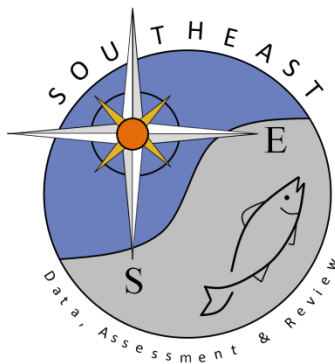Estimates of vital rates and population dynamics parameters of interest of blacktip sharks (*Carcharhinus limbatus*) in the Atlantic Ocean

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Estimates of vital rates and population dynamics parameters of interest of blacktip sharks (*Carcharhinus limbatus*) in the Atlantic Ocean

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ABSTRACT

Estimates of vital rates and population dynamics parameters of the western North Atlantic population of blacktip shark for use as inputs into Stock Synthesis were computed based on biological information provided in the SEDAR 65 Data Workshop Report. Population dynamics parameters included maximum population growth rate (r_{max}), generation time ($\overline{A}$), steepness of the Beverton-Holt stock-recruitment relationship (h), position of the inflection point of population growth curves (R), and spawning potential ratio at maximum excess recruitment (SPR$_{MER}$). Six methods were used to compute r_{max}: four age-aggregated methods and two analogous age-structured methods. Additionally, a Leslie matrix approach was used to incorporate uncertainty in growth parameters, the maturity ogive, natural mortality, and lifespan. Productivity (r_{max}) ranged from 0.057 to 0.092 yr^{-1} and from 0.039 to 0.092 yr^{-1} for the deterministic methods when using the theoretical longevity and the observed lifespan, respectively. For the stochastic Leslie matrix, age-specific median values of M obtained through six life-history invariant methods ranged from 0.12 to 0.29 yr^{-1}, and median r_{max} = 0.042 yr^{-1}(95% CI = -0.027 – 0.085), h = 0.28 (95% CI = 0.20 – 0.42), R = 0.72 (95% CI = 0.61 – 1.00), $\overline{A}$ = 12.5 years (95% CI = 11.2 – 20.1), and SPR$_{MER}$ = 0.81 (95% CI = 0.59– 1.00). A range of steepness of 0.32 to 0.52 (mean = 0.40) was also inferred from the deterministic methods used to compute r_{max}, not used in the simulations. It is suggested that the estimates of instantaneous natural mortality rates corresponding to the deterministic age-structured Euler-Lotka/Leslie Matrix approaches be used as inputs for the Stock Synthesis reference case. For steepness, given the low median value obtained in the simulations and that the lower confidence limit for r_{max} was negative or hit the lower bound for h (0.20) or, alternatively, the upper bound for R and SPR$_{MER}$ (1), which indicate that the population growth rates and steepness values obtained are not the theoretical maxima, using a value of steepness on the order of 0.40 for the reference case seems like a reasonable approach. The lower and upper end values of the range obtained with the deterministic methods (0.32 and 0.52) could be used in low and high productivity plausible states of nature, respectively. Additionally, the estimates of generation time obtained here can help inform the time horizon for projections.

1. Introduction

The maximum theoretical population growth rate, or intrinsic rate of population increase (r_{max}), is a fundamental metric in population biology and, together with carrying capacity (K), one of the two driving parameters in Schaefer and other production models (e.g., Schaefer 1954). In general formulations of production models, such as in the Pella-Tomlinson (1969) or Fletcher (1978) models, it is also important—but very difficult—to estimate the shape parameter, which is then used to obtain the inflection point. The inflection point of population growth curves (R; Fowler 1981) can be estimated independently of a stock assessment because it is also a function of r_{max} and generation time ($\overline{A}$). Generation time, typically described as the mean age of parents in a population (Cortés and Cailliet 2019), is also required to formulate rebuilding timeframes and generally in projections of future stock status and is a measure of stock resilience. Steepness (h), or the fraction of recruitment from an unfished population when the spawning stock size declines to 20% of its unfished level, is also a measure of stock resilience in the context of stock-recruitment relationships (Mangel et al. 2013). Finally, the spawning potential ratio at maximum excess recruitment (SPR_{MER}; Goodyear 1980) is yet another measure of stock resilience, with the closer the %SPR is to 100%, the less exploitation the stock can sustain (Brooks et al. 2010).

The purpose of this paper was to generate values of r_{max} and the associated h, as well as provide a vector of M values used in the computation of these metrics, to use as input into Stock Synthesis. Additionally, generation time is also provided to help identify the time horizon for stock projections.

