

ESTIMATES OF VITAL RATES AND POPULATION DYNAMICS PARAMETERS OF INTEREST FOR PORBEAGLE SHARK IN THE WESTERN NORTH ATLANTIC AND SOUTH ATLANTIC OCEAN

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SUMMARY

We updated vital rates and population dynamics parameters for input into stock assessments of the western North Atlantic and South Atlantic Ocean porbeagle shark. These included maximum population growth rate (r_{max}), generation time (\bar{A}), steepness (h), and spawning potential ratio at maximum excess recruitment (SPR_{MER}). We used six methods to compute r_{max} deterministically and incorporated uncertainty in vital rates through a Leslie matrix approach. Productivity (r_{max}) for the western North Atlantic assuming an equally probable 1 or 2 year breeding frequency was 0.045-0.068 yr⁻¹ for the six deterministic methods. For the stochastic Leslie matrix, $r_{max}=0.059$ yr⁻¹ (CIs=0.03–0.081), $h=0.45$ (0.31–0.59), $\bar{A}=20.1$ years (17.3–21.3), and $SPR_{MER}=0.56$ (0.41–0.74). The South Atlantic was data deficient and we had to use life history data from the South Pacific. Because the stochastic Leslie matrix resulted in very low or implausible values of productivity and other population parameters we recommend using results of the deterministic scenario with an annual reproductive cycle and longevity obtained through bomb radiocarbon (65 years), which yields $r_{max}=0.059$ yr⁻¹, $h=0.45$, and $SPR_{MER}=0.55$.

RÉSUMÉ

Nous avons mis à jour les taux vitaux et les paramètres de la dynamique des populations afin de les intégrer dans les évaluations des stocks de requins-taupes communs de l'Atlantique Nord-Ouest et de l'Atlantique Sud. Ceux-ci comprennent le taux de croissance maximal de la population (r_{max}), le temps de génération (\bar{A}), la pente (steepness) (h) et le ratio du potentiel reproducteur au recrutement excédentaire maximum (SPR_{MER}). Nous avons utilisé six méthodes pour calculer r_{max} de manière déterministe et avons intégré l'incertitude dans les taux vitaux au moyen d'une approche de matrice de Leslie. La productivité (r_{max}) pour l'Atlantique Nord-Ouest en postulant une fréquence de reproduction tout aussi probable sur 1 ou 2 ans était de 0,045-0,068 an⁻¹ pour les six méthodes déterministes. Pour la matrice stochastique de Leslie, $r_{max}=0,059$ an⁻¹ (CI=0,03-0,081), $h=0,45$ (0,31-0,59), $\bar{A}=20,1$ ans (17,3- 21,3), et $SPR_{MER}=0,56$ (0,41-0,74). Les données de l'Atlantique Sud étaient insuffisantes et nous avons dû utiliser les données sur le cycle vital dans le Pacifique Sud. Étant donné que la matrice stochastique de Leslie a donné des valeurs très faibles ou peu plausibles de la productivité et d'autres paramètres de population, nous recommandons d'utiliser les résultats du scénario déterministe avec un cycle de reproduction annuel et une longévité obtenus par radiocarbone (65 ans), qui donne $r_{max}=0,059$ yr⁻¹, $h=0,45$ et $SPR_{MER}=0,55$.

RESUMEN

Se actualizaron las tasas vitales y los parámetros de dinámica de la población para las entradas de las evaluaciones de stock de marrajo sardinero del Atlántico noroccidental y del Atlántico sur. Entre ellas figuraban la tasa máxima de crecimiento de la población (r_{max}), el tiempo de generación (\bar{A}) la inclinación (h) y la ratio potencial de desove en el reclutamiento excedentario máximo (SPR_{MER}). Se utilizaron seis métodos para calcular r_{max} de forma

