ESTIMATES OF VITAL RATES AND POPULATION DYNAMICS PARAMETERS OF INTEREST FOR BLUE SHARKS IN THE NORTH AND SOUTH ATLANTIC OCEAN

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SUMMARY

*Estimates of vital rates and population dynamics parameters of the North and South Atlantic stocks of blue shark (*Prionace glauca*) for potential use as inputs into production and integrated stock assessment models were computed based on biological information gathered at the 2023 Data Preparatory meeting. Six methods were used to compute deterministic estimates of r_{max} and a Leslie matrix approach was also used to incorporate uncertainty in growth parameters, the maturity ogive, fecundity, natural mortality, and lifespan by assigning statistical distributions to these biological traits. Productivity (r_{max}) estimated with the Euler-Lotka deterministic method using a length-based mortality estimator was 0.283 yr^{-1} (North); 0.142 yr^{-1} (South) and increased to 0.386 yr^{-1} (North) and 0.291 yr^{-1} (South) when using the mean of six life-history invariant mortality estimators. Productivity estimated with the stochastic Leslie matrix was very similar to that estimated with the deterministic method using the mean of the six M estimators: r_{max}=0.385; 95% CI: 0.224-0.596 (North); r_{max}=0.299; 95% CI: 0.165-0.389 (South). The corresponding values of steepness were h=0.86, 95% CI: 0.57-0.96 (North); h =0.80, 95% CI: 0.46-0.93 (South).*

RÉSUMÉ

*Les estimations des taux vitaux et des paramètres de la dynamique des populations des stocks de requin peau bleue (*Prionace glauca*) de l'Atlantique Nord et Sud ont été calculées aux fins de leur possible utilisation comme valeurs d'entrée dans les modèles de production et les modèles d'évaluation des stocks intégrés en se basant sur les informations biologiques collectées à la Réunion de préparation des données de 2023. Six méthodes ont été utilisées pour calculer les estimations déterministes de r_{max} ; une approche de matrice de Leslie a également été utilisée pour inclure l'incertitude dans les paramètres de croissance, l'ogive de maturité, la fécondité, la mortalité naturelle et la durée de vie en attribuant des distributions statistiques à ces caractéristiques biologiques. La productivité (r_{max}) estimée avec la méthode déterministe d'Euler-Lotka utilisant un estimateur de la mortalité basé sur la longueur était de 0,283 an^{-1} (Nord) ; 0,142 an^{-1} (Sud), passant à 0,386 an^{-1} (Nord) et à 0,291 an^{-1} (Sud) lorsque l'on utilisait la moyenne des six estimateurs de la mortalité invariable du cycle vital. La productivité estimée avec la matrice stochastique de Leslie était très similaire à celle estimée avec la méthode déterministe utilisant la moyenne des six estimateurs de M : r_{max}=0,385 ; IC 95% : 0,224-0,596 (Nord) ; r_{max}=0,299 ; IC 95% : 0,165-0,389 (Sud). Les valeurs de pente correspondantes étaient h=0,86, IC 95% : 0,57-0,96 (Nord) ; h =0,80, IC 95% : 0,46-0,93 (Sud).*

RESUMEN

Las estimaciones de las tasas vitales y los parámetros de dinámica de la población de los stocks de tiburón azul (Prionace glauca) del Atlántico norte y sur para su posible uso como datos de entrada en los modelos de producción y modelos integrado de evaluación de stock se calcularon a partir de la información biológica recopilada en la reunión de preparación de datos de 2023. Se emplearon seis métodos para calcular estimaciones deterministas de r_{max} y también se utilizó un enfoque de matriz de Leslie para incorporar la incertidumbre en los parámetros de crecimiento, la ojiva de madurez, la fecundidad, la mortalidad natural y el ciclo vital asignando distribuciones estadísticas a estos rasgos biológicos. La productividad (r_{max}) estimada con el método determinista de Euler-Lotka utilizando un estimador de mortalidad basado en la talla

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fue de 0,283 yr^{-1} (norte); 0,142 yr^{-1} (sur) y aumentó a 0,386 yr^{-1} (norte) y 0,291 yr^{-1} (sur) cuando se utilizó la mediana de seis estimadores de mortalidad invariables del ciclo vital. La productividad estimada con la matriz estocástica de Leslie fue muy similar a la estimada con el método determinista utilizando la mediana de los seis estimadores de M: r_{max}=0,385; intervalo de confianza del 95 %: 0,224-0,596 (norte); r_{max}=0,299; intervalo de confianza del 95 %: 0,165-0,389 (sur). Los valores correspondientes de inclinación fueron h=0,86, intervalo de confianza del 95 %: 0,57-0,96 (norte); h=0,80; intervalo de confianza del 95 %: 0,46-0,93 (sur).

