

# Life history of the silvertip shark *Carcharhinus albimarginatus* from Papua New Guinea

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**Abstract** Growth and maturity of the silvertip shark *Carcharhinus albimarginatus* from Papua New Guinea were estimated to form the basis of future population assessments. Samples were collected from commercial longline vessels targeting sharks in the Bismarck and Solomon Seas. A total of 48 *C. albimarginatus*—28 males (95–219 cm total length, TL) and 20 females (116–250 cm TL)—provided data for the analyses. Employing back-calculation techniques accounted for missing juvenile length classes and supplemented the sample size. A multi-model framework incorporating the Akaike information criterion was used to estimate growth parameters. The von Bertalanffy growth function (VBGF) provided the best-fit growth estimates. Parameter estimates were  $L_0 = 72.1$  cm TL,  $k = 0.04$  yr<sup>-1</sup> and  $L_\infty = 311.3$  cm TL for males; and  $L_0 = 70.8$  cm TL,  $k = 0.02$  yr<sup>-1</sup> and  $L_\infty = 497.9$  cm TL for females. The biologically implausible  $L_\infty$  occurred for females as their growth did not asymptote; a typical trait of large shark species. The maximum age estimated from vertebral analysis was 18 yr for both sexes, while the calculated longevity from the VBGF parameters was 27.4 yr

for males and 32.2 yr for females. Males matured at 174.7 cm TL and 10.5 yr old, while females matured at 208.9 cm TL and 14.8 yr old.

**Keywords** Reef shark · Growth · Maturity ogives · Akaike information criterion (AIC) · Fisheries · Elasmobranch

## Introduction

The silvertip shark, *Carcharhinus albimarginatus*, is one of the largest reef-associated shark species in the Indo-Pacific (Last and Stevens 2009). It is highly mobile in comparison with other reef-associated shark species (Espinoza et al. 2015b) and is known to spend time in deeper pelagic waters near drop offs (Forster et al. 1970; Bond et al. 2015). Despite its wide distribution, *C. albimarginatus* has been poorly studied and we know little of its life history and population status (Espinoza et al. 2015a; Osgood and Baum 2015). Records suggest that *C. albimarginatus* has a wide-ranging but fragmented distribution across the tropical Indo-Pacific (Bass et al. 1973; Ebert et al. 2013). However, little to no information is available regarding abundances and/or fisheries interactions from any part of its range. Recent studies have examined the habitat use and movement of *C. albimarginatus*, providing useful information about how marine parks may contribute to the species' management and conservation (Bond et al. 2015; Espinoza et al. 2015a, b). However, very little life-history information is available for *C. albimarginatus* (White 2007), precluding accurate population assessments.

*Carcharhinus albimarginatus* are born at 70–80 cm and can reach a maximum total length (TL) of 275 cm (Last and Stevens 2009). No length-at-age estimates are available, although a tagging study in the western Pacific Ocean

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determined that growth was fairly slow (Stevens 1984). According to the limited information available, this species has a gestation period of ca. 12 months and has litters of 1–11 pups with a mean of 6 (Wheeler 1962; Bass et al. 1973). The length at maturity of *C. albimarginatus* is poorly understood as mature females have rarely been sampled (Stevens 1984; White 2007). Based on the limited information available, males and females are estimated to mature at 160–180 cm TL and 160–199 cm TL, respectively (Ebert et al. 2013).

*Carcharhinus albimarginatus* are caught in longline, subsistence and artisanal fisheries in Papua New Guinea (PNG). Until July 2014, a dedicated shark longline fishery operated in the Bismarck and Solomon Seas of PNG (Kumoru 2003b). As some of the longline vessels operated in pelagic waters adjacent to coral reefs, *C. albimarginatus* were caught regularly (Kumoru 2003b). While they were not one of the main species caught by the shark longline fishery, *C. albimarginatus* composed ~6% of the annual catch prior to 2002 (Kumoru 2003a, b). However, after the enactment of a shark longline management plan in 2003, their catch had dropped markedly to <1% by 2007 (Usu 2011). Due to the paucity of data from the PNG region, the cause of this catch decline is unknown. Catches of *C. albimarginatus* were region specific with the majority of the catch coming from the Bismarck Sea in northern PNG (Kumoru 2003b). It is therefore unclear whether catch rates declined after 2003 as a result of unsustainable fishing or a redistribution of effort away from the areas where *C. albimarginatus* were caught. If population declines have occurred, the recent closure of the shark longline fishery now provides opportunity for *C. albimarginatus* to recover.

The National Fisheries Authority (NFA) of PNG has identified a need to develop better fisheries management practices, underpinned by increased knowledge of the key species exploited. In order to develop these practices, basic life-history information such as age, growth and maturity is required to form the basis of population assessments. *Carcharhinus albimarginatus* is caught by several fisheries in PNG waters, including coastal artisanal fisheries. The main aim of this study was to determine the life-history characteristics of *C. albimarginatus* in PNG and provide this information towards future demographic assessments.

## Materials and methods

### Sample collection

Samples were collected in May and June 2014 by NFA observers on board commercial longline vessels in the Bismarck and Solomon Seas. The longline vessels targeted sharks by setting a maximum of 1200 hooks close to the surface with a soak time of 8–10 h. Observers collected samples from the catch by recording biological information

including stretched TL, sex and maturation. The TL was measured to the nearest mm following Francis (2006). A section of the vertebral column was removed from a position anterior to the first dorsal fin and stored frozen. Species identification was verified using specimen photographs taken by observers to minimise the effects of species misidentification on the analyses (Smart et al. 2016b). All of the observers received pre-trip training at workshops which included species identification, specimen photography, data recording and maturity staging. Each observer was also supplied with a training and protocol manual for use at sea.

### Vertebrae sectioning

Vertebrae were processed following protocols described by Cailliet and Goldman (2004). Once transported to the laboratory, the vertebrae were defrosted and remaining muscle tissue was removed using a scalpel. Individual vertebral centra were then separated and soaked in a 4% sodium hypochlorite solution for 30 min to remove any remaining tissue. Centra were then dried in an oven at 60 °C for 24 h. A low-speed circular saw with two diamond-tipped blades (Buehler, Illinois, USA) was used to section individual centra. These longitudinal sections were made through the centrum focus at a thickness of 400 µm. Sections were mounted onto microscope slides using Crystal Bond adhesive (SPI supplies, Pennsylvania, USA).