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determinista y se incorporó la incertidumbre en las tasas vitales mediante un enfoque de matriz de Leslie. La productividad (r_{max}) para el Atlántico noroccidental suponiendo una frecuencia de cría igualmente probable de 1 o 2 años fue de 0,045-0,068 años⁻¹ para los seis métodos deterministas. Para la matriz estocástica de Leslie, $r_{max}=0,059$ año⁻¹ (CI=0,03-0,081), $h=0,45$ (0,31-0,59), $\bar{A}=20,1$ años (17,3- 21,3), y $SPR_{MER}=0,56$ (0,41-0,74). El Atlántico sur era deficiente en datos y hubo que utilizar los datos de ciclo vital del Pacífico sur. Debido a que la matriz estocástica de Leslie tuvo como resultado valores muy bajos o no plausibles de productividad y otros parámetros de población, recomendamos utilizar los resultados del escenario determinístico con un ciclo reproductivo anual y longevidad obtenidos a través de la bomba de radiocarbono (65 años), que arroja $r_{max}=0,059$ año⁻¹, $h=0,45$, y $SPR_{MER}=0,55$.

KEYWORDS

Productivity, Steepness, Lifespan, SPR, Porbeagle

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 (\bar{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). 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). Furthermore, if a reliable index of current abundance is available, it can be compared to the level of depletion at MER to determine stock status relative to the overfished criterion (Brooks *et al.* 2010). The associated productivity (expressed as steepness or as the related maximum lifetime reproductive rate, $\hat{\alpha}$) can further be used to identify F -based reference points (e.g. F_{MSY}) (Cortés and Brooks 2018).

The purpose of this paper was to generate values of productivity (r_{max} , h , $\hat{\alpha}$, and SPR_{MER}) and \bar{A} of porbeagle for use in data-limited or other approaches.

2. Materials and methods

Inputs

Western North Atlantic—Life history inputs were obtained from previously published data, as first summarized in the 2014 intersessional meeting of the Shark Species Group (see Appendix 7 of the report), recently published data, and unpublished data on maturity (**Table 1**). All values are for females.

We used growth function parameters from Natanson *et al.* (2002) and reproductive biology information, including a maturity ogive, litter size, and gestation period from Jensen *et al.* (2002). Recently published information showing a resting period for the western North Atlantic population, which is indicative of a biennial cycle, was considered in the analyses (Natanson *et al.* 2019). Fecundity was set to a constant value of 4 and a 1:1 female to male ratio at birth was assumed. Unpublished data on maturity (L. Natanson. NOAA Fisheries, NEFSC, pers. comm.) were added to the previously available data from Jensen *et al.* (2002).

Annual survival at age (obtained from the instantaneous natural mortality rate at age as e^{-M}) was obtained through five 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), and the mass-based estimator of Peterson and Wroblewski (1996) (**Appendix 1**). The first

four 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 from Kohler *et al.* (1995). Lifespan (ω) was set at 25 years (Natanson *et al.* 2002) (**Table 1**).

South Atlantic— The only life history inputs available for the South Atlantic were from Morinobu (1996). These included growth parameters, observed lifespan, and weight-length conversions, but no reproductive parameters. Specimens used for the estimation of growth parameters were obtained from the South Atlantic, South Indian Ocean, and South Pacific Ocean. In contrast, there was more information available for the South Pacific as summarized in Clarke *et al.* (2015) and Francis *et al.* (2015) (**Table 2**). Use of Morinobu’s (1996) South Atlantic growth data in the modeling with reproductive parameters from the South Pacific resulted in negative population growth rates and undefined steepness for the 2-year and 1.5-year reproductive cycle scenarios and a very low value of r_{max} (0.018) and steepness (0.23) for the 1-year reproductive cycle. We thus decided to use the life history information from the South Pacific as described below because sampling in the Morinobu (1996) study was biased towards smaller animals (mostly < 150cm precaudal length) and thus not representative of the population.

We thus used growth function parameters from Francis *et al.* (2015) and reproductive biology information from Francis and Stevens (2000). There was no maturity ogive available for the South Pacific, but we used the maturity ogive from the western North Atlantic from Jensen *et al.* (2002) because the predicted median age at maturity (14.1 years) is very similar to the mid-point of the range of values reported in Francis (2015). As for the western North Atlantic we also considered the possibility of a biennial reproductive cycle. Fecundity was set to a constant value of 3.74 and a 1:1 female to male ratio at birth was assumed.

