly during the 1970s and 1980s. To prevent overfishing, the FMP imposed an annual quota of 2570 t dw from 1994 to 1996 for the large coastal fishery, required mandatory reporting of landings, and prohibited the removal of fins (NMFS, 1993). At the 1996 stock evaluation workshop (SEW), scientists found no evidence of improvements in the large coastal stocks and recommended reducing fishing mortality by 50% (NMFS, 1996). In response, the National Marine Fisheries Service (NMFS) reduced the annual quota in 1997 by 50% to 1285 t dw and reported to Congress that large coastal sharks were

overfished (NMFS, 1997). The most recent data indicate that fishing mortality rates have not declined as much as expected and may still be too high to stabilize the sandbar shark stock (NMFS⁴). A size limit equivalent to approximately 12–13 years of age (140 cm fork length) was recommended.

The NMFS is mandated, through the Magnuson-Stevens Fishery Conservation and Management Act, to

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¹ 1996. Report of the shark evaluation workshop. Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Miami, FL, 80 p.

² Branstetter, S., and G. Burgess. 1997. Continuation of an observer program to characterize and compare regional efforts in the directed commercial shark fishery in the eastern Gulf of Mexico and South Atlantic. Gulf and South Atlantic Fisheries Development Foundation, Inc., Tampa, FL. University of Florida, Gainesville, FL., 83 p.

³ 1997. Shark evaluation annual report. Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Miami, FL, 12 p.

⁴ 1998. Report of the shark evaluation workshop. Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Panama City, FL.

rebuild the large coastal stocks to the optimum yield level. In October 1998, the NMFS released a draft FMP for Atlantic tunas, swordfish, and sharks. The measures in this FMP were designed to halt over-fishing and to rebuild these stocks. Management options under consideration for large coastal sharks included restrictions on effort, size limits, and area closures that were focused on nursery grounds.

Many traditional approaches that could be used to compare management options, such as surplus production models or age- and size-structured approaches, rely on catch or effort data, or both. However, because logbook reporting in the shark fishery was not mandatory until 1993, fishery-dependent time series have been insufficiently long to permit reliable application of these approaches. Yet a comparison of the efficacy of the potential management options is still required. The paucity of fishery-dependent data suggests that demographic approaches, such as life-table or stage-based analyses, may be the appropriate tools to explore the potential response of shark populations to management actions.

Life-table analysis is a common age-structured demographic approach with a long history in population dynamics (Kingsland, 1985). It is a matrix projection approach that estimates the contribution of each age class to future generations. Sminkey and Musick (1996) applied a life-table approach to sandbar sharks. From the intrinsic rate of natural increase, r , predicted by the model, they concluded that the population could not sustain the observed rates of fishing mortality. Heppell et al. (1999) developed matrix-based life tables for leopard (*Triakis semifasciata*) and angel (*Squatina californica*) sharks. Heppell et al. calculated the elasticity or proportional sensitivity of the population growth rate to changes in survival and fecundity and concluded that the two species differ in the degree to which each can compensate for changes in exploitation. Simpfendorfer (1999) developed a life table for the dusky shark (*Carcharhinus obscurus*). He concluded that in the absence of exploitation, dusky shark populations in southwestern Australia would increase at 4.3% annually. Analysis also indicated that current patterns of exploitation were sustainable. However, there are problems in application of life-table analysis to long-lived marine species. The intrinsic rate of natural increase predicted is dependent on the products of survival and fecundity for all ages and the estimated generation time. Thus, life tables require estimates of the schedules of mortality (survival) and fecundity over the entire age range (Gotelli, 1995). Consequently, in a long-lived species such as the sandbar shark, small errors in parameter estimates can become magnified.

Stage-based modeling is a matrix-based demographic approach that considers aggregate stages (defined in terms of size or life history stages) that represent functional biological units (Gotelli, 1995). It too has a long history in the field of ecological population dynamics (Kingsland, 1985). A stage-based model can be formed by collapsing a life table into discrete stages. Thus, unlike the life-table analysis that requires estimates for every year the organism lives, the stage-based model requires only estimates for each stage. Therefore, the realism of a many-staged model can be balanced with the precision of a simpler model when parameter estimation error is of concern. As with life tables, stage-based projection models can easily be solved analytically to permit formal sensitivity analysis (Caswell, 1989). Anderson (1990), and Hoenig and Gruber (1990) have suggested that stage-based models may provide a more realistic view of the dynamics of some populations.

The population dynamics of several marine species, including sandbar sharks (Cortés, 1999), sea turtles (Crouse et al., 1987; Crowder et al., 1994), blue crabs (Miller and Houde⁵), sardines (Lo et al., 1995), and anchovies (Perterra et al., 1997) have been explored by using stage-based models. Cortés (1999) developed a stochastic stage-based model for sandbar sharks in the western North Atlantic. He used the model to explore the implications of three different harvest strategies on population viability when fecundity varies. He concluded that in the absence of exploitation, the sandbar shark population should increase slowly by about 1.3% annually. Additionally, Cortés concluded that all three patterns of exploitation would cause declines in population abundance. Cortés' model and results indicate the utility of stage-based models in exploring potential management alternatives for sandbar sharks.

Here, we develop a deterministic stage-based model for sandbar shark populations. The model includes the two-year reproductive cycle of fertile and resting periods known to occur in sandbar sharks, but which were not included in Cortés's (1999) original description. We chose to use a deterministic framework to permit a formal elasticity (proportional sensitivity) analysis of the basic model. Stages to which the population dynamics are most sensitive can be interpreted either as being stages at which management action is likely to have the most impact or as stages at which parameter estimates have to be most precise because of impacts of potential environmental stochasticity. We use the model to examine the expected change in population growth resulting from

⁵ Miller, T. J., and E. D. Houde. 1998. Blue crab targeting. U.S. EPA Chesapeake Bay Program Report, Annapolis, MD, 167 p.

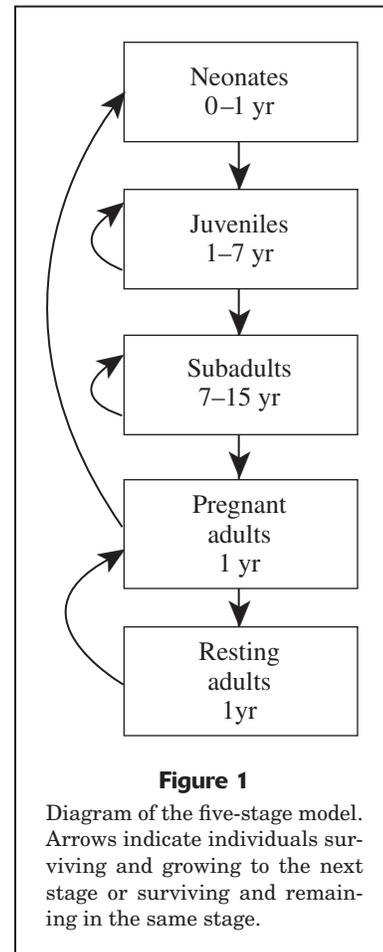
two particular management options, nursery ground closures and size limits. We exercised the general model framework to address four fundamental questions. What is the intrinsic rate of increase of sandbar shark populations under current patterns of exploitation? What is the sustainable level of fishing mortality ($F_{CRITICAL}$)? What is the effect of eliminating fishing mortality on early stages, either through nursery ground closures or through the introduction of size limits? For each question, we provide the results, predictions, and interpretation of sensitivity analyses to indicate the reliability of our conclusions.

