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AGE, GROWTH AND MATURITY OF BLUE SHARK (*PRIONACE GLAUCA*) IN THE NORTHWEST ATLANTIC OCEAN

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SUMMARY

*Age, growth, and maturity estimates for the northwest Atlantic population of blue shark (*Prionace glauca*) were updated from previous studies with samples collected from 2002-2019. Growth rates from three models were developed from aged vertebrae and from tag-recaptured individuals and maturity estimated from aged sharks rather than back-transforming length into age from growth equations. The best fitting model was von Bertalanffy growth equation and the estimates were similar to those previously derived. Von Bertalanffy growth parameters (sexes combined) derived from vertebral length-at-age data are L_∞ = 292 cm FL, K= 0.157 yr^{-1}, and t_0 =-1.80 yr^{-1} whereas those developed from the tag-recapture model were L∞ = 249 cm FL, K= 0.29 yr^{-1}. The median size and age at maturity estimates were 197 cm FL and 4.9 years for males and 191 cm FL and 5.3 years for females. Overall, growth and maturity estimates for blue shark suggest the species is fast growing and matures earlier than many other species of sharks, in agreement with previously published estimates for this population.*

RÉSUMÉ

*Les estimations de l'âge, de la croissance et de la maturité du stock de requin peau bleue (*Prionace glauca*) de l'Atlantique Nord-Ouest ont été mises à jour à partir d'études antérieures avec des échantillons collectés entre 2002 et 2019. Les taux de croissance de trois modèles ont été développés à partir de vertèbres dont l'âge a été déterminé et de spécimens marqués et recapturés, et la maturité a été estimée à partir de requins dont l'âge a été déterminé plutôt que de rétro-transformer la taille en âge à partir d'équations de croissance. Le modèle présentant le meilleur ajustement était l'équation de croissance de von Bertalanffy et les estimations étaient similaires à celles obtenues précédemment. Les paramètres de croissance de Von Bertalanffy (sexes combinés) dérivés des données de taille par âge des vertèbres sont L∞ = 292 cm FL, K= 0,157 an-1, et t0 =-1,80 an-1 alors que ceux développés à partir du modèle de marquage-recapture étaient L∞ = 249 cm FL, K= 0,29 an-1. La médiane de la taille et de l'âge à la maturité estimés étaient de 197 cm FL et 4,9 ans pour les mâles et de 191 cm FL et 5,3 ans pour les femelles. Dans l'ensemble, les estimations de croissance et de maturité du requin peau bleue suggèrent que l'espèce a une croissance rapide et arrive à maturité plus tôt que de nombreuses autres espèces de requins, ce qui est conforme aux estimations précédemment publiées pour cette population.*

RESUMEN

Se actualizaron las estimaciones de edad, crecimiento y madurez de stock de tiburón azul (Prionace glauca) del Atlántico noroccidental a partir de estudios previos con muestras recogidas entre 2002 y 2019. Las tasas de crecimiento de los tres modelos se desarrollaron a partir de la determinación de la edad de vértebras y de ejemplares marcados y recuperados; y la madurez se estimó a partir de la determinación de la edad de los tiburones en vez de mediante la retrotransformación de la talla en edad a partir de ecuaciones de crecimiento. El modelo que mejor se ajustaba era la ecuación de crecimiento de von Bertalanffy, y las estimaciones fueron similares a las derivadas anteriormente. Los parámetros de crecimiento de von Bertalanffy (sexos combinados) derivados de los datos de talla por edad de las vértebras son L∞ = 292 cm FL, K= 0,157 yr^{-1} , y t0 =-1,80 yr^{-1} , mientras que los desarrollados a partir del modelo de marcado y recuperación fueron L∞ = 249 cm FL, K= 0,29 yr^{-1} . Las estimaciones de la mediana de la talla de madurez y de la edad de madurez se situaron en 196 cm FL y 4,9 años para los machos y 191 cm FL y 5,3 años para las hembras, respectivamente. En general, las estimaciones

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de crecimiento y madurez del tiburón azul sugieren que la especie crece rápidamente y madura antes que muchas otras especies de tiburones, lo que concuerda con las estimaciones publicadas anteriormente para esta población.

KEYWORDS

Vertebrae, von Bertalanffy, tag-recapture, oogive,

1. Introduction

An understanding of the age structure and growth dynamics of a population is crucial for the application of biologically realistic stock assessment models and, ultimately, for effective conservation and management. Information on age and growth is often used to estimate natural mortality or total mortality, which are important components of stock assessment models, and in the calculation of population and demographic parameters such as population growth rates and generation times. Successful fisheries management thus requires precise and accurate age information to make informed decisions, and inaccurate age estimates can lead to serious errors in stock assessments and possibly to overexploitation (Campana, 2001). Stock assessment scientists are often forced to rely on decades-old life history information to determine current stock status for shark species.