2. Materials and methods

Inputs

Life history inputs were obtained from Table 1 of the HMS Atlantic Blacktip Shark Data Workshop report (reproduced here in Table 1). All values are for females.

Annual survival at age (obtained from the instantaneous natural mortality rate at age as e^{-M}) was obtained through six life history invariant estimators: Jensen's (1996) K-based and age at maturity estimators, a modified growth-based Pauly (1980) estimator (Then et al. 2015), a modified longevity-based Hoenig (1983) estimator (Then et al. 2015), Chen and Yuan's (2006) estimator, and the mass-based estimator of Peterson and Wroblewski (1984) (Appendix 1 and Appendix Table 1). The first five estimators provide a constant value of mortality, whereas the last method provides size- specific estimates, which are then transformed to age-specific values. Conversions of length into weight were done using the power equation listed in Table 1. Lifespan was set equal to the maximum age obtained from ageing vertebrae (18 years) or, alternatively, as the theoretical age corresponding to 7 half-lives ($7*\ln(2)/K = 31$ years; Table 1).

Modeling and outputs

Maximum population growth rate (r_{max}) was estimated with six methods. Four methods were age-aggregated modifications of the Euler-Lotka equation (Eberhardt et al. (1982); Skalski et al. (2008); Au et al. (2016); and Niel and Lebreton's (2005) demographically invariant method)

and two methods were age structured (life table/Euler-Lotka equation and a Leslie matrix) (Appendix 2).

Uncertainty was introduced in the Leslie matrix approach through Monte Carlo simulation by randomly selecting vital rates/parameters from predefined statistical distributions (n=100,000). The quantities varied were the parameters from the von Bertalanffy growth function (VBGF; L_{inf}, K, t_0), intercept and slope parameters from the maturity ogive at age (a, b), age at maturity, lifespan, and survivorship at age.

The parameter estimates from the VBGF and the maturity ogive were assigned a multivariate normal distribution with a vector of means and a covariance matrix to take into account covariance among parameters. Because the original studies of age and growth and reproduction did not report parameter correlations, the data used to fit the models originally were obtained from the authors and the models re-fit to obtain correlation matrices. Lifespan was given a uniform distribution with the lower bound set equal to "observed" longevity from vertebral ageing (18 years) and the upper bound set to a theoretical seven half-lives (7*log(2)/K or 31 years). The values of the VBGF parameters, median age at maturity, and lifespan were then used to populate the mortality estimators and generate survivorship at age. The maximum value of age-specific survival (or minimum value of age-specific natural mortality) from the six methods used was selected at each iteration.

In addition to r_{max}, the net reproductive rate (R_0 or virgin spawners per recruit in fisheries terms), $\overline{A}$, generation time defined as the mean age of parents of offspring in a stable age distribution, the maximum lifetime reproductive rate $\hat{\alpha}$ (Myers et al. 1997, 1999), which is the product of R_0 and S_0 (age-0 survival) (Brooks et al. 2010), steepness, computed as

$$h = \frac{\hat{\alpha}}{4+\hat{\alpha}} \text{, and} \quad SPR_{MER} = \frac{1}{\sqrt{\hat{\alpha}}} \text{ were calculated.}$$

All models were run in R (R Core Team 2019).

3. Results and Discussion

The minimum estimates of M (corresponding to maximum annual survivorship) from the six mortality estimators used in the deterministic analyses ranged from 0.198 yr^{-1} for age 0 to 0.125 yr^{-1} for age 18 sharks, or from 0.198 yr^{-1} for age 0 to 0.121 yr^{-1} for age 31 sharks (Table 2). For the stochastic analysis, median M from the five estimators that yield a single constant value for all ages ranged from 0.14 to 0.24 yr^{-1} (minimum values ranged from 0.11 to 0.19 yr^{-1} and maximum values ranged from 0.17 to 0.29 yr^{-1}), whereas median M for the age-specific estimator ranged from 0.29 yr^{-1} for age 0 sharks to 0.12 yr^{-1} for age 18 sharks (Table 3).

Estimated productivity ranged from r_{max} = 0.039 to 0.092 yr^{-1} for a lifespan of 18 years, or from r_{max} = 0.057 to 0.092 yr^{-1} for a lifespan of 31 years for the six deterministic methods (Table 4). For the stochastic Leslie matrix method, median r_{max} = 0.042 yr^{-1} (95% CI = -0.027 – 0.085), h = 0.28 (95% CI = 0.20 – 0.42), R = 0.72 (95% CI = 0.61 – 1.00), $\overline{A}$ = 12.5 years (95% CI = 11.2 – 20.1), and SPR$_{MER}$ = 0.81 (95% CI = 0.59– 1.00) (Table 5).

