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Estimates of vital rates and population dynamics parameters of interest for hammerhead sharks (*Sphyrna lewini, S. mokarran, and S. zygaena*) in the western North Atlantic Ocean

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ABSTRACT

Estimates of vital rates and population dynamics parameters of the western North Atlantic populations of scalloped (Gulf of Mexico, Atlantic, and both areas combined), great, and smooth hammerhead sharks for use as inputs into production and integrated stock assessment models were computed based on biological information provided in the SEDAR 77 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), spawning potential ratio at maximum excess recruitment (SPR_{MER}), position of the inflection point of population growth curves (R), and natural mortality (M). Seven methods were used to compute deterministic estimates of r_{max}: five 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, fecundity, natural mortality, and lifespan.

- For scalloped hammerhead (Gulf of Mexico and South Atlantic combined), productivity ($r_{\max}$) from the seven deterministic methods ranged from 0.039 to 0.099 yr^{-1} (mean = 0.080) and the stochastic Leslie matrix yielded a median $r_{\max}$ = 0.104 yr^{-1} (95% CI = 0.039 – 0.189), $\overline{A}$ = 20.1 years (95% CI = 10.0 – 74.0), h = 0.69 (95% CI = 0.44 – 0.87), SPR_{MER} = 0.33 (95% CI = 0.19– 0.56), R = 0.48 (95% CI = 0.33 – 0.60), and M = 0.117 (95% CI = 0.092 – 0.164)
- For scalloped hammerhead (Gulf of Mexico), $r_{\max}$ from the seven deterministic methods ranged from 0.043 to 0.122 yr^{-1} (mean = 0.095) and the stochastic Leslie matrix yielded a median $r_{\max}$ = 0.107 yr^{-1} (95% CI = 0.029 – 0.217), $\overline{A}$ = 20.1 years (95% CI = 9.3 – 80.3), h = 0.71 (95% CI = 0.37 – 0.89), SPR_{MER} = 0.32 (95% CI = 0.18– 0.65), R = 0.48 (95% CI = 0.33 – 0.65), and M = 0.109 (95% CI = 0.099 – 0.167)
- For scalloped hammerhead (Atlantic), $r_{\max}$ from the seven deterministic methods ranged from 0.039 to 0.096 yr^{-1} (mean = 0.078) and the stochastic Leslie matrix yielded a median $r_{\max}$ = 0.101 yr^{-1} (95% CI = 0.036 – 0.190), $\overline{A}$ = 20.0 years (95% CI = 8.7 – 73.8), h = 0.67 (95% CI = 0.41 – 0.86), SPR_{MER} = 0.35 (95% CI = 0.20– 0.60), R = 0.49 (95% CI = 0.34 – 0.62), and M = 0.114 (95% CI = 0.083 – 0.162)

- For great hammerhead, $r_{\max}$ from the seven deterministic methods ranged from 0.080 to 0.186 yr^{-1} (mean = 0.136) and the stochastic Leslie matrix yielded a median $r_{\max}$ = 0.146 yr^{-1} (95% CI = 0.059 – 0.199), $\overline{A}$ = 14.5 years (95% CI = 12.7 – 60.7), h = 0.71 (95% CI = 0.46 – 0.87), SPR_{MER} = 0.32 (95% CI = 0.20– 0.53), R = 0.48 (95% CI = 0.30 – 0.57), and M = 0.156 (95% CI = 0.080 – 0.206)
- For smooth hammerhead, $r_{\max}$ from the seven deterministic methods ranged from 0.063 to 0.154 yr^{-1} (mean = 0.120) and the stochastic Leslie matrix yielded a median $r_{\max}$ = 0.182 yr^{-1} (95% CI = 0.139 – 0.423), $\overline{A}$ = 13.0 years (95% CI = 3.4 – 35.5), h = 0.78 (95% CI = 0.66 – 0.88), SPR_{MER} = 0.27 (95% CI = 0.19– 0.36), R = 0.48 (95% CI = 0.33 – 0.56), and M = 0.129 (95% CI = 0.081 – 0.138)

The estimates of r_{max} and of the position of the inflection point of the production curve (R) can be used to generate priors for production models, the estimates of generation time can help identify the time horizon for projections, and the estimates of steepness and natural mortality can also be used as fixed parameter values or priors in Stock Synthesis.

KEYWORDS

Productivity, Steepness, Lifespan, Generation time, SPR, Hammerhead sharks

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 can then used to obtain the inflection point. 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} and R 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

Inputs

Life history inputs were obtained from Tables 1, 3, and 4 of the HMS Hammerhead Sharks Data Workshop Life History (section 2) report (relevant values reproduced here in Tables 1 to 5). All values are for females.

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:

$$M_L = M_r \frac{L_r}{L} \tag{1}$$

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:

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

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

$$\widehat{t_{max}} = \frac{1}{k}\ln((L_\infty - L_0)/((1-0.99)L_\infty) \quad (3)$$

with 0.99 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):

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

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 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 equations listed in Tables 1-5. Lifespan was set equal to the maximum "observed" age obtained from ageing vertebrae or, alternatively, as the theoretical age corresponding to when 99% of L_∞ is reached (equation 3; see Tables 1-5).

Modeling and outputs

Maximum population growth rate ($r_{\max}$) was estimated with seven methods. Five methods were age-aggregated modifications of the Euler-Lotka equation (Eberhardt et al. (1982); Skalski et al. (2008); Pardo et al. (2016); 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=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), 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 99% of L_∞ is reached. Litter size was assigned a truncated normal distribution, with mean and SD and lower and upper bounds reflecting the minimum and maximum observed litter sizes. 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.

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 $R = 0.633 - 0.187 \times \ln(r_{\max} \times \bar{A})$ 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. All models were run in R (R Core Team 2021, version 4.1.2).

3. Results

Scalloped hammerhead (GOM and ATL combined)—The age-specific deterministic estimates of M obtained from the Dureuil et al. (2021) method ranged from 0.353 yr^{-1} for age 0 sharks to 0.065 yr^{-1} for a maximum theoretical age of 51 years (Table 6). Estimated productivity ranged from $r_{\max}$ = 0.039 yr^{-1} for the DIM method to 0.099 yr^{-1} for three of the other methods (Eberhardt et al. (1982), Skalski et al. (2008), and Pardo et al. (2016); Table 7).

The median estimate of M from the six mortality estimators used in the Leslie matrix stochastic analyses was 0.117 yr^{-1} (95% CI = 0.092 – 0.164), median $r_{\max}$ = 0.104 yr^{-1} (95% CI = 0.039 – 0.089), $\bar{A}$ = 20.1 years (95% CI = 10.0 – 74.0), h = 0.69 (95% CI = 0.44 – 0.87), SPR_{MER} = 0.33 (95% CI = 0.19– 0.56), and R = 0.48 (95% CI = 0.33 – 0.60) (Table 8A).