Materials and methods

Life history of sandbar sharks

The first step in developing a stage-based model is to review the life history of a species to identify appropriate stages. Results of tagging and age and growth studies (Springer, 1960; Casey et al., 1985; Casey and Natanson, 1992; Sminkey and Musick, 1995, 1996) indicate that sandbar sharks are a long-lived species with low fecundity. These studies also indicate that females, males, and juveniles segregate by water depth and distance from shore. However, estimates of key vital rates are inconsistent. The generally accepted estimate of mortality and fecundity schedules indicates that sandbar sharks mature between 12 and 15 years of age and live to around 30 years of age (Casey et al., 1985; Sminkey and Musick, 1996). Another estimate suggests that sandbar sharks may not mature until age 29 and may live past 50 (Casey and Natanson, 1992). In our model we used an age at maturity of 15 years. From the biological function and the migration pathways determined by these studies, we identified five stages in the life history of the sandbar shark: neonates, juveniles, subadults, pregnant adults, and resting adults (Fig. 1).

Neonates are young-of-the-year sharks. Sandbar shark neonates are born fully developed at a fork length (FL) between 43 and 52 cm (Castro, 1983; Branstetter and Burgess¹). They remain in this stage for one year before becoming juveniles. Juveniles are the first stage to show a seasonal pattern of movement. In the winter, juveniles migrate to warmer waters, often to the edge of the Gulf Stream off North Carolina. In the summer, juveniles return to their nursery grounds. They continue this seasonal migration until they are between 6 and 10 years old (Casey et al., 1985; Branstetter and Burgess¹). In contrast, subadults, while still not yet mature, follow the adult migration pattern. This migration pattern consists of swimming along the Atlantic coast of the United States as far north as New England



in the summer and traveling south to warmer waters in the winter (Castro, 1983). In this model, individuals remain in the subadults stage for 8 years, at which point they may be 15 years of age, and then join the reproductive population.

Fifty percent of female sandbar sharks are mature at about 150 cm FL (Springer, 1960; Casey et al., 1985; Sminkey and Musick, 1996) or 12 to 15 years of age depending on the von Bertalanffy model. Female sandbar sharks give birth to an average of 8 or 9 pups once every other year (Springer, 1960; Sminkey and Musick, 1996). Larger sharks do not appear to give birth to a greater number of pups (Sminkey and Musick, 1996). Gestation lasts between 9 and 12 months (Castro, 1983). Pregnant females pup in shallow bays and estuaries along the east coast of North America, including Chesapeake Bay (Sminkey and Musick, 1996), Delaware Bay (Pratt and Merson⁶) and the waters off the coast of South Caro-

⁶ Pratt Jr., H. L., and R. R. Merson. 1996. Report of the 1996 apex predators investigation: sandbar shark nursery grounds project. Apex predators investigation. Northeast Fisheries Science Center, Natl. Mar., Fish. Serv., NOAA, Narragansett, RI.

lina (Castro, 1993). In the model, females alternate between pregnant and resting adult stages, spending one year in each. Thus, the stage durations used in the model were the following: 1 year for neonates; 6 years for juveniles; 8 years for subadults; 1 year for pregnant females; and 1 year for resting females.

Model development

The approach we present below is based on the general framework presented by Caswell (1989). Details on the general background of the approach can be found in Caswell (1989). In all equations, matrices and vectors are shown in boldface type, parameters in italic type.

The model is a postbreeding census, follows only females, and uses a yearly time step. The total number of sharks in the population at time t can be expressed in vector form as \mathbf{N}_t . Each element of \mathbf{N}_t represents the number of sharks in the appropriate stage at time t . There are three possible transitions for each individual in each stage: the probability of surviving and growing to the next stage, G_i ; the probability of surviving yet remaining in the same stage, P_i ; or the probability of dying, $1-G_i-P_i$. The individual transition probabilities G_i and P_i may range between 0 and 1. The sum of G_i and P_i is further constrained such that when a stage is not subject to mortality, $G_i + P_i = 1$. One other parameter, stage-specific fecundity, is required to estimate the number of young females produced per breeding female per year.

The vital rates governing the dynamics of the shark population can be expressed mathematically in a 5×5 transition matrix, \mathbf{A} . The fundamental equation to estimate the stage-structure in the population at any time t is given by

$$\mathbf{N}_t = \mathbf{A}^t - \mathbf{N}_0, \tag{1}$$

where \mathbf{N}_t = a vector of the number of individuals in each stage at time t ; and

\mathbf{A} = the transition matrix \mathbf{A} for sandbar sharks given by

$$\begin{bmatrix} 0 & 0 & 0 & G_4 \times f_4 & 0 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & 0 & G_5 \\ 0 & 0 & 0 & G_4 & 0 \end{bmatrix}. \tag{2}$$

For large values of t , $\mathbf{A}\mathbf{N}_t = \lambda\mathbf{N}_t = \mathbf{N}_{t+1}$, where the scalar λ is the finite rate of population increase. Further, $\ln\lambda = r$, the intrinsic rate of increase.

The columns of the matrix represent the fates of individuals in each stage. For example, surviving neo-

nates can grow only to the juvenile stage (G_1) whereas surviving juveniles can either remain a juvenile (P_2) or survive and grow into a subadult (G_2). Surviving pregnant adults can give birth and become resting adults (G_4). Surviving resting adults (G_5) can grow only into a pregnant female. The rows represent the origins of individuals in each stage. Neonates arise from pregnant adults who survive ($G_4 \times f_4$) whereas juveniles arise from neonates surviving and growing into juveniles (G_1) or from juveniles surviving and remaining juveniles (P_2). Pregnant adults can arise from subadults surviving and growing into a pregnant female (G_3) or from resting adults surviving and becoming pregnant adults (G_5). Resting adults can arise only from pregnant adults that survive (G_4).

The transition probabilities, P_i and G_i , can be calculated from estimates of the probability that during a single time step an individual of stage i survives, σ_i , and an individual of stage i grows, γ_i . In this way G_i , the probability of surviving and growing to the next stage is given by

$$G_i = \sigma_i \gamma_i. \tag{3}$$

Consequently P_i , the probability of surviving, but not growing to the next stage is given by

$$P_i = \sigma_i(1 - \gamma_i). \tag{4}$$

The probability of survival, σ_i over a single time step can be expressed as

$$\sigma_i = e^{-Z_i}. \tag{5}$$

Following traditional fisheries models, total mortality (Z_i) is calculated by using the equation $Z_i = F_i + M_i$, where F_i is the rate of fishing mortality and M_i is the rate of natural mortality at stage i .

