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ARTICLE

Age and Growth of the Shortfin Mako Shark in the Southern Indian Ocean

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Abstract
The Shortfin Mako *Isurus oxyrinchus* is one of the major shark bycatch species in the longline fishery for tuna *Thunnus* spp. in the Indian Ocean; however, its biological information is still little known. This study estimated the age and growth of Shortfin Makos in the southern Indian Ocean. In total, 178 specimens (72 females and 106 males) were opportunistically collected by the scientific observers onboard Taiwanese large-scale longline fishing vessels from February 2013 to September 2016 in the southern Indian Ocean. The relationship of gutted weight (GW; in kg) to curved fork length (CFL; in cm) for both sexes combined was estimated as GW = 0.00001 × CFL$^{2.517}$ (n = 170, r^2 = 0.85). Growth band pairs (including translucent and opaque bands) were counted based on sectioned vertebral centra from the caudal peduncle region. The periodicity of band-pair deposition on vertebral centra was estimated to be 1 year, with opaque bands deposited around August based on edge analysis. On this basis, the maximum observed ages of females and males were 18 and 14 years, respectively. The von Bertalanffy growth function best fitted the observed sexes-combined length-at-age data, with growth parameter estimates as L_∞ = 267.6 cm CFL, k = 0.123/year, and t_0 = −2.487 years (n = 159). The growth model could be improved for future stock assessments by increasing the sample size, particularly on very small (neonates and small subadults) and very large female Shortfin Makos.

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Sharks (class Chondrichthyes) are the top predators in the ocean, and they are particularly vulnerable to overexploitation because of their life history characteristics of slow growth, late maturity, few offspring, extended longevity, and close stock–recruitment relationship (Holden 1974, 1977). Shark conservation and management have become issues of great concern with the decline of populations of several pelagic shark species (Fowler et al. 2005; Dulvy et al. 2008; Cortés et al. 2010). In recent years, the stock assessments of sharks have been conducted by various regional fisheries management organizations. For example, the Blue Shark *Prionace glauca* and Shortfin Mako *Isurus oxyrinchus* in the North Pacific Ocean have been assessed by the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC 2015, 2017), whereas the Blue Shark in the Atlantic Ocean and the Indian Ocean have been assessed by the International Commission for the Conservation of Atlantic Tunas and the Indian Ocean Tuna Commission (ICCAT 2015; IOTC 2015). However, management and conservation for most other shark species are hindered by a lack of fisheries data and biological information (Hoff and Musick 1990).

The Shortfin Mako is widely distributed in tropical and temperate waters (Compagno 2001). It has typical shark life history characteristics, such as low fecundity (Stevens 1983; Semba et al. 2011), late maturity (Mollet et al. 2000; Francis and Duffy 2005), and an extended reproductive cycle (2 or 3 years) (Mollet et al. 2000; Joung and Hsu 2005; Semba et al. 2011). It has been identified as "vulnerable" on the International Union for Conservation of Nature Red List of Threatened Species (IUCN 2013).

The Shortfin Mako is one of the major shark bycatch species in the Taiwanese longline fishery targeting tuna *Thunnus* spp. or Swordfish *Xiphias gladius* in the open ocean (Chang and Liu 2009). In the Taiwanese tuna longline fishery in the Indian Ocean, it follows after Blue Shark and Silky Shark *Carcharhinus falciformis* as the main bycatch species (Huang and Liu 2010). The average annual reported catch of Shortfin Makos in the Indian Ocean was 1,503 metric tons for 2012–2016 (IOTC 2017). Due to the large amount of this species caught by various fisheries, it has been identified as the key (major) shark species by various regional fisheries management organizations. However, the current stock status of the Shortfin Mako in the Indian Ocean is unknown because no quantitative stock assessment has been conducted due to considerable uncertainty in both the fisheries and the biological information, and a precautionary approach to manage this stock has been suggested (IOTC 2017).

The major uncertainties in the life history traits of Shortfin Makos are the length of their reproductive cycle and the periodicity of band-pair (i.e., ring) deposition in their vertebral centra, which leads to uncertainty in age assignment. Pratt and Casey (1983) assumed a biannual periodicity (two band pairs per year) in the North Atlantic Ocean, whereas Cailliet et al. (1983) assumed an annual periodicity (one band pair per year) in the North Pacific Ocean. In the past two decades, most research on the age and growth of Shortfin Makos has supported an annual cycle of band-pair deposition, for instance, Ribot-Carballal et al. (2005) and Semba et al. (2009) in the North Pacific Ocean, Cerna and Licandeo (2009) in the South Pacific Ocean, and Campana et al. (2002), Ardizzone et al. (2006), and Natanson et al. (2006) in the North Atlantic Ocean. In addition, Bishop et al. (2006), Doño et al. (2015), and Barreto et al. (2016) assumed an annual cycle of band-pair deposition on vertebral centra for Shortfin Makos in the western South Atlantic Ocean and in tropical Brazilian waters. However, Chan (2001) suggested a biannual cycle of band-pair deposition for the Shortfin Makos in Australian waters. Among these studies, only Campana et al. (2002), Ardizzone et al. (2006), and Natanson et al. (2006) validated the annual periodicity with bomb radiocarbon techniques or oxytetracycline-tagged sharks. In addition, the periodicity of band-pair deposition may change throughout the life of a fish, and Wells et al. (2013) concluded a biannual cycle of vertebral band-pair deposition for Shortfin Makos up to 5 years old, whereas Kinney et al. (2016) concluded an annual cycle for those older than 5 years old in the eastern North Pacific Ocean based on tagging coupled with oxytetracycline marking.

Age and growth information is essential for stock assessment and fishery management. However, the growth parameters of Shortfin Makos in the southern Indian Ocean are still relatively unknown. Groeneveld et al. (2014) reported the only sexes-combined growth model of Shortfin Makos from South Africa (southwestern Indian Ocean) based on vertebral band-pair counts of 89 sharks. To fill this research gap, we estimated the age and growth of Shortfin Makos collected by scientific observers onboard the Taiwanese large-scale tuna longline vessels in the southern Indian Ocean.