A lognormal distribution was fitted to the values of $r_{\max}$ obtained from the stochastic simulation yielding a back-transformed mean=0.099 and SD=0.435 (Fig. 1 top). Similarly, a normal distribution was fitted to the R values yielding a mean=0.479 and SD=0.063 (Fig. 1 bottom).

Scalloped hammerhead (GOM)—The values of the SEs of the intercept and slope of the age-based maturity ogive in the SEDAR 77 DW report were extremely high (SE(a)=62741.45 and SE(b)=4967.34). To address this, the same CV for these parameters used in the scalloped hammerhead analysis for areas combined (~32% for a and b) were applied to the scalloped hammerhead (GOM) analysis, yielding SE values of 17.71 for a and 1.28 for b.

The age-specific deterministic estimates of M obtained from the Dureuil et al. (2021) method ranged from 0.345 yr^{-1} for age 0 sharks to 0.064 yr^{-1} for a maximum theoretical age of 52 years

(Table 6). Estimated productivity ranged from $r_{max} = 0.043$ yr^{-1} for the DIM method to 0.122 yr^{-1} for the Pardo et al. (2016) method (Table 7).

The median estimate of M from the six mortality estimators used in the Leslie matrix stochastic analyses was 0.109 yr^{-1} (95% CI = 0.099 – 0.167), median $r_{max} = 0.107$ yr^{-1} (95% CI = 0.029 – 0.217), $\overline{A} = 20.1$ years (95% CI = 9.3 –80.3), $h = 0.71$ (95% CI = 0.37 – 0.89), $SPR_{MER} = 0.32$ (95% CI = 0.18– 0.65), and $R = 0.48$ (95% CI = 0.33 – 0.65) (Table 8B).

A lognormal distribution was fitted to the values of r_{max} obtained from the stochastic simulation yielding a back-transformed mean=0.097 and SD=0.598 (Fig. 2 top). Similarly, a normal distribution was fitted to the R values yielding a mean=0.485 and SD=0.080 (Fig. 2 bottom).

Scalloped hammerhead (ATL)—The age-specific deterministic estimates of M obtained from the Dureuil et al. (2021) method ranged from 0.364 yr^{-1} for age 0 sharks to 0.068 yr^{-1} for a maximum theoretical age of 50 years (Table 6). Estimated productivity ranged from $r_{max} = 0.039$ yr^{-1} for the DIM method to 0.096 yr^{-1} for two of the other methods (Eberhardt et al. (1982) and Skalski et al. (2008); Table 7).

The median estimate of M from the six mortality estimators used in the Leslie matrix stochastic analyses was 0.114 yr^{-1} (95% CI = 0.083 – 0.162), median $r_{max} = 0.101$ yr^{-1} (95% CI = 0.036 – 0.190), $\overline{A} = 20.0$ years (95% CI = 8.7 – 73.8), $h = 0.67$ (95% CI = 0.41 – 0.86), $SPR_{MER} = 0.35$ (95% CI = 0.20– 0.60), and $R = 0.49$ (95% CI = 0.34 – 0.62) (Table 8C).

A lognormal distribution was fitted to the values of r_{max} obtained from the stochastic simulation yielding a back-transformed mean=0.096 and SD=0.454 (Fig. 3 top). Similarly, a normal distribution was fitted to the R values yielding a mean=0.486 and SD=0.068 (Fig. 3 bottom).

Great hammerhead—The age-specific deterministic estimates of M obtained from the Dureuil et al. (2021) method ranged from 0.418 yr^{-1} for age 0 sharks to 0.086 yr^{-1} for a maximum theoretical age of 40 years (Table 6). Estimated productivity ranged from $r_{max} = 0.067$ yr^{-1} for the DIM method to 0.186 yr^{-1} for the Pardo et al. (2016) method; Table 7).

The median estimate of M from the six mortality estimators used in the Leslie matrix stochastic analyses was 0.156 yr^{-1} (95% CI = 0.080 – 0.206), median $r_{max} = 0.146$ yr^{-1} (95% CI = 0.059 – 0.199), $\overline{A} = 14.5$ years (95% CI = 12.7 – 60.7), $h = 0.71$ (95% CI = 0.46 – 0.87), $SPR_{MER} = 0.32$ (95% CI = 0.20– 0.53), and $R = 0.48$ (95% CI = 0.30 – 0.57) (Table 8D).

A normal distribution was fitted to the values of r_{max} obtained from the stochastic simulation yielding a mean=0.144 and SD=0.036 (Fig. 4 top). Similarly, a normal distribution was fitted to the R values yielding a mean=0.467 and SD=0.102 (Fig. 4 bottom).

Smooth hammerhead—There were no SEs available for the von Bertalanffy growth curve parameters from the Rosa et al. (2017) study listed in the SEDAR 77 DW report. To address this, the same CVs for these parameters used in the scalloped hammerhead analysis for areas combined (~2.37% for L_∞, 5.81% for K, and 4.68% for t_0) were applied to the smooth hammerhead analysis, yielding SE values of 6.96, 0.005, and 0.103 for L_∞, K, and t_0, respectively. Rosa et al. (2017) reported a value of L_0=52.7 cm FL, which was converted to t_0 through the von Bertalanffy growth curve. Additionally, there was no maturity ogive available for smooth hammerhead so the intercept and slope were approximated iteratively by finding values that yielded a median age at maturity of 10.5 years for females, as listed in the SEDAR 77 DW report. SEs for *a* and *b* were also obtained by applying the CVs for these parameters used in the scalloped hammerhead analysis for areas combined (~32% for *a* and *b*). Finally, the correlation matrices for growth and maturity parameters used in the scalloped hammerhead analysis for areas combined were used for smooth hammerhead.

The age-specific deterministic estimates of *M* obtained from the Dureuil et al. (2021) method ranged from 0.378 yr^{-1} for age 0 sharks to 0.069 yr^{-1} for a maximum theoretical age of 49 years (Table 6). Estimated productivity ranged from r_{max} = 0.053 yr^{-1} for the DIM method to 0.154 yr^{-1} for the Pardo et al. (2016) method and the Euler-Lotka and Leslie matrix methods (Table 7).

