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ORIGINAL PAPER

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^{-1} and $L_\infty = 311.3$ cm TL for males; and $L_0 = 70.8$ cm TL, $k = 0.02$ yr^{-1} and $L_\infty = 497.9$ cm TL for females. The biologically implausible L_∞ 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 $\sim$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 ± 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 ± 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 µm. 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_∞) 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 $AIC = nlog(\sigma^2) + 2k$, k is the total number of parameters +1 for variance (σ^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	$L_t = L_0\exp\left(\ln\left(\frac{L_\infty}{L_0}\right)(1 - \exp(-g_{gom}t))\right)$	Ricker (1975)
Logistic function	$L_t = \frac{L_\infty L_0(\exp(g_{log}t))}{L_\infty + L_0(\exp(g_{log}t) - 1)}$	Ricker (1979)

L_t is Length-at-age t, L_0 is length at age 0, L_∞ is asymptotic length, k, g_{log}, and g_{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 (Δ) which was calculated for each model ($i = 1$–3) as:

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

Models with Δ of 0–2 had the highest support, while models with Δ of 2–10 had considerably less support and models with Δ 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 $\mathrm{AIC_c}$, model-averaged length-at-age estimates, parameters and standard errors were calculated. Only L_∞ 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:

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

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

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

where $var(L_{\infty,i}|g_i)$ is the variance of parameter L_∞ 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
	$U = 4$	*In utero* 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 ± 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).

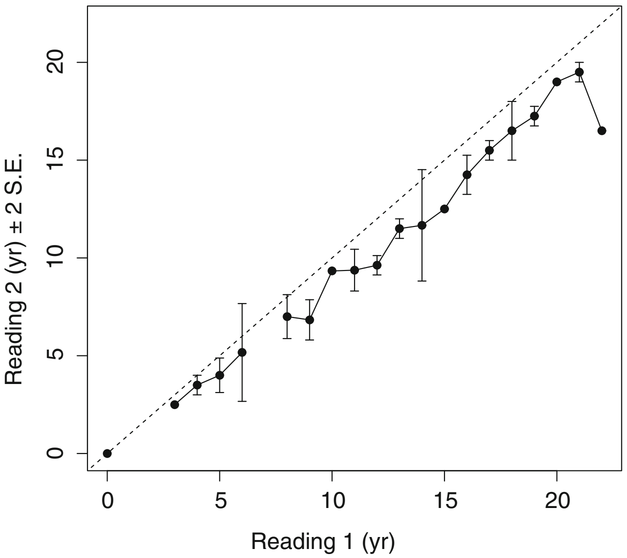
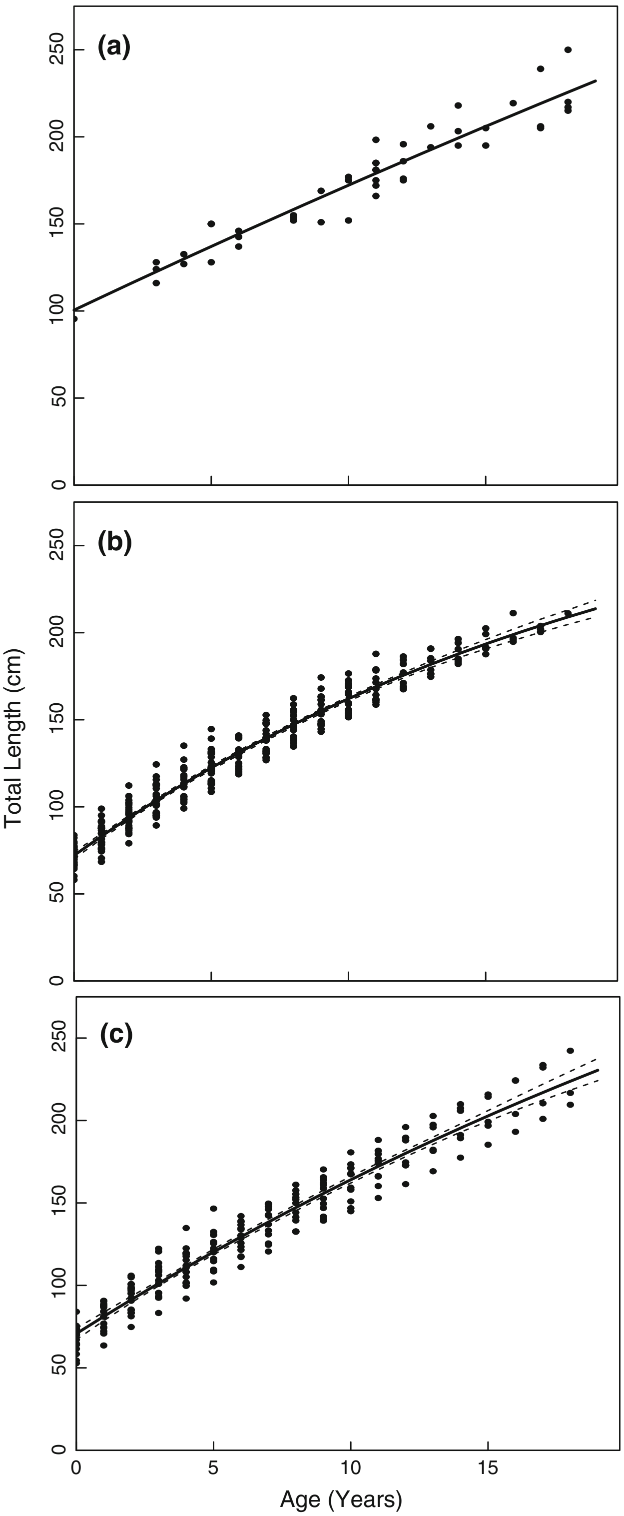


Fig. 1 Age-bias plot for *Carcharhinus albimarginatus* incorporating the age-specific agreements between Readers 1 and 2. Mean age-specific agreements ±2 standard errors are plotted along a 1:1 equivalence line. The average percent error (APE) and coefficient of variation (CV) were 17.24 and 24.38 respectively

There was no significant difference in growth curves between the sexes (likelihood ratio test using the observed 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, $\overline{L}_\infty$ and $\overline{L}_0$ estimates. These estimates were $\overline{L}_0 = 101.9$ cm TL and $\overline{L}_\infty = 598.7$ cm

Table 3 Percent agreement (PA) and percent agreement ±1 yr (PA ± 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 ± 1 yr	PA	PA ± 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



◀**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 $\mathrm{AIC_c}$ 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

TL. A large $\overline{L}_\infty$ was not unexpected as the growth curve lacked a clear asymptote. Therefore, $\overline{L}_\infty$ was in this instance not equivalent to maximum size as it is often considered. However, a $\overline{L}_0$ value of 101.9 cm TL was considerably larger than empirical length-at-birth estimates 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 $\overline{L}_0$ 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_∞ (497.9 cm TL) in comparison with the males (311.3 cm TL). The high VBGF L_∞ 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_∞ 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 tests. Multi-model inference was used to produce model-averaged L_∞ 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 $w > 0.9$

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

n is the sample size, AIC_C is the small sample bias adjusted form of Akaike's information criterion, Δ is the difference in AIC_C values between models, *w* (%) are the AIC_C weights, L_∞ is asymptotic length parameter in cm, L_0 is the length-at-birth parameter in cm, *k* is the growth completion parameter in 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

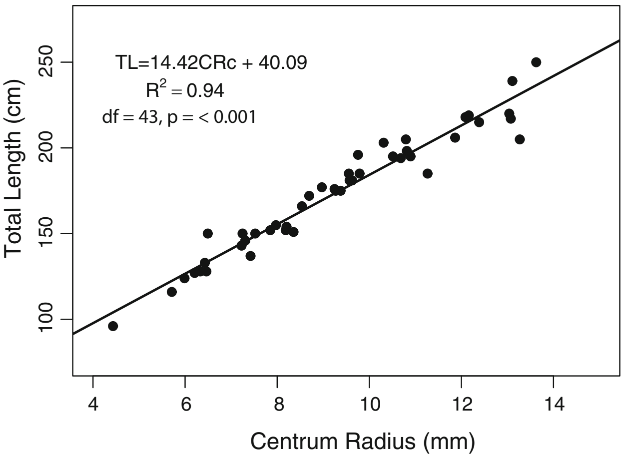


Fig. 3 Relationship between centrum radius (CR_c) and stretched total length (TL) for *Carcharhinus albimarginatus*

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 ± 1.8 cm TL and 10.5 ± 0.8 yr old, respectively (Fig. 5a, c). Female estimates of l_{50} and a_{50} were 208.9 ± 6.9 cm TL and 14.8 ± 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).

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

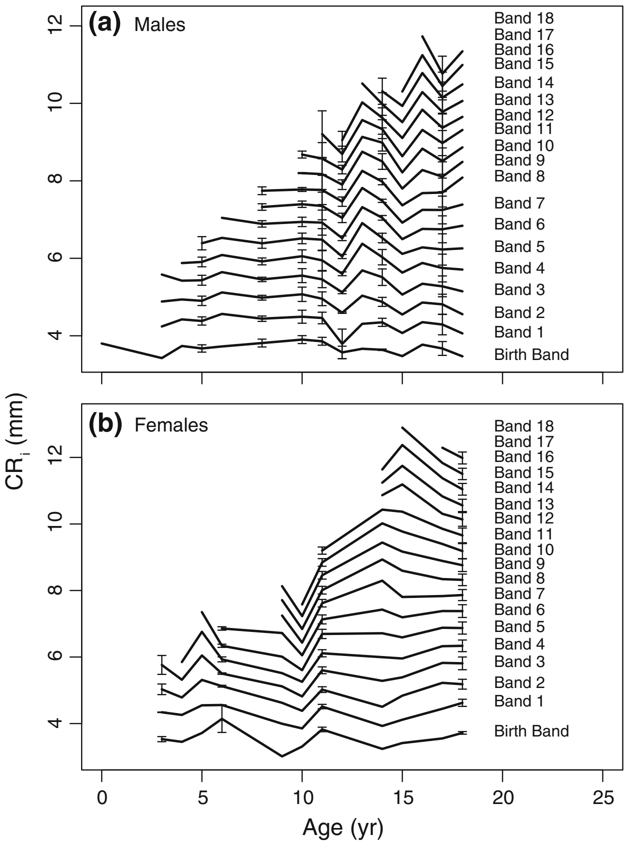


Fig. 4 Mean growth band radius (±SE) for each age at capture of **a** males and **b** females

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_{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 multimodel 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,

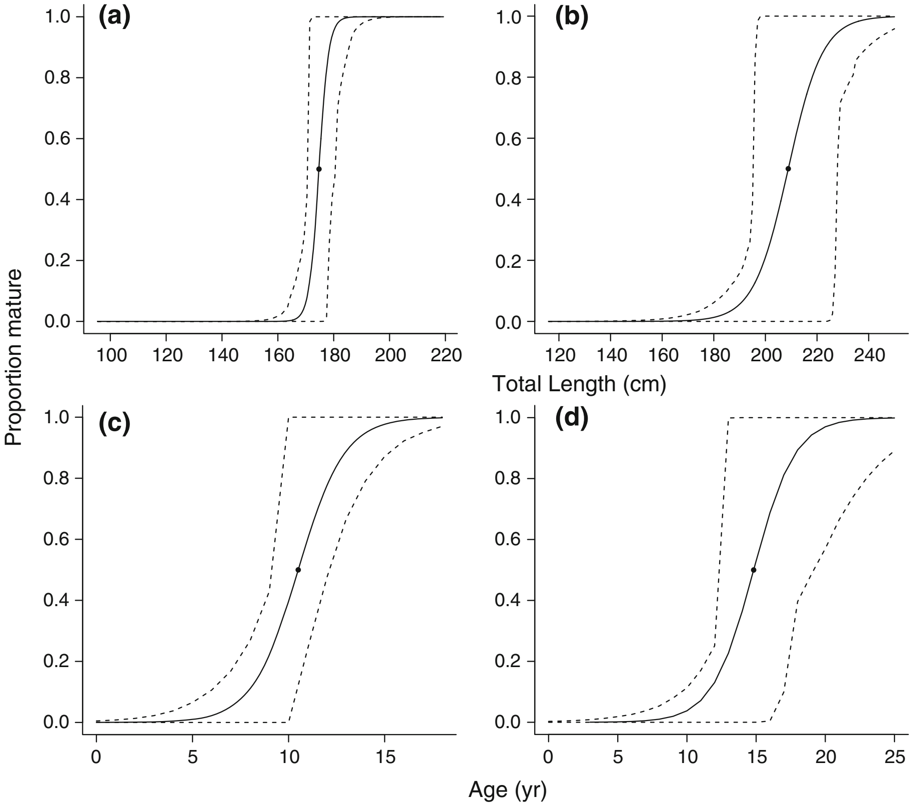


Fig. 5 Length- and age-at-maturity ogives for male (**a**, **c**) and female (**b**, **d**) *Carcharhinus albimarginatus*. *Black points* indicate l_{50} (**a**, **b)** and a_{50} (**c**, **d**), respectively, and the *dashed lines* represent bootstrapped 95% confidence intervals

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_∞ 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_∞ 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_∞ parameter or the growth curve. Instead, the L_∞ 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 underaged 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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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: $L_\infty = 316.7$ 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.

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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 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 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

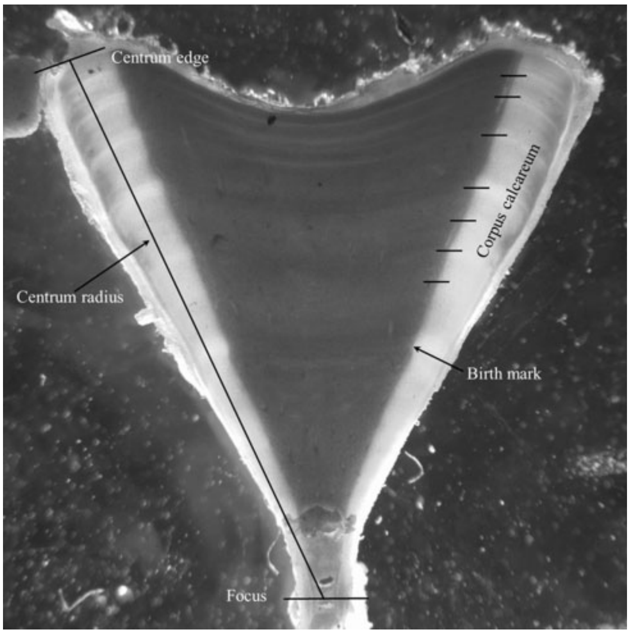

Fig. 1. Photograph of a vertebral section from a male *Carcharhinus longimanus* estimated to be 7 years old at 157.8-cm total length, from the Western Central Pacific Ocean, Papua New Guinea. The approximate locations of the focus, birth mark, vertebral bands (black dashes; 1–7) and centrum edge are 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 ± 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 ± 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:

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

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	$L_t = \frac{L_\infty \times L_0\left(\exp\left(g_{Log}t\right)\right)}{L_\infty + L_0\left(\exp\left(g_{Log}t - 1\right)\right)}$	Ricker (1979)
Gompertz function	$L_t = L_0 \times \exp(\ln\left(\frac{L_\infty}{L_0}\right)\left(1 - \exp\left(-g_{Log}t\right)\right)$	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):

$$\mathrm{TL} = 1.37 \times \mathrm{PCL}$$

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. 4*a*), 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. 4*b, 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. 4*b, 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

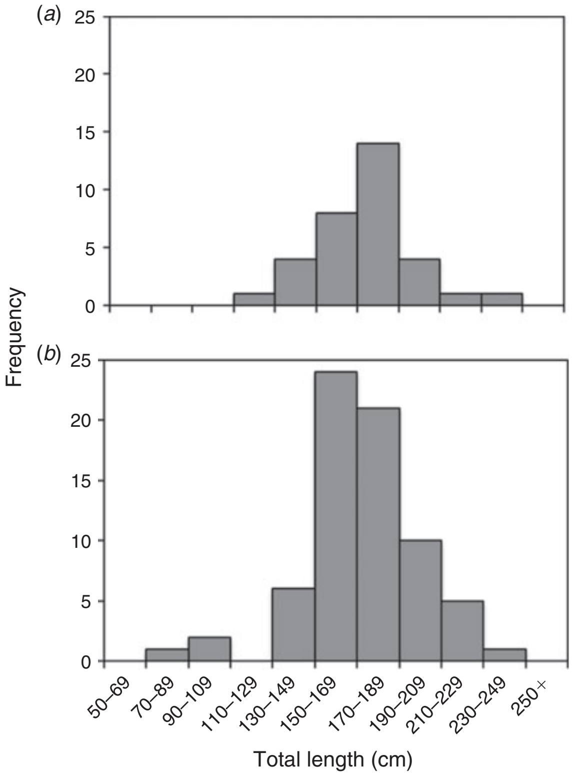

Fig. 2. Length–frequency of individuals sampled, grouped into 20-cm size classes for (*a*) female (*n* = 33) and (*b*) male (*n* = 70) *Carcharhinus longimanus* from the Western Central Pacific Ocean, Papua New Guinea. Samples were collected between May and July 2014.

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 *in utero* 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 (±s.e.) maximum likelihood estimates of l_{50} and l_{95} for females were 224 ± 15 and 258 ± 29 cm TL respectively (Fig. 5*a*). 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. 5*c*). 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. 5*b*). The A_{50} and A_{95} for males were predicted as 10.0 ± 0.5 and 12.5 ± 1.2 years respectively (Fig. 5*d*). Therefore, female *C. longimanus* mature at an older age and greater length than males.