The lower confidence limit for r_{max} was negative or hit the lower bound for h (0.20) or, alternatively, the upper bound for R and SPR$_{MER}$ (1). Although this can be due to some extent

to stochasticity, the occurrence of negative growth rates and such low values of steepness for this population is suspect.

The other four methods used to compute r_{max} deterministically do not provide estimates of steepness, but using the r_{max} and steepness values obtained with the Euler-Lotka/Leslie matrix approach, a range of steepness of 0.32 to 0.52 is inferred from the other methods. In all, mean steepness from the five deterministic methods (since the Euler-Lotka and Leslie matrix approaches are essentially the same) is 0.40. For reference, published values of the maximum lifetime reproductive rate $\hat{\alpha}$ for 33 shark stock assessments ranged from 1.0 to 19.2 (Cortés and Brooks 2018), which corresponds to steepness values ranging from 0.20 to 0.83, or a mean of 0.46 (SD = 0.20).

The low values of steepness found here are not entirely unexpected because the combination of the relatively high age-0 mortality and the reduced lifetime reproductive rate for this stock results in low estimates. It is also important to note that the values of r and steepness found here are likely underestimates since this population may be closer to carrying capacity and therefore the life history variables (age and growth, lifespan, reproduction) used to compute population growth and steepness are likely not representative of ideal conditions after exploitation has ceased and there is very little density dependence. Considering all of these caveats, using a value of steepness on the order of 0.40 for the reference case seems like a reasonable approach. The lower and upper end values of the range obtained with the deterministic methods (0.32 and 0.52) could be used in low and high productivity plausible states of nature, respectively. The estimates of generation time obtained here can also help inform the time horizon for projections.

References

Au, D.W., Smith, S.E., and Show, C. 2008. Shark productivity and reproductive protection, and a comparison with teleosts. In: Camhi, M.D., Pikitch, E.K., and Babcock, E.A. (Eds.), Sharks of the Open Ocean. Blackwell Publishing, Oxford, pp. 298–308.

Au, D.W., Smith, S.E., and Show, C. 2016. New abbreviated calculation for measuring intrinsic rebound potential in exploited fish populations – example for sharks. Can. J. Fish. Aquat. Sci. 72: 767-773.

Pikitch, E.K., and Babcock, E.A. (Eds.), Sharks of the Open Ocean. Blackwell Publishing, Oxford, pp. 298–308

Brooks, E.N, J.E. Powers, and E. Cortés. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. ICES J. Mar. Sci. 67:165-175.

Chen, P., and Yuan, W. 2006. Demographic analysis based on the growth parameter of sharks. Fish Res. 78:374-379.

Cortés, E. and E.N. Brooks. 2018. Stock status and reference points for sharks using data-limited methods and life history. Fish and Fisheries 19: 1110-1129.

Cortés, E., and Cailliet, GM. 2019. Generation time. (pp 381-383) In (B. Fath, ed.) Encyclopedia of Ecology, 2nd ed. Vol. 3.

Dillingham, P.W. 2010. Generation time and the maximum growth rate for populations with age-specific fecundities and unknown juvenile survival. Ecol. Model. 221: 895–899.

Dillingham, P.W., Moore, J. E., Fletcher, D., Cortés, E., Curtis, K.A., James, K.C., and Lewison, R. 2016. Improved estimation of intrinsic growth r_{max} for long-lived species: integrating matrix models and allometry. Ecol. Applications 26: 322-333.

Eberhardt, L.L., Majorowicz, A.K. & Wilcox, J.A. 1982. Apparent rates of increase for two feral horse herds. J. Wildlife Management 46: 367–374.

Fletcher, R.I. 1978. Time-dependent solutions and efficient parameters for stock-production models. Fish. Bull. 76:377-388.

Fowler, C. W. 1988. Population dynamics as related to rate of increase per generation. Evol. Ecol. 2: 197-204.

Goodyear, C. P. 1980. Compensation in fish populations. In Biological Monitoring of Fish, pp. 253–280. Ed. by C. H. Hocutt, and J. R. Stauffer. Lexington Books, D. C. Heath and Co, Lexington, MA.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898–903.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. 53:820–822.