The median estimate of *M* from the six mortality estimators used in the Leslie matrix stochastic analyses was 0.129 yr^{-1} (95% CI = 0.081 – 0.138), median r_{max} = 0.182 yr^{-1} (95% CI = 0.139 – 0.423), $\overline{A}$ = 13.0 years (95% CI = 3.4 – 35.5), h = 0.78 (95% CI = 0.66 – 0.88), SPR_{MER} = 0.27 (95% CI = 0.19– 0.36), and R = 0.48 (95% CI = 0.33 – 0.56) (Table 8E).

A lognormal distribution was fitted to the values of r_{max} obtained from the stochastic simulation yielding a back-transformed mean=0.192 and SD=0.291 (Fig. 5 top). Similarly, a normal distribution was fitted to the R values yielding a mean=0.462 and SD=0.060 (Fig. 5 bottom).

4. Discussion

The median estimates of r_{max} obtained through Monte Carlo simulation of a Leslie matrix were similar to the corresponding deterministic estimates also obtained with a Leslie matrix/Euler-Lotka equation approach, especially for the scalloped hammerhead stocks, despite the fact that the deterministic estimates relied on age-specific natural mortality values obtained from the Dureuil et al. (2021) method and the stochastic estimates used six other alternative methods to estimate *M*. The mean r_{max} from the seven deterministic estimates fell within the 95% confidence intervals of the stochastic method, with the exception of smooth hammerhead, probably due to larger uncertainty for this stock.

The median estimates of R ranged from 0.476 to 0.491 and the corresponding values of the shape parameter, n (where $R = n^{-\frac{1}{n-1}}$), ranged from 1.77 to 1.91 so were very close to those of a Schaefer model (R=0.5 and n=2). The means of the distributions fitted to r_{max} and R were very close to the median values of these parameters obtained in the Monte Carlo simulation.

The median steepness values obtained for the different hammerhead stocks were rather high, ranging from 0.67 to 0.78. 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. The high values of steepness for hammerhead sharks can be explained by the combination of the relatively low age-0 mortality and the elevated lifetime reproductive rate for these fecund stocks.

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Table 1. Biological input values for females used to compute r_{max}, steepness, and other parameters of interest for scalloped hammerhead (GOM+ATL combined).

Parameter	Definition	Value	Unit	References
L_{∞}	Theoretical maximum length	229.2 (5.44)	cm FL	DW report life history section
K	Brody growth coefficient	0.086 (0.005)	yr^{-1}	DW report life history section
t_0	Theoretical age at zero length	-2.352 (0.11)	yr	DW report life history section
a	Intercept of maturity ogive	-11.979 (3.80)	dimensionless	DW report life history section
b	Slope of maturity ogive	0.744 (0.24)	dimensionless	DW report life history section
c	Scalar coefficient of weight on length	5.774E-06	dimensionless	DW report life history section
d	Power coefficient of weight on length	3.128	dimensionless	DW report life history section
w	Observed lifespan	29.5	yr	DW report life history section
	Theoretical lifespan (99% of Linf)	51.2	yr	DW report life history section
	Sex ratio at birth	1:1	dimensionless	DW report life history section
	Reproductive cycle	annual	yr	DW report life history section
mx	Constant litter size	18.0 (SD=7.67; 7-30)	pups per litter	DW report life history section
e	Intercept of maternal age vs. fecundity	n/a	dimensionless	DW report life history section
f	Slope of maternal age vs. fecundity	n/a	dimensionless	DW report life history section
GP	Gestation period	11	months	DW report life history section

Values in parentheses are SEs.

Table 2. Biological input values for females used to compute r_{max}, steepness, and other parameters of interest for scalloped hammerhead (GOM).

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length	234.5 (12.89)	cm FL	DW report life history section
K	Brody growth coefficient	0.084 (0.009)	yr^{-1}	DW report life history section
t_0	Theoretical age at zero length	-2.407 (0.17)	yr	DW report life history section
a	Intercept of maturity ogive	-55.68 (62741.55)	dimensionless	DW report life history section
b	Slope of maturity ogive	4.009 (4967.34)	dimensionless	DW report life history section
c	Scalar coefficient of weight on length	5.774E-06	dimensionless	DW report life history section
d	Power coefficient of weight on length	3.128	dimensionless	DW report life history section
w	Observed lifespan	24.5	yr	DW report life history section
	Theoretical lifespan (99% of Linf)	52.4	yr	DW report life history section
	Sex ratio at birth	1:1	dimensionless	DW report life history section
	Reproductive cycle	annual	yr	DW report life history section
mx	Constant litter size	18.0 (SD=7.67; 7-30)	pups per litter	DW report life history section
e	Intercept of maternal age vs. fecundity	n/a	dimensionless	DW report life history section
f	Slope of maternal age vs. fecundity	n/a	dimensionless	DW report life history section
GP	Gestation period	11	months	DW report life history section

Values in parentheses are SEs.

Table 3. Biological input values for females used to compute $r_{\max}$, steepness, and other parameters of interest for scalloped hammerhead (ATL).

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length	225.8 (6.33)	cm FL	DW report life history section
K	Brody growth coefficient	0.089 (0.006)	yr^{-1}	DW report life history section
t_0	Theoretical age at zero length	-2.29 (0.14)	yr	DW report life history section
a	Intercept of maturity ogive	-11.652 (3.84)	dimensionless	DW report life history section
b	Slope of maturity ogive	0.721 (0.25)	dimensionless	DW report life history section
c	Scalar coefficient of weight on length	5.774E-06	dimensionless	DW report life history section
d	Power coefficient of weight on length	3.128	dimensionless	DW report life history section
w	Observed lifespan	29.5	yr	DW report life history section
	Theoretical lifespan (99% of Linf)	49.5	yr	DW report life history section
	Sex ratio at birth	1:1	dimensionless	DW report life history section
	Reproductive cycle	annual	yr	DW report life history section
mx	Constant litter size	18.0 (SD=7.67; 7-30)	pups per litter	DW report life history section
e	Intercept of maternal age vs. fecundity	n/a	dimensionless	DW report life history section
f	Slope of maternal age vs. fecundity	n/a	dimensionless	DW report life history section
GP	Gestation period	11	months	DW report life history section

Values in parentheses are SEs.

Table 4. Biological input values for females used to compute r_{max}, steepness, and other parameters of interest for great hammerhead.