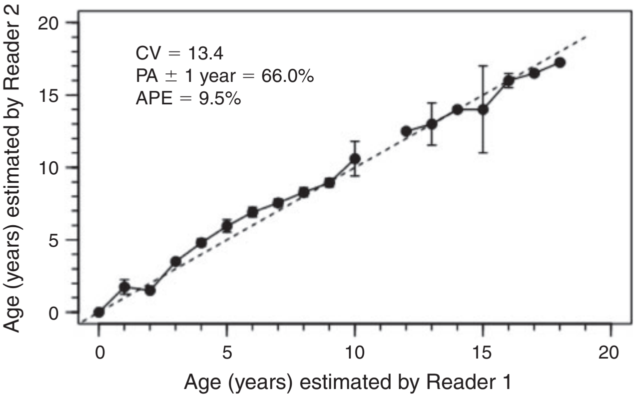

Fig. 3. Age-bias plot for 103 *Carcharhinus longimanus* vertebral counts with age-specific agreements between two independent readers used for Bowker's test of symmetry. Mean (± 2 s.e.) age-specific agreements are plotted with a 1 : 1 equivalence line for comparison. The CV, percentage agreement (PA)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

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 ± 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, AIC$_C$ 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 ± 8.54**	**342.5 ± 90.1**	**0.045 ± 0.023**	–	–
	Gompertz	103	862.6	7.58	0.02	88.09 ± 8.51	240.0 ± 15.1	–	0.146 ± 0.028	
	Logistic	103	939.3	84.2	0.00	88.10 ± 10.1	240.0 ± 32.7	–		0.146 ± 0.043
Back-calculated data										
Male	**VBGF**	**630**	**4973**	**0.00**	**0.74**	**75.11 ± 1.13**	**315.6 ± 20.7**	**0.059 ± 0.007**	–	–
	Gompertz	630	4975	2.15	0.25	78.13 ± 1.04	251.8 ± 7.90	–	0.134 ± 0.007	
	Logistic	630	4984	10.7	0.00	78.13 ± 0.98	230.3 ± 5.10	–	–	0.207 ± 0.008
Female	**VBGF**	**315**	**2463**	**0.00**	**0.94**	**74.68 ± 1.52**	**316.7 ± 27.6**	**0.057 ± 0.008**	–	–
	Gompertz	315	2468	5.46	0.06	76.37 ± 1.42	252.4 ± 10.6	–	0.127 ± 0.009	
	Logistic	315	2477	14.1	0.00	78.00 ± 1.13	230.9 ± 6.90	–	–	0.197 ± 0.010

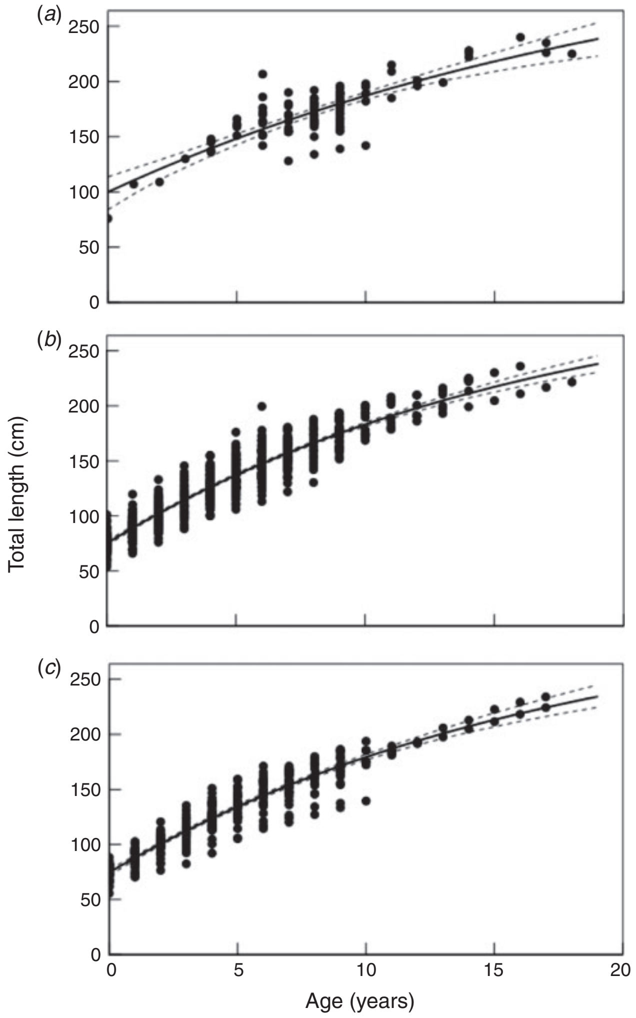

Fig. 4. Length-at-age growth curves for *Carcharhinus longimanus* from the Western Central Pacific Ocean, Papua New Guinea, for (*a*) observed data with males and females combined, (*b*) back-calculated data for males and (*c*) back calculated data for females, fitted with fitted von Bertalanffy growth 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

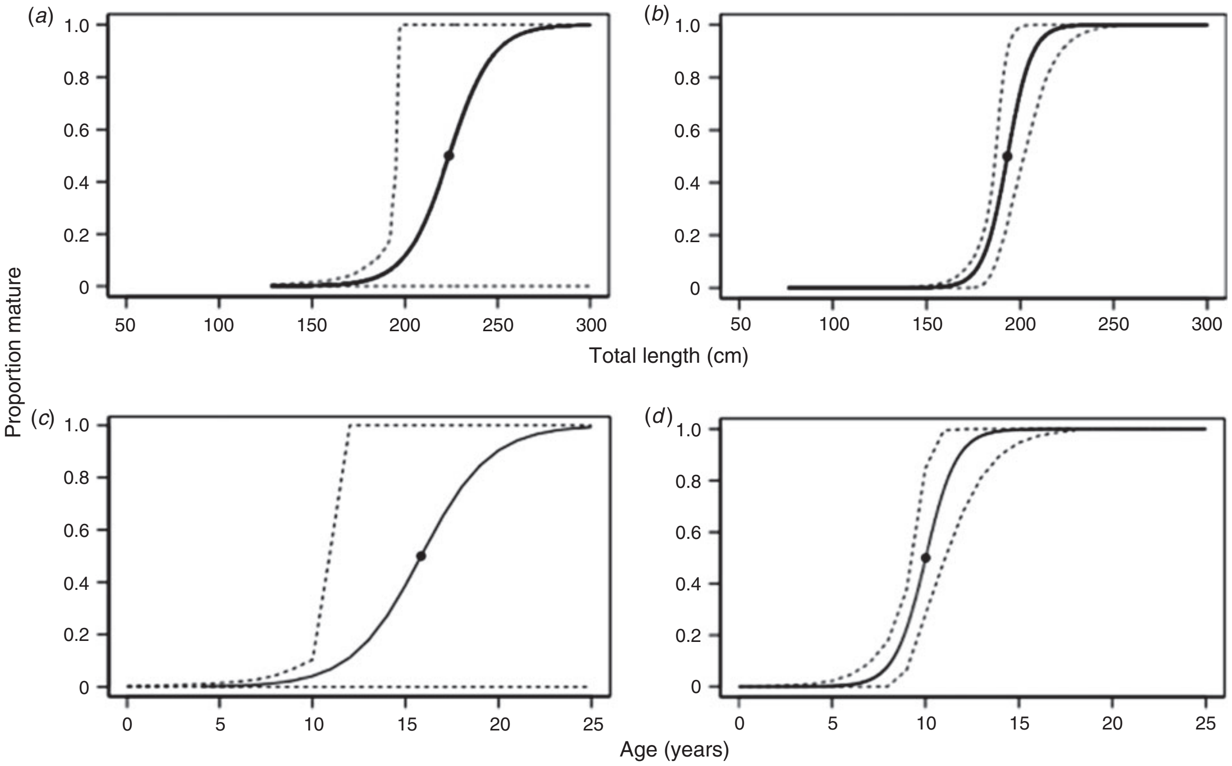

Fig. 5. (*a*, *b*) Length- and (*c*, *d*) age-at-maturity ogives for female (*a*, *c*) and male (*b*, *d*) *Carcharhinus longimanus* from. The black points represent the length and age at which 50% of the population was mature (l_{50} and A_{50} respectively) and dashed lines indicate bootstrapped 95% 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.* 2011*a*, 2011*b*). 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
		Female	BC	74.7	316.7	0.057	–	15.8	223.8	235.0	17	24.9
Seki *et al.* (1998)	North Pacific	Combined	Observed	69.8	341.7	0.103	−2.7	4.5	182.0	272.2	11	20.7^{A} 36.0^{B}
Joung *et al.* (2016)	North-west Pacific	Combined	Observed	64.0	309.4	0.085	–	8.7	193.9	268.0	12	22.1^{A}
Lessa *et al.* (1999)	South-west Atlantic	Combined	Observed	71.0	284.9	0.099	−3.4	7.0	185.0	250.0	17	21.0^{A}

^{A}Calculated during the present study.

^{B}Estimate based on theoretical maximum length by Rice and Harley (2012).

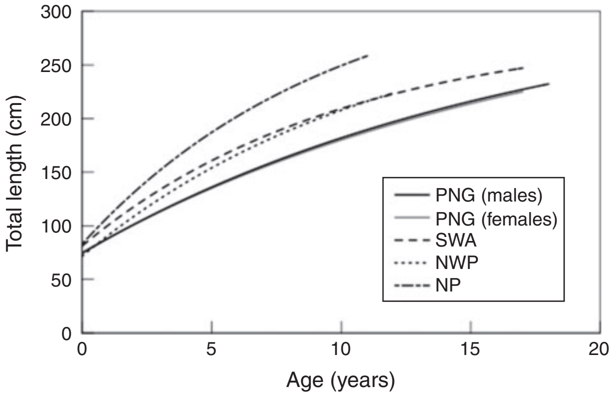

Fig. 6. Comparison of von Bertalanffy growth curves for *Carcharhinus longimanus* from the Western Central Pacific Ocean, Papua New Guinea (PNG; separate sexes, present study), North Pacific Ocean (NP; Seki *et al.* 1998), North-west Pacific Ocean (NWP; Joung *et al.* 2016) and South-west Atlantic Ocean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

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Life history characteristics of the silky shark *Carcharhinus falciformis* from the central west Pacific

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Abstract. In the central west Pacific region, silky sharks (*Carcharhinus falciformis*) are commonly taken in fisheries, forming up to 95% of incidental elasmobranch bycatch. The present study examined the life history of silky sharks ($n = 553$) from Papua New Guinean waters. Age was analysed using sectioned vertebrae, and a multimodel approach was applied to the length-at-age data to fit growth models. Females ranged in length from 65.0- to 253.0-cm total length (TL), with the oldest estimated at 28 years. Males ranged in length from 68.4 to 271.3 cm TL and were aged to a maximum of 23 years. The logistic model provided the best fitting growth parameter estimates of length at birth $L_0 = 82.7$ cm TL, growth coefficient $g = 0.14\ \text{year}^{-1}$ and asymptotic length $L_\infty = 261.3$ cm TL for the sexes combined. Females reached sexual maturity at 204 cm TL and 14.0 years, whereas males reached maturity at 183 cm TL and 11.6 years. The average litter size from 28 pregnant females was 8 (range of 3–13). The growth parameters and late ages of sexual maturation for silky sharks in the central west Pacific suggest a significant risk from fisheries exploitation without careful population management.

Additional keywords: intraspecific variation, logistic growth function, pelagic shark fisheries, vertebral ageing.

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Introduction

Detailed biological information on life history (age, growth, reproductive traits and demography) of species exposed to fishing is critical to their sustainable management (Cailliet 2015). Aspects of the life history of chondrichthyans (sharks, rays and chimaeras) remain one of the most poorly understood among marine vertebrate groups. Although many elasmobranch species are widely distributed, considerable intraspecific variation in life history traits has been shown to exist between some populations in different geographic locations (e.g. Yamaguchi *et al.* 1998; Lombardi-Carlson *et al.* 2003; Smart *et al.* 2015). Therefore, region-specific life history data of a species is required to properly inform sustainable management plans (Simpfendorfer *et al.* 2011). Using life history parameters derived from one population to conspecifics in another region increases the risk of inaccuracies in population modelling (Chin *et al.* 2013; Smart *et al.* 2015). This can lead to inappropriate management approaches that risk negative consequences for those species and may lead to economic loss for those using the resource.

Sharks life histories are typically characterised by slow growth, low fecundity, late age of sexual maturation and often considerable longevity (Cortés 2000; Au *et al.* 2008). These traits collectively manifest low intrinsic population growth rates, reducing their resilience to fishing mortality (Campana 2001: Au *et al.* 2008). In recent decades, sharks have increasingly become a valuable commodity as catch of traditional teleost species has become more restrained (Dulvy *et al.* 2008) and demand for shark products has increased (Dent and Clarke 2015). Fuelled largely by the high market value of fins and demand for cheap sources of animal protein (Simpfendorfer and Dulvy 2017), targeted fishing effort for sharks, as well as the retention of incidentally caught sharks, has increased considerably both in coastal areas and on the high seas (Clarke *et al.* 2006; Dulvy *et al.* 2008). As exploitation increases, and the status of populations declines (Davidson *et al.* 2016), life history

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data on key species taken in fisheries are needed to help improve their fisheries management and assessment.

The silky shark *Carcharhinus falciformis* is a pantropically distributed oceanic–epipelagic species (Last and Stevens 1994; Rigby *et al.* 2016) commonly caught by fisheries throughout their range. This species is placental viviparous and likely has a biennial reproductive cycle (Galván-Tirado *et al.* 2015). Maximum size is reported to be 371 cm and length-at-maturity ranges from 180 to 246 cm, with males and females estimated to reach maturity at 5–13 and 6–15 years respectively (Rigby *et al.* 2016). Silky sharks have a strong tendency to aggregate under floating oceanic debris and artificial fish aggregation devices (FADs), where they are commonly observed to follow schooling tuna (Strasburg 1958; Yoshimura and Kawasaki 1985). The tendency of silky sharks to migrate within schools of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*), both of which are heavily fished, has resulted in them being one of the most incidentally caught elasmobranch species (Hutchinson *et al.* 2015). Commercial purse seine and longline fishing operations report large amounts of silky shark catch (Poisson *et al.* 2014; Hutchinson *et al.* 2015). In addition, entanglement in FADs significantly contributes to the mortality of juvenile age classes in the Indo-Pacific and Indian Ocean regions (Filmalter *et al.* 2013). In recent years, the incidental catch rate of silky shark has fallen by 60% in the east Pacific (Minami *et al.* 2007), by up to 90% on longlines in the Atlantic (Baum and Myers 2004) and in the central Pacific, catch rate trends have fallen with decreases in the median size of individuals caught also observed (Clarke *et al.* 2011). Currently, the Western and Central Pacific Fisheries Commission (WCPFC) and International Commission for Conservation of Atlantic Tunas prohibit the retention of silky shark (Rice *et al.* 2015). In the Indian and east Pacific oceans, the deteriorating status of silky sharks has been noted (Minami *et al.* 2007; Hall *et al.* 2012), although adoption of conservation measures has yet to be reviewed and implemented. The Convention on International Trade in Endangered Species (CITES) lists the silky shark in appendix II (international trade only allowed if shown to have no detrimental to a population) and the silky shark is listed under the Conservation of Migratory Sharks (CMS) Memorandum of Understanding for Migratory Sharks (Rigby *et al.* 2016). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species assesses the silky shark as ‘near threatened’ throughout its range (Rigby *et al.* 2016).

Despite silky sharks being a common constituent of bycatch throughout their geographic range, life history parameters are lacking for some regions. Furthermore, previous studies on aspects of their growth and reproductive biology have produced variable results, underlining the need for region-specific data (Branstetter 1987; Oshitani *et al.* 2003; Hall *et al.* 2012). The central west Pacific is one such area where no detailed life history information exists for silky sharks. A dedicated shark longline fishery that operated in Papua New Guinea (PNG) until 2014 reported catch per unit effort (CPUE) of silky sharks to be as high as 17 per 1000 hooks set, with the species comprising ~50% of total landings (Kumoru 2003). Furthermore, silky shark reportedly constituted up to 95% of incidentally caught elasmobranchs in some areas of the WCPFC’s range (Lawson 2011). High catch rates of this species since the inception of management in 1995 indicate that the central west Pacific is an important region to this species and likely supports a large population (Clarke *et al.* 2013). However, gradual decreases in the median size of individuals caught since 1995 suggest this population may be declining as a result of prolonged fisheries exploitation (Rice and Harley 2013).

The aim of the present study was to estimate growth parameters from length-at-age analysis and to describe aspects of the reproductive biology for the silky shark in PNG waters. Information gathered was intended to produce sufficient life history data to inform improved fisheries management in PNG and the greater central west Pacific region.

Materials and methods

Samples were collected from seven commercial longline operators in the Bismarck and Solomon seas in May and June 2014 by fisheries observers from the PNG National Fisheries Authority. The vessels targeted various shark species by setting gear close to the surface (up to 1200 hooks per set) for 8–10 h (Kumoru 2003). In all, 553 silky sharks were collected for examination. Total length (TL) was measured to the nearest 1 mm for all individuals and photographs were taken for identification purposes. On-board observers recorded their reproductive status (see below) and a section of six to eight vertebrae was removed from 527 individuals anterior to the first dorsal fin. Vertebral samples were stripped of excess flesh and tissue before being stored frozen. Species validation of each individual was performed through the examination of the photographs taken.