KEYWORDS

Natural mortality, Productivity, Steepness, Lifespan, Generation time, SPR, Stochastic models, Life history, Blue shark

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 (m), which can then be used to obtain the inflection point or vice versa. The position of the inflection point of population growth curves (R; Fowler 1981), or inflection point of the production curve, can be estimated independently of a stock assessment because it is also a function of the product 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 document was to generate values of r_{max}, R, and m to generate informative priors of these parameters for production models as well as values of h and M for potential use as fixed parameter values or priors in Stock Synthesis. Additionally, generation time estimates are also provided to help identify the time horizon for stock projections.

2. Materials and methods

2.1 Data inputs

Life history inputs were obtained from data assembled at the 2023 Blue Shark Data Preparatory meeting (**Tables 1** and **2**). All values used in the analyses are for females unless otherwise noted.

2.2 Modelling and outputs

2.2.1 Deterministic estimates

For the computation of deterministic estimates of r_{max}, annual natural mortality at age was obtained from a method developed by Dureuil *et al.* (2021) based on the Lorenzen (2000) method. According to these methods M scales inversely proportional to body length and M at length is obtained as:

$$M_L = M_r \frac{L_r}{L} \quad (1)$$

where M_r is a constant M rate at a specific reference length (L_r), In this method M_r is obtained using the predicted constant adult M rate from another estimator (T_{max}), which is obtained from the expression:

$$M = e^{(1.551-1.066\ln(t_{max}))} \quad (2)$$

where t_{max} is obtained from the von Bertalanffy growth curve as:

$$\widehat{t_{max}} = \frac{1}{k}\ln\left((L_\infty - L_0)/((1-0.95)L_\infty\right) \quad (3)$$

with 0.95 indicating the proportion of L_∞ at which t_{max} is reached.

The reference length, L_r, is defined as the length at the age after which M can be assumed constant, L_{ta}. Simplifying (see Dureuil *et al*. (2021) for details), t_a is obtained from the expression:

$$t_a = \left(\frac{2}{\ln(P)} + 1\right) t_{max} \quad (4)$$

where the estimator P is the proportion of the cohort P that remains alive at t_{max}, which was found to be 0.0178 for elasmobranchs (Dureuil *et al.* 2021):

$$M = \frac{-\ln(0.0178)}{t_{max}} \quad (5)$$

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 1**).

2.2.2 Stochastic estimates

For the computation of stochastic estimates of r_{max}, annual survival at age (obtained from the instantaneous natural mortality rate at age as e^{-M}) was obtained through six alternative 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 2**). 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 equations listed in **Tables 1** and **2**. Lifespan was set equal to the maximum "observed" age obtained from ageing vertebrae or, alternatively, as the theoretical age corresponding to when 95% of L_∞ is reached (equation 3; see Tables 1 and 2).

Maximum population growth rate (r_{max}) was estimated through an age-structured Leslie matrix approach (Leslie 1945; Caswell 2001) assuming a birth-pulse, post-breeding census (survival first, then reproduction) where each element in the first row of the matrix is expressed as $F_x = m_{x+1}P_x$ (where P_x is the probability of survival at age x and m_{x+1} is fecundity or the number of female offspring produced annually by a female of age $x+1$), and a yearly time step applied to females only. Uncertainty was introduced in the Leslie matrix through Monte Carlo simulation by randomly selecting vital rates/parameters from predefined statistical distributions (n=10,000). The quantities varied were the parameters from the von Bertalanffy growth function (VBGF; L_∞, K, t_0), intercept and slope parameters from the maturity ogive at age (a, b), litter size or fecundity relationship, lifespan, and survivorship (mortality).

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. Lifespan was given a uniform distribution with the lower bound set equal to "observed" longevity from vertebral ageing and the upper bound set to the age corresponding to when 95% of L_∞ is reached. Litter size was assigned a truncated normal distribution, with mean, SD, and lower and upper bounds reflecting the minimum and maximum observed litter sizes, or alternatively a maternal vs. fecundity relationship was used. 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. A value of mortality was then randomly selected from the six estimators at each iteration. A 1:1 female to male ratio at birth, an annual reproductive cycle, and an 11-month time lapse to account for the gestation period before females can contribute offspring to the population were also used. Finally, litter size was divided by two to account for female pups only.

