SCRS/1999/045 Rev. Col.Vol.Sci.Pap. ICCAT, 51 (6) : 1822-1828 (2000)

POTENTIAL RATES OF INCREASE AND RATES OF INCREASE PER GENERATION FOR THREE SPECIES OF PELAGIC SHARKS FROM THE ATLANTIC OCEAN

by

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SUMMARY

Age at maturity and longevity estimates, combined with vital rate information, were used to construct life tables for three representative species of pelagic sharks occurring in the Atlantic Ocean (the blue shark Prionace glauca, the shortfin mako Isurus oxyrinchus, and the porbeagle Lamna nasus). Uncertainty and variability associated with vital rates was incorporated through Monte Carlo simulation and estimates of potential rates of increase and generation length were produced and combined into rates of increase per generation. The proportion of the carrying capacity at which MSY is predicted to be reached for these pelagic species also was investigated.

RÉSUMÉ

Des estimations de l'âge de maturité et de la longévité, combinées avec l'information sur le cycle vital, ont été utilisées pour élaborer des tables du cycle vital pour trois espèces représentatives de requins pélagiques présentes dans l'Atlantique (le requin peau bleue, Prionace glauca, le requin-taupe bleu, Isurus oxyrinchus, et le requin-taupe commun Lamna nasus). Les incertitudes et la variabilité liées au cycle vital ont été incorporées par la simulation de Monte-Carlo, et des estimations du taux potentiel d'accroissement et de la taille de la génération ont été calculées et combinées en taux d'accroissement par génération. On a également recherché la proportion de la capacité de cale à laquelle on prévoit que la PME sera atteinte en ce qui concerne ces espèces pélagiques.

RESUMEN

Se usaron estimaciones de edad de madurez y de longevidad, combinadas con información sobre tasa vital, para diseñar tablas de vida de tres especies *representativas de tiburones pelágicos que habitan el Atlántico (tintorera, Prionace glauca, tiburón maco, Isurus oxirinchus y el marrajo, Lamna nasus). La incertidumbre y variabilidad asociadas con las tasas vitales se incorporaron por medio de una simulación Montecarlo y se hicieron estimaciones de tasas potenciales de incremento y de duración de una generación, que se combinaron en tasas de incremento por generación. Se investigó la proporción de la capacidad del stock a la cual se podría alcanzar el RMS en estas especies pelágicas.*

Introduction

Life tables have been used to produce estimates of potential rates of increase (r) and other demographic parameters for several species of sharks. In this approach the best biological information available on longevity, age at maturity, reproduction, and natural mortality is used to generate output demographic parameters. However, with the exception of Cortés (1999) and Cortés and Scott (1998), previous demographic analyses of sharks have only produced point estimates or examined a limited number of scenarios through sensitivity analysis. In this paper some of the uncertainty and variability associated with the vital rates of pelagic sharks is incorporated through Monte Carlo simulation.

The intrinsic rate of increase and generation length are both correlated with body size (Peters 1983, Hoenig and Gruber 1990). However, Fowler (1988) showed that the position of the inflection point of population growth curves (a measure of where Maximum Sustainable Yield or Catch can be attained) is related to the rate of increase per generation (rT), and that this relationship is independent of body size. In a plot of log transformed rate of increase per generation vs. R (position of the inflection point), in which both sets of values were obtained from the literature, he further showed that several species of marine mammals reached MSY at over 50% of carrying capacity (K).

I used published values and the best available biological information on vital rates, age at maturity and lifespan to calculate potential rates of increase (r) and mean generation lengths (T; also known as average T [Caughley 1966]) for three species of pelagic sharks (the blue shark *Prionace glauca*, the shortfin mako *Isurus oxyrinchus*, and the porbeagle *Lamna nasus*).

Materials and Methods

Age-specific reproductive output was calculated by randomly choosing the number of pups per female from a normal distribution with a mean and standard deviation of 37 and 7.3 (blue shark; Castro and Mejuto 1995) and 12.5 and 2.8 (shortfin mako; Mollet et al. 1997), and from a discrete distribution with a range of 2-5 for the porbeagle (Gauld 1989). That figure was divided by two to account for a biennial reproductive cycle in these three species, and by two again to consider a sex ratio of offspring at birth of 1:1. It was assumed that 100% of females were mature after the age at maturity and that all mature females were reproductively active in any given year.

