

Age, growth and maturity of oceanic whitetip shark (*Carcharhinus longimanus*) from Papua New Guinea

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Abstract. Oceanic whitetip sharks (*Carcharhinus longimanus*) in the Western Central Pacific have been overfished and require improved assessment and management to enable planning of recovery actions. Samples from 103 individuals (70 males and 33 females; 76.0–240- and 128–235-cm total length (TL) respectively) were used to estimate age, growth and maturity parameters from sharks retained by longline fisheries in Papua New Guinea. Back-calculation was used because of the low number of juveniles and a multimodel framework with Akaike's information criterion corrected for small sample size (AIC_c) estimated growth parameters. The von Bertalanffy growth model provided the best fitting growth model for both sexes. Parameter estimates for males were: asymptotic length (L_{∞}) = 315.6 cm TL; growth coefficient (k) = 0.059 year⁻¹; and length at birth (L_0) = 75.1 cm TL. For females, the parameter estimates were: L_{∞} = 316.7 cm TL; k = 0.057 year⁻¹; and L_0 = 74.7 cm TL. Maximum age was estimated to be 18 years for males and 17 years for females, with a calculated longevity of 24.6 and 24.9 years respectively. Males matured at 10.0 years and 193 cm TL, whereas females matured at 15.8 years and 224 cm TL. *C. longimanus* is a slow-growing, late-maturity species, with regional variation in life history parameters, highlighting increased vulnerability to fishing pressure in this region.

Additional keywords: pelagic shark fisheries, vertebral analysis, Western Central Pacific Ocean.

Received 3 May 2016, accepted 3 August 2016, published online 14 September 2016

Introduction

Accurately describing the life history characteristics (e.g. age, growth and reproduction) of species is the foundation for an understanding of the species biology, population dynamics and status (Hoenig and Gruber 1990). Characterising these traits is crucial for fisheries stock assessment, management and conservation, especially for long-lived, slow-growing, late-maturing and less-fecund species, such as sharks and rays (Cortés 2000). The life history characteristics of many sharks and rays results in a lower productivity compared with teleost fish, increasing their vulnerability to human pressures (e.g. sustained direct or incidental fishing pressure) and prolonging recovery times from population declines (Compagno 1990; Dulvy *et al.* 2014). Life history traits of sharks and rays can vary considerably between species, as well as between conspecific populations (García *et al.* 2008; Kyne and Simpfendorfer 2010; Rigby and Simpfendorfer 2013). Regional differences in life history characteristics may reflect regional selection pressures and alternative population dynamics, and can also affect the

capacity for each population to withstand exploitation and so affect fisheries assessment and management (Cortés 2008; Francis *et al.* 2008). As such, life history studies from local populations are critical to providing more accurate and robust assessment of current fisheries sustainability and an understanding of the status of shark populations (Lombardi-Carlson *et al.* 2003; Cailliet and Goldman 2004; Goldman *et al.* 2012; Smart *et al.* 2015).

There is global concern over rapidly declining populations of oceanic sharks, with many species being caught in large numbers in longline, purse seine and gill net fisheries on the high seas (Dulvy *et al.* 2008, 2014). Oceanic pelagic sharks are widely distributed and highly mobile species that primarily inhabit open ocean habitats. Although the declines of pelagic sharks highlight the need for improved management and conservation, their inaccessibility and the historically low management priority have hampered management efforts and resulted in limited and ambiguous data (Cortés *et al.* 2010). Thus, in order to manage data-poor pelagic shark species for sustainable outcomes, an

understanding of the basic life history information and population trajectory of a species is required.

The oceanic whitetip shark (*Carcharhinus longimanus*; family Carcharhinidae) is a highly migratory, large-bodied whaler shark (maximum size 350–395-cm total length (TL)) with a circumglobal distribution in tropical and subtropical seas (Bigelow and Schroeder 1948; Lessa *et al.* 1999). It is a strictly oceanic species, primarily occupying the epipelagic water column (0–150 m; Musyl *et al.* 2011; Howey-Jordan *et al.* 2013). *C. longimanus* is currently listed by the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species as globally 'Vulnerable' and 'Critically Endangered' in the North-west and Western Central Atlantic Ocean due to extensive population declines across its distribution (Baum *et al.* 2015). Despite its global distribution and relatively high interaction with fisheries, there is limited life history information for *C. longimanus*. Currently, the main information regarding the age, growth and reproductive biology of this species is limited to three studies, one in the North Pacific Ocean (Seki *et al.* 1998), one in the North-west Pacific Ocean (Joung *et al.* 2016) and one in the South-west Atlantic Ocean (Lessa *et al.* 1999). Individuals in the North-west Pacific Ocean are reported to have slower growth (von Bertalanffy growth coefficient (k) = 0.085 year⁻¹; Joung *et al.* 2016) than individuals from the North Pacific Ocean and South-west Atlantic Ocean (k = 0.099–0.103 year⁻¹; Seki *et al.* 1998; Lessa *et al.* 1999), but sexual maturity (5–9 years and 175–194 cm TL) and size at birth (63.0–77.0 cm TL) of *C. longimanus* does not appear to differ between sexes and regions (Seki *et al.* 1998; Lessa *et al.* 1999; Joung *et al.* 2016). The longevity of this species was estimated to be 35–36 years (Seki *et al.* 1998). Life history information is lacking for *C. longimanus* in the Western Central Pacific Ocean (WCPO), particularly in Papua New Guinea (PNG) waters.

C. longimanus was one of the five key species taken in the PNG shark longline fishery in the WCPO (Kumoru 2003). The fishery operated primarily in oceanic habitats and targeted sharks until the fishery closed in mid-2014 because of a ban on silky shark retention (Western and Central Pacific Fisheries Commission 2013; conservation and management measure, CMM, 2013–08). *C. longimanus* is now caught as bycatch in the tuna longline and purse seine fisheries in PNG and throughout the wider region. Prior to 2002, *C. longimanus* accounted for ~9.1% of the annual catch for the fishery (Kumoru 2003). However, the catch rate estimates and catch per unit effort (CPUE) have experienced steep and consistent declines (~70%) over the past decade in the WCPO and the stock is currently considered overfished (Rice and Harley 2012). The Western Central Pacific Fishery Commission (WCPFC) has prohibited the retention, selling or storing of the carcass or any part of *C. longimanus*, following the other tuna-focused Regional Fisheries Management Organisations (RFMOs; Inter-American Tropical Tuna Commission Recommendation C-11-10, see <https://www.iattc.org/PDFFiles2/Resolutions/C-11-10-Conservation-of-oceanic-whitetip-sharks.pdf>, accessed 17 August 2016; Indian Ocean Tuna Commission Resolution 13/06, see <http://www.iotc.org/cmm/resolution-1306-scientific-and-management-frameworkconservation-sharks-species-caught>; International Commission for the Conservation of Atlantic Tuna Recommendation 10-07, see