METHODS

Shark sampling.— Shortfin Makos were opportunistically sampled by scientific observers onboard vessels in the Taiwanese large-scale tuna longline fleet in the southern Indian Ocean (Figure 1) from February 2013 to September 2016 (except March). The Taiwanese government launched an observer program for the large-scale tuna longline fleet fishery in 2002, and the duty of these scientific observers was to record fishing information, including effort, catch, and bycatch, as well as collect biological information (Huang and Liu 2010).

Measurements of curved fork length (CFL; in cm), taken over the curve of the body, gutted weight (GW; in

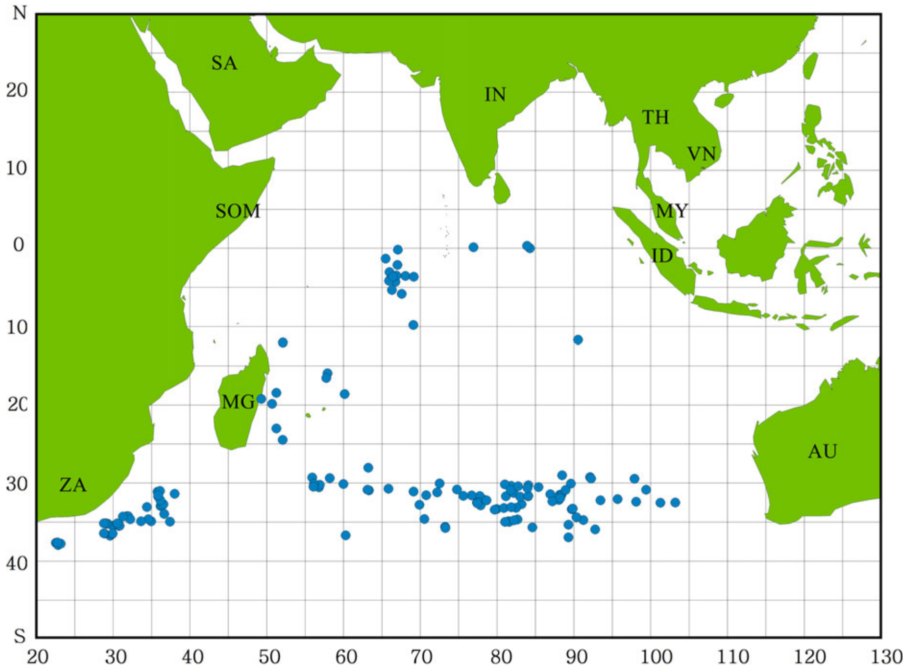

FIGURE 1. Sampling area for Shortfin Makos in the southern Indian Ocean. The dots represent the sampling locations. Abbreviations are as follows: AU = Australia, ID = Indonesia, IN = India, MG = Madagascar, MY = Malaysia, SA = Saudi Arabia, SOM = Somalia, TH = Thailand, VN = Vietnam, and ZA = South Africa.

kg), and sex were recorded for each Shortfin Mako, along with catch date and location (latitude and longitude). A block of one to eight vertebral centra was taken from the caudal peduncle region (the only area of vertebrae available for sampling) of each sampled shark processed on the deck. Sampling vertebrae in this region was considered acceptable for aging because Natanson et al. (2006) previously concluded that band-pair counts in different regions of the vertebral column were the same for Shortfin Makos in the North Atlantic Ocean. In addition, vertebrae in this region have been successfully used to estimate the age of several pelagic shark species (Joung et al. 2005, 2008, 2015, 2016). Vertebrae from Shortfin Makos were stored frozen onboard and transported back to Taiwan and stored frozen in the laboratory until processed.

Processing of vertebral centra and age estimation.— Two vertebral centra from each sample were removed, thawed, and had excess tissue removed. The centra were then soaked in 10% KOH (potassium hydroxide) aqueous solution for 8–12 h (depending on the size of the vertebrae) to remove residual connective tissue and rinsed with running water for 24 h (Joung et al. 2004). The diameter of the vertebral centra (VD) was measured to the nearest millimeter using calipers. After being soaked in ethyl alcohol and t-butyl alcohol for 48 h (24 h for each), centra were embedded in paraffin and sectioned along the lateral plane using an Isomet low-speed saw (Buehler) at a thickness of 1–1.44 mm.

Sectioned vertebrae were photographed by a soft X-ray (Laiko XL-080 1359, Japan) using 35 kV and 25 mA for 3–6 min, depending on the size of the vertebral centrum. The X-ray films were put on a negatoscope and the images (Figure 2) were photographed with a digital camera (Canon PowerShot D10). A translucent band (appearing dark in X-ray film) and an opaque band (appearing light in X-ray film) were assumed to represent one complete band pair. If the vertebral centra images photographed from X-ray film were not clear, then the sectioned centra were also examined using a stereomicroscope (ZEISS Stemi SV 6) (Figure 2) with reflected light under a black background at 2–4 times magnification. Vertebral images were obtained by taking photographs with a digital camera (Canon 700D). Opaque bands were counted on the sectioned vertebral centra images by using Adobe Photoshop CS4 version 11.0, which was used for increasing the brightness and contrast of the images to enhance the banding pattern.

Opaque bands on each vertebral centrum were counted twice by one reader based on the X-ray images. The interval between the two readings was at least 2 weeks. If the second count was different from the first one, a third count was conducted, and the final count was accepted if it agreed with one of the previous counts. If the third count was different from the previous two counts, the vertebral centrum was discarded. If the X-ray images were not clear, the band-pair counts were done using the images of sectioned vertebral centra from the stereomicroscope instead.

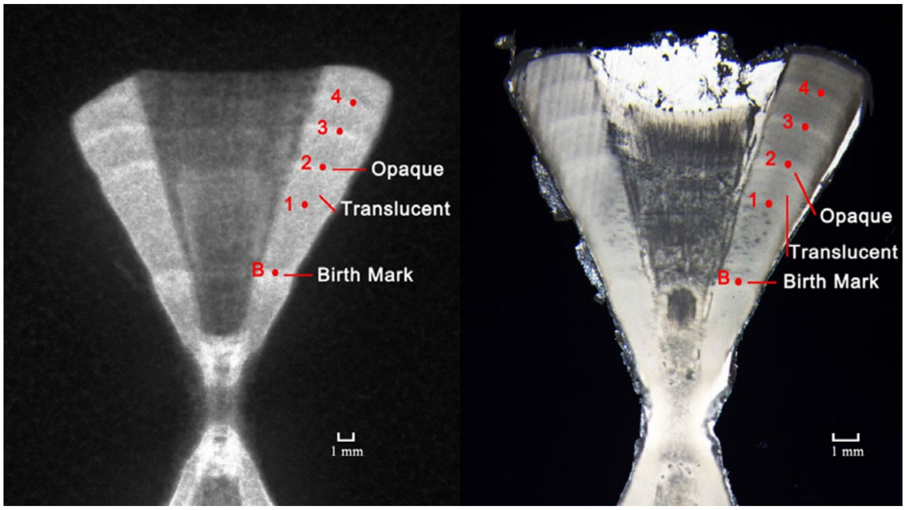

FIGURE 2. Images of sectioned vertebral centrum on soft X-ray (left image) and under a microscope (right image) from Shortfin Makos sampled in the southern Indian Ocean. Numbers indicate opaque bands.