Age-specific survivorship was calculated from natural mortality estimates obtained through up to three life history methods: (1) an equation by Hoenig (1983) relating longevity to total instantaneous mortality rate (Z), (2) an equation by Pauly (1980) that relates instantaneous mortality rate (M) to von Bertalanffy growth function (VBGF) parameters and an estimate of the mean annual water temperature where the population occurs, and (3) an equation by Peterson and Wroblewski (1984) that relates M to body weight (see Cortés and Parsons 1996 and Cortés 1999 for details on these methods) and thus allows calculation of size-specific mortality rates. Parameters from the VBGF (Aasen 1963; Pratt and Casey 1983; Skomal 1990) and length-length and length-weight relationships were obtained from published accounts (Kohler et al. 1995) (Table 1). For earlier life stages, age-specific survivorship was obtained from method (3); once the survivorship value estimated through method (3) exceeded the values estimated through methods (1) and (2), age-specific survivorship was randomlychosen from the three alternative life history methods assuming an equal probability of occurrence.

Both age at maturity and maximum age were obtained from published studies and held constant (Table 1). The estimate of longevity was based on the oldest female sharks of each species aged through analysis of vertebrae, not on theoretical values or extrapolations from the VBGF. Monte Carlo simulations for each species were run to generate 1000 values of r and T. Confidence intervals were calculated as the 2.5th and 97.5th percentiles to account for non-normality of the data. Since values of R (position of the inflection point) were not available from the literature, they were obtained by solving the linear equation derived empirically by Fowler (1988):

$$R = 0.633 - 0.187\ (\ln(rT))$$

Table 1. Parameters used in the calculation of natural mortality/survivorship estimates at age for females, and values of longevity, age at maturity, and litter size used to calculate demographic parameters for three species of pelagic sharks.

	Blue	*Mako*	*Porbeagle*
L_∞	375	373.4	280
K	-0.15	-0.203	-0.116
t_o	-0.87	1.0	72[1]
(a)	0.0000031841	0.0000052432	0.000014823
(b)	3.1313	3.1407	2.9641
(y)	1.3908	-1.7101	1.7939
(x)	0.8313	0.9286	0.8971
Temperature (C)	20	18	18
Longevity	13	12	19
Maturity	4.5	7	7.5
Litter size[2]	37 (7.3)	12.5 (2.8)	2-5

[1] Length at birth
[2]Mean litter size with standard deviation in parentheses; litter size for porbeagle is a range
t_o is the X-axis intercept from the von Bertalanffy equation
a and b are parameters from the weight-length relationship: $W=aL^b$
y and x are parameters from the fork to total length relationship: FL=y+(TL)x