Estimates of γ_i can be obtained in several different ways. Caswell (1989) recommended assuming constant stage duration for all individuals in the stage when only a relatively crude estimate of survival over broad age ranges is available. For this approach, individuals entering the stage have an equal probability of survival as individuals nearing the end of the stage. Employing this assumption yields an estimate of γ_i as

$$\gamma_i = \frac{(\sigma_i/\lambda_{init})^{T_i} - (\sigma_i/\lambda_{init})^{T_i-1}}{(\sigma_i/\lambda_{init})^{T_i-1}} \tag{6}$$

where T = the expected stage duration of a single stage; and

λ = the finite rate of population increase given by the dominant eigenvector of \mathbf{A} ($\ln \lambda = r$, the intrinsic rate of increase).

We began with an initial value of $\lambda_{init} = 1$. We then iterated λ until the value of λ given by an eigenanalysis of the matrix \mathbf{A} (see below), equaled the value of λ_{init} used in Equation 6. Together, Equations 1–6 described above allow estimates of G_i and P_i within \mathbf{A} to be defined.

Fecundity must also be defined. The fecundity term, f_i , is simply the expected number of female offspring produced by a female in stage i . For sandbar sharks only one stage is reproductively active and thus the only fecundity term in the matrix \mathbf{A} is $f_4 = 4.5$. This estimate is based on an equal sex ratio, 9 pups per brood, and one brood per year. However, as the model is a postbreeding census, the fecundity has to be discounted by the probability that a pregnant female will survive the gestation year to pup. Thus the realized fecundity term used in the model is $G_4 \times f_4$. All parameters within the matrix \mathbf{A} are now defined.

One feature of stage-based projection models that motivated their use was that they allowed us to solve \mathbf{A} analytically in order to calculate important demographic features and find the sensitivity of the model to parameter estimates. The two demographic features that can be calculated from \mathbf{A} are the stable stage distribution and the reproductive value of each stage. Once the stable stage distribution has been reached, the relative proportion of individuals in each stage remains constant over time. The reproductive value is the relative number of offspring that are yet to be born by individuals in a given age (Gotelli, 1995). This value depends on individuals surviving to maturity and reproducing. Thus, the youngest stages should have the lowest reproductive values because individuals in those stages must survive and reach maturity before they can reproduce. Both features can be calculated from an eigenanalysis of \mathbf{A} . For any $\{n \times n\}$ matrix one may define up to n scalar values ($\lambda_{1..n}$) and n -associated right and left vectors such that

$$\mathbf{A}\mathbf{w} = \lambda\mathbf{w} \quad (7)$$

$$\mathbf{v}\mathbf{A}^T = \lambda\mathbf{v} \quad (8)$$

where \mathbf{A}^T = the transpose of \mathbf{A} ;

λ = the eigenvalue; and

\mathbf{w} and \mathbf{v} = the right and left eigenvectors of \mathbf{A} .

The sandbar shark transition matrix has five possible eigenvalues and eigenvectors. However, our

interpretation is simplified for the sandbar shark transition matrix, \mathbf{A} , because it is non-negative, irreducible, and primitive. Thus, we are guaranteed that there is a single, dominant eigenvalue, λ_1 , that is real, positive, and strictly greater than all other possible λ s. This dominant eigenvalue, λ_1 will eventually describe the population rate of increase and $\ln \lambda_1 = r$, the intrinsic rate of increase of the population. Moreover, the right and left eigenvectors associated with λ_1 will be strictly positive. The population structure will eventually become proportional to a single stable stage distribution, given by \mathbf{w}_1 . Finally, there will be a single vector, \mathbf{v}_1 , associated with λ_1 , that expresses the relative contributions of each stage to the future population—a vector of reproductive values. Reproductive values are standardized so that the reproductive value of an individual in the first stage is one.

We were interested in calculating the change in λ following a change in vital rates expressing a transition from stage i to any other stage (including remaining in i) that may have been caused by management activities. This change reflects the sensitivity of λ to the transition probability. If entries in the transition matrix \mathbf{A} are represented as a_{ij} , it can be shown that

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (9)$$

where $\langle \mathbf{w}, \mathbf{v} \rangle$ = the scalar product of the two vectors.

Simply stated, the sensitivity of the population growth rate to changes in any vital rate is the product of the reproductive value of stage i and the proportional level of stage j in the stable stage distribution.

Because transition probabilities are censored parameters, varying only between 0 and 1, and fecundity is uncensored, it is more helpful to report the elasticity of λ . This is defined as the proportional change in λ for proportional changes in a_{ij} . Elasticities are calculated as

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (10)$$

Importantly, elasticities are additive, such that the sum of elasticities for each stage defines the proportional contribution of a_{ij} to overall population growth, λ , as

$$\sum_i \sum_j e_{ij} = 1.$$

Elasticities depend on a stable stage distribution and should be compared qualitatively.

Transition probability estimation for management options

Current conditions Fishing mortality (F) and especially natural mortality (M) are difficult to estimate. Owing to the uncertainty in estimates and in order to simplify the model, we used an estimate of $M = 0.1$ for all stages and all projections (NMFS¹; Sminkey and Musick, 1996). We projected the population forward using $F = 0.20$ for juveniles and older stages, as estimated in the 1996 shark evaluation workshop (SEW) for sandbar sharks only (NMFS³). For neonates a lower value of $F = 0.10$ was used because small sharks may be, but are not as likely to be, caught on the same gear as older sharks (Branstetter and Burgess¹). Using these values of F and M and $f_4 = 4.5$, we iterated Equation 6 to estimate all P_i and G_i values. We initialized the population with 1000 neonates. Then we estimated the initial number in subsequent stages using the 90% survival schedule for sandbar sharks given in Sminkey and Musick (1996). These calculations yielded an initial population of 9640 sharks (N_0).

Estimate of $F_{CRITICAL}$ We defined $F_{CRITICAL}$ as the limiting level of fishing mortality that is sustainable, i.e. the F for which $r = 0$ or $\lambda = 1$, where $r = \ln \lambda$. We systematically reduced F on all stages to define the relationship between F and r . For our estimations, F_1 remained 0.10 as long as $F_{2,3,4,5}$ was ≥ 0.10 . For any $F_{2,3,4,5} < 0.10$, $F_1 = F_{2,3,4,5}$. Thus, the fishing mortality of neonates was never greater than the fishing mortality on other stages.

Protecting neonates and pregnant adults: an extreme example We used the model to determine how efficient protecting different stages would be in promoting recovery of sandbar shark stocks. We asked the question: If neonates and pregnant adults are removed from the commercial fishery, how much will F on other stages need to be reduced to arrive at a sustainable population level? To address this question, we modified the model to remove all mortality on neonates ($F_1 = 0$, $M_1 = 0$) and to protect all pregnant adults from fishing pressure ($F_4 = 0$). In reality, we could not completely protect neonates from mortality (i.e. $M_1 > 0$) and we could not fully protect pregnant adults from commercial fishing. Thus the scenario represents an idealized nursery closure scheme. Fishing mortality on juveniles, subadults, and resting adults remained at 0.20. The fecundity for pregnant adults was left at 4.5.