https://www.iccat.int/Documents/Recs/ACT_COMP_2015_ENG.pdf, all accessed 17 August 2016). Although the no-retention policies have been implemented for *C. longimanus* for the tuna longline fisheries globally, this species is highly susceptible to longline fishing practices (e.g. depth of longline hooks; Tolotti *et al.* 2015) and is a key bycatch species in tuna fisheries that deploy fish aggregating devices (FADs; Dagorn *et al.* 2013). The ongoing management of *C. longimanus* in PNG and regional tuna fisheries requires accurate, regionally appropriate, biological information. With that in mind, the present study investigated the life history of *C. longimanus* caught in the WCPO in the seas around PNG. The information can be used to provide regional specific life history information, which will assist in further understanding the status of this species in the WCPO and help refine future assessments and management strategies.

Materials and methods

Sample collection

Samples were collected between May and July 2014 by PNG National Fisheries Authority (NFA) fisheries observers on board seven commercial longline vessels operating under the Shark Management Plan. Sharks were targeted by setting a maximum of 1200 hooks at an average depth of 72.3 m (depth range 35–108 m; Kumoru 2003), with a soak time of 8–10 h. Biological information was recorded for each individual, including sex, TL (measured from the snout to the tip of the caudal fin in a straight line; Francis 2006) and maturity. A section of the thoracic vertebrae was taken from below the anterior margin of the first dorsal fin and was stored frozen until processed. Although *C. longimanus* is a distinctive, easily identifiable species, the accuracy of species identification was verified using photographs taken by observers using digital cameras (Smart *et al.* 2016).

Vertebral processing and sectioning

Vertebral processing followed the standard protocols described in Cailliet and Goldman (2004). Vertebrae were defrosted and the haemal arch, neural arch and extraneous tissues were removed using a scalpel. Individual vertebral centra were separated and soaked in 5% sodium hypochlorite for 30 min to remove residual soft tissue. Centra were then thoroughly rinsed under tap water and dried in an oven for 24 h at 60°C. Longitudinal sections of the centra (~400 µm) were made through the focus of the vertebra with a low-speed rotary saw with twin diamond-tipped saw blades (Beuhler). Sections were mounted on microscope slides for storage and analysis using Crystal Bond adhesive (SPI Supplies).

Age determination

Sectioned vertebrae were examined using a dissecting microscope under transmitted light. Individual ages were estimated by counting the pairs of opaque and translucent growth bands present in the corpus calcareum after the birth mark (Goldman 2004). The birth mark was identified as the change in angle of the corpus calcareum and represented an age of zero (Goldman 2004; Fig. 1). Each subsequent growth band pair was assumed to represent 1 year of growth. Validation of annual growth band

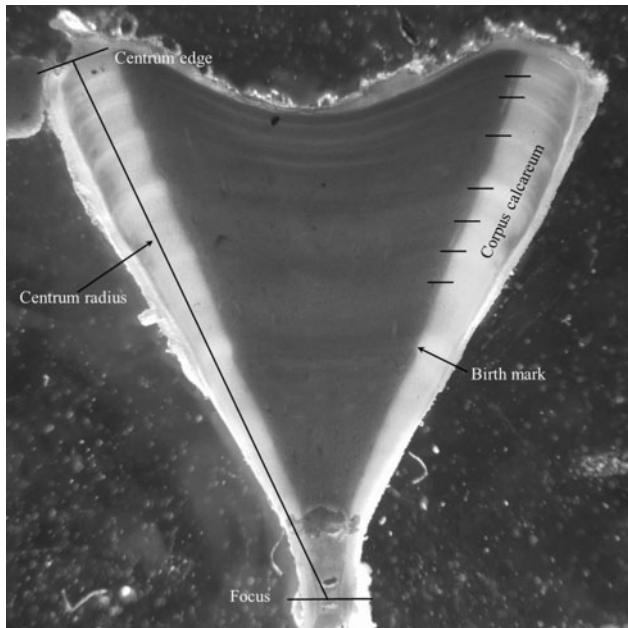


Fig. 1. Photograph of a vertebral section from a male *Carcharhinus longimanus* estimated to be 7 years old at 157.8-cm total length, from the Western Central Pacific Ocean, Papua New Guinea. The approximate locations of the focus, birth mark, vertebral bands (black dashes; 1–7) and centrum edge are shown, as is the centrum radius along which the back calculation measurements were made.

pair deposition could not be conducted during the present study because of the low sample size. Marginal increment analysis (MIA) could not be performed because the data only sampled during 3 months of the year. Previous studies by Seki *et al.* (1998), Lessa *et al.* (1999) and Joung *et al.* (2016) have verified annual growth band pair deposition for *C. longimanus* through MIA in the North Pacific Ocean, south-western Atlantic Ocean and north-west Pacific Ocean respectively, thus annual band pair deposition was also assumed in the present study.

Age estimation was conducted independently by two readers in order to reduce age estimate bias. Vertebral samples were selected at random and neither reader had prior knowledge of the sex or TL of the specimen (Cailliet and Goldman 2004). The age estimates from the two readers were then compared. Where counts differed between readers, the vertebra was re-examined collaboratively by both readers and a consensus age was decided. If no consensus age could be agreed, those centra were omitted from analysis. Precision and bias between readers before consensus reads and across the sample range were calculated using several methods, as recommended by Cailliet *et al.* (2006): percentage agreement (PA \pm 1 year), average percentage error (APE), Bowker's test of symmetry and Chang's CV (Campana *et al.* 1995; Cailliet *et al.* 2006). The PA \pm 1 year and APE were calculated with individuals grouped by 25 cm TL classes. For long-lived species, PA can be variable across age classes because of difficulty ageing older individuals. Thus, the variability in calculating PA across ages was accounted for because length is an empirical measurement, whereas age is an estimate (Goldman and Musick 2006). Statistics were calculated using the FSA package (D. H. Ogle,

see <https://fishr.wordpress.com/fsa/>, accessed September 2015) in the R program environment (R Foundation for Statistical Computing).

