AGE AND GROWTH OF THE BLUE SHARK *(PRIONACE GLAUCA)* IN THE SOUTH ATLANTIC OCEAN

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SUMMARY

The blue shark Prionace glauca*, an oceanic migratory elasmobranchii species, was one of the most commonly bycatch species caught by long-liners. A total of 337 male, 311 female, and 137 sex unknown blue sharks caught by Taiwanese far sea long-line vessels in the South Atlantic (50˚35´W-13˚51´E, 40˚6´S-0˚57´S) between December 2006 and December 2011 were collected for age and growth analysis. The vertebrae from caudal peduncle region sampled by observers were used for aging. Growth band pairs were read via images photographed from X-ray films. Marginal increment ratio and centrum edge analysis indicated that the growth band pair (including translucent and opaque bands) on vertebral central was formed once a year. The Akaike's information criterion indicated that the von Bertalanffy growth function (VBGF) best fit the observed total length (TL) at age data. The VBGFs were not significantly different between sexes using likelihood ratio test ($P > 0.05$). Growth parameters were estimated to be $L_\infty = 352.1$ cm TL, $k = 0.13$ yr^{-1}, and $t_0 = -1.31$ yrs for sex combined blue shark. The longevity was estimated to be 21.4 years at least.*

RÉSUMÉ

*Le requin peau bleue (*Prionace glauca*), espèce d'elasmobranchii océanique migratoire, était l'une des espèces accessoires les plus communément capturées par les palangriers. Un total de 337 mâles, 311 femelles et 137 spécimens de sexe indéterminé de requin peau bleue capturés par des palangriers du Taipei chinois opérant en haute mer dans l'Atlantique Sud (50˚35´W-13˚51´E, 40˚6´S-0˚57´S) entre décembre 2006 et décembre 2011 a été prélevé afin d'être soumis à des analyses d'âge et de croissance. Les vertèbres du pédoncule caudal échantillonnées par des observateurs ont été utilisées pour déterminer l'âge. Les paires de bandes de croissance ont été lues par le biais d'images photographiées aux rayons x. L'analyse de la bordure du centre et du taux de croissance marginal ont fait apparaître que la paire de bande de croissance (y compris les bandes translucides et opaques) de l'axe vertébral se formait une fois par an. Le critère d'information Akaike a indiqué que la fonction de croissance de von Bertalanffy (VBGF) est celle qui ajuste le mieux la longueur totale observée (LT) aux données d'âge. Les fonctions VBGF ne présentaient pas de différences significatives entre les sexes utilisant le test du rapport des vraisemblances (P > 0,05). Les paramètres de croissance ont été estimés comme suit : L∞ = 352,1 cm TL, k = 0,13 yr-1, et t0 = -1,31 yrs pour le requin peau bleue de sexe combiné. Il est estimé que la durée de vie s'élève au moins à 21,4 ans.*

RESUMEN

La tintorera, Prionace glauca, una especie de elasmobranquio oceánico migratorio, es una de las especies de captura fortuita más comúnmente capturada por los palangreros. Entre diciembre de 2006 y diciembre de 2011 los palangreros de Taipei Chino de aguas distantes en el Atlántico sur (50˚35´W-13˚51´E, 40˚6´S-0˚57´S) capturaron un total de 337 machos, 311 hembras y 137 tintoreras de sexo desconocido recopilados para análisis de edad y crecimiento. Para la determinación de la edad se utilizaron vértebras de la región del pedúnculo caudal muestreadas por observadores. Los pares de bandas de crecimiento se leyeron a través de imágenes fotografiadas a partir de películas de rayos X. La ratio de incremento marginal y el análisis del borde del centrum indicaron que el par de bandas de crecimiento (incluidas bandas translúcidas y opacas) en la vértebra central se formaba una vez al año. El criterio de información de Akaike indicaba que la función de crecimiento de von Bertalanffy (VBGF) ajustaba mejor la talla total observada (TL) a los datos de edad. Las VBGF no eran significativamente diferentes entre sexos utilizando la prueba de ratio de verosimilitud (P > 0,05). Se estimó que los parámetros de crecimiento eran L∞ = 352,1 cm TL, k = 0,13 yr-1, y t0 = -1,31 yrs para los sexos combinados. Se estimó que la longevidad era de 21,4 como mínimo.