### Age determination

Individual ages were estimated by counting translucent and opaque centrum band pairs in the corpus calcareum under a microscope using transmitted light (Cailliet and Goldman 2004). The transition from pre- to post-natal growth was identified from a change in the angle of the corpus calcareum and marked an age of zero. Each subsequent growth band pair was assumed to be 1 yr of growth. Validation of annual growth band deposition was not possible in this study as the limited sample size made mark-recapture impractical, and marginal increment analysis was precluded as monthly samples were not available. However, a strong body of the literature has shown that carcharhinid sharks typically deposit growth band pairs annually (e.g. Barreto et al. 2011; Chin et al. 2013; Harry et al. 2013).

Growth bands of individual centra were counted independently by two readers to reduce band-reading estimate bias (Cailliet and Goldman 2004). Neither reader had any prior knowledge of the TL or sex of the individuals. When counts differed between readers, those centra were re-examined by both readers until a consensus age was reached. If no consensus age was reached, those individuals were omitted from further analyses.

Inter-reader precision analyses were conducted on the original counts of both readers. Percent agreement (PA) and  $PA \pm 1$  yr were calculated with individuals grouped in 10-cm TL classes. For long-lived species, greater variation in growth band reading occurs as age increases. By grouping individuals by length class, the variability in calculating PA and  $PA \pm 1$  yr as age increases was accounted for. Grouping individuals by length rather than age avoids introducing bias to this approach as length is an empirical measurement, whereas age is estimated (Cailliet and Goldman 2004; Goldman et al. 2006). Average percent error (APE) and Chang's coefficient of variation (CV) (Chang 1982) were used to test precision of inter-reader growth band reads (Campana 2001). These statistics were calculated using the FSA package (Ogle 2016) in the 'R' programme environment (R Core Team 2013).

### Back calculation

Back-calculation techniques were applied to overcome the limited number of juveniles in the sample (Cailliet and Goldman 2004). Individual centrum sections were photographed using a compound video microscope, and the distances between growth band pairs were measured using image analysis software (Image Pro Plus version 6.2 for Windows, Media Cybernetics, 2002). The centrum radius (CR) was measured as a straight line from the focus to the centrum edge. The birth mark and each growth band pair were measured along this line as the distance from the focus to the nearest  $1 \mu\text{m}$ . A Dahl–Lea direct proportions back-calculation technique was applied (Carlander 1969):

$$L_i = \left( \frac{L_c}{CR_c} \right) \times CR_i$$

where  $L_i$  = length at growth band pair 'i',  $L_c$  = length at capture,  $CR_c$  = centrum radius at capture and  $CR_i$  = centrum radius at growth band pair 'i'.

An assumption of the Dahl–Lea direct proportions method is that there is a linear relationship between  $L_c$  and  $CR_c$ . This was tested by performing a linear regression between these two measurements.

A Rosa Lee phenomenon can occur when using back-calculation techniques as some fisheries can selectively harvest the fast-growing individuals from among the youngest age classes and the slow-growing individuals from among the oldest age classes. To determine whether the Rosa Lee phenomenon occurred in this study, the average radius of each growth band was calculated for each age class to determine whether there were differences in band deposition (and therefore growth) in older individuals (Walker et al. 1998). A repeated-measures ANOVA was applied to determine whether there were differences among ages at capture.

### Growth modelling

Growth was estimated using a multi-model framework that included three candidate growth functions a priori (Table 1) (Smart et al. 2016a). Model selection was determined using Akaike's information criterion (Akaike 1973) with a small sample size adjusted bias correction ( $AIC_c$ ) as recommended for sample sizes less than 200 (Zhu et al. 2009). A multi-model approach was used because use of only one model such as the VBGF can generate biased growth estimates if it is inappropriate for species' growth patterns (Katsanevakis 2006). Using a multi-model framework which incorporates  $AIC_c$  circumvents the risk of using an inappropriate model and produces the most robust growth estimates possible (Smart et al. 2016a). A parameterisation that included length at birth ( $L_0$ ) and asymptotic length parameters ( $L_\infty$ ) was used for all three candidate models (Table 1). Best-fit parameter estimates were determined for all three candidate models using the 'nls' function in the 'R' programme environment (R Core Team 2013).  $AIC_c$  was also calculated in the 'R' programme environment as

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

where  $AIC = n \log(\sigma^2) + 2k$ ,  $k$  is the total number of parameters +1 for variance ( $\sigma^2$ ), and  $n$  is the sample size. The model with the lowest  $AIC_c$  value ( $AIC_{\min}$ ) had the best fit to the data and was thus identified as the most

**Table 1** Model equations of the three a priori growth functions used to estimate Length-at-age

Growth function	Equation	References
von Bertalanffy growth function	$L_t = L_0 + (L_\infty - L_0)(1 - \exp(-kt))$	von Bertalanffy (1938)
Gompertz function	$L_t = L_0 \exp\left(\ln\left(\frac{L_\infty}{L_0}\right)(1 - \exp(-g_{\text{gom}}t))\right)$	Ricker (1975)
Logistic function	$L_t = \frac{L_\infty L_0 (\exp(g_{\text{log}}t))}{L_\infty + L_0 (\exp(g_{\text{log}}t) - 1)}$	Ricker (1979)

$L_t$  is Length-at-age  $t$ ,  $L_0$  is length at age 0,  $L_\infty$  is asymptotic length,  $k$ ,  $g_{\text{log}}$ , and  $g_{\text{gom}}$  are the different growth coefficients of the respective models (which are incomparable)

appropriate of the candidate models. The remaining models were ranked using the AIC difference ( $\Delta$ ) which was calculated for each model ( $i = 1-3$ ) as:

$$\Delta = AIC_c - AIC_{min}.$$

Models with  $\Delta$  of 0–2 had the highest support, while models with  $\Delta$  of 2–10 had considerably less support and models with  $\Delta$  of >10 had little or no support (Burnham and Anderson 2001). AIC weights ( $w$ ) represent the probability of choosing the correct model from the set of candidate models and were calculated for each model ( $i = 1-3$ ) as:

$$w_i = \frac{\exp\left(-\frac{\Delta_i}{2}\right)}{\sum_{j=1}^3 \exp\left(-\frac{\Delta_j}{2}\right)}.$$