Back-calculation techniques

Back-calculation was used to compensate for the small number of juveniles (immature individuals) in the sample and limited sample sizes (Cailliet and Goldman 2004; Smart *et al.* 2013). Individual centra were photographed using a compound video microscope and the distances between growth band pairs were measured using an image analysis program (Image Pro Plus version 6.2 for Windows; Media Cybernetics). The centrum radius (CR) was measured in a straight line from the focus to the edge of the vertebra (Fig. 1). Along this straight line, the distance from the focus to each opaque growth band and the birth mark was measured. All distances were measured to the nearest 0.001 mm. A Dahl Lea direct-proportions back-calculation technique (Carlander 1969) was applied to the data using the following equation:

$$L_i = \left(\frac{L_C}{CR_C} \right) CR_i$$

where L_i is the length at growth band pair i , L_C is the length at capture (cm TL), CR_C is the centrum radius at capture and CR_i is the centrum radius at growth band pair i . For comparison with the Dahl Lea method, a length-at-birth modified Fraser Lee back-calculation technique (Campana 1990) was applied to the data using the following equation:

$$L_i = L_C \left(\frac{(CR_i - CR_C)(L_C - L_{\text{birth}})}{(CR_C - CR_{\text{birth}})} \right)$$

where L_{birth} is the length at birth and CR_{birth} is the centrum radius at the birth mark. L_{birth} was set to 76.0 cm, the known length at birth from the present study. Upon visual inspection, it was determined that the Dahl Lea direct-proportions method presented more reasonable estimates of length compared with the observed length-at-age data available for the older age classes (Smart *et al.* 2013). The Dahl Lea direct-proportion method provided estimates of length at birth, rather than a fixed length used in the Fraser Lee method, and was therefore used in all further analyses.

Growth models and analysis

An information-theoretic multimodel inference (MMI) approach, incorporating Akaike's information criterion (AIC), was used to model the growth of *C. longimanus*. A set of three candidate models commonly used in elasmobranch growth studies was selected *a priori* (Thorson and Simpfendorfer 2009): von Bertalanffy growth function (VBGF), logistic function and Gompertz function (Table 1). This approach was taken because the use of a single model, such as the VBGF, can bias growth estimations if it is an inappropriate model; using a multimodel framework removes this bias and generates the most robust growth estimate (Katsanevakis 2006; Katsanevakis and Maravelias 2008; Smart *et al.* 2016). Models were fitted using the biologically relevant length-at-birth parameter (L_0), instead of a time at size zero parameter (t_0 ; Cailliet *et al.* 2006). The

Table 1. Model equations of the three *a priori* growth functions used to estimate length at age using the multimodel, Akaike's information criterion corrected for small sample size (AIC_c) analysis

L_t , length at age t ; L_0 , length at age 0; L_∞ , asymptotic length; k , g_{Log} and g_{Gom} , growth coefficients of the respective models (which are incomparable); VBGF, von Bertalanffy growth function

Model	Growth function equation	References
VBGF	$L_t = L_0 + (L_\infty - L_0)(1 - \exp(-kt))$	von Bertalanffy (1938)
Logistic function	$L_t = \frac{L_\infty \times L_0 (\exp(g_{Log} t))}{L_\infty + L_0 (\exp(g_{Log} t - 1))}$	Ricker (1979)
Gompertz function	$L_t = L_0 \times \exp(\ln(\frac{L_\infty}{L_0}) (1 - \exp(-g_{Log} t)))$	Ricker (1975)

models were fit to the length-at-age data in the R statistical environment (R Foundation for Statistical Computing). Parameter estimates for each growth function were estimated using non-linear least-squares regression methods in R. The standard errors for the parameters were calculated for parameter estimates using a bootstrapping method with the 'nlstools' package (F. Baty and M. L. Delignette-Muller, see <http://cran.r-project.org/web/packages/nlstools>, accessed 16 September 2015) in R program environment (R Foundation for Statistical Computing).

The performance of the models relative to each other was evaluated and selected using AIC with a small sample size bias correction algorithm (AIC_C, Akaike 1973; Burnham and Anderson 2002; D. H. Ogle, see <https://fishr.wordpress.com/fsa/>). Compared with the standard AIC, the AIC_C has been demonstrated to perform better when the sample size is below 200 (Zhu *et al.* 2009). The AIC_C provided a measure of model fit and complexity, allowing for the simultaneous comparison of the growth models (Natanson *et al.* 2014). The AIC_C was calculated as follows:

$$AIC_C = AIC + \left(\frac{2k(k+1)}{n-k-1} \right)$$

where $AIC = n \log(\sigma^2) + 2k$, k is the total number of parameters + 1 for variance (σ^2) and n is the sample size. The model that had the lowest AIC_C value (AIC_{min}) was considered the most appropriate. The AIC difference (Δ) was calculated for each model ($i = 1-3$) and used to rank the remaining models as follows:

$$\Delta_i = AIC_{C,i} - AIC_{min}$$

Models with Δ values from 0 to 2 had the highest support, whereas models in which $\Delta = 2-10$ had considerably less support, and models with little or no support had Δ values >10 (Burnham and Anderson 2002). The probability of choosing the correct model was calculated using Akaike weights (w_i) from the AIC_C differences for each model (Burnham and Anderson 2002). The weights were calculated as follows:

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

A likelihood ratio test was conducted to determine whether sexes should be modelled separately or combined (Kimura 1980). This was performed for the best fitting model, determined by the AIC_C analysis for both observed and back-calculated data, using the method described by Haddon (2001), which was modified for the R program environment (R Foundation for Statistical Computing). If a significant difference between male and female growth curves was detected for either dataset, then separate growth curves were produced.

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

$$t_{max} = 7 \times \ln(2 \div k)$$

where t_{max} is the longevity in years (Mollet *et al.* 2002).

Maturity estimation

The maturity of each individual was staged using an index modified from Walker (2005; Table 2). The maturity stage of males was based on clasper condition ($C = 1-3$), whereas the stage of female maturity was based on uterus condition ($U = 1-5$; Table 2). Maturity stage data were converted to a binary maturity category (immature = 0, mature = 1) for statistical analysis. Population estimates of length at maturity were produced for males and females using a logistic regression equation (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 at which 50 and 95% of the population were mature (l_{50} and l_{95}) were estimated using a generalised linear model (GLM) with a binomial error structure and a logit link function in the R program environment (R Foundation for Statistical Computing). 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.