The International Commission for the Conservation of Atlantic Tunas (ICCAT) assessed blue shark (*Prionace glauca*) in 2015 and determined that the status of the North Atlantic stock is unlikely to be overfished nor subject to overfishing. However, due to the level of overall uncertainty in the assessment outcomes, a consensus on specific management recommendations could not be reached as participants disagreed on the level of fishing mortality to be included. Among the main obstacles for obtaining reliable estimates of current stock status were uncertainty in some important biological parameters such as age and growth. Age reading data needs to be improved to provide better growth estimates for the North Atlantic. The most current age and growth model for blue shark in the North Atlantic is over 20 years old (Skomal and Natanson 2003) and there has been improvement in our ability to differentiate growth bands in shark vertebrae (e.g., Natanson et al. 2018). In addition, reassessing maturity including data from Viducic et al. (2022) and other new samples collected since that publication is also warranted. Given the re-assessment of blue shark status by ICCAT scheduled for 2023, there is an immediate need to provide a better understanding of the life history to improve the quality of the forthcoming assessment. Herein, we provide an update to the age, growth, maturity of blue shark from samples collected in the northwest Atlantic Ocean from 1966-2019.

2. Methods

2.1 Vertebral ageing

Blue shark vertebrae were collected from various sources in the US and Canada, including NOAA archives, fishery observer programs, fisheries-independent surveys and sport fishing tournaments. Vertebrae and associated length information were obtained from 288 blue sharks (176 males, 112 females) captured in the north Atlantic, for addition to samples previously aged in Skomal and Natanson (2003) (n = 411). The newly aged sharks ranged in size from 66-307 cm fork length (FL), while the overall data set spanned 44-312 cm FL (**Figure 1**). Vertebrae were stored in various manners (e.g. submerged in ethanol, frozen and uncleaned). Individual vertebrae remained stored in their original state unless they had not been previously cleaned. In the latter case, all tissue were removed using a scalpel followed by soaking in a sodium hypochlorite solution (common household bleach) to remove remaining adhering tissue prior to vertebrae being stored in 95% ethanol. As the current study is an update to growth models presented in Skomal and Natanson (2003), we employed identical ageing criteria for identifying band pairs (annuli). Following Skomal and Natanson (2003), a growth layer was defined as a clear indentation of the corpus calcareum at the position of an opaque band within the vertebra, and was considered the annulus. Each layer was considered a temporal growth zone. The first opaque band distal to the focus that coincided with an angle change in the corpus calcareum was defined as the birth mark (B). To allow for the combining of new age data with that of Skomal and Natanson (2003), two authors (Carlson and Passerotti) performed an ageing calibration by counting growth bands from images of vertebrae from Skomal and Natanson (2003) and then compared their counts with the original author of that study (Skomal). Ageing criteria were reviewed for any vertebrae with count discrepancies, and once the band counts for the calibration samples were agreed upon by all three age readers, two readers (Carlson and Passerotti) randomly aged the new samples. Ages were produced from counts of growth bands using digitized images of vertebral sections, which were read independently without knowledge of sex or length of specimens. Images were enhanced for improved visualization of growth bands based on Campana (2014). Vertebrae for which age estimates disagreed were re-read simultaneously and a consensus age was determined. If no agreement was reached, samples were discarded. Several methods were used to evaluate precision and bias among individual reader ages.

Percent agreement [(PA=Number agreed/Number read)*100] and percent agreement plus or minus one year were calculated to evaluate precision. The Index of Average Percent Error (IAPE; Beamish and Fournier, 1981) was calculated to compare the average deviation of readings from the means of all readings for each vertebral section:

$$\text{IAPE} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|x_{ij}-x_j|}{x_j}\right]$$

where N = number of sharks aged; R = number of readings; x_{ij} = i_{th} age estimation of j_{th} shark, and x_j = mean age calculated for the j_{th} shark. Bias plots were used to assess graphically the ageing accuracy between the readings (Campana, 2001). Precision analysis was carried out using the R language for statistical computing version 3.2.5 (R Core Team 2016).

Several models were fitted to combined and sex-specific observed size-at-age data to estimate growth parameters. The von Bertalanffy growth model (von Bertalanffy, 1938) was described using the equation:

$$\boldsymbol{L_t = L_\infty(1 - e^{-k(t-t_o)})}$$

A modified equation of the von Bertalanffy growth model, with a size-at-birth (L_0) intercept rather than the t_o parameter (Fabens, 1965) was described as:

$$L_t = L_\infty\ (1\text{-}be^{-kt})$$

where b = $(L_\infty\text{-}L_0)/L_\infty$. Estimated length at birth for the blue shark is 40 cm FL based on the median from a range reported in Pratt (1977).

We also used the 3-parameter Gompertz growth model (Liu et al., 2021) described as:

$$\boldsymbol{L_t = L_\infty e\left(-e^{-c_g(k_g t)}\right)}$$

where L_t = mean fork length at time t; L_∞ = theoretical asymptotic length; k = growth coefficient; t_o = theoretical age (t, years from birth) at zero length, and c_g and k_g are the parameters of the Gompertz model. All growth model parameters were estimated using Marquardt least-squares non-linear regression using SAS statistical software PROC NONLIN (SAS Institute, Inc., Cary, NC, USA). Akaike's Information Criterion (AIC) was used to determine the model that provided the best fit to length-at-age data (Buckland et al. 1997; Burnham and Anderson 2002).

$$\text{AIC} = n\ \ln(\hat{\sigma}^2) + 2p$$

where n is sample size; $\hat{\sigma}$ is residual sum of squares divided by n; and p is number of parameters.