Vertebrae preparation and sectioning

Vertebral sections were prepared for ageing following standard protocols (Goldman 2005). Vertebral samples were defrosted before being separated into individual centra. The neural arch, haemal arch and any residual tissue were cut from each centrum. Individual centra were then soaked in a 5% sodium hypochlorite solution for 30 min to remove any remaining soft tissue. Centra were rinsed thoroughly under running tap water and placed in a drying oven for 24 h at 60°C. One centrum from each individual was randomly selected to be sectioned for analysis. Centra were sectioned on a sagittal axis through the centrum focus using a low-speed circular saw with two diamond-tipped blades (Beuhler, Lake Bluff, IL, USA). Sections were cut to a thickness of ~400 μm, measured with digital callipers. Vertebral sections were mounted on microscope slides using Crystal Bond adhesive (SPI Supplies, West Chester, PA, USA). A binocular dissecting microscope with a transmitted light source was used to examine each section

Age determination

Ages were determined by counting translucent and opaque band pairs in the corpus calcareum of each centrum as per Cailliet and Goldman (2004). The birthmark was identified as a change in angle on the inner margins of the corpus calcareum representing the shift from embryonic development to postnatal growth (Cailliet and Goldman 2004). Following Cailliet *et al.* (2006), each pair of translucent and opaque bands thereafter was deemed to represent 1 year of growth (Fig. 1). No attempt to

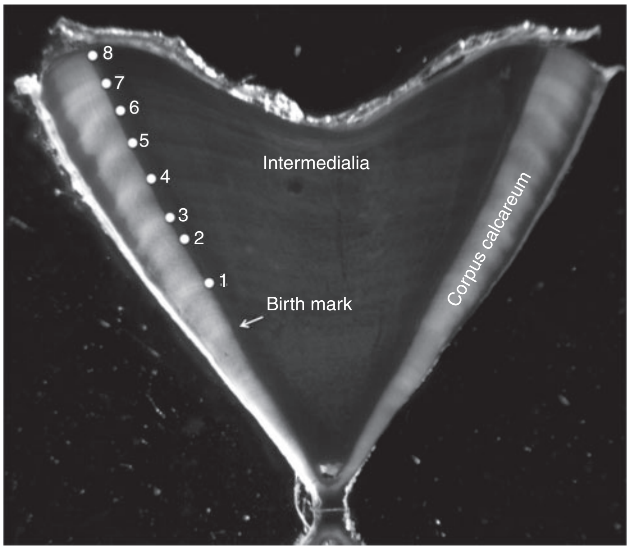

Fig. 1. Vertebral section of an immature male *Carcharhinus falciformis*, 148.8-cm total length, estimated to be 8 years old. The locations of the translucent annulus bands (white dots 1–8), the birthmark, intermedialia and corpus calcareum are shown.

determine the periodicity of band pair deposition could be made in the present study because samples were only collected over a 2-month period and hence methods of marginal increment analysis were not possible. However, annual band pair deposition has been verified by this method for silky sharks in regions adjacent to the present study site (Joung *et al.* 2008; Hall *et al.* 2012), and so annual band pair deposition was assumed for the present study.

Two readers independently counted band pairs on all sectioned vertebrae without prior knowledge of the length of the specimens. Each vertebral section was read twice by the primary reader (M. I. Grant) and once by an experienced second reader (J. J. Smart). A consensus age was recorded when primary reader counts agreed with the second reader count. All vertebrae with a band pair count discrepancy between readers were re-examined by both readers together to reach a consensus age. Vertebrae were disregarded from further analysis where a consensus age could not be agreed. Intra- and interreader precision was measured by indices of average percentage error (APE) and CV (Chang 1982), as recommended by Cailliet and Goldman (2004). Age bias plots were also constructed between each set of reads to identify the presence of systematic bias, which was formally tested by Bowker's test of symmetry (Bowker 1948; Evans and Hoenig 1998). All accuracy and precision calculations were conducted using the FSA package (D. H. Ogle, see https://fishr.wordpress.com/fsa/, accessed September 2016) in the R program environment (R Foundation for Statistical Computing, Vienna, Austria).

Modelling growth

A multimodel approach incorporating Akaike's information criterion (AIC; Akaike 1973) was used to select the most appropriate growth model (Smart *et al.* 2016). Three candidate models were selected *a priori* and each applied to the length-at-age data. The candidate models chosen were the von Bertalanffy growth function (VBGF; von Bertalanffy 1938), the logistic function (Ricker 1979) and the Gompertz function (Ricker 1975; Table 1). A form of each model incorporating the length-at-birth parameter L_0 was used because it has biological meaning and can be directly compared between models. The asymptotic length (L_∞) can also be directly compared between each of the candidate models, but the respective growth coefficient of each model (i.e. k for the VBGF, g for the logistic model and g for the Gompertz model) cannot because these coefficients represent different mathematical principles.

Table 1. Three *a priori* model candidate equations used in the multimodel Akaike information criterion analysis

L_t, length at age t; L_0, length at age 0; L_∞, asymptotic length; k and g, respective growth coefficients of each model

Model	Growth function equation
Von Bertalanffy growth function	$L_t = L_0 + (L_\infty - L_0)\,(1 - \exp(-kt))$
Logistic function	$L_t = (L_\infty\, L_0\,(\exp(gt))) \div (L_\infty + L_0\,(\exp(gt) - 1))$
Gompertz function	$L_t = L_0\exp(\log(L_\infty \div L_0)\,(1 - \exp(-gt)))$

The best-fit parameter estimates for each model were identified using the non-linear least squares (nls) function in the R program environment (R Foundation for Statistical Computing). Each model was applied to the sexes combined data and to each sex separately. The AIC was then used to determine the 'best-fit' model for each of these datasets as follows:

$$\mathrm{AIC} = n\log\left(\sigma^2\right) + 2k$$

where k is the total number of parameters being considered $+1$ for variance (σ^2) and n is the sample size. The model with the lowest AIC value ($\mathrm{AIC}_{\mathrm{min}}$) was selected as the most appropriate representation of the length-at-age data. Differences in AIC values (ΔAIC) were calculated for subsequently poorer fitting models as follows:

$$\Delta\mathrm{AIC} = \mathrm{AIC}_i - \mathrm{AIC}_{\mathrm{min}}$$

whereby a ΔAIC of 0–2 had the highest support, ΔAIC of 2–10 had considerably less support and $\Delta\mathrm{AIC} > 10$ had no support (Burnham and Anderson 2002). AIC weights (w_i) were also calculated from AIC values, which described the probability of selecting the most suited model to the length-at-age dataset, as follows:

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

where Δ_i is ΔAIC of each specified model and Δ_j is the ΔAIC of each individual model. Likelihood ratio tests (LRTs; Kimura 1980) were used to determine whether models for separate sexes should be used over a single model for combined sexes. The LRT was used to test whether the growth curves of each sex were coincident for all growth parameters combined, as well as each parameter individually, using Microsoft Excel (Bellevue, WA,

Table 2. Characteristics used to classify maturity stages of female and male *Carcharhinus falciformis*

Adapted from White *et al.* (2001)

Maturity stage classification	Indicating characteristics
Females	
Stage 1: immature	Very small ovaries; uteri similar in size, thin and flaccid
Stage 2: maturing virgin	Functional (right) ovary contains small yolked ova; the two functional uteri beginning to enlarge but mostly thin and flaccid
Stage 3: mature, non-pregnant	Right ovary contains yolked ova >2.0 mm in diameter; uteri enlarged along entire length
Stage 4: mature, pregnant	Fertilised eggs or embryos in both uteri
Stage 5: mature, postpartum	Uteri very enlarged and flaccid from having recently released young
Males	
Immature	Claspers small, flexible and non-calcified
Maturing	Claspers enlarging and beginning to calcify and thus become rigid
Mature	Claspers fully developed and rigid from complete calcification

USA) according to the method outlined by Haddon (2001). Growth curves were tested only for equivalent age ranges (0–23 years) as per the assumptions of the LRT used (Haddon 2001).

Maturity analysis

The reproductive maturity status of 518 silky sharks was determined by examination of external and internal features. Male maturity was assessed by observers at the time of capture by inspection of clasper calcification. Female maturity was also examined at the time of capture by internal inspection of ovaries, uteri and ova (Table 2). Female silky sharks classified as Stage 1 and 2 were identified as those possessing an undeveloped right (functional) uterus and thus are not capable of conceiving, despite some small ova with indication of vitellogenic development. Females in Stage 3 contained larger (at least >2.0 mm) ova in conjunction with a developed uterus and were deemed capable of conceiving and were thus considered mature (White *et al.* 2001; Hall *et al.* 2012). Female maturity stages were later verified for each individual by reviewing photographs taken at the time of inspection. For pregnant females, the litter size and sex of embryos were recorded and the TL of each embryo measured. A Chi-Square test was used to test for any significant difference in the sex ratio of litters examined.

The TL at which 50% (L_{50}) and 95% (L_{95}) of females and males had attained maturity was calculated using the generalised linear model (GLM) with a logit-link function in the R environment (R Foundation for Statistical Computing). Following Hall *et al.* (2012), 1000 bootstrap estimates of the logistic parameters were produced to identify the probability of each individual of a given TL being mature. The 95% confidence limits were taken as the 2.5 and 97.5 percentiles of the 1000 estimates for the logistic parameters and probabilities of each individual being mature. The same process was used to estimate the age-at-maturity for the population at 50% mature (A_{50}) and 95% mature (A_{95}).

Results

Age estimates

Band pair counts by the primary reader (M. I. Grant) had a CV of 10.8% and an APE of 7.6%, both within reasonable limits for chondrichthyan age studies (Campana 2001). However, systematic bias was present between Read 1 and Read 2 (both M. I. Grant) (Fig. 2), as detected by Bowker's test of symmetry (d.f. = 72, $\chi^2 = 149.2$, $P < 0.001$). There were also levels of systematic bias detected between readers for both Read 1 (M. I. Grant) and Read 3 (J. J. Smart) (d.f. = 86, $\chi^2 = 229.6$, $P < 0.001$) and Read 2 and Read 3 (d.f. = 92, $\chi^2 = 338.6$, $P < 0.001$). Differences in age estimates were more pronounced in larger length classes (Fig. 2). To rectify age discrepancies, consensus counts were conducted for all age estimates that differed within all length classes. A third reader was used before commencing consensus counts to ensure consistency in first band pair identification, which is often the main systematic error source in chondrichthyan ageing techniques (Campana 2001). Age estimates were agreed upon for 526 samples (females = 254, males = 272) with only one vertebra deemed uninterpretable and omitted from the length-at-age data. Samples in the present study produced the oldest age estimates by vertebral analysis for both female and male silky sharks, with estimated ages ranging from 0 to 28 years for females and from 0 to 23 years for males. The sample size encompassed individuals ranging from 65 to 271 cm TL (Fig. 3).

Growth estimation

Results of the multimodel AIC analysis indicated that the logistic model was the best fit for the observed length-at-age data for sexes combined (Table 3; Fig. 4). Kimura's LRT showed that logistic growth curves for each sex separately were coincident, with no significant difference detected between curves ($\chi^2 = 2.49$, d.f. = 3, $P < 0.05$). Furthermore, no significant difference was detected for each growth parameter produced by the logistic growth model between sexes ($P < 0.05$). Hence, the sexes combined logistic model growth parameter estimates ($L_0 = 82.7$ cm TL, $g = 0.14\ \text{year}^{-1}$, $L_\infty = 268.3$ cm TL) were considered to appropriately represent the growth of both sexes (Fig. 4). Parameter estimates for length at birth (L_0) were within a reasonable biological range for this species across all models for both sexes combined and sexes separated.

Maturity analysis

Maturity status data were collected for 518 individuals (248 females, 269 males). The smallest observed mature female was 192 cm TL, whereas the largest observed immature female was

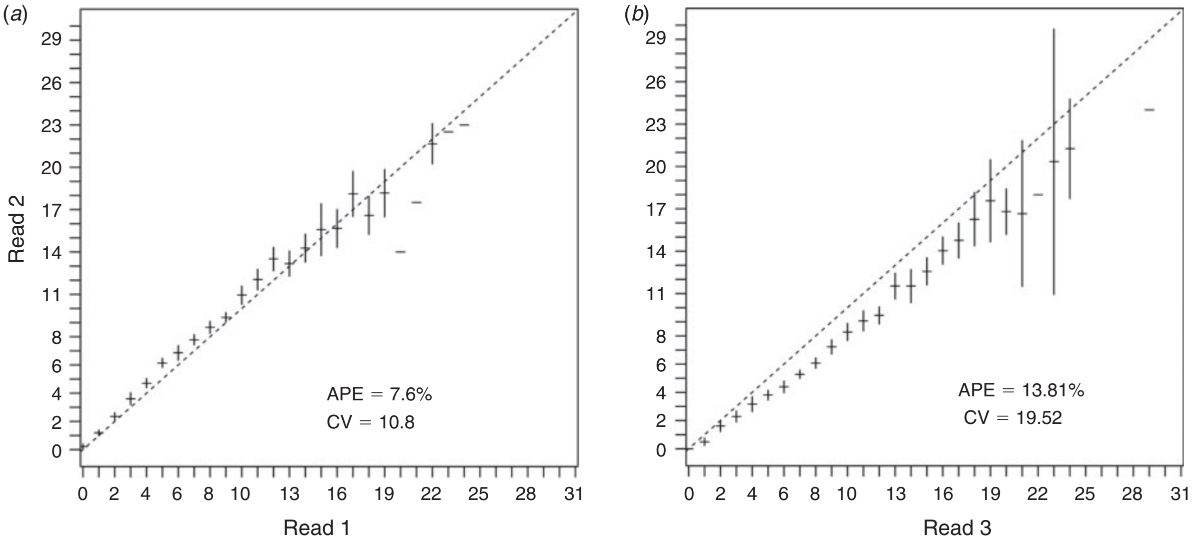

Fig. 2. Age-bias plots for *Carcharhinus falciformis*. Mean age-specific agreements between (*a*) Read 1 and Read 2 (both M. I. Grant) and (*b*) Read 2 (M. I. Grant) and Read 3 (J. J. Smart). The 95% confidence limits are plotted along a 1 : 1 equivalence line for comparison. APE, average percentage error. (The age-bias plot between Read 1 and Read 3 is shown in Fig. S1, available as Supplementary material to this paper.)

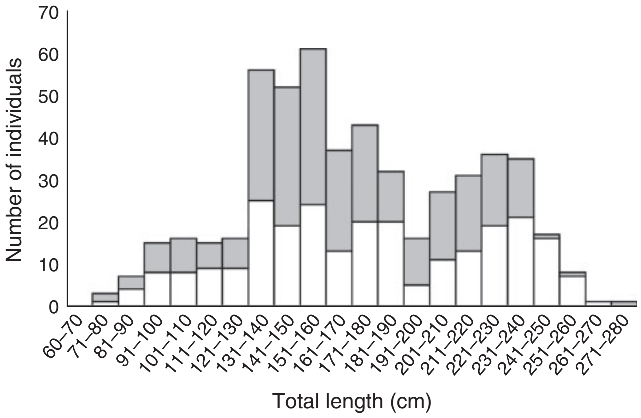

Fig. 3. Length–frequency distribution showing the range of *Carcharhinus falciformis* males (shaded) and females (white) used in the present study

213 cm TL. For males, the size range of mature individuals was greater, with the smallest mature male being 167 cm TL and the largest immature male being 200 cm TL. The length and age at which 50% and 95% of both females and males were mature showed a considerable difference, with males maturing earlier and at smaller sizes (Table 4). For males, L_{50} and L_{95} were 183 and 198 cm TL respectively, corresponding to an A_{50} and A_{95} of 11.6 and 13.7 years respectively. For females, L_{50} and L_{95} were 204 and 219 cm TL respectively, corresponding to an A_{50} and A_{95} of 14.0 and 16.5 years respectively (Figs 5, 6).

Of the mature females collected for ageing, 28 were pregnant with a mean (±s.d.) litter size of 8.6 ± 2.65. In total, there were 242 embryos (120 male, 122 female). The embryonic sex ratio did not differ significantly from 1 : 1 ($\chi^2 = 0.017$, d.f. = 1, $P = 0.90$). The largest observed litter size was 13 and the smallest was 3. No consistency in the length of embryos was observed during the sampling period, with individuals between litters ranging from 9–12 to 66–71 cm TL.

Discussion

The results of the present study provide evidence that the growth characteristics of the silky shark vary throughout its pantropical distribution. Compared with previous length-at-age studies, silky sharks in the central west Pacific grow slower, mature later and possibly attain a smaller maximum size than conspecifics in the Atlantic (Branstetter 1987; Bonfil *et al.* 1993), Taiwan (Joung *et al.* 2008) and the central Pacific (Oshitani *et al.* 2003; Fig. 7; Table 5), whereas the results for growth parameters and ages at maturity were similar to those reported from Indonesia (Hall *et al.* 2012). Fecundity data and sex ratios for the western central Pacific showed similar trends to all other study regions (Oshitani *et al.* 2003; Hall *et al.* 2012).

