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ESTIMATES OF MAXIMUM POPULATION GROWTH RATE AND STEEPNESS FOR SHORTFIN MAKOS IN THE NORTH AND SOUTH ATLANTIC OCEAN

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SUMMARY

Maximum population growth rates and steepness values of the Beverton-Holt stock-recruitment relationship were computed for North and South Atlantic stocks of shortfin mako (Isurus oxyrinchus) *based on biological information provided at the 2017 Shortfin Mako Data Preparatory meeting and soon thereafter. I used a dual life table/Leslie matrix approach to obtain estimates of the intrinsic rate of increase (r_{max}), net reproductive rate (R_0), generation time (μ_1), and derived steepness (h) analytically. To encompass a plausible range of biological values, different assumptions on growth, reproduction, and natural mortality were considered. Estimated productivity ranged from r_{max}=0.031 to 0.060 yr^{-1} for the North Atlantic stock and from r_{max}=0.066 to 0.123 yr^{-1} for the South Atlantic stock and steepness ranged from h=0.34 to 0.52 for the North Atlantic stock and h=0.44 to 0.72 for the South Atlantic stock. These estimates can be used to formulate informative priors of r_{max} and h in production and age-structured stock assessment models, respectively.*

RÉSUMÉ

Les taux de croissance maximale de la population et les valeurs de la pente à l'origine de la relation stock-recrutement de Beverton-Holt ont été calculés pour les stocks de l'Atlantique Nord et Sud du requin-taupe bleu (Isurus oxyrinchus) reposant sur les informations biologiques fournies lors de la réunion de préparation des données sur le requin-taupe bleu de 2017, et peu de temps après celle-ci. Une double approche de tableau du cycle vital et de matrice de Leslie a été appliquée afin d'obtenir des estimations du taux intrinsèque d'augmentation (r_{max}), du taux net de reproduction (R0), du temps de génération ((μ_1) et de la pente dérivée (h) analytiquement. Dans le but d'englober une gamme plausible de valeurs biologiques, différentes hypothèses sur la croissance, la reproduction et la mortalité naturelle ont été prises en considération. La productivité estimée variait de r_{max} = 0,031 à 0,060 an-1 pour le stock de l'Atlantique Nord et de r_{max} = 0,066 à 0,123 an-1 pour le stock de l'Atlantique Sud et l'inclinaison variait de h = 0,34 à 0,52 pour le stock de l'Atlantique Nord et de h = 0,44 à 0,72 pour le stock de l'Atlantique Sud. Ces estimations peuvent être utilisées pour formuler des priors informatifs de r_{max} et de h dans des modèles d'évaluation des stocks structurés par âge et de production, respectivement.

RESUMEN

*Se calcularon las tasas de crecimiento máximo de la población y los valores de la inclinación de la relación stock reclutamiento de Beverton-Holt para los stocks del Atlántico norte y sur de marrajo dientuso (*Isurus oxyrinchus*) basándose en la información biológica presentada en la reunión de preparación de datos de marrajo dientuso de 2017 y posteriormente. Se utilizó un enfoque dual de matriz de Leslie/tabla vital para obtener de forma analítica estimaciones de la tasa intrínseca de crecimiento (r_{max}), de la tasa reproductiva neta (R0), del tiempo de generación (μ_1), y de la inclinación derivada (h). Para abarcar un rango probable de valores biológicos, se consideraron diferentes supuestos sobre crecimiento, reproducción y mortalidad natural. La productividad estimada oscilaba entre r_{max}=0,031 a 0,060 yr-1 para el stock del Atlántico norte y entre r_{max}=0,066 a 0,123 yr-1 para el stock del Atlántico sur, y la inclinación oscilaba entre h=0,34 a 0,52 para el stock del Atlántico norte y h=0,44 a 0,72 para el stock del Atlántico sur. Estas estimaciones pueden utilizarse para formular distribuciones previas informativas de r_{max} y h en los modelos de evaluación de stock de producción y estructurados por edad, respectivamente.*

KEYWORDS

Natural mortality, Life history, Longevity, Sexual maturity, Shortfin mako

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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). 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 purpose of this paper was to generate values of r_{max} to use in constructing priors of this parameter in surplus production models of shortfin mako stocks in the North and South Atlantic Ocean, and values of *h* for use in the age-structured stock assessment model, SS3 (Methot 2013), for the North Atlantic shortfin mako stock.