In developing theoretical growth models, we assumed that (1) the birth mark is the band associated with a pronounced change in angle in the intermedialia, and (2) subsequent narrow translucent growth bands occur annually thereafter. Thus, ages (years) were calculated following the algorithm: age = birth mark + number of translucent bands -1. If only the birth mark was present, the age was 0+ years. All age estimates from growth band counts were assumed to represent annual growth band deposition based on Skomal and Natanson (2003). Theoretical longevity was estimated as the age at which 95% of L_∞ is reached (5(ln2)/K; Fabens, 1965; Cailliet et al. 1992).

2.2 Tag-Recapture

Growth parameters were estimated with mark-recapture data from the NOAA Fisheries Cooperative Shark Tagging Program (CSTP) using both the Fabens (1965) and Francis (1988) model frameworks based on the von Bertalanffy equation. Bayesian implementation of both models was also used for parameter estimation. The Bayesian implementations are based on the Dureuil et al. (2022) simulation study. Their analyses showed that multiple methods produce similar results with clean data, but when data is limited and errors are introduced the Fabens and Francis Bayesian methods were the most reliable and produced biologically reasonable estimates for elasmobranchs. Prior information used to inform the model was based on age and growth work done by Skomal and Natanson (2003). A lognormal prior distribution was generated for asymptotic total length, L_∞ (cm), with a median L_∞ = Lmax/0.99, using the given mean and standard deviation on the log scale for narrow and wide priors. A uniform prior distribution was used for the von Bertalanffy growth constant, k (year^{-1}), with minimum and maximum bounds. The wide priors for k were set between 10^{-10} year^{-1} and 100 year^{-1} (Dureuil et al. 2022). For a detailed description of the models and R code see Dureuil et al. (2022) and associated supplementary materials.

CSTP data used in this study consisted only of sharks that were measured at both tagging and recapture events. The analyses in this study were done using fork length. Measurements that needed to be converted from one measured value to FL were done using conversion equations found in Kohler et al. 1996. Data resulting in negative length increment values between tagging and recapture events and data for fish that were at liberty less than one year were excluded from the study dataset. This removed most outliers due to amplification of measurement error when calculating annual growth for short time spans.

2.3 Maturity

Using maturity data from Viducic et al. (2022) and new information collected since that publication, we re-calculated median size at maturity for male and female blue sharks. Median FL and age at maturity were calculated for both sexes by using maturity ogives fit to binomial data on reproductive maturity status. The relationship is described with a logistic equation by the maximum likelihood method: $Y = 1[e^{(a+bLT)}]^{-1}$, where Y are binomial maturity data (0, juvenile; 1, mature). As Viducic et al. (2022) found no temporal difference in age or size at maturity over the length of sample collection (1971-2016), all data from that study were combined with more recent information. When fitting the logistic equation to age data, we used observed ages in lieu of back-transforming length into age from the von Bertalanffy equation as had been done in Viducic et al. (2022). Additionally, we compiled previously unpublished data collected by Pratt to evaluate the relationship between maternal size and litter size (fecundity).

3. Results and Discussion

3.1 Vertebral ageing

Of the new set of vertebral images, 39 were removed due to the poor quality of the section and inability to visualize and count accurately the growth bands. The remaining vertebrae (n=248) were moderately difficult to interpret, with tendency for clearer band patterns in younger sharks (Figure 2) relative to older sharks. After initial age reading and assignment of consensus counts for all samples, any band count that was considerably greater or smaller than expected relative to measured FL was re-examined and a new random count was conducted. The percent agreement ±1 year across all size classes between the two readers was 87%. The age bias plot showed minimal variation around the 1:1 line. There was a slight bias for ages 12 and 14 (Figure 3). The Index of Average Percent Error of 6.1%.

All growth models fit the data well and were significant ($p<0.001$). AIC values were lowest for von Bertalanffy growth models (**Table 1**), and fits to the observed data were best for the sex specific von Bertalanffy models (**Figure 3**). The values of k and L_∞ from all equations varied slightly, but best-fit von Bertalanffy parameters and growth rates were similar to that estimated by Skomal and Natanson (2003) (**Table 2**). The maximum observed age for this study was 16 years but theoretical longevity was 22 years using estimates from the sex combined von Bertalanffy growth model.

3.2 Tag-recapture

A total of 295 mark-recapture events (117 males, 165 females, and 11 without sex determination) met our criteria. These data include the following size ranges: tagged males (46-277 cm FL), recapped males (112-305 cm FL), tagged females (61-167 cm FL), recapped females (117-305 cm FL), tagged unknown sex (85-246 cm FL), and recapped unknown sex (105-266 cm FL). Estimated growth parameters for males, females, and all sharks combined are reported in **Table 3**.