In addition to r_{max} (obtained as the logarithm of the dominant eigenvalue of the matrix), generation time defined as the mean age of parents of offspring in a stable age distribution ($\bar{A}$), the net reproductive rate (R_0 or virgin spawners per recruit in fisheries terms), age-0 survivorship (S_0), steepness (h) obtained from the maximum lifetime reproductive rate $\hat{\alpha}$ (Myers *et al.* 1997, 1999), which is itself the product of R_0 and S_0 (Brooks *et al*. 2010), $h = \frac{\hat{\alpha}}{4+\hat{\alpha}}$, $SPR_{MER} = \frac{1}{\sqrt{\hat{\alpha}}}$, and R (the position of the inflection point of population growth curves/production functions

obtained from the equation $R = 0.633 - 0.187 \times \ln(r_{max} \times \overline{A})$ were calculated. A density function was then fitted to the probability distributions of r_{max} and R to use as priors for these parameters in production models. The shape parameter was derived from R (B_{MSY}/K) based on the relationship (Winker *et al.* 2018):

$$\frac{B_{MSY}}{K} = m^{-\frac{1}{(m-1)}} \quad (6)$$

All models were run in R (R Core Team 2023, version 4.2.3).

North Atlantic stock—In addition to the values shown in **Table 1,** the following correlation matrix of von Bertalanffy growth function parameters was obtained based on Carlson *et al.* (2023; J. Carlson pers. comm. to EC):

	L_{INF}	K	t_0
L_{INF}	1	-0.9779	-0.7656
K	-0.9779	1	0.8735
t_0	-0.7656	0.873497	1

and the following correlation between the intercept and slope parameters of the maturity ogive:

	Intercept	slope
Intercept	1	-0.9869
slope	-0.9869	1

Fecundity at age was assumed to follow a truncated normal distribution with mean=39 and minimum and maximum values of 1 and 96, respectively **(Table 1**). Since no SD was specified in the DW report, a value of 13 (≈0.33 x mean for the right uterus), was assumed based on Castro and Mejuto (1995). In an alternative scenario, the litter size (LS) vs. maternal length (ML) relationship reported by the DW based on data from the South Atlantic stock was used: LS = -23.65501 + 0.27966*FL (cm).

South Atlantic stock— In addition to the values shown in **Table 2**, the same correlation matrix of von Bertalanffy growth function parameters from the North Atlantic stock was used because it was not reported for the South Atlantic stock in Joung *et al*. (2017):

	L_{INF}	K	t_0
L_{INF}	1	-0.9779	-0.7656
K	-0.9779	1	0.8735
t_0	-0.7656	0.873497	1

Similarly, because SEs of the von Bertalanffy parameter estimates were not reported in Joung *et al.* (2017), the CVs of these parameters for the North Atlantic stock were used to derive SEs for the South Atlantic stock.

The following correlation between the intercept and slope parameters of the maturity ogive was obtained based on Mas *et al.* (2023; F. Mas, pers. comm. to EC):

	Intercept	slope
Intercept	1	-0.992
slope	-0.992	1

Fecundity at age was obtained from the litter size (LS) vs. maternal length (ML) relationship reported by the DW for the South Atlantic stock: LS = -23.65501 + 0.27966*FL (cm).

3. Results

North Atlantic stock—The age-specific deterministic estimates of *M* obtained from the Dureuil *et al.* (2021) method with the Euler-Lotka/Leslie matrix approach ranged from 0.524 yr^{-1} for age 0 sharks to 0.126 yr^{-1} for a maximum theoretical age of 26 years (**Table 3**). Estimated productivity ranged from r_{max} = 0.104 yr^{-1} for the DIM method to 0.311 yr^{-1} for the Skalski *et al*. (2008) method for a lifespan of 15 years and from r_{max} = 0.101 yr^{-1} for the DIM method to 0.315 yr^{-1} for both the Skalski *et al.* (2008) and Eberhardt *et al.* (1982) methods for a lifespan of 26 years (**Table 4**). Using the fecundity vs. maternal size relationship instead of constant fecundity had very little effect on the estimate of productivity obtained with the Euler-Lotka/Leslie matrix approach using the Dureuil *et al.* (2021) method to estimate *M* (r_{max} = 0.283 yr^{-1} with constant fecundity vs. r_{max} = 0.284 yr^{-1} with the fecundity-maternal length relationship). In contrast, the deterministic Euler-Lotka/Leslie matrix approach using the mean of the six life-history invariant *M* estimators yielded higher productivity (r_{max} = 0.386 yr^{-1}).