Multimodel growth analysis

The present study is the first to use a multimodel approach to the fitting of growth functions for the silky shark. All previous studies have *a priori* selected only the VBGF to fit length-at-age data, because the VBGF has traditionally been assumed to sufficiently estimate viviparous shark growth (Smart *et al.* 2016). However, it has been demonstrated that the VBGF does not always provide the best fit to shark length-at-age data and, in some instances, provides growth parameter estimates that are likely to be inaccurate (Katsanevakis 2006; Smart *et al.* 2016). The absence of a defined asymptote is not uncommon in many shark growth curves (Simpfendorfer *et al.* 2002; Smart *et al.* 2017), which can lead to biologically unrealistic L_∞ estimates, such as those observed for the VBGF in the present study. Comparatively, the logistic model L_∞ estimate was more comparable to the maximum size observed in the present study. Similarly, Carlson and Baremore (2005) found the logistic

Table 3. Summary of Akaike information criterion (AIC) results and model parameters for the length-at-age data

Where appropriate, data are given as the mean ± s.d. Bold values indicate the AIC selected logistic model growth parameters, *n*, number of individuals; Δ, difference in AIC values between models; *w*, AIC weight; L_∞, asymptotic length parameter; L_0, length-at-birth parameter; *k*, growth rate parameter for the von Bertalanffy growth function (VBGF). Both the Gompertz and logistic models use '*g*' to represent their respective growth coefficient, so subscripts have been used to indicate which growth function '*g*' refers to (i.e. g_{Gomp} and g_{Log} respectively). Confidence limits (95%) for parameter estimates are given in parenthesis. Only parameter values of L_∞ and L_0 are comparable between models

Sex	Model	*n*	AIC	Δ	*w*	L_∞ (cm)	L_0 (cm)	*k* (year^{-1})	g_{Gomp} (year^{-1})	g_{Log} (year^{-1})
Combined	VBGF	526	4292.3	26.9	0.0	386.8 ± 57.4	77.6 ± 4.1	0.04 ± 0.01	–	–
	Logistic	**526**	**4264.1**	**0.0**	**100**	**268.3** ± 11.4	**82.7** ± 3.1	**–**	**–**	**0.14** ± 0.01
	Gompertz	526	4275.6	11.1	0.0	296.4 ± 19.0	80.3 ± 3.5	–	0.09 ± 0.01	–
Male	VBGF	272	2234.0	2.8	24.2	659.1 ± 509.6	82.3 ± 6.0	0.02 ± 0.02	–	–
	Logistic	**272**	**2231.2**	**0.0**	**67.6**	**287.3** ± 31.8	**85.8** ± 4.9	**–**	**–**	**0.12** ± 0.02
	Gompertz	272	2236.2	5.0	8.2	342.0 ± 61.4	84.0 ± 5.5	–	0.07 ± 0.02	–
Female	VBGF	254	2057.4	22.7	0.0	342.6 ± 45.1	74.8 ± 5.7	0.05 ± 0.01	–	–
	Logistic	**254**	**2034.7**	**0.0**	**99.9**	**261.6** ± 11.4	**80.6** ± 4.3	**–**	**–**	**0.15** ± 0.02
	Gompertz	254	2044.0	9.3	0.01	282.7 ± 18.2	77.8 ± 4.9	–	0.09 ± 0.01	–

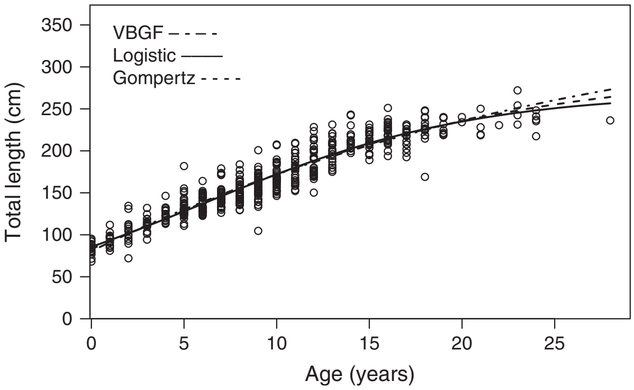

Fig. 4. Length-at-age data of *Carcharhinus falciformis* fitted with the three candidate models, namely the von Bertalanffy growth function (VBGF), logistic and Gompertz. Circles indicate the length at age of each individual. The logistic model provided the best fit for the observed length-at-age data.

Table 4. Total length (L_{50} and L_{95}) and age (A_{50} and A_{95}) estimates at which 50 and 95% of females and males are mature, together with 95% confidence limits (CL)

Maturity index	Females	Males
L_{50} (cm)	204.19	183.44
Lower CL	199.90	179.40
Upper CL	208.36	187.68
L_{95} (cm)	218.91	198.90
Lower CL	212.32	190.60
Upper CL	234.53	205.95
A_{50} (years)	14.0	11.6
Lower CL	13.4	11.2
Upper CL	14.5	12.0
A_{95} (years)	16.5	13.7
Lower CL	15.1	12.9
Upper CL	17.6	14.3

model also provided the best fit to length-at-age data for the spinner shark (*Carcharhinus brevipinna*), despite traditional *a priori* use of the VBGF for this species.

No significant difference was detected between growth parameters of each sex for the logistic models. Uniform growth between sexes has also been observed in all previous length-at-age studies of silky sharks and appears to be characteristic of this species. The growth coefficient attained from the logistic model ($g = 0.14\ \text{year}^{-1}$) suggests that silky sharks in the central west Pacific reach their asymptotic length slowly compared with other regions (Fig. 7). For example, the blacktip reef shark *Carcharhinus melanopterus* from north-eastern Australia had an estimated *g* of 0.25 year^{-1} and was also considered to be a slow-growing species (Chin *et al.* 2013). A low growth coefficient for the silky shark was also observed in an adjacent study site, in Indonesia (Hall *et al.* 2012), whereas in the Gulf of Mexico (Branstetter 1987) and east (Sánchez-de Ita *et al.* 2011) and central Pacific (Oshitani *et al.* 2003) regions, silky sharks appear to reach their asymptotic length faster (Fig. 7; Table 5). Variation in the growth coefficient has been observed for other *Carcharhinus* species between regions, and may be a reflection of natural variation or differences in methodology and sampling design between studies (Casey and Natanson 1992; Smart *et al.* 2015).

Despite more individuals in larger size classes being sampled in the present study compared with the adjacent Pacific study sites, namely the central Pacific (Oshitani *et al.* 2003) and Taiwan (Joung *et al.* 2008), the L_∞ parameter estimated (268.3 cm TL) is still considerably lower than the observed maximum length of 371 cm TL for silky sharks (Serafy *et al.* 2012) in the Atlantic. Large (>300 cm TL) silky sharks are reported in the Atlantic (Bonfil *et al.* 1993) and occasionally in the east Pacific (Sánchez-de Ita *et al.* 2011), whereas around the Indo-Pacific reports of individuals >300 cm TL are rare. Sampling was only conducted over a 2-month period in the present study and it is possible that extremely large individuals were not present in the area at this time. However, the largest individuals observed in the present study are similar to those

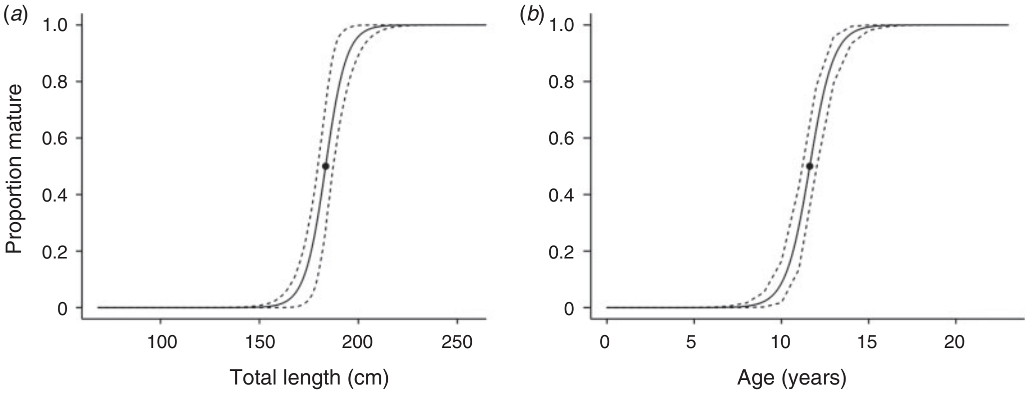

Fig. 5. Maturity ogives for male *Carcharhinus falciformis* from logistic generalised linear models of (*a*) observed length and (*b*) estimated age. Curves show the proportion of males that appear to be mature at a given length and age. Dotted lines indicate 95% confidence limits. The black circle indicates the point where the proportion mature is 50% (L_{50}, A_{50}).

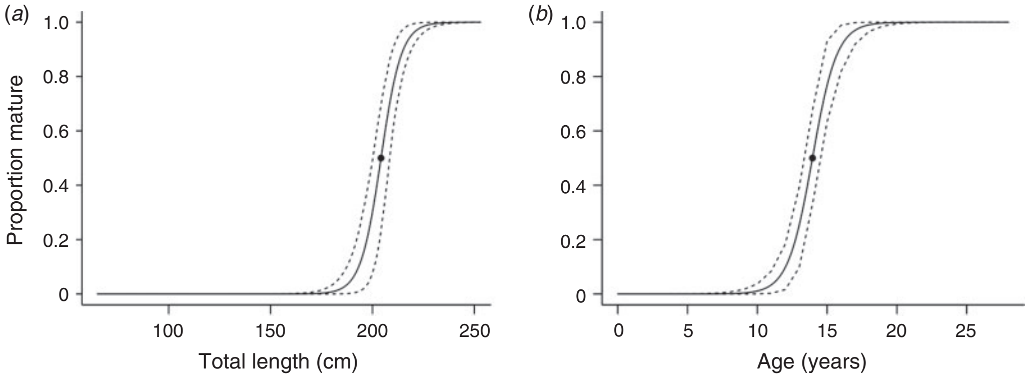

Fig. 6. Maturity ogives for female *Carcharhinus falciformis* from logistic generalised linear models of (*a*) observed length and (*b*) estimated age. Curves show the proportion of males which appear to be mature at a given length and age. Dotted lines indicate 95% confidence limits. The black circle indicates the point where the proportion mature is 50% (L_{50}, A_{50}).

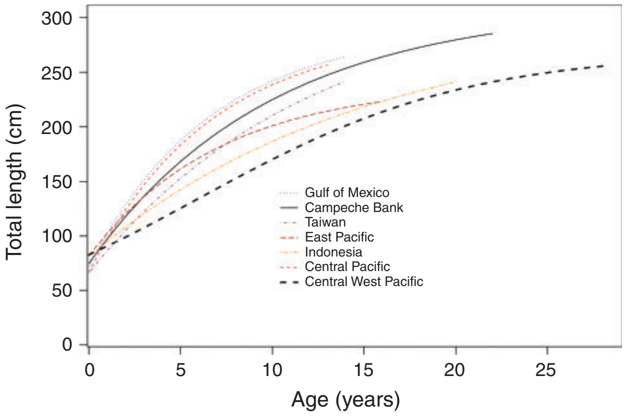

Fig. 7. Comparison of growth curves for *Carcharhinus falciformis* from the Gulf of Mexico (Branstetter 1987), Campeche Bank (Bonfil *et al.* 1993), Taiwan (Joung *et al.* 2008), east Pacific (Sánchez-de Ita *et al.* 2011), Indonesia (Hall *et al.* 2012), central Pacific (Oshitani *et al.*, 2003) and central west Pacific (present study). The von Bertalanffy growth function was used in all regions to fit length-at-age data, except for the central west Pacific, where the logistic growth function provided the best fit from Akaike information criterion analysis.

reported by Hall *et al.* (2012), who sampled year-round in comparable latitudes in Indonesia. It is possible that silky shark populations around the Indo-Pacific do not reach the maximum sizes that conspecifics do in the Atlantic. This is supported by older age estimates derived in the present study, which indicate that several individuals of 20–28 years have only attained lengths of ~250 cm TL. Silky sharks at similar lengths were also aged at ~20 years by Hall *et al.* (2012) in Indonesia, whereas in the Atlantic Branstetter (1987) estimated his largest specimen, measuring 267 cm TL, to be 13 years old. However, the absence of large (>300 cm TL) silky sharks in the Indo-Pacific may be a consequence of intensive historical targeting of large sharks for the Asian fin trade (Clarke *et al.* 2006, 2013). Within the WCPFC's range particularly, silky sharks have incurred very heavy fisheries pressure since the mid-1990s, with an average of ~175 000 individuals caught annually in longline and purse seine fisheries since 1995 (Lawson 2011).

Sources of variation between silky shark studies

There are a few possible sources of variation within silky shark length-at-age studies that may have been responsible for the observed regional differences in growth parameters (Table 5)

Table 5. Comparison of life history characteristics presented for *Carcharhinus falciformis* in each region studied

TL, total length; L_0, length-at-birth parameter; L_∞, asymptotic length parameter; k, von Bertalanffy growth coefficient; g, logistic growth function growth coefficient; A_{50}, age at which 50% of individuals sampled have obtained maturity, calculated using a generalised linear model (GLM); L_{50}, length at which 50% of individuals sampled have obtained maturity, calculated using a GLM; F, female; M, male

Region	Maximum observed age (years)	Maximum observed TL (cm)	Growth parameter estimates				Sexual maturation			Study
			L_0 (cm TL)	L_∞ (cm TL)	k (year^{-1})	g (year^{-1})		Age (years)	TL (cm)	
Atlantic										
Gulf of Mexico	14	267	72	291	0.15	–	F	7–9	>225	Branstetter (1987)
							M	6–7	210–220	
Campeche Bank	22	314	74.7	311	0.1	–	F	>12	232–245	Bonfil *et al.* (1993)
							M	10	>225	
Pacific										
East Pacific	16	260	81.9	240	0.14	–	F	8	180–182	Hoyos-Padilla *et al.* (2012),
							M	8	180–182	Sánchez-de Ita *et al.* (2011)
Central Pacific	13	292	66.8	288	0.15	–	F	6–7	204	Oshitani *et al.* (2003)
							M	5–6	>186	
Taiwan	14	256	68.3	332	0.083	–	F	9–10	210–220	Joung *et al.* (2008)
							M	9 (A_{50})	213 (L_{50})	
Central west Pacific	28	271	82.7	268	–	0.14	F	14 (A_{50})	204 (L_{50})	Present study
							M	12 (A_{50})	183 (L_{50})	
Indian										
Indonesia	20	260	81.2	299	0.066	–	F	15 (A_{50})	216 (L_{50})	Hall *et al.* (2012)
							M	13 (A_{50})	208 (L_{50})	

and subsequent growth curves (Fig. 7). There is a paucity of information available with regard to distributional patterns of silky shark stocks and a better understanding is needed of population structure and size segregations within populations. Clarke *et al.* (2015) investigated the global population connectivity of silky sharks using mitochondrial DNA markers and suggested one population in the west Atlantic and two distinct populations (east and west) in both the Pacific and Indian oceans. Hence, variations in growth parameters between regions studied may be attributed to natural variation between these suggested populations. However, differences between growth parameters in west Pacific study sites, namely Taiwan (Joung *et al.* 2008), the central Pacific (Oshitani *et al.* 2003) and the present study, are inconsistent with the population structure proposed by Clarke *et al.* (2015), although latitudinally segregated populations were not considered in their study.

Differences in sampling design and methodology may have contributed to regional growth parameter variances. Growth models are sensitive to missing data points on either end of the length spectrum and a lack of juvenile or large adult size classes can lead to false inferences of growth rate (Smart *et al.* 2016). Bonfil *et al.* (1993) noted size class distributions within the sample size of the two respective Atlantic silky shark studies likely contributed to the observed growth parameter differences between these geographically adjacent regions. A lack of large samples in the Gulf of Mexico (Branstetter 1987) produced a low asymptotic length and higher growth coefficient estimate compared with Campeche Bank to the south (Bonfil *et al.* 1993). The variation in growth models produced between these studies is significant because Clarke *et al.* (2015) suggest one population in the west Atlantic. This indicates that these variations in growth parameters are likely to have resulted from methodological differences or sampling design. In the east (Sánchez-de Ita *et al.* 2011) and central (Oshitani *et al.* 2003) Pacific studies, most individuals collected were <240 cm TL and, similarly, these regions had comparatively high growth coefficient estimates compared with the present study and that in Taiwan (Joung *et al.* 2008), where more individuals in larger size classes were sampled (Table 5).

From data presented within silky shark length-at-age studies, it is not possible to deduce whether the apparent limitations on the availability of size classes sampled is due to temporal gear selectivity or undocumented segregation of size classes in each study region. All previous length-at-age studies on silky sharks have obtained samples from longline fishing methods, although little comparable information is given for soak time, depth and hook size. However, location of habitat fished may be a factor. For example, between the Atlantic studies, larger individuals (>240 cm TL) were caught on the continental shelf (Bonfil *et al.* 1993), whereas Branstetter (1987) collected samples from a pelagic swordfish fishery resulting in smaller size classes ranging from 100 to 210 cm TL. Conversely, in Indonesia, Hall *et al.* (2012) noted a higher presence of smaller individuals (<140 cm TL) in gill net fisheries operating on the outer continental shelf and larger individuals (>140 cm TL) were collected from longline fisheries off the continental shelf in pelagic environments. Thus, size class segregations may occur between shelf and pelagic habitats for silky sharks, although it is unclear whether this is a function of gear selectivity. In the Pacific, seasonal size class segregations are observed in the east (Sánchez-de Ita *et al.* 2011; Galván-Tirado *et al.* 2015) although similar data are lacking for other regions within the Pacific.

Further to methodological differences in sample collection, it is also possible that differences in the interpretation of vertebral growth band pairs have affected growth curves between studies. Silky shark age and growth studies have been conducted over the past 30 years and, throughout this period, the methodological approaches to length-at-age estimation for elasmobranchs have become more refined (Cailliet 2015). All studies used the traditional technique of counting opaque and translucent band pairs to estimate ages (Cailliet and Goldman 2004), except for Oshitani *et al.* (2003) in the central Pacific, who counted convex and concave structures on vertebral sections. Maximum observed age estimates of females and males in the central Pacific were only 13 and 8 years respectively. Low maximum observed age estimates were also reported in the east Pacific (females 16 years, males 14 years; Sánchez-de Ita *et al.* 2011), Taiwan (females 11 years, males 14 years; Joung *et al.* 2008) and in the Gulf of Mexico (females 14 years, males 13 years; Branstetter 1987). These observations are substantially lower than studies in the Campeche Bank (females 22 years, males 20 years; Bonfil *et al.* 1993), Indonesia (females 19 years, males 20 years; Hall *et al.* 2012) and the present study (females 28 years, males 23 years). It is suggested that growth band counts incorporate at least two readers with some form of precision, accuracy and bias measurement (Cailliet and Goldman 2004). Previous length-at-age studies on silky sharks (Branstetter 1987; Bonfil *et al.* 1993; Oshitani *et al.* 2003; Joung *et al.* 2008; Sánchez-de Ita *et al.* 2011; Hall *et al.* 2012) did not always use multiple readers and, where they did, there has been no indication of precision and bias in growth band counts, limiting the confidence that can be taken from length-at-age estimates and subsequent growth parameter estimates. It is likely that the intraspecific variation observed for the silky shark between regions can be attributed, in part, to a combination of sampling differences and limitations or varied band pair interpretation across studies. Between-laboratory comparisons would be useful to test the assumptions about the interpretation of band pairs for the purpose of ageing by different institutions and remains an area in need of further investigation (Cailliet *et al.* 1990; Tanaka *et al.* 1990).