3.3 Maturity

Maturity status information was available for n = 202 blue sharks. Median length at maturity was 197.0 cm and 190.7 cm for males and females, respectively (**Table 4**). For age-at-maturity, the age at which 50% of males were mature was 4.95 years, and 5.3 years for females. Both males and females matured quickly with the ogive demonstrating a "knife-edge" rather than a logistic curve (**Figure 5**). Age and length at maturity estimates did not differ greatly from Viducic et al. (2022). Percent maturity by age and FL for males and females are given in Tables 5 and 6, respectively. There is no new data on litter size since Pratt (1979). Fecundity data were compiled from 16 litters observed from 1971-1977. There was no significant relationship between female size and litter size ($p = 0.863$; **Figure 6**).

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Table 1. Akaike's information criterion (AIC) values for fitted growth models for blue shark from von Bertalanffy, von Bertalanffy modified with size at birth intercept, and Gompertz growth models for male, female, and combined sex models. Δ-AIC is the difference between the AIC of the best-fit model and those of the other models tested.

Model	*AIC*	*Parameters*	*Δ-AIC*	*Akaike weight*
Male				
von Bertalanffy	1058.7	3	0.0	0.9980
Gompertz	1071.2	3	12.5	0.0020
von Bertalanffy (modified)	1090.4	2	31.7	0.0000
Female				
von Bertalanffy	517.2	3	0.0	0.9144
Gompertz	521.9	3	4.7	0.0856
von Bertalanffy (modified)	555.4	2	38.2	0.0000
Combined Sexes				
Gompertz	1597.6	3	0.0	0.9935
von Bertalanffy	1607.7	2	10.1	0.0065
von Bertalanffy (modified)	1664.9	2	67.3	0.0000

Table 2. Estimates of growth parameters for blue shark from von Bertalanffy, von Bertalanffy modified with size at birth intercept, and Gompertz growth models for male, female, and combined sex models. Values in parentheses are standard errors, FL=fork length. Values are provided from Skomal and Natanson (2003) for comparison.

Model	*Sex*	*L_∞ (cm FL)*	*K (yr^{-1})*	*t_0 (yr^{-1})*
von Bertalanffy	Male	282.4 (3.46)	0.179 (0.008)	-1.59 (0.11)
von Bertalanffy (modified)		270.9 (2.507)	0.226 (0.007)	
Gompertz		268.6 (2.45)	0.276 (0.010)	0.82 (0.07)
Skomal and Natanson (2003)		282.3 (7.15)	0.18 (0.02)	-1.35 (0.23)
von Bertalanffy	Female	337.3 (23.68)	0.107 (0.015)	-2.43 (0.23)
von Bertalanffy (modified)		263.2 (9.48)	0.219 (0.017)	
Gompertz		288.8 (12.04)	0.212 (0.017)	1.12 (0.19)
Skomal and Natanson (2003)		310.8 (334.8)	0.13 (0.03)	-1.77 (0.50)
von Bertalanffy	Combined	292.4 (3.95)	0.157 (0.006)	-1.80 (0.09)
von Bertalanffy (modified)		273.8 (2.62)	0.213 (0.006)	
Gompertz		273.3 (2.58)	0.255 (0.008)	0.90 (0.05)
Skomal and Natanson (2003)		286.8 (7.32)	0.17 (0.01)	−1.43 (0.20)

Table 3. Growth estimates produced from two mark-recapture models and the Bayesian forms of these models, by sex.

model	male	female	all sharks
Fabens VB (1965)			
Linf (cm FL)	244.2 (7.15)	272.6 (14.30)	248.6 (5.80)
k	0.41 (0.044)	0.27 (0.041)	0.37 (0.031)
AIC	1083.6	1531.5	2721.63
Bayesian Fabens			
Linf (cm FL)	276.4 (2.73)	308.8 (2.82)	301.1 (2.74)
k	0.28 (0.013)	0.19 (0.006)	0.21 (0.007)
AIC	1126.5	1513.78	2752.94
Francis VB (1988)			
Linf (cm FL)	276.9 (0.002)	269.3 (14.13)	249.1 (5.05)
k	0.23 (0.004)	0.21 (25.93)	0.29 (11.68)
AIC	1060.28	1482.12	2663.71
Bayesian Francis			
Linf (cm FL)	276.41 (2.72)	308.8 (2.81)	301.1 (2.77)
k	0.27 (.013)	0.19 (0.006)	0.21 (0.007)
AIC	1126.52	1513.78	2752.94

Table 4. Age and size of maturity for blue shark. Values from Viducic et al. (2022), which were produced using size at maturity data only, are provided as comparison.

	Sample size	*Sex*	*Median age (yr)*	*Median fork length (cm)*
This study	120	Male	4.95	197.0
Viducic *et al.* (2022)	488		5.0	192.5
This study	81	Female	5.34	190.7
Viducic *et al.* (2022)	315		5.0	190.9
This study	202	Sex Combined	5.15	194.6
Viducic *et al.* (2022)	--		--	--

Table 5. Percent maturity for male blue shark by fork length (FL, cm) and age.