Comparisons of regional life history characteristics

In order to compare the life history characteristics of *C. longimanus* between regions, the VBGF fits for the other populations were reproduced (Smart *et al.* 2015). Parameter

estimates were used from previously published length-at-age studies from populations in the North Pacific Ocean (Seki et al. 1998), North-west Pacific Ocean (Joung et al. 2016) and South-west Atlantic Ocean (Lessa et al. 1999). Length was converted from precadual length (PCL) to TL using the following formula (Seki et al. 1998):

$$TL = 1.37 \times PCL$$

In instances where a range of values was reported, the mid-point was used in the calculations. The theoretical longevity was calculated using the VBGF parameters for the other populations.

Results

Vertebrae samples were collected from 103 *C. longimanus*, consisting of 70 males (76.0–240 cm TL) and 33 females (128–235 cm TL; Fig. 2). The age range for males and females was 0–18 and 4–17 years respectively. Vertebrae were moderately easy to interpret. The PA ± 1 year and APE ± 1 year across 25-cm TL classes between the two readers were 66.0 and 9.5% respectively. The age bias plot showed minimal variation around the 1 : 1 line. There was a slight bias for ages 4–7 (Fig. 3). However, no systematic bias across the entire age range was detected between the readers (Bowker’s test of symmetry, d.f. = 27, $\chi^2 = 47.39, P = 8.973$). The CV was 13.4%. Although values of APE and CV are considered high for teleost fish ageing studies, values in the present study are comparable to chondrichthyan age and growth studies, because long-lived species have a greater number of growth band pairs to read (Campana 2001; Cailliet et al. 2006).

Vertebral growth analysis

The VBGF provided the best fit for the observed and back-calculated data, and the logistic and Gompertz models provided little support for both datasets (Table 3). A combined growth curve for males and females was produced for the observed length-at-age data (Fig. 4a), because growth did not differ significantly between the sexes for the observed length-at-age data (likelihood ratio test; VBGF, d.f. = 3, $\chi^2 = 5.70, P = 0.127$). The observed data models lacked clear biological realism, with an unrealistically large L_0 estimate of 99.0 cm TL compared with the empirical length-at-birth estimates of 63.0–77.0 cm TL (Seki et al. 1998). Therefore, the missing size classes were accounted for using back-calculation techniques, which increased the

number of length-at-age data points from 103 to 945 through the addition of interpolated data (Table 3).

The back-calculated dataset provided far more reasonable estimates of L_0 and L_∞ than estimates produced using the observed data (Table 3). Separate growth curves were produced for males and females for the back-calculated data (Fig. 4b, c) because growth differed significantly between sexes for the back-calculated dataset (likelihood ratio test; VBGF, d.f. = 3, $\chi^2 = 9.64, P = 0.02$). There was considerable variation in the estimates for the back-calculated length-at-birth for both sexes (Fig. 4b, c). However, the VBGF L_0 estimates for male and females were within the known length-at-birth range (Seki et al. 1998). Estimates of L_∞ for males and females were smaller than

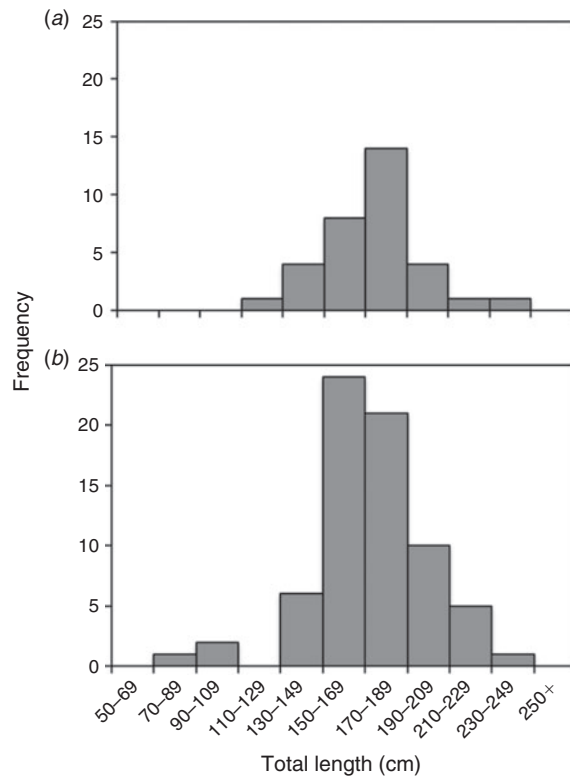


Fig. 2. Length–frequency of individuals sampled, grouped into 20-cm size classes for (a) female (n = 33) and (b) male (n = 70) *Carcharhinus longimanus* from the Western Central Pacific Ocean, Papua New Guinea. Samples were collected between May and July 2014.

Table 2. Reproductive indices used for staging the maturity condition
Adapted from Walker (2005)

Organ	Index	Description	Binary maturity condition
Female uterus	U = 1	Uteri uniformly thin and white tubular structures; small ovaries and with no yolked ova	Immature
	U = 2	Uterus thin, tubular structure that is partly enlarged posteriorly; small yolked ova developing in ovary	Immature
	U = 3	Uterus uniformly enlarged tubular structure; yolked ova developing in ovary	Mature
	U = 4	Uterus enlarged with <i>in utero</i> eggs or embryos macroscopically visible: pregnant	Mature
	U = 5	Uterus enlarged, flaccid and distended tubular structure: postpartum	Mature
Male clasper	C = 1	Pliable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

those from the observed data (Table 3), whereas k was higher than the observed length-at-age data, and males had a slightly higher k than females (Table 3). A pronounced asymptote was not observed in growth curves from either sex, and the asymptotic lengths were greater than the largest individual observed (Table 3; Fig. 4). The estimates of longevity were similar for males and females, and were calculated to be 24.6 and 24.9 years respectively.