Jensen, C.F., L.J. Natanson, H.L. Pratt Jr., N. E. Kohler,and S. E. Campana. 2002. The reproductive biology of the porbeagle shark (Lamna nasus) in the western North Atlantic Ocean. Fish. Bull. 100:727–738.

Mangel, M. , A.D. MacCall, J. Brodziak, E.J. Dick, R. E. Forrest, R. Pourzand, and S. Ralston. 2013. A perspective on steepness, reference points, and stock assessment. Can. J. Fish. Aquat. Sci 70:930-940.

Myers, R.A., G. Mertz, and P.S. Fowlow. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fish. Bull. 95:762–772.

Myers, R.A., K.G. Bowen, and N.J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Can J. Fish. Aquat. Sci. 56:2404–2419.

NMFS 2018. Update assessment to SEDAR 29 HMS Gulf of Mexico blacktip shark. SEDAR, North Charleston, SC 29405.

Niel, C. and Lebreton, J.D. 2005. Using demographic invariants to detect overharvested bird populations from incomplete data. Cons. Biol. 19: 826–835.

Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39:175–192.

Pella, J.J., and Tomlinson, P.K. 1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. 13:419–496.

Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41:1117-1120.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter American Tropical Tuna Commission Bulletin 2:247–285.

Skalski, J.R, Millspaugh, J.J. & Ryding, K.E. 2008. Effects of asymptotic and maximum age estimates on calculated rates of population change. Ecol. Model. 212: 528–535.

Smith, S.E., Au, D.W., and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Mar. Freshwater Res. 49: 663–678.

Then, A.Y., J.M. Hoenig, N.G. Hall, and D.A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72: 82-92.

Table 1. Biological input values for females used to compute r_{max} and steepness for Atlantic blacktip shark.

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length	166.23 (2.47)	cm FL	SEDAR65-DW-02
K	Brody growth coefficient	0.16 (0.01)	yr^{-1}	SEDAR65-DW-02
t_0	Theoretical age at zero length	-2.59 (0.16)	yr	SEDAR65-DW-02
a	Intercept of maturity ogive	-12.07 (2.52)	dimensionless	SEDAR65-DW-01
b	Slope of maturity ogive	1.80 (0.35)	dimensionless	SEDAR65-DW-01
c	Scalar coefficient of weight on length	4.630E-06	dimensionless	SEDAR65-DW-15
d	Power coefficient of weight on length	3.21575	dimensionless	SEDAR65-DW-15
w	Observed lifespan	18	yr	SEDAR65-DW-02
	Theoretical lifespan (7 half lives)	31	yr	This document
	Sex ratio at birth	1:1	dimensionless	SEDAR65-DW-02
	Reproductive cycle	2	yr	Castro 1996
mx	Constant litter size	4.09 (SD=0.13)	pups per litter	SEDAR65-DW-01
e	Intercept of maternal age vs. fecundity	-0.04078	dimensionless	SEDAR65-DW-01
f	Slope of maternal age vs. fecundity	0.38445	dimensionless	SEDAR65-DW-01
GP	Gestation period	11	months	Castro 1996

Values in parentheses are SEs.

Table 2. Minimum estimates of instantaneous natural mortality rates (yr^{-1}) obtained with six life-history invariant estimators and used in the Euler-Lotka and Leslie matrix approaches.

Age	M
0	0.198
1	0.198
2	0.198
3	0.185
4	0.171
5	0.161
6	0.153
7	0.147
8	0.143
9	0.139
10	0.136
11	0.133
12	0.131
13	0.130
14	0.128
15	0.127
16	0.126
17	0.125
18	0.125
19	0.124
20	0.123
21	0.123
22	0.123
23	0.122
24	0.122
25	0.122
26	0.122
27	0.122
28	0.121
29	0.121
30	0.121
31	0.121

Table 3. Estimates of instantaneous natural mortality rates (yr^{-1}) obtained through Monte Carlo simulation of six life-history invariant estimators. The first five methods yield a single constant value for all age classes.