Males				
FL (cm)	Percent		**Age**	Percent
50.0	0.00		0	0.00
60.0	0.00		1	0.00
70.0	0.00		2	0.01
80.0	0.00		3	0.05
90.0	0.00		4	0.19
100.0	0.00		5	0.52
110.0	0.00		6	0.84
120.0	0.00		7	0.96
130.0	0.00		8	0.99
140.0	0.00		9	1.00
150.0	0.01		10	1.00
160.0	0.03		11	1.00
170.0	0.09		12	1.00
180.0	0.24		13	1.00
190.0	0.49		14	1.00
200.0	0.74		15	1.00
210.0	0.90		16	1.00
220.0	0.96		17	1.00
230.0	0.99		18	1.00
240.0	1.00		19	1.00
250.0	1.00		20	1.00
260.0	1.00			
270.0	1.00			
280.0	1.00			
290.0	1.00			
300.0	1.00			
310.0	1.00			
320.0	1.00			

Table 6. Percent maturity for female blue shark by fork length (FL, cm) and age.

Females			
FL (cm)	*Percent Mature*	***Age***	*Percent Mature*
50.0	0.00	0	0.00
60.0	0.00	1	0.00
70.0	0.00	2	0.00
80.0	0.00	3	0.01
90.0	0.00	4	0.06
100.0	0.00	5	0.33
110.0	0.00	6	0.79
120.0	0.00	7	0.97
130.0	0.00	8	1.00
140.0	0.00	9	1.00
150.0	0.00	10	1.00
160.0	0.00	11	1.00
170.0	0.02	12	1.00
180.0	0.09	13	1.00
190.0	0.33	14	1.00
200.0	0.69	15	1.00
210.0	0.91	16	1.00
220.0	0.98	17	1.00
230.0	1.00	18	1.00
240.0	1.00	19	1.00
250.0	1.00	20	1.00
260.0	1.00		
270.0	1.00		
280.0	1.00		
290.0	1.00		
300.0	1.00		
310.0	1.00		
320.0	1.00		

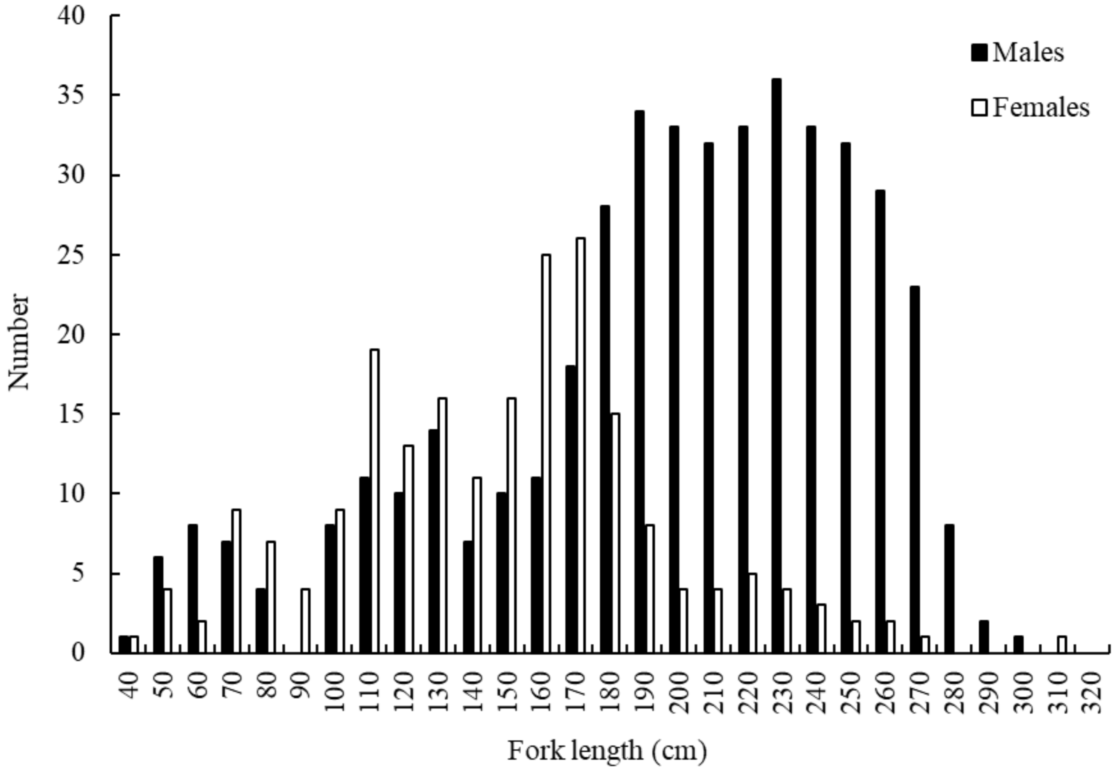

Figure 1. Distribution of age samples (n=654) used to develop growth models for blue shark (1967-2019).