2. Materials and Methods

Life history inputs were obtained from the data assembled at the 2017 Shortfin Mako Data Preparatory meeting (see Table 9 of report) and some additional data obtained after the meeting (**Table 1**). The specific values used in this paper are listed in **Table 2** and **Table 3**. All values refer to females.

North Atlantic stock—I used growth function parameters from SCRS/2017/111 and Natanson *et al.* (2006). Parameters from Natanson *et al.* (2006) were both from a Gompertz and a von Bertalanffy growth curve, although these authors indicated that the Gompertz curve provided the most biologically reasonable estimates. Parameters from the maturity ogive presented in Mollet *et al.* (2000; their Figure 4) were not reported in that publication but were obtained from the first author. A two-year time lapse was assumed to account for some time (6 months) for the females to mate after they become mature and gestate (18 months) before they can contribute offspring to the population.

Fecundity at age was obtained from the power female size to litter size relationship in Mollet *et al.* (2000) or, alternatively, was set to a constant value of 12.5 (Mollet *et al.* 2000). A 1:1 female to male ratio at birth and a triennial reproductive cycle were further used and litter size was divided by two to account for female pups only.

Annual survival at age was obtained through five life history invariant methods: Jensen's (1996) *K*-based estimator, 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 estimators from Peterson and Wroblewski (1984) and Lorenzen (1996) (see Kenchington 2013 and references therein for details). Note that the first three estimators provide a constant value of mortality, whereas the last two provide 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.* (1993). Lifespan (ω) was set at 32 years (Natanson *et al.* 2006) (**Table 2**).

South Atlantic stock—von Bertalanffy growth function parameters from two separate studies were used: Barreto *et al.* (2016) and Doño *et al.* (2015), both from the Southwest Atlantic. Parameters from the maturity ogive presented in Mollet *et al.* (2000; their Figure 4) were not reported in that publication and were also obtained from the first author as for the North Atlantic. However, as the use of that ogive with the available growth functions resulted in implausible maturity schedules and negative growth rates, maturity was alternatively assumed to be knife-edged at an age at maturity (α) of 12 (or 18) years, i.e. zero for ages 0 to $\alpha-1$, 0.5 for α, and 1 for ages $\alpha+1$. As for the North Atlantic, a two-year time lapse was assumed to account for some time (6 months) for the females to mate after they become mature and gestate (18 months) before they can contribute offspring to the population.

Fecundity at age was obtained using the same values as for the North Atlantic as Mollet *et al.* (2000) reported these parameters for the whole Atlantic. Annual survival at age was also derived in the same way as for the North Atlantic. Conversions of length into weight were done using the power equation from Garcia-Cortés and Mejuto (2002). Lifespan (ω) was set at 23 years (Barreto *et al.* 2016) or 28 years (Doño *et al.* 2015) (**Table 3**).

Modeling - Maximum population growth rate (r_{max}) was estimated with an age-structured life table (by iteratively solving the Euler-Lotka equation) and an age-structured Leslie matrix (Leslie 1945; Caswell 2001) 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. Both approaches yield identical results. In addition, the net reproductive rate (R_0), which is also virgin spawners per recruit, and μ_1, generation time defined as the mean age of parents of offspring produced by a cohort over its lifetime, were computed in the life table approach. Steepness was then computed as $h = \frac{\hat{\alpha}}{4 + \hat{\alpha}}$ where $\hat{\alpha}$ is the maximum lifetime reproductive rate (Myers *et al.* 1997, 1999), which in turn is the product of R_0 and p_0 (Brooks *et al.* 2010).

3. Results and discussion

Productivity ranged from 0.031 to 0.060 yr^{-1} for the North Atlantic stock and from 0.066 to 0.123 yr^{-1} for the South Atlantic stock; steepness ranged from 0.34 to 0.52 for the North Atlantic stock and from 0.44 to 0.72 for the South Atlantic stock; and generation time ranged from 25 to 26 years for the North Atlantic stock and from 18 to 21 for the South Atlantic stock (**Table 4**).