Annual survival at age (obtained from the instantaneous natural mortality rate at age as e^{-M}) was obtained in the same manner as for the western North Atlantic population. Conversions of length into weight were done using the power equation from Morinobu (1996). Lifespan (ω) was set at 25 years (Francis 2015) (**Table 2**).

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); Smith *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** and **Appendix Table 1**).

Uncertainty was introduced in the Leslie matrix approach 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_{inf} , K , t_0), intercept and slope parameters from the maturity ogive at age (a , b), median 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 for the western North Atlantic population 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. The parameter correlation matrices from the western North Atlantic were used for the South Atlantic. Lifespan was given a uniform distribution with the lower bound set equal to “observed” longevity from vertebral ageing (25 years for both the western North Atlantic and South Atlantic) and the upper bound set to a theoretical seven half-lives ($7 \cdot \log(2)/K$) for the western North Atlantic. For the South Atlantic the upper bound was set to the age determined from using bomb radiocarbon (65 years) because the theoretical seven half-lives estimate was lower (56 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 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), \bar{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 $h = \frac{\hat{\alpha}}{4 + \hat{\alpha}}$, and $SPR_{MER} = \frac{1}{\sqrt{\hat{\alpha}}}$ were calculated.

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

3. Results and discussion

Western North Atlantic— The minimum estimates of M (corresponding to maximum annual survivorship) from the four mortality estimators used in the stochastic analysis that yield a single constant value for all ages ranged from 0.05 to 0.13 yr^{-1} , whereas M for the age-specific estimator ranged from 0.18 to 0.21 yr^{-1} for age 0 sharks to 0.09 to 0.10 yr^{-1} for age 25 sharks.

Estimated productivity ranged from $r_{max} = 0.045$ to 0.068 yr^{-1} for the six deterministic methods when considering an equally probable annual or biennial reproductive cycle (1.5 years). For an annual breeding frequency, r_{max} ranged from 0.045 to 0.088 yr^{-1} and for a biennial frequency, from 0.039 to 0.055 yr^{-1} (**Table 3**).

For the stochastic Leslie matrix method, median r_{max} was 0.059 yr^{-1} (approximate 95% confidence limits computed as the 2.5th and 97.5th percentiles = 0.037 – 0.081), median $h = 0.45$ (0.31 – 0.59), median $R = 0.60$ (0.54 – 0.70), median $\bar{A} = 20.1$ years (17.3 – 21.3), and median $\text{SPR}_{\text{MER}} = 0.56$ (0.41– 0.74) for a 1.5 yr reproductive cycle. For the annual cycle, median $r_{max} = 0.080$ yr^{-1} (0.057 – 0.101), median $h = 0.55$ (0.40 – 0.68), median $R = 0.55$ (0.51 – 0.62), median $\bar{A} = 19.3$ years (17.0 – 20.4), and median $\text{SPR}_{\text{MER}} = 0.45$ (0.34– 0.61). For the biennial cycle, median $r_{max} = 0.045$ yr^{-1} (0.022 – 0.067), median $h = 0.38$ (0.26 – 0.52), median $R = 0.65$ (0.57 – 0.79), median $\bar{A} = 20.8$ years (17.6 – 22.0), and mean $\text{SPR}_{\text{MER}} = 0.64$ (0.48– 0.85) (**Table 4**).

South Atlantic— The minimum estimates of M (corresponding to maximum annual survivorship) from the four mortality estimators used in the stochastic analysis that yield a single constant value for all ages ranged from 0.06 to 0.19 yr^{-1} , whereas M for the age-specific estimator ranged from 0.18 to 0.22 yr^{-1} for age 0 sharks to 0.10 to 0.12 yr^{-1} for age 25 sharks.