Nursery closures and size limits We also ran the model using more realistic scenarios. In this case F on neonates and juveniles was 0, and F on the older stages was 0.20. Natural mortality for all stages remained at 0.10. This scenario is a fairly realistic size limit or nursery ground closure because sandbar sharks segregate by size. This scenario is similar to, but not as strict as, the 1998 SEW's recommended size limit.

Size limits protecting only one stage are another management option available. This method can be used to reduce the fishing mortality on any range of sizes. In this paper, two scenarios of this type are presented: 1) a size limit which reduces the F on juveniles to 0; and 2) a size limit which reduces the F on subadults to 0. Fishing mortality was equal to 0.20 in all other stages except neonates, where $F = 0.10$. Implementing such management actions would be difficult because the gear (longlines) cannot realistically avoid catching only the restricted stage, but the results would be indicative of the potential of these mechanisms to improve stocks.

Using the relationships (Eqs. 1–10) and vital rate estimates defined above, we now proceed with an analysis of the population dynamics of sandbar sharks. For each scenario, we calculate the stable stage distribution, the proportional reproductive value for each stage, and the elasticity of λ to changes in each matrix parameter, and compare the population growth rate and potential population reduction after 20 years for each scenario.

Results

Current conditions

When $F = 0.20$ for all stages except neonates, the population decreases (Table 1). The model predicts the intrinsic rate of natural increase, r , of the population as $r = -0.124$. The population is 13% of the initial abundance when projected 20 years forward. Population growth rate, stable stage distribution, and reproductive values are not affected by choice of the actual numbers used for initial abundance. The stable stage distribution is reached after 21 years in this scenario.

The largest proportion of the population (>0.56) are juveniles (Table 2). The smallest proportions (0.04, 0.03) are pregnant and resting adults, respectively. Adults have much larger reproductive values than prereproductive stages (Table 3).

The pattern of model proportional sensitivity is shown in Figure 2. The elasticity of λ to a small change in fecundity was expressed only in the preg-

Table 1
The reduction in population abundance after 20 years of each scenario.

Scenario	Fishing and natural mortality rates used	Intrinsic rate of increase, r	Reduction (%) in population abundance after 20 years ¹
Current conditions	$F_1=0.10; F_{2-5}=0.20$ $M=0.10$	-0.124	87
Protecting neonates and pregnant adults	$F_{1,4}=0; F_{2,3,5}=0.20$ $M_1=0; M_{2-5}=0.10$	-0.079	62
Protecting neonates and juveniles	$F_{1,2}=0; F_{3-5}=0.20$ $M=0.10$	-0.058	51
Protecting juveniles only	$F_1=0.10; F_2=0$ $F_{3-5}=0.20; M=0.10$	-0.069	62
Protecting subadults only	$F_1=0.10; F_3=0$ $F_{2,4,5}=0.20; M=0.10$	-0.048	50

¹ This percent reduction in population abundance is based on numbers generated in the model. Population abundance can also be calculated by using the equation

$$1 - e^{rt},$$

where r = the intrinsic rate of increase; and

t = the number of years.

Use of this equation results in a greater reduction in the population abundance.

Table 2

The stable stage distributions for each stage of the model and each scenario. The values of all stages under a scenario should sum to one.

Model stage	Current conditions, unstablized	Current conditions, stablized	Protecting neonates and pregnant adults	Protecting neonates and juveniles	Protecting juveniles	Protecting subadults
Neonate	0.15	0.16	0.15	0.10	0.12	0.19
Juvenile	0.56	0.54	0.60	0.54	0.51	0.51
Subadults	0.22	0.22	0.18	0.31	0.31	0.21
Pregnant adults	0.04	0.04	0.03	0.03	0.03	0.05
Resting adults	0.03	0.04	0.03	0.02	0.03	0.04

nant adult stage (because this is the only stage that is reproductively active). The highest elasticities were for the transition from neonate to juvenile and juvenile to subadult stages (Fig. 2). The elasticities for sharks remaining in the stage were equal for neonate, juvenile, subadult, and pregnant female stages. As discussed, the individual elasticities can be summed to estimate the overall contribution of each stage to λ . It is clear from Figure 2 that the peak elasticity occurs in the subadult stage. Estimates of elasticity suggest that the model is 2.3 times more sensitive to changes in this stage than in pregnant adults.

Estimate of $F_{CRITICAL}$

The relation between F and r is linear (Fig. 3). $F_{CRITICAL} = 0.071$ when $M = 0.10$. Therefore, the population is sustainable if $F = 0.071$. The value of $F_{CRITICAL}$ will vary with the value of M that is chosen. Our analyses showed that total mortality (Z) must be less than 0.17 for all stages if the population is to increase (Fig. 4). The population will increase at a rate $r = 0.05$ if $Z = 0.122$, and the population will decrease at a rate $r = -0.05$ if $Z = 0.222$.

At $F_{CRITICAL}$, the population abundance stabilizes and the population reaches a stable stage distribu-

Table 3
The proportional standardized reproductive values of each stage under each scenario. Neonates will always equal one.

Model stage	Current conditions, unstablized	Current conditions, stablized	Protecting neonates and pregnant adults	Protecting neonates and juveniles	Protecting juveniles	Protecting subadults
Neonate	1.00	1.00	1.00	1.00	1.00	1.00
Juvenile	1.08	1.19	0.92	1.04	1.26	1.29
Subadults	3.10	3.32	3.48	1.34	1.52	5.83
Pregnant adults	12.72	13.06	20.44	9.23	9.65	8.84
Resting adults	10.67	11.00	16.38	7.25	7.66	6.87

tion (Table 2). In this scenario, the proportion of neonates, pregnant adults, and resting adults in the population has increased compared with the proportion of stages in previous scenarios. The pattern in reproductive values remains largely unchanged (Table 3). As with the baseline scenario, the elasticities show the model to be the most sensitive to changes at the juvenile and subadult stages.

In summary, these model runs suggest that to stabilize and increase the sandbar shark population, F needs to be reduced below 0.07 ($Z \leq 0.17$). An F of this magnitude requires more than the full 50% quota reduction to be implemented.