For the stochastic Leslie matrix approach, median r_{max} was 0.385 yr^{-1} (95% CI = 0.224 – 0.596), median *M* from the six mortality estimators was 0.178 yr^{-1} (95% CI = 0.148 – 0.210, $\overline{A}$ = 7.60 years (95% CI = 4.14 – 14.13), *h* = 0.86 (95% CI = 0.57 – 0.96), SPR_{MER} = 0.20 (95% CI = 0.11– 0.43), *R* = 0.43 (95% CI = 0.32 – 0.53), and *m* = 1.41 (95% CI >1.0 – 2.39) (**Table 5**).

A lognormal distribution was fitted to the values of r_{max} obtained from the stochastic simulation yielding a back-transformed mean=0.387 and SD=0.287 (**Figure 1 top**). Similarly, a normal distribution was fitted to the R values yielding a mean=0.429 and SD=0.055 **(Figure 1 bottom**).

South Atlantic stock— The age-specific deterministic estimates of *M* obtained from the Dureuil *et al*. (2021) method with the Euler-Lotka/Leslie matrix approach ranged from 0.901 yr^{-1} for age 0 sharks to 0.148 yr^{-1} for a maximum theoretical age of 22 years (**Table 3**). Estimated productivity ranged from r_{max} = 0.094 yr^{-1} for the DIM method to 0.163 yr^{-1} for the Skalski *et al*. (2008) method for a lifespan of 15 years and from r_{max} = 0.093 yr^{-1} for the DIM method to 0.166 yr^{-1} for the Skalski *et al.* (2008) method for a lifespan of 22 years (**Table 4**). The estimate of productivity obtained with the Euler-Lotka/Leslie matrix approach using the Dureuil *et al.* (2021) method to estimate *M* was r_{max} = 0.142 yr^{-1}, whereas using the mean of the six life-history invariant *M* estimators yielded about double that productivity value (r_{max} = 0.291 yr^{-1}).

For the stochastic Leslie matrix approach, median r_{max} was 0.299 yr^{-1} (95% CI = 0.165 – 0.389), median *M* from the six mortality estimators was 0.197 yr^{-1} (95% CI = 0.162 – 0.235, $\overline{A}$ = 9.16 years (95% CI = 7.99 – 20.36), *h* = 0.80 (95% CI = 0.46 – 0.93), SPR_{MER} = 0.25 (95% CI = 0.13– 0.54), *R* = 0.45 (95% CI = 0.28 – 0.56), and *m* = 1.53 (95% CI >1.0 – 2.69) (**Table 5**).

A normal distribution was fitted to the values of r_{max} obtained from the stochastic simulation yielding a mean=0.293 and SD=0.057 (**Figure 2 top**). Similarly, a normal distribution was fitted to the R values yielding a mean=0.429 and SD=0.076 **(Figure 2 bottom**).

4. Discussion

For both stocks, using the deterministic Euler-Lotka/Leslie matrix approach with the length-specific Dureuil *et al.* (2021) method to estimate *M* yielded considerably lower values of productivity than when using the mean of the six life-history invariant *M* estimators. This is because the values of *M* obtained with the Dureuil *et al.* (2021) method for the first age groups are considerably higher than those obtained when using the mean of the six *M* estimators, resulting in lower survivorship and thus lower productivity. The deterministic productivity values obtained with the Dureuil *et al.* (2021) method should thus be regarded as minimum estimates that fell within the confidence intervals of the stochastic estimates for the North Atlantic stock, but not for the South Atlantic stock (**Table 5**).

Productivity for the North Atlantic stock was higher than for the South Atlantic stock. This was due in part to the combination of von Bertalanffy growth function parameter estimates and the weight-length relationships used in the simulation, which resulted in smaller age-0 and other young animals for the South Atlantic than for the North Atlantic, with the corresponding higher mortality values and thus lower productivity for the South Atlantic stock.

In all, the high values of productivity and steepness obtained herein are not dissimilar to previously reported values for these and other stocks of blue shark. For comparison, Cortés (SCRS-2015-142) reported mean productivity and steepness values ranging from 0.31 to 0.44 yr^{-1} and 0.73 to 0.93, respectively, for the North Atlantic stock and from 0.22 to 0.34 yr^{-1} and 0.55-0.84, respectively, for the South Atlantic stock. A stock assessment of blue shark in the Indian Ocean (Rice 2017) reported a value of steepness of 0.79, whereas another stock assessment of blue shark in the North Pacific reported a lower value of steepness of 0.67 (Carvalho et al. 2017).