To be able to estimate the GW of a sampled Shortfin Mako when only its CFL was available, or to estimate the CFL when only a vertebral centrum sample was collected, the relationships between GW–CFL and CFL–VD were estimated using nonlinear and linear regression models as follows: GW = a CFL^b and CFL = a + b VD, where a and b are constants. A maximum-likelihood ratio test and an analysis of covariance (ANCOVA) (Kimura 1980) were used to compare the GW–CFL and CFL–VD relationships between sexes, respectively.

The index of average percentage error (IAPE) (Beamish and Fournier 1981) and the coefficient of variation (Chang 1982), along with an age-bias plot (Campana et al. 1995), were used to estimate the within-reader reproducibility (precision) of age estimates between the two readings (Campana 2001; Lessa et al. 2004). Band pairs were counted without knowledge of the length or sex of the Shortfin Mako.

Edge analysis was used to examine the periodicity of band-pair deposition on vertebral centra. The centrum edge of each vertebra was categorized as either an opaque or a translucent band. The percentage of centra showing each edge type was then plotted over all months sampled to examine whether there was one minimum (annual periodicity) or two minima (biannual periodicity). The periodicity obtained from the edge analysis was further verified by Okamura and Semba's (2009) approach that combines binary data with a statistical model for circular data with a sine pattern. No cycle, annual cycle, and biannual cycle were examined in this analysis.

Growth models.— Four growth functions were used to fit the observed CFL as a function of observed age data of Shortfin Makos.

The first was the von Bertalanffy growth function (VBGF; Von Bertalanffy 1938), where L_t is the length at age t, L_∞ is the asymptotic length, k is Brody's growth coefficient of the von Bertalanffy function, t is the age (year from birth), and t_0 is the theoretical age at length 0:

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

The second was the two-parameter VBGF (Fabens 1965), where L_0 is the length at birth, set as 63 cm FL based on Mollet et al. (2000):

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt} \tag{2}$$

The third was the Robertson (logistic) growth function (Robertson 1923), where k_R and b_R are the growth coefficient and constant of the Robertson function, respectively:

$$L_t = \frac{L_\infty}{1 + e^{(b_R - k_R t)}} \tag{3}$$

The fourth was the Gompertz growth function (Gompertz 1825), where k_G is the growth coefficient of the Gompertz function and c_G is the constant to be estimated:

$$L_t = L_\infty e^{-e(c_G - k_G t)} \tag{4}$$

The nonlinear regression procedure (NLIN) in the statistical package SAS version 9.4 (SAS Institute 2014, Cary, North Carolina) was used to estimate the growth parameters. The goodness of fit of the four growth functions was compared based on the bias-corrected Akaike information criterion (AIC$_c$) (Hurvich and Tsai 1989). The AIC$_c$ was expressed as follows: AIC$_c$ = AIC + $\frac{2k(k+1)}{N-k-1}$, AIC = $N \times \ln(\text{MSE}) + 2K$ (Akaike et al. 1973), where N is the total sample size, MSE is the mean square of residuals, and K is the number of parameters estimated in the growth function.

A chi-square test (χ^2) of maximum likelihood ratios (Kimura 1980) was used to examine whether growth functions differed between sexes. It can be expressed as follows: $\chi^2 = -2\ln(\frac{LR}{LF})$, where L_F is the maximum likelihood for the full model and L_R is the maximum likelihood for the reduced model.

RESULTS

Shark Sampling

A total of 178 Shortfin Makos (72 females and 106 males) were collected in this study. There were 19 of 178 vertebral centra that were discarded due to a failure in processing or because the third count did not agree with one of the former two counts. Consequently the age and growth of Shortfin Makos was described based on 159 vertebral centra (60 females and 99 males). Females ranged in size from 84 to 273 cm CFL (Figure 3) and 6 to 128 kg GW, whereas males ranged from 65 to 253 cm CFL (Figure 3) and 3 to 138 kg GW.

No significant difference in the GW as a function of CFL was found between sexes using the maximum likelihood ratio test ($P > 0.05$). Therefore, the GW–CFL relationship (sexes combined) was described as follows (Figure 4):

$$\text{GW} = (1.0 \times 10^{-4})\text{CFL}^{2.517} \quad (r^2 = 0.845, n = 170) \quad (5)$$

There was no significant difference in CFL as a function of VD between sexes (ANCOVA: $P > 0.05$). Thus, the sexes-combined CFL–VD relationship was as follows (Figure 5):

$$\text{CFL} = -0.7567 + 9.2053\text{VD} \quad (r^2 - 0.896, n = 159) \quad (6)$$

Growth-Band-Pair Formation

Images of band pairs of sectioned vertebral centra viewed using soft X-ray and a negatoscope or viewed with a stereomicroscope showed similar counts and banding features (Figure 2). The first opaque band was assumed to be the birth mark (Natanson et al. 2006). A slight angle change on the vertebral centrum coincided with the birth mark. Thus, the first complete band pair after the birth mark was assumed to be age 1. The number of band pairs counted ranged from 0 (84 cm CFL) to 18 (273 cm CFL) for females and from 0 (65 cm CFL) to 14 (253 cm CFL) for males. The IAPE for within-reader ages was 4.04%, and the coefficient of variation was 5.94%. The age-bias plot indicated no systematic bias between the first and second band-pair counts made by the reader (Figure 6).