Maturity analysis

Female and male *C. longimanus* mature at different lengths and ages. There were two mature females and 15 mature males in the sample. The youngest mature female was estimated to be 12 years old at 196 cm TL. The oldest immature female (Stage 2) was 17 years old at 226 cm TL. The mean (\pm s.e.) maximum

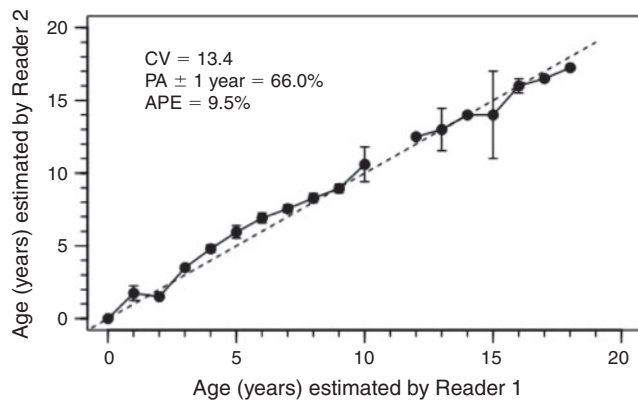


Fig. 3. Age-bias plot for 103 *Carcharhinus longimanus* vertebral counts with age-specific agreements between two independent readers used for Bowker’s test of symmetry. Mean (\pm 2 s.e.) age-specific agreements are plotted with a 1 : 1 equivalence line for comparison. The CV, percentage agreement (PA) \pm 1 year and average percentage error (APE) are shown.

likelihood estimates of l_{50} and l_{95} for females were 224 ± 15 and 258 ± 29 cm TL respectively (Fig. 5a). The female age at maturity of A_{50} and A_{95} was estimated to be 15.8 ± 2.3 and 21.3 ± 4.3 years respectively (Fig. 5c). The youngest mature male was 7 years old at 190 cm TL, whereas the oldest immature male was 10 years old at 195 cm TL. The mean (\pm s.e.) maximum likelihood estimates of l_{50} and l_{95} for males were 193 ± 3 and 212 ± 8 cm TL respectively (Fig. 5b). The A_{50} and A_{95} for males were predicted as 10.0 ± 0.5 and 12.5 ± 1.2 years respectively (Fig. 5d). Therefore, female *C. longimanus* mature at an older age and greater length than males.

Comparison of regional life history characteristics

There was a considerable difference in the growth of *C. longimanus* from PNG (WCPO) compared with other populations (Table 4; Fig. 6). For example, k for male and female *C. longimanus* from PNG (WCPO) was approximately half that of k values for the North Pacific Ocean (Seki *et al.* 1998) and the south-west Atlantic Ocean (Lessa *et al.* 1999) populations (Table 4; Fig. 6). Furthermore, individuals from the north-west Pacific Ocean grow at a slower rate than those from the North Pacific and south-west Atlantic, but faster than individuals from PNG (Table 4; Fig. 6). In addition, L_{∞} varied between populations (Table 4; Fig. 6). However, L_0 for *C. longimanus* was similar between the four regions (Table 4). The PNG population had the highest maximum observed age for males and the highest theoretical longevity (Table 4). Females and males from PNG mature at a later age than other conspecifics (Table 4). Males from all four regions mature at similar lengths, but males from PNG mature at a later age. Female *C. longimanus* from PNG mature a considerably greater length than other conspecifics (Table 4). The maximum observed age and theoretical longevity for North Pacific *C. longimanus* were younger than those for *C. longimanus* from PNG, despite the former attaining a larger L_{max} (Table 4).

Table 3. Summary of parameter estimates and Akaike’s information criterion corrected for small sample size (AIC_c) performance of the three models used for observed length at age and back-calculated length at age of *Carcharhinus longimanus* from the Western Central Pacific Ocean, sampled between May and July 2014

Unless indicated otherwise, data are given as the mean \pm s.e. The best fitting model is highlighted in bold. n , sample size; VBGF, the von Bertalanffy growth function; L_0 , length at birth; TL, total length; L_{∞} , asymptotic length; k , von Bertalanffy model growth coefficient; g_{Log} , logistic model growth coefficient; g_{Gom} , Gompertz model growth coefficient; Δ , the difference between AICc values; w , AICc weights

Sex	Model	n	Model performance			Model estimates				
			AIC _c	Δ	w	L_0 (cm)	L_{∞} (cm)	k (year ⁻¹)	g_{Gom} (year ⁻¹)	g_{Log} (year ⁻¹)
Observed data										
Combined	VBGF	103	855.0	0.00	0.98	99.90 \pm 8.54	342.5 \pm 90.1	0.045 \pm 0.023	–	–
	Gompertz	103	862.6	7.58	0.02	88.09 \pm 8.51	240.0 \pm 15.1	–	0.146 \pm 0.028	–
	Logistic	103	939.3	84.2	0.00	88.10 \pm 10.1	240.0 \pm 32.7	–	–	0.146 \pm 0.043
Back-calculated data										
Male	VBGF	630	4973	0.00	0.74	75.11 \pm 1.13	315.6 \pm 20.7	0.059 \pm 0.007	–	–
	Gompertz	630	4975	2.15	0.25	78.13 \pm 1.04	251.8 \pm 7.90	–	0.134 \pm 0.007	–
	Logistic	630	4984	10.7	0.00	78.13 \pm 0.98	230.3 \pm 5.10	–	–	0.207 \pm 0.008
Female	VBGF	315	2463	0.00	0.94	74.68 \pm 1.52	316.7 \pm 27.6	0.057 \pm 0.008	–	–
	Gompertz	315	2468	5.46	0.06	76.37 \pm 1.42	252.4 \pm 10.6	–	0.127 \pm 0.009	–
	Logistic	315	2477	14.1	0.00	78.00 \pm 1.13	230.9 \pm 6.90	–	–	0.197 \pm 0.010