KEYWORDS

Blue shark, Age and growth, Vertebra, South Atlantic

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Introduction

The blue shark, *Prionace glauca*, is a pelagic species with a circum-global distribution in tropical, subtropical and temperate waters (Compagno 1984). It is also the top one shark bycach for Taiwanese long-line fishery. This species has been concerned by the regional fisheries management organizations (RFMOs) such as ISC, WCPFC, and ICCAT due to its large amount of catch.

The growth parameters essential for stock assessment of the blue shark in the North Atlantic have been well documented. Henderson et al. (2001) reported a sexes- combined von Bertalanffy growth function (VBGF) for blue sharks as: L_∞ = 377 cm total length (TL), k = 0.12 year^{-1}, and t_0 = -1.33 years in the North-east Atlantic. In the North Atlantic, the VBGF parameters were estimated to be L_∞ = 282 cm fork length (FL), k = 0.18 year^{-1}, and t_0 = -1.35 years for male, and L_∞ = 310 cm FL, k = 0.13 year^{-1}, and t_0 = -1.77 years for female, respectively (Skomal and Natanson 2003). Despite of the estimates of sexes-combined VBGF parameters, L_∞ = 352 cm FL, k = 0.157 year^{-1}, and t_0 = -1.01 years, derived from back-calculated TLs in the Northeastern Brazil waters (Lessa et al. 2004), the growth information of blue sharks in the South Atlantic is little known especially the east South Atlantic.

In this study, the age and growth of blue sharks in the east South Atlantic was estimated based on the vertebrae collected by the observers of Taiwanese long-line fishing vessel in the South Atlantic. It is hoped the results derived from this study can fill the research gap to better understand the life history of blue sharks in the South Atlantic.

Materials and Methods

Sample collection and preparation

A total of 337 male, 311 female, and 137 sex unknown blue sharks caught by Taiwanese far sea long-line vessels in the South Atlantic (50˚35´W-13˚51´E, 40˚6´S-0˚57´S) between December 2006 and December 2011 (**Table 1 and Figure 1**) were collected by observers. Fishing date, location, sex and TL (in cm) of the specimens were recorded. The size of specimens ranges 110-310 cm TL, 100-323 cm TL, and 171-325 cm TL for males, females, and sex unknown individuals, respectively (**Table 1, Figure 2**).

Vertebral samples from the caudal peduncle region were used for aging in this study. Vertebral samples were frozen after removing from the sharks and were sent back to our laboratory. Vertebrae were cleaned, infiltrated and embedded by using KOH, ethanol, t-butyl alcohol and paraffin to prevent deforming. The ventrodorsal radius (VR) of the processed vertebrae was measured to the nearest mm.

Age assignment and validation

Processed vertebrae from 318 males, 295 females, and 129 sex unknown individuals were photographed by soft X-ray (Laiko XL-080 1359) in the condition of 36 kv and 25 mA for 2.5 minutes. The X-ray film was put on the light box, and the vertebral images were photographed using digital camera (PowerShot D10, Canon). Growth band pairs were counted via vertebral images using the image manipulation program (Adobe Photoshop CS4 11.0) (**Figure 3**). One band pair comprises one calcified (opaque) and one less calcified (translucent) band (Cailliet *et al.* 2006). Each image was read by two readers, if any two readings matched, the matching reading was adopted.

The index of average percentage error (IAPE) and the coefficient of variation (CV) were calculated for each set of two readings, as described by Campana (2001) and Lessa et al. (2004). The equation used for IAPE and CV were as follow:

$IAPE = 1/N \sum [1/R \sum (|X_{ij} - X_j| / X_j)] \times 100\%$;
$CV = 1/N \sum (s_i / X_j) \times 100\%$;

where N is the number of sharks aged, R is the number of readings, X_{ij} is the count from the jth shark at the ith reading, X_j is the mean count of the jth shark from i readings, and s_i is the standard deviation of i counts from the jth shark.

Periodicity of band pair formation was estimated from edge analysis and marginal increment ratio (MIR) using vertebrae with 2-8 band pairs. The definition of MIR followed Joung et al.'s (2004) description: MIR = $(VR - R_n) / (R_n - R_{n-1})$, in which VR is the vertebral radius, R_n is the radius of the ultimate band pair, and R_{n-1} is the radius of the next to last complete band pair. Okamura and Semba's (2009) centrum edge analysis (CEA) statistic method was used to validate the periodicity of band pair formation.