Estimated productivity ranged from $r_{max} = 0.015$ to 0.054 yr^{-1} for the six deterministic methods when considering an equally probable annual or biennial reproductive cycle (1.5 years) and a maximum age of 25 years and from $r_{max} = 0.040$ to 0.053 yr^{-1} for a maximum age of 65 years. For an annual breeding frequency and a maximum age of 25 years, r_{max} ranged from 0.036 to 0.054 yr^{-1} and from 0.046 to 0.059 yr^{-1} for a maximum age of 65 years. For biennial breeding frequency, r_{max} ranged from -0.001 to 0.054 yr^{-1} for a maximum age of 25 years and from 0.026 to 0.053 yr^{-1} for a maximum age of 65 years (**Table 5**).

For the stochastic Leslie matrix method, median r_{max} was 0.018 yr^{-1} (-0.018 – 0.054), median $h = 0.24$ (0.13 – 0.42), median $R = 0.79$ (0.62 – 1.26), median $\bar{A} = 20.0$ years (17.2 – 21.3), and median $\text{SPR}_{\text{MER}} = 0.89$ (0.59 – 1.30) for a 1.5 yr reproductive cycle. For the annual cycle, median $r_{max} = 0.038$ yr^{-1} (0.002 – 0.075), median $h = 0.32$ (0.18 – 0.52), median $R = 0.69$ (0.57 – 1.01), median $\bar{A} = 19.2$ years (16.9 – 20.4), and median $\text{SPR}_{\text{MER}} = 0.73$ (0.48– 1.06). For the biennial cycle, median $r_{max} = 0.004$ yr^{-1} (-0.033 – 0.040), median $h = 0.19$ (0.10 – 0.35), median $R = 0.87$ (0.65 – 1.45), median $\bar{A} = 20.6$ years (17.4 – 22.0), and mean $\text{SPR}_{\text{MER}} = 1.03$ (0.68– 1.51) (**Table 6**). Several of the parameter estimates (denoted in red font in **Table 6**) were thus out of bounds/undefined ($R_0 < 1$; $\hat{\alpha} < 1$; steepness < 0.2 ; $\text{SPR}_{\text{MER}} > 1$; $R > 1$) even for some of the 95% confidence limits for an annual reproductive cycle. Although these results may be due to some extent to stochasticity, the occurrence of negative growth rates and undefined values for several of the parameters reflective of productivity is suspect and indicative of problems with some of the life history inputs used in the simulation. Based on this, we believe that the most plausible scenario is that reflected in the deterministic scenario for an annual reproductive cycle with a maximum age of 65 years as determined from the bomb radiocarbon analysis (**Table 5**). The steepness value corresponding to that scenario is 0.45, $\hat{\alpha} = 3.253$, and $\text{SPR}_{\text{MER}} = 0.55$, which coincidentally are almost exactly the same as estimated for the western North Atlantic population with the stochastic Leslie matrix approach for an equally probable annual or biennial cycle.

These estimates can be used to formulate informative priors of r_{max} and the shape parameter in production models, steepness in age-structured/integrated stock assessment models, to inform the time horizon for projections in all models, and SPR_{MER} and $\hat{\alpha}$ can also be used to generate biological reference points for data-limited stock assessment approaches.

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Table 1. Biological input values used in computing population dynamics parameter of interest for the western North Atlantic population of porbeagle.

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length	309.8 (13.36)	cm FL	Natanson et al. (2002)
K	Brody growth coefficient	0.061 (0.007)	yr ⁻¹	Natanson et al. (2002)
t_0	Theoretical age at zero length	-5.9 (0.474)	yr	Natanson et al. (2002)
a	Intercept of maturity ogive	-10.2899 (1.679)	dimensionless	Jensen et al. (2002), Natanson (pers. comm.)
b	Slope of maturity ogive	0.7299 (0.118)	dimensionless	Jensen et al. (2002), Natanson (pers. comm.)
e	Scalar coefficient of weight on length	1.482E-05	dimensionless	Kohler et al. (1995)
f	Power coefficient of weight on length	2.9641	dimensionless	Kohler et al. (1995)
w	Observed lifespan	25	yr	Natanson et al. (2002)
t_{max}	Theoretical lifespan (7 half lives)	79	yr	This document
	Sex ratio at birth	1:1	dimensionless	Jensen et al. (2002)
BF	Breeding frequency	1 or 2	yr	Natanson et al. (2019)
m_x	Constant litter size	4	pups	Jensen et al. (2002)
GP	Gestation period	9	months	Jensen et al. (2002)

Values in parentheses are SEs.