Multi-model inference (MMI) is recommended when no model candidate is the outright best model for the data ( $w > 0.9$ ) (Katsanevakis and Maravelias 2008). Therefore, in instances where candidate models performed similar according to  $AIC_c$ , model-averaged length-at-age estimates, parameters and standard errors were calculated. Only  $L_\infty$  and  $L_0$  were comparable among the three model candidates as the three growth completion parameters ( $k$ ,  $g_{log}$  and  $g_{Gom}$ ) are incomparable between them. Therefore, a model-averaged value was calculated as:

$$\bar{L}_\infty = \sum_{i=1}^3 w_i * L_{\infty,i}$$

where  $\bar{L}_\infty$  was the model-averaged asymptotic length (Burnham and Anderson 2002; Katsanevakis 2006). The unconditional standard error of  $\bar{L}_\infty$  was estimated as:

$$SE(\bar{L}_\infty) = \sum_{i=1}^3 w_i * (var(L_{\infty,i}|g_i) + (L_{\infty,i} - \bar{L}_\infty)^2)^{1/2}$$

where  $var(L_{\infty,i}|g_i)$  is the variance of parameter  $L_\infty$  of model  $g_i$  (Katsanevakis and Maravelias 2008). A model-averaged estimate and standard error of  $L_0$  were calculated using the same equations.

A likelihood ratio test was performed to determine whether sexes should be combined or separated (Kimura 1980). This was performed for each candidate model of both the observed and back-calculated data using the method outlined by Haddon (2001) modified for the ‘R’ programme environment (R Core Team 2013). Growth curves were produced for separate sexes if the likelihood ratio test of the best-fitting model (or any individual candidate model where MMI was required) determined a significant difference existed for either data set.

Where the VBGF was the best-fitting growth model, estimates of longevity were calculated as:

$$t_{max} = 7 * \ln\left(\frac{2}{k}\right)$$

where  $t_{max}$  is longevity in years and  $k$  is the growth coefficient of the VBGF (Mollet et al. 2002).

### Maturity estimation

The maturity of each individual was determined on board vessels by fisheries observers using an index modified from Walker (2005) (Table 2). These maturity stages were verified post-cruise by using photographs of the gonads taken by the observers. Male maturity stages were based on clasper condition ( $C = 1-3$ ), and female maturity stages were based on uterus condition ( $U = 1-5$ ) (Table 2). Maturity stage data were converted to a binary maturity category (immature = 0 or mature = 1) for statistical analysis. Estimates of length at maturity were produced for males and females using a logistic regression model (Walker 2005):

$$P(l) = P_{max} \left( 1 + e^{-\ln(19) \left( \frac{l-l_{50}}{l_{95}-l_{50}} \right)} \right)^{-1}$$

where  $P(l)$  is the proportion of the population mature at TL  $l$  and  $P_{max}$  is the maximum proportion of mature individuals. The lengths that 50 and 95% of the population were mature ( $l_{50}$  and  $l_{95}$ ) were estimated using a generalised linear model with a binomial error structure and a logit-link function in the ‘R’ programme environment (R Core Team

**Table 2** Indices for staging maturity condition. Adapted from Walker (2005)

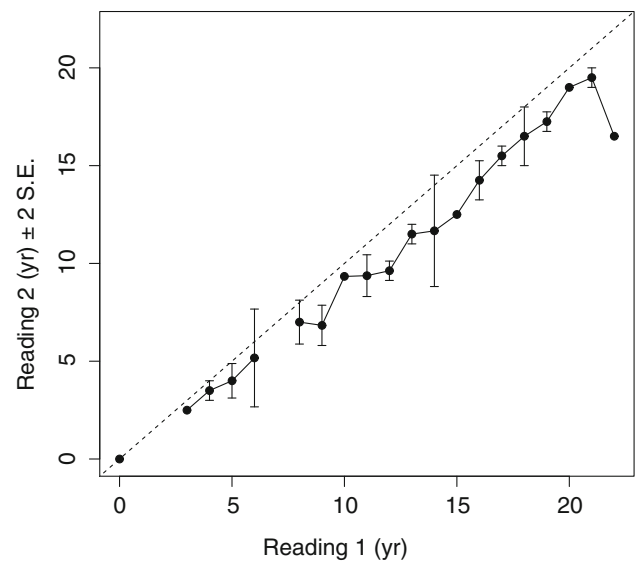
Organ	Index	Description	Binary maturity condition
Female uterus	$U = 1$	Uniformly thin tubular structure. Ovaries small and without yolked ova	Immature
	$U = 2$	Thin, tubular structure which is partly enlarged posteriorly. Small yolked ova developing	Immature
	$U = 3$	Uniformly enlarged tubular structure. Yolked ova developed	Mature
	$U = 4$	<i>In utero</i> eggs or embryos macroscopically visible	Mature
	$U = 5$	Post-partum—enlarged tubular structure distended	Mature
Male clasper	$C = 1$	Pliable with no calcification	Immature
	$C = 2$	Partly calcified	Immature
	$C = 3$	Rigid and fully calcified	Mature

2013). Population estimates of age at maturity ( $a_{50}$  and  $a_{95}$ ) were estimated using the same methods.  $l_{50}$  and  $a_{50}$  were used as metrics to describe the approximate length-and-age-at-maturity for the population.