The present study produced the oldest age estimations for female and male silky sharks. In the management of exploited populations, longevity of the species is an important consideration and underestimation can seriously impede management (Cailliet and Andrews 2008; Cailliet 2015; Harry 2017). However, maximum ages derived from vertebral ageing techniques have proven to underestimate longevity in several *Carcharhinus* species. Determinate methods of validation confirm that the maximum age of adult sandbar sharks *Carcharhinus plumbeus* and blacktip reef sharks may be underestimated by more than 11 years by vertebral analysis techniques (Andrews *et al.* 2011; Chin *et al.* 2013). Based on these and similar studies, it is apparent that adult sharks may cease annual band pair deposition in vertebral centra, despite validation in juveniles and subadults, (Casey and Natanson 1992; Harry *et al.* 2013; Passerotti *et al.* 2014; Harry 2017). For silky sharks, there is reasonably good evidence that band pair depositions occur on an annual basis until at least the age of 20 years in the Indo-Pacific, as evidenced by methods of marginal increment analysis (Joung *et al.* 2008; Hall *et al.* 2012). Moreover, in the east Pacific during an annual period of high sea surface temperature, vertebrae with opaque borders were observed in subadult and adult silky sharks (Sánchez-de Ita *et al.* 2011). This supports evidence from marginal increment analysis that the translucent band forms in winter months during early development in silky sharks throughout their geographic range (Branstetter 1987; Bonfil *et al.* 1993; Joung *et al.* 2008; Hall *et al.* 2012). However, the absence of deterministic age validation on silky sharks in different regions and throughout different age classes limits the confidence that can be taken in directly comparing growth parameter estimates between studies. There is a need for validation of the periodicity of silky shark band pair formation throughout their geographic distribution and within different age classes.

Reproductive biology

Lengths of embryos were highly variable across a short time span (weeks), supporting the conclusion of asynchronous parturition for silky sharks in the Indo-Pacific (Oshitani *et al.* 2003; Hall *et al.* 2012; Galván-Tirado *et al.* 2015). The litter sizes observed in the present study were also consistent with previous observations of fecundity suggesting silky sharks most commonly birth 8–12 young (Oshitani *et al.* 2003). The smallest neonate observed in the present study was 65 cm TL, whereas the largest embryo was 71 cm TL. The estimated size-at-birth parameter L_0 was marginally larger than reported in previous studies (Table 5). Collectively, these observations and L_0 estimates are within the range of birth sizes (65–85 cm TL) commonly observed for this species, supporting evidence that silky sharks can have a relatively wide length range at birth (Oshitani *et al.* 2003).

Maturity ogives indicate that males reach sexual maturity at a younger age and smaller size than females. Lengths estimated in the present study were smaller than at other study sites, although it has been suggested here that silky sharks in the central west Pacific may not reach the maximum lengths observed in other regions. Interestingly, the lengths at maturity are very similar to the lengths proposed for the central Pacific (Oshitani *et al.* 2003), although the ages at which those lengths are reached vary considerably (Table 5). However, this may be due to the different technique used in estimating age in the central Pacific study (Oshitani *et al.* 2003). The ages at maturity estimated in the present study are most comparable to those reported for studies in Indonesia (Hall *et al.* 2012) and Campeche Bank (Bonfil *et al.* 1993), suggesting that silky sharks are slow to reach sexual maturity. This late onset of sexual maturity indicates slow population growth potential and a higher risk of exploitation from fisheries (Smith *et al.* 1998; Musick 1999).

Conclusions

The growth parameters estimated herein provide the requisite biological information for further demographic analysis and are intended to inform fisheries and conservation sectors in the central west Pacific region. Data from the present study indicate that silky sharks have a slow growth rate and late age of sexual maturity. Coupled with previous studies on fecundity and evidence of a biennial reproductive cycle, it is suggested here that this species is vulnerable to the intensive fishing pressure it currently faces in the central west Pacific region. Information on population structure and validation of annual band pair deposition for silky sharks is recommended in future studies to further refine the life history data for this cosmopolitan species.

Conflicts of interest

The authors declare that they have no conflicts of interest for any material contained within this manuscript.

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Age, growth and maturity of the Australian sharpnose shark *Rhizoprionodon taylori* from the Gulf of Papua

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Abstract

Coastal sharks with small body sizes may be among the most productive species of chondrichthyans. The Australian sharpnose shark (*Rhizoprionodon taylori*) is considered to be one of the most productive members of this group based on work in northern and eastern Australia. However, life history information throughout the remainder of its range is lacking. To address this knowledge gap, the age, growth and maturity of *R. taylori* caught in the Gulf of Papua prawn trawl fishery in Papua New Guinea, were studied. One hundred and eighty six individuals, comprising 131 females (31-66 cm TL) and 55 males (31-53 cm TL) were aged using vertebral analysis and growth was modelled using a multi-model approach. The von Bertalanffy growth model provided the best fit to the data when used with a fixed size at birth

(L_0 = 26 cm TL). This study found that for males (L_∞= 46 cm TL, k = 3.69 yr^{-1}, L_{50} = 41.7 cm TL and A_{50} = 0.5 years) grew at a faster rate and matured at smaller sizes then females (L_∞ = 58 cm TL, k = 1.98 yr^{-1}, L_{50} = 47.0 cm TL and A_{50} = 0.93 years). These results reaffirm the rapid growth of this species and suggest that the Gulf of Papua population grows at a faster rate than Australian populations. *Rhizoprionodon taylori* is possibly well placed to withstand current fishing pressure despite being a common bycatch species in the Gulf of Papua prawn trawl fishery. However, further research needs to be undertaken to estimate other key life history parameters to fully assess the population status of this exploited shark species and its vulnerability to fishing in the Gulf of Papua.

Key Words: Australian Sharpnose Shark, Growth, Elasmobranch, Fisheries, Gulf of Papua.

Introduction

A general view on the life history characteristics of sharks assumes slow growth, late maturity, and a low number of offspring resulting in populations that have low intrinsic rates of population growth and are highly vulnerable to overfishing (Smith *et al.*, 1999; Stevens *et al.*, 2000). However, not all shark species share these characteristics. In particular, small bodied carcharhinids such as the milk shark *Rhizoprionodon acutus* and the sliteye shark *Loxodon macrorhinus* are characterised by relatively rapid growth and early maturity resulting in higher population turnover rates (Harry *et al.*, 2010; Gutteridge *et al.*, 2013). Fast population turnover rates for these species make them potentially more resilient to fishing (Goldman *et al.*, 2012), although this is not the only factor in determining if a species can be fished sustainably (Simpfendorfer and Dulvy, 2017).

The Australian sharpnose shark *Rhizoprionodon taylori* is a small carcharhinid species known to have one of the fastest growth rates of all shark species (Simpfendorfer, 1993; Cortés, 2004). Initial studies suggested it grows rapidly in the first year of life, on average increasing to 140% of its length-at-birth, and attains a maximum length of only 67 and 97 cm TL respectively in different locations in Australia (Simpfendorfer, 1993; Taylor *et al.*, 2016). Maturity is reached after only one year with a litter of 1–10 pups produced every year following maturity (Simpfendorfer, 1992; 1993). *Rhizoprionodon taylori* is also one of the few elasmobranch species that can halt embryonic development (diapause), possibly to facilitate increased litter sizes (Simpfendorfer, 1992; Waltrick *et al.*, 2012). Occurring only in southern New Guinean and tropical and sub-tropical nearshore waters of Australia from Carnarvon in Western Australia to Moreton Bay is southern Queensland, it is a .locally abundant species often incidentally caught in trawl and gillnet fisheries (Last and Stevens, 2009; Harry *et al.*, 2011).

All known biological information about *R. taylori* has been established from populations in Australia (Stevens and McLoughlin, 1991; Simpfendorfer, 1992; 1993; 1998; 1999). Recent trawl fisheries data from Papua New Guinea (PNG) confirm that *R. taylori* is also frequently caught as bycatch in the Gulf of Papua (GOP) (Baje unpubl. data). Prawn trawling has occurred in the area since the late 1960's and bycatch levels can comprise up to 85% of the total catch (Matsuoka and Kan, 1991). However, the effect of trawling on the sustainability of bycatch populations cannot be properly assessed without determining species compositions and locally relevant biological parameters.

Life history traits can differ for populations in separate localities (Lombardi-Carlson *et al.*, 2003; White, 2007). The Gulf of Papua (GOP) is in close proximity to the northern coast of Australia. However, *R. taylori* has been observed to maintain residency in embayments and nearshore habitats, travelling short distances and rarely moving greater than 100 km within 6 months to one year (Munroe *et al.*, 2015). These limited movements mean that there may be differences in the life history of this species between the GOP and other regions. These differences need to be investigated since variations in size at birth and length at maturity could affect fisheries risk assessments, and have already been documented between different locations in Australia (Stevens and McLoughlin, 1991; Simpfendorfer, 1992; Taylor *et al.*, 2016).

Age and growth studies provide essential information for wider population analyses such as stock assessments (Cortés *et al.*, 2012). Growth parameters for *R. taylori* were determined by Simpfendorfer (1993) prior to the development and use of multiple growth models within an information theoretic framework, which is now the recommended approach for age and growth studies (Cailliet and Goldman, 2004; Smart *et al.*, 2016b). This study used the more contemporary multi-model approach to determine growth and maturity parameters for *R. taylori* in the GOP. The specific aims were: (1) to determine the age, growth and maturity of *R. taylori*; (2) compare life history parameters to previous work to determine if the use of the multiple model approach substantially changed the outcomes; and (3) examine spatial variation in life history of this species. This study also contributes new knowledge from a data poor region that can be used to inform fisheries management and conservation in PNG.

Materials and methods

Sample collection

Commercial trawling in the GOP occurs between Parama Island in the West, just south of the mouth of the Fly River, and the border of the Central and Gulf Provinces in the East (Fig. 1). Trawl fishing is permitted all year round throughout the GOP except in a section of the Gulf between Iokea and Cape Blackwood which is closed to fishing between the 1st of December and the 31st of March, a measure put in place to protect the growth and survival of prawn recruits (Evans *et al.*, 1997). Samples of *R. taylori* were collected by National Fisheries Authority fishery observers on commercial vessels from June 2014 to August 2015. Whole samples were kept frozen and brought ashore at the end of each trip for confirmation of identification and processing. In a laboratory samples were defrosted, total length (TL) measured, and sex recorded. For each individual, maturity was also determined using an index modified from (Walker, 2005a). Reproductive organs were examined and categorised according to the developmental stage of the ovaries and uteri in females, and claspers in males. Females were categorised into one of five stages and males into one of three stages (Table 2). A section of the vertebral column from beneath the first dorsal fin was retained and stored frozen for subsequent age determination (Cailliet and Goldman, 2004).

Vertebrae preparation

Vertebrae processing and aging followed protocols described by Cailliet *et al.*, (2006). Frozen vertebrae were thawed and any excess tissue was removed using a scalpel. Vertebrae were separated into individual centra and immersed in 4% sodium hypochlorite solution for 3–5 minutes to clean remaining soft tissue from the small sized vertebrae. The centra were then rinsed using water and dried in an oven at 60 °C for 24 hours. To obtain a thin section a single centrum was selected from each individual and mounted on a microscope slide using Crystal bond adhesive (SPI supplies, Pennsylvania, USA). To achieve the desired thickness of <400 µm the vertebrae was sanded towards the centre of the centrum using 400-1200 grit wet and dry abrasive paper. After one side was complete the centrum was remounted and sanded again on the other side until the desired thickness was achieved (Simpfendorfer, 1993).

Age determination

To estimate the age of each individual, mounted sections of vertebrae were observed using a dissecting microscope. Growth increments appeared as a pair of alternating wide opaque band and a narrow translucent band, referred to as a band pair after Cailliet *et al*. (2006). The birth mark was identified where there was an obvious change in angle along the *corpus calcareum*. Subsequent band pairs that spanned from one side of the *corpus calcareum* to the other side were interpreted to represent annual growth (Cailliet and Goldman, 2004). The age of each individual was estimated as the number of band pairs present after the birth mark. The annual deposition of bands for this species has been validated using marginal increment analysis and size frequency data by Simpfendorfer (1993).

Precision and bias

Reader bias is inherent in estimating age (Cailliet and Goldman, 2004). Therefore, to minimise this bias, two independent counts were conducted without knowledge of the sex or size of individuals. A second experienced reader also aged all of the samples. Final ages were the result of a consensus process between the readers – where counts were different readers examined the section and agreed on a final age. Where differences could not be resolved those centra were removed from the analyses. To assess the precision of counts the average percent error (APE) (Beamish and Fournier, 1981), Chang's coefficient of variation (CV) (Chang, 1982) and percent agreement (PA ± 1 year) (Cailliet and Goldman, 2004) were used. Bowkers test of symmetry was used to estimate bias between readers (Bowker, 1948). Analyses were carried out using 'FSA' package (Ogle, 2016) in the R program environment (R Core Team, 2015).

Partial ages

For a species that reproduces seasonally, and the period of parturition is known, it is possible to assign partial ages and therefore improve age estimation (Smart *et al.*, 2013). The pupping season for *R. taylori* was observed in January in Queensland (Simpfendorfer, 1993). In this study the largest embryo (22 cm TL) was caught in the month of December, confirming a similar timing in the GOP. Partial ages were calculated by choosing a birth date of 15th of January and determining the total number of days between this date and the date of capture which was then divided by the number of days in a year. This value was added to the number of full annual band pairs for each individual to give the final age. For example, samples aged at 1 year caught in May and October, respectively, were given partial ages of 1.4 and 1.9 years.

Growth model fitting

The growth of *R. taylori* was modelled using a multi-model framework. This method incorporated the Akaike Information Criterion (AIC) (Akaike, 1973) which either selected the best model fit based on the lowest AIC value or when all candidate models perform similarly, provides model weightings that can be used in multi-model inference (MMI) (Smart *et al.*, 2016a). Preference for the use of multiple growth models over an *a priori* approach, using only the von Bertalanffy growth model (VBGM) is now becoming standard methodology in elasmobranch growth literature (Smart *et al.*, 2016b). The multi-model approach is considered to provide better growth estimates as it avoids model mis-specification and biases compared to the use of a single model (Cailliet *et al.*, 2006; Thorson and Simpfendorfer, 2009; Smart *et al.*, 2016b). The lack of small juveniles in the sample, and their likely very rapid growth required a variety of models to determine the most suitable growth parameters. Three candidate models were used: VBGM, logistic model, and Gompertz model (Table 1). However, because of the limited data from very young individuals, versions of the growth models with a fixed size at birth (which ensured that models accounted for the rapid early growth; 2 parameter version) and estimateable length-at-birth (3 parameter versions) were both run. Separate growth models were constructed for males, females, and combined sexes.

The 3-parameter models estimated length-at-birth (L_0), asymptotic length (L_∞) and growth coefficient (k, g_{log} and g_{gom}). The 2 parameter models incorporated a fixed known value for L_0 and thus the models only estimated L_∞ and the growth coefficients. Umbilical scars were not recorded in this study which meant that a L_0 for *R. taylori* in the GOP was not identified, but could be estimated using other data available from the sample as well as published information. In this study the smallest free swimming individuals were 30 cm (TL) and largest embryos were 22 cm (TL) observed in December (a month prior to pupping). The literature estimates of L_0 are 25–30 cm (Stevens and McLoughlin, 1991) from northern Australia and 22–26 cm in north eastern Australia (Simpfendorfer, 1993). A possible estimate for the L_0 would therefore be 22–30 cm, however in the GOP *R. taylori* are still embryos at 22 cm and are possibly born at a larger size. The midpoint between 22 and 30 cm (26 cm) was chosen because this value was within the L_0 range suggested by both previous studies and was biologically plausible given embryo sizes on the GOP. Growth models were fit using the ‘nls’ function, multi-model analysis was conducted using the ‘MuMIn package’ (Barton, 2016) and bootstrapped confidence intervals were produced using the ‘nlstools package’ (Baty *et al.*, 2015) in the R program environment (R Core Team, 2015).

As the sample size was less than 200, the AIC_C, a size adjusted bias correction, was used (Zhu *et al.*, 2009) :

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

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

$$\Delta_i = AIC_{CI} - AIC_{min}$$

Models were ranked according to the value of Δ. Values from 0-2 were considered to have the strongest support, less support was given to values between 2-10 and the least support for Δ values > 10 (Anderson and Burnham, 2002). The AIC weights were calculated by the expression:

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

To test if there were differences in the growth curves for males and females, a likelihood ratio test was carried out (Kimura, 1980). This was conducted on the model with the best fit based on the AIC$_C$ results for the sexes combined. The method used to carry out the likelihood ratio test was described by (Haddon, 2001) and incorporated into the R program environment for this analysis.