Table 2. Biological input values used in computing population dynamics parameter of interest for a South Atlantic population of porbeagle.

Parameter	Definition	Value	Unit	References
L_{∞}	Theoretical maximum length	210.86 (9.62)	cm FL	Francis (2015)
		214	cm PCL	Morinobu (1996)
K	Brody growth coefficient	0.086 (0.012)	yr ⁻¹	Francis (2015)
		0.082	yr ⁻¹	Morinobu (1996)
t_0	Theoretical age at zero length	-6.10 (0.665)	yr	Francis (2015)
		-4.43	yr	Morinobu (1996)
a	Intercept of maturity ogive	-10.2899 (1.679)	dimensionless	Jensen et al. (2002), Natanson (pers. comm.) ¹
b	Slope of maturity ogive	0.7299 (0.118)	dimensionless	Jensen et al. (2002), Natanson (pers. comm.) ¹
e	Scalar coefficient of weight on length	3.556E-05	dimensionless	Morinobu (1996)
f	Power coefficient of weight on length	2.894	dimensionless	Morinobu (1996)
w	Observed lifespan (from vertebrae)	25	yr	Francis (2015)
		19	yr	Morinobu (1996)
t_{max}	Lifespan (from bomb radiocarbon)	65	yr	Francis et al. (2007)
	Theoretical lifespan (7 half lives)	59	yr	This document ²
	Sex ratio at birth	1:1	dimensionless	Francis and Stevens (2000)
BF	Breeding frequency	1 or 2?	yr	Francis and Stevens (2000)
m_x	Constant litter size	3.74	pups	Francis (unpublished data)
GP	Gestation period	8-9	months	Francis and Stevens (2000)
Values in parentheses are SEs.				
¹ Values used are from the western North Atlantic because the maturity ogive predicts a median age at maturity (14.1) very similar to the mid-point of those reported in Francis (2015) for the South Pacific (14.6 years)				
² using Morinobu's K value				

Table 3. Estimates of productivity (r_{max}) for the western North Atlantic population of porbeagle obtained through six methods.

	BF = 1 year	BF= 2 years	BF= 1.5 years
Euler-Lotka / Leslie matrix	0.078 (0.49)	0.039 (0.32)	0.055 (0.32)
Au et al. (2016)	0.050	0.050	0.050
Eberhardt et al. (1982)	0.074	0.036	0.052
Skalski et al. (2008)	0.088	0.055	0.068
Neil and Lebreton's (2005) DIM*	0.045	0.045	0.045
Mean	0.067	0.045	0.045
BF=breeding frequency			
Values in parentheses are steepness			
*DIM=Demographically Invariant Method			

Table 4. Productivity (r_{max}), generation time (\bar{A}), net reproductive rate (R_0), 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 through a Leslie matrix for the western North Atlantic population of porbeagle shark under different assumptions for breeding frequency (BF). LCL and UCL are approximate lower and upper confidence limits computed as the 2.5th and 97.5th percentiles.