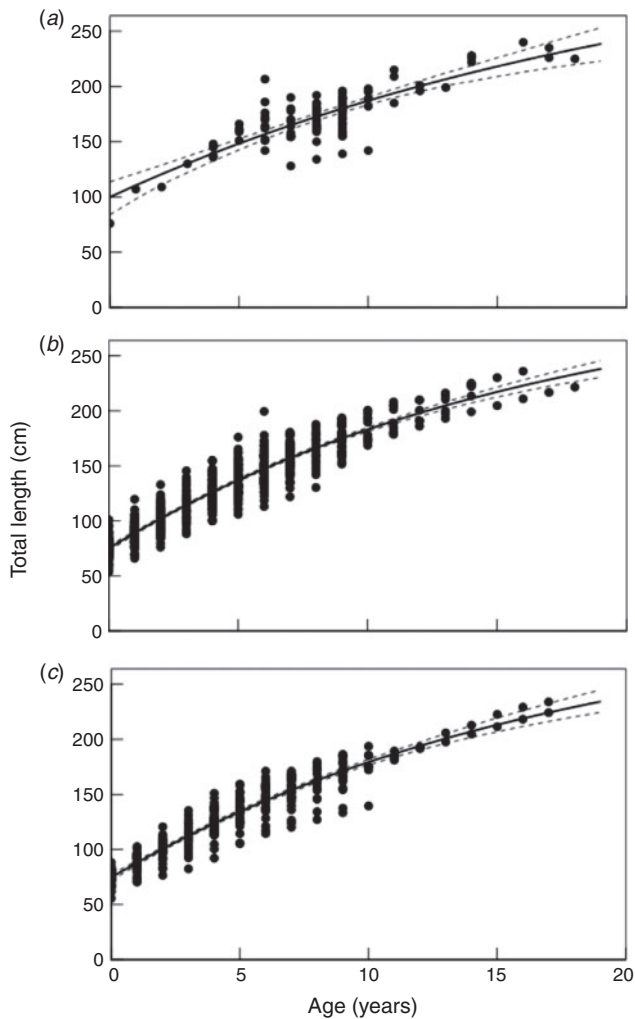


Fig. 4. Length-at-age growth curves for *Carcharhinus longimanus* from the Western Central Pacific Ocean, Papua New Guinea, for (a) observed data with males and females combined, (b) back-calculated data for males and (c) back calculated data for females, fitted with fitted von Bertalanffy growth model (solid line) and bootstrapped 95% confidence intervals (dashed line). A direct proportion Dahl Lea equation was used for the back calculation.

Discussion

Conducting regional life history studies is imperative to understanding the biology of a species and to provide the most accurate parameter estimates. Life history traits of shark species can differ between conspecific populations, reflecting varying population dynamics and resilience to exploitation (Dulvy *et al.* 2008; Rigby and Simpfendorfer 2013). Life history parameters of *C. longimanus* from the PNG (WCPO) population revealed a substantial regional variation compared with populations in the North Pacific Ocean (Seki *et al.* 1998), North-west Pacific Ocean (Joung *et al.* 2016) and South-west Atlantic Ocean (Lessa *et al.* 1999). Male and female *C. longimanus* from PNG (WCPO) have considerably slower growth than populations from the North Pacific Ocean (Seki *et al.* 1998) and South-west Atlantic Ocean (Lessa *et al.* 1999). Both sexes of *C. longimanus* from PNG (WCPO) mature at an older age, and females mature at an

larger size, than conspecifics from the other regions. Size at birth was similar among all four populations (Seki *et al.* 1998; Lessa *et al.* 1999; Joung *et al.* 2016). These regional differences in life history traits may reflect different population dynamics and resilience to fishing pressure (Chin *et al.* 2013; Smart *et al.* 2015). Therefore, these results provide more representative life history estimates towards local population assessments, avoiding the use of potentially inaccurate surrogate information from other regions.

Regional variations may reduce the accuracy of population assessment when proxy data are used from conspecifics from other regions (Chin *et al.* 2013; Smart *et al.* 2015). Similar levels of regional variation have been well documented for a number shark species, such as bonnethead sharks (*Sphyrna tiburo*; Lombardi-Carlson *et al.* 2003), blacknose shark (*Carcharhinus acronotus*; Driggers *et al.* 2004), blacktip reef shark (*Carcharhinus melanopterus*; Chin *et al.* 2013), Australian blacktip sharks (*Carcharhinus tilstoni*; Harry *et al.* 2013) and common blacktip sharks (*Carcharhinus limbatus*; Smart *et al.* 2015). The most recent stock assessment for *C. longimanus* from the WCPO was conducted using proxy data from the conspecifics from North Pacific Ocean (Seki *et al.* 1998) and south-west Atlantic Ocean (Lessa *et al.* 1999). The life history characteristics of *C. longimanus* from PNG (WCPO) suggest that this region is more susceptible to population declines and that the population in this area has a slower ability to recover. However, the causes of observed regional variation in *C. longimanus* are unknown and may be related to several factors, including varying environmental conditions between regions, regional genetic adaptation and limited samples (Tanaka *et al.* 1990; Carlson *et al.* 2006; Jolly *et al.* 2013). Thus, using the regional life history parameters of *C. longimanus* from the PNG in the present study can significantly improve demographic analysis and stock assessments for this population, thereby improving PNG and WCPO fisheries management and conservation.

C. longimanus were aged to a maximum of 18 years for females and 17 years for males through vertebral band counts, providing the oldest age estimation to date. However, the age estimates reported in the present study are likely to be an underestimation. Age underestimation can arise when interpreting terminal band pairs in large individuals because band compression can occur (where the most recent band pair is deposited close together and is poorly defined) or growth band formation can cease past a certain age when the animal stops growing (Cailliet *et al.* 2006; Chin *et al.* 2013; Natanson *et al.* 2014). This can be problematic, because several species have been documented to live twice as long as the vertebral band pair counts estimated, such as the porbeagle *Lamna nasus* (Francis *et al.* 2007) and school shark *Galeorhinus galeus* (Kalish and Johnston 2001). Comprehensive age validation studies (e.g. mark and recapture using tetracycline injection or bomb radiocarbon dating) are difficult to conduct for pelagic sharks because these species are typically highly migratory, attain large sizes and are difficult to sample regularly throughout the year (Natanson *et al.* 2002; Cailliet *et al.* 2006). In the present study, theoretical longevity estimates were calculated for *C. longimanus* using parameters from the VBGF. These estimates (24.5 and 24.9 years for males and females respectively) were considerably lower than previous estimates