The parturition period of the blue shark in the south hemisphere was estimated in September to December (Stevens 1984; Hazin et al. 1994) and thus birth month of the blue shark in the South Atlantic was assumed in November and the opaque band deposition was assumed to be restricted to November for annual band pair formation (see Results). With these assumptions, the age (years) of each specimen could be estimated with the following formulae:

$Age = (BN\text{-}1) + (M_a - 11) / 12 \; (11 \leqq M_a \leqq 12)$
$Age = (BN\text{-}1) + (M_b + 12 - 11) / 12 \; (M_b < 11)$

where BN is the number of band pairs, and M_a and M_b are the capture time (month) of sharks.

Growth functions

Four growth functions were used to fit the observed total length at age data. The von Bertalanffy (VBGF, von Bertalanffy 1938), the VBGF with size at birth (VBGF2, Fabens 1965), the Robertson (Robertson 1923), and the Gompertz (Gompertz 1825) growth functions were described as follows:

(1) von Bertalanffy growth function (VBGF, von Bertalanffy 1938)

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is the growth coefficient, t is the age (year from birth), and t_0 is the theoretical age at length 0.

(2) Two-parameter VBGF (Fabens 1965)

$$L_t = L_\infty + (L_\infty - L_0)(1 - e^{(-kt)})$$

where L_0 is the length at birth.

(3) Robertson (Logistic) growth function (Robertson 1923)

$$L_t = \frac{L_\infty}{1 + e^{(b_R - k_R t)}}$$

where b_R and k_R are the parameter and the growth coefficient of Robertson function, respectively.

(4) Gompertz growth function (Gompertz 1825)

$$L_t = L_\infty e^{-e^{(c - k_G t)}}.$$

where k_G is the growth coefficient of Gompertz function, and c is the parameters to be estimated.

Observed length at age data and size at birth (45 cm TL, Joung et al. (2011)) were fitted using the nonlinear regression (PROC NLIN) with SAS software. The Akaike's information criterion (AIC) (Akaike 1973) was used to determine the best growth function. In addition, a Chi-square test of maximum likelihood ratios (Kimura 1980) was used to examine the difference between the sexes in the growth functions.

Longevity

Theoretical longevity (t_{max}) was estimated using the sizes at which 95% and 99% of L_∞ are attained following Taylor (1958) and Fabens (1965) respectively. The equations of the longevity were described as follow:
$t_{max} = t_0 + 2.966/k$ (Taylor 1958);
$t_{max} = 5(\ln 2)/k$ (Fabens 1965).

Results and Discussion

Vertebral sample measurement

The sex-specific relationship between TL (cm) and VR (mm) showed linear trend and was not significantly different between sexes (ANCOVA, $P > 0.05$) as follow:

$TL = 0.222 + 258.89\ VR$ ($r = 0.82$, $n = 785$, $p < 0.05$).

Growth band pair formation

According to vertebral readings between two readers, high reading consistency was showed in the reading bios plot based on 295 vertebral samples (**Figure 4**). The IAPE and CV based on 785 vertebrae were also estimated as low as 3.82% and 4.96% under Campana's (2001) suggestion of 5.5% and 7.6%, respectively. No band pair deposition was found before birth and growth band pairs were counted up to 15 for both females and males, respectively.

The MIRs were significant different between September and October using Kruskal-Wallis test ($P < 0.05$) based on 2-8 band pairs sexes-combined data (170 females, 113 males, and 50 sex unknown individuals) (**Figure 5**). For CEA, the translucent band peaked in November and the opaque peaked in May (**Figure 6**). Both results suggested that the growth band pair was formed once a year. The opaque band of vertebral centrum started to be formed in November-December (**Table 2 and Figure 5-6**) which is similar to that in Brazil waters (Lessa et al. 2004), but a little later to that in the northwestern and south Pacific (Hsu et al. 2011, 2012).

Growth parameters

There was no significant difference between sexes in all four growth functions via the maximum likelihood ratio test ($P > 0.05$), therefore age and TL data of 742 specimens including males, females and sex unknown individuals were combined to estimate growth parameters. The AIC values showed that the VBGF best fit the observed length at age data for both males and females (**Table 3**). The parameters of the VBGF were estimated to be $L_\infty = 352.1$ cm TL, $k = 0.13$ year^{-1}, and $t_0 = -1.31$ years. These values are comparable to those in the western South Atlantic (Lessa et al. 2004) and in the North Atlantic (Skomal and Natanson 2003) (**Table 4, Figure 7**).

The estimated L_∞ of male blue sharks is larger than that of females in all Pacific studies (**Table 4**), but similar finding was not observed in the Atlantic (**Table 4**). The k value is larger than 0.1 year^{-1} for the blue shark in all reports indicated that this species grows faster than most other large sharks. Relative higher fecundity (litter size: 29-56, Joung et al. 2011; Compagno 1984) and faster growth rate than most other pelagic sharks might explain why blue sharks outnumber other shark species in the seas.