## Results

The sample consisted of 48 *C. albimarginatus*, which included 28 males (95–219 cm TL) and 20 females (116–250 cm TL). Male ages ranged between 0 and 18 yr and females between 3 and 18 yr. The APE and CV of the age estimates were 17.2 and 24.4%, respectively. The  $PA \pm 1$  yr was 24.5% with differences in age estimates occurring increasingly with age (Table 3). These differences occurred as the growth band pairs were poorly defined throughout the centrum regardless of CR. Therefore, ageing differences occurred with Reader 2 consistently estimating lower than Reader 1 (Fig. 1). Additionally, growth band pairs were compressed at the edges of larger individuals suggesting a cessation in formation. This growth band compression meant that the largest ageing discrepancies occurred for the largest individuals in the sample (Table 3; Fig. 1). However, this discrepancy was overcome during the consensus reads with no individuals requiring omission from the growth analyses. Visual inspection of the growth curve indicates that the consensus reads show little variation either side of the growth curve (Fig. 2a).

There was no significant difference in growth curves between the sexes (likelihood ratio test using the observed



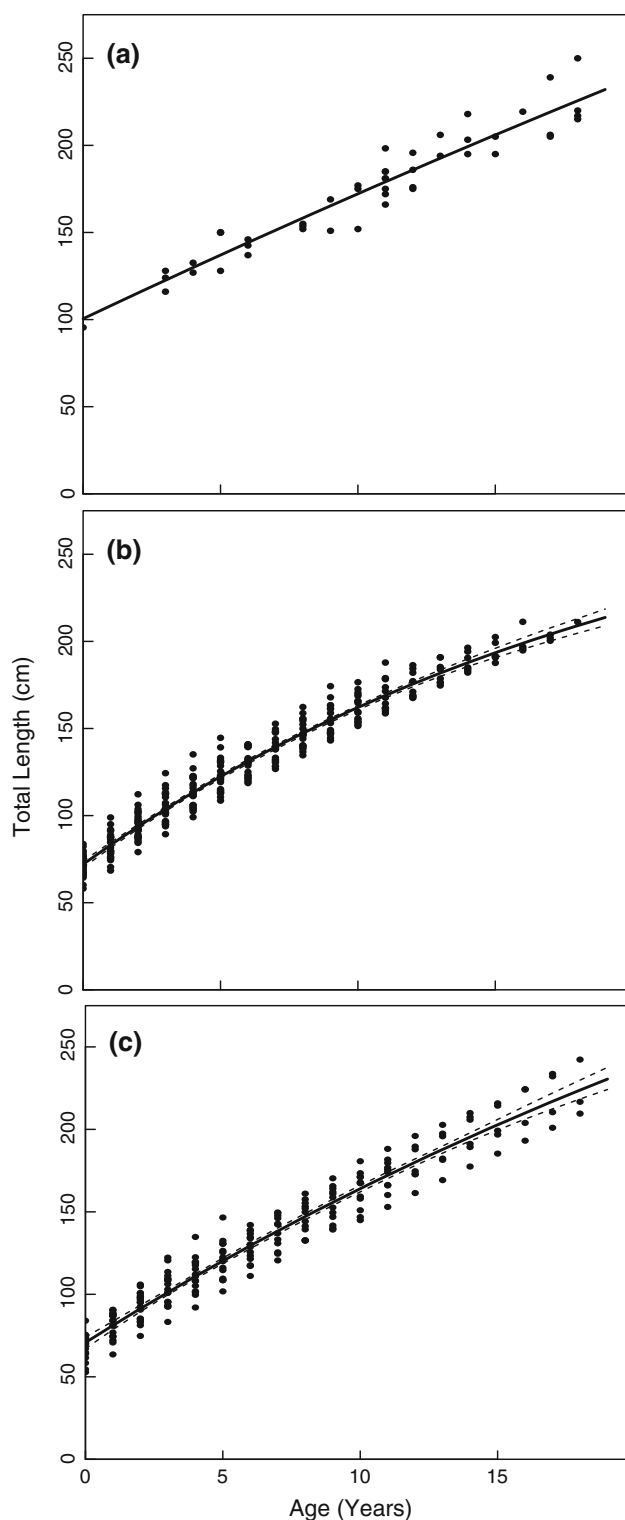
**Fig. 1** Age-bias plot for *Carcharhinus albimarginatus* incorporating the age-specific agreements between Readers 1 and 2. Mean age-specific agreements  $\pm 2$  standard errors are plotted along a 1:1 equivalence line. The average percent error (APE) and coefficient of variation (CV) were 17.24 and 24.38 respectively

data; VBGF [ $df = 3$ ,  $\chi^2 = 6.55$ ,  $p = 0.08$ ]; Logistic [ $df = 3$ ,  $\chi^2 = 7.6$ ,  $p = 0.055$ ]; Gompertz [ $df = 3$ ,  $\chi^2 = 7.79$ ,  $p = 0.051$ ]). Therefore, a growth curve was produced with the sexes combined (Fig. 2a). All three candidate models provided equivalent  $w$  for the observed data (Table 4). Therefore, MMI was used to provide model-averaged length-at-age,  $\bar{L}_\infty$  and  $\bar{L}_0$  estimates. These estimates were  $\bar{L}_0 = 101.9$  cm TL and  $\bar{L}_\infty = 598.7$  cm

**Table 3** Percent agreement (PA) and percent agreement  $\pm 1$  yr ( $PA \pm 1$ ) between growth band readers for *Carcharhinus albimarginatus* divided into 10-cm-total-length (TL) classes

TL class (cm)	Number of readings	Number agreed	Number agreed $\pm 1$ yr	PA	PA $\pm 1$
90–100	1	1	1	100	100
110–120	1	0	0	0	0
120–130	4	1	2	25	50
130–140	2	1	1	50	50
140–150	3	0	1	0	33.34
150–160	7	0	1	0	14.29
160–170	2	0	0	0	0
170–180	6	0	1	0	16.67
180–190	6	1	2	16.67	33.34
190–200	5	1	1	20	20
200–210	5	0	1	0	20
210–220	4	0	0	0	0
220–230	1	0	0	0	0
230–240	1	0	1	0	100
240–250	1	0	0	0	0
n	49	5	12	–	–
Percent agreement	–	–	–	10.20	24.49