The estimates of life-history traits used herein were collected during different time periods, but the age, growth, maturity, and lifespan information is associated with samples collected fairly recently. This means that at this time blue shark stocks have been exposed to fishing for multiple decades and their biomasses are likely far from their unexploited levels. It is therefore expected that the parameter estimates used here are only moderately, if at all, influenced by density dependence, and hence the derived productivity should not be very different from the true intrinsic, or maximum, rate of increase.

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Table 1. Biological input values for females used to compute r_{max}, steepness, and other parameters of interest for North Atlantic blue shark.

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length (FL)	337.3 (23.68)	cm FL	DP meeting (2023)
K	Brody growth coefficient	0.107 (0.015)	yr^{-1}	DP meeting (2023)
t_0	Theoretical age at zero length	-2.43 (0.235)	yr	DP meeting (2023)
a	Intercept of maturity ogive	-10.81 (3.45)	dimensionless	DP meeting (2023)
b	Slope of maturity ogive	2.02 (0.65)	dimensionless	DP meeting (2023)
c	Scalar coefficient of weight on length (FL)	3.180E-06	dimensionless	DP meeting (2023)
d	Power coefficient of weight on length (FL)	3.1313	dimensionless	DP meeting (2023)
w	Observed lifespan	15	yr	DP meeting (2023)
	Theoretical lifespan (95% of Linf)	25.6	yr	DP meeting (2023)
	Sex ratio at birth	1:1	dimensionless	DP meeting (2023)
	Reproductive cycle	annual	yr	DP meeting (2023)
mx	Constant litter size	39 (SD=13[a]; 1-96)	pups per litter	DP meeting (2023)
e	Intercept of maternal length (FL) vs. fecundity	-23.655	dimensionless	DP meeting (2023)
f	Slope of maternal length (FL) vs. fecundity	0.2797	dimensionless	DP meeting (2023)
GP	Gestation period	9-12	months	DP meeting (2023)

[a] Approximated from Mejuto et al. (1995)

Values in parentheses are SEs.

Table 2. Biological input values for females used to compute r_{max}, steepness, and other parameters of interest for South Atlantic blue shark.

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length (TL)	352.1 (24.72) [a]	cm FL	DP meeting (2023)
K	Brody growth coefficient	0.13 (0.018)	yr^{-1}	DP meeting (2023)
t_0	Theoretical age at zero length	-1.31 (0.127)	yr	DP meeting (2023)
a	Intercept of maturity ogive	-11.93 (3.18)	dimensionless	DP meeting (2023)
b	Slope of maturity ogive	1.85 (0.49)	dimensionless	DP meeting (2023)
c	Scalar coefficient of weight on length (FL)	1.100E-06	dimensionless	DP meeting (2023)
d	Power coefficient of weight on length (FL)	3.35	dimensionless	DP meeting (2023)
w	Observed lifespan	15	yr	DP meeting (2023)
	Theoretical lifespan (95% of Linf)	21.7	yr	DP meeting (2023)
	Sex ratio at birth	1:1	dimensionless	DP meeting (2023)
	Reproductive cycle	annual	yr	DP meeting (2023)
mx	Constant litter size	37 (SD=)	pups per litter	DP meeting (2023)
e	Intercept of maternal length vs. fecundity	-23.655	dimensionless	DP meeting (2023)
f	Slope of maternal length vs. fecundity	0.2797	dimensionless	DP meeting (2023)
GP	Gestation period	9-12	months	DP meeting (2023)
g	Intercept of TL to FL relationship	1.613	dimensionless	DP meeting (2023)
h	Slope of TL to FL relationship	1.201	dimensionless	DP meeting (2023)

[a] SEs from the original paper (Joung et al. 2017) were not available so the CVs from the North Atlantic stock were applied to obtain the SEs

Table 3. Estimates of instantaneous natural mortality rates (yr^{-1}) obtained with the Dureuil *et al.* (2021) method used with the deterministic methods to estimate r_{max}.