Protecting neonates and pregnant adults: an extreme example

Results show that, even after protection of neonates and pregnant females, at current levels of F the population still decreases rapidly ($r = -0.079$). The population, projected 20 years forward, is only 38% of the initial abundance (Table 1). This percentage compares with reductions to 13% of initial abundance and $r = -0.124$ in the base run, where $F_{2,3,4,5} = 0.2$. In order to have a stable population ($r = 0$) under this scenario, we needed to decrease F to 0.097. Without protecting neonates and pregnant females, F must be reduced to 0.07. Thus, protecting neonates and pregnant females provides a 37% increase in the F required to maintain a sustainable population (Table 4). However, it must be emphasized that although

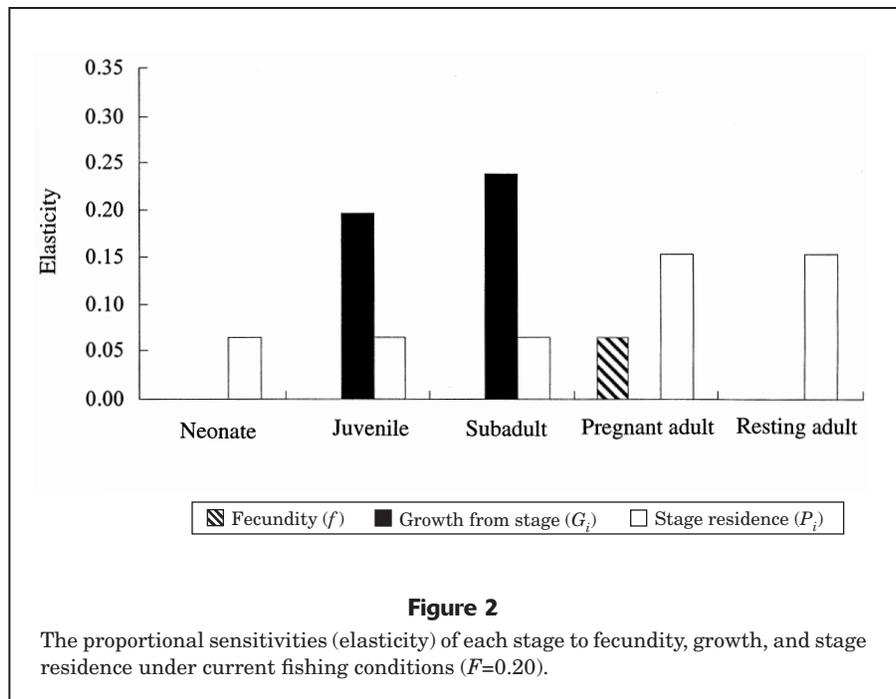


Figure 2
The proportional sensitivities (elasticity) of each stage to fecundity, growth, and stage residence under current fishing conditions ($F=0.20$).

this option does provide some protection, implementation would still require a 52% reduction in F over those levels currently estimated to be operating in the fishery. This reduction is in contrast to the 64% reduction in F required to reach sustainable rates of exploitation in the absence of this protection.

Juveniles had the highest proportion of individuals in the stable stage distribution (Table 2). Pregnant females and resting adults have the highest reproductive values (Table 3). Similar to the previous scenario, projections show the highest overall sensitivity to transitions involving the abundance of subadults (Fig. 5). However, in contrast with earlier simulations, projections show additional substantial sensitivity to transitions into the resting adult stage (Fig. 5).

Nursery ground closures and size limits

Results of this scenario show that the protection of neonates and juveniles from all fishing mortality slowed the decline ($r=-0.058$) but could not stabilize the population. When projected forward 20 years, the population abundance is 49% of the initial abundance (Table 1). In order to stabilize this model, F had to be reduced on subadults and adults to 0.109. Thus, this closure provides a 54% increase in the F

required to maintain a sustainable population over that required in the absence of nursery closures and a 12% increase in F over the extreme option modeled above (Table 4). Protecting neonates and juveniles through nursery ground closures or size limits would require a 46% reduction in F over those levels currently estimated to be operating in the fishery.

Juveniles have the highest proportion of individuals in the stable stage distribution (Table 2). Pregnant adults and resting adults have the highest reproductive values (Table 3). Again, the model shows the highest sensitivities to the juvenile and subadults stages (Fig. 6).

Protecting either juveniles or subadults alone still leads to a declining population. When $F_2=0$, after 20 years the population is 38% that of the initial population (Table 1). When $F_3=0$, the population at 20 years is 50% that of the initial population (Table 1). Further runs indicated that the population is stabilized if $F_{3,4,5} = 0.101$ (when $F_2=0$) or if $F_{2,4,5} = 0.120$ (when $F_3=0$). Quota reductions of 50% and 40%, respectively, are required to achieve these critical levels of F . In both cases the stable stage distribution is achieved within 24 years. The stable stage distribution proportions and reproductive values of each stage are listed in Tables 2 and 3. Figure 7 shows the sensitivity of the model to fecundity, growth, and stage residence when $F_2 = 0$. These sensitivities were approximately the same when $F_3 = 0$. As in the other models, juveniles and subadults have the highest sensitivity.

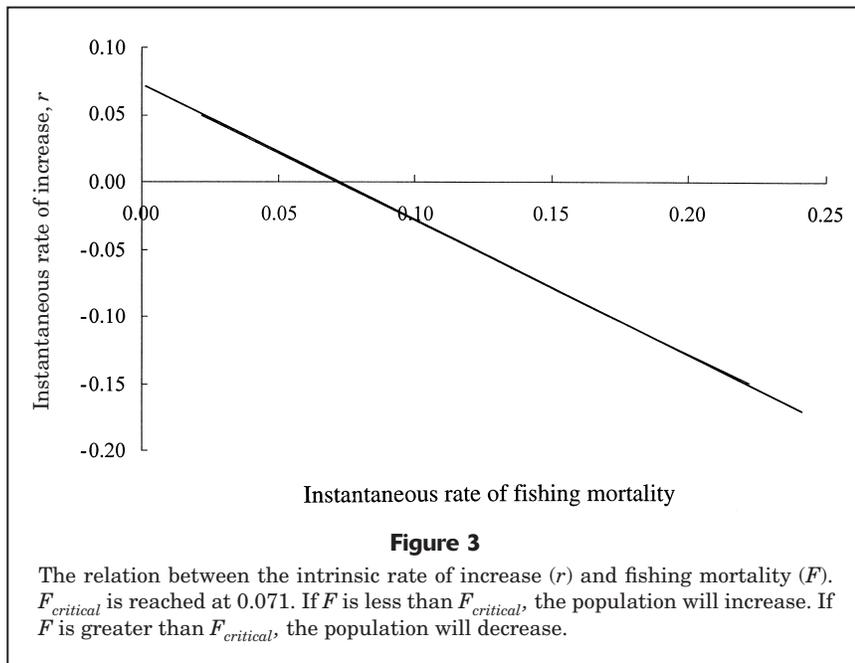


Figure 3

The relation between the intrinsic rate of increase (r) and fishing mortality (F). $F_{critical}$ is reached at 0.071. If F is less than $F_{critical}$, the population will increase. If F is greater than $F_{critical}$, the population will decrease.