TL. A large  $\bar{L}_\infty$  was not unexpected as the growth curve lacked a clear asymptote. Therefore,  $\bar{L}_\infty$  was in this instance not equivalent to maximum size as it is often considered. However, a  $\bar{L}_0$  value of 101.9 cm TL was considerably larger than empirical length-at-birth estimates

**Fig. 2** Length-at-age curves for **a** the observed data for sexes combined, **b** the back-calculated data for males and **c** the back-calculated data for females. Growth curve **a** was predicted using multi-model inference results as all three model candidates performed similarly for the observed data with sexes combined. Growth curves **b** and **c** were both predicted from the von Bertalanffy growth function parameters as this model had an  $AIC_c$  weight ( $w$ ) > 0.9 for both males and females for the back-calculated data. Likelihood ratio tests identified sexual dimorphism in growth for the back-calculated data but not the observed data. The dashed line represents bootstrapped 95% confidence intervals for the VBGF estimates. 95% confidence intervals are not applicable for MMI results

of 70–80 cm TL (Last and Stevens 2009). Therefore, the growth curve of the observed data lacked clear biological realism and required back-calculation techniques to supplement the observed data and correct for the low number of juveniles in the sample that caused an overestimated  $\bar{L}_0$  value.

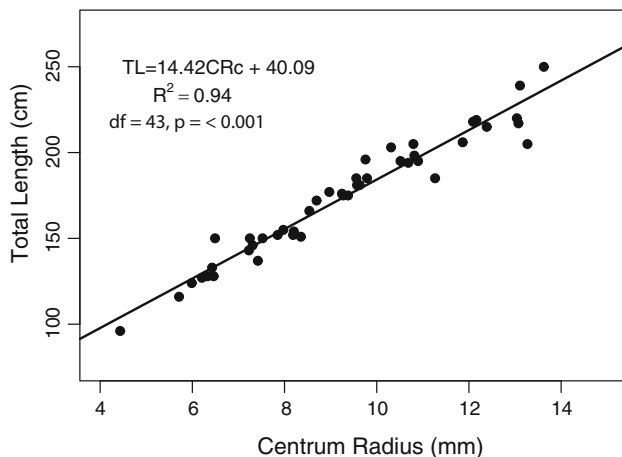
A linear relationship was determined between  $L_c$  and  $CR_c$  (Fig. 3). Therefore, the Dahl–Lea direct proportions technique was appropriate for this species. Using the back-calculated data, the likelihood ratio test revealed a significant difference between the growth of males and females (VBGF [ $df = 3$ ,  $\chi^2 = 22.86$ ,  $p = < 0.001$ ]; Logistic [ $df = 3$ ,  $\chi^2 = 26.35$ ,  $p = < 0.001$ ]; Gompertz [ $df = 3$ ,  $\chi^2 = 24.64$ ,  $p = < 0.001$ ]). Therefore, separate growth curves were produced for males and females (Fig. 2b, c). The VBGF provided the best fit and had a  $w > 0.9$  for both sexes (Table 4). Therefore, MMI was not necessary and estimates of longevity were calculated as 27.4 yr for males and 32.2 yr for females. The VBGF  $L_0$  and  $k$  estimates were both similar for males and females (Table 4). However, females had a much larger  $L_\infty$  (497.9 cm TL) in comparison with the males (311.3 cm TL). The high VBGF  $L_\infty$  value produced for females is far larger than their reported maximum size of 275 cm TL (Last and Stevens 2009). This is not indicative of a poorly fitting growth curve, but that asymptotic growth has not occurred. The narrow confidence intervals indicate that the model has high precision (Fig. 2c), as does the low standard error (SE) of the  $L_0$  and  $k$  parameters. The SE was inflated for the  $L_\infty$  parameter as the theoretical age that the species would reach to achieve it lies too far outside of the data. Therefore, it does not represent low precision for the growth curve but instead identifies the lack of asymptotic growth due to an absence of maximum-age individuals.

There was no significant difference in the distance between growth band pairs for different ages at capture ( $df = 1$ ,  $F = 2.543$ ,  $p = 0.112$ ). While some variation occurred at certain ages, it was negligible and likely caused by a low number of individuals in those age classes (Fig. 4). These results demonstrate that the Rosa Lee phenomenon did not occur in this study.

**Table 4** Summary of model parameters and adjusted Akaike information criterion ( $AIC_C$ ) results for the observed length-at-age and back-calculated data for *Carcharhinus albimarginatus*. Model parameters were produced for separate sexes for the back-calculated data as sexual dimorphism in growth was determined by likelihood ratio

Sex	Model	$n$	$AIC_C$	$\Delta$	$w$ (%)	$L_\infty$ ( $\pm$ SE)	$L_0$ ( $\pm$ SE)	$k$ ( $\pm$ SE)	$g_{\text{Gom}}$ ( $\pm$ SE)	$g_{\text{log}}$ ( $\pm$ SE)	$RSE$
Observed data											
Combined	VBGF	48	365.75	0.00	0.35	1044.5 ( $\pm$ 2015.9)	100.5 ( $\pm$ 6.35)	0.01 ( $\pm$ 0.02)	–	–	10.32
	Logistic	48	365.94	0.19	0.32	319.58 ( $\pm$ 57.16)	103.25 ( $\pm$ 5.2)	–	–	0.09 ( $\pm$ 0.02)	10.34
	Gompertz	48	365.85	0.10	0.33	397.1 ( $\pm$ 127.9)	103.3 ( $\pm$ 5.2)	–	0.05 ( $\pm$ 0.02)	–	10.33
	Model average	–	–	–	–	598.7 ( $\pm$ 891.5)	101.9 ( $\pm$ 5.9)	–	–	–	–
Back calculated											
Males	VBGF	300	2081.69	0.00	0.92	311.3 ( $\pm$ 20.7)	72.1 ( $\pm$ 1.0)	0.04 ( $\pm$ 0.00)	–	–	7.79
	Logistic	300	2095.55	13.85	0.00	220.6 ( $\pm$ 4.5)	75.0 ( $\pm$ 0.9)	–	–	0.17 ( $\pm$ 0.00)	7.97
	Gompertz	300	2086.45	4.75	0.08	242.8 ( $\pm$ 7.3)	73.6 ( $\pm$ 1.0)	–	0.11 ( $\pm$ 0.00)	–	7.85
Females	VBGF	209	1571.59	0.00	0.93	497.9 ( $\pm$ 101.2)	70.8 ( $\pm$ 1.6)	0.02 ( $\pm$ 0.00)	–	–	10.26
	Logistic	209	1582.64	11.05	0.00	256.7 ( $\pm$ 9.8)	74.3 ( $\pm$ 1.4)	–	–	0.14 ( $\pm$ 0.00)	10.54
	Gompertz	209	1576.49	4.90	0.07	297.8 ( $\pm$ 18.1)	72.6 ( $\pm$ 1.5)	–	0.08 ( $\pm$ 0.00)	–	10.39

