
Incorporating Uncertainty into Demographic Modeling: Application to Shark Populations and Their Conservation

ENRIC CORTÉS

National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32408, U.S.A., email cortes@bio.fsu.edu

Abstract: *I explored the effect of uncertainty in demographic traits on demographic analyses of sharks, an approach not used before for this taxon. I used age-structured life tables and Leslie matrices based on a pre-breeding survey and a yearly time step applied only to females to model the demography of 41 populations from 38 species of sharks representing four orders and nine families. I used Monte Carlo simulation to reflect uncertainty in the estimates of demographic traits and to calculate population statistics and elasticities for these populations; I used correlation analysis to identify the demographic traits that explained most of the variation in population growth rates (λ). The populations I examined fell along a continuum of life-history characteristics that can be linked to elasticity patterns. Sharks characterized by early age at maturity, short lifespan, and large litter size had high λ values and short generation times, whereas sharks that mature late and have long lifespans and small litters have low λ values and long generation times. Sharks at the "fast" end of the spectrum tended to have comparable adult and juvenile survival elasticities, whereas sharks at the "slow" end of the continuum had high juvenile survival elasticity and low age-zero survival (or fertility) elasticity. Ratios of adult survival to fertility elasticities and juvenile survival to fertility elasticities suggest that many of the populations studied do not possess the biological attributes necessary to restore λ to its original level after moderate levels of exploitation. Elasticity analysis suggests that changes in juvenile survival would have the greatest effect on λ , and correlation analysis indicates that variation in juvenile survival, age at maturity, and reproduction account for most of the variation in λ . In general, combined results from elasticity and correlation analyses suggest that research, conservation, and management efforts should focus on these demographic traits.*

Incorporación de la Incertidumbre en el Modelado Demográfico: Aplicación en Poblaciones de Tiburones y Su Conservación

Resumen: *Exploré los efectos de la incertidumbre en los caracteres demográficos en análisis demográficos de tiburones, un método no empleado con anterioridad para este taxón. Utilicé tablas de vida estructuradas por edades y matrices de Leslie basadas en evaluaciones pre-gestación y pasos de tiempo de un año aplicados solo a las hembras para modelar la demografía de 41 poblaciones de 38 especies de tiburones que representan cuatro órdenes y nueve familias. Utilicé la simulación de Monte Carlo para reflejar la incertidumbre en las estimaciones de caracteres demográficos y calcular las estadísticas y elasticidades poblacionales para estas poblaciones y el análisis de correlación para identificar los caracteres demográficos que explican la mayoría de la variación en las tasas de crecimiento poblacional (λ). Las poblaciones examinadas caen dentro de un continuo de características de historias de vida que pueden estar vinculadas con los patrones de elasticidad. Los tiburones que maduran a temprana edad y tienen corta duración de vida y grupos grandes de crías tuvieron valores altos de λ y tiempos generacionales cortos, mientras que los tiburones que maduran tarde y tienen una duración de vida larga y grupos pequeños de crías tienen valores bajos de λ y tiempos generacionales largos. Los tiburones que se encuentran en el punto final "rápido" del espectro tendieron a tener elasticidades de supervivencia de adultos y juveniles comparables, mientras que los tiburones en el*

Paper submitted October 3, 2000; revised manuscript accepted September 19, 2001.

1048

punto final "lento" del continuo tuvieron una alta elasticidad de supervivencia de juveniles y una baja elasticidad en supervivencia a la edad cero (o fertilidad). Las proporciones de elasticidades de supervivencia de adultos y fertilidad y de elasticidades de supervivencia de juveniles y fertilidad sugieren que muchas de las poblaciones estudiadas no poseen los atributos biológicos necesarios para restaurar λ a su nivel original después de niveles moderados de explotación. El análisis de elasticidad sugiere que en la supervivencia de juveniles se podría tener el efecto mayor de λ y el análisis de correlación indica que la variación en la supervivencia de juveniles, la edad de maduración y reproducción explican la mayor parte de la variación en λ . En general, los resultados combinados de los análisis de elasticidad y correlación sugieren que los esfuerzos de investigación, conservación y manejo deberían enfocarse a estas características demográficas.

Introduction

The use of matrix population models to address conservation issues has increased in recent years. In particular, the usefulness of elasticity analysis as a tool in population ecology has been recently re-emphasized (Benton & Grant 1999 and references therein; Heppell et al. 2000a). Previous demographic analyses of shark populations have used deterministic life tables to calculate intrinsic rates of increase and other population parameters of interest to estimate their potential for exploitation. These analyses have included calculation of life-table sensitivities or have considered only a reduced number of scenarios to evaluate the effect of variation of a single demographic parameter at a time on population growth rates. Only two studies have calculated mean matrix elasticities, one for leopard sharks (*Triakis semifasciata*) and angel sharks (*Squatina californica*) (Heppell et al. 1999) and the other for sandbar sharks (*Carcharhinus plumbeus*) (Brewster-Geisz & Miller 2000).

Incorporating the effect of uncertainty in vital rates into demographic analyses is a useful approach that is increasingly being applied in conservation biology. It is important to consider the effect that uncertainty and variability in vital rates can have on population parameters, especially for marine species, for which estimates of vital rates are difficult to obtain and often result in high uncertainty (Caswell et al. 1998). A better understanding of how life histories and population dynamics will respond to exploitation under uncertainty would be beneficial for fishery managers dealing with marine taxa. With the exception of a study by Cortés (1999), who used a Monte Carlo simulation in a stage-based population model of *C. plumbeus*, no published studies have attempted to incorporate uncertainty or known variation in vital rates for sharks.

When elasticity analysis of a single deterministic projection matrix is used to rank the importance of life-history stages, inappropriate management actions can result (Benton & Grant 1999; Mills et al. 1999; Heppell et al. 2000a). To circumvent potential shortcomings of deterministic methods, Wisdom et al. (2000) developed life-stage simulation analysis, a technique that combines

aspects of both prospective and retrospective analysis of matrix population models (Horvitz et al. 1997). This simulation approach provides a useful framework within which to account for the effect of uncertainty and variability in vital rates on population growth rates (λ) by resampling the vital rates to produce matrix replicates from which λ values can be obtained.

Deterministic elasticity analysis measures the relative effect on λ of small, proportional changes in single matrix elements or vital rates, while all the other matrix elements or vital rates are held constant (De Kroon et al. 1986; Wisdom & Mills 1997). Randomization procedures have been proposed as a complementary tool through which elasticity and regression analyses can be used in tandem to provide useful insight into the effects of vital rates on λ (Wisdom & Mills 1997). With randomization and regression procedures, elasticities can be evaluated across a wide range of vital rates, and the effects on λ of simultaneous, stochastic, and disproportionate changes in vital rates can be considered.

Life-table or matrix-based approaches also assume density independence and time invariance of vital rates, although density-dependent compensation can be incorporated into these models (Getz & Haight 1989; Grant 1998; Grant & Benton 2000). Heppell et al. (1999) used the ratio of adult survival elasticity to age-0 survival (or fertility) elasticity to predict the level of compensation or the management efforts required to restore population growth rates to their original levels in several long-lived species. Smith et al. (1998) calculated rebound potentials for 26 species of sharks through a modified demographic technique incorporating density dependence in the pre-adult stages. These studies were based on mean, invariant vital-rate values.

In light of our lack of understanding of how uncertainty can affect estimates of vital rates and conclusions from demographic and elasticity analyses of shark populations, my objectives were as follows. First, I wanted to incorporate uncertainty in estimates of demographic traits in a consistent manner to compare, on a relative scale, predictions of future population growth rates, generation times (\bar{A}), and elasticities across species. Second, I was interested in identifying which vital rates λ is

most sensitive to and determining which demographic traits used in constructing life-table or matrix population models accounted for more variation in λ . Third, I sought to determine how likely it is that density-dependent or other responses could offset the effects of exploitation by restoring λ to original levels given the life-history constraints for each species. Finally, I wanted to examine elasticity patterns of shark populations and potentially link them to life-history characteristics to ultimately categorize those populations according to their likely response to perturbation of the various life stages, as was recently done for other taxa (Heppell et al. 2000b; Sæther & Bakke 2000).

Methods

Estimation of Population Growth Rates, Generation Times, and Elasticities

I used age-structured life tables and Leslie matrices based on prebreeding surveys and a yearly time step applied only to females to model the demography of 41 populations from 38 species of sharks representing four orders and nine families. I used Monte Carlo simulation to incorporate uncertainty in demographic parameters and generate population growth rates, generation times, and elasticities for a large set of matrices that spanned a range of possible parameter values.

I randomly selected age at maturity, maximum age, age-specific fecundity, and age-specific survivorship from assumed statistical distributions, based on knowledge of demographic traits for each population taken from published accounts. I assumed that age at maturity (α) was represented by a triangular distribution when only a single value was reported in the literature (Appendix 1). I set that value as the likeliest and obtained the lower and upper bounds using ± 1 or more years as an approximation. If a range was reported in the literature, I assumed a uniform distribution. I represented lifespan (ω) by a linearly decreasing distribution scaled to a total relative probability of 1. I used the highest empirical value of lifespan reported in the literature as the likeliest or maximum value and set the minimum value by arbitrarily adding 30% to the likeliest value. I opted for this approach because, for comparative purposes, it is preferable to using theoretically derived values. In a few cases, I sought an opinion from experts to estimate the minimum value.

I estimated the probability of annual survival at the beginning of each age through six life-history methods, those of (1) Hoenig (1983); (2) Pauly (1980); (3) Chen and Watanabe (1989); (4) Peterson and Wroblewski (1984); and (5) and (6) Jensen (1996). (See Cortés [1998] for a description of methods 1 and 2; Cortés [1999] and Roff [1992] for a description of methods 3 and 4; and Sim-

pfendorfer [1999] for a description of methods 5 and 6). Method 1 relies on an estimate of lifespan, whereas all the other methods except 4 rely on parameter estimates derived from the von Bertalanffy growth function, which is typically used to describe the growth and aging dynamics of elasmobranchs.