Longevity

The maximum observed age of this study were 15 years for both males and females. Estimated theoretical longevity of the blue shark was considerably greater than the maximum observed age. Longevity estimates were estimated to be 21.4 and 26.6 years following Taylor's (1958) and Fabens' (1965) methods, respectively.

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Table 1. Specimens of the blue shark (*Prionace glauca*) used in this study from the South Atlantic between 2006 and 2011.

Data	**Female**		**Male**		**Sex unknown**		**Total**
	n	Range of TL (cm)	n	Range of TL (cm)	n	Range of TL (cm)	
Jan.	35	168-247	13	167-291	5	199-265	53
Feb.	15	177-255	18	167-289	32	171-292	65
Mar.	29	162-260	22	175-269	11	175-282	62
Apr.	28	181-265	45	161-265	18	181-255	91
May	37	150-280	51	152-286	22	191-288	110
Jun.	38	180-279	53	139-295	15	196-283	106
Jul.	13	169-293	29	164-310	13	205-325	55
Aug.	7	190-260	15	158-310	5	211-320	27
Sep.	9	190-250	28	180-282	4	210-260	41
Oct.	8	202-254	16	210-272	4	210-261	28
Nov.	4	245-276	6	215-262	4	218-276	14
Dec.	88	100-323	39	110-270	4	228-275	131
Total	311	100-323	337	110-310	137	171-325	785

TL: total length.

Table 2. Compare goodness-of-fit among different models for of vertebral growth band formation.

Periodicity of band pair formation	*No cycle*	*Annual cycle*	*Biannual cycle*
Akaike's information criterion	505.1	456.2	500.7

Table 3. Comparison of goodness-of-fit among different functions for the blue shark in the South Atlantic.

Growth model	*Akaike's information criterion*
Von Bertalanffy	4022.8
Von Bertalanffy with L_0	4047.2
Robertson	4059.8
Gompertz	4034.9

Table 4. Comparison of the growth parameters for the blue shark in different studies.

Region	*Sex*	*n*	L_∞ *(TL, cm)*	*k*	t_0	A_{max}	*References*
South Atlantic	Both sexes	742	352.1	0.13	-1.31	15	This study
North Atlantic	Both sexes	82	423.0	0.11	-1.04	6	Stevens (1975)
North Atlantic	Male	287	337.6	0.18	-1.35	16	Skomal and Natanson (2003)
	Female	119	371.2	0.16	-1.56	15	
Western South Atlantic	Both sexes	236	352.0	0.16	-1.01	12	Lessa et al. (2004)
Eastern North Pacific	Male	38	295.3	0.18	-1.11	9	Cailliet et al. (1983)
	Female	88	241.9	0.25	-0.80	9	
Western North Pacific	Male	43	369.0	0.10	-1.38	7	Tanaka et al. (1990)
	Female	152	304.0	0.16	-1.01	8	
North Pacific	Male	148	378.8	0.13	-0.76	10	Nakano (1994)
	Female	123	318.5	0.14	-0.85	10	
Western South Pacific	Male	593	299.9	0.10	-2.44	16	Blanco-Parra *et al.* (2008)
	Female	324	237.5	0.15	-2.15	12	
Western North Pacific	Male	181	375.8	0.12	-1.55	14	Hsu *et al.* 2011
	Female	250	317.4	0.17	-1.12	12	
Central South Pacific	Male	164	366.9	0.13	-1.33	14	Hsu *et al.* 2012
	Female	81	348.0	0.16	-1.01	11	

Continued

A_{max} : maximum observed age.

