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ESTIMATES OF MAXIMUM POPULATION GROWTH RATE AND STEEPNESS FOR BLUE SHARKS 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 blue shark (Prionace glauca) *based on the latest biological information available gathered at the 2015 Blue Shark Data Preparatory meeting. To encompass a plausible range of values, uncertainty in the estimates of life history inputs (reproductive age, lifespan, fecundity, von Bertalanffy growth parameters, and natural mortality) was incorporated through Monte Carlo simulation by assigning statistical distributions to those biological traits in a Leslie matrix approach. Estimated productivity was high (r_{max}=0.31-0.44 yr^{-1} for the North Atlantic stock; r_{max}=0.22-0.34 yr^{-1} for the South Atlantic stock) as previously found for these and other populations of this species. Consequently analytically derived values of steepness were also high (h=0.73-0.93 for the North Atlantic stock; h=0.55-0.84 for the South Atlantic stock). These estimates can be used as inputs into both surplus production (r_{max}) and age-structured (steepness) stock assessment models.*

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 peau bleue (Prionace glauca) *reposant sur les informations biologiques les plus récentes recueillies lors de la réunion de préparation des données sur le requin peau bleue de 2015. Afin d'inclure une gamme plausible de valeurs, l'incertitude entourant les estimations des entrées du cycle vital (âge de reproduction, durée de vie, fécondité, paramètres de croissance von Bertalanffy et mortalité naturelle) a été incorporée au moyen de la simulation Monte Carlo en attribuant des distributions statistiques aux caractéristiques biologiques dans une approche de matrice de Leslie. La productivité estimée était élevée (r_{max}=0,31-0,44 yr^{-1} pour le stock de l'Atlantique Nord ; r_{max}=0,22-0,34 yr^{-1} pour le stock de l'Atlantique Sud), comme cela avait été préalablement observé pour ces espèces et d'autres populations de cette espèce. Par conséquent, les valeurs de la steepness dérivées analytiquement étaient également élevées (h=0,73 - 0,93 pour le stock de l'Atlantique Nord ; h=0,55-0,84 pour le stock de l'Atlantique Sud). Ces estimations peuvent être utilisées comme données d'entrée dans les modèles d'évaluation des stocks de production excédentaire (r_{max}) et structuré par âge (steepness).*

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 tintorera (*Prionace glauca*) basándose en la última información biológica disponible reunida en la reunión de preparación de datos de tintorera de 2015. Para incluir un rango plausible de valores, se incorporó la incertidumbre en las estimaciones de los valores de entrada del ciclo vital (edad reproductiva, ciclo de vida, fecundidad, parámetros de crecimiento de von Bertalanffy y mortalidad natural) mediante una simulación Monte Carlo asignando distribuciones estadísticas a estas características biológicas en un enfoque de matriz de Leslie. La productividad estimada era elevada (r_{max}=0,31-0,44 yr^{-1} para el stock del Atlántico norte; r_{max}=0,22-0,34 yr^{-1} para el stock del Atlántico sur), como ya se había hallado para estas y otras poblaciones de esta especie. Por consiguiente, los valores de la inclinación analíticamente derivados eran también elevados (h=0,73-0,93 para el stock del Atlántico*

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norte; h=0,55-0,84 para el stock del Atlántico sur). Estas estimaciones pueden utilizarse como valores de entrada tanto en los modelos de producción excedente (r_{max}) como en los modelos de evaluación de stock estructurados por edad (inclinación).

KEYWORDS

Natural mortality, stochastic models, life history, longevity, sexual maturity, blue shark

1. Introduction

The maximum theoretical population growth rate or intrinsic rate of population change (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 blue shark 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 blue shark stock.

2. Materials and methods

Life history inputs were obtained from data first assembled at the 2014 Intersessional Meeting of the Shark Species Group (Anon. 2015) and additional information provided during the 2015 Blue Shark Data Preparatory meeting and thereafter (**Table 1**).