For Peterson and Wroblewski's method (4), I used wet weight as a proxy for dry weight because this method seems to yield more realistic estimates of survival for sharks (E.C., unpublished data). I assumed that dry weight was 20% of wet weight in all cases. This method is the only one of the six I applied that uses empirical estimates of weight to predict survivorship, thus allowing estimation of size- and age-specific survivorship. It also provides a benchmark for comparison with the other methods, which—except in part for method 3—make identical predictions of survivorship for animals of very different size but with similar lifespan and growth characteristics. Based on these considerations, I chose this method as the likeliest for developing probability density functions for survivorship. Length-at-age and weight-at-age estimates were obtained from published von Bertalanffy growth functions and by transforming length into weight through published length-weight relationships, respectively.

I took a liberal approach and discarded the lowest of the other five estimates of survivorship to minimize the occurrence of unrealistically low values. I then used the lowest and highest values from the remaining four estimates as lower and upper bounds (Appendix 1). If the estimate of survivorship obtained through method 4 fell between those bounds, I used it as the likeliest value in a triangular distribution. If the estimate from method 4 was the lowest of the five estimates, I assumed a linearly decreasing distribution scaled to a total relative probability of 1, with the estimate from method 4 being the likeliest and the highest estimate the unlikeliest. Conversely, if the estimate from method 4 was the highest of the five estimates, I assumed a linearly ascending distribution scaled to a total relative probability of 1, with the lowest estimate being the unlikeliest and the estimate from method 4 the likeliest (Fig. 1).

I generally represented fecundity-at-age by a normal distribution, with the mean and standard deviation obtained from the literature (Appendix 1). In cases where the standard deviation was not reported, I assumed it was 30% of the mean, based on the observation that it generally ranged between 20% and 40% of the mean in reported cases. I further truncated the normal distribution to reflect the biological knowledge of litter size (i.e., I used the minimum and maximum litter sizes reported to bound the distribution). When the mode was reported instead of the mean, I assumed a triangular distribution with the mode being the likeliest value and the range used to bound the distribution. I assumed a uniform distribution when only a range was reported. In cases

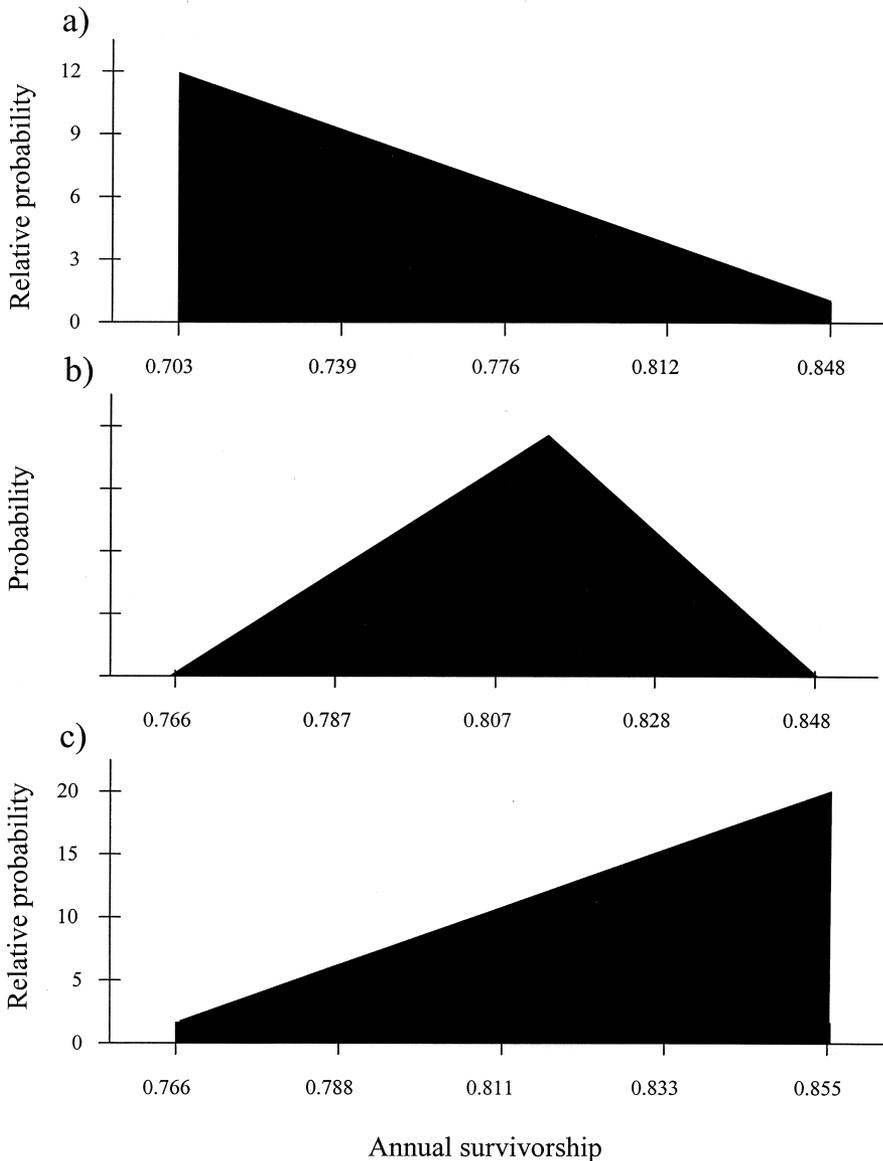


Figure 1. Statistical distributions of annual survivorship-at-age. These examples are for the tiger shark (*Galeocerdo cuvier*) and show (a) a linearly decreasing distribution describing survivorship for age-0 individuals, (b) a triangular distribution of age-1 sharks, and (c) a linearly increasing distribution of age-2 individuals. In (a) the estimate from the Peterson and Wroblewski (1984) method survivorship was the lowest of five estimates, in (b) it fell between the lowest and highest of the other four estimates, and in (c) it was the highest of five estimates (see text for a full explanation).

where such information was available, I increased fecundity with body size and age. I assumed a 1:1 male to female ratio in all cases and that 100% of females were reproductively active after reaching maturity, unless otherwise noted. I expressed annual fecundity as the number of female offspring at birth, divided by the length of the reproductive cycle in years.

I used life tables and age-structured Leslie matrices to calculate population statistics, which produce nearly identical results. For life tables, I used the discrete form of the Euler (Lotka) equation, generation time, reproductive value, and stable age distributions.

Annual population growth rates ($\lambda = e^r$) were obtained from per capita rates of population increase (r) calculated by iteratively solving the Euler equation:

$$1 = \sum_{x=1}^{\omega} l_x m_x e^{-rx}$$

where l_x is the probability of an individual being alive at the beginning of age x , m_x is the number of female offspring produced annually by a female at age x , and ω is maximum age. I calculated generation time (\bar{A}) as

$$\bar{A} = \frac{\sum_{x=1}^{\omega} x l_x m_x e^{-rx}}{\sum_{x=1}^{\omega} l_x m_x e^{-rx}}$$

The distribution of reproductive values (v_x) was obtained through

$$\frac{v_x}{v_0} = \frac{e^{rx}}{l_x} \sum_{t=x}^{\omega} e^{-rt} l_t m_t$$

where v_0 is the reproductive value at birth, which is equal to 1, and t denotes all the ages a female will pass through from x to ω .

The stable age distribution (c_x) was obtained through

$$c_x = \frac{l_x e^{-rx}}{\sum_{x=1}^{\omega} l_x e^{-rx}}.$$

In matrix formulation, λ was calculated as the dominant eigenvalue of a Leslie matrix. The vectors of reproductive value (\mathbf{v}) and stable age (\mathbf{w}) distribution were obtained as the left and right eigenvectors, respectively, associated with the dominant eigenvalue of the Leslie matrix.

Elasticities of matrix elements (e_{ij}) were calculated (Caswell 2001) as

$$e_{ij} = \frac{a_{ij} v_i w_j}{\lambda \langle \mathbf{w}, \mathbf{v} \rangle},$$

where a_{ij} is the matrix element corresponding to row i and column j , v_i is the value of row i in reproductive value vector \mathbf{v} , w_j is the value of column j in stable-age distribution vector \mathbf{w} , and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of vectors \mathbf{w} and \mathbf{v} .

I calculated elasticities for age-0 survival (fertility), juvenile survival, and adult survival by summation of matrix element elasticities across relevant age classes (e.g., age-0 survival or fertility elasticity is the sum of all first-row elasticities). The sum of all matrix-element elasticities is 1. Each matrix element in the first row of the Leslie matrix was expressed as $f_x = m_x p_0$, where p_0 is the probability of survival of age-0 individuals. Thus, the fertility term (f_x) in matrix methodology includes survival to age 1.

Monte Carlo Simulation of Life Tables and Projection Matrices

I randomly selected a set of demographic traits—age-specific survival and fecundity, age at maturity, and lifespan—from the probability distribution describing each individual trait. I then used the set of variables to construct a life table or age-based matrix population model from which the demographic results of interest (λ , \bar{A} , fertility, juvenile survival, and adult survival elasticities summed over age classes) were estimated. I repeated this process 10,000 times for each population analyzed and calculated the mean for each of the demographic results. Confidence intervals for the demographic results were at the 2.5th and 97.5th percentiles of each distribution. Because elasticities calculated from a mean matrix can be imprecise and ranking of elasticities—and their magnitude—can vary substantially when different combinations of vital rates are used, I recorded the frequency of reversals in the ranking order of the elasticities summed over age classes (Wisdom et al.

2000). To examine the effect of generation time and age at maturity on elasticity patterns, I plotted the relative contribution of each of the three mean elasticities summed over age classes to population growth rate grouped by mean age at maturity and ordered by increasing generation time.

To evaluate the potential for density-dependent or other compensation and to identify management efforts required to restore population growth rates to their original levels, I calculated ratios of mean adult survival elasticity to mean fertility elasticity (Heppell et al. 1999) and mean juvenile survival elasticity to mean fertility elasticity. For example, a ratio of juvenile survival to fertility elasticities of 4.0 indicates that a 10% decrease in juvenile survival would have to be compensated by a 40% increase in fertility to return the population to its original λ (Heppell et al. 1999). The required compensatory response for a 10% decrease in juvenile or adult survival was not deemed possible if its magnitude exceeded the biological limits for age-0 survival (1) or fecundity for a given population.

