

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

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SUMMARY

Vital rates and population dynamics parameters for use as inputs in stock assessment models were computed for the western North Atlantic population of porbeagle based on published biological information. Population dynamics parameters included maximum population growth rate (r_{max}), generation time (\bar{A}), steepness of the Beverton-Holt stock-recruitment relationship (h), position of the inflection point of population growth curves (R), and spawning potential ratio at maximum excess recruitment (SPR_{MER}). I used multiple methods to compute r_{max} : four age-aggregated methods and two age-structured methods. I used a Leslie matrix approach to incorporate uncertainty in growth parameters, maturity ogive, natural mortality, and lifespan. Productivity (r_{max}) was 0.046-0.059 yr⁻¹ for the six deterministic methods. For the stochastic Leslie matrix, mean values were: $r_{max} = 0.051$ yr⁻¹ (IQR=0.034 – 0.068), $h = 0.36$ (IQR=0.29 – 0.43), $R = 0.66$ (IQR=0.61 – 0.73), $\bar{A} = 16.9$ years (IQR=16.2 – 17.3), and $SPR_{MER} = 0.68$ (IQR=0.58– 0.79). These estimates can be used to formulate informative priors in production and age-structured/integrated stock assessment models, to inform the time horizon for projections in all models, and for potential use in data-limited stock assessment approaches.

RÉSUMÉ

Les taux vitaux et les paramètres de dynamique de population à utiliser comme données d'entrée dans les modèles d'évaluation des stocks ont été calculés pour la population de requin-taube commun de l'Atlantique Nord-Ouest sur la base des informations biologiques publiées. Les paramètres de dynamique de la population comprenaient le taux de croissance maximal de la population (r_{max}), le temps de génération (\bar{A}), l'inclinaison de la pente à l'origine de la relation stock-recrutement de Beverton-Holt (h), la position du point d'inflexion des courbes de croissance de la population (R) et le ratio du potentiel reproducteur au recrutement excédentaire maximum (SPR_{MER}). Plusieurs méthodes ont été utilisées pour calculer r_{max} : quatre méthodes agrégées par âge et deux méthodes structurées par âge. Une approche de matrice de Leslie a été employée pour intégrer l'incertitude dans les paramètres de croissance, l'ogive de maturité, la mortalité naturelle et la durée de vie. La productivité (r_{max}) était de 0,046-0,059 an⁻¹ pour les six méthodes déterministes. Les valeurs moyennes de la matrice de Leslie stochastique étaient: $r_{max} = 0,051$ an⁻¹ (IQR = 0,034 - 0,068), $h = 0,36$ (IQR = 0,29 - 0,43), $R = 0,66$ (IQR = 0,61 - 0,73), $\bar{A} = 16,9$ ans (IQR = 16,2 - 17,3) et $SPR_{MER} = 0,68$ (IQR = 0,58 à 0,79). Ces estimations peuvent être utilisées pour formuler des priors informatifs dans les modèles d'évaluation des stocks intégrés de production et structurés par âge, pour éclairer l'horizon temporel des projections dans tous les modèles et pour une utilisation potentielle dans les approches d'évaluation des stocks à données limitées.

RESUMEN

Las tasas vitales y los parámetros de dinámica de población para su uso como valores de entrada en los modelos de evaluación de stocks se calcularon para la población del Atlántico noroccidental de marrajo sardinero sobre la base de la información biológica publicada. Los parámetros de dinámica población incluyen la tasa máxima de crecimiento de la población

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(r_{max}), el tiempo de generación (\bar{A}), la pendiente de la relación stock-reclutamiento de Beverton-Holt (h), la posición del punto de inflexión de las curvas de crecimiento de la población (R), y la ratio potencial de desove en el máximo excedente de reclutamiento (SPR_{MER}). Se han utilizado varios métodos para calcular r_{max} : cuatro métodos agregados por edad y dos métodos estructurados por edad. Se utilizó un enfoque de matriz de Leslie para incorporar la incertidumbre en los parámetros de crecimiento, ojiva de madurez, mortalidad natural y tiempo de vida. La productividad (r_{max}) fue 0,046-0,059 yr^{-1} para los seis métodos deterministas. Para la matriz estocástica Leslie, los valores medios fueron: $r_{max} = 0,051$ yr^{-1} ($IQR=0,034 - 0,068$), $h = 0,36$ ($IQR=0,29 - 0,43$), $R = 0,66$ ($IQR=0,61 - 0,73$), $\bar{A} = 16,9$ años ($IQR=16,2 - 17,3$), y $SPR_{MER} = 0,68$ ($IQR=0,58 - 0,79$). Estas estimaciones se pueden utilizar para formular distribuciones previas informativas en los modelos de evaluación de stocks estructurados por edad/integrados y de producción, para aportar información al horizonte temporal de las proyecciones en todos los modelos y para su posible uso en enfoques de evaluación de stocks con datos limitados.