Age	ChenYuan			Jensen (K)			Jensen (maturity)			Then et al. (Hoenig)			Then et al. (Pauly)			Peterson & Wroblewski		
	Minimum	Maximum	Median	Minimum	Maximum	Median	Minimum	Maximum	Median	Minimum	Maximum	Median	Minimum	Maximum	Median	Minimum	Maximum	Median
constant	0.11	0.17	0.14	0.19	0.29	0.24	0.18	0.24	0.21	0.17	0.26	0.21	0.17	0.23	0.20			
0																0.27	0.31	0.29
1																0.23	0.25	0.24
2																0.20	0.21	0.21
3																0.18	0.19	0.19
4																0.17	0.18	0.17
5																0.16	0.17	0.16
6																0.15	0.16	0.15
7																0.15	0.15	0.15
8																0.14	0.15	0.14
9																0.14	0.14	0.14
10																0.13	0.14	0.14
11																0.13	0.14	0.13
12																0.13	0.13	0.13
13																0.13	0.13	0.13
14																0.13	0.13	0.13
15																0.13	0.13	0.13
16																0.12	0.13	0.13
17																0.12	0.13	0.13
18																0.12	0.13	0.12

Table 4. Estimates of productivity (r_{max}) obtained through six methods.

	Lifespan=18 yr	Lifespan=31 yr
Euler-Lotka	0.039 (0.25)	0.060 (0.34)
Leslie matrix	0.039 (0.25)	0.060 (0.34)
Au et al. (2016)	0.092	0.092
Eberhardt et al. (1982)	0.058	0.058
Skalski et al. (2008)	0.040	0.057
Neil and Lebreton's (2005) DIM*	0.084	0.084
Mean	0.059	0.069
Values in parentheses are steepness		
*DIM=Demographically Invariant Method		

Table 5. Productivity (r_{max}), generation time ($\overline{A}$), net reproductive rate (R0), age-0 survivorship (S_0), steepness (h), spawning potential ratio at maximum excess recruitment (SPR$_{MER}$), and position of the inflection point of population growth curves (R) obtained from Monte Carlo simulation of vital rates with a Leslie matrix approach. LCL and UCL are approximate lower and upper confidence limits computed as the 2.5th and 97.5th percentiles.

	Median	LCL	UCL
r_{max}	0.042	-0.027	0.085
Generation time	12.5	11.2	20.1
Net reproductive rate (R_0)	1.815	0.781	3.307
Age-0 survivorship (S_0)	0.84	0.79	0.88
Steepness (h)	0.28	0.20	0.42
SPR$_{MER}$	0.81	0.59	1.00
R	0.72	0.61	1.00

Appendix 1. Life-history invariant methods used to estimate M.

Methods 1 and 2 — Jensen's (1996) estimators based on K and age at maturity:

$$M = 1.5K$$

and

$$M = \frac{1.65}{a_{mat}}$$

Method 3 — Then et al.'s (2015) modified longevity-based Hoenig (1983) estimator:

$$M = 4.899 a_{max}^{-0.916}$$

Method 4 — Then et al.'s (2015) modified growth-based Pauly (1980) estimator:

$$M = 4.118 k^{0.73} L_{\infty}^{-0.33}$$

Method 5 — Chen and Yuan's (2006) estimator:

$$\ln(M) = 1.46 - 1.01 \ln\left(t_0 - \frac{\ln(0.05)}{K} \right)$$

Method 6 — Peterson and Wroblewski (1984) mass-based estimator:

$$M = 1.92 W^{-0.25}$$

where W is weight in g.

Appendix Table 1. Data requirements for six methods used to estimate r_{max}.

Method	Age at maturity/ first breeding	Maximum age	Fecundity	M	Survival to age at maturity/ first breeding
Euler-Lotka/Leslie matrix	Yes	Yes	Age-dependent	Age-dependent	Yes
Rebound potential (Au et al. 2009)	Yes	Yes	Constant	Constant	Yes
Eberhardt et al. (1992)	Yes	Yes	Constant	Constant	Yes
Skalski et al. ()	Yes	No	Constant	Constant	Yes
DIM	Yes	No	No	Constant	No

Appendix 2. Methods used to estimate r_{max}.

Method 1 — Eberhardt et al. (1982):

$$e^{ra} - e^{-M}(e^r)^{a-1} - ml_a\left(1 - \left(\frac{e^{-M}}{e^r}\right)^{w-a+1}\right) = 0$$

where a is age at first breeding, e^{-M} is probability of adult survival from natural mortality only, m is constant fecundity, l_a is the cumulative survival from age 0 to age at maturity, w is maximum life expectancy, and r is the population rate of increase.