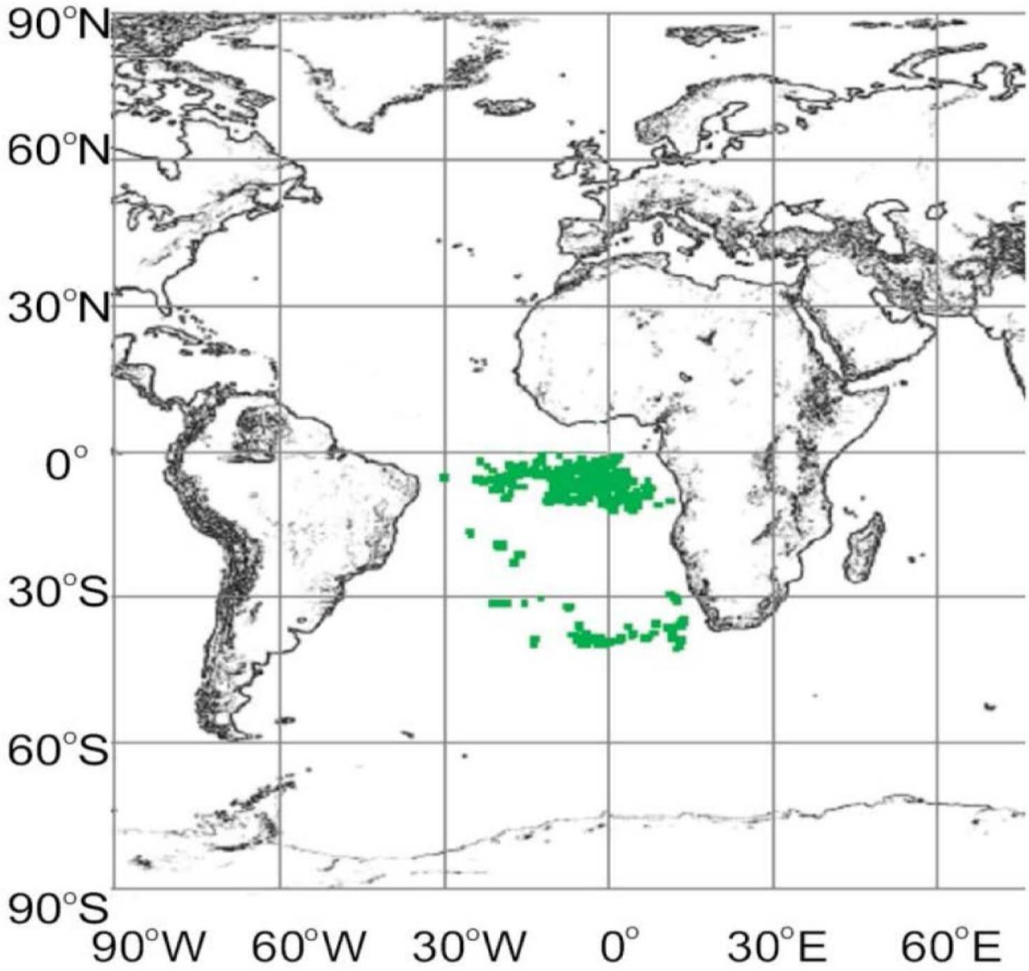

Figure 1. Sampling area of the blue shark (*Prionace glauca*) in the South Atlantic. Green dots indicate the locations of specimens collected.

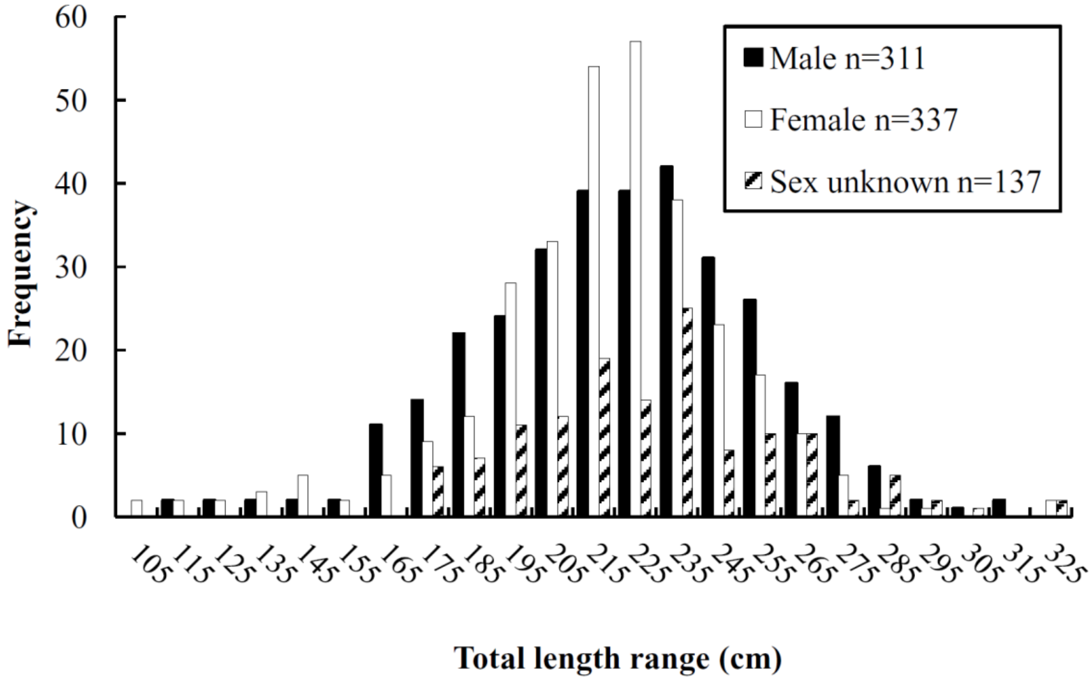

Figure 2. Total length frequency distribution of the blue shark in this study.