To measure the contribution of each demographic trait to the variance in λ , I calculated the correlation of the forecasted values of λ for each population to each of the assumed demographic traits used in the simulation by computing Spearman rank correlation coefficients corrected for ties, an approach analogous to the regression analysis advocated by Wisdom and Mills (1997). I assigned correlation values for age-0 survival (s_0) and reproduction (m_x values) to fertility and survival values for juveniles (s_x values, with $x < \alpha$) and adults (s_x values, with $x \geq \alpha$) to juvenile and adult survival, respectively. I did not include values for age at maturity (α) and maximum age (ω) in these three categories because they cannot be broken down into their individual components in the age-based model I used (α and ω contribute to both survival and reproduction). I then summed the correlation coefficients of the demographic traits with the 10 highest values into the appropriate categories and expressed them as a percentage on a scale from 0 to 100%. All simulations were implemented with Microsoft Excel spreadsheet software equipped with proprietary add-in risk-assessment software (Crystal Ball; Decisioneering Inc.) and matrix-function software (MatriXL V4.5; MathTools Ltd.) and with Microsoft Visual Basic for Applications.

Results

Simulation of Population Growth Rates and Generation Times

Population growth rates for the species of sharks analyzed varied widely, ranging from the highest values for the oviparous lesser-spotted dogfish (*Scyliorbinus canicula*) to the lowest values ($\lambda < 1$) for the blacknose

shark (*Carcharbinus acronotus*) (Appendix 2). Values of λ were not correlated with body size ($r_s = 0.12$, $p = 0.4702$, $n = 41$) but were negatively correlated with age at maturity ($r_s = -0.53$, $p = 0.0004$, $n = 41$). The precision of the λ estimates, as measured by the magnitude of the 95% confidence intervals, tended to decrease with decreasing age at maturity and increasing λ .

Generation times ranged from 2.9 years in the Australian sharpnose shark (*Rhizoprionodon taylori*) to 55.6 years for the northeastern Pacific population of the spiny dogfish (*Squalus acanthias*) (Appendix 2). As expected, λ and \bar{A} were negatively correlated ($r_s = -0.55$, $p = 0.0002$, $n = 41$) and α and \bar{A} were highly positively correlated ($r_s = 0.98$, $p < 0.001$, $n = 41$). A three-dimensional plot of population growth rate versus generation time and age at maturity revealed a “fast-slow” continuum, with species characterized by early age at maturity, short generation times, and generally high λ at the fast end of the spectrum and species characterized by late age at maturity, long generation times, and generally low λ at the slow end of the spectrum (Fig. 2a). Species at the fast end, such as *S. canicula*, *S. lewini*, and *P. glauca*, also had large litter sizes, whereas species at the slow end, such as several large carcharhinid and lamniform sharks, tended to have small litter sizes. Especially noticeable is the long generation time and late age at maturity for the Pacific population of *S. acanthias*, which resulted in simulated λ values of <1 . Species at the slow end of the spectrum also tended to be larger than those at the fast end, although there were exceptions (e.g., *P. glauca* and *S. lewini* are large but are fast sharks, and *S. acanthias* are small but are slow sharks) (Fig. 2b).

Elasticity Patterns and Ratios

Juvenile and/or adult survival elasticities were always higher than fertility elasticities (Fig. 3; Appendix 2). Mean fertility elasticities ranged from 1.8% in the Pacific population of *S. acanthias* to 26.1% in *R. taylori*. Mean juvenile survival elasticities ranged from 22.7% in *R. taylori* to 82.1% in the northwestern Gulf of Mexico population of *S. lewini*. Mean adult survival elasticities ranged from 12.2% in the northwestern Gulf of Mexico population of *S. lewini* to 47.5% in the brown smoothhound (*Mustelus henlei*). Juvenile survival elasticities were generally the highest, except in *S. tiburo*, *M. henlei*, *Carcharbinus tilstoni*, *Mustelus californicus*, *Alopias vulpinus*, *Carcharbinus sorrab*, and *R. taylori*, whose adult survival elasticities were the highest (Appendix 2). All these species exhibit early age at maturity (≤ 5 years).

Ranking of elasticities did not vary in general, except in those cases where the confidence intervals overlapped (Appendix 2). The relative ranking of elasticities between adult (first) and juvenile (second) survival elasticities was reversed in the early maturing species mentioned above, notably *A. vulpinus* (47.6% of the cases),

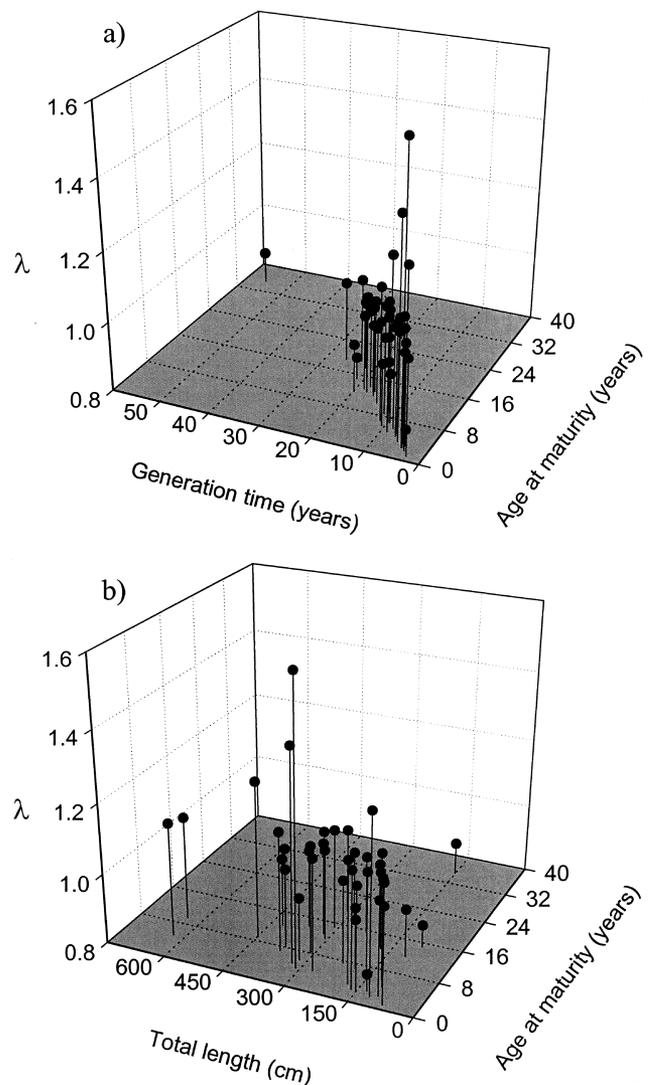


Figure 2. Mean population growth rates (λ) of 41 shark populations from 38 species expressed as a function of (a) generation time (\bar{A}) and mean age at maturity and (b) total length and mean age at maturity. Mean values of λ and \bar{A} obtained through Monte Carlo simulation.

S. tiburo, and *C. tilstoni* (46.2%). Fertility elasticity and adult survival elasticity tended to decrease and juvenile survival elasticity tended to increase with increasing generation time (Fig. 3). This trend was more pronounced in the early maturing species.

Fast sharks had low ratios of adult survival to fertility and juvenile survival to fertility elasticity (Appendix 2), indicating that they could compensate for a 10% decrease in adult or juvenile survival by increasing fertility. In contrast, slow sharks had higher elasticity ratios and do not appear to have the biological attributes that would enable them to return to their original population level of λ after moderate exploitation of the juvenile and adult stages. A plot of the elasticity ratios of adult sur-

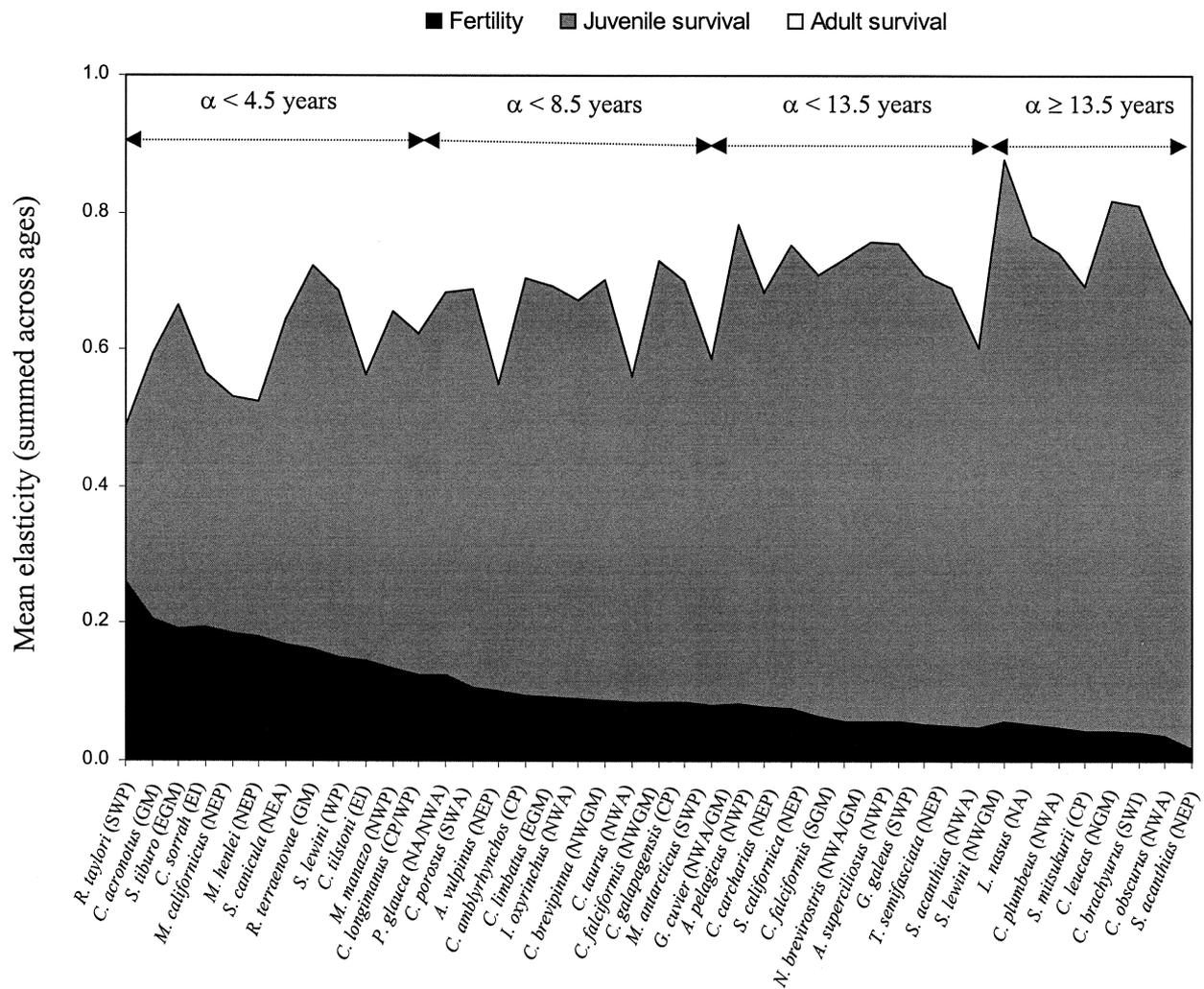


Figure 3. Mean elasticities (summed across ages) of 41 shark populations from 38 species obtained through Monte Carlo simulation. Populations are grouped by age at maturity (α) and ordered by increasing generation time. Geographical codes in parentheses after species names are as follows: GM, Gulf of Mexico; NWGM, northwestern Gulf of Mexico; SGM, southern Gulf of Mexico; EGM, eastern Gulf of Mexico; NWA, northwestern Atlantic; NA, northern Atlantic; NEA, northeastern Atlantic; SWA, southwestern Atlantic; CP, central Pacific; WP, western Pacific; NEP, northeastern Pacific; NWP, northwestern Pacific; SWP, southwestern Pacific; SWI, southwestern Indian; EI, eastern Indian.