For the North Atlantic, considering a constant vs. increasing fecundity with age had little effect on results. Using the Gompertz growth function from Natanson *et al.* (2006) produced lower estimates than using their von Bertalanffy growth function, and using the von Bertalanffy growth function from SCRS/2017/111, which includes more data than those used by Natanson *et al.* (2006), yielded lower estimates. For the South Atlantic, considering a constant vs. increasing fecundity with age had a considerable effect on results, probably because of the use of the knife-edge maturity, and using the growth function from Barreto *et al.* (2016) or Doño *et al.* (2015) impacted results much less.

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Table 1. Life history parameters for shortfin mako (North and South) stocks. The table is an update of Table 9 in the Data Preparatory meeting report.

	NA	SA	References
Reproduction			
L_{mat} (♂)		180	Mas et al. (2017) [SCRS]
L_{50} (♂)	180-185 FL	166	Natanson et al. (2006) Maia et al. (2006) Mas et al. (2017) [SCRS]
T_{mat} (♂)	8	6-8*	Campana et al. (2005) Barreto et al. (2016) Doño et al. (2015)
T_{50} (♂)	8		Natanson et al. (2006)
L_{mat} (♀)			
L_{50} (♀)	275-298 FL		Mollet et al. (2000), Natanson et al. (2006)
T_{mat} (♀)	18	12-18*	Campana et al. (2005) Barreto et al. (2016) Doño et al. (2015)
T_{50} (♀)	18		Natanson et al. (2006)
Sex ratio	1:1		Mollet et al. (2000)
Cycle	3		Mollet et al. (2000)
GP (months)	16.5 (15-18)		Mollet et al. (2000)
L_0	70 FL-63 FL	81M-88F (FL)*	Natanson et al. (2006) Mollet et al. (2000) Doño et al. (2015)
Mean litter size (LS)	12.5		Mollet et al. 2000 (n=24)
Min LS	2		Mollet et al. 2000 (n=24)
Max LS	30		Mollet et al. 2000 (n=24)
LS vs MS relation	LS=0.81*TL^2.346		Mollet et al. 2000 (n=24)
Maturity ogive (♀)	Mat=1/(1+exp-(-27.81+9.332*MS))	Use fit to clasper index (♂)	Mollet et al. 2000 (n=24); SCRS/2017/058
Age & Growth			
L_{inf} (♀)	366 (393) [350.6]**	244*; 408	Natanson et al. (2006) Doño et al. (2015) Barreto et al. (2016)
k (♀)	0.087 (0.054) [0.064]**	0.04	Natanson et al. (2006) Barreto et al. (2016)
T_o / L_o (♀)	88.4 (70 fixed) [63] **	-7.08	Natanson et al. (2006) Barreto et al. (2016)
T_{max} (♀)	32	23-28*	Natanson et al. (2006) Barreto et al. (2016) Doño et al. (2015)
L_{inf} (♂)	253 ***	261*; 329	Natanson et al. (2006) Doño et al. (2015) Barreto et al. (2016)
k (♂)	0.125	0.08	Natanson et al. (2006) Barreto et al. (2016)
T_o / L_o (♂)	71.6	-4.47	Natanson et al. (2006) Barreto et al. (2016)
T_{max} (♂)	29	11-18*	Natanson et al. (2006) Doño et al. (2015) Barreto et al. (2016)
Conversion Factors			
Length-length [cm]	FL=0.9286TL-1.7101	TL=1.127FL+0.358	Megalofonou et al. (2005) Kohler (1995)
	W=5.2432E-06FL^3.1407	W=3.1142E-05FL^2.7243	Kohler (1995) García-Cortes & Mejuto (2002)
Length-weight (b) [cm,kg]		HG=7.5443x10^{-6}x (FL ^{2,9568})****	Mas et al. (2017) [SCRS]

* Derived with the Schnute model; ** Gompertz (VBGF in parentheses) [Coelho et al. VBGF in brackets]; *** VBGF with Lo; **** HG is eviscerated weight

Table 2. Biological input values used in computing r_{max} and steepness with life tables/Leslie matrices for the North Atlantic shortfin mako stock.