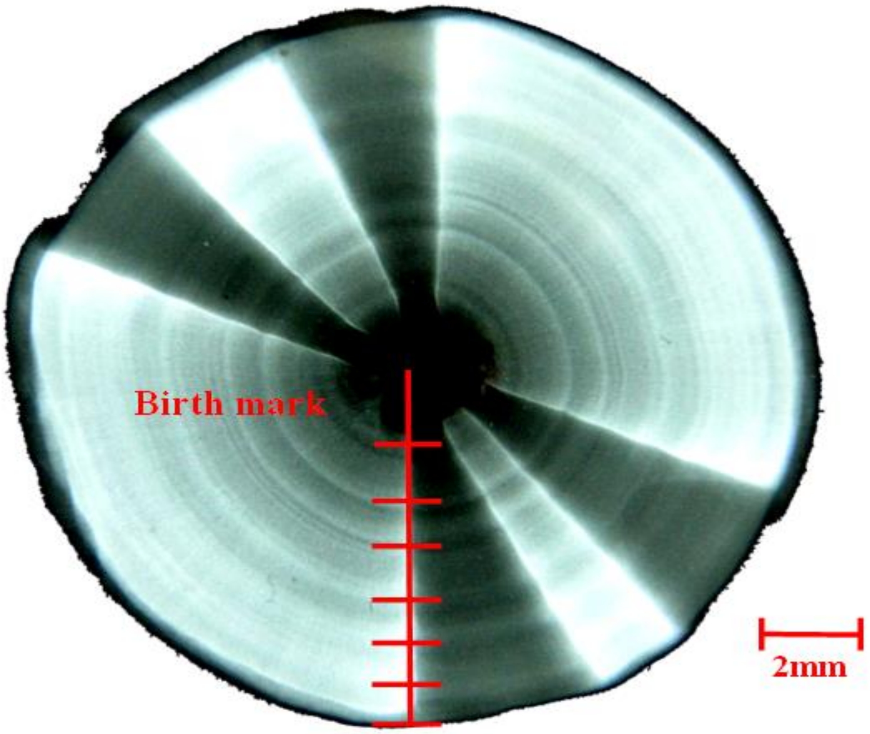

Figure 3. Vertebral image magnified by Adobe Photoshop CS4 11.0 program and displayed on screen of a 205 cm TL female blue shark.