vival to fertility and juvenile survival to fertility in relation to generation time (Fig. 4) suggests that the magnitude of both ratios, especially that of juvenile survival to fertility, increases with increasing generation time from fast to slow sharks. In other words, the species analyzed became progressively less capable of withstanding removal of adult and especially juvenile individuals as one moves along the fast-slow continuum.

Contribution of Demographic Traits to Population Growth Rate

Age at maturity generally accounted for the greatest proportion of variation in λ . The other demographic traits

explained less of the variation in λ , with a majority accounting only for minute portions of that variation. The general trends of decreasing importance of fertility and increasing importance of juvenile survival with increasing generation time found in elasticity analysis were maintained, but no clear trend was apparent in the correlation of adult survival or age at maturity (α) with increasing generation time (Fig. 5). Correlation analysis revealed a fairly substantial contribution of fertility to the variance of λ (Fig. 5), due mostly to the contribution of reproductive rates (m_x values) rather than to that of age-0 survival (s_0). Correlation analysis also indicated a generally high contribution of juvenile survival and low contribution of adult survival (Fig. 5) to the variation in λ ,

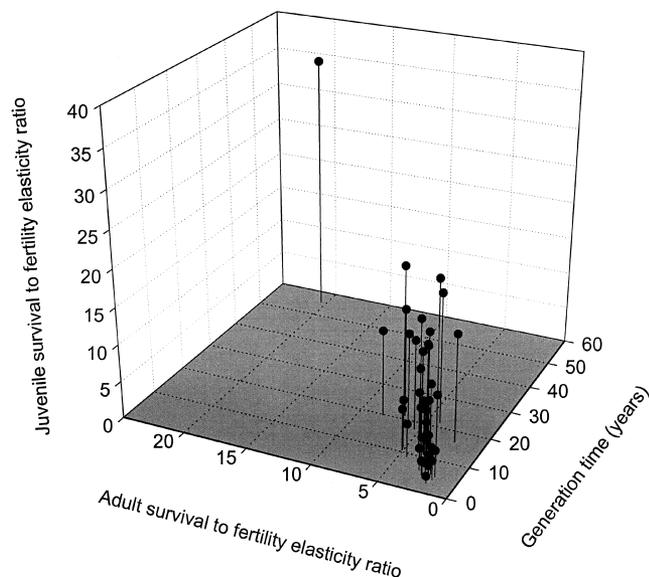


Figure 4. Elasticity ratios of adult survival to fertility and juvenile survival to fertility as a function of generation time for 41 shark populations from 38 species.

although the contribution of α could have accounted for some of the variation not assigned to adult survival.

Discussion

Utility and Limitations of the Simulation Framework and the Role of Uncertainty and Density Dependence

The simulations yielded widely varying population growth rates and generation times. Some fecund and early-maturing species had unexpectedly high values of λ for shark species, whereas several other species had low values ($\lambda < 1$). The variability and extremes in population growth rates may be the result, at least in part, of violations of the assumptions of demographic analysis. For example, the demographic framework I used assumes density independence and invariability in vital rates over time. We know that vital rates vary over time, but it is simply not possible to collect and update biological information on a periodic basis for most species of shark.

Most of the populations of sharks I examined have been exploited to varying degrees, which may have violated the assumption of a stable age distribution, thus making the demographic framework I used inappropriate. The populations I compared may also be at varying proportions of their maximum carrying capacity (K) (Smith et al. 1998) because of different exploitation levels. Density-dependent exploitation theory predicts that the value of the per capita rate of increase tends to decrease to zero when population size approaches K (equi-

librium populations) and tends to increase to a maximum when population size approaches zero.

Use of unreliable or incorrect demographic traits may lead to incorrect interpretations of population statistics (Wisdom et al. 2000). I addressed this problem by including in the analysis only populations with published life-history information, but some of the demographic traits I used may still have been inaccurate or incorrect. For example, age has been partially validated through direct methods in only 10 of the 41 populations I examined. *Sphyrna lewini* provides a good example of the uncertainty in aging because the differences in published age and growth parameters between the Western Pacific and Gulf of Mexico populations may be methodological rather than real.

I used Monte Carlo simulation to compensate in part for the potential use of unreliable or incorrect demographic traits, because this probabilistic approach allows inclusion of a wide range of values reflecting uncertainty in the estimates of demographic traits. I used distributions that I thought approximated reasonably well the biology of each population in an attempt to minimize the occurrence of unrealistic combinations of demographic traits. In that respect, my findings of several species with values of $\lambda < 1$ were somewhat surprising, especially for some species perceived to be abundant, such as the blacktip shark (*C. limbatus*), *S. acanthias*, and *C. acronotus*. Although applied consistently to all the species analyzed, it is possible that my methods of estimating natural mortality did not describe equally well the biology of all species. In the case of the heavily exploited *C. limbatus* and *S. acanthias*, it is also possible that the mortality rates I used implicitly included the effects of fishing, implying that survival rates in the absence of fishing would be higher, resulting in higher λ values.

The choice of statistical distributions used to describe survivorship at age, which was based on six indirect methods, may also have affected the population statistics. Except for the Peterson and Wroblewski (1984) method and in part the Chen and Watanabe (1989) method, the other four methods provided a single estimate of natural mortality for adult individuals. In addition, predictions from the Peterson and Wroblewski (1984) method are based on empirical rather than estimated parameters. Based on these considerations, I assigned a higher probability of occurrence to the estimates derived from this method. An example may help clarify why this method provides a good benchmark with which to compare the other methods. According to the Hoening (1983) method, an age-0 spiny dogfish 25 cm in length and 75 g in weight would have a higher survivorship than an age-40 adult dusky shark 3.5 m in length and over 200 kg in weight. In contrast, survivorship estimates obtained through the Peterson and Wroblewski (1984) method progressively increased from age-0 to the largest individuals. In its original form, this method uses dry weight to predict

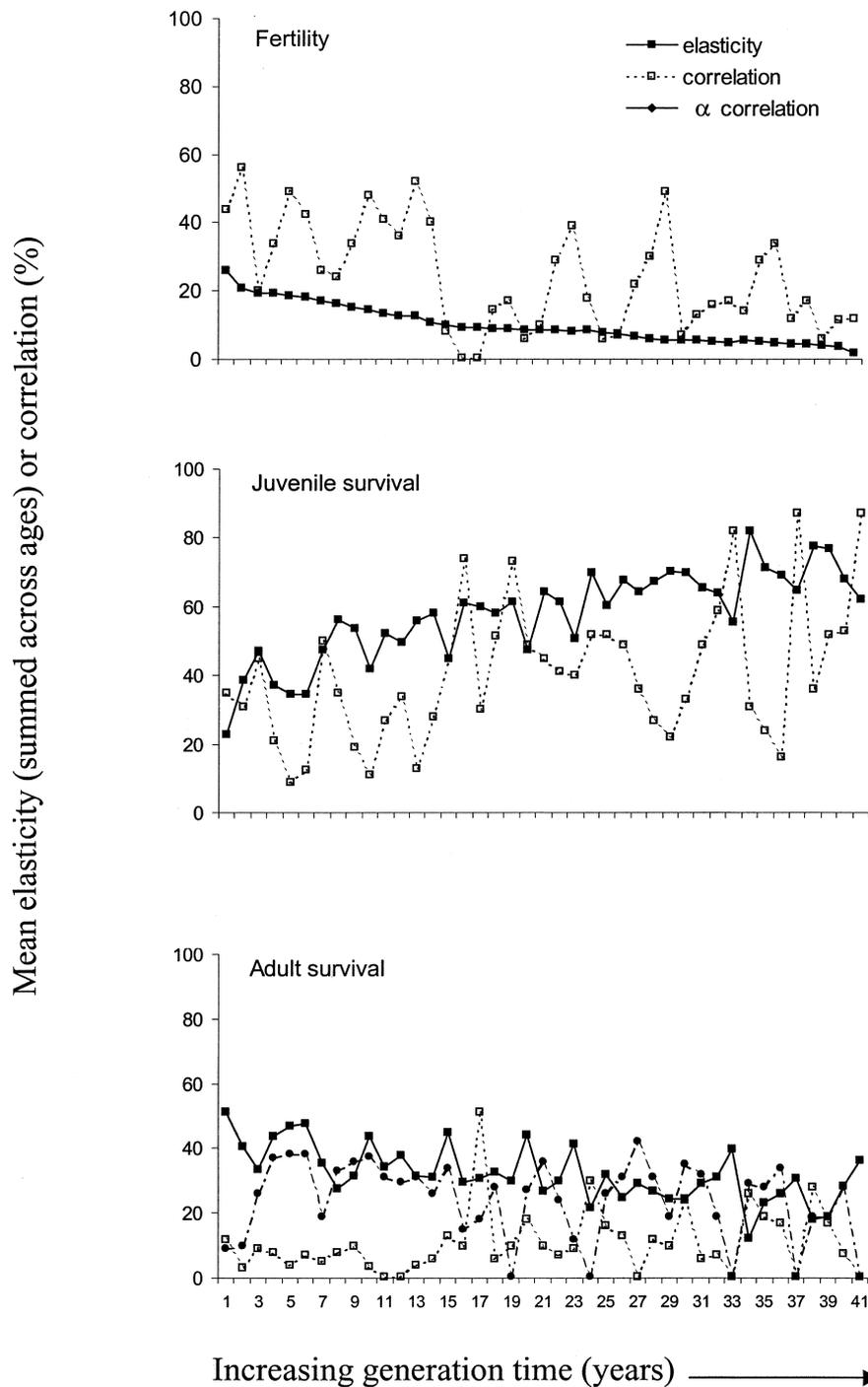


Figure 5. Mean elasticity for fertility, juvenile survival, and adult survival obtained from Monte Carlo simulation compared to results from a correlation analysis of each category with population growth rate (λ) for 41 shark populations from 38 species ordered by increasing generation time. The correlation of age at maturity (α) with λ is included for comparison to that of adult survival with λ (bottom panel).

