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*_\(_\infty\)) = 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*_\(_\infty\) = 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.

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 (Compagnon 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; Rugby 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 inhibit 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 fishery 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.iatc.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.ioc.org/cmm/resolution-1306-scientific-and-management-framework-conservation-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; Dagnor 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).

Ventral processing and sectioning

Ventral 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
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 decided. If no consensus age could be agreed, those centra were omitted from analysis. Peace and bias between readers 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. Peace and bias between readers.

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:

\[ L_i = \frac{L_C}{CR_C} CR_i \]

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:

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

where \( L_{\text{birth}} \) is the length at birth and \( CR_{\text{birth}} \) is the centrum radius at the birth mark. \( L_{\text{birth}} \) 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-proportions 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 (VBF), 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 zero parameter \( (t_0) \). See https://fishr.wordpress.com/fsa/, accessed September 2015 in the R program environment (R Foundation for Statistical Computing).

**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.
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 (AICc, Akaike 1973; Burnham and Anderson 2002; D. H. Ogle, see https://fishr.wordpress.com/). Compared with the standard AIC, the AICc has been evaluated and selected using AIC with a small sample size bias correction algorithm (AICC, Akaike 1973; Burnham and Anderson 2002; D. H. Ogle, see https://fishr.wordpress.com/). The weights were calculated as follows: $w_i = \frac{\exp(-\Delta_i/2)}{\sum_{j=1}^3 \exp(-\Delta_j/2)}$ where $\Delta_i = \text{AIC}_{C,i} - \text{AIC}_{\text{min}}$

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 AICc 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: $t_{\text{max}} = 7 \times \ln(2 - k)$ where $t_{\text{max}}$ 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):

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

where $P(l)$ is the proportion of the population mature at TL, $l$ and $P_{\text{max}}$ 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 $l_{95}$ 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

<table>
<thead>
<tr>
<th>Model</th>
<th>Growth function equation</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>VBGF</td>
<td>$L_t = L_0 + (L_{\infty} - L_0)(1 - \exp(-kt))$</td>
<td>von Bertalanffy (1938)</td>
</tr>
<tr>
<td>Logistic function</td>
<td>$L_t = L_{\infty} \left(1 - \exp\left(-\frac{kt}{L_{\infty}}\right)\right)$</td>
<td>Ricker (1979)</td>
</tr>
<tr>
<td>Gompertz function</td>
<td>$L_t = L_0 \times \exp\left(\ln\left(\frac{L_{\infty}}{L_0}\right)(1 - \exp(-kt))\right)$</td>
<td>Ricker (1975)</td>
</tr>
</tbody>
</table>

**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 (AICc) analysis**

$L_t$, length at age $t$; $L_0$, length at age 0; $L_{\infty}$, asymptotic length; $k$, $g_{\text{Gomp}}$, and $g_{\text{Log}}$. Growth coefficients of the respective models (which are incomparable); VBGF, von Bertalanffy growth function.
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 precaudal 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 \( L_b \) 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 \( L_b \) and \( L_o \), 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 \( L_o \) estimates for male and females were within the known length-at-birth range (Seki et al. 1998). Estimates of \( L_o \) for males and females were smaller than

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### Table 2. Reproductive indices used for staging the maturity condition

Adapted from Walker (2005)

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

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![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.](image-url)
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 (± s.e.) maximum 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 for \( A_{50} \) 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 (± 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, \( L_{\infty} \) 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 \( L_{\text{max}} \) (Table 4).

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**Table 3. Summary of parameter estimates and Akaike’s information criterion corrected for small sample size (AIC,) 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**

<table>
<thead>
<tr>
<th>Sex</th>
<th>Model</th>
<th>( n )</th>
<th>Model performance</th>
<th>Model estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AIC( _C )</td>
<td>( \Delta )</td>
<td>( w )</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Observed data</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Combined</td>
<td>VBGF</td>
<td>103</td>
<td>855.0</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Gompertz</td>
<td>103</td>
<td>862.6</td>
<td>7.58</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>103</td>
<td>939.3</td>
<td>84.2</td>
</tr>
<tr>
<td><strong>Back-calculated data</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>VBGF</td>
<td>630</td>
<td>4973</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Gompertz</td>
<td>630</td>
<td>4975</td>
<td>2.15</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>630</td>
<td>4984</td>
<td>10.7</td>
</tr>
<tr>
<td>Female</td>
<td>VBGF</td>
<td>315</td>
<td>2463</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Gompertz</td>
<td>315</td>
<td>2468</td>
<td>5.46</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>315</td>
<td>2477</td>
<td>14.1</td>
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North Pacific Ocean (Seki et al. 1999). Substantial regional variation compared with populations in the Ocean (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 (Sphyraena 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 tibstoni; 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 conspecics 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

**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.

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**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.
(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 (L0) 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 L0 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

![Fig. 5.](image-url)
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. 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 carcharhinid shark populations that have been fished to low population sizes (Smirkin 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.

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