2.1 North Atlantic stock

Von Bertalanffy growth function parameters were from Skomal and Natanson (2003). The 95% confidence interval (CI) and sample size for parameter estimates reported by these authors were used to derive SDs for parameterizing lognormal distributions such that L_∞~LN(310.8,17.8), k~LN(0.13,0.015), and t_0~LN(-1.77,-0.26). Median age at maturity (α) was given a uniform distribution ranging from 5 to 7 years based on Skomal and Natanson (2003) and Stevens (1979). Since no maturity ogive was available, maturity was assumed to be knife-edged at the prescribed age at maturity, i.e. zero for ages 0 to $\alpha-1$, 0.5 for α, and 1 for ages $\alpha+1$. A one-year time lapse was allowed to account for the gestation period before females can contribute offspring to the population. Lifespan (ω) was also given a uniform distribution ranging from 15 to 17 years based on values reported by Skomal and Natanson (2003) for females and males.

Fecundity at age was assumed to follow a lognormal distribution with mean=39 (Mejuto and Garcia-Cortés 2005; data for North Atlantic) and SD taken from Castro and Mejuto (1995; ≈0.33mean for the right uterus), which yielded an SD≈13. In an alternative scenario, a litter size (LS) vs. maternal length (ML) relationship from Castro and Mejuto (1995) was used: LS=-91.97+0.6052ML (cm FL). A 1:1 female to male ratio at birth and an annual 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 six life history invariant methods: Jensen (1996) age at maturity-based estimator, a modified growth-based Pauly (1980) estimator (Then *et al*. 2015), a modified longevity-based Hoenig (1983) estimator (Then *et al*. 2015), the growth-based Chen and Watanabe (1989) estimator, and the weight-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 second three provide size-specific estimates, which are then transformed to age-specific estimates. Conversions of length into weight were done using the power equation from Kohler *et al*. (1993).

2.2 South Atlantic stock

Von Bertalanffy growth function parameters were available from three separate studies: Montealegre (2007) and Mas (2015) for the Southwest Atlantic, and Jolly *et al*. (2013) for the Southeast Atlantic. Given the range of estimates available, uniform distributions were used to parameterize L_∞, k, and t_0 such that L_∞~U(246,283), k~U(0.11,0.18), and t_0~U(-2.19,-1.55). Median age at maturity (α) was given a uniform distribution ranging from 5 to 7 years based on these studies and additionally a maternity ogive was available from Montealegre *et al*. (2014). Lifespan (ω) was also given a uniform distribution ranging from 12 to 16 years based on these studies.

Fecundity at age was assumed to follow a lognormal distribution with mean=33.5 and SD=12.5 (Montealegre *et al*. 2014). In an alternative scenario, a litter size (LS) vs. maternal length (ML) relationship from Montealegre *et al*. (2014) was used: LS=-54.547+0.4334ML (cm FL). A 1:1 female to male ratio at birth and an annual 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 six life history invariant methods: Jensen (1996) age at maturity-based estimator, a modified growth-based Pauly (1980) estimator (Then *et al*. 2015), a modified longevity-based Hoenig (1983) estimator (Then *et al*. 2015), the growth-based Chen and Watanabe (1989) estimator, and the weight-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 second three provide size-specific estimates, which are then transformed to age-specific estimates. Conversions of length into weight were done using the power equation from Montealegre and Vooren (2010).

2.3 Modeling

Maximum population growth rate (r_{max}) was estimated through an age-structured Leslie matrix approach (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. Uncertainty in life history variables (age at maturity, lifespan, age-specific fecundity and age-specific survival) was incorporated through Monte Carlo simulation by randomly drawing values from assumed statistical distributions for each of these variables. In addition, variability in the von Bertalanffy growth function used to describe growth of female blue sharks was introduced by drawing parameters L_∞, k, and t_0 from statistical distributions.

Steepness was computed as alpha_hat/4+alpha_hat, where alpha_hat is the maximum lifetime reproductive rate (Myers *et al*. 1997, 1999), which in turn is the product of R_0 (the net reproductive rate obtained from a life table or Leslie matrix) and p_0 (Brooks *et al*. 2010).

A total of 10,000 iterations were run and descriptive statistics for r_{max} and h computed, including the approximate 95% confidence intervals (expressed as the 2.5th and 97.5th percentiles). Including the variability in life history inputs described above, four stochastic scenarios were explored for each stock: 1) constant fecundity, average annual survivorship; 2) increasing fecundity, average annual survivorship; 3) constant fecundity, maximum annual survivorship, and 4) increasing fecundity, maximum annual survivorship.