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). Finally, the spawning potential ratio at maximum excess recruitment (SPR_{MER} ; Goodyear 1980) is yet another measure of stock resilience, with the closer the %SPR is to 100%, the less exploitation the stock can sustain (Brooks et al. 2010).

The purpose of this paper was to generate values of: r_{max} to use in constructing informative priors of r_{max} in production models; R to compute the shape parameter in generalized production models; \bar{A} for use in stock projections; h to use in age-structured/integrated stock assessment models (e.g. Stock Synthesis), and SPR_{MER} for potential use in data-limited stock assessment approaches (e.g., Cortés and Brooks 2018).

2. Materials and methods

Inputs

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) and recently published data (**Table 1**). All values are for females.

I 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). Newly published information showing a resting period for the western North Atlantic population, which is indicative of a biennial cycle, was incorporated 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.

Annual survival at age (obtained from the instantaneous natural mortality rate at age as e^{-M}) was obtained through multiple 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), the mass-based estimator of Lorenzen (1996), and the Chen and Watanabe (1989) estimator (see Kenchington 2013 and references therein for details). Note that the first four estimators provide a constant value of mortality, whereas the last two provide size- and age-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**).

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 1**).

Uncertainty was introduced in the Leslie matrix approach through Monte Carlo simulation by randomly selecting vital rates/parameters from predefined statistical distributions (n=100,000). The quantities varied were the parameters from the von Bertalanffy growth function (VBGF; L_{inf} , K , t_0), intercept and slope parameters from the maturity ogive at age (a , b), age at maturity, lifespan, and survivorship at age. The parameter estimates from the VBGF and the maturity ogive were assigned a multivariate normal distribution with a vector of means and a covariance matrix to take into account covariance among parameters. Because the original studies of age and growth and reproduction did not report parameter correlations, the data used to fit the models originally were obtained from the authors and the models re-fit to obtain correlation matrices. Lifespan was given a uniform distribution with the lower bound set equal to "observed" longevity from vertebral ageing (25 years) and the upper bound set to a theoretical seven half-lives ($7 \cdot \log(2)/K$). 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.

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 P_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 CoreTeam 2019).

3. Results and discussion

Estimated productivity ranged from $r_{max}=0.046$ to 0.059 yr^{-1} for the six deterministic methods. For the stochastic Leslie matrix method, mean r_{max} was 0.051 yr^{-1} (IQR=0.034 – 0.068), mean h was 0.36 (IQR=0.29 to 0.43), mean R was 0.66 (IQR=0.61-0.73), mean \bar{A} was 16.9 years (IQR=16.2 to 17.3), and mean SPR_{MER} was 0.68 (IQR=0.58-0.79) (**Table 2**). 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} can also be used potentially in data-limited stock assessment approaches. If new life history information becomes available, input values can be easily changed.