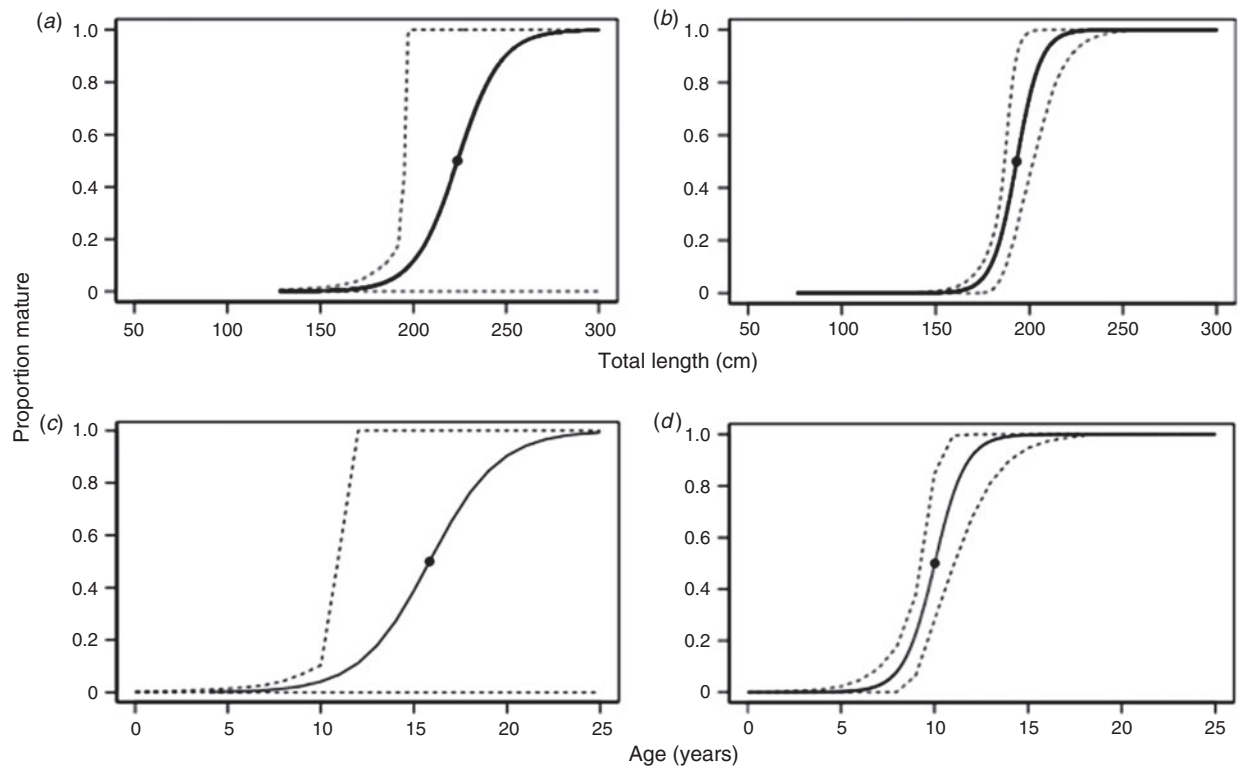


Fig. 5. (a, b) Length- and (c, d) age-at-maturity ogives for female (a, c) and male (b, d) *Carcharhinus longimanus* from PNG. The black points represent the length and age at which 50% of the population was mature (l_{50} and A_{50} respectively) and dashed lines indicate bootstrapped 95% confidence intervals.

(36 years for males and females; Rice and Harley 2012) based on the theoretical maximum length from the North Pacific Ocean population (Seki *et al.* 1998). This estimate was considered unreliable by Clarke *et al.* (2015, pp. 12–13) and, for comparison, theoretical longevity estimates using the parameters from respective VBGFs were also calculated for the North Pacific Ocean population (combined sexes, 20.7 years), north-west Pacific Ocean (combined sexes, 22.1 years) and south-west Atlantic Ocean population (combined sexes, 21.0 years). The theoretical longevity estimates for the conspecific populations suggest *C. longimanus* may have a shorter life span than previously estimated. Although no individual from either population has been caught and aged beyond 18 years, the longevity estimates derived from growth models are more reasonable and conservative than the vertebral counts, and should be used in assessment when validation studies have not been conducted.

Fitting a VBGF to the back-calculated data provided the most appropriate growth estimates for both sexes. The observed data for *C. longimanus* lacked juveniles (between 76.0 and 175 cm TL) and larger individuals (>200 cm TL), which resulted in overestimation of length at birth (L_0) and underestimation of asymptotic length (L_∞) in the three candidate growth models. Growth models are sensitive to incomplete datasets (e.g. missing smallest and largest individuals in the sample) and can produce biased growth parameters in these cases (Haddon 2001; Pilling *et al.* 2002; Smart *et al.* 2015). The use of back-calculation techniques allowed for more biologically reasonable growth estimates, within the known ranges for birth size

(63.0–77.0 cm TL), and realistic larger asymptotic length. There was a significant difference between male and female growth curves using the back-calculated data, whereas there was no difference between the growth curves using the combined data. This disparity between the male and female back-calculated growth may be a function of the greater sample size in the back-calculated data. The absence of young juveniles (<4 years old; between 76.0 and 175 cm TL) in the present study suggests longline gear selectivity occurs for *C. longimanus*. Longline fisheries are inherently length selective, with the tendency to capture larger *C. longimanus* (White *et al.* 2008). Juveniles have been reported to inhabit deep reef areas along the continental shelf (Seki *et al.* 1998), which may be out of the depth range (35–108 m) of the longlines used in the WCPO fishery (Kumoru 2003). The smaller, younger individuals are more likely to be caught using purse seine nets (Clarke *et al.* 2011a, 2011b). Introduction of as little as five juveniles into the sample has been demonstrated to correct the L_0 estimates (Smart *et al.* 2015). Using both methods for sampling, as well as targeted sampling of individuals (e.g. nursery areas; Smart *et al.* 2015), may be highly beneficial to overcome gear-selective sampling and result in the collection of a well-represented sample of all length classes. If access to juvenile individuals is not possible, then back-calculation techniques can be used successfully to account for the juveniles and produce biologically realistic estimates (Smart *et al.* 2013). Although back-calculation techniques can account for the missing juvenile length classes, these techniques are limited to the oldest age estimate in the sample and cannot

Table 4. Comparison of life history parameters for *Carcharhinus longimanus* between the Papua New Guinea Western Central Pacific Ocean, North Pacific Ocean, North-west Pacific Ocean and South-west Atlantic Ocean

BC, back calculated; L_0 , length at birth; TL, total length; L_∞ , asymptotic length; k , von Bertalanffy model growth coefficient; t_0 , theoretical age at zero length; t_{mat} , estimated age at maturity; L_{mat} , length at maturity; L_{max} , maximum observed length; $O_{t_{max}}$, observed maximum age; $T_{t_{max}}$, calculated theoretical longevity from von Bertalanffy parameters. TL values for *C. longimanus* from Seki et al. (1998) were converted from precadual length (PCL) using the length relationship reported in their study

Study	Location	Sex	Data type	VBGF parameters				t_{mat} (years)	L_{mat} (cm TL)	L_{max} (cm TL)	$O_{t_{max}}$ (years)	$T_{t_{max}}$ (years)
				L_0 (cm TL)	L_∞ (cm TL)	k (year ⁻¹)	t_0 (years)					
Present study	Western Central Pacific	Male	BC	75.1	315.6	0.059	-	10.0	193.1	240.0	18	24.6
Seki et al. (1998)	North Pacific	Female	BC	74.7	316.7	0.057	-	15.8	223.8	235.0	17	24.9
		Combined	Observed	69.8	341.7	0.103	-2.7	4.5	182.0	272.2	11	20.7 ^A
Joung et al. (2016)	North-west Pacific	Combined	Observed	64.0	309.4	0.085	-	8.7	193.9	268.0	12	36.0 ^B
Lessa et al. (1999)	South-west Atlantic	Combined	Observed	71.0	284.9	0.099	-3.4	7.0	185.0	250.0	17	22.1 ^A
												21.0 ^A

^ACalculated during the present study.