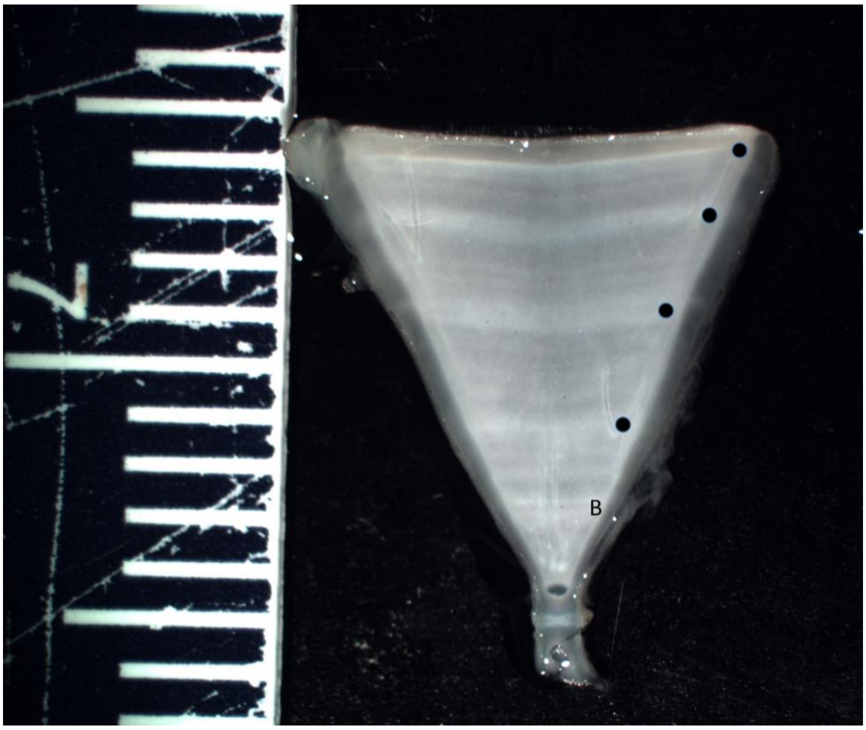

Figure 2. Example image of a vertebral section from a blue shark estimated to be 4 years old. Birth band is denoted with "B" and annuli are denoted with black circles.

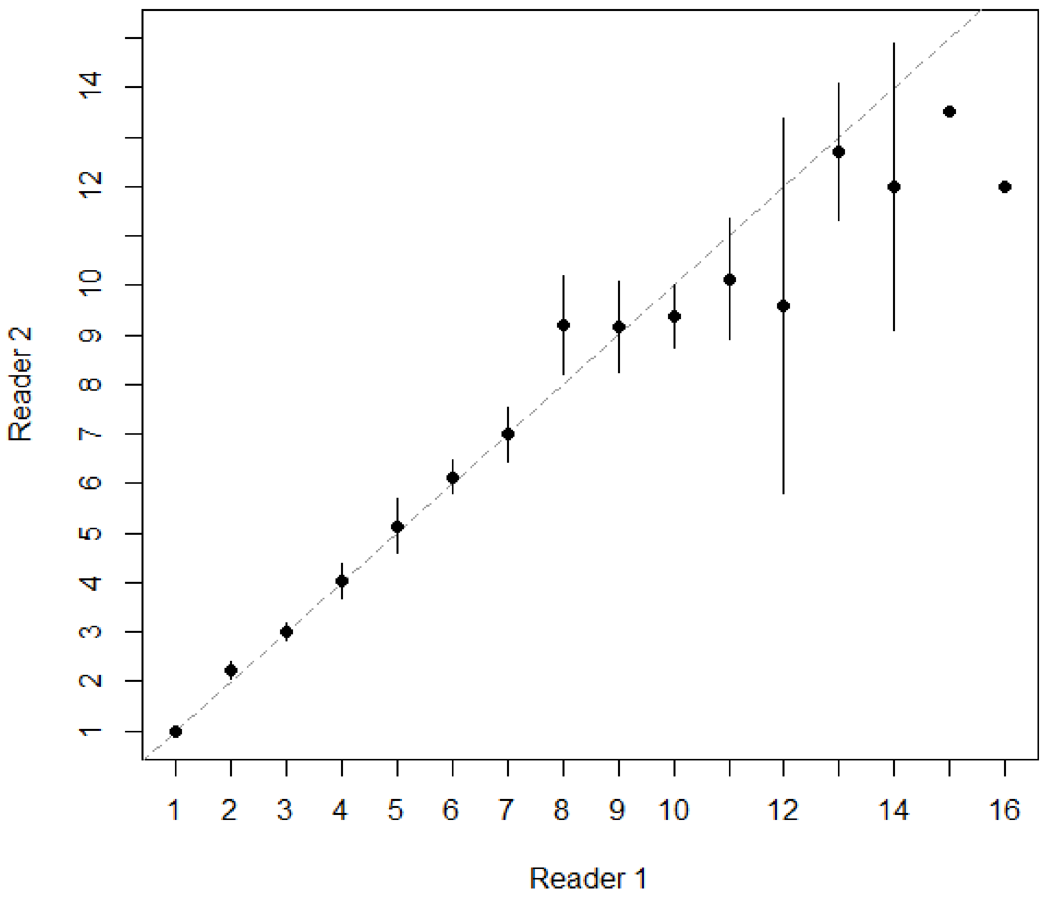

Figure 3. Age bias graph for pairwise comparison of blue shark vertebral counts from two independent readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by reader 1. The one-to-one equivalence line (dashed line) is also presented.