Parameter	Definition	Value	Unit	References
L_{∞}	Theoretical maximum length	323.9 (7.49)	cm FL	DW report life history section
K	Brody growth coefficient	0.11 (0.011)	yr^{-1}	DW report life history section
t_0	Theoretical age at zero length	-2.06 (0.20)	yr	DW report life history section
a	Intercept of maturity ogive	-7.569 (2.67)	dimensionless	DW report life history section
b	Slope of maturity ogive	0.937 (0.32)	dimensionless	DW report life history section
c	Scalar coefficient of weight on length	9.275E-06	dimensionless	DW report life history section
d	Power coefficient of weight on length	3.028	dimensionless	DW report life history section
w	Observed lifespan	35	yr	DW report life history section
	Theoretical lifespan (99% of Linf)	40	yr	DW report life history section
	Sex ratio at birth	1:1	dimensionless	DW report life history section
	Reproductive cycle	biennial	yr	DW report life history section
mx	Constant litter size	30.93 (SD=10.74; 13-56)	pups per litter	DW report life history section
e	Intercept of maternal length vs. fecundity	-67.9565	dimensionless	DW report life history section
f	Slope of maternal length vs. fecundity	0.3453	dimensionless	DW report life history section
GP	Gestation period	12	months	DW report life history section

Values in parentheses are SEs.

Table 5. Biological input values for females used to compute r_{max}, steepness, and other parameters of interest for smooth hammerhead.

Parameter	Definition	Value	Unit	References
L_∞	Theoretical maximum length	293.9	cm FL	DW report life history section
K	Brody growth coefficient	0.09	yr^{-1}	DW report life history section
t_0	Theoretical age at zero length	-2.195*	yr	DW report life history section
a	Intercept of maturity ogive	n/a	dimensionless	DW report life history section
b	Slope of maturity ogive	n/a	dimensionless	DW report life history section
c	Scalar coefficient of weight on length	2.000E-06	dimensionless	DW report life history section
d	Power coefficient of weight on length	3.329	dimensionless	DW report life history section
w	Observed lifespan	25	yr	DW report life history section
	Theoretical lifespan (99% of Linf)	49	yr	DW report life history section
	Sex ratio at birth	1:1	dimensionless	DW report life history section
	Reproductive cycle	biennial	yr	DW report life history section
mx	Constant litter size	33.5	pups per litter	DW report life history section
e	Intercept of maternal length vs. fecundity	n/a	dimensionless	DW report life history section
f	Slope of maternal length vs. fecundity	n/a	dimensionless	DW report life history section
GP	Gestation period	11	months	DW report life history section

* Obtained from an L_0 of 52.7 cm FL.

Table 6. 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}.

	M				
Age	Scalloped hammerhead (GOM +ATL)	Scalloped hammerhead (GOM)	Scalloped hammerhead (ATL)	Great hammerhead	Smooth hammerhead
0	0.353	0.345	0.364	0.418	0.378
1	0.258	0.254	0.265	0.296	0.271
2	0.207	0.204	0.212	0.235	0.216
3	0.175	0.173	0.179	0.199	0.182
4	0.154	0.152	0.157	0.174	0.159
5	0.138	0.136	0.141	0.157	0.142
6	0.126	0.125	0.129	0.144	0.130
7	0.117	0.116	0.119	0.134	0.121
8	0.110	0.108	0.112	0.127	0.113
9	0.104	0.102	0.106	0.120	0.107
10	0.099	0.098	0.101	0.115	0.102
11	0.095	0.093	0.097	0.111	0.098
12	0.091	0.090	0.093	0.108	0.094
13	0.088	0.087	0.090	0.105	0.091
14	0.086	0.084	0.088	0.102	0.088
15	0.084	0.082	0.086	0.100	0.086
16	0.082	0.080	0.084	0.098	0.084
17	0.080	0.078	0.082	0.097	0.083
18	0.078	0.077	0.080	0.095	0.081
19	0.077	0.076	0.079	0.094	0.080
20	0.076	0.074	0.078	0.093	0.078
21	0.075	0.073	0.077	0.092	0.077
22	0.074	0.072	0.076	0.091	0.077
23	0.073	0.072	0.075	0.090	0.076
24	0.072	0.071	0.074	0.090	0.075
25	0.072	0.070	0.074	0.089	0.074
26	0.071	0.070	0.073	0.089	0.074
27	0.070	0.069	0.073	0.088	0.073
28	0.070	0.068	0.072	0.088	0.073
29	0.069	0.068	0.072	0.088	0.072
30	0.069	0.068	0.071	0.087	0.072
31	0.069	0.067	0.071	0.087	0.071
32	0.068	0.067	0.070	0.087	0.071
33	0.068	0.067	0.070	0.087	0.071
34	0.068	0.066	0.070	0.086	0.071
35	0.067	0.066	0.070	0.086	0.070
36	0.067	0.066	0.069	0.086	0.070
37	0.067	0.066	0.069	0.086	0.070
38	0.067	0.065	0.069	0.086	0.070
39	0.067	0.065	0.069	0.086	0.070
40	0.066	0.065	0.069	0.086	0.069
41	0.066	0.065	0.069		0.069
42	0.066	0.065	0.068		0.069
43	0.066	0.065	0.068		0.069
44	0.066	0.064	0.068		0.069
45	0.066	0.064	0.068		0.069
46	0.066	0.064	0.068		0.069
47	0.066	0.064	0.068		0.069
48	0.066	0.064	0.068		0.069
49	0.066	0.064	0.068		0.069
50	0.065	0.064	0.068		
51	0.065	0.064			
52		0.064			

Table 7. Estimates of productivity (r_{max}) obtained through seven methods.

	Stock				
Method	Scalloped hammerhead (GOM +ATL)	Scalloped hammerhead (GOM)	Scalloped hammerhead (ATL)	Great hammerhead	Smooth hammerhead
Eberhardt et al. (1982)	0.099	0.120	0.096	0.177	0.149
Skalski et al. (2008)	0.099	0.120	0.096	0.177	0.149
Au et al. (2016)	0.048	0.052	0.048	0.080	0.063
Neil and Lebreton's (2005) DIM*	0.039	0.043	0.039	0.067	0.053
Euler-Lotka/Leslie matrix	0.098	0.114	0.095	0.131	0.154
Pardo et al. (2016)	0.099	0.122	0.095	0.186	0.154
Mean	0.080	0.095	0.078	0.136	0.120

Table 8. 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}), 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 different stocks of hammerhead sharks. LCL and UCL are approximate lower and upper confidence limits computed as the 2.5th and 97.5th percentiles. "Deterministic" shows the results obtained with a life table/Leslie matrix using the Dureuil et al. (2021) method to estimate M at age.