Edge Analysis

Edge analysis showed that the percentage of opaque band formation at the edge of the vertebral centra

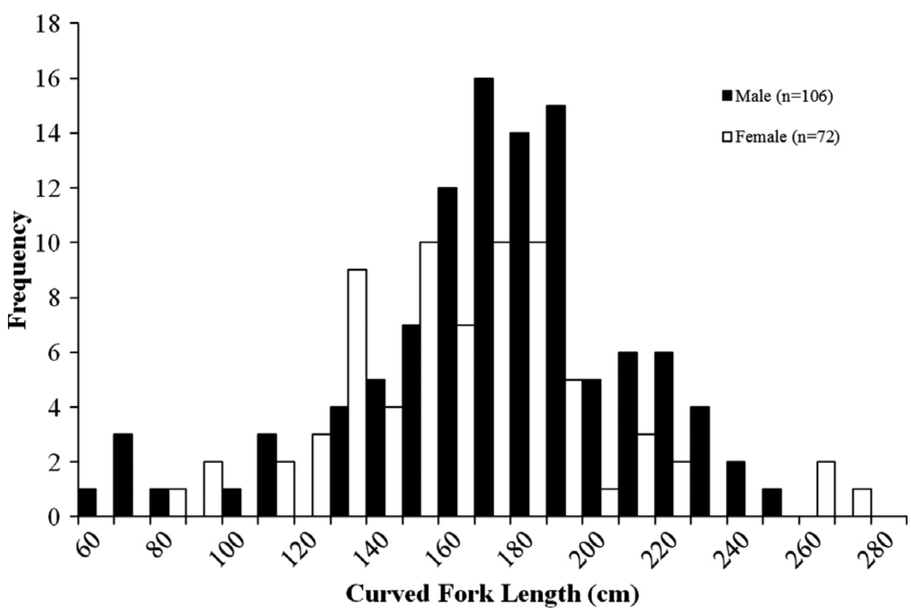

FIGURE 3. Curved fork length frequency distribution of the Shortfin Makos used in this study.

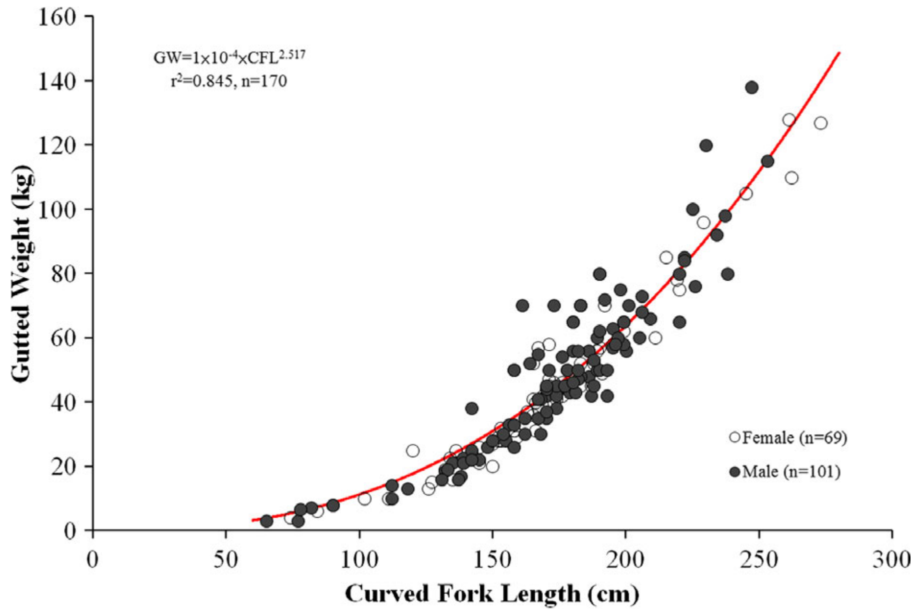

FIGURE 4. Relationship between gutted weight (GW) and curved fork length (CFL) for Shortfin Makos (both sexes combined) in the southern Indian Ocean.

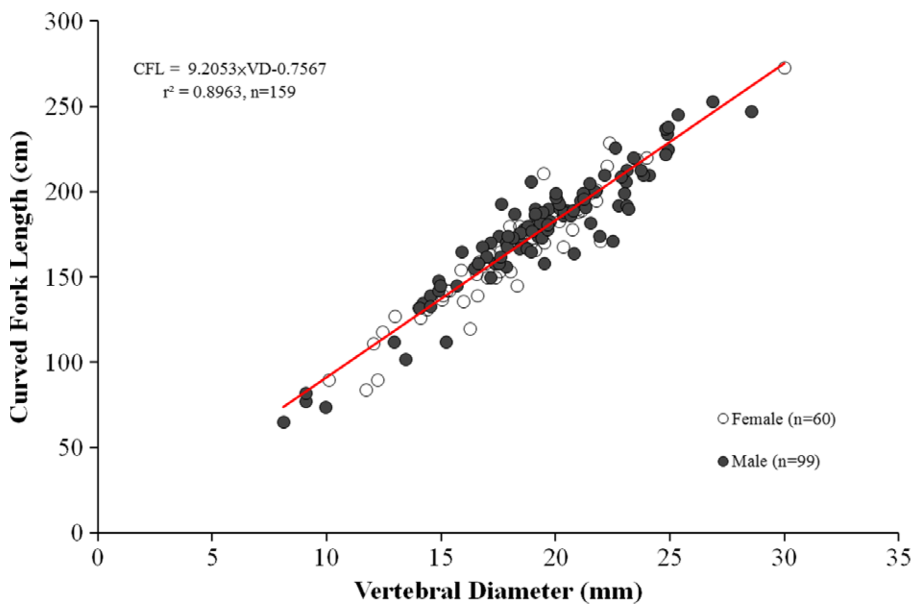

FIGURE 5. Relationship between curved fork length (CFL) and vertebral centra diameter (VD) for Shortfin Makos in the southern Indian Ocean.

increased from April and reached a peak during August to November, suggesting that the band pair was deposited annually (Figure 7). The Okamura and Semba (2009) analysis also suggested that the one-band-pair-per-year model had the highest support with the lowest AIC_c (216.1) compared with the no-cycle (221.0) and biannual cycle (220.4) models.

Growth Models

Significant differences were found between the sexes (maximum likelihood ratio, χ^2 test: $P < 0.05$) in the four growth functions applied to the observed length at age for Shortfin Makos (Table 1). The VBGF had the lowest AIC_c (281.29) for females (Figure 8A) and males (513.61) (Figure 8B; Table 1).