^BEstimate based on theoretical maximum length by Rice and Harley (2012).

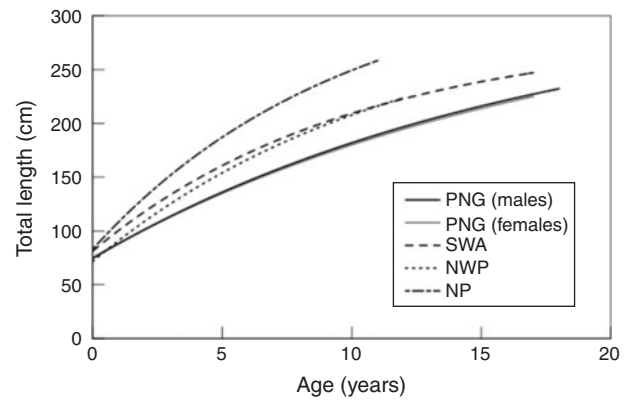


Fig. 6. Comparison of von Bertalanffy growth curves for *Carcharhinus longimanus* from the Western Central Pacific Ocean, Papua New Guinea (PNG; separate sexes, present study), North Pacific Ocean (NP; Seki et al. 1998), North-west Pacific Ocean (NWP; Joung et al. 2016) and South-west Atlantic Ocean (SWA; Lessa et al. 1999).

account for the absence of fully grown individuals (Cailliet et al. 2006; Smart et al. 2015).

Despite *C. longimanus* having been described as a large-bodied species and one of the most abundant pelagic sharks in tropical and subtropical oceans, along with the blue shark (*Prionace glauca*) and silky shark (*Carcharhinus falciformis*; Compagno 1984; Nakano and Stevens 2008; Castro 2011; Baum et al. 2015), there was a lack of large individuals >200 cm TL in the present study. The absence of these large individuals can affect the growth parameters (Haddon 2001; Pilling et al. 2002; Smart et al. 2015), but there is no method that can retrospectively account for the missing large individuals. The absence of large individuals in the present study may be attributed to several reasons, such as size and sexual segregation, seasonal migratory behaviours and length-selective fishing mortality. Currently, very little is known about the population organisation, movements and habitat use in the Pacific Ocean. The lack of females, particularly mature females, in the present study suggests sexual segregation in the WCPO and the Pacific Ocean. Evidence of sexual and size segregation of *C. longimanus* has been reported in the Maldives, where females within the length range 110–179 cm TL were caught more frequently than males in the same size range (Anderson and Ahmed 1993). In the WCPO, most of the males in the present study caught were between 150 and 189 cm TL, whereas most of the females sampled were between 170 and 189 cm TL. Furthermore, because *C. longimanus* is a highly migratory species, it is possible that a 3-month sampling period was an inadequate time frame to collect a representative and equal sample in PNG (WCPO), and further studies into the population structure and migration behaviours of *C. longimanus* in the WCPO are required.

C. longimanus exhibits a strong preference for warm and shallow waters above 120 m and is highly susceptible to longline gear, particularly in fisheries that deploy FADs (Tolotti et al. 2013; Tolotti et al. 2015). The absence of large individuals is likely the result of length-selective fishing mortality, given the history of extensive fishing in the WCPO, as well as migration

behaviour and sampling time frame. Shifts in the length composition to smaller sizes due to length-selective fishing mortality have been attributed to the exploitation of a range of shark species (Ricker 1969; Jennings and Kaiser 1998; Walker *et al.* 1998; Stevens *et al.* 2000). Length-selective fishing mortality occurs when larger, older individuals are removed from the population, resulting in a smaller maximum size and younger maximum age (Thorson and Simpfendorfer 2009). *C. longimanus* was one of the main eight species in the WCPO shark longline fishery, but it is now considered overfished and well below maximum sustainable yields (Clarke 2011; Rice and Harley 2012). The largest observed specimen of *C. longimanus* was 350 cm TL in the North Atlantic Ocean in the 1940s (Bigelow and Schroeder 1948). However, no individual was caught at such length either in the present study in PNG (largest 240 cm TL male) or in previous studies in the North Pacific Ocean (largest 272 cm TL female; Seki *et al.* 1998), north-western Pacific (largest 268 cm TL male; Joung *et al.* 2016) and south-west Atlantic Ocean (largest 250 cm TL female; Lessa *et al.* 1999). The median size of *C. longimanus* was observed to be decreasing significantly, until samples became too scarce in the Pacific Ocean, based on long-term catch data (Clarke 2011). Thus, the rarity of individuals larger than 270 cm TL in the present study and in catches obtained worldwide imply the length composition of this species has been significantly altered, and median length and maximum size have been reduced (Lessa *et al.* 1999). The decrease in size can affect the parameters of the growth models (Pilling *et al.* 2002) and may explain the lack of a distinct asymptote in the growth model. It is also possible that the growth rates of the species have changed over time as a result of length-selective fishing mortality (Walker *et al.* 1998). Compensatory (density-dependent) growth has been demonstrated for carcharinid shark populations that have been fished to low population sizes (Sminkey and Musick 1995).

C. longimanus from PNG and WCPO have a slower growth rate and mature later and at a larger size than other conspecific populations. These life history traits suggest that the population from the WCPO has a higher vulnerability to fishing pressure and low ability to recover from perturbations than other populations for which data are available. The recent no-retention policy and the closure of the shark longline fishery in PNG present an opportunity for this overfished species to recover in this region. However, *C. longimanus* is still being taken as bycatch, especially in the tuna longline fisheries and fisheries that deploy FADs (Dagorn *et al.* 2013), and ongoing management for this species is required. The regional life history information presented herein provides an important step towards understanding the population status of *C. longimanus* in PNG and the WCPO.

Acknowledgements

This project was co-funded by the National Fisheries Authority (NFA) and the Australian Centre for International Agricultural Research (ACIAR; project FIS/2012/102). The authors thank Brian Kumasi, Luanah Yaman, Leban Gisawa and Ludwig Kumoru from the NFA, as well as the fishers and the NFA on-board fisheries observers: Jackson Maravee, Noah Lurang Jr, Daniel Sau, Murphy John, Paliu Parkop, Towai Peli and Udill Jotham. The authors also thank Samantha Sherman, Satoshi Shiratsuchi and Andrea Cabrera Garcia for laboratory assistance.

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