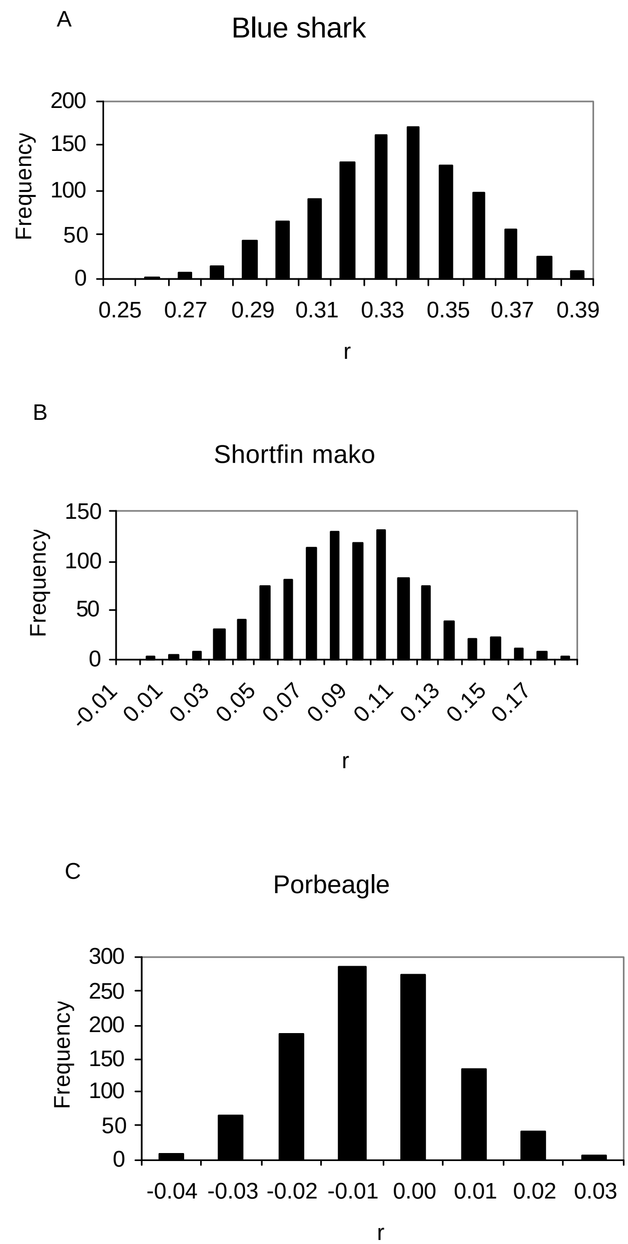
Results and Discussion

Mean generation lengths estimated for the blue shark, shortfin mako, and porbeagle were approximately 7, 9, and 11 yr, and estimates of potential rate of increase were 39%/yr, 8.5%/yr, and -0.8%/yr, respectively (Table 2). Rates of increase ranged from 0.255 to 0.394 in the blue shark (Fig. 1a), -0.013 to 0.176 in the shortfin mako (Fig. 1b), and -0.047 to 0.031 in the porbeagle (Fig. 1c).

Table 2. Longevity, age at maturity, mean intrinsic rate of increase (r), and mean generation length (T) for three species of pelagic sharks. Values in parentheses are lower and upper confidence intervals.

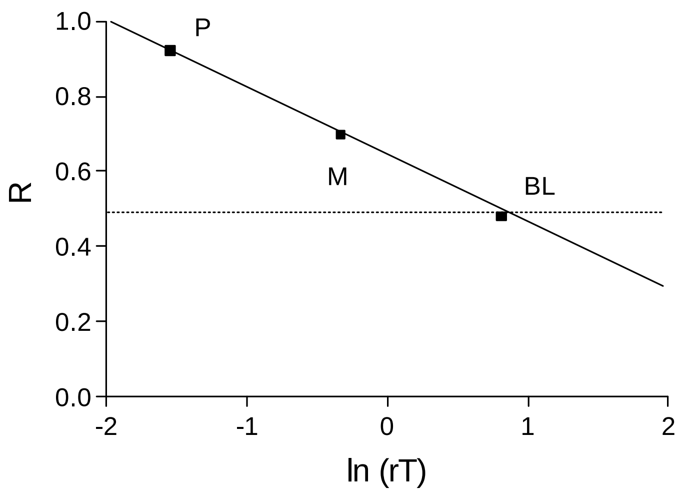
Species	*Longevity*	*Maturity*	*r*	*T*
Blue shark	13	4.5	0.328 (0.281-0.373)	6.89 (6.52-7.31)
Mako	12	7	0.082 (0.024-0.147)	8.74 (8.40-9.13)
Porbeagle	19	7.5	-0.008 (-0.033--0.019)	10.65 (10.28-11.09)

Figure 1. Histogram of the relative frequency of various levels of potential population rate of increase for the blue shark (a), the shortfin mako (b), and the porbeagle (c) obtained through simulation (1000 iterations).



A plot modified from the diagram presented in Fowler (1988) reveals differences in the proportion of carrying capacity at which these three pelagic species are predicted to reach the inflection point (Fig. 2). The blue shark is the most productive species with an inflection point near 50% of K. In contrast, the shortfin mako, and especially the porbeagle, are predicted to reach MSY at 70% and 92% of K, respectively. Note that the upper confidence limit for the rate of increase found in the simulations was used to allow calculation of ln(rT) for the porbeagle.

Figure 2. Relationship between the log-transformed rate of increase per generation and the relative position of the inflection point (R) for three pelagic species of sharks. BL is blue shark; M, shortfin mako; P, porbeagle. The dotted line indicates the position at which 50% of K is reached.



Intrinsic rates of increase and generation lengths describe the life history strategy of a population or species by reflecting the vital rates that operate over the life span of individuals. The rate of increase per generation goes one step beyond by integrating these related aspects of life history strategy (Fowler 1988) and is thus important for studying the relationships between life history strategies and population dynamics. To the extent that the rate of increase per generation is indicative of the concepts of r- and K- selection (Fowler 1988), the three pelagic species of sharks examined herein exhibit considerable variability. Like other species of long-lived, large coastal sharks studied (Cortés and Scott 1998), the porbeagle appears to be more "K-selected" and reach MSY very close to carrying capacity. In contrast, the blue shark is a more productive species that may reach MSY at approximately 50% of K as predicted for many commercial fish species, whereas the shortfin mako falls somewhere in between the porbeagle and the blue shark.

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