$n$  is the sample size,  $AIC_C$  is the small sample bias adjusted form of Akaike's information criterion,  $\Delta$  is the difference in  $AIC_C$  values between models,  $w$  (%) are the  $AIC_C$  weights,  $L_\infty$  is asymptotic length parameter in cm,  $L_0$  is the length-at-birth parameter in cm,  $k$  is the growth completion parameter in  $\text{yr}^{-1}$  for the VBGF,  $g$  is the growth parameter for Logistic and Gompertz functions (but is incomparable between the two),  $SE$  is the standard error of the adjacent parameter, and  $RSE$  is the residual standard error of the model



**Fig. 3** Relationship between centrum radius ( $CR_c$ ) and stretched total length (TL) for *Carcharhinus albimarginatus*

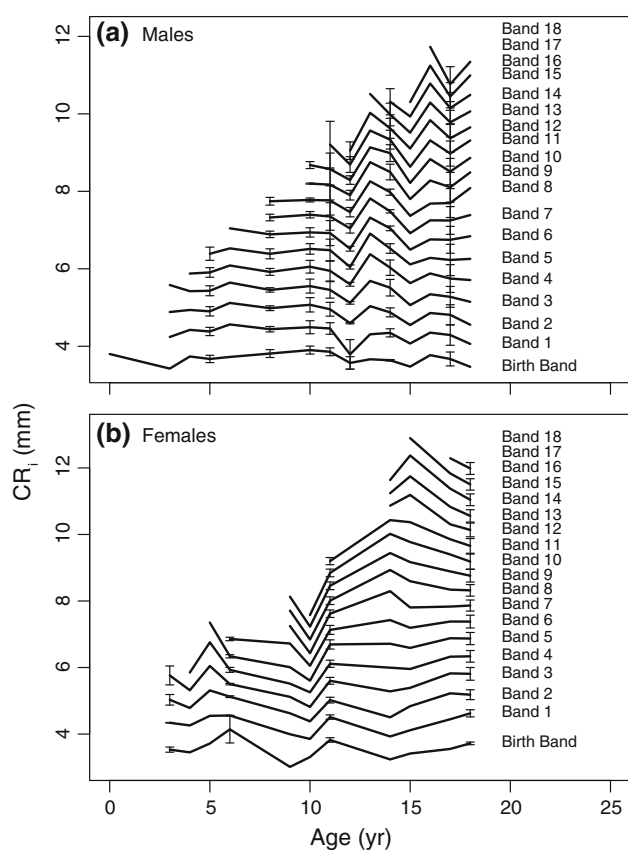
Male and female *C. albimarginatus* mature at different ages and lengths. The maximum likelihood estimates of  $l_{50}$  and  $a_{50}$  for males were  $174.7 \pm 1.8$  cm TL and  $10.5 \pm 0.8$  yr old, respectively (Fig. 5a, c). Female estimates of  $l_{50}$  and  $a_{50}$  were  $208.9 \pm 6.9$  cm TL and  $14.8 \pm 1.3$  yr, respectively, showing that females mature at greater lengths and older ages than males (Fig. 5b, d). Both  $l_{50}$  values resemble previously estimated values of 170 cm TL for males and 195 cm TL for females (Last and Stevens 2009).

tests. Multi-model inference was used to produce model-averaged  $L_\infty$  and  $L_0$  estimates for the observed data due to similar  $w$ . This was not required for the back-calculated data as the von Bertalanffy growth function (VBGF) had  $w > 0.9$

## Discussion

*Carcharhinus albimarginatus* had been poorly studied in comparison with many other species of reef-associated sharks (Osgood and Baum 2015), and consequently little was known about many aspects of its biology (White 2007). The life-history estimates presented in this study provide an important foundation for future population assessments and the development of management and conservation strategies. These estimates indicate that *C. albimarginatus* grows slowly and matures late as had previously been suspected (Stevens 1984). Asymptotic growth was not observed, suggesting that either maximum age has been underestimated or that maximum-age individuals were not included in the sample, a scenario often encountered with large shark species (Cailliet et al. 1985; Natanson et al. 1995; Simpfendorfer et al. 2002). This study provides the most robust maturity estimates for the species so far, especially for females. However, the late age at maturity for females also suggests the maximum age has either been underestimated by vertebral analysis or that minimum-age individuals were not included in the sample.

The application of back-calculation techniques produced length-at-age estimates that better modelled the early growth of *C. albimarginatus*. The observed data lacked young of the year (YOY) individuals, which meant that  $L_0$  was overestimated by all three candidate models and subsequently the MMI. This occurs because growth models are



**Fig. 4** Mean growth band radius ( $\pm$ SE) for each age at capture of **a** males and **b** females

most sensitive to the smallest and largest individuals in the sample (Haddon 2001). Therefore, when YOY are missing, the growth curve will overestimate  $L_0$  and underestimate the growth completion parameters ( $k$ ,  $g_{\log}$  and  $g_{\text{Gom}}$ ). Recent research has shown that as few as five YOY individuals are sufficient to overcome this issue (Smart et al. 2015). These individuals do not necessarily need to be aged using vertebral analysis, so long as they can be confirmed as YOY by unhealed umbilical scars (Bishop et al. 2006). However, the length-selective nature of many fisheries means that YOY individuals can be difficult to sample (Gwinn et al. 2010). In this study, young juveniles (ages 0–3 yr) were not caught by the fishery, and therefore the application of back-calculation techniques was necessary to account for missing YOY for both sexes.