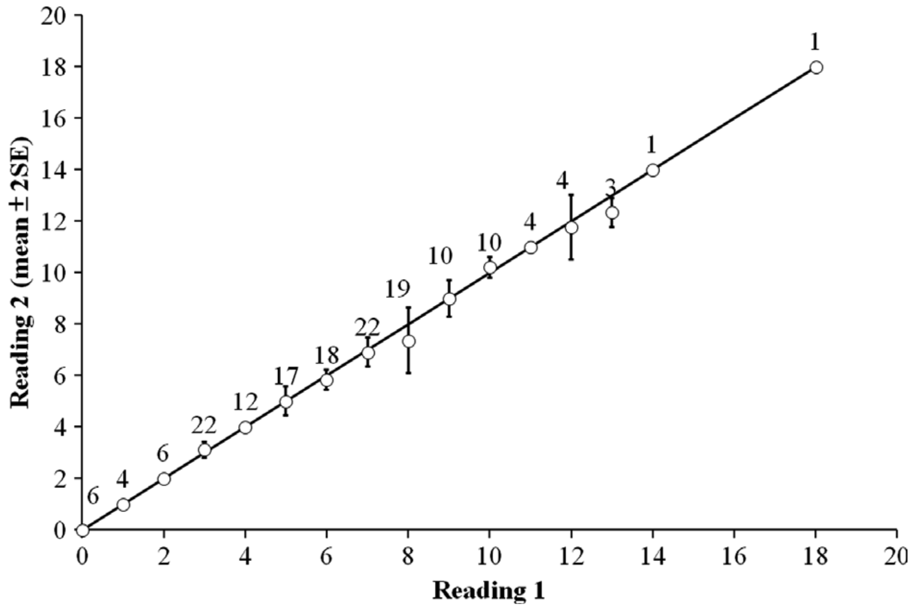

FIGURE 6. Age-bias plot of vertebral band-pair counts for Shortfin Makos in the southern Indian Ocean. The numbers above the dots represent sample size, and the dots with error bars are the mean ± 2 SE counts of reading 2 relative to reading 1.

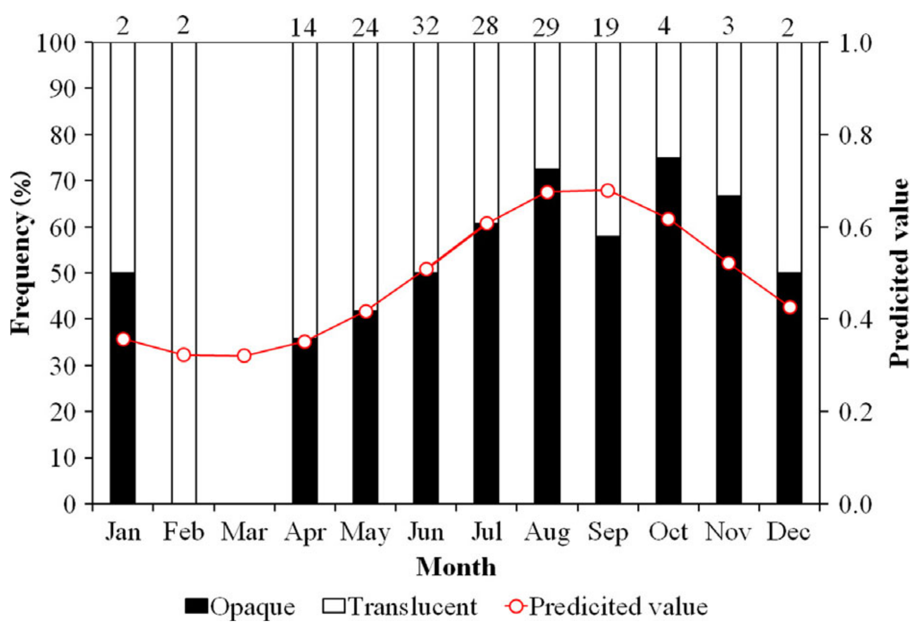

FIGURE 7. Monthly edge analysis of growth band formation in Shortfin Makos in the southern Indian Ocean. The numbers along the top of the graph are the sample size (both sexes combined). The predicted values are based on Okamura and Semba's (2009) one-cycle model.

Growth models with sexes pooled were also derived due to the relatively low sample size, especially of females. In addition, Natanson et al. (2006) and Doño et al. (2015) have previously shown that male and female Shortfin Makos grow similarly up to 11 and 15 years of age, respectively. For the sexes-combined data, the VBGF had the lowest value of AIC_c (802.20) (Figure 8C; Table 1).

DISCUSSION

The present study provides an important contribution on the age and growth of Shortfin Makos in the southern Indian Ocean, which can be used as biological input parameters for a future stock assessment.

Although the length of Shortfin Makos ranged from 65 to 273 cm CFL in this study, only a few specimens <

TABLE 1. Comparison of growth parameters for Shortfin Makos estimated by different growth functions based on observed length at age. The values in parentheses are 95% confidence intervals. The growth functions are as follows: VBGF = the von Bertalanffy growth function (Von Bertalanffy 1938), 2-VGBF = the two-parameter VBGF, Robertson = the Robertson logistic growth function (Robertson 1923), and Gompertz = the Gompertz growth function (Gompertz 1825).

Sex	Growth function	L_∞ (CFL in cm)	k (year^{-1})	t_0 (year)	AIC$_c$
Combined	VBGF	267.6 (245.3–289.9)	0.123 (0.094–0.152)	−2.987 (−3.698 to −2.275)	802.20
	2-VBGF[a]	242.5 (231.3–253.7)	0.179 (0.157–0.201)		819.99
	Robertson	239.0 (226.7–251.4)	0.262 (0.220–0.303)	1.799 (1.3915–2.206)	826.23
	Gompertz	248.1 (230.2–266.0)	0.195 (0.153–0.236)	0.218 (−0.113 to +0.549)	814.38
Female	VBGF	323.8 (252.1–395.5)	0.075 (0.039–0.111)	−4.360 (−5.826 to −2.893)	281.29
	2-VBGF[a]	248.4 (227.7–269.0)	0.164 (0.131–0.196)		299.60
	Robertson	279.0 (244.3–313.7)	0.180 (0.139–0.222)	3.206 (1.795–4.617)	289.50
	Gompertz	292.1 (243.1–341.1)	0.128 (0.085–0.172)	0.830 (−0.276 to +1.935)	285.56
Male	VBGF	251.6 (231.0–272.2)	0.151 (0.112–0.189)	−2.488 (−3.247 to −1.730)	513.61
	2-VBGF[a]	238.8 (225.5–252.2)	0.191 (0.161–0.221)		519.48
	Robertson	228.1 (216.9–239.2)	0.315 (0.256–0.374)	1.581 (1.165–1.996)	526.87
	Gompertz	235.8 (220.2–251.5)	0.234 (0.180–0.289)	0.216 (−0.194 to +0.626)	520.02

[a] L_0 was fixed at 63 cm CFL.