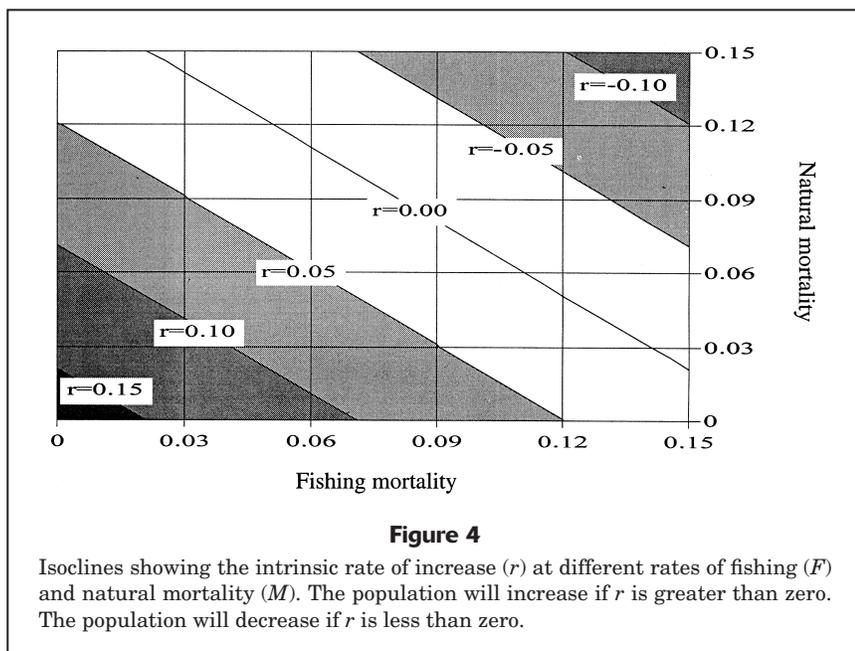


Figure 4

Isoclines showing the intrinsic rate of increase (r) at different rates of fishing (F) and natural mortality (M). The population will increase if r is greater than zero. The population will decrease if r is less than zero.

Discussion

The model projects that the sandbar shark population is unlikely to increase unless F is reduced below $F_{CRITICAL}$. The value calculated here is less than the $F_{CRITICAL}$ value of 0.10 that Sminkey and Musick (1996) predicted by using a life table. Both Sminkey and Musick's (1996) and Cortés's (1999) results and those presented here indicate that current estimates of F are

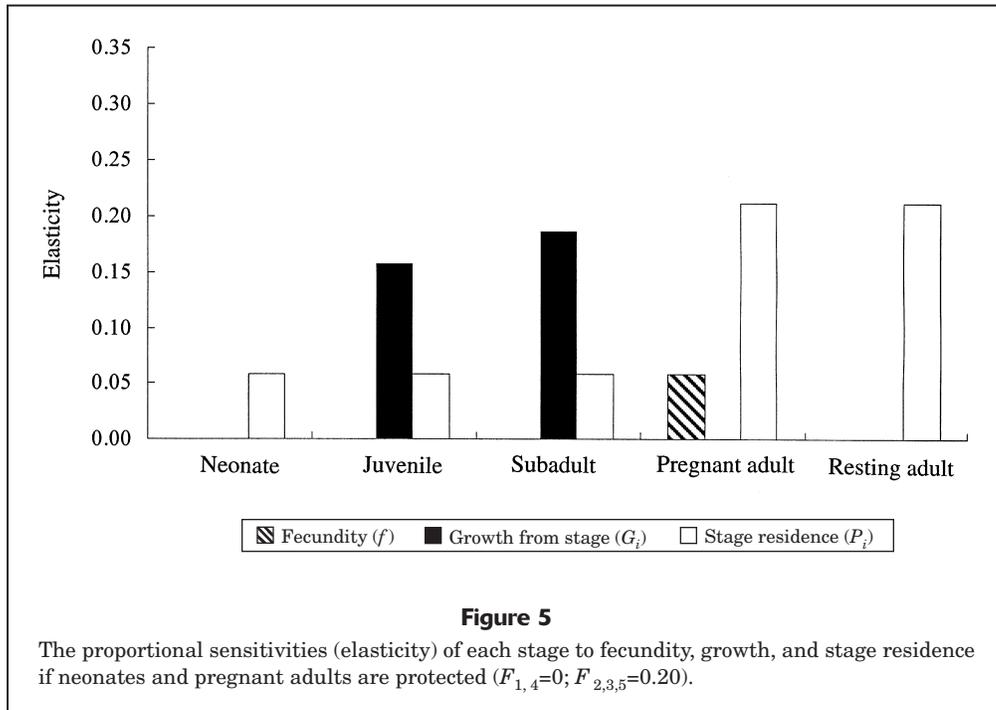


Table 4

The percent reduction in fishing mortality needed to stabilize the population if $F_{Current} = 0.20$. $F_{Critical}$ is the fishing mortality level at which the population abundance is stable. $F_{Current}$ is the fishing mortality level estimated in the 1996 stock assessment.

Scenario	Fishing and natural mortality rates used	$F_{Critical}$	% reduction needed
Current conditions	$F_1=0.10$; $F_{2-5}=0.20$ $M=0.10$	0.071	64
Protecting neonates and pregnant adults	$F_{1,4}=0$; $F_{2,3,5}=0.20$ $M_1=0$; $M_{2-5}=0.10$	0.097	52
Protecting neonates and juveniles	$F_{1,2}=0$; $F_{3-5}=0.20$ $M=0.10$	0.109	46
Protecting juveniles only	$F_1=0.10$; $F_2=0$ $F_{3-5}=0.20$; $M=0.10$	0.101	50
Protecting subadults only	$F_1=0.10$; $F_3=0$ $F_{2,4,5}=0.20$; $M=0.10$	0.120	40

too high to maintain the population and must be reduced. At the 1996 SEW, it was determined that reducing F levels by 50% was likely to increase the chances of recovering the large coastal stock (NMFS¹). In response to this, NMFS reduced the quota in 1997 for Atlantic large coastal sharks by 50% in order to reduce F by 50%. Assuming that the estimate of F from the SEW is accurate, that a 50% quota reduction is equivalent to a 50% decrease in F , and that the reduction in F is equally distrib-

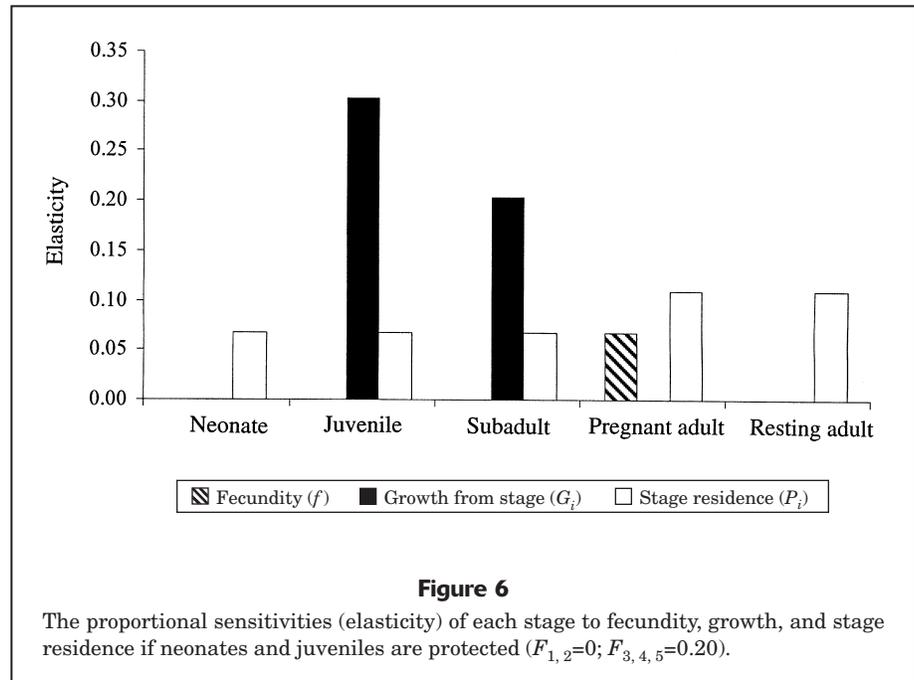
uted across age classes, we believe our results indicate that a 50% quota reduction may not stabilize the stock. Our model predicts that without alternative management strategies, the population will not begin to recover unless F on sandbar sharks is reduced to below 0.07, requiring a reduction in current estimates of F of greater than 50%.