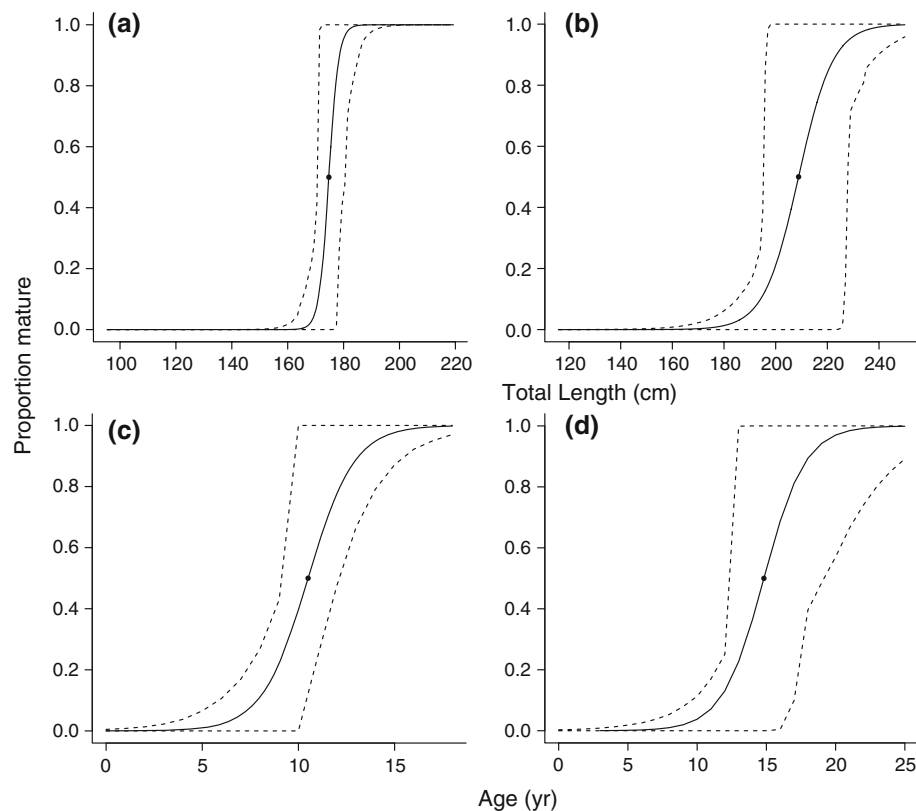
Back-calculation techniques must be used with caution when applied to exploited populations due to the potential effects of the Rosa Lee phenomenon (Lee 1912; Ricker 1969; Walker et al. 1998). This phenomenon occurs as some fisheries selectively harvest the fast-growing individuals from among the youngest age classes and the slow-growing individuals from among the oldest age classes (Walker et al. 1998). When this occurs, growth estimates can be biased as individuals with varying growth rates have

unequal probabilities of being included in the sample. Furthermore, back calculation can introduce error into length-at-age estimates as it adds interpolated data rather than increasing the sample size. As these interpolated data are not independent, small ageing errors can potentially be magnified through back calculation. In this study, the back-calculated data provided similar length estimates to the corresponding age classes in the observed data. This demonstrates that there were no gross errors in the back-calculation estimates, although it should be noted that small amounts of bias cannot be detected in this approach (Francis 1990). In addition, the  $L_0$  estimate produced by the back-calculation matched empirical length-at-birth estimates for the species (Last and Stevens 2009), demonstrating realistic values. The presence of the Rosa Lee phenomenon was tested in this study using the method of Walker et al. (1998) which compares the distance between growth bands of sharks caught at different ages. A lack of differentiation in the growth of older and younger sharks demonstrated that the Rosa Lee phenomenon was not present in this study. Therefore, the use of back-calculation was appropriate as neither biased estimates nor the Rosa Lee phenomenon occurred.

The VBGF best fitted the back-calculated data. MMI is an approach that can improve final growth estimates by avoiding the use of an inappropriate model a priori (Katsanevakis 2006; Katsanevakis and Maravelias 2008). However, MMI is not necessary when an individual growth function receives an AIC  $w > 0.9$  (Katsanevakis and Maravelias 2008). This occurred for both the male and female growth curves for the back-calculated data with the VBGF selected for both sexes. However, for the observed data, the three candidate models produced equal  $w$ , and therefore MMI was used. It is not unusual for MMI to be necessary for observed data but not required when the same sample is back calculated. This occurs as back calculation is required most often when sample sizes are small (Smart et al. 2013). However, when the sample is small, all candidate models will often provide similar fits as there are insufficient data for them to attain their divergent shapes (Smart et al. 2016a). Once interpolated data are added through back calculation, the sample size is increased and individual candidate models can assume their individual shapes. In this instance, the VBGF provided a better fit than the logistic and Gompertz functions. Therefore, even though a multi-model approach was not required in this case, greater confidence can be placed on the estimates of the VBGF as alternate growth functions have been applied and rejected.

The VBGF estimated that males live until ca. 27 yr old and females until ca. 32 yr old. While *C. albimarginatus* were aged to a maximum of 18 yr by directly counting vertebral rings, these results were likely underestimates. Larger individuals showed signs of growth band compression,





**Fig. 5** Length- and age-at-maturity ogives for male (a, c) and female (b, d) *Carcharhinus albimarginatus*. Black points indicate  $L_{50}$  (a, b) and  $a_{50}$  (c, d), respectively, and the dashed lines represent bootstrapped 95% confidence intervals

where the most recent growth bands in older individuals were laid close together, poorly defined and difficult to distinguish. *Carcharhinus albimarginatus* may cease to lay annual growth bands past a certain age because growth is insufficient to produce discernible growth bands. This has been documented in numerous shark species, suggesting that growth band deposition can in many instances be ontogenetic (Cailliet 2015). For example, *Lamna nasus* has been shown to live almost twice as long as was estimated from vertebral analysis (Francis et al. 2007). In the present study, longevity estimates were calculated for *C. albimarginatus* using parameters from the VBGF. These estimates (27.4 and 32.2 yr for males and females, respectively) appear far more reasonable than those derived from direct vertebral counts as they are consistent with the longevity of similar-sized species (Francis et al. 2007). This uncertainty in longevity should be accounted for when conducting demographic analyses by running multiple scenarios where longevity is varied. The length-at-age estimates presented here remain valid, although they only range from 0 to 18 yr and represent a probably incomplete growth curve due to the absence of the maximum-age individuals.