100 cm CFL were collected. This may be because the sampling did not cover the pupping and nursery time periods and areas of Shortfin Makos, which are presumed in part to be in the coastal shelf waters off the eastern coast of South Africa (Cliff et al. 1990). Gear selectivity and the release (discard) of small sharks as the gear was hauled back (i.e., not brought onboard) could have also contributed to the paucity of small sharks in the sample.

The maximum length of Shortfin Makos in this study (273 cm CFL) and that reported by Groeneveld et al. (2014) (311 cm FL which is 315 cm CFL[1,2]) in the southwestern Indian Ocean were much smaller than those reported in the North Atlantic Ocean (396 cm TL which is 366 cm CFL[1]; Bigelow and Schroeder 1948), in the eastern North Pacific Ocean (362 cm TL which is 334 cm CFL[2]; Carreón-Zapiain et al. 2018), and in the western North Pacific Ocean (383 cm TL which is 356 cm CFL[2]; K. M. Liu, unpublished data). Geographic variation, gear selectivity, and longline configuration, as well as the relatively small sample size in this study, are all possible factors that could cause the marked difference in the maximum observed length of Shortfin Makos among oceans. Pratt and Casey (1983) reported that the lack of sampling large Shortfin Makos might be because large sharks have sharp teeth that can cut the line when they are hooked. Sippel et al. (2015) indicated that large Shortfin Makos were mainly found in tropical waters but small individuals were mainly distributed in the high-latitude waters of the North Pacific Ocean. The sharks used in this study were mainly caught in temperate waters (south of 30°s; Figure 1), and only a small portion of the sharks were taken from tropical and subtropical waters. If Shortfin Makos in the Indian Ocean have similar distribution patterns as those in the North Pacific Ocean, then this could explain why only a few large-size specimens were collected and the maximum observed size in this study was smaller than that of other studies.

The coefficient of variation and the IAPE in this study (4.04% and 5.94%, respectively) were lower than the criteria of 5.5% and 7.6%, respectively, for between-reader age estimates (Campana 2001). These values were also smaller than those from other aging studies on Shortfin Makos, such as 6.6% and 9.3% (Bishop et al. 2006), 11.5% and 10.8% (Ardizzone et al. 2006), 9.77% and 13.82% (Cerna and Licandeo 2009), and 6.45% and 9.12% (Barreto et al. 2016), respectively. The smaller values of IAPE and coefficient of variation in this study (i.e., higher precision) may be because the age readings were made by the same reader (within reader), while the readings were made by different readers in other studies (between reader). Nevertheless, the aging criteria used by the single reader were precise and the band-pair counts in this study were therefore assumed to be reliable.

Based on the results of edge analysis and the cycle analysis, the periodicity of band-pair deposition was assumed to be 1 year in this study. Annual band-pair deposition was also assumed by other authors for Shortfin Makos in the southern hemisphere, including the southwestern Indian Ocean (Groeneveld et al. 2014), the western and central South Atlantic Ocean (Barreto et al. 2016), and the western South Atlantic Ocean (Doño et al. 2015). Although annual band-pair deposition has been validated

[1] The FL to TL conversion was based on Wells et al. (2013).

[2] The TL to CFL conversion for Shortfin Mako is available at https://www.nefsc.noaa.gov/nefsc/Narragansett/sharks/calc.html.