natural mortality. I used wet weight instead because I obtained substantially higher predictions of survivorship for age-0 and early life stages, especially for small species of sharks, when using wet weight. The median difference in predictions of survivorship for age-0 individuals of the 41 populations analyzed was 18.3% (8.4% and 42.9% lower and upper 95% confidence intervals), whereas differences in predictions for adults were much smaller (median = 6.4%, 3.6%, and 23.7%). Thus, the rationale for using wet weight was to eliminate low estimates of

survivorship for early life stages that might have resulted in values of $\lambda < 1$ for small species perceived to be abundant. Regardless of the choice of statistical distribution, I applied the same rationale and methods consistently across populations to make predictions comparable on a relative scale.

Overall, the general trends I found seem robust to deviations in the assumptions of traditional density-independent population models. Although the demography of the species analyzed may have been captured more or

less accurately, one of my main goals was to provide a framework for relative comparison of population statistics among species by consistently using the same assumptions to specify the statistical distributions describing demographic traits. In particular, the values of λ I presented should be regarded as indices rather than predictors of absolute population growth through time. The 95% confidence intervals of λ for the populations I examined generally included published point values of λ for sharks, but there were exceptions. My estimated elasticities matched well the deterministic results of Heppell et al. (1999) for leopard and angel sharks and of Brewster-Geisz and Miller (2000) for sandbar sharks. Differences between my results and those of other authors were most likely due to the use of different survivorship schedules and highlight the potential risk of using one set of deterministic estimates of demographic traits to produce population statistics given the high degree of uncertainty in many of these traits, especially the survivorship schedules.

The general trends I identified also seem robust to deviations in the assumptions of traditional fisheries models. The relative placement of the populations I examined along the fast-slow continuum of shark life-history characteristics linked to the stage elasticity patterns I identified (Fig. 3) matched well with the corresponding position along an “ r continuum” of the shark populations also examined by Smith et al. (1998). This is encouraging because the approach used by Smith et al. (1998) assumed density dependence and was deterministic, yet they also identified a continuum of fast-slow sharks in relation to population growth rates. My study provides further support for such a continuum of life-history characteristics in sharks (Cortés 2000) and links it to the elasticity landscape, allowing classification of sharks according to their likely response to stage-specific perturbations.

The correlation analysis indicated that age at maturity generally accounted for more variability in λ than any other individual demographic trait. Smith et al. (1998) also found that rebound potentials resulting from a hypothetical density-dependent increase in survival of pre-adult stages were strongly affected by age at maturity in the species they examined. Few cases of density-dependent compensation have been described for sharks, however (Cortés 1998, 1999; Walker 1998). Population compensation through increased adult survival does not seem to be a likely mechanism in shark populations, because the values of survival are generally assumed to be high and fairly constant in adults. Increased pup production is constrained by the limited space females possess to carry young, and changes in reproductive periodicity in response to exploitation are possible but have not been described for shark populations.

In addition to increased age-0 and juvenile survival, decreased age at maturity could be one of the main mecha-

nisms through which shark populations could compensate for exploitation. A study of the age and growth of *C. plumbeus* before and after exploitation (Sminkey & Musick 1995) detected increased growth rate after population depletion, but it was not accompanied by decreased age at maturity. This lack of detection of compensation through earlier age at maturity may be due, at least in part, to methodological issues, because age at maturity is obtained by back-transforming size at maturity into age through a growth curve, but is almost never determined directly (Cortés 2000).

The elasticity ratios I calculated suggest that particular care should be taken in considering the harvesting of generally large, slow-growing, long-lived species. Even moderate removal of adult, but especially of juvenile, individuals in populations of these species requires a level of compensation in the form of increased age-0 survival or fecundity that these species may not be able to provide. Indeed, application of a 10% decrease in annual survival of adults or juveniles requires that age-0 survival increase to impossible levels (>1) or that fecundity be increased beyond the biological limits of the majority of these populations as given by the observed range in litter size.

The elasticity ratios I examined, however, may not provide the full picture of a population's ability to withstand exploitation. Compensatory increases in survival of the juvenile stage or reduced age at maturity, for example, could offset the effect of decreasing survival in the adult stage. Future work should investigate more systematically all potential sources of compensation that can counter removals in the various life stages. Regardless of the source and feasibility of compensation, recovery times would likely be long owing to the long generation times of these populations. In contrast, species such as *S. canicula*, *S. lewini*, or *P. glauca* probably have a much higher ability to compensate because they potentially have high productivity, owing to their high fecundity and early age at maturity, and thus could sustain much higher removal levels.

The two methods of analysis, correlation and elasticity analysis, I used in concert help us to more fully understand the influence of demographic uncertainty on λ and its variance. Elasticity analysis identified juvenile survival as the factor to which λ is most sensitive (elastic), with adult survival and especially fertility having less influence on λ . Correlation analysis also revealed that variability in age at maturity and juvenile survival contributed the most to the variance in λ . With this latter approach, fecundity and age-zero survival also contributed substantially to the variance in λ , whereas adult survival did not.

Finally, the use of age at maturity and longevity as demographic traits in the age-based model I applied is analogous to a stage-based or size-based model incorporating growth transitions. Regardless of the type of model

used, the number of ages, stages, or size classes chosen affects the calculation of elasticity and correlation values. The results of elasticity and correlation analyses could have been affected by a number of additional factors, including the different types of statistical distributions I used to describe demographic traits, the range of variation in the values of these distributions, and covariance among demographic traits. In addition, the correlation values may be inaccurate when a nonmonotonic relationship exists between the demographic trait and λ . Despite these limitations, the results obtained through elasticity and correlation analyses suggest not only that a probabilistic approach is necessary to capture the uncertainty in demographic traits, but also that the effect of that uncertainty should be investigated in depth before strong conclusions are drawn or management recommendations are made.

Links between Elasticity Patterns and Life-History Characteristics in Sharks

The probability-based demographic and elasticity analyses indicated that population growth rates are generally much more sensitive to survival of the juvenile and adult stages than to survival of age-0 individuals or fecundity across shark species. These results agree with the general patterns outlined for other long-lived marine species (Heppell et al. 1999) and suggest that protection of age-0 individuals is insufficient to recover declining populations of sharks. Thus, management efforts targeted at juveniles or adults are likely to be most effective for recovery.

The juvenile and adult stages seem to affect λ equally for some species of sharks. This is the case for fast-growing, early maturing, short-lived, and generally small-sized species such as *Sphyrna tiburo*, the two *Rhizoprionodon* species, the *Mustelus* species, and small carcharhinids such as *C. sorrah*, *C. tilstoni*, and *C. acronotus*, all of which can be placed at the fast end of the fast-slow continuum of shark life-history characteristics. The relative importance of fertility is also higher in the species found near this fast end. In contrast, at the other end of the continuum lie slow-growing, late-maturing, long-lived, and generally large species such as *Carcharhinus leucas*, *C. brachyurus*, and *C. obscurus* (with the two squaliform sharks *Squalus mitsukurii* and *S. acanthias* being notable exceptions in terms of size). In these species juvenile survival is important, whereas fertility is not.

My results for sharks are supported by previous work that proposes a slow-fast continuum of life histories in other taxa, such as mammals (Promislow & Harvey 1990; Heppell et al. 2000b), birds (Sæther 1988; Sæther & Bakke 2000), and plants (Franco & Silvertown 1996). A decreasing trend in fertility elasticity from the fast to the slow end of the life-history continuum was also found in mammals (Heppell et al. 2000b) and birds (Sæther & Bakke 2000), whereas the increasing trend in juvenile survival

elasticity was also observed in mammals (Heppell et al. 2000b). The decreasing trend in adult survival elasticity with generation time observed in sharks opposes the pattern found for most long-lived vertebrates (Pianka 1970; Wisdom et al. 2000). Fast mammals are also more sensitive to fertility elasticity (Heppell et al. 2000b) than fast sharks.

Conclusions and Implications for Conservation and Management

Caution should be taken when using elasticities alone to guide conservation efforts because it is still unclear how actions directed at one particular life stage may affect other life stages (Heppell et al. 2000b). It is also essential to consider the uncertainty in the estimates of demographic traits, the biological constraints on the potential variability of those traits, and the degree of effectiveness of the management options directed to specific life stages (De Kroon et al. 2000).

Past studies of shark demography have evaluated the effects of uncertainty through life-table sensitivity analysis, which involves changing the value of a single parameter at a time and recalculating the life-table output parameters. This deterministic approach may completely omit predictions of population statistics obtained from plausible combinations of demographic traits, because it considers only a limited number of scenarios that involve changing the value of a single demographic trait at a time. My simulation approach overcame this limitation, because it considered ranges of values of demographic traits reflecting uncertainty, randomized the values within these ranges, and simultaneously varied the values of all the demographic traits.

The use of Monte Carlo simulation does not eliminate the need for further sensitivity tests. It is still necessary to conduct an extensive examination of the sensitivity of population metrics and elasticities to the choice of the distributions used to describe each demographic trait, the magnitude of the total variation in each demographic trait, and the correlation between these variables. Also, the effects of various forms of density dependence on equilibrium and nonequilibrium populations, which may require different sorts of elasticity analysis, should be incorporated into the simulation process (Grant & Benton 2000).