The results of the VBGF show that *C. albimarginatus* is a slow-growing species with  $k$  values that were similar to

other large whaler sharks (Casey and Natanson 1992; Natanson et al. 1995; Simpfendorfer 2000). The values of  $k$  for both males and females were low, which indicates that the species takes a long time to reach maximum size. In this instance, it should be noted the  $L_{\infty}$  of *C. albimarginatus* is not equivalent to maximum size. This is because asymptotic growth was not observed due to the possible under ageing or absence of maximum-age individuals (due to sampling limitations or their absence from the population from the effects of fishing). Therefore, the  $L_{\infty}$  parameter was inflated and outside the size range of the species. This is often the case with large shark species (Cailliet et al. 1985; Natanson et al. 1995; Simpfendorfer et al. 2002) and does not invalidate the  $L_{\infty}$  parameter or the growth curve. Instead, the  $L_{\infty}$  parameter is the value which is needed to calculate length-at-age estimates over the age range included in the sample (0–18 yr in this study). The  $L_0$  of the back-calculated data was within range of empirical values recorded for *C. albimarginatus* (Last and Stevens 2009), indicating that missing YOY have been adequately accounted for. Therefore, the results of this study represent biologically realistic length-at-age estimates for *C. albimarginatus* until an age of 18 yr.

Limited maturity information is available for *C. albimarginatus* with some disparity between studies. Male *C.*

*albimarginatus* from Indonesia were estimated to mature at ca. 193–199 cm TL (White 2007), while maturity in the western Indian Ocean was estimated to be 170–180 cm TL (Stevens 1984). This study found that male  $l_{50}$  (174.7 cm TL) was similar to the western Indian Ocean population (Stevens 1984). However, low numbers of mature females impeded the ability to estimate an accurate length at maturity in both Indonesia and the western Indian Ocean (Stevens 1984; White 2007). Two mature females were dissected by Stevens (1984); one 188.1 cm TL individual that was virgin and a 204.7 cm TL individual that was not virgin. In Indonesia, two pregnant females were encountered that were both larger than 230 cm TL, providing a preliminary length at first reproduction (White 2007). In the present study, five mature females were examined (205–250 cm TL) along with a further eight which were maturing (stage 2), providing the most complete data set to date from which to estimate female maturity. The resulting  $l_{50}$  estimate for females was 208.9 cm TL with the largest immature (stage 2) female at 196 cm TL. Given this  $l_{50}$  is larger than confirmed pregnant or post-partum females it is likely that *C. albimarginatus* females mature at sizes ranging from 190 to 210 cm TL. The  $a_{50}$  estimated for females in this study was 14.8 yr, and the approximate age of the smallest mature female from Stevens (1984) (extrapolated from length-at-age estimates from the present study) was 13 yr old. This indicates that *C. albimarginatus* mature at 40–46% of their maximum age according to the calculated longevity. According to maximum vertebral age, this value would be 80% which further suggests that *C. albimarginatus* live longer than 18 yr. Therefore, *C. albimarginatus* could be at risk of recruitment overfishing if mature individuals are taken in large numbers by the fishery (Musick et al. 2000).

Conducting life-history studies on heavily exploited populations has been shown to yield estimates that are different from an unfished (or lightly fished) population (Walker et al. 1998). This occurs for three reasons: (1) length-selective fishing mortality results in a biased sample (Walker et al. 1998); (2) high levels of exploitation have caused changes to population life history, possibly through compensation (Sminkey and Musick 1995); or (3) heavy exploitation has caused a truncated age distribution (Hsieh et al. 2010; Rouyer et al. 2011; Stewart 2011). The absence of the Rosa Lee phenomenon indicates that this sample was likely representative of the current population structure as individuals of different ages displayed similar growth rates. However, the dome-shaped selectivity of fisheries may reduce the likelihood of *C. albimarginatus* from reaching maximum age (Taylor and Methot 2013). As this study aged *C. albimarginatus* to 18 yr and determined that females mature at 14.8 yr, it is likely that some level of age truncation may have occurred in this stock. This is difficult

to determine as no historical data on age distributions are available for *C. albimarginatus*. However, future work should aim to validate the ages of larger individuals. This will determine whether these individuals have been under-aged and possibly indicate whether the maximum age of this population has been decreased due to exploitation. Given the uncertainty around the maximum age of *C. albimarginatus*, future studies should focus on producing life-history information from a larger sample size that includes the largest size classes. However, until such a study can be conducted, the present study provides realistic life-history estimates for an exploited population.

The population status of *C. albimarginatus* in PNG waters is not currently understood. The recent closure of the shark longline fishery has likely reduced the number of *C. albimarginatus* harvested in PNG. However, they continue to be taken as bycatch in PNG tuna fisheries (Nicol et al. 2009) as well as in coastal artisanal and subsistence fisheries. The full extent of their catch is unknown as PNG, and artisanal fisheries are particularly data poor (Teh et al. 2014). Future studies should focus on producing demography estimates for the PNG *C. albimarginatus* population using these life-history data and accounting for their uncertainty (particularly longevity and age at female maturity). Given the lack of life-history data from other parts of its range, the life-history information for *C. albimarginatus* from PNG can be used for populations from other regions until further studies are conducted. However, it should be used with caution as regional variation in life-history estimates has been documented in other shark species (Driggers et al. 2004; Carlson et al. 2006; Smart et al. 2015). The fragmented distribution and limited dispersal of *C. albimarginatus* (Ebert et al. 2013) makes this species potentially susceptible to this regional variation.

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