Method 2 — Skalski et al. (2008):

$$e^{ra} - e^{-M}(e^r)^{a-1} - ml_a = 0$$

Method 3 — Au et al.'s (2016) modified rebound potentials:

The premise of this method is that the growth potential of each species can be approximated for a given level of exploitation, which then becomes its potential population growth rate after harvest is removed, or its "rebound" potential. The density-dependent compensation is assumed to be manifested in pre-adult survival as a result of increased mortality in the adult ages. Starting from the Euler-Lotka equation:

$$\sum_{x=a}^{w} l_x m_x e^{-rx} - 1 = 0$$

if l_x is expressed in terms of survival to age at maturity $l_a e^{-M(x-a)}$ and m_x is replaced with a constant fecundity m (average number of female pups per female), completing the summation term yields:

$$e^{-(M+r)} + l_a m e^{-ra}\left(1 - e^{-(M+r)(w-a+1)}\right) - 1 = 0.$$

Pre-adult survival $l_a = l_{a,Z}$ that makes increased mortality Z $(=M+F)$ sustainable $(r=0)$ is calculated from the following equation by setting $M=Z$ and $r=0$:

$$e^{-(Z)} + l_{a,Z} m\left(1 - e^{-(Z)(w-a+1)}\right) - 1 = 0.$$

If F is then removed ($Z=M$), the population under survival $l_{a,Z}$ will rebound at a productivity rate of r_z, which is found by substituting $l_{a,Z}$ into the first equation and solving it iteratively. The rebound potential r_z thus represents the population growth rate at Maximum Sustainable Yield (MSY).

Smith et al. (1998) multiplied the fecundity term m in the first equation by 1.25 to allow for an arbitrary 25% increase which they felt was appropriate because, even if fecundity was constant with age, the average m value of a population would increase as it expands under reduced mortality because there would be more, older and larger fish that would survive. They also acknowledged that, based on density-dependent theory under a logistic function, $r_{max}=2r_z$, or in other words that their rebound potentials should be doubled to obtain r_{max}. Au et al. (2008) later arrived at the conclusion that $Z_{MSY}=1.5M$ is a more appropriate level of MSY for determining the intrinsic rebound potential of sharks compared to pelagic teleosts (for which $Z_{MSY}=2M$) by linking stock-recruitment and abundance-per-recruit relationships via the Euler-Lotka equation, thus the rebound potential for sharks should be $r_z=r_{1.5M}$ and $r_{max}=2r_{1.5M}$.

Method 4 — Neil and Lebreton's Demographically Invariant Method:

Niel & Lebreton (2005) developed a method that combines an age-based matrix model with an allometric model. The age-based matrix model assumes constant adult survival ($s=e^{-M}$) and fecundity and a mean generation time $T=a+s/(\lambda-s)$, where a is age at first breeding, is also derived. The allometric model is based on relationships between r_{max} and T and body mass (M), such that $r_{max}=a_rM^{-0.25}$ and $T=a_TM^{-0.25}$, which when multiplied yield the dimensionless maximum rate of increase per generation or $r_{max}T=a_ra_T=a_{rT}$. When combined with the matrix model, the allometric model provides an equation for the demographic invariant method (DIM) (Niel & Lebreton; Dillingham 2010) which can be written as:

$$e^r = e^{\left(a_{rT} \dfrac{1}{\left(a+\dfrac{e^{-M}}{e^r - e^{-M}}\right)} \right)}$$

and can be solved iteratively. Niel & Lebreton (2005) found that $a_{rT}\approx1$ for birds and Dillingham *et al.* (2016) recently found that $a_{rT}\approx1$ for several vertebrate taxa (birds, mammals, and elasmobranchs), thus r_{max} can be obtained from knowledge of a and s only.

Method 5 — Euler-Lotka equation:

$$\sum_{x=a}^{w} l_x m_x e^{-rx} - 1 = 0$$

Method 6 — Leslie matrix:

$$
\mathbf{A} = \begin{pmatrix}
F_1 & F_2 & F_3 & \dots & F_{n-1} & F_n \\
P_1 & 0 & 0 & \dots & 0 & 0 \\
0 & P_2 & 0 & \dots & 0 & 0 \\
0 & 0 & P_3 & \dots & 0 & 0 \\
. & . & . & \dots & . & . \\
0 & 0 & 0 & \dots & P_{n-1} & 0
\end{pmatrix}
$$

assuming a birth-pulse, prebreeding census (i.e., each element in the first row of the matrix is expressed as $F_x = m_x P_0$, where P_0 is the probability of survival of age-0 individuals and m_x is fecundity or the number of female offspring produced annually by a female of age x), and a yearly time step applied to females only, and P_x is the probability of survival at age.