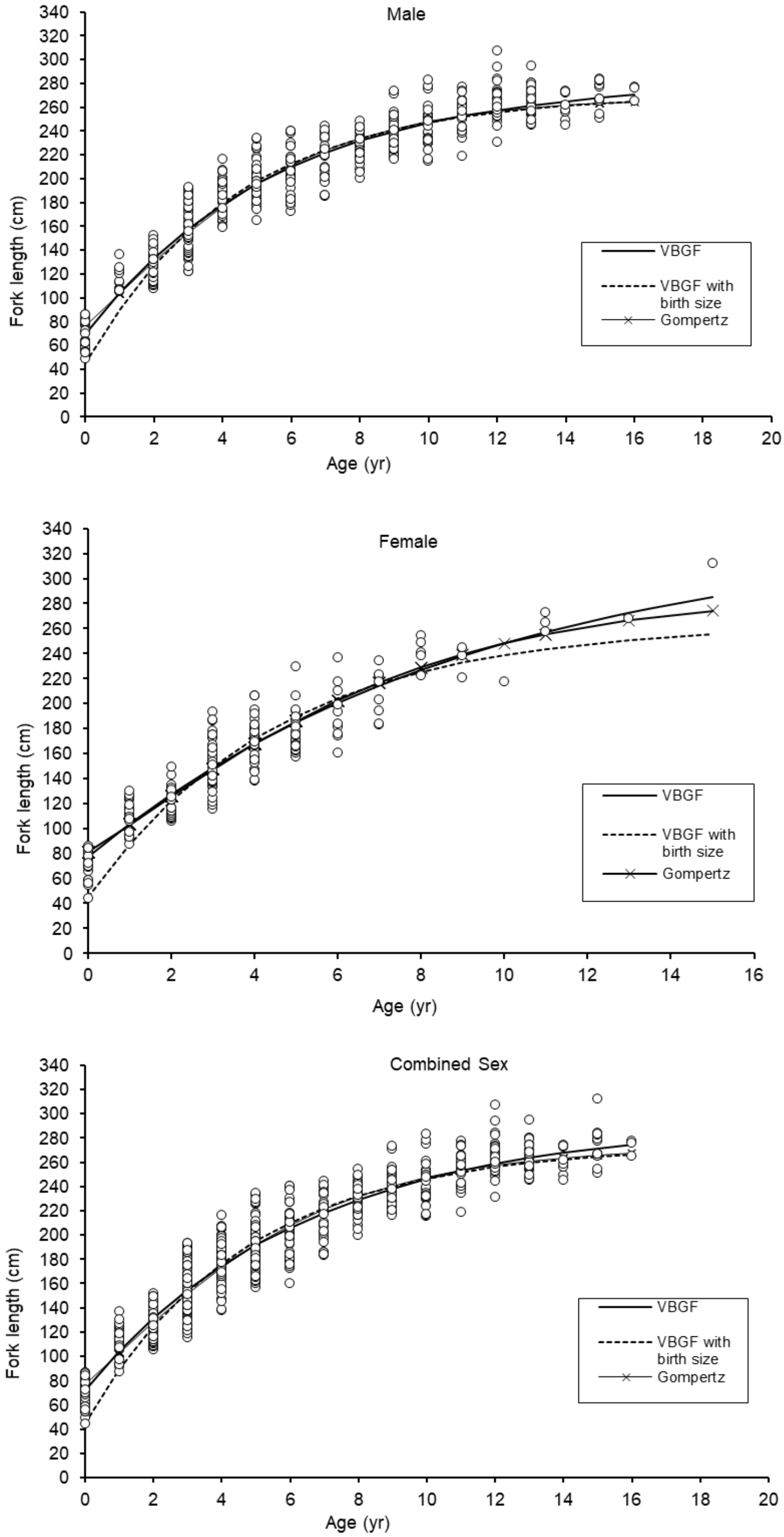

Figure 4. Von Bertalanffy, von Bertalanffy with size at birth intercept, and Gompertz growth models for male, female, and sex combined blue shark.