Nursery ground closures and size limits are possible management strategies. These strategies would protect neonates, pregnant adults who are in the

nursery grounds to pup, and any juveniles who may have returned for the summer. One of the scenarios we ran is extreme in that every neonate survives ($Z=0$) and pregnant adults are not fished for the entire time they are pregnant. But in this scenario, juveniles are not protected. If F is not reduced on juveniles, subadults, and resting adults, the model shows that the population will decrease until F is reduced to 0.097. This is higher than the $F = 0.07$ which would be needed to stabilize the population without any protection for neonates, and would almost be met by the 50% reduction in quota as suggested by the 1996 SEW. However, these scenarios assume complete protection of protected stages from either fishing or natural mortality. Thus, they probably over-estimate the effectiveness of the potential management action. Overall, these models indicate that nursery ground closures or size limits that protect only neonates and juveniles, or neonates and pregnant adults, are not likely to be the ultimate solution. Additional measures will need to be taken to protect the sandbar shark.

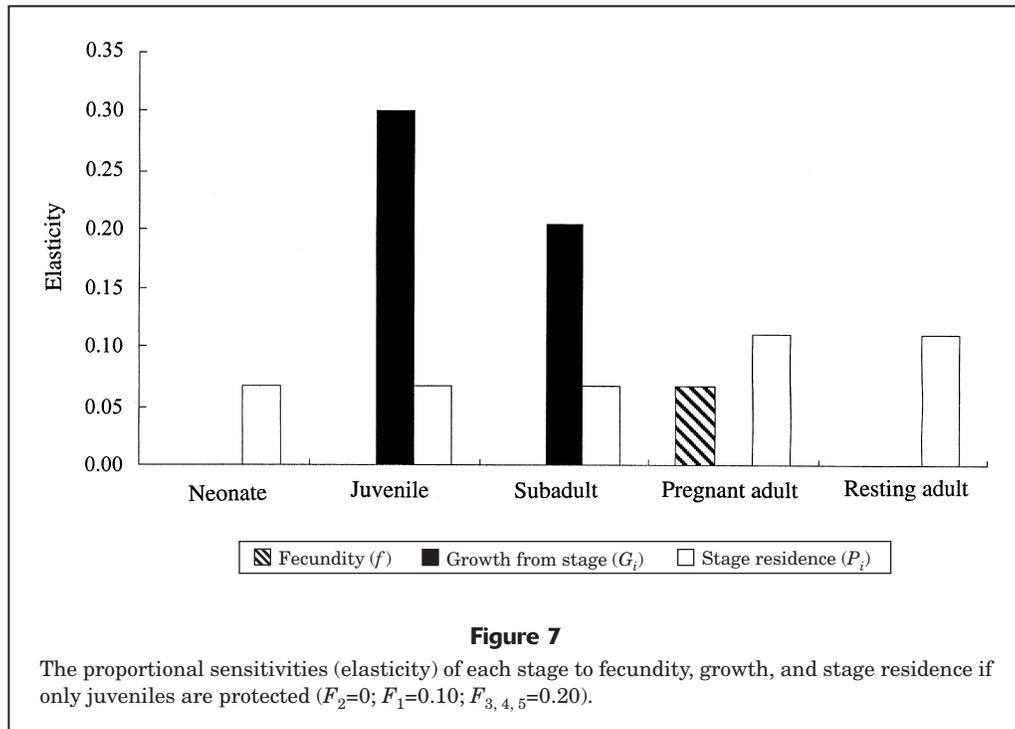
Subsequent runs of the model showed that size limits that protect juvenile and subadult stages will not act to rebuild the population alone, despite the fact that the model indicates these stages are the most sensitive to survival. In these cases, F needs to be reduced to 0.10 or 0.12, respectively. If the current F estimate of 0.20 is correct and if a 50% reduction in quota reduces F by 50%, size limits to protect either stage and a reduction in quota of between 40% and 50% may be sufficient to stabilize the population.

All scenarios indicate that the sandbar shark stock will most likely be rebuilt through a combination of management strategies. With nursery closures or size limits that protect only one stage, the stock will decline if fishing mortality remains the same as that currently estimated. Because the model's estimates of population growth are sensitive to survival at the juvenile and subadult stages, because these stages have the highest proportion of the population in the stable stage distribution, and because subadults have relatively high reproductive values, ideally any management strategies selected should be those that conserve these stages.



Most of the model projections indicate that the total sensitivities of juveniles and subadults are the greatest. The sensitivity of population growth to events during these stages suggests two things: management needs to focus on protecting juveniles and subadults, and scientists need to collect accurate estimates of F and M for juveniles and subadults. Possible conservation efforts could include minimum sizes to protect immature sandbar sharks or time-area closures to protect both juveniles and subadults during their migrations. If our model is correct, it is important to take measures to protect these stages soon, not only because the model shows that the population abundance decreases quickly at current estimates of F , but also because there is evidence of strong year classes of immature sandbar sharks entering the fishery (Branstetter and Burgess¹). In 1994, Sminkey suggested that the 1987, 1989, and 1992 year classes in Chesapeake Bay were exceptionally strong. It will be easier for the fishery to recover if we have strong year classes on which to build.

This is not the first time the use of a stage-based model has concluded that conservation efforts should target juveniles and subadults of a long-lived species more than newborns. Rates of population growth in many marine species are effected more by changes in survival of juvenile and subadult stages than by changes in survival of other stages, or by changes in fecundity (Heppell et al., 1999). For example, Crouse et al. (1987) and Crowder et al. (1994) concluded that population growth rate was most sensitive to the survival of large juvenile loggerhead sea turtles.



They suggested that the use of turtle excluder devices would protect juvenile sea turtles and aid in conservation and recovery of this species. Additionally, Heppell et al. (1996) indicated that population enhancement by means of hatchery production of sea turtles would likely not be successful. In contrast, marine mammals show a different pattern of sensitivity. For these taxa, population growth appears most sensitive to events occurring during the adult stages (Heppell et al., 1999). Studies indicate that marine fish may also show a different pattern of sensitivity, where there is increased sensitivity to events in the early life history (Heppell et al. 1999; Quinlan and Crowder, 1999).

Three features of our approach require one to use caution in interpreting our conclusions. First, there are problems in using stage-based models, or demographic models of all types, with highly migratory animals such as sharks. For instance, most demographic models assume that the population is closed. In the case of the sandbar shark this assumption may not hold true. Tagging studies show that a small percentage of sandbar sharks tagged in U.S. waters are caught in Mexican waters. Because it is currently unknown if there are nursery grounds in Mexican waters, this migration to Mexico may represent an additional source of loss to the population that may not be replaced. The model does not consider this loss. If a significant number of sandbar sharks are found to migrate to Mexican waters, current estimates of F may be underestimates. If this is

the case, even greater reductions in F may be necessary to help the stock recover.