A) Scalloped hammerhead (GOM and ATL combined)

	Median	LCL	UCL	Deterministic
r_{max}	0.104	0.039	0.189	0.098
Generation time	20.1	10.0	74.0	21.8
Net reproductive rate (R_0)	10.732	3.656	29.320	10.769
Age-0 survivorship (S_0)	0.88	0.68	0.92	0.70
Steepness (h)	0.69	0.44	0.87	0.65
SPR_{MER}	0.33	0.19	0.56	0.36
R (inflection point)	0.483	0.335	0.597	0.47
M	0.117	0.092	0.164	0.091

B) Scalloped hammerhead (GOM)

	Median	LCL	UCL	Deterministic
r_{max}	0.107	0.029	0.217	0.114
Generation time	20.1	9.3	80.3	20.2
Net reproductive rate (R_0)	11.341	2.734	34.351	13.286
Age-0 survivorship (S_0)	0.89	0.68	0.93	0.71
Steepness (h)	0.71	0.37	0.89	0.70
SPR_{MER}	0.32	0.18	0.65	0.33
R (inflection point)	0.479	0.332	0.648	0.46
M	0.109	0.099	0.167	0.089

C) Scalloped hammerhead (ATL)

	Median	LCL	UCL	Deterministic
r_{max}	0.101	0.036	0.190	0.095
Generation time	20.0	8.7	73.8	21.8
Net reproductive rate (R_0)	9.873	3.239	27.213	9.804
Age-0 survivorship (S_0)	0.88	0.68	0.92	0.70
Steepness (h)	0.67	0.41	0.86	0.63
SPR_{MER}	0.35	0.20	0.60	0.38
R (inflection point)	0.491	0.340	0.617	0.48
M	0.114	0.083	0.162	0.094

Table 8 (continued).

D) Great hammerhead

	Median	LCL	UCL	Deterministic
r_{max}	0.146	0.059	0.199	0.131
Generation time	14.5	12.7	60.7	14.8
Net reproductive rate (R_0)	11.193	4.053	33.844	9.553
Age-0 survivorship (S_0)	0.85	0.76	0.90	0.66
Steepness (h)	0.71	0.46	0.87	0.61
SPR_{MER}	0.32	0.20	0.53	0.40
R (inflection point)	0.476	0.296	0.571	0.48
M	0.156	0.080	0.206	0.117

E) Smooth hammerhead

	Median	LCL	UCL	Deterministic
r_{max}	0.182	0.139	0.423	0.154
Generation time	13.0	3.4	35.5	14.1
Net reproductive rate (R_0)	15.850	9.209	34.783	13.940
Age-0 survivorship (S_0)	0.87	0.71	0.91	0.69
Steepness (h)	0.78	0.66	0.88	0.70
SPR_{MER}	0.27	0.19	0.36	0.32
R (inflection point)	0.476	0.327	0.559	0.45
M	0.129	0.081	0.138	0.095

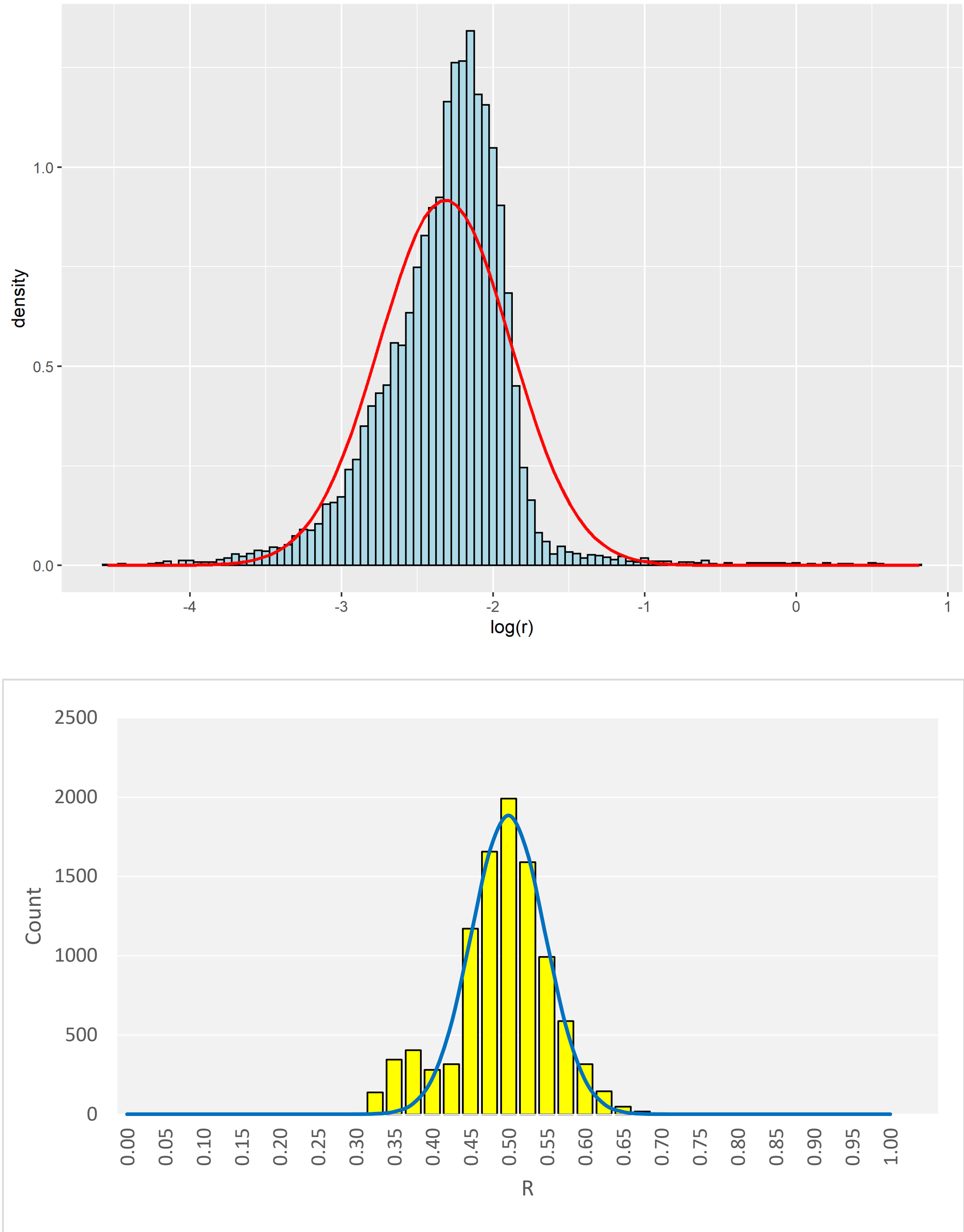
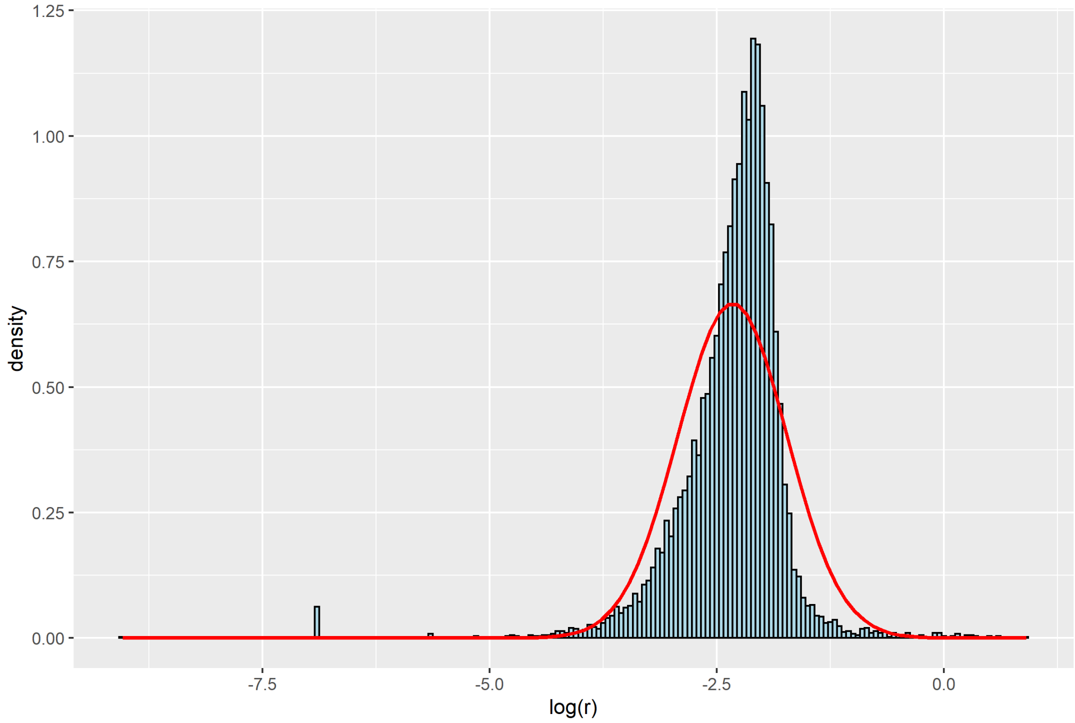