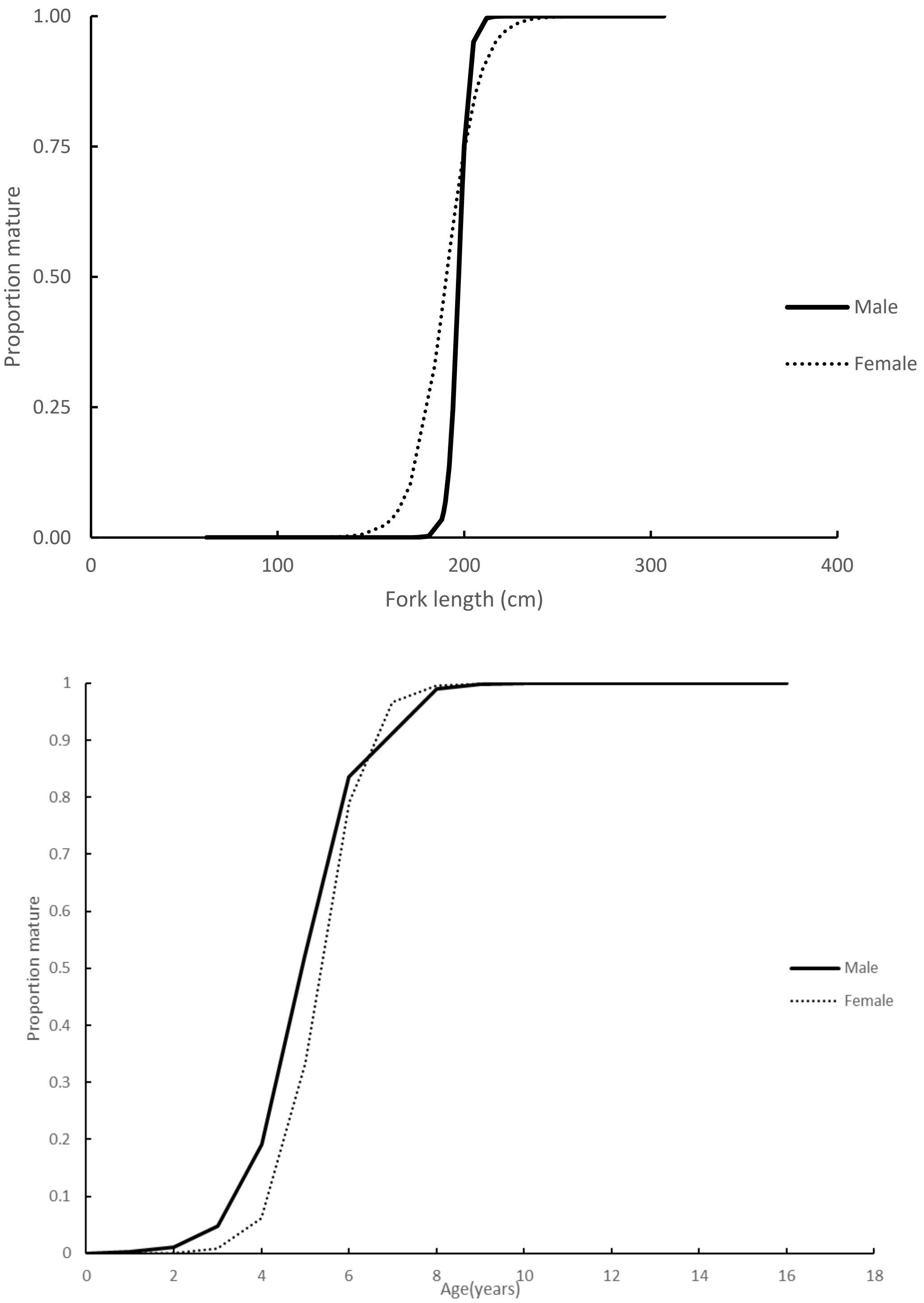

Figure 5. Proportion mature at fork length (top) and age (bottom) for blue shark.

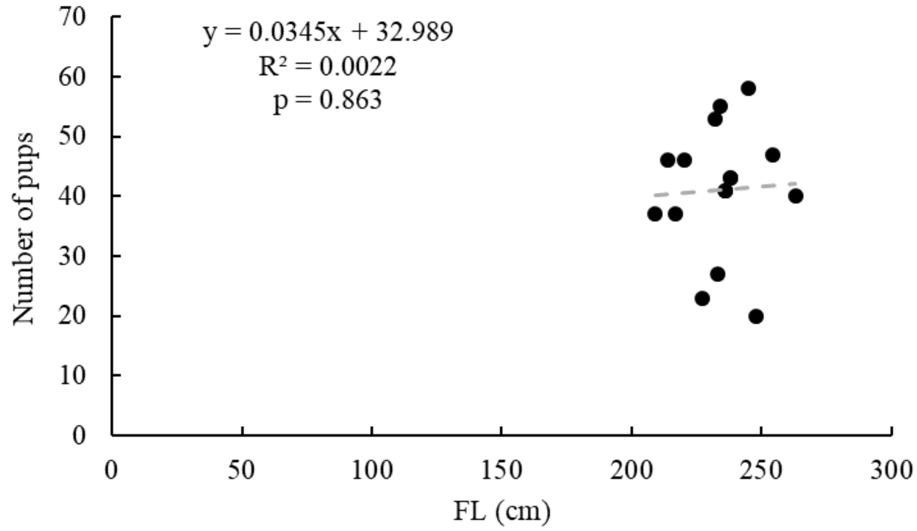

Figure 6. Fecundity relationship for female blue shark based on fork length (FL) and litter size (number of pups).