		Growth curve				
Parameter	Definition	VB	Gompertz	VB	Unit	References
		Natanson et al. (2006)	Natanson et al. (2006)	SCRS/2017/111		
L_∞	Theoretical maximum length	393	366	350.6	cm FL	
K	Brody growth coefficient	0.054	0.087	0.064	yr^{-1}	
L_0	Length at birth	70	88.4	63	cm FL	
a	Intercept of maturity ogive	-27.81			dimensionless	Mollet et al. (2000) and Mollet (pers.comm.)
b	Slope of maturity ogive	9.332			dimensionless	Mollet et al. (2000) and Mollet (pers.comm.)
c	Slope of TL to FL length relationship	0.929			dimensionless	Kohler et al. (1995)
d	Intercept of TL to FL length relationship	1.7101			dimensionless	Kohler et al. (1995)
e	Scalar coefficient of weight on length	5.243E-06			dimensionless	Kohler et al. (1995)
f	Power coefficient of weight on length	3.1407			dimensionless	Kohler et al. (1995)
ω	Lifespan	32			yr	Natanson et al. (2006)
	Sex ratio at birth	1:1			dimensionless	Mollet et al. (2000)
	Reproductive cycle	3			yr	Mollet et al. (2000)
m_x	Constant litter size	12.5			pups	Mollet et al. (2000)
g	Scalar coefficient of litter size on TL	0.810			dimensionless	Mollet et al. (2000)
h	Power coefficient of litter size on TL	2.346			dimensionless	Mollet et al. (2000)

Table 3. Biological input values used in computing r_{max} and steepness with life tables/Leslie matrices for the South Atlantic shortfin mako stock.

		Growth curve				
Parameter	Definition	VB	VB		Unit	References
		Barreto et al. (2016)	Doño et al. (2015)			
L_{∞}	Theoretical maximum length	407.7	416		cm FL	
K	Brody growth coefficient	0.04	0.035		yr^{-1}	
t_0	Age at zero length	-7	-6.18		yr	
a	Intercept of maturity ogive	-53.13			dimensionless	Mollet et al. (2000) and Mollet (pers.comm.)
b	Slope of maturity ogive	19.46			dimensionless	Mollet et al. (2000) and Mollet (pers.comm.)
	Median age for knife-edge maturity	12	18			Barreto et al. (2016) and Doño et al. (2015)
c	Slope of TL to FL length relationship	1.127			dimensionless	Kohler et al. (1995)
d	Intercept of TL to FL length relationship	0.358			dimensionless	Kohler et al. (1995)
e	Scalar coefficient of weight on length	3.114E-05			dimensionless	Garcia-Cortes and Mejuto (2002)
f	Power coefficient of weight on length	2.7243			dimensionless	Garcia-Cortes and Mejuto (2002)
ω	Lifespan	23 or 28			yr	Barreto et al. (2016) and Doño et al. (2015)
	Sex ratio at birth	1:1			dimensionless	Mollet et al. (2000)
	Reproductive cycle	3			yr	Mollet et al. (2000)
m_x	Constant litter size	12.5			pups	Mollet et al. (2000)
g	Scalar coefficient of litter size on TL	0.810			dimensionless	Mollet et al. (2000)
h	Power coefficient of litter size on TL	2.346			dimensionless	Mollet et al. (2000)

Table 4. Productivity (r_{max}), steepness (h), and generation time (μ_1) obtained with different assumptions on growth and reproduction for the North and South Atlantic stocks of shortfin mako (see text for details).

North Atlantic					
Growth curve	Fecundity	r_{max}	h	μ_1	
VBGF (Natanson et al. 2006)	length-based	0.060	0.519	25.8	
VBGF (Natanson et al. 2006)	constant	0.058	0.494	25.3	
Gompertz (Natanson et al. 2006)	length-based	0.038	0.371	25.6	
Gompertz (Natanson et al. 2006)	constant	0.034	0.347	25.1	
VBGF (SCRS/2017/111)	length-based	0.031	0.345	26.5	
VBGF (SCRS/2017/111)	constant	0.032	0.347	26.1	

South Atlantic					
Growth curve	Fecundity	Maturity	r_{max}	h	μ_1
VBGF(Barreto et al. 2016)	length-based	knife-edge	0.066	0.44	18.7
VBGF(Barreto et al. 2016)	constant	knife-edge	0.111	0.63	18.3
VBGF(Dono et al. 2015)	length-based	knife-edge	0.075	0.52	21.3
VBGF(Dono et al. 2015)	constant	knife-edge	0.123	0.72	20.4