Figure 1. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted lognormal distribution for r_{max} and normal distribution for R for scalloped hammerhead (GOM and ATL combined).



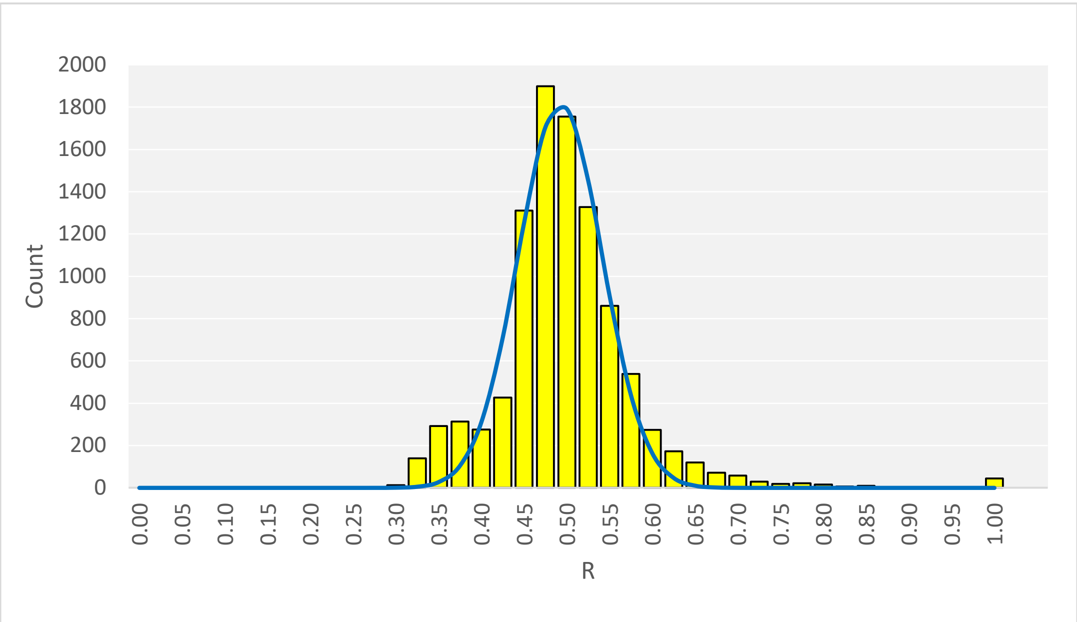
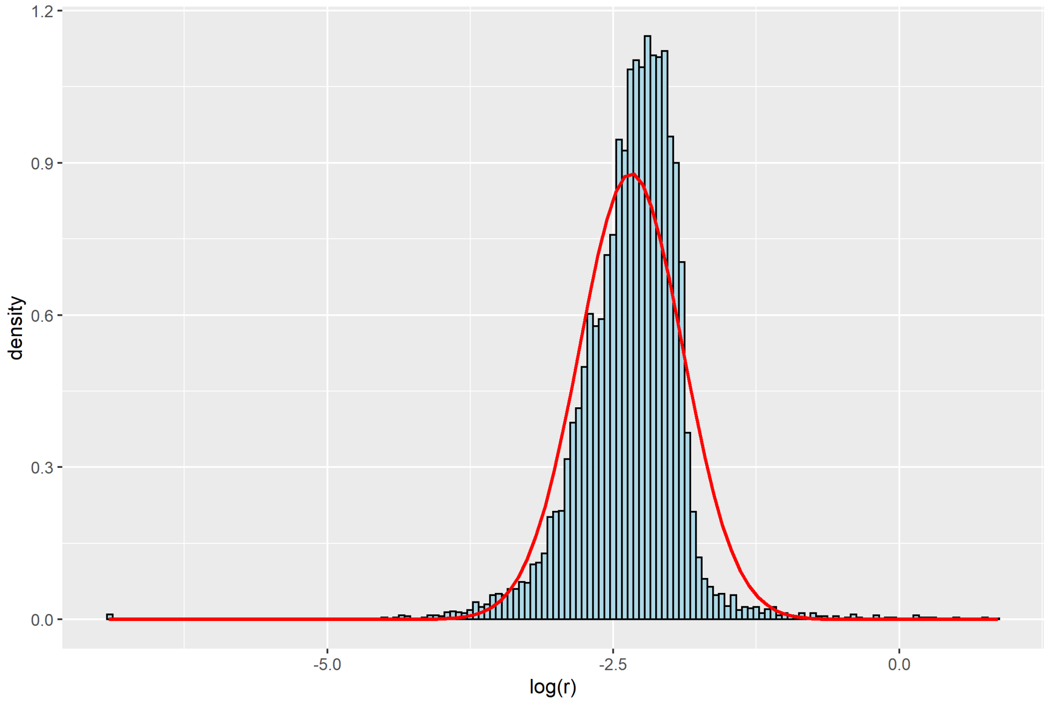


Figure 2. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted lognormal distribution for r_{max} and normal distribution for R for scalloped hammerhead (GOM).