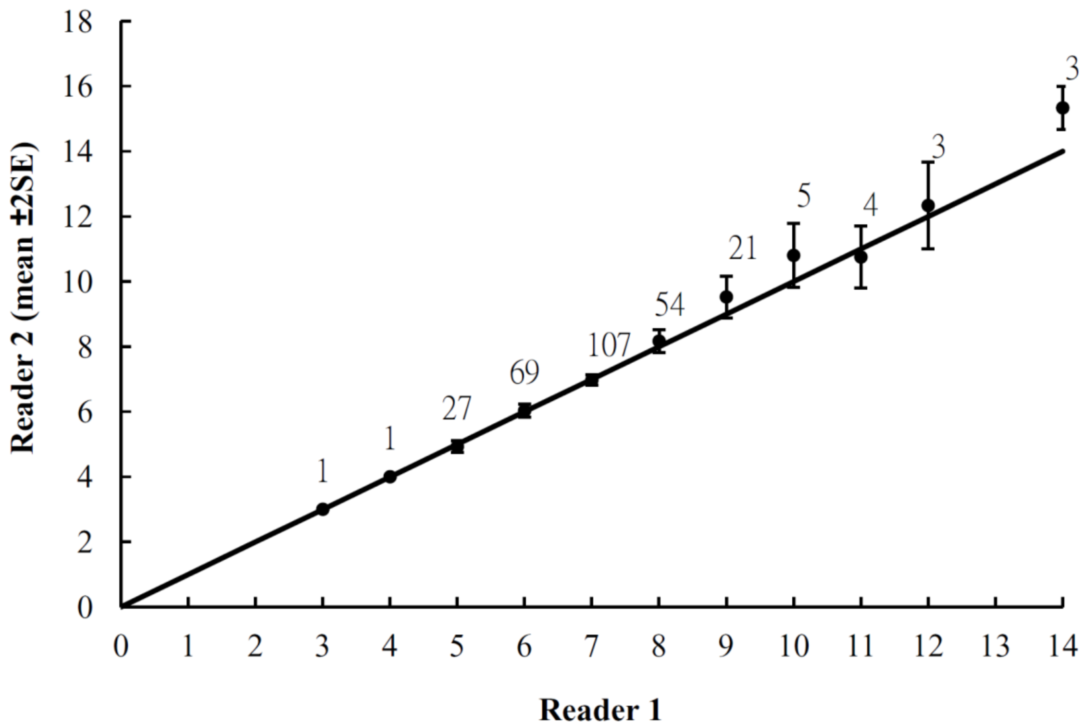

Figure 4. Age-bias plot of vertebral band pairs counts for *P*. *glauca* numbers represent sample size, and dots with error bars are the mean counts of reader 2 (±2SE) relative to reader 1.

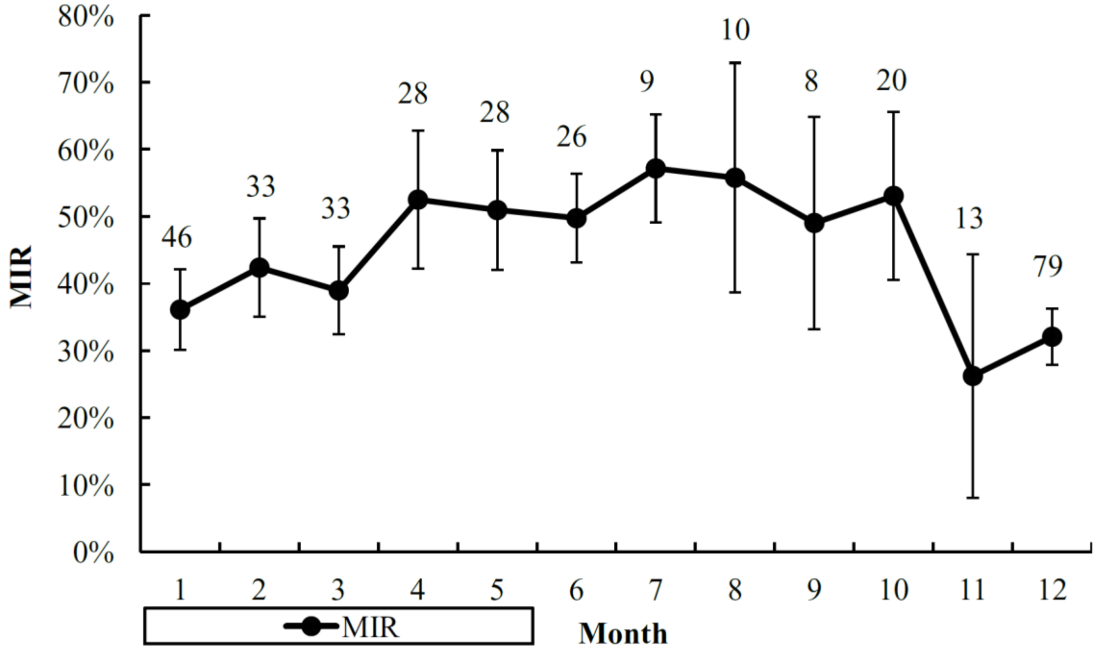

Figure 5. Monthly change of marginal increment ratio (MIR) of growth band pair for the blue shark in the South Atlantic. Vertical bars indicate ± 2SE and numbers above vertical bars mean sample size.