Second, we have presented a deterministic model of sandbar shark population dynamics. Thus, we have ignored uncertainty of and plasticity in vital rates such as growth and fecundity. Tuljapurkar (1997) and Nations and Boyce (1997) have discussed the potential biases that may result from basing harvest strategies on results from a deterministic model, particularly when juvenile survival is closely tied to environmental conditions. In addition to potential biases in the results, a deterministic model yields only a point estimate of population growth rate. Cortés (1999) included a stochastic term for fecundity in his model for sandbar sharks. Subsequently, he used Monte Carlo simulations to generate distributions of predicted population growth rates when fecundity varies stochastically. His results indicate that predicted population growth rates may vary by 2–3% when fecundity is allowed to vary. The impact of stochasticity in survival and growth on the predicted population growth rates is unknown. However, given the sensitivity of the model to transition involving growth and survival for juvenile and subadult animals, its impact may be substantial.

Finally, unlike many traditional fishery models, our demographic model does not take into account density dependence or compensation. However, given the longevity and age to maturity of sandbar sharks, and sharks in general, compensation may not be as signif-

icant or as observable as that for teleost fish. Sminkey and Musick (1995) have suggested three mechanisms of compensation in sharks: decreases in natural mortality of younger sharks as the abundance of predatory larger sharks is reduced; compensatory increases in fecundity when food is more available or when uterine mortality is reduced; and an increase in growth rate and thus a decrease in natural mortality and possibly earlier maturity when food is abundant. In Chesapeake Bay, they found evidence of a slight increase in growth rate of juvenile sharks after the population had been depleted but were not able to ascertain if the age of maturity had also been reduced. Late age at maturity due to relatively slow growth rates reduces the probability that small increases in growth or increased neonate survival through density-dependent mechanisms will compensate for fishing mortality (Heppell et al., 1999).

In summary, the results when $F = 0.20$ for older stages indicate that sandbar shark stocks are currently being fished above their ability to replace themselves (i.e. r is negative for the best estimate of F). Thus, management action (e.g. time area closures, reduced quota, minimum size) is needed to reduce F to the level where r is zero or positive. Because the model is highly sensitive to juvenile and subadult survival, management actions that reduce the mortality rates of these stages would likely be more effective than nursery closures that protect only neonates and pregnant females.

Although our study suggests that the protection of juvenile and subadult sandbar sharks may aid in recovery of sandbar sharks, our method may not work as well on other shark species, because life history traits differ. Sandbar sharks are often confused with other shark species such as the dusky shark; therefore, whichever management strategy is chosen, it should work for all large coastal shark species. These problems, combined with a paucity of data on pupping grounds, age at maturity, and other traits, make selection of a conservation method difficult. The model in our study should be viewed as a starting point for looking at the effect of the different options available and for comparing these options among the shark species involved.

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Literature cited

- Anderson, E. D.**
1990. Fishery models as applied to elasmobranch fisheries. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematic, and the status of the fisheries (H. L. Pratt, S. H. Gruber, T. Taniuchi, eds.), p. 473–484. U.S. Dep. Commer., NOAA Technical Report NMFS 90.
- Casey, J. G., and L. J. Natanson.**
1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *C. J. Fish. Aquat. Sci.* 49:1474–1477.
- Casey, J. G., H. L. Pratt Jr., and C. E. Stillwell.**
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Can. J. Fish. Aquat. Sci.* 42:963–975.
- Castro, J.**
1983. The sharks of North American waters. Texas A&M Univ. Press, College Station, TX, 180 p.
1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environ. Biol. Fish.* 38:37–48.
- Caswell, H.**
1989. Matrix population models. Sinauer Associates, Inc., Sunderland, MA, 328 p.
- Cortés, E.**
1999. A stochastic stage-based population model of the sandbar shark in the western North Atlantic. *Am. Fish. Soc. Symp.* 23:115–136.
- Crouse, D. T., L. B. Crowder, and H. Caswell.**
1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412–1423.
- Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin.**
1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecol. Appl.* 4:437–445.
- Gotelli, N. J.**
1995. A primer of ecology. Sinauer Associates, Sunderland, MA, 206 p.
- Heppell, S. L., L. B. Crowder, and D. T. Crouse.**
1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecol. Appl.* 6:556–565.
- Heppell, S., L. B. Crowder, T. R. Menzel.**
1999. Life table analysis of long-lived marine species, with implications for conservation and management. *Am. Fish. Soc. Symp.* 23:137–148.
- Hoenig, J. M., and S. H. Gruber.**
1990. Life history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematic, and the status of the fisheries (H. L. Pratt, S. H. Gruber, T. Taniuchi, eds.), p. 1–16. U.S. Dep. Commer., NOAA, Tech. Report NMFS 90.
- Kingsland, S. E.**
1985. Modeling nature: episodes in the history of population ecology. Chicago Univ. Press, Chicago, IL, 267 p.
- Lo, N. C. H., P. E. Smith, and J. L. Butler.**
1995. Population growth of northern anchovy and Pacific sardine using stage-specific matrix models. *Mar. Ecol. Prog. Ser.* 127:15–26.

NMFS (National Marine Fisheries Service).

1993. Fishery management plan for sharks of the Atlantic ocean. Office of Sustainable Fisheries. U.S. Dep. Commer., National Oceanic and Atmospheric Administration (NOAA), NMFS, Silver Spring, MD, 173 p.

1997. Report to Congress: status of fisheries of the United States. U.S. Dep. Commer., NOAA, Silver Spring, MD, 75 p.

Nations, C. S., and M. S. Boyce.

1997. Stochastic demography for conservation biology. *In* Structured models in marine, terrestrial and freshwater systems (S. Tuljapurkar and H. Caswell, eds.), p. 450–469. Chapman and Hall. New York, NY, 643 p.

Pertierra, J. P., J. Lleonart, and N. C. H. Lo.

1997. Application of a stage-specific matrix model and length-cohort based analysis to assess the anchovy fishery in Catalan coastal waters (NW Mediterranean Sea). *Fish. Res.* 30:127–137.

Quinlan, J. A., and L. B. Crowder.

In press. Searching for sensitivity in the life history of Atlantic menhaden: inferences from a matrix model. *Fish. Oceanog.*

Simpfendorfer, C. A.

1999. Demographic analysis of the dusky shark fishery in southwestern Australia. *Am. Fish. Soc. Symp.* 23:149–160.

Sminkey, T. R., and J. A. Musick.

1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* 4:871–883.

1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fish. Bull.* 94:341–347.

Springer, S.

1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv. Fish. Bull. 61:1–38

Tuljapurkar, S.

1997. Stochastic matrix models. *In* Structured models in marine, terrestrial and freshwater systems (S. Tuljapurkar and H. Caswell, eds.), p. 59–87. Chapman and Hall. New York, NY, 643 p.