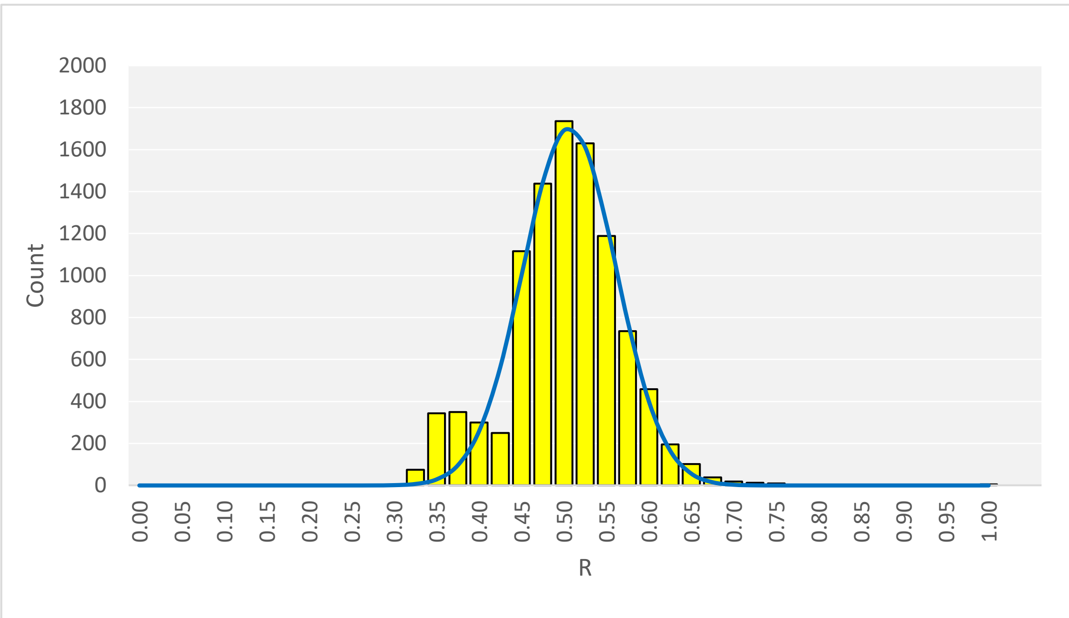
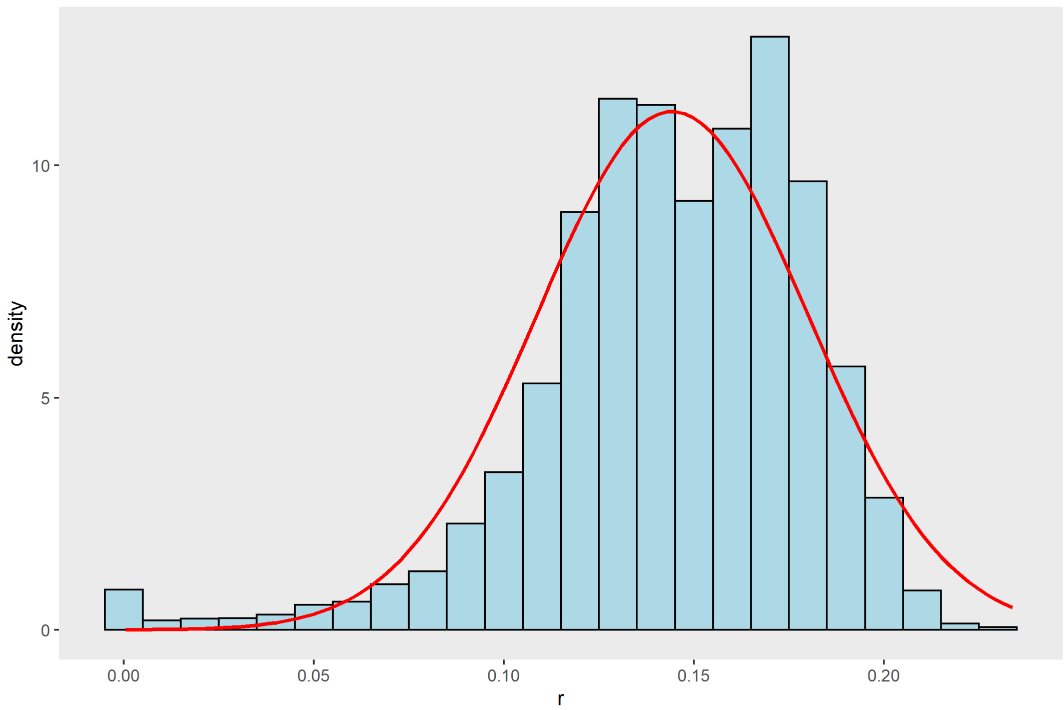


Figure 3. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted lognormal distribution for r_{max} and normal distribution for R for scalloped hammerhead (ATL).