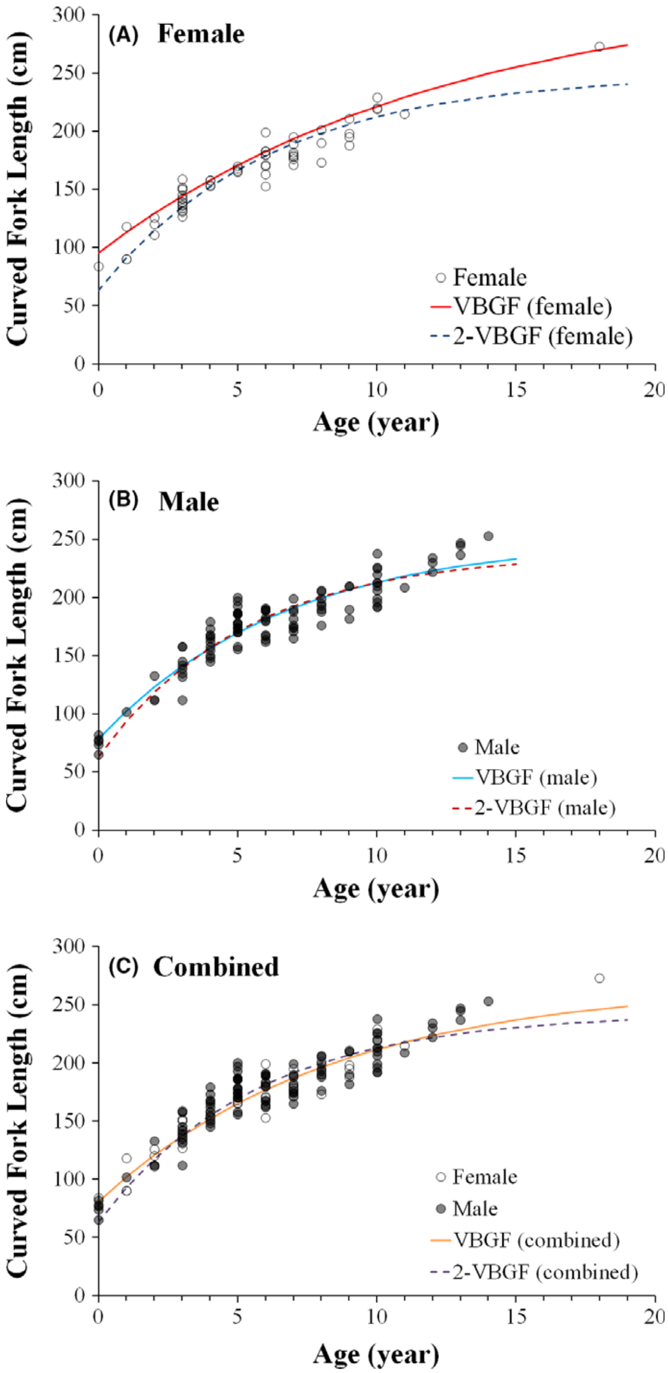

FIGURE 8. The best-fit growth functions for observed length-at-age data for Shortfin Makos in the southern Indian Ocean for **(A)** females, **(B)** males, and **(C)** both sexes combined.

by Campana et al. (2002), Ardizzone et al. (2006), and Natanson et al. (2006) based on bomb-radiocarbon chronologies and recaptured oxytetracycline-tagged Shortfin Makos, these authors did not reject the possibility of biannual band-pair deposition for the first few years of age. Wells et al. (2013) concluded biannual band-pair deposition for juvenile Shortfin Makos (up to 5 years old), which may be associated with the seasonal movement between their two feeding grounds in California and Mexico. However, the annual deposition of band pairs becomes regular when sharks grow older (>5 years old) and move to offshore waters, where the environment is more stable in the northeastern Pacific Ocean (Kinney et al. 2016). This transition (from biannual to annual band-pair deposition) may be related to their ontogenetic change (Wells et al. 2013). Whether this phenomenon occurs in the southern Indian Ocean needs further examination using oxytetracycline-tagged sharks in the future.

Based on the assumption of annual deposition of band pairs in the vertebral centra of Shortfin Makos in the southern Indian Ocean, the maximum age of males and females observed in this study was 14 and 18 years, respectively. These maximum observed ages are comparable with those reported by Semba et al. (2009) (13 and 19 years for males and females, respectively) and females in the eastern North Pacific Ocean (18 years in Ribot-Carballal et al. 2005); males in the eastern North Pacific Ocean were reported by Ribot-Carballal et al. (2005) to only reach a maximum age of 8 years). However, the maximum observed ages for Shortfin Makos in the southern Indian Ocean were much younger than those in the western North Pacific Ocean (24 and 31 years for males and females, respectively, in Chang and Liu 2009), the South Pacific Ocean (28 years in Bishop et al. 2006; 25 years in Cerna and Licandeo 2009), and the North Atlantic Ocean (21–24 years in Campana et al. 2002; 21 and 38 years for males and females, respectively, in Natanson et al. 2006). In addition, Ardizzone et al. (2006) validated the maximum age of 31 years for Shortfin Makos in the North Atlantic Ocean using a radiocarbon technique. The younger maximum ages observed in this study may be because large-size females were not collected, and the maximum observed size in this study was smaller than that of other studies (Table 2). In addition, peripheral bands become narrow and difficult to distinguish and count in older sharks (Francis et al. 2007), and different interpretation of peripheral band pairs among studies may lead the differences in maximum ages.

Most age and growth studies for Shortfin Makos have used the three-parameter VBGF to describe the growth. The VBGF best fit the observed length at age data of females, males, and sexes-combined Shortfin Makos in this study, similar to studies by Cailliet and Bedford (1983), Ribot-Carballal et al. (2005), Cerna and Licandeo (2009), Chan (2001), Pratt and Casey (1983), and Barreto et al. (2016) (Table 2). The Gompertz model best fit female Shortfin Makos in the North Atlantic Ocean (Natanson et al. 2006) and also provided the second best fit of all the growth models for females and sexes-combined for Shortfin Makos in the present study after the VBGF (Table 1).

TABLE 2. Comparison of growth parameters of Shortfin Makos from different studies. Abbreviations are as follows: BP = band-pair periodicity.

Reference	Model	Sex	CFL (cm)	L_∞	k/k_G	t_0/L_0	n	Location	BP (year)
Cailliet et al. (1983)	VBGF	Combined	81–295	294.6	0.07	−3.75	44	North Pacific Ocean	1
Ribot-Carballal et al. (2005)	VBGF	Combined	69–267	381.0	0.05	−4.70	109	North Pacific Ocean	1
Cerna and Licandeo (2009)	VBGF	Female	69–305	299.7	0.07	−3.18	304	North Pacific Ocean	1
		Male	69–262	274.3	0.08	−3.58	243		1
Semba et al. (2009)	2-VBGF	Female	64–333	340.4	0.09	67	147	North Pacific Ocean	1
		Male	58–264	256.5	0.16	67	128		1
Chan (2001)	VBGF	Female	74–314	349.0	0.15	−1.97	52	South Pacific Ocean	2
		Male	66–274	267.0	0.31	−0.95	24		2
Bishop et al. (2006)	VBGF	Female	100–347	820.1	0.01	−11.30	111	South Pacific Ocean	1
		Male	100–347	302.2	0.05	−9.04	145		1
Pratt and Casey (1983)	VBGF	Female	69–238	345.0	0.20	−1	54	North Atlantic Ocean	2
		Male	69–238	302.0	0.26	−1	49		2
Natanson et al. (2006)	Gompertz	Female	64–340	365.6	0.08	88	140	North Atlantic Ocean	1
	2-VBGF	Male	72–260	253.3	0.12	72	118		1
Doño et al. (2015)	Schnute	Female	104–343	434.3	0.04	−6.18	126	South Atlantic Ocean	1
		Male	84–259	604.5	0.02	−7.52	116		1
Barreto et al. (2016)	VBGF	Female	73–296	407.7	0.04	−7.08	109	South Atlantic Ocean	1
		Male	79–250	328.7	0.08	−4.47	129	Southwestern Indian	1
Groeneveld et al. (2014)	2-VBGF	Combined	99–302	289.6	0.113	90	89	Ocean	1
This study	VBGF	Combined	65–273	267.6	0.12	−2.49	159	Southern Indian Ocean	1
		Female	84–273	323.8	0.08	−3.86	60		1
		Male	65–253	251.6	0.15	−1.99	99		1
	2-VBGF	Combined	65–273	256.6	0.14	63	159		1
		Female	84–273	268.8	0.12	63	60		1
		Male	65–253	249.6	0.16	63	99		1

Different size ranges, sample sizes, and band-pair counting criteria among studies may result in the selection of different growth functions.