MATURITY

The maturity stage data was converted to a binary maturity category (immature = 0 or mature =1) for statistical analyses. The length-at-maturity was estimated for both males and females using logistic regression (Walker, 2005b):

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

where $P(l)$ is the proportion mature at TL, l; and P_{max} is the maximum proportion of mature individuals. The lengths of which 50 and 95% of the population are 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 Core Team, 2015)

Results

Age Determination

In total 186 individuals were collected: 131 females and 55 males. Males ranged in size from 31–53 cm TL and females from 31–66 cm TL. The majority of sharks were aged between 0 and 1 years (i.e. birth mark but no fully formed 1st band pair). Final partial ages ranged from 0.2 to 4.6 years. The oldest female was 64 cm TL and aged at 4.6 years. The oldest male was 51 cm TL and aged at 3.6 years. The APE, Chang's CV and PA ± 1 year were 29.1, 42.4 and 62.4, respectively. The APE and Chang's CV were considerably higher than for other elasmobranchs (Campana, 2001; Natanson *et al.*, 2007; Gutteridge *et al.*, 2013) but reflect that for short lived species where small differences in band pair counts can produce inflated error estimates in comparison to longer lived species (Simpfendorfer, 1993). Bowkers test for symmetry (df = 8, $x^2 = 16.4$, $P = 0.037$) indicated some systematic bias between readers. The age bias plot (Fig. 2) showed that this bias was associated with reader 1 estimating younger counts of band pairs at 3 and 4 years relative to reader 2. The use of consensus counts to produce final ages overcame this ageing bias.

Growth Model Fitting

The 3 parameter models had similar AIC weights for combined and individual sexes (Table 3). However, without data from small newly born animals 3 parameter models were unsuitable as the projected L_0 values were too high and biologically unreasonable for *R. taylori* (give the values her; e.g. XX – YY cm). The 2 parameter von Bertalanffy model performed best as neither logistic and Gompertz models had Δ values > 2, although there was some weak support for the Gompertz model for males (*w* = 0.24) (Table 4) . The 2 parameter models projected much higher growth completion rates (k, g(log), g (gomp) than 3 parameter models however, the L_0 values were more realistic (give the values her; e.g. XX – YY cm). Therefore the 2 parameter von Bertalanffy model is recommended to describe the growth of *R. taylori* in the GOP (Figure 3), with a growth estimate (k) of 1.27 for both sexes combined (Table 4). A likelihood ratio test showed significant difference (df = 3, $x^2 = 23.3$, $P = 3.5$) between males and females demonstrating that results from individual sexes should be used.

Maturity

Maturity estimates for male and female *R. taylori* differed slightly. Females grew larger than males, and males matured earlier in terms of both length and age (Fig. 5, 6). The smallest mature female was 42 cm TL and lengths at maturity L_{50} and L_{95} were 47.0 cm TL ± 0.68 S.E. and 53.5 cm TL ± 1.2 S.E. The A_{50} and A_{95} were 0.93 years ± 0.1 S.E. and 2.95 years ± 0.4 S.E., respectively for females. The smallest mature male was 39 cm TL. L_{50} and L_{95} for males were 41.7 cm TL ± 0.8 S.E. and 47.2 cm TL ± 1.5 S.E. The ages at maturity A_{50} and A_{95} for males were 0.5 years ± 0.2 S.E. and 2.2 years ± 0.6 S.E.

Discussion

The results of this study reaffirm the very rapid growth and maturity of *R. taylori* in comparison to the majority of chondrichthyan species. For sharks, von Bertlanffy growth completion rates (*k*) of >1, as seen in *R. taylori*, are rare and indicate very rapid growth compared to larger species which grow at much slower rates. For example *Isurus oxyrinchus* (k = 0.052 year^{-1}) and *Carcharhinus plumbeus* (k = 0.040 year^{-1}) (Bishop *et al.*, 2006; McAuley *et al.*, 2006) both have much lower growth completion rates. Other small bodied coastal shark species grow at faster rates such as *Rhizoprionodon terraenovae* (k = 0.5 year^{-1}) and *Rhizoprionodon acutus* (k = 0.63 yerar-1 for females, k = 0.94 year^{-1} for males) (Loefer and Sedberry, 2003; Harry *et al.*, 2010). However, *R.taylori* has the fastest growth completion rate estimated for a shark species. In the GOP *R. taylori* appear to grow even faster than previously found in Australia. The 2 parameter von Bertalanffy model estimated k = 1.165 year^{-1} for females which was similar to that reported by (Simpfendorfer, 1993) (k=1.013). Males in the GOP however, had an estimated k value of 3.69 year $^{-1}$ which was much higher than previously reported for any shark species and also substantially higher than that reported by (Simpfendorfer, 1993).

Generally for sharks, males tend to grow faster than females (Cortés, 2000), and that was observed in this study. However, the large difference in k between Simpfendorfer (1993) and the present study, and its difference to female estimate, is unusual. This result may be influenced by the relatively small number of males in the sample, as well as the model being constrained by fixing L_0 (Pardo *et al.*, 2013). There are also methodological differences between this study and Simpfendorfer (1993) who fitted growth curves by eye. The very high value of k and the large difference between males and females means that further investigation is warranted to confirm this result.

The maturity estimates for *R. taylori* in the GOP showed that males matured within 6 months of birth while females reached maturity as they approached 12 months of age. The only other age-at-maturity estimates for *R. taylori* were observed by Simpfendorfer (1993) and although the female age–at-maturity observed in the GOP corresponds to this study, the males in the GOP appear to reach maturity within half the time noted in Queensland. Length-at-maturity estimates for the GOP showed that males also matured at smaller sizes then females. The length at which both 50% of males and females (data from sexes combined) in the GOP reached maturity resembled data from north and western Australia recorded by Stevens and Mcloughlin (1991) which were smaller than that observed by Simpfendorfer (1993) and Taylor *et al.* (2016). These findings highlight latitudinal variation for this species suggesting length-at-maturity increases with higher latitudes. The underlying causes for latitudinal variation remain unexplained (Taylor *et al.*, 2016) but for other shark species have been attributed to differences in water temperatures between latitudes (Yamaguchi *et al.*, 2000; Lombardi-Carlson *et al.*, 2003).

The rapid growth and early onset of maturity in sharks has been hypothesised to be a survival strategy to counter high levels of predation experienced by these species (Branstetter, 1990). Small bodied sharks are an important intermediate link in the food chain as they are often preyed upon by larger predators (Heupel *et al.*, 2014). Harry *et al.* (2010) working on *R. acutus* also noted high natural mortality experienced by a species may be balanced by early maturity. Certainly in the GOP where the trawl fishery operates throughout the year, both natural and fishing mortality are likely high for the *R. taylori* population which may account for their very young age at maturity.

Commercial trawling has taken place in the GOP for over forty years. At the onset of this fishery as many as 30 vessels were licensed. The total number of vessels and fishing effort has fluctuated over the years peaking at 95 000 trawl hours in 1989 before decreasing when effort control measures were introduced (Evans *et al.*, 1995). Currently only 6 vessels are actively trawling in the GOP. Rapid growth and early maturity are biological characteristics associated with the ability of a species to withstand fishing pressure (Smith *et al.*, 1999), therefore it is probable that *R. taylori* in the GOP are well placed to withstand current fishing levels than other shark species.

It is important to correctly determine age in sharks as errors can lead to inaccurate projections of parameters such as age-at-maturity which can have a sizable impact on population models (Loefer and Sedberry, 2003), and stock assessments. Achieving accuracy and precision in vertebral aging relies on the clarity of growth markings and the ability of the readers to identify and differentiate growth bands. Several studies focused on small shark species have noted difficulties in detecting the correct number of growth bands particularly on the edge of the vertebrae, where bands are deposited very close to each other and as a consequence maximum age may be underestimated (Loefer and Sedberry, 2003; Gutteridge *et al.*, 2013). Furthermore as temperate seasonality may influence the deposition of growth bands (Goldman *et al.*, 2012), they appear more pronounced in temperate sharks as opposed to tropical sharks where seasonality is limited. For instance the appearance of check marks in the GOP vertebrae were not as pronounced as that observed by Simpfendorfer (1993). Discrepancies among readings for fast growing sharks with few age classes will produce a more pronounced level of bias (Simpfendorfer, 1993). The measures of precision – Chang's CV and APE were relatively high in this study compared to those of most other shark species.

Assumptions on annual growth band deposition and length at birth for *R. taylori* were made in this study because validation was not possible due to logistic constraints. Simpfendorfer

(1993) verified the annual periodicity of band formation for *R. taylori* in northern Queensland based on marginal increment analysis and length frequency data. This assumption has strong support given the geographic proximity of this study, and annual band formation being the typical pattern observed in carcharhinid sharks (Simpfendorfer *et al.*, 2002; Harry *et al.*, 2013).

The improvement in the biological representativeness provided by the two parameter growth models over the three parameter versions is somewhat unusual. Although this option for modelling growth is discouraged as biases can be introduced, longer lived species are more susceptible to this risk (Pardo *et al.*, 2013). The use of two parameter models is recommended under stringent conditions where: there is limited data for smaller juveniles; low sample sizes; and where the L_0 cannot be estimated from the study population but can be deduced from a representative population in the same geographic region (Thorson and Simpfendorfer, 2009). Given the lack of data from younger *R. taylori* close to the size at birth, and the inability to back calculate to alleviate this problem in short-lived species (Smart *et al.*, 2013), the use of two parameter models in this study was the only way to ensure that biologically plausible parameters were produced.

The foundations of managing fish stocks and attaining sustainable fisheries rely upon accurate biological data of fish populations (Cailliet and Goldman, 2004; Heupel and Simpfendorfer, 2010). Until recently, information for sharks in PNG has been scarce (White *et al.*, 2015; D'Alberto *et al.*, 2016; Smart *et al.*, 2016a; Smart *et al.*, 2017). This study is one of the first attempts to determine biological parameters of a small-bodied, commonly caught carcharhinid species in PNG. However, further work is needed to provide critical biological data for population assessments as well as to understand the ecological functions of shark species in order to fine tune management and conservation measures to suit the PNG context. Advancement in elasmobranch research in PNG will also address important data gaps for the

Indo-Australasian region which supports the highest diversity of sharks globally (White and Kyne, 2010).

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Tables

Table 1: Equations of the three growth functions used in the multi model analysis.

Model	Growth function
von Bertalanffy	$L(t) = L_0 + (L_\infty - L_0)(1-exp(-kt))$
Logistic	$L(t) = \frac{L_\infty L_0 (g_{log} t)}{L_\infty + L_0 (exp(g_{log} t) - 1)}$
Gompertz	$L(t) = L_\infty exp(-L_0 exp(-g_{(gom)} t))$

Table 2: The maturity of male and female samples were determined by the state of the uteri and ovaries in females, and claspers in males. Maturity stages were assigned a binary category for statistical analysis.

Female stage		**Description**	**Binary category**
1	Immature	Uteri very thin, ovaries small and without yolked eggs.	0
2	Maturing	Uteri slightly becoming enlarged at one end, ovaries becoming larger and small yolked eggs developing.	0

3	Mature	Uteri large along entire length, ovaries containing some large yolked eggs.	1
4	Pregnant	Uteri containing embryos or large eggs.	1
5	Post-partum	Uteri very large but without embryos.	1
Male stage			
NC	Not Calcified	Clasper very short not extending past the pelvic fin tip.	0
PC	Partially Calcified	Claspers longer, extending past the pelvic fin tip, not entirely hard, still flexible.	0
FC	Fully Calcified	Claspers long, hard along almost the entire length.	1

Table 3: Summary of results from the multi model inference framework (MMI) incorporating Akaike's information Criterion (AIC) using 3 parameter versions of models.

Sex	**Model**	**n**	**AIC_C**	**Δ**	**W (%)**	**L_0(±SE)**	**L_∞(±SE)**	**k(±SE)**	**$g_{(log)}$(±SE)**	**$g_{(gom)}$(±SE**
Combined	VB3	190	1166.85	0	0.45	35.12±1.32	63.88±4.03	0.48±0.14		
	Logistic	190	1168.21	1.96	0.23	35.98±1.14	61.75±2.87		0.73±0.15	
	Gompertz	190	1167.59	0.73	0.32	35.59±1.22	62.65±3.33			0.60±0.14
Male	VB3	57	330.66	0	0.39	34.55±1.87	50.42±2.57	1.01±0.43		
	Logistic	57	331.28	0.62	0.28	35.28±0.92	50.41±2.47		1.17±0.25	
	Gompertz	57	331.01	0.35	0.33	34.96±1.76	50.44±2.53			1.08±0.44
Female	VB3	133	819.85	0	0.44	34.91±1.96	63.77±3.92	0.53±0.17		
	Logistic	133	821.06	1.21	0.24	36.22±1.38	62.27±3.04		0.77±0.15	
	Gompertz	133	820.51	0.66	0.32	35.64±1.8	62.92±3.41			0.65±0.18

n is the sample size, AIC_C is the small-sample bias adjusted from the Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_0 and L_∞ are the length-at-birth and asymptotic length in cm respectively, k is the growth completion rate in ($year^{-1}$) for the VB3, $g_{(log)}$ and $g_{(gom)}$ are the growth parameters for Logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the model.

Table 4: Summary of results from the multi model inference framework (MMI) incorporating Akaike's information Criterion (AIC) in 2 parameter versions of growth model for *Rhizopriondon taylori* from the Gulf of Papua.

Sex	**Model**	**n**	**AIC_C**	**Δ**	**W (%)**	**L_∞(±SE)**	**k(±SE)**	**$g_{(log)}$(±SE)**	**$g_{(gom)}$(±SE)**	**RSE**
Combined	VB2	186	1193.71	0	0.99	55.95±0.95	1.27±0.11			5.54
	Logistic	186	1213.08	19.38	0	54.41±0.75		2.12±0.14		5.83
	Gompertz	186	1203.61	9.9	0.01	55.07±0.82			1.67±0.13	5.68
Male	VB2	55	336.13	0	0.64	46.11±0.9	3.69±0.68			4.44
	Logistic	55	339.47	3.34	0.12	45.08±0.77		6.73±1.23		4.57
	Gompertz	55	338.1	1.97	0.24	45.52±0.82			5.04±0.92	4.52
Female	VB2	131	830.37	0	0.96	57.78±1.12	1.17±0.12			5.40
	Logistic	131	842.88	12.52	0.00	56.08±0.84		1.98±0.15		5.66
	Gompertz	131	836.6	6.23	0.04	56.8±0.94			1.55±0.13	5.53

n is the sample size, AIC_C is the small-sample bias adjusted from the Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_∞

is the asymptotic length in cm, k is the growth completion rate in (year^{-1}) for the VB2, $g_{(log)}$ and $g_{(gom)}$ are the growth parameters for logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the model.

Figure Captions

Fig 1. Location of the Gulf of Papua along the southern coast of Papua New Guinea.

Fig 2. Length-at-age curve for *Rhizoprionodon taylori* with both sexes combined from the Gulf of Papua fitted with a 2 parameter von Bertalanffy growth model (solid line) and 95% bootstrapped confidence intervals (dashed line).

Fig 3. Length-at-age curves for male (a) and female (b) *Rhizoprionodon taylori* from the Gulf of Papua fitted with the 2 parameter von Bertalanffy growth curve (solid line). Dashed lines indicated 95% bootstrapped confidence intervals.

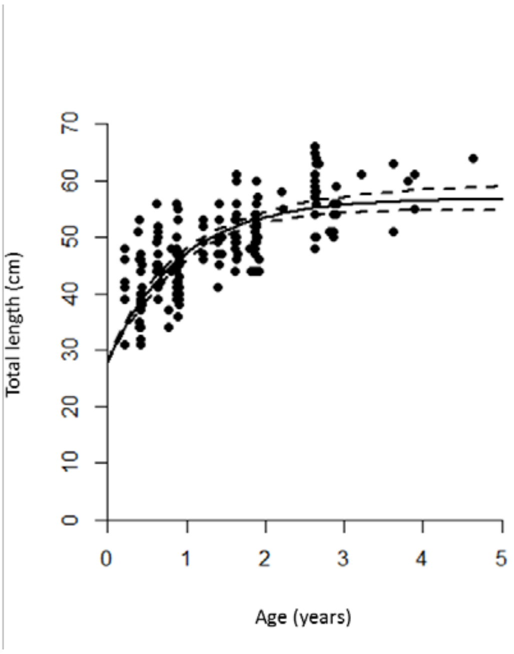
Fig 4. Age bias plot showing agreement between two independent readers. The PA ± 1 year was 62.4 %, APE was 29.1 and Chang's coefficient of variation (CV) was 42.4.

Fig 5. Length-at-maturity ogives for male (a) and female (b) *Rhizoporionodon taylori* from the Gulf of Papua. The points represent the length at which 50% of population reaches maturity. 95% bootstrapped confidence intervals are indicated with dashed lines.

Fig 6. Age-at-maturity ogives for male (a) and female (b) *Rhizoprionodon taylori* from the Gulf of Papua. The points represent the ages where 50% of the population reaches maturity. 95% bootstrapped confidence intervals are indicated with dashed lines.