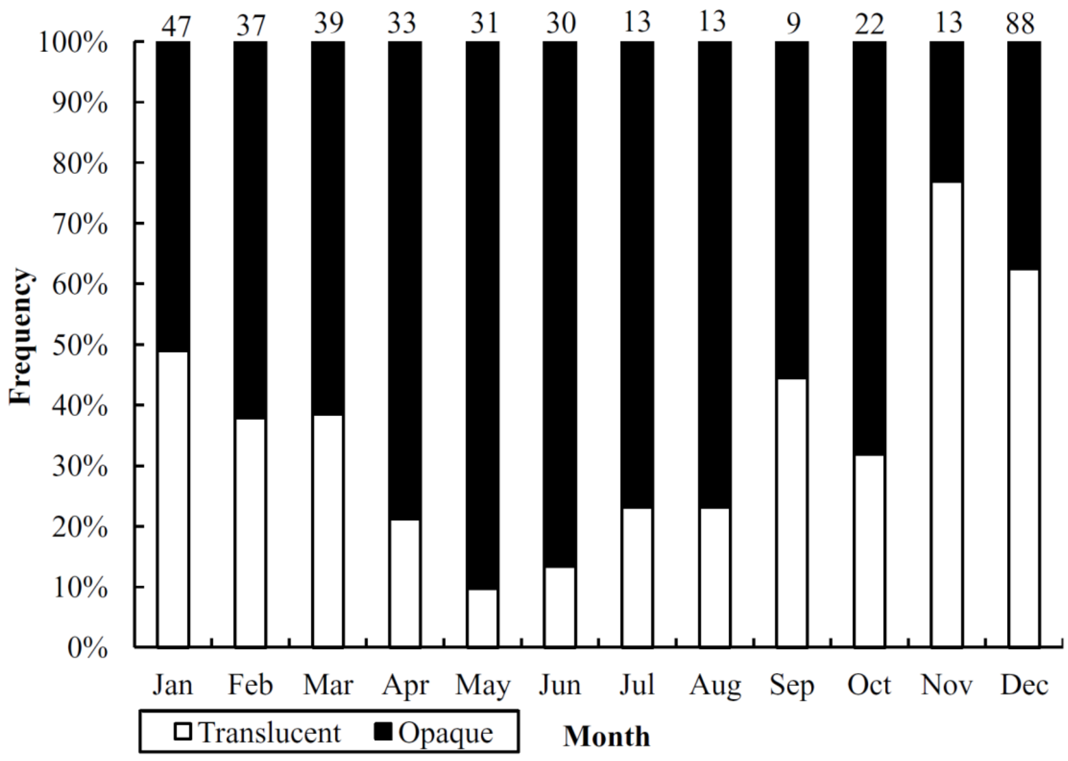

Figure 6. Centrum edge analysis (CEA) of growth bands formation for the blue shark in the South Atlantic. The numbers above represent sample size based on sexes combined data.

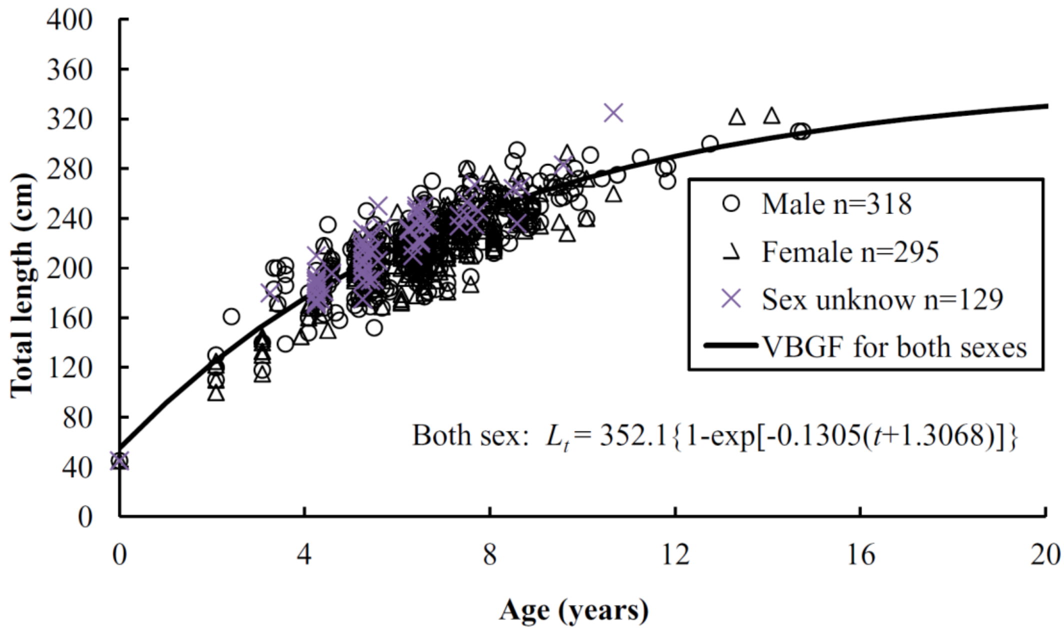

Figure 7. Von Bertalanffy growth function (VBGF) fitted to observed length at age data for the blue shark in the South Atlantic.