	Stock	
	Blue shark	Blue shark
Age	North Atlantic	South Atlantic
0	0.524	0.901
1	0.391	0.544
2	0.318	0.403
3	0.272	0.329
4	0.241	0.283
5	0.219	0.252
6	0.202	0.230
7	0.189	0.214
8	0.178	0.201
9	0.170	0.191
10	0.163	0.183
11	0.157	0.177
12	0.153	0.171
13	0.148	0.167
14	0.145	0.163
15	0.142	0.160
16	0.139	0.158
17	0.137	0.155
18	0.135	0.154
19	0.133	0.152
20	0.132	0.151
21	0.131	0.149
22	0.129	0.148
23	0.128	
24	0.128	
25	0.127	
26	0.126	

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

		Stock			
Method		North Atlantic		South Atlantic	
		Lifespan=15 yr	Lifespan=26 yr	Lifespan=15 yr	Lifespan=22 yr
Euler-Lotka/Leslie matrix		0.279	0.283	0.129	0.142
Au et al. (2016)		0.117	0.112	0.108	0.106
Eberhardt et al. (1982)		0.308	0.315	0.151	0.165
Skalski et al. (2008)		0.311	0.315	0.163	0.166
Neil and Lebreton's (2005) DIM		0.104	0.101	0.094	0.093
Mean		0.224	0.225	0.129	0.134

Table 5. Productivity (r_{max}), generation time ($\overline{A}$), net reproductive rate (R_0), age-0 survivorship (S_0), steepness (h), spawning potential ratio at maximum excess recruitment (SPR_{MER}), position of the inflection point of population growth curves (R), and natural mortality (M) obtained from Monte Carlo simulation of vital rates with a Leslie matrix approach for the two stocks of blue sharks. The shape parameter (m) was derived from R based on equation (6). The LCL and UCL are approximate lower and upper confidence limits computed as the 2.5th and 97.5th percentiles. Stochastic results are based on six methods to estimate M, whereas deterministic results are based on the Dureuil *et al.* (2021) method to estimate M at age or on the mean of six methods to estimate M. All results were obtained with a Leslie matrix approach.

A) North Atlantic stock

	Median	LCL	UCL	Deterministic [a]	Deterministic [b]
r_{max}	0.385	0.224	0.596	0.283	0.386
Generation time	7.60	4.14	14.13	8.16	7.64
Net reproductive rate (R_0)	29.77	6.96	103.75	14.81	31.86
Age-0 survivorship (S_0)	0.79	0.72	0.90	0.59	0.81
Steepness (h)	0.86	0.57	0.96	0.69	0.87
SPR_{MER}	0.20	0.11	0.43	0.34	0.20
R (inflection point)	0.43	0.32	0.53	0.45	0.40
M	0.178	0.148	0.210	0.183	0.178
Shape parameter (m)	1.41	1.00	2.39	1.53	1.20
[a] Using Dureuil et al. (2020) method to estimate age-specific M					
[b] Using mean of six methods to estimate M					

B) South Atlantic stock

	Median	LCL	UCL	Deterministic [a]	Deterministic [b]
r_{max}	0.299	0.165	0.389	0.142	0.291
Generation time	9.16	7.99	20.36	10.58	9.41
Net reproductive rate (R_0)	19.03	4.78	77.01	5.05	21.68
Age-0 survivorship (S_0)	0.81	0.68	0.89	0.41	0.78
Steepness (h)	0.80	0.46	0.93	0.34	0.81
SPR_{MER}	0.25	0.13	0.54	0.70	0.24
R (inflection point)	0.45	0.28	0.56	0.54	0.42
M	0.197	0.162	0.235	0.233	0.192
Shape parameter (m)	1.53	1.00	2.69	2.50	1.34
[a] Using Dureuil et al. (2020) method to estimate age-specific M					
[b] Using mean of six methods to estimate M					