	BF = 1 year			BF = 2 years			BF = 1.5 years		
	Median	LCL	UCL	Median	LCL	UCL	Median	LCL	UCL
r_{max}	0.080	0.057	0.101	0.045	0.022	0.067	0.059	0.037	0.081
Generation time	19.3	17.0	20.4	20.8	17.6	22.0	20.1	17.3	21.3
Net reproductive rate (R_0)	5.321	3.037	9.339	2.641	1.524	4.745	3.533	2.040	6.288
Age-0 survivorship (S_0)	0.91	0.89	0.93	0.91	0.89	0.93	0.91	0.89	0.93
Alpha hat	4.86	2.72	8.69	2.41	1.37	4.42	3.22	1.84	5.84
Steepness (h)	0.55	0.40	0.68	0.38	0.26	0.52	0.45	0.31	0.59
SPR_{MER}	0.45	0.34	0.61	0.64	0.48	0.85	0.56	0.41	0.74
R	0.55	0.51	0.62	0.65	0.57	0.79	0.60	0.54	0.70

Table 5. Estimates of productivity (r_{max}) for the South Atlantic population of porbeagle obtained through six methods.

	Max age=25 yr	Max age=65 yr	Max age=25 yr	Max age=65 yr	Max age=25 yr	Max age=65 yr
	BF = 1 year	BF = 1 year	BF= 2 years	BF= 2 years	BF= 1.5 years	BF= 1.5 years
Euler-Lotka / Leslie matrix	0.043 (0.33)	0.059 (0.45)	0.005 (0.20)	0.026 (0.29)	0.021 (0.25)	0.040 (0.35)
Au et al. (2016)	0.054	0.053	0.054	0.053	0.054	0.053
Eberhardt et al. (1982)	0.053	0.059	0.021	0.027	0.034	0.040
Skalski et al. (2008)	0.036	0.059	-0.001	0.027	0.015	0.040
Neil and Lebreton's (2005) DIM*	0.046	0.046	0.046	0.046	0.046	0.046
Mean	0.046	0.055	0.025	0.036	0.034	0.044
BF=breeding frequency						
Values in parentheses are steepness						
*DIM=Demographically Invariant Method						

Table 6. Productivity (r_{max}), generation time (\bar{A}), net reproductive rate (R_0), 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 through a Leslie matrix for the South Atlantic population of porbeagle shark under different assumptions for breeding frequency (BF). LCL and UCL are approximate lower and upper confidence limits computed as the 2.5th and 97.5th percentiles. Red font indicates parameter estimates were out of bounds ($R_0 < 1$; $\alpha_{hat} < 1$; steepness < 0.2 ; $SPR_{MER} > 1$; $R > 1$).

	BF = 1 year			BF = 2 years			BF = 1.5 years		
	Median	LCL	UCL	Median	LCL	UCL	Median	LCL	UCL
r_{max}	0.038	0.002	0.075	0.004	-0.033	0.040	0.018	-0.018	0.054
Generation time	19.2	16.9	20.4	20.6	17.4	22.0	20.0	17.2	21.3
Net reproductive rate (R_0)	2.123	1.041	4.762	1.068	0.516	2.379	1.440	0.695	3.133
Age-0 survivorship (S_0)	0.88	0.85	0.91	0.88	0.85	0.91	0.88	0.85	0.91
Alpha hat	1.86	0.88	4.33	0.94	0.44	2.16	1.27	0.59	2.85
Steepness (h)	0.32	0.18	0.52	0.19	0.10	0.35	0.24	0.13	0.42
SPR_{MER}	0.73	0.48	1.06	1.03	0.68	1.51	0.89	0.59	1.30
R	0.69	0.57	1.01	0.87	0.65	1.45	0.79	0.62	1.27

Life-history invariant methods used to estimate natural mortality

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:

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

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

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

Method 5 — Peterson and Wroblewski (1984) mass-based estimator:

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

where W is weight in g.

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. (1998):

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

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 $r_{max}T=a_r a_T=a_{rT}$. 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:

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

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:

$$\mathbf{A} = \begin{pmatrix} \mathbf{F}_1 & \mathbf{F}_2 & \mathbf{F}_3 & \dots & \mathbf{F}_{n-1} & \mathbf{F}_n \\ \mathbf{P}_1 & \mathbf{0} & \mathbf{0} & \dots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{P}_2 & \mathbf{0} & \dots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{P}_3 & \dots & \mathbf{0} & \mathbf{0} \\ \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \dots & \mathbf{P}_{n-1} & \mathbf{0} \end{pmatrix}$$

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.

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