Figures


5°0'0"S
Gulf Province
Western Province
Cape Blackwood
Iokea
Central Province
Gulf of Papua
Parama Island
10°0'0"S
144°0'0"E
146°0'0"E
148°0'0"E


Total length (cm)
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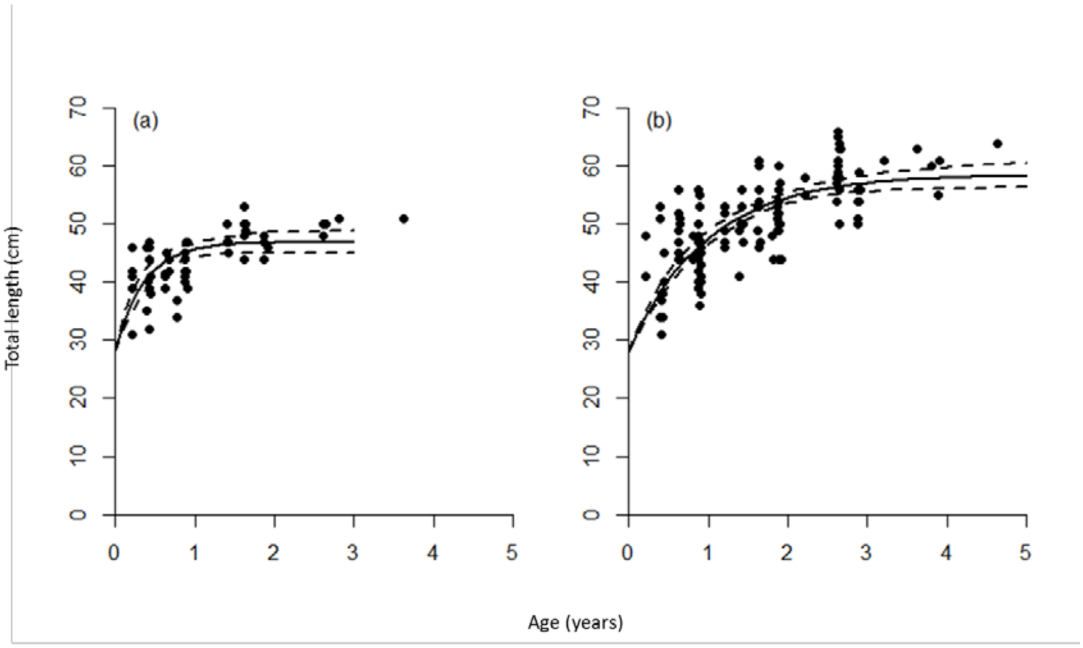
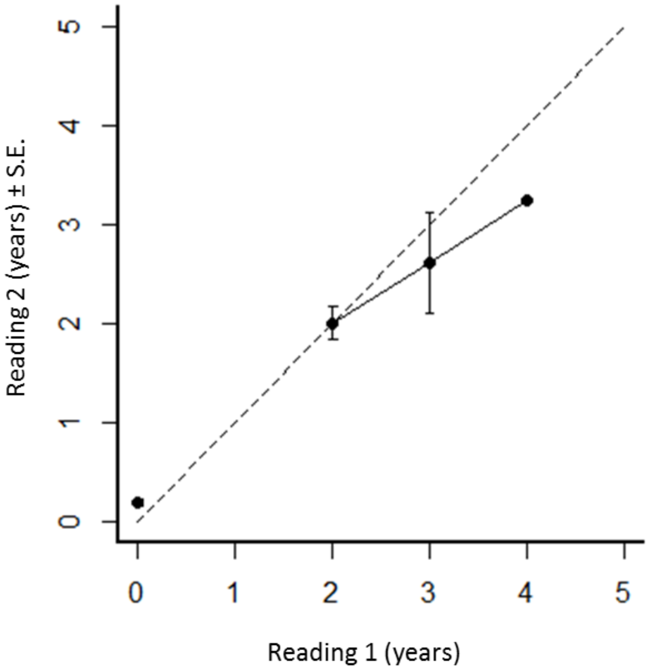
10
20
30
40
50
60
70
0
1
2
3
4
5
Age (years)


(a)
(b)
Total length (cm)
0
10
20
30
40
50
60
70
0
1
2
3
4
5
Age (years)


Reading 2 (years) ± S.E.
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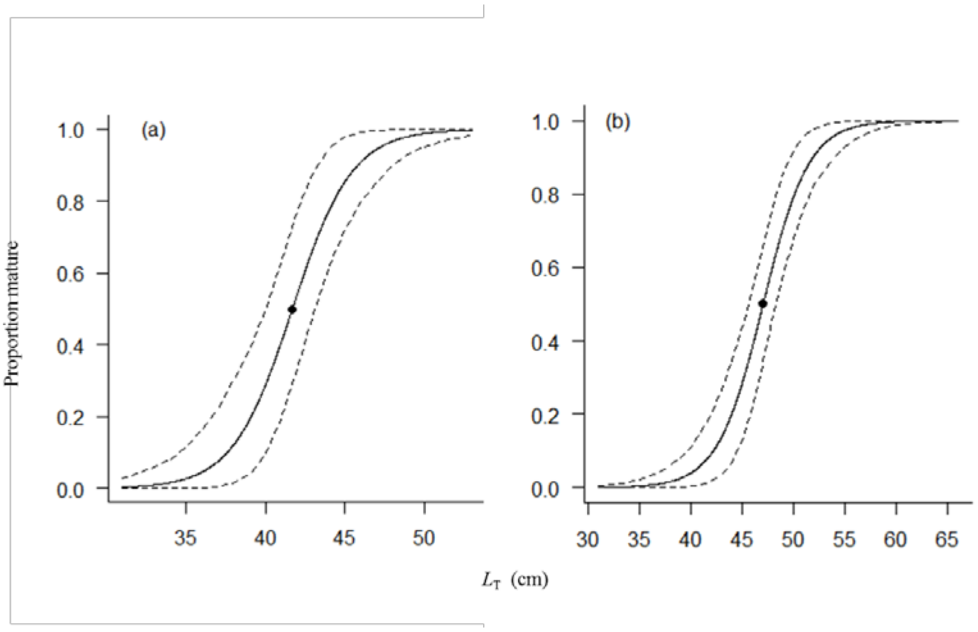
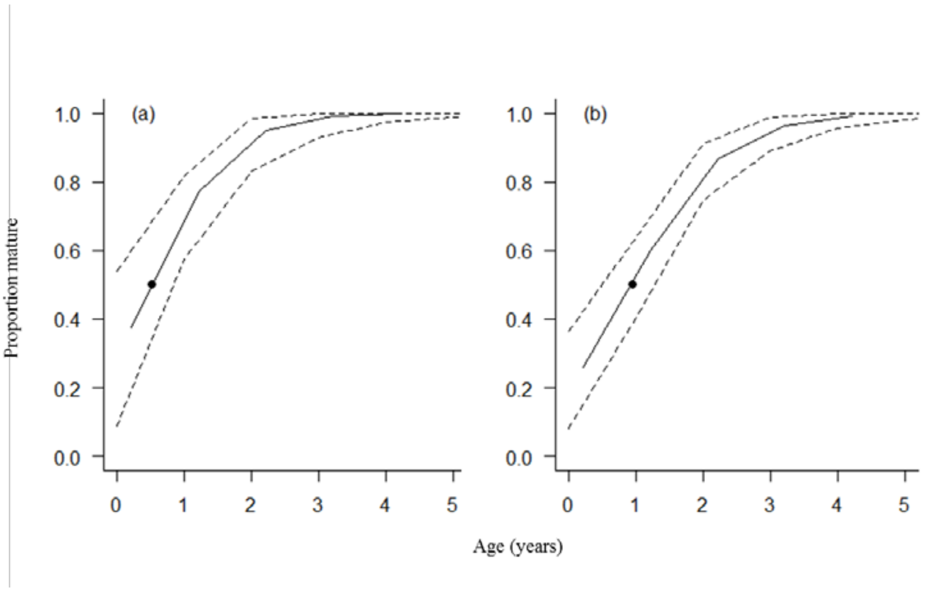
1
2
3
4
5
0
1
2
3
4
5
Reading 1 (years)


(a)
(b)
Proportion mature
1.0
0.8
0.6
0.4
0.2
0.0
30
35
40
45
50
55
60
65
L_T (cm)


(a)
(b)
Proportion mature
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
Age (years)

Age, growth and maturity of *Carcharhinus coatesi* captured by prawn trawlers in the Gulf of Papua

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Abstract:

Small bodied coastal sharks are often caught as bycatch in fishing operations. Life history information for these sharks is needed to ascertain the level at which these populations are potentially affected by fishing. This study determined the age, growth and maturity of *Carcharhinus coatesi* captured by prawn trawlers in the Gulf of Papua. Using vertebral aging and the information theoretic multi-model approach, the von Bertalanffy growth parameters were L_0 = 40.61 ± 0.81 SE, L_∞ = 74.84 ± 2.05 SE, k = 0.33 ± 0.06 SE. Length at maturity analysis indicated that that males (L_{50} = 66.2 ± 1.5 SE, L_{95} = 72.1 ± 1.6 SE) attained maturity at smaller sizes than females (L_{50} = 71. 0 ± 312.5 SE, L_{95} = 71.2 ± 303.8 SE). Age at maturity estimates showed that both males (A_{50} = 5.1 years ± 0.3 SE, A_{95} = 6.4 years ± 0.4 SE) and females (A_{50} = 5.3 years ± 0.9 SE and A_{95} = 7.4 ± 1.3 SE) reach maturity at about 5 years of age. This study addresses the need for specific life history information for a data deficient species in a region that has remained relatively under-researched.

Additional keywords: Elasmobranch, bycatch, fisheries, management, Papua New Guinea, trawl

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Introduction

In recent years many species of chondrichthyans have faced large declines in population numbers (Dulvy et al., 2014). The main causes are habitat degradation, pollution and other factors but most notably the effects of harvesting through various fishing practices (Dulvy et al., 2017, Stevens et al., 2000). The need to make fishing more sustainable and less ecologically damaging is urgent yet hampered by the lack of taxonomic and fundamental life history information for many species in vast regions of the world (Frisk et al., 2001). Without an understanding of basic biological parameters such as reproductive and growth characteristics of a species it is difficult to carry out stock assessments and understand population dynamics, which are needed to improve management for threatened and exploited shark stocks.

Small bodied sharks that typically grow to a maximum length of less than one meter are commonly caught in coastal areas by a range of fishing gears (Cortés, 2002, Stobutzki et al., 2002, Harry et al., 2011). This group of sharks have relatively fast growth, and thus are thought to be more resilient to fishing pressure than larger, slower growing shark species (Smith et al., 1998). Despite this general understanding it is also known that the biology of a single shark species can differ between localities within its range (Taylor et al., 2016, White, 2007). Region or population specific information is therefore required to produce more accurate stock assessments.

The whitecheek shark *Carcharhinus coatesi* is a common small bodied carcharhinid shark found throughout northern Australia and southern Papua New Guinea. Taxonomic uncertainty led to earlier identification of this species in Australia as *Carcharhinus dussumieri* (Stevens and McLoughlin, 1991, Stobutzki et al., 2002). However, recent taxonomic work combining molecular techniques with more traditional morphological characteristics distinguished *C. coatesi* as a separate species (White, 2012). Preliminary age and growth assessments of *C. coatesi* were conducted by Smart et al. (2013) from the Great Barrier Reef region, Australia. However, there have been no other studies on the biology of *C. coatesi* elsewhere within its range.

Papua New Guinea (PNG) is located within the Coral Triangle and is designated as an area of high elasmobranch diversity (White and Kyne, 2010, White et al., 2017). However very little research has been carried out to determine the biological characteristics of PNG sharks despite the impact of fishing at industrial and artisanal levels (Sabetian and Foale, 2006, Kumoru and Lewis, 2003, Vieira et al., 2017). Bycatch data from the Gulf of Papua prawn trawl fishery

(NFA unpublished data) identified *C. coatesi* as one of the most abundant shark species present. This fishery has been in existence for over four decades and bycatch levels vary between 60–85% by weight of the total catch (Matsuoka and Kan, 1991, Evans et al., 1995). Previous work has focused on the target crustacean species in this fishery (Evans et al., 1995, Evans et al., 1997, Gwyther, 1982) and bycatch reduction technology (Matsuoka and Kan, 1991). However, little to no research has focused on the biology of bycatch species in order to understand the broader impact of the trawl fishery in the Gulf of Papua (GoP). In an effort to address these data gaps and subsequently provide fishery managers with local information this study aims to: (1) present new information about the age, growth and maturity of *C. coatesi* in the GoP, and (2) compare this information with previous work in Australia to investigate regional variation in life history.

Materials and methods

The Gulf of Papua is the semi enclosed body of water on the southern side of PNG covering an area of over 50,000 km^2 (Wolanski et al., 1995). Several rivers flowing from the interior of PNG converge onto the gulf. The larger Fly River is located in the north-west and several smaller rivers occur eastward (Fig. 1). Extensive mangrove swamps and estuarine areas line the coastline providing important habitat and nursery areas which support a diverse array of marine and freshwater species (Pernetta and Hill, 1981). Several commercially valuable crustacean species occur in the region and are harvested annually via the GoPPTF (Gwyther, 1982).

Fishery observers were deployed on 7 prawn trawl fishing trips between June 2014 and August 2015 to collect shark bycatch samples and data. Samples were kept whole, frozen on board and brought back to shore. In a laboratory sharks were thawed, total length (TL) measured, and sex and maturity recorded. Maturity stages were assessed by inspecting the appearance and development of the ovaries and uteri in females and the claspers in males based on Walker (2005a) (Table 1). A section of the vertebrae beneath the first dorsal fin was extracted and kept frozen for further preparation to determine the age of the sharks.

Vertebrae preparation

Protocols described by Cailliet et al. (2006) were used to prepare vertebrae for aging. Frozen vertebrae were thawed, any excess tissue was removed using a scalpel, and the sample separated into individual centra. All centra from an individual shark were placed in separate vials and immersed in 4% sodium hypochlorite solution for 3–5 minutes to remove any remaining soft tissue. Small vertebrae from juvenile sharks were immersed for a maximum of 3 minutes while larger vertebrae were immersed for up to 5 minutes. The centra were then rinsed with water and dried in an oven at 60 $^{\circ}$C for 24 hours. Vertebrae large enough to be sectioned were mounted onto a low speed circular saw (Beuhler, Illinois USA) and a section approximately 400 µm was cut using two diamond tip blades. Each section was attached onto a microscope slide using Crystal Bond adhesive (SPI supplies, Pennsylvania, USA). Centra that were too small to be sectioned using the circular saw were mounted on a microscope slide using the same adhesive and were sanded towards the centre on either side using 400-1200 grit wet and dry abrasive paper. After one side was complete each centrum was remounted and sanded again on the other side to achieve the desired thickness (Simpfendorfer, 1993).

Age determination

Mounted sections of vertebrae were examined using a dissecting microscope. Growth increments appeared as wide and narrow bands. The wide banding is usually opaque while the narrow band is translucent and together are referred to as a band pair as recommended by Cailliet et al. (2006). The birthmark was identified as an obvious change in angle along the inner margin of the corpus calcareum. Complete band pairs that could be seen from one side of the corpus calcareum to the other side were assumed to represent annual growth (Cailliet and Goldman, 2004) (Fig. 2). The age of each shark was indicated by the number of band pairs present after the birth mark. Annual growth band deposition could not be verified using marginal increment analysis because length and age data was not acquired consistently in each month over a period of one year due to logistical issues. However, it was assumed that *C. coatesi* deposited bands annually based on strong evidence in literature that supports annual growth band deposition for sharks belonging to the family Carcharhinidae (McAuley et al., 2006, Harry et al., 2011).

Precision and bias

The appearance of growth band pairs differs between species and may be affected by the light source and method of preparation (Cailliet and Goldman, 2004). In addition, readers may also interpret growth bands differently from each other. To reduce variability and bias, independent age readings were carried out by two separate readers without knowledge of the size and sex of individual sharks. Readers then compared their results and a consensus read was conducted in any instance where counts differed. Samples were excluded from further analysis where an agreed age could not be reached. The precision of the counts was analysed by the average percentage error (APE) (Beamish and Fournier, 1981), Chang's coefficient of variation (CV) (Chang, 1982) and percentage agreement (PA ± 1 year) (Cailliet and Goldman, 2004). Bias between readers was calculated using the Bowker's test of symmetry (Bowker, 1948). Analyses were carried out using 'FSA' package (Ogle, 2016) in the R program environment (R Core Team, 2015).

Growth model fitting

A multi-model approach was used to determine the growth of *C. coatesi* by assessing the level of fit between several candidate models as opposed to only the von Bertalanffy growth model (VBGM). The traditional *a priori* use of the VBGM to fit length-at-age data is now being replaced by the multi-model approach which has been recommended as best practice in recent elasmobranch growth studies (Smart et al., 2016). The multi-model approach uses the Akaike Information Criterion (AIC) (Akaike, 1973) to rank the performance of each model thereby indicating the model with the best fit to the length at age data. When all models perform similarly, the Multi Model Inference approach calculates model averaged parameters based on Akaike weights from each respective model (Katsanevakis and Maravelias, 2008). The use of the multi-model approach minimises the risk model-misrepresentation and associated biases (Cailliet et al., 2006, Thorson and Simpfendorfer, 2009, Smart et al., 2016). Three candidate models were used: VBGM, logistic model, and Gompertz model (Table 2). The models estimated length at birth (L_0), the asymptotic length (L_∞) and growth coefficient (k). Growth models were fit using the 'nls' function, multi-model analysis was conducted using the 'MuMIn package' (Barton, 2016) and bootstrapped confidence intervals were produced from 1000 bootstraps using the 'nlstools package' (Baty et al., 2015) in the R program environment (R Core Team, 2015).

As the sample size was less than 200, the AIC_C, a size adjusted bias correction, was used (Zhu et al., 2009) :

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

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

$$\Delta_i = AIC_{CI} - AIC_{min}$$

Models were ranked according to the value of Δ. Values from 0-2 were considered to have the strongest support, less support was given to values between 2-10 and the least support for Δ values > 10 (Anderson and Burnham, 2002). The AIC weights were calculated by the expression:

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

To test if there were differences in the growth curves for males and females, a likelihood ratio test was carried out (Kimura, 1980). This was conducted for all candidate models included in the analysis. The method used to carry out the likelihood ratio test was described by Haddon (2001) and incorporated into the R program environment for this analysis.