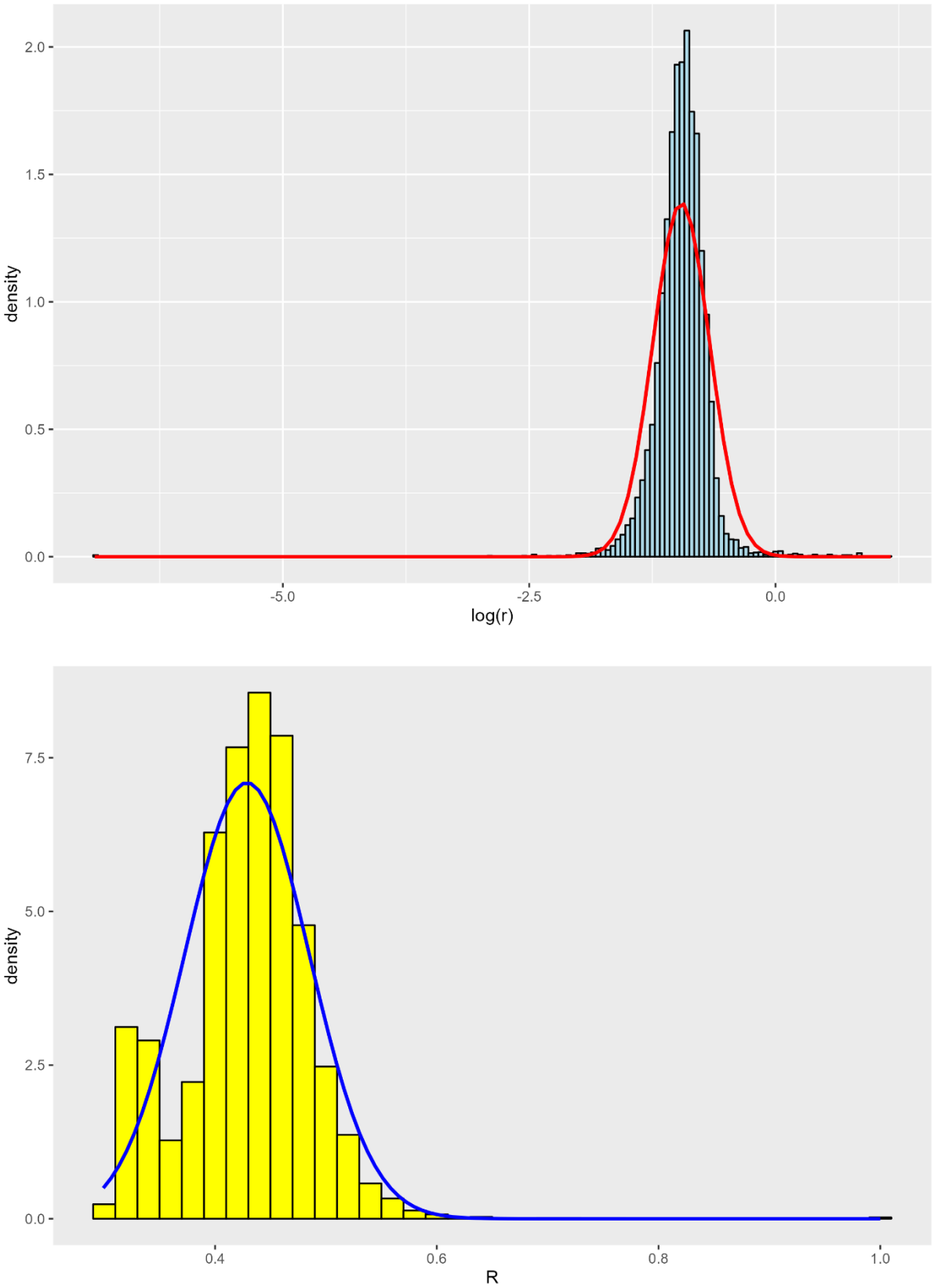

Figure 1. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted lognormal distribution for r_{max} and normal distribution for R for the North Atlantic blue shark stock.