The significant difference in growth between male and female Shortfin Makos found in this study has also been reported in the North Pacific Ocean (Cerna and Licandeo 2009; Semba et al. 2009), the South Pacific Ocean (Chan 2001; Bishop et al. 2006), the North Atlantic Ocean (Pratt and Casey 1983; Natanson et al. 2006), and the South Atlantic Ocean (Doño et al. 2015; Barreto et al. 2016) (Table 2). Females have a greater L_∞ than that of males, with males having greater growth coefficients (k) and therefore attaining L_∞ at smaller sizes than females (Bishop et al. 2006; Natanson et al. 2006). This sexual dimorphism in growth is also commonly found in other elasmobranchs (Skomal and Natanson 2003; Goldman 2005; Francis et al. 2007). However, some studies have concluded that there is no significant difference in the growth between sexes for Shortfin Makos in the southwestern Indian Ocean (Groeneveld et al. 2014) and in the North Pacific Ocean (Cailliet and Bedford 1983; Ribot-Carballal et al. 2005). The sample size for females in the present study was low (n = 60), and few very small or very large females were sampled, which may have limited a complete description and modeling of female growth. Although sex-specific differences were observed statistically, both sexes appeared visually to grow similarly in this study (Figure 8C), and hence a sexes-combined growth equation was provided to better describe the overall observed size-at-age data of Shortfin Makos in the southern Indian Ocean.

The sex-specific asymptotic lengths estimated in this study (324 and 252 cm CFL for females and males, respectively) were comparable with those reported for females (340 cm CFL^2) and for males (257 cm CFL^2) in the North Pacific Ocean (Semba et al. 2009) and those in the North Atlantic Ocean (366 cm CFL for females and 253 cm CFL for males in Natanson et al. 2006). However, the L_∞ estimated from this study is smaller than that from the North Pacific Ocean (381 cm CFL^2 in Ribot-Carballal et al. 2005) and from the South Atlantic Ocean (408 and 329 cm CFL for females and males, respectively, in

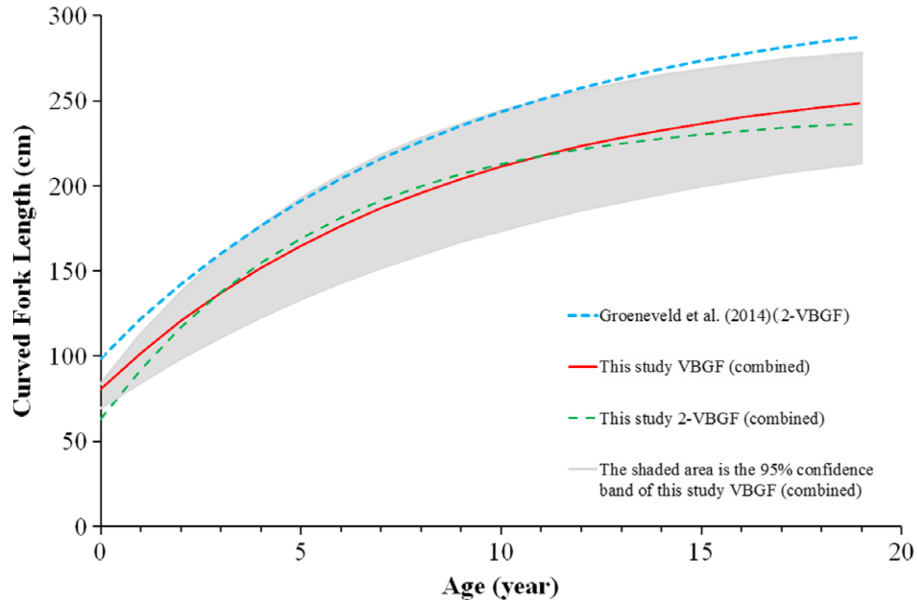

FIGURE 9. Comparison of growth curves for Shortfin Makos (both sexes combined) from the present study in comparison with results from Groeneveld et al. (2014) from the southwestern Indian Ocean.

Barreto et al. 2016). The estimated L_∞ for sexes-combined data was smaller than that from the southwestern Indian Ocean (Groeneveld et al. 2014; Table 2).

The estimated k for sexes-combined data in this study is comparable with that in the southwestern Indian Ocean (0.11/year in Groeneveld et al. 2014) but is smaller than those from Pratt and Casey (1983) and Chan (2001), which assumed biannual band-pair deposition. Natanson et al. (2006) documented that larger L_∞ and smaller k were expected when using annual band-pair deposition compared with when using two band pairs per year.

The predicted length at age modeled by a VBGF or a two-parameter VBGF in this study was consistently smaller than for Shortfin Makos sampled by Groeneveld et al. (2014) in the southwestern Indian Ocean off South Africa, but the upper 95% confidence band overlapped for sharks 3–12 years of age (Figure 9). The L_∞ and k derived from these two studies are similar, but L_0 (90 cm CFL) estimated by Groeneveld et al. (2014) was much larger than the size at birth in this region (63 cm CFL). As the sample size in this study was markedly larger (159 versus 89 aged sharks in this study versus Groeneveld et al. 2014), the variation in size at age is smaller than in Groeneveld et al. (2014). In addition, the small area sampled in Groeneveld et al.'s (2014) study off the eastern coast of South Africa was also sampled in the present study's more geographically comprehensive coverage in the southern Indian Ocean. Increased sample size in combination with greater geographical coverage makes the results derived from the present study on the age and growth of Shortfin Makos in the southern Indian Ocean useful for future stock assessments.

In conclusion, this study has provided detailed information of age and growth for Shortfin Makos in the southern Indian Ocean. However, the results derived from this study may not fully describe the growth of females, in particular, due to the lack of larger sharks in the collection. Future research should focus on increasing the sample size, especially for very small sharks (neonates and small subadults not landed in the fisheries) and very large sharks (females > 200 cm FL) to improve the estimates of the growth parameters. In addition, validation of the band-pair deposition in Shortfin Makos of various ages using a chemical-marking and tagging study is also needed in the future.

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