The use of elasticity and correlation analyses in concert appears to have yielded robust predictions of the vital rates that exert the greatest effect on λ and that contribute the most to its variance. Although λ is most sensitive to juvenile survival, age at maturity and juvenile survival are also important explanations of variations in λ . Survival of age-0 and older adult individuals generally has a smaller influence on λ in terms of its elasticity and contribution to its variance, whereas variability in fecundity contributes substantially to the variance

in λ . Based on these predictions, research on shark populations should focus on obtaining better estimates of juvenile survival, age at maturity, and reproductive rates, and conservation efforts should focus on monitoring these variables rather than those that appear to have a smaller effect on λ , such as age-0 or adult survival. From a management perspective, minimum size limits imposed on fisheries and protection of reproductive females could be effective measures to enhance juvenile survival and reproductive output, respectively.

The combined application of a simulation approach to elasticity analysis and correlation analysis in conjunction with the ability to place the population of interest along the continuum of life-history characteristics linked to the elasticity patterns I identified provide a useful framework for classifying shark populations according to their likely response to perturbation of the various life stages and demographic traits. Those species at the slow end of the life-history and elasticity continuum (Fig. 3) with high elasticity ratios (Appendix 2), especially those with high uncertainty in their demographic traits, should be given the highest priority in research and conservation efforts.

Acknowledgments

I appreciate the helpful comments from D. Au and S. Smith on an earlier draft of this paper. I thank M. Wisdom, G. Cailliet, and H. Mollet for carefully reviewing the manuscript and providing very useful comments. I especially thank S. Heppell for reviewing the manuscript and providing thoughtful insights that helped to improve it. The views expressed in this paper are solely those of the author. Reference to trade names does not imply endorsement by the National Oceanographic and Atmospheric Administration or any of its subagencies.

Literature Cited

- Benton, T. G., and A. Grant. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution* **14**:467-471.
- Brewster-Geisz, K. K., and T. J. Miller. 2000. Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model. *Fishery Bulletin* **98**:236-249.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
- Caswell, H., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. *Ecological Applications* **8**:1226-1238.
- Chen, S. B., and S. Watanabe. 1989. Age dependence of natural mortality coefficient in fish population dynamics. *Nippon Suisan Gakkai-shi* **55**:205-208.
- Cortés, E. 1998. Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research* **39**:199-208.
- Cortés, E. 1999. A stochastic stage-based population model of the sandbar shark in the western North Atlantic. Pages 115-136 in J. A. Musick, editor. *Life in the slow lane: ecology and conservation of long-lived marine animals*. Symposium 23. American Fisheries Society, Bethesda, Maryland.
- Cortés, E. 2000. Life-history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**:299-344.
- De Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427-1431.
- De Kroon, H., J. van Groenendael, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* **81**:607-618.
- Franco, M., and J. Silvertown. 1996. Life history variation in plants: an exploration of the slow-fast continuum hypothesis. *Philosophical Transactions of the Royal Society, London B* **351**:1341-1348.
- Getz, W. N., and R. G. Haight. 1989. *Population harvesting*. Princeton University Press, Princeton, New Jersey.
- Grant, A. 1998. Population consequences of chronic toxicity: incorporating density dependence into the analysis of life table response experiments. *Ecological Modeling* **105**:325-335.
- Grant, A., and T. G. Benton. 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* **81**:680-693.
- Heppell, S. S., L. B. Crowder, and T. R. Menzel. 1999. Life table analysis of long-lived marine species, with implications for conservation and management. Pages 137-148 in J. A. Musick, editor. *Life in the slow lane: ecology and conservation of long-lived marine animals*. Symposium 23. American Fisheries Society, Bethesda, Maryland.
- Heppell, S. S., C. Pfister, and H. De Kroon. 2000a. Elasticity analysis in population biology: methods and applications. *Ecology* **81**:605-606.
- Heppell, S. S., H. Caswell, and L. B. Crowder. 2000b. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* **81**:654-665.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **82**:898-903.
- Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The relative "importance" of life history stages to population growth: prospective and retrospective approaches. Pages 247-272 in S. Tuljapurjar and H. Caswell, editors. *Structured population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York.
- Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:820-822.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* **13**:815-829.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* **39**:175-192.
- Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1117-1120.
- Pianka, E. R. 1970. On r and K selection. *The American Naturalist* **104**:592-597.
- Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life history variation in mammals. *Journal of Zoology (London)* **232**:417-437.
- Roff, D. A. 1992. *The evolution of life histories*. Chapman and Hall, New York.
- Sæther, B.-E. 1988. Pattern of covariation between life history traits of European birds. *Nature* **331**:616-627.
- Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642-653.
- Simpfendorfer, C. A. 1999. Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia. *Fishery Bulletin* **97**:978-986.
- Sminkey, T. R., and J. A. Musick. 1995. Age and growth of the sandbar

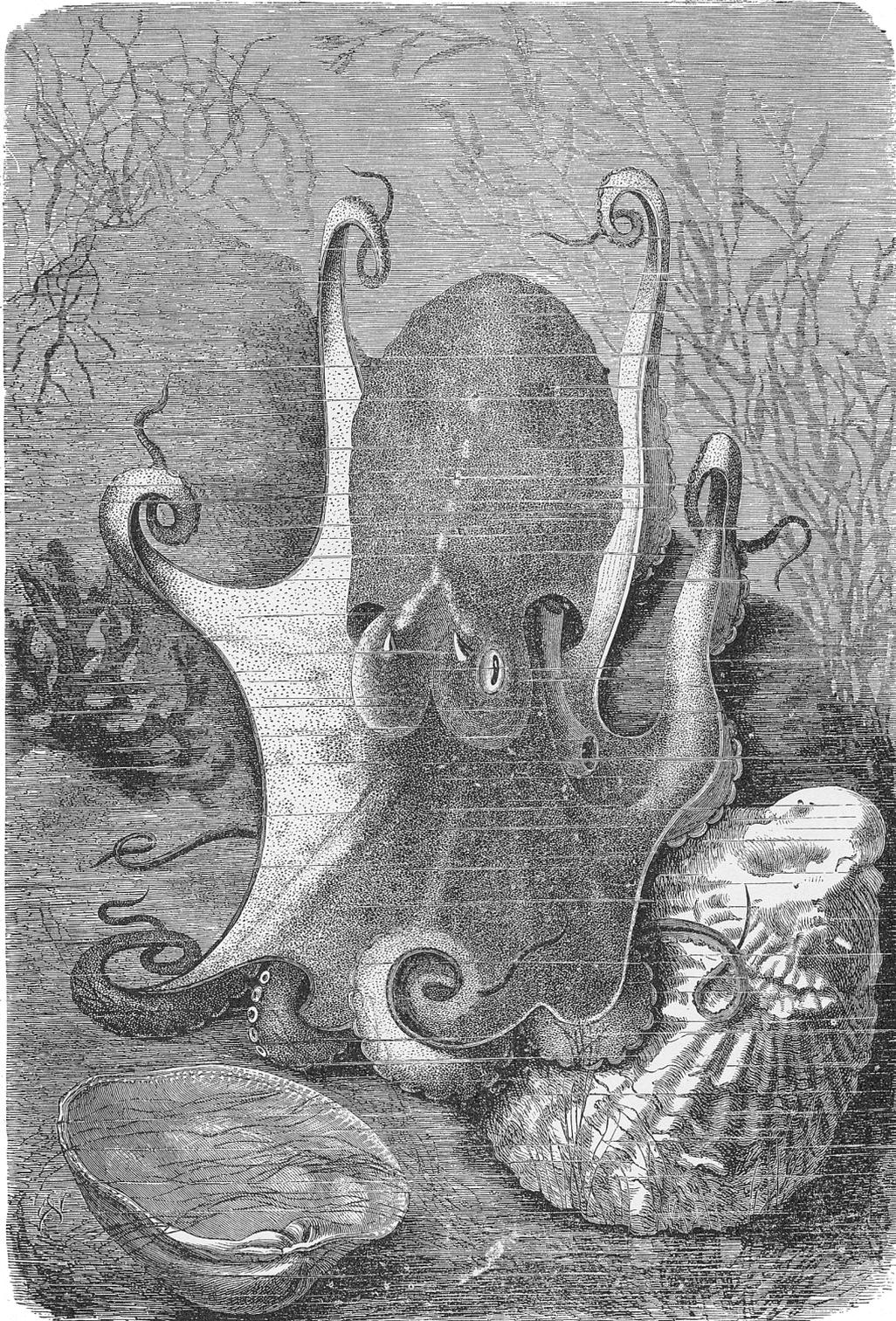
shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* **1995**:871-883.

Smith, S. E., D. W. Au, and C. Show. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine Freshwater Research* **49**:663-678.

Walker, T. I. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine Freshwater Research* **49**:553-572.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *Journal of Wildlife Management* **61**:302-312.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* **81**:628-641.