Maturity

The maturity stage data was converted to a binary maturity category (immature = 0 or mature =1) for statistical analyses. The length at maturity was estimated for both males and females using logistic regression (Walker, 2005b):

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

where $P(l)$ is the proportion mature at TL, l; and P_{max} is the maximum proportion of mature individuals. The lengths of which 50 and 95% of the population are 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 Core Team, 2015).

Results

Age Determination

A total of 115 sharks were used in this study, 81 were male and 34 were female. Males ranged in size from 33–79 cm TL, and females from 35–75cm TL. The majority of samples were smaller sized juveniles. Maximum ages were the same for both sexes at 10.5 years; the male measured 76 cm TL while the female was 73 cm TL. The measures of precision in determining ages were 9.93, 14.05 and 58.7 for the APE, Chang’s CV and PA ± 1 year respectively. The age bias plot (Fig. 3) shows some level of discrepancy particularly with older age classes however, the Bowker’s test of symmetry results (df = 23, x = 30.13, P = 0.14) demonstrate that there was no significant bias between readers.

Growth Model Fitting

The AICc values were similar for all candidate models. All models (Table 3) had a Δ of < 2 and w < 0.9. However, the VBGM was selected as the best model given that each of the candidate growth models produced almost identical growth estimates and therefore there was no need to perform model averaging (Table 3). Sexes were combined because the likelihood ratio test showed no significant difference between sexes for all three models (VBGM $df = 3, \chi^2 = 3.78, P = 0.29$; logistic $df = 3, \chi^2 = 4.05, P = 0.26$; Gompertz $df = 3, \chi^2 = 3.90, P = 0.27$).

Maturity

The size at which 50% and 95% of individuals became sexually mature showed that males (L_{50} = 66.2 cm ± 1.5 SE, L_{95} = 72.1 cm ± 1.6 SE) attained maturity at smaller sizes than females (L_{50} = 71.0 cm ± 312.5 SE, L_{95} = 71.2 cm ± 303.8 SE) (Fig. 5). Age at maturity estimates indicate that males (A_{50} = 5.1 years ± 0.3 SE, A_{95} = 6.4 years ± 0.4 SE) and females (A_{50} = 5.3 years ± 0.9 SE and A_{95} = 7.4 years ± 1.3 SE) reach maturity at about 5 years of age (Fig. 6). A large proportion of individuals in the sample were in the first year of life or had not reached maturity (Fig. 7).

Discussion

Sharks display different life history strategies with varying growth and reproductive patterns (Cortés, 2000). Typically sharks that grow beyond one meter in total length possess life history traits such as slow growth, late maturity and low fecundity that place them at greater risk of population decline (Frisk et al., 2001). In contrast, smaller coastal sharks such as carcharhinids that grow to maximum lengths less than a meter, usually grow rapidly after birth and reach maturity within a short period of time (Smart et al., 2013, Loefer and Sedberry, 2003, Harry et al., 2010, Gutteridge et al., 2013). However despite general patterns individual variability in growth is common among species.

Among small bodied carcharhinids, growth completion rates range from k = 0.18 for female *Loxodon macrorhinus* (Gutteridge et al., 2013) to k = 1.33 for male *Rhizoprionodon taylori* (Simpfendorfer, 1993). With a growth completion rate of k = 0.33 *C. coatesi* in the GoP can be considered as a slower growing small bodied coastal shark. This is exemplified in the lack of a distinctive steep increase in growth straight after birth, which is observed in other small bodied species such as *R. taylori*, *Rhizoprionodon terraenovae* and *Rhizoprionodon acutus*. However, young *C. coatesi* are born at large sizes and growth occurs gradually after birth (Fig. 8).

Carcharhinus coatesi in the GoP were smaller in size and slower in growth compared to studies in Australia (Stevens and McLoughlin, 1991, Smart et al., 2013). A notable difference is that the smallest individuals were about 5 cm smaller indicating a reduced size at birth. Smart et al. (2013) used back calculation to derive a preliminary growth completion rate for *C. coatesi* in the GBR (k = 0.83), which implies faster growth than observed in the present study. However the GBR study had a sample size of only 56 individuals and further work on a larger sample is required to confirm the growth projections. The difference in growth completion rates and potentially size at birth may imply latitudinal variation in growth characteristics, which has been suggested for other shark species (Taylor et al., 2016, Lombardi-Carlson et al., 2003). The AIC multi-model approach has been found to improve the accuracy of growth model fitting but low samples sizes may be a limiting factor (Thorson and Simpfendorfer, 2009). Given that there were very small differences between model outputs in this study, calculating model averaged parameters would have yielded very similar results and therefore was not undertaken.

Carcharhinus coatesi is an aseasonally reproducing species (Stevens and McLoughlin, 1991). The estimation of ages therefore took into account the variability of parturition throughout the year to be more accurate (Harry et al., 2010). Smart et al. (2013) aged *C. coatesi* to up to 6.5 years, however the maximum age observed for the GoP was 10.5 years. The measures of reader precision did not indicate bias between readers but did show greater level of differences between readers in the older age classes. Bands deposited towards the edge of the vertebrae can be very difficult to read because band pairs are deposited in closer proximity to each other reflecting slower growth later in life. Therefore, it is possible that ages may be underestimated for older individuals that have reached their maximum size but are still depositing growth band pairs. This has been observed in other studies on small bodied sharks (Gutteridge et al., 2013, Loefer and Sedberry, 2003, Huveneers et al., 2013), and Harry (2017) reported widespread age under-estimation in elasmobranch aging studies.

This study provides the first age-at-maturity estimates for *C. coatesi*. Whereas other small bodied carcharhinids take 1–2 years to mature (Harry et al., 2010, Gutteridge et al., 2013, Simpfendorfer, 1993, Carlson and Baremore, 2003) both male and female *C. coatesi* attain sexual maturity at 5 years of age. This characteristic suggests that this species may be less productive, but demographic models should be investigated further. Length at maturity analysis indicate that males attain maturity at sizes smaller than females, unlike northern Australia where both sexes reach maturity at the same length (Stevens and McLoughlin, 1991). This is consistent with shark life history patterns that show males tend to grow faster though reach maximum sizes that are smaller than females (Cortés, 2000). Given that the number of females in the sample was low the standard error reported for female size and age at maturity was high, estimates should be treated as preliminary and be further investigated with additional sampling.

The advantages of fast growth and early maturity are reduced for *C. coastesi* given it matures over more than double the time it takes for other small bodied carcharhinids. Fast growth and the earlier onset of maturity is predicted to be an evolutionary counter response to high levels of predation (Simpfendorfer, 1993, Heupel et al., 2014) mainly in the early stages of life (Heupel and Simpfendorfer, 2002, Heupel and Simpfendorfer, 2011). This life history increases the survivorship of juveniles (Heupel et al., 2007) and the ability of adults to reproduce within relatively short life spans. For *C. coatesi* however, a longer period of immaturity could mean that other life history characteristics have been developed to compensate for the late maturity one of which may be a larger size at birth.

Trawl fisheries contribute to large numbers of elasmobranch bycatch (Oliver et al., 2015). Commercial vessels in the GoP fish for 24 hours a day for about 250 days per year. Historical records over a 19 year period (1974 -1993) indicate that fishing effort had varied over time, being at its lowest in 1975 (17,000 trawl hours) and peaked in 1989 (95,000 trawl hours) (Evans et al., 1997). In 2011 eight vessels were actively fishing with an overall effort of 14,000 trawl hours (Suuronen et al., 2013), but currently only six vessels are in operation. The total amount of bycatch taken in the fishery is expected to have fluctuated in proportion with fishing effort, however in recent years bycatch may be at much lower levels given that effort appears to have decreased. Bycatch reduction devices have yet to be introduced to the fishery and their use is currently being explored. However, the effectiveness of such devices to reduce small bodied shark bycatch may be minimal (Stobutzki et al., 2002).

The effect of fishing on several coastal shark populations has led to population declines (Dulvy et al., 2014). This could potentially cause changes in life history parameters. Carlson and Baremore (2003) recorded a higher growth rate and reduced age at maturity in *R. terraenovae* after more than a decade noting increased fishing pressure and a reduction in stock size over this time. The extent to which biological traits of *C. coatesi* may have changed due to the effects of fishing in the GoP over four decades remains unknown due to the lack of data on previous abundance, catch trends over time and previous life history information. The current growth and maturity information for *C. coatesi* gathered in this study implies that although it is a fast growing species, it may be more vulnerable to fishing pressure than other small carcharhinids (e.g. *R. taylori*, Baje et al., in review) due to its older age at maturity. As such, increases in exploitation may differentially have greater effects on the population.

Sustainable fisheries management relies on an understanding of the biology of both targeted fish stocks for commercial markets and those that are impacted as bycatch. In order to carry out wider demographic and stock assessment analysis as well as ecological risk assessments determining local life history parameters is fundamental. Research on bycatch species have been overlooked mainly in the Indo Pacific (Molina and Cooke, 2012) but are increasingly needed for a more holistic approach to managing fisheries in view of wider sustainability concerns (Pikitch et al., 2004). This study highlights the case of *Carcharhinus coatesi* that is potentially more vulnerable to population decline in the event of increased fishing pressure in the GoP. The information provided here can be used to assess the ecological consequences of trawl fishing in the GoP and evaluate the conservation status of *C. coatesi*. Further research should be encouraged in regions of high biodiversity where fishing regularly occurs as population declines and the threat of extinction may easily go unnoticed in the absence of quantitative data (Edgar et al., 2005).

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Conflicts of interest

The authors declare no conflict of interests.

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Figures and captions

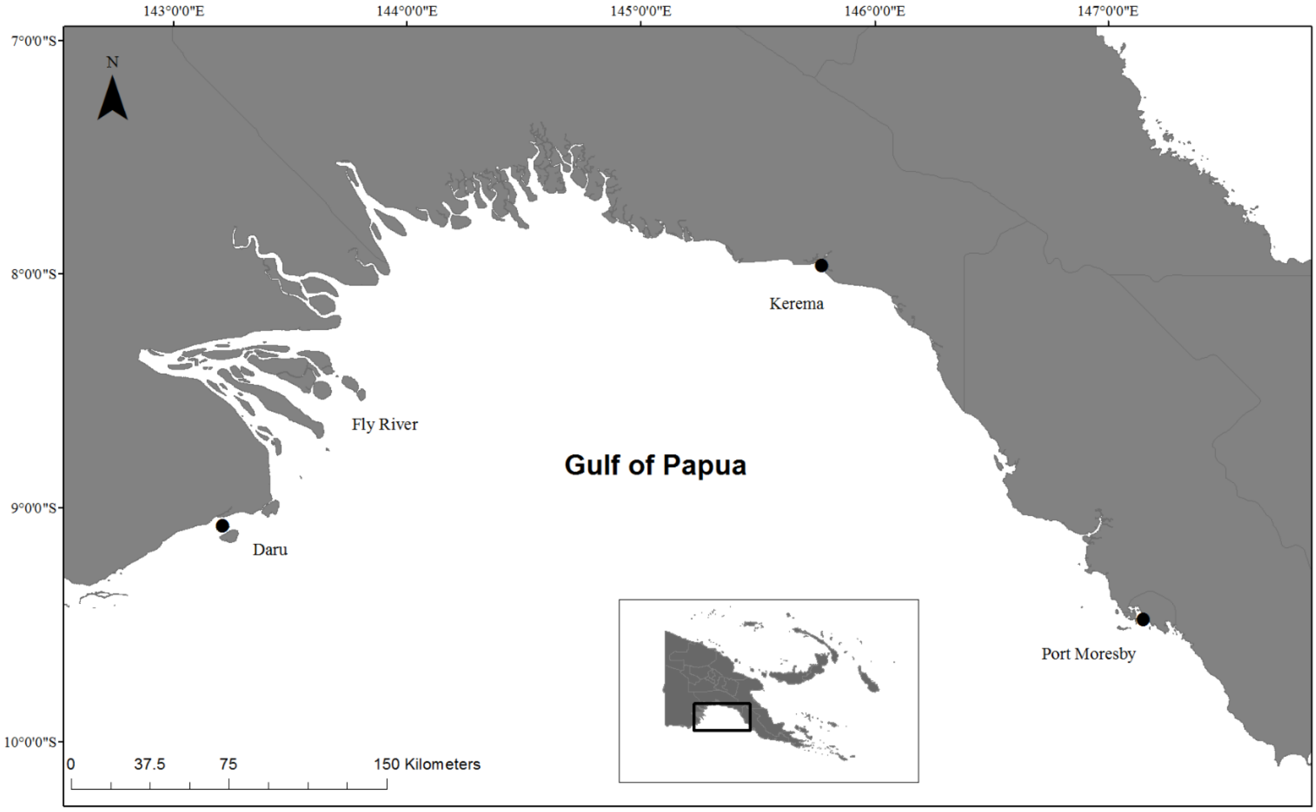


Figure 1. Gulf of Papua situated along the southern coastline of Papua New Guinea.

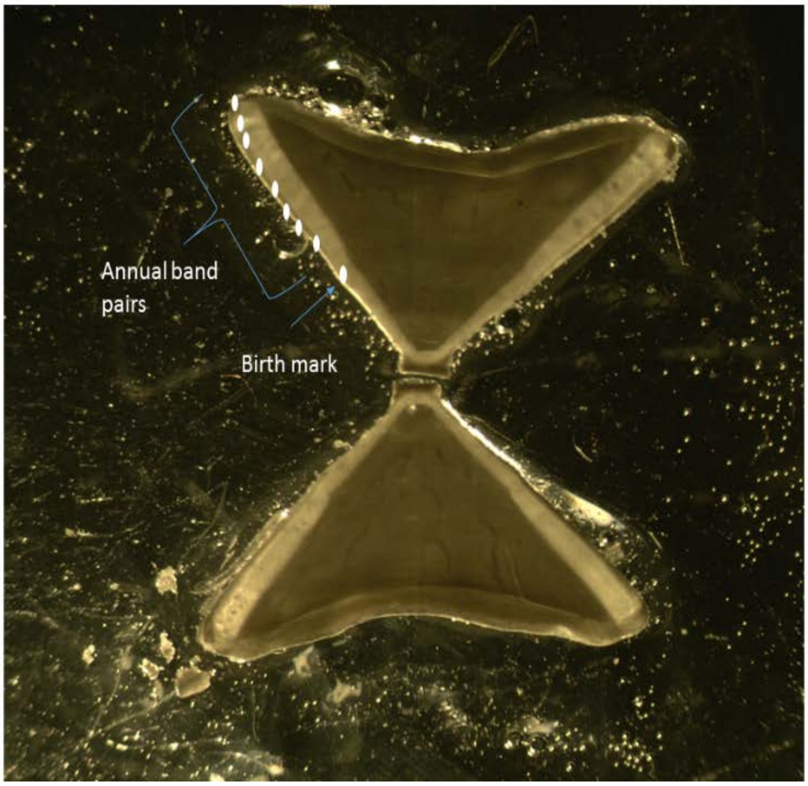


Figure 2: Vertebrae cross section viewed under a microscope. Birth mark and annual band pairs indicated.

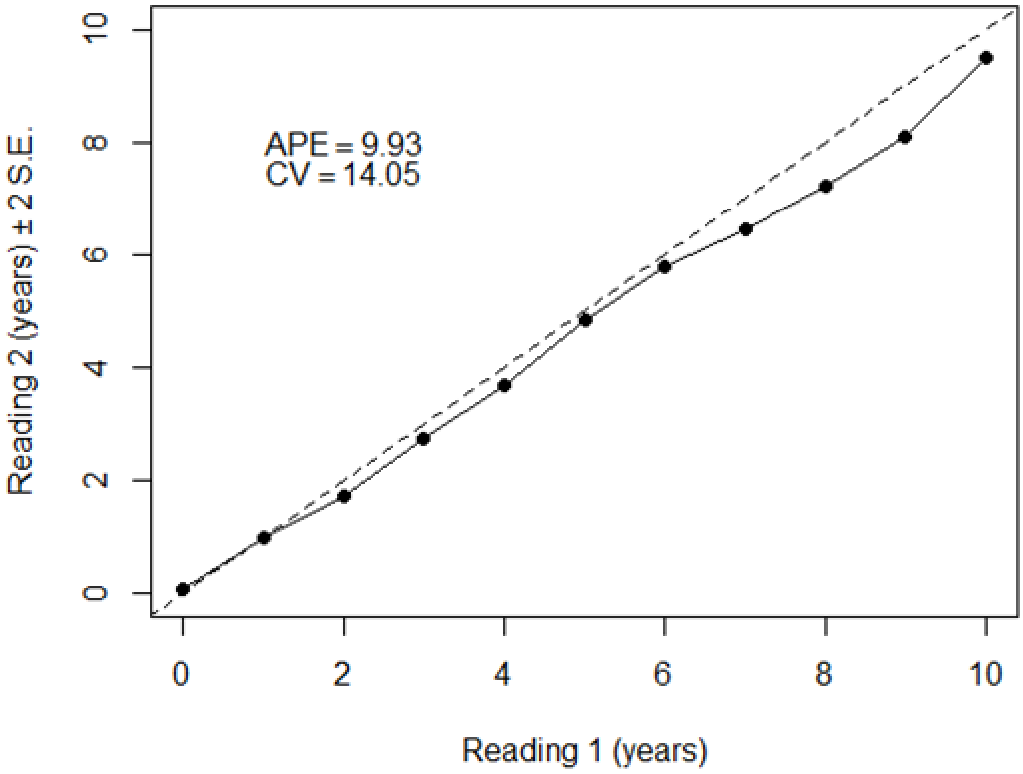


Figure 3. Age bias plot showing agreement between two independent readers. The PA ± 1 year was 58.73 % coefficient of variation (CV) was 14.05.