References

- Au, D.W., Smith, S.E., and Show, C. (2008). Shark productivity and reproductive protection, and a comparison with teleosts. In: Camhi, M.D., Pikitch, E.K., and Babcock, E.A. (Eds.), *Sharks of the Open Ocean*. Blackwell Publishing, Oxford, pp. 298–308.
- Brooks, E.N, J.E. Powers, and E. Cortés. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. *ICES J. Mar. Sci.* 67:165-175.
- Cortes, E., and E.N. Brooks. 2018. Stock status and reference points for sharks using data-limited methods and life history. *Fish and Fisheries* 19:1110-1129.
- Cortes, E., and CAILLIET, GM. 2019. Generation time. (pp 381-383) In (B. Fath, ed.) *Encyclopedia of Ecology*, 2nd ed. Vol. 3.
- Dillingham, P.W. 2010. Generation time and the maximum growth rate for populations with age-specific fecundities and unknown juvenile survival. *Ecol. Model.* 221: 895–899.
- Eberhardt, L.L., Majorowicz, A.K. & Wilcox, J.A. 1982. Apparent rates of increase for two feral horse herds. *J. Wildlife Management* 46: 367–374.
- Fletcher, R.I. 1978. Time-dependent solutions and efficient parameters for stock-production models. *Fish. Bull.* 76:377-388.
- Fowler, C. W. 1988. Population dynamics as related to rate of increase per generation. *Evol. Ecol.* 2: 197-204.
- Goodyear, C. P. 1980. Compensation in fish populations. In *Biological Monitoring of Fish*, pp. 253–280. Ed. by C. H. Hocutt, and J. R. Stauffer. Lexington Books, D. C. Heath and Co, Lexington, MA.
- Hoening, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 82:898–903.
- Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* 53:820–822.
- Jensen, C.F., L.J. Natanson, H.L. Pratt Jr., N. E. Kohler, and S. E. Campana. 2002. The reproductive biology of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fish. Bull.* 100:727–738.
- Kenchington, T.J. 2014. Natural mortality estimators for information-limited fisheries. *Fish and Fisheries* 15:533-562.
- Kohler, N. E., J.G. Casey, and P.A. Turner. 1995. Length-weight relationships for 13 species of sharks from the western North Atlantic. *Fish. Bull.* 93:412–418.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J. Fish. Biol.* 49: 627–647.
- Mangel, M., A.D. MacCall, J. Brodziak, E.J. Dick, R. E. Forrest, R. Pourzand, and S. Ralston. 2013. A perspective on steepness, reference points, and stock assessment. *Can. J. Fish. Aquat. Sci* 70:930-940.
- Myers, R.A., G. Mertz, and P.S. Fowlow. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. *Fish. Bull.* 95:762–772.
- Myers, R.A., K.G. Bowen, and N.J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. *Can J. Fish. Aquat. Sci.* 56:2404–2419.
- Natanson, L. J., J. J. Mello, and S. E. Campana. 2002. Validated age and growth of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. *Fish. Bull.* 100:266–278.

- Natanson, L.J., B.M. Deacy, W. Joyce, and J. Sulikowski. 2019. Presence of a resting population of female porbeagles (*Lamna nasus*), indicating a biennial reproductive cycle, in the western North Atlantic Ocean. *Fish. Bull.* 117: 70-77.
- Niel, C. and Lebreton, J.D. 2005. Using demographic invariants to detect overharvested bird populations from incomplete data. *Cons. Biol.* 19: 826–835.
- Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer* 39:175–192.
- Pella, J.J., and Tomlinson, P.K. (1969). A generalized stock production model. *Inter-Am. Trop. Tuna Comm. Bull.* 13:419–496.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Inter American Tropical Tuna Commission Bulletin* 2:247–285.
- Skalski, J.R, Millsbaugh, J.J. & Ryding, K.E. (2008) Effects of asymptotic and maximum age estimates on calculated rates of population change. *Ecol. Model.* 212: 528–535.
- Smith, S.E., Au, D.W., and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Mar. Freshwater Res.* 49: 663–678.
- Then, A.Y., J.M. Hoenig, N.G. Hall, and D.A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES J. Mar. Sci.* 72: 82-92.

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

Parameter	Definition	Value	Unit	References
L_{∞}	Theoretical maximum length	309.8	cm FL	Natanson et al. (2002)
K	Brody growth coefficient	0.061	yr ⁻¹	Natanson et al. (2002)
t_0	Theoretical age at zero length	-5.9	yr	Natanson et al. (2002)
a	Intercept of maturity ogive	-14.3072	dimensionless	Jensen et al. (2002)
b	Slope of maturity ogive	1.0951	dimensionless	Jensen et al. (2002)
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	Lifespan	25	yr	Natanson et al. (2002)
	Sex ratio at birth	1:1	dimensionless	Jensen et al. (2002)
	Reproductive cycle	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)

Table 2. Productivity (r_{max}), generation time (\bar{A}), 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 for the western North Atlantic population of porbeagle shark. LCL and UCL are approximate lower and upper confidence limits computed as the 2.5th and 97.5th percentiles.

	Mean	LCL	UCL
r_{max}	0.051	0.034	0.068
Generation time	16.9	16.2	17.3
Net reproductive rate	2.421	1.768	3.225
Age-0 survivorship	0.923	0.908	0.937
Steepness	0.36	0.29	0.43
SPR_{MER}	0.68	0.58	0.79
R	0.66	0.61	0.73

Life-history invariant methods used to estimate natural mortality

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:

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

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:

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

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