Appendix 1. Statistical distributions and values of demographic traits (age at maturity, life span, age-specific fecundity, and age-specific survivorship) used in Monte Carlo simulations of population growth rates (λ), generation times (\bar{A}), and elasticities of 41 populations from 38 species of sharks.^a

Population ^b	Maximum size (cm) ^c	Age at maturity (years) ^d	Life span (years) ^e	Fecundity ^f		Survivorship ^g
				distribution	range	
<i>Carcharhinus acronotus</i> (GM)	130	triangular (2,3,4)	5 (7)	uniform ^b	4–6	0.44–0.77 (0.63–0.84)
<i>C. amblyrhynchos</i> (CP)	190	uniform (6–8)	12 (16)	normal ^b (4.1,1.4)	3–6	0.64–0.81 (0.72–0.88)
<i>C. brachyurus</i> (SWI)	315	triangular (18,19,5,21)	30 (39)	normal ^b (15,4.5 ^h)	8–20	0.90–0.95 (0.76–0.91)
<i>C. brevipinna</i> (NWGM)	225	triangular (6,7,5,9)	12 (16)	normal ^b (7,2.1 ⁱ)	6–10	0.73–0.83 (0.76–0.88)
<i>C. falciformis</i> (NWGM)	305	triangular (7,8,9)	14 (18)	triangular ^b (11)	10–15	0.79–0.83 (0.77–0.91)
<i>C. falciformis</i> (SGM)	308	triangular (11,12,13)	22 (29)	normal ^b (10.2,1.3)	6–14	0.85–0.80 (0.77–0.91)
<i>C. galapagensis</i> (CP)	370	triangular (6.5,8,9)	15 (20)	normal ^b (8.7,2.6 ⁱ)	4–16	0.76–0.83 (0.78–0.92)
<i>C. leucas</i> (NWGM)	285	triangular (17,18,19)	24 (31)	triangular ^b (8)	5–10	0.86–0.92 (0.76–0.91)
<i>C. limbatus</i> (EGM)	191	uniform (6–8)	10 (20)	normal ^b (4.9,1.5 ^h)	3–6	0.76–0.81 (0.72–0.88)
<i>C. longimanus</i> (CP/WP)	272	triangular (3,4,5,6)	11 (15)	normal ^b (6.2,1.9 ^j)	1–14	0.68–0.88 (0.81–0.92)
<i>C. obscurus</i> (NWA)	371	triangular (17,19,21)	39 (51)	normal ^j (7.7,2.3 ⁱ)	6–12	0.91–0.95 (0.81–0.92)
<i>C. plumbeus</i> (NWA)	234	triangular (12,15,5,17)	24 (40)	normal ^b (8.4,2.3)	4–12	0.85–0.91 (0.75–0.90)
<i>C. porosus</i> (SWA)	120	triangular (5,6,7)	12 (16)	normal ^b (6,1.8 ^h)	2–9	0.72–0.88 (0.64–0.83)
<i>C. sorrah</i> (EI)	152	triangular (1,2,5,4)	7 (9)	normal ^k (3.1,1.1)	1–8	0.54–0.67 (0.70–0.83)
<i>C. tilstoni</i> (EI)	180	triangular (2,3,5,5)	12 (16)	normal ^k (3,0,1.0)	1–6	0.70–0.85 (0.73–0.87)
<i>Galeocerdo cuvier</i> (NWA)	>450	uniform (8–10)	16 (21)	normal ^b (55,16.5 ^l)	30–70	0.77–0.85 (0.70–0.93)
<i>Negaprion brevirostris</i> (NWA)	320	triangular (12,13,14)	21 (27)	normal ^b (10.8,4.1)	4–17	0.86–0.91 (0.74–0.93)
<i>Prionace glauca</i> (NWA/NA)	327	triangular (4,5,6)	16 (21)	normal ^b (37,14.6)	4–75	0.76–0.85 (0.64–0.91)
<i>Rhizoprionodon taylori</i> (SWP)	>78	uniform (0.9–2)	7 (9)	normal ^k (4.5,1.3 ⁱ)	1–10	0.22–0.63 (0.49–0.75)
<i>R. terraenovae</i> (GM)	107	triangular (2,8,3,4,4)	7 (9)	uniform ^k	4–6	0.55–0.67 (0.61–0.79)
<i>Sphyrna lewini</i> (NWGM)	310	triangular (14,15,16)	17 (22)	uniform ^k	30–40	0.83–0.90 (0.67–0.90)
<i>S. lewini</i> (WP)	324	triangular (3,1,4,1,5,1)	14 (18)	normal ^k (26,7.8 ^l)	12–38	0.70–0.79 (0.70–0.91)
<i>S. tiburo</i> (EGM)	116	uniform (1.9–3)	7 (9)	normal ^k (7.5,2.5)	3–15	0.55–0.68 (0.60–0.81)
<i>Galeorhinus galeus</i> (SWP)	174	uniform (10–15)	53 (69)	normal ^j (28.4,7.1)	17–41	0.87–0.94 (0.59–0.87)
<i>Mustelus antarcticus</i> (SWP)	164	uniform (5–8)	16 (21)	normal ^{l,m}	1–38	0.79–0.90 (0.59–0.85)
<i>M. californicus</i> (NEP)	163	triangular (1,2,5,4)	9 (12)	uniform ^k	2–5	0.63–0.78 (0.53–0.83)
<i>M. benlei</i> (NEP)	100	triangular (1,2,5,4)	13 (17)	uniform ^k	3–5	0.66–0.78 (0.49–0.77)
<i>M. manazo</i> (NWP)	107	triangular (3,4,5,6)	10 (13)	normal ^k (6,1.8 ^h)	2–13	0.66–0.87 (0.53–0.79)
<i>Triakis semifasciata</i> (NEP)	160	triangular (10,13,16)	24 (31)	normal ^{k,m}	7–36	0.84–0.92 (0.53–0.83)
<i>Scyliorhinus canicula</i> (NEA)	100	uniform (3–5)	9 (12)	uniform ^k	96–115	0.63–0.83 (0.33–0.72)
<i>Carcharodon carcharias</i> (NEP)	640	triangular (8,9,5,11)	15 (20)	uniform ^b	8–10	0.81–0.92 (0.86–0.95)
<i>Isurus oxyrinchus</i> (NWA)	375	triangular (6,7,8)	17 (22)	normal ^j (12.7,3.0)	9–18	0.76–0.83 (0.76–0.93)
<i>Lamna nasus</i> (NWA)	365	triangular (13,14,15)	22 (29)	triangular ^k (4)	2–5	0.84–0.90 (0.83–0.91)
<i>Alopias pelagicus</i> (NWP)	375	triangular (7,8,6,10,2)	16 (21)	fixed ^k	2	0.79–0.91 (0.85–0.90)
<i>A. superciliosus</i> (NWP)	422	triangular (11,12,8,14)	20 (26)	fixed ^k	2	0.85–0.90 (0.82–0.91)
<i>A. vulpinus</i> (NEP)	630	triangular (3,5,7)	15 (20)	triangular ^k (4)	2–4	0.76–0.84 (0.83–0.93)
<i>Carcharias taurus</i> (NWA)	318	triangular (5,6,7)	17 (22)	fixed ^b	2	0.78–0.85 (0.77–0.90)
<i>Squalus acanthias</i> (NEP)	130	triangular (34,35,36)	81 (105)	normal ^b (7.1,2.1 ⁱ)	2–17	0.94–0.96 (0.52–0.82)
<i>S. acanthias</i> (NWA)	110	triangular (11,12,13)	40 (52)	normal ^b (6,6,1.8)	1–15	0.85–0.92 (0.49–0.79)
<i>S. mitsukurii</i> (CP)	91	triangular (14,15,16)	27 (35)	normal ^b (3,6,1.1)	1–6	0.89–0.95 (0.54–0.77)
<i>Squatina californica</i> (NEP)	152	uniform (8–13)	22 (29)	normal ^k (6,2,6)	1–11	0.78–0.88 (0.65–0.84)

^aVariation in the values represents uncertainty. All literature sources for the life-history data listed can be obtained from the author.

^bGeographical codes are as follows: GM, Gulf of Mexico; NWGM, northwestern Gulf of Mexico; SGM, southern Gulf of Mexico; EGM, eastern Gulf of Mexico; NWA, northwestern Atlantic; NA, northern Atlantic; NEA, northeastern Atlantic; SWA, southwestern Atlantic; CP, central Pacific; WP, western Pacific; NEP, northeastern Pacific; NWP, northwestern Pacific; SWP, southwestern Pacific; SWI, southwestern Indian; EI, eastern Indian.

^cTotal length.

^dFor the triangular distribution, values in parentheses are low, likeliest, and high respectively; for uniform distribution, the range is shown.

^eMaximum empirical age. Value in parentheses is +30% of the first value, unless other expert opinion was available (in brackets).

^fValues in parentheses are mean and SD (normal distribution) or likeliest value (triangular distribution). All values extracted from these distributions were divided by two to account for an assumed 1:1 male-to-female embryo ratio and then by one, two, or three according to the length of the reproductive cycle.

^gRange of annual survivorship values obtained through four life-history methods; values in parentheses show the range of age-specific estimates obtained through the Peterson and Wroblewski (1984) method, which is based on weight (see text for an explanation).

^hBiennial reproductive cycle.

ⁱThe SD was not reported in the original study but was assumed to be 30% of the mean.

^jBiennial or triennial reproductive cycle.

^kAnnual reproductive cycle.

^lAnnual or biennial reproductive cycle.

^mIncreasing fecundity with body size and age.

Appendix 2. Population growth rates (λ), generation times (\bar{A}), mean elasticities (summed across ages), and elasticity ratios of 41 populations from 38 species of sharks obtained through Monte Carlo simulation (populations listed by decreasing value of λ).^a