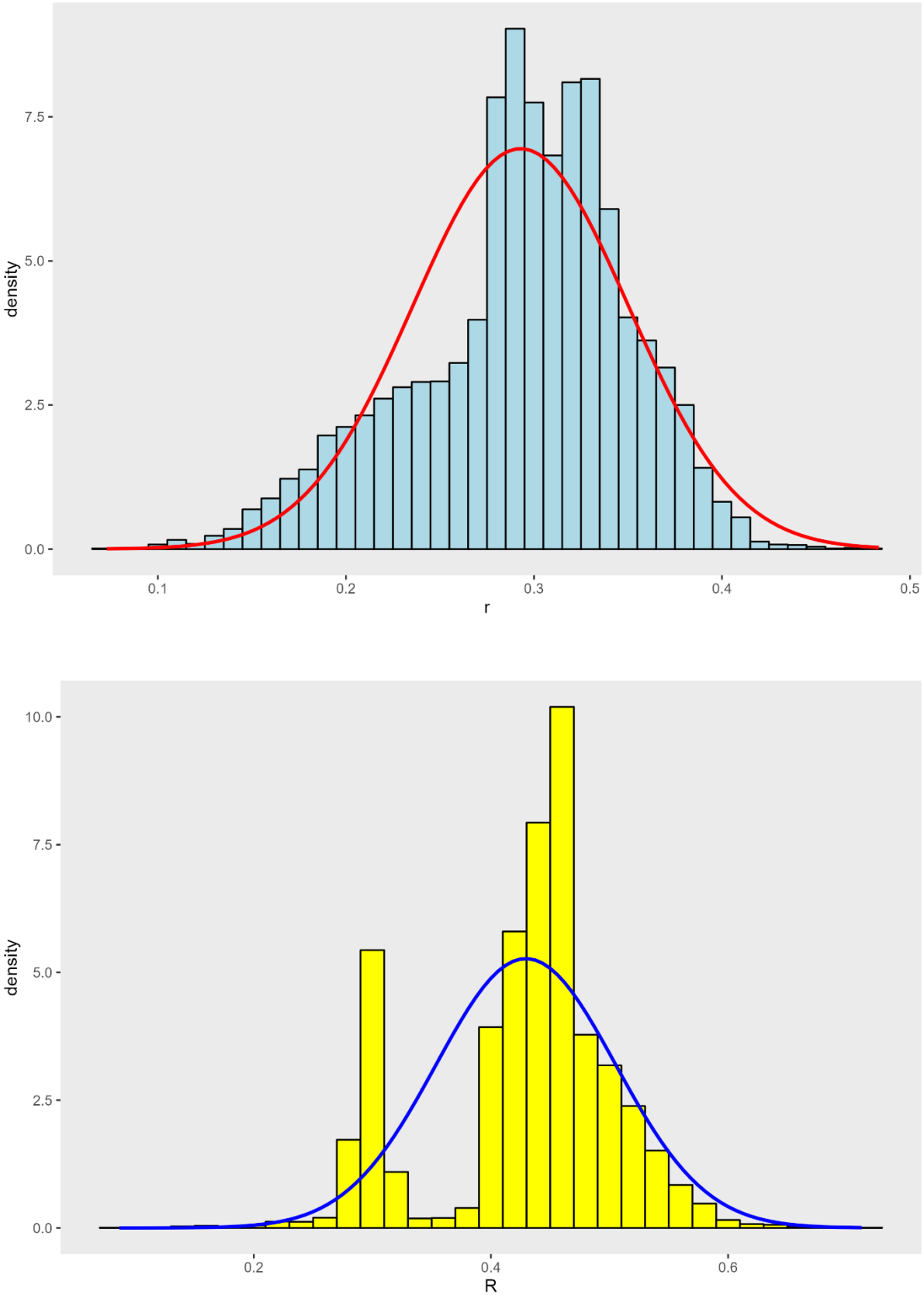

Figure 2. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted normal distribution for r_{max} and normal distribution for R for the South Atlantic blue shark stock.

Appendix 1

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 first breeding, w is maximum life expectancy, and r is the population rate of increase, which can be obtained by iteratively solving the above equation.

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 (DIM):

Niel and 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 $r_{max}=a_r M^{-0.25}$ and $T=a_T M^{-0.25}$, which when multiplied yield the dimensionless maximum rate of increase per generation or $r_{max}\,T=a_r a_T=a_{rT}$. 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:

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

and can be solved iteratively. Niel & Lebreton (2005) found that $a_{rT}\approx 1$ for birds and Dillingham *et al.* (2016) recently found that $a_{rT}\approx 1$ 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:

$$\begin{pmatrix} F_0 & F_1 & F_2 & \dots & F_{n-1} & F_n \\ P_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & P_2 & \dots & 0 & 0 \\ . & . & . & \dots & . & . \\ 0 & 0 & 0 & \dots & P_{n-1} & 0 \end{pmatrix}$$

assuming a birth-pulse, post-breeding census (survival first, then reproduction). Each element in the first row of the matrix is expressed as $F_x = m_{x+1}P_x$, where P_x is the probability of survival at age x and m_{x+1} is fecundity or the number of female offspring produced annually by a female of age $x+1$. A yearly time step is assumed, applied to females only.

Appendix 2

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 growth-based Pauly (1980) estimator:

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

Method 4 — Then *et al*.'s (2015) modified longevity-based Hoenig (1983) estimator:

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

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:

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

where W is weight in g.

Table 1.2 Data requirements for seven methods used to estimate r_{max}.

Method	Age at maturity/ first breeding	Maximum age	Fecundity	M	Survival to age at maturity/ first breeding
Eberhardt et al. (1992)	Yes	Yes	Constant	Constant	Yes
Skalski et al. (2008)	Yes	No	Constant	Constant	Yes
Rebound potential (Au et al. 2009)	Yes	Yes	Constant	Constant	Yes
Neil and Lebreton's (2005) DIM	Yes	No	No	Constant	No
Euler-Lotka/Leslie matrix	Yes	Yes	Age-dependent	Age-dependent	Yes