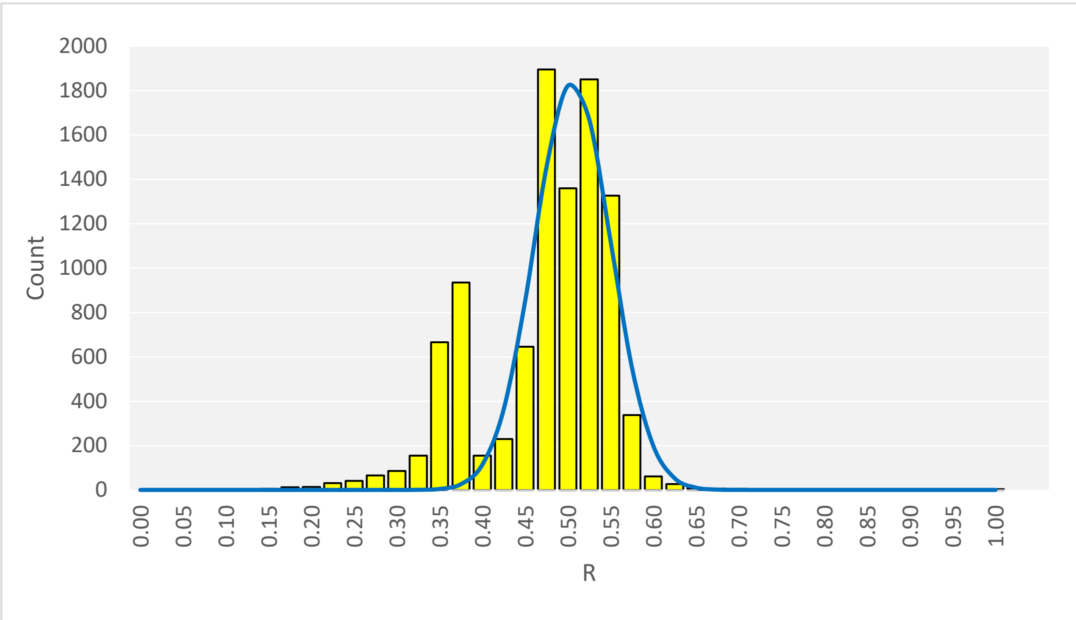
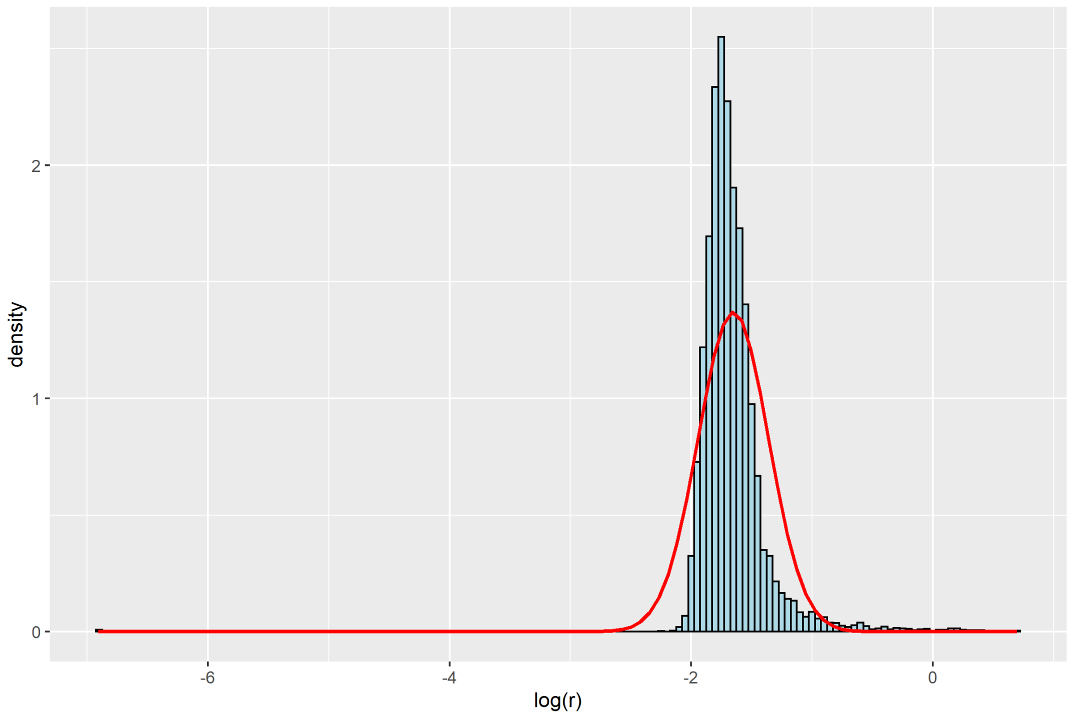


Figure 4. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted normal distribution for r_{max} and normal distribution for R for great hammerhead.



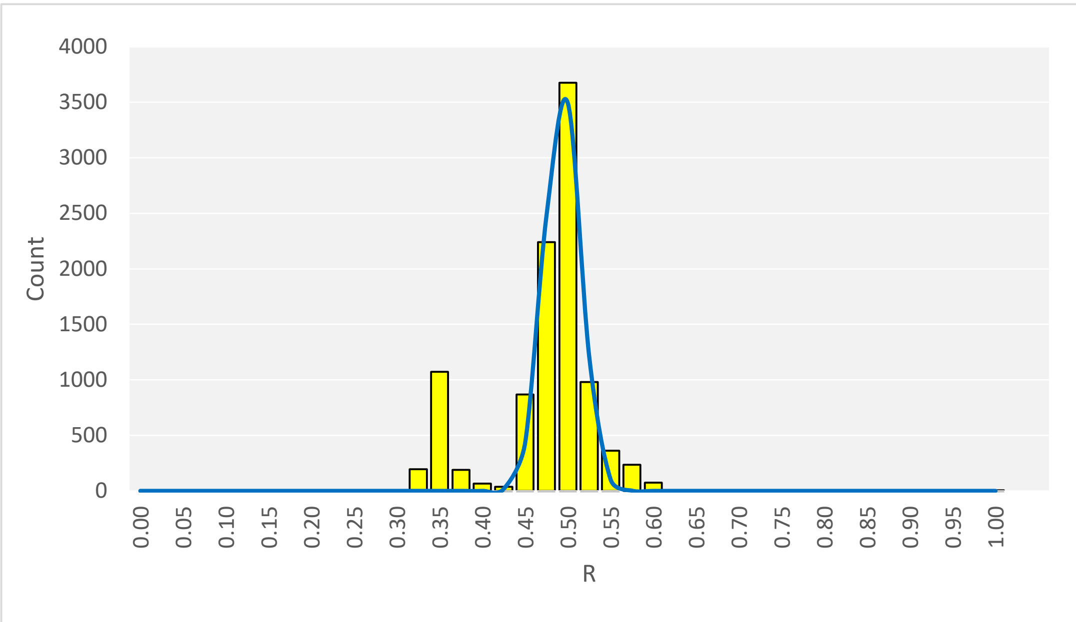


Figure 5. Distribution of simulated r_{max} (top) and R (bottom) values obtained from a Leslie matrix approach with fitted lognormal distribution for r_{max} and normal distribution for R for smooth hammerhead.

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 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.

Appendix Table 1. 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
Pardo et al. (2016)	Yes	No	Constant	Constant	Yes

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 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 $r_{\max}=a_rM^{-0.25}$ 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:

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

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:

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

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.

Method 7 — Pardo et al. (2016):

Pardo et al. (2016) developed an identical equation to that previously published by Skalski et al. (2008), only differing in that they defined *a* as age at maturity, not age at first breeding:

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