Population ^b	λ	\bar{A}	Elasticity				Elasticity ratios ^c	
			fertility	juvenile survival	adult survival	reversals (%)	1	2
<i>Scyliorhinus canicula</i> (NEA)	1.659 (1.377–2.060)	5.2 (4.5–6.0)	16.2 (14.3–18.2)	56.1 (52.1–59.9)	27.6 (25.1–30.5)	0	1.70	3.46
<i>Sphyrna lewini</i> (WP)	1.600 (1.446–1.809)	5.7 (4.7–6.6)	15.1 (13.1–17.6)	53.5 (47.8–57.9)	31.4 (27.6–36.3)	0	2.08	3.54
<i>Prionace glauca</i> (NWA/NA)	1.401 (1.284–1.534)	7.0 (6.0–8.4)	12.6 (10.6–14.3)	55.8 (50.1–61.4)	31.7 (26.3–38.0)	0	2.52	4.44
<i>Sphyrna tiburo</i> (EGM)	1.304 (1.150–1.655)	3.9 (2.6–4.5)	20.6 (18.3–27.6)	38.8 (26.0–43.1)	40.6 (35.4–48.0)	46.2 ^d (0.2 ^e)	1.97	1.88
<i>Galeocerdo cuvier</i> (NWA/GM)	1.246 (1.199–1.294)	10.9 (10.2–11.8)	8.4 (7.8–9.0)	69.9 (67.3–72.4)	21.7 (19.3–24.3)	0	2.59	8.31 ^f
<i>Mustelus benlei</i> (NEP)	1.163 (1.021–1.427)	4.7 (3.0–6.4)	18.1 (13.5–25.2)	34.4 (22.6–43.7)	47.5 (41.6–54.7)	6.9 ^d (1.4 ^e)	2.62	1.90
<i>Carcharhinus tilstoni</i> (EI)	1.145 (1.052–1.277)	6.0 (4.3–7.8)	14.5 (11.4–18.7)	41.9 (32.6–50.1)	43.6 (37.0–51.0)	46.2 ^d	3.00	2.89
<i>Isurus oxyrinchus</i> (NWA)	1.141 (1.098–1.181)	10.1 (9.2–11.1)	9.0 (8.3–9.8)	58.2 (54.6–61.9)	32.8 (29.2–36.2)	0	3.65	6.47 ^f
<i>Mustelus californicus</i> (NEP)	1.132 (0.996–1.364)	4.6 (2.9–6.1)	18.5 (14.0–25.5)	34.7 (21.8–45.7)	46.8 (38.9–56.3)	15.1 ^d (2.0 ^e)	2.53	1.87
<i>Alopias vulpinus</i> (NEP)	1.125 (1.078–1.178)	8.9 (7.1–10.6)	10.2 (8.6–12.3)	44.8 (35.3–53.5)	45.0 (37.5–52.9)	47.6 ^d	4.42 ^f	4.40 ^f
<i>Carcharhinus longimanus</i> (CP/WP)	1.117 (1.039–1.218)	7.0 (5.5–8.6)	12.6 (10.4–15.3)	50.0 (41.8–56.8)	37.7 (31.9–44.2)	6.0 ^d	3.00	3.95
<i>Carcharhinus falciformis</i> (NWGM)	1.108 (1.075–1.139)	10.6 (9.9–11.5)	8.6 (8.0–9.2)	64.4 (60.8–68.0)	27.0 (23.4–30.5)	0	3.12	7.46 ^f
<i>Carcharodon carcharias</i> (NEP)	1.098 (1.069–1.131)	12.3 (11.0–13.8)	7.6 (6.7–8.3)	67.7 (65.1–70.3)	24.7 (22.2–27.1)	0	3.28 ^f	8.97 ^f
<i>Mustelus manazo</i> (NWP)	1.096 (0.998–1.235)	6.6 (5.2–8.1)	13.3 (11.0–16.1)	52.4 (44.1–59.3)	34.3 (28.7–41.1)	0.5 ^d	2.58	3.94
<i>Carcharhinus sorrah</i> (EI)	1.093 (0.930–1.360)	4.3 (2.8–5.6)	19.4 (15.1–26.3)	37.0 (22.3–49.3)	43.5 (34.2–55.2)	28.2 ^d (1.3 ^e)	2.24	1.91
<i>Carcharhinus porosus</i> (SWA)	1.086 (1.030–1.145)	8.4 (7.5–9.6)	10.7 (9.5–11.8)	58.2 (54.0–62.5)	31.2 (27.1–35.2)	0	2.92	5.45
<i>Carcharhinus galapagensis</i> (CP)	1.086 (1.046–1.136)	10.8 (9.2–12.2)	8.5 (7.6–9.8)	61.4 (56.8–65.1)	30.0 (26.4–34.2)	0	3.52	7.20
<i>Sphyrna lewini</i> (NWGM)	1.086 (1.057–1.111)	16.7 (15.8–17.9)	5.7 (5.3–5.9)	82.1 (79.4–84.3)	12.2 (10.1–15.3)	0	2.15	14.48 ^f
<i>Mustelus antarcticus</i> (SWP/SEI)	1.082 (1.042–1.126)	11.5 (10.3–12.8)	8.0 (7.3–8.9)	50.6 (45.7–55.9)	41.3 (36.1–46.7)	4.1 ^d	5.16	6.32
<i>Galeorhinus galeus</i> (SWP)	1.077 (1.037–1.128)	17.7 (14.4–21.0)	5.4 (4.5–6.5)	65.4 (61.3–71.3)	29.2 (22.2–33.4)	0	5.39 ^f	12.09 ^f
<i>Rhizoprionodon taylori</i> (SWP)	1.073 (0.778–1.686)	2.9 (1.4–3.8)	26.1 (20.6–40.9)	22.7 (0.0–28.3)	51.2 (43.4–38.0)	32.7 ^e	1.96	0.87
<i>Negaprion brevirostris</i> (NWA/GM)	1.064 (1.042–1.087)	16.4 (15.4–17.7)	5.7 (5.3–6.1)	70.0 (65.9–74.2)	24.2 (20.1–28.4)	0	4.22	12.21 ^f
<i>Carcharhinus falciformis</i> (SGM)	1.057 (1.044–1.071)	16.1 (15.1–17.2)	5.9 (5.5–6.2)	67.3 (65.6–69.2)	26.8 (24.9–28.7)	0	4.57	11.47 ^f
<i>Rhizoprionodon terraenovae</i> (GM)	1.056 (0.970–1.195)	4.9 (4.0–5.4)	16.9 (15.7–20.1)	47.5 (38.5–50.9)	35.6 (32.1–42.2)	13.6 ^d	2.10	2.80
<i>Carcharhinus brachyurus</i> (SWI)	1.043 (1.028–1.059)	23.3 (21.9–25.0)	4.1 (3.8–4.4)	76.9 (74.7–79.0)	19.0 (16.8–21.3)	0	4.61 ^f	18.69 ^f
<i>Carcharhinus brevipinna</i> (NWGM)	1.037 (1.007–1.065)	10.4 (9.7–10.8)	8.8 (8.4–9.3)	61.4 (59.1–65.3)	29.8 (25.3–32.4)	0	3.40	7.00 ^f
<i>Carcharhinus obscurus</i> (NWA)	1.030 (1.017–1.042)	26.2 (24.2–28.2)	3.7 (3.4–4.0)	67.9 (64.9–70.9)	28.5 (25.5–31.3)	0	7.73 ^f	18.44 ^f
<i>Carcharhinus plumbeus</i> (NWA)	1.022 (1.007–1.042)	19.8 (16.7–22.7)	4.8 (4.2–5.6)	69.3 (66.2–72.4)	25.9 (22.5–29.2)	0	5.34	14.29 ^f
<i>Lamna nasus</i> (NWA)	1.022 (1.011–1.035)	17.9 (16.8–19.2)	5.3 (4.9–5.6)	71.4 (69.0–73.6)	23.3 (21.0–25.9)	0	4.41 ^f	13.50 ^f
<i>Alopias pelagicus</i> (NWP)	1.020 (1.001–1.041)	11.8 (10.8–13.4)	7.8 (6.9–8.5)	60.4 (58.0–63.2)	31.7 (28.9–34.0)	0	4.05 ^f	7.70 ^f
<i>Squatina californica</i> (NEP)	1.019 (0.971–1.073)	14.4 (11.7–17.0)	14.4 (11.7–17.0)	64.3 (57.1–70.9)	29.1 (23.1–36.1)	0	4.44	9.80 ^f
<i>Triakis semifasciata</i> (NEP)	1.016 (0.984–1.052)	18.5 (16.0–20.6)	5.1 (4.6–5.9)	63.9 (57.8–71.0)	31.0 (24.2–36.6)	0	6.03	12.43
<i>Carcharhinus leucas</i> (NWGM)	0.998 (0.986–1.010)	21.6 (20.5–23.1)	4.4 (4.1–4.7)	77.4 (74.5–79.8)	18.1 (15.7–21.4)	0	4.10 ^f	17.50 ^f
<i>Alopias superciliosus</i> (NWP)	0.996 (0.978–1.014)	16.7 (15.2–18.1)	5.7 (5.2–6.2)	70.0 (65.3–74.1)	24.4 (20.2–28.9)	0	4.30 ^f	12.34 ^f
<i>Carcharias taurus</i> (NWA)	0.978 (0.957–0.996)	10.6 (9.8–11.6)	8.6 (7.9–9.3)	47.4 (43.3–51.4)	43.9 (40.0–48.0)	30.8 ^d	5.08 ^f	5.49 ^f
<i>Carcharhinus limbatus</i> (EGM)	0.974 (0.925–1.068)	10.0 (8.2–14.8)	9.3 (5.9–10.9)	60.0 (41.5–66.3)	30.6 (23.2–49.5)	4.9 ^d	3.29	6.45 ^f
<i>Carcharhinus amblyrhynchos</i> (CP)	0.941 (0.897–0.984)	9.6 (8.7–10.8)	9.4 (8.5–10.2)	60.9 (57.2–65.0)	29.7 (25.7–33.3)	0	3.15	6.45 ^f
<i>Squalus acanthias</i> (NWA)	0.938 (0.908–0.973)	19.9 (17.4–22.4)	4.8 (4.3–5.4)	55.5 (50.4–60.7)	39.7 (33.8–45.1)	0.4 ^d	8.27	11.56
<i>Squalus acanthias</i> (NEP)	0.893 (0.876–0.912)	55.6 (50.0–62.2)	1.8 (1.6–2.0)	62.0 (56.2–67.9)	36.2 (30.0–42.0)	0	20.5 ^f	34.99 ^f
<i>Squalus mitsukurini</i> (CP)	0.864 (0.832–0.901)	21.3 (19.5–23.5)	4.5 (4.1–4.9)	64.8 (60.6–68.8)	30.7 (26.3–35.1)	0	6.84 ^f	14.46 ^f
<i>Carcharhinus acronotus</i> (GM)	0.847 (0.709–0.972)	4.2 (3.7–5.0)	19.1 (16.7–21.4)	47.2 (40.4–55.6)	33.6 (25.9–39.4)	0.9 ^d	1.75	2.46

^a Values in parentheses are lower and upper 95% confidence intervals calculated as the 2.5th and 97.5th percentiles.

^b Geographical codes are as follows: GM, Gulf of Mexico; NWGM, northwestern Gulf of Mexico; SGM, southern Gulf of Mexico; EGM, eastern Gulf of Mexico; NWA, northwestern Atlantic; NA, northern Atlantic; NEA, northeastern Atlantic; SWA, southwestern Atlantic; CP, central Pacific; WP, western Pacific; NEP, northeastern Pacific; NWP, northwestern Pacific; SWP, southwestern Pacific; SWI, southwestern Indian; EI, eastern Indian.

^c Ratio of adult survival elasticity to fertility elasticity (column 1) and ratio of juvenile survival elasticity to fertility elasticity (column 2).

^d Percentage of times in which the ranking order of juvenile survival elasticity and adult survival elasticity was reversed.

^e Percentage of times in which the ranking order of fertility elasticity and juvenile survival elasticity was reversed.

^f Compensation required for a 10% decrease in adult survival or juvenile survival is beyond the biological limits thought to be possible for the population in question.