3. Results and discussion

Mean productivity ranged from 0.31 to 0.44 yr^{-1} for the North Atlantic stock and from 0.22 to 0.34 yr^{-1} for the South Atlantic stock. Considering a constant vs. increasing fecundity with age had little effect on r_{max}, but as expected using the average vs. the maximum value of annual survivorship had a significant effect (**Table 2**). Mean steepness ranged from 0.73 to 0.93 for the North Atlantic stock and from 0.55 to 0.84 for the South Atlantic stock. Considering a constant vs. increasing fecundity with age had a little more effect on h in this case and using the average vs. the maximum value of annual survivorship also had a pronounced effect, as for productivity (**Table 2**).

The values of productivity and steepness found using the average survivorship approach seem more reasonable than those obtained with the maximum survivorship approach, which seem too high even for a very productive elasmobranch species such as the blue shark.

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Table 1. Biological input values and statistical distributions used to describe vital rates for blue shark simulations of r_{max} and steepness.

Parameter	Definition	North Atlantic	References	South Atlantic	References	Unit
K	Brody growth coefficient	LN (0.13,0.015)	Skomal and Natanson (2003)	U (0.106,0.183)	Montealegre (2007), Mas (2015), Jolly et al. (2013)	yr^{-1}
L_∞	Theoretical maximum length	LN (310.8,17.8)	Skomal and Natanson (2003)	U (246,283)	Montealegre (2007), Mas (2015), Jolly et al. (2013)	cm FL
t_0	Age at zero length	LN (1.77,0.26)	Skomal and Natanson (2003)	U (-2.19,-1.55)	Montealegre (2007), Mas (2015), Jolly et al. (2013)	yr
α	Median age at maturity	U (5,7)	Skomal and Natanson (2003); Stevens (1975)	U (5,7)	Montealegre (2007), Mas (2015), Jolly et al. (2013)	yr
β_0	Parameter 1 of logit maternity model			-2.8	Montealegre et al. (2014)	dimensionless
β_1	Parameter 2 of logit maternity model			0.1	Montealegre et al. (2014)	dimensionless
FLmn	Mean length in logit maternity model			162.5	Montealegre et al. (2014)	cm FL
ω	Lifespan	U (15,17)	Skomal and Natanson (2003)	U (12,16)	Montealegre (2007), Mas (2015), Jolly et al. (2013)	yr
	Sex ratio at birth	1:1		1:1		dimensionless
	Reproductive cycle	1	Hazin et al. (1994)	1	Hazin et al. (1994)	yr
m_x	Litter size	LN (39,13)	Mejuto and Garcia-Cortes (2005); Castro and Mejuto (1995)	LN (33.5,12.5)	Montealegre et al. (2014)	pups
a	Scalar coefficient of weight on length	3.18E-06	Kohler et al. (1995)	1.00E-06	Montealegre and Vooren (2010)	dimensionless
b	Power coefficient of weight on length	3.1313	Kohler et al. (1995)	3.35	Montealegre and Vooren (2010)	dimensionless

Table 2. Productivity (r_{max}) and steepness (h) descriptive statistics obtained through 4 stochastic simulation scenarios (see text for details).

	Scenario 1		Scenario 2		Scenario 3		Scenario 4	
	r	h	r	h	r	h	r	h
North Atlantic								
Mean	0.313	0.730	0.325	0.781	0.427	0.903	0.438	0.933
Median	0.314	0.736	0.325	0.788	0.427	0.906	0.439	0.935
SD	0.043	0.067	0.037	0.052	0.047	0.030	0.036	0.015
LCL	0.230	0.582	0.247	0.662	0.338	0.836	0.368	0.899
UCL	0.399	0.842	0.393	0.864	0.520	0.950	0.505	0.956
South Atlantic								
Mean	0.216	0.552	0.223	0.581	0.330	0.811	0.341	0.838
Median	0.220	0.568	0.228	0.613	0.332	0.826	0.349	0.856
SD	0.071	0.130	0.072	0.130	0.068	0.075	0.066	0.064
LCL	0.067	0.272	0.073	0.271	0.196	0.635	0.205	0.681
UCL	0.347	0.778	0.346	0.758	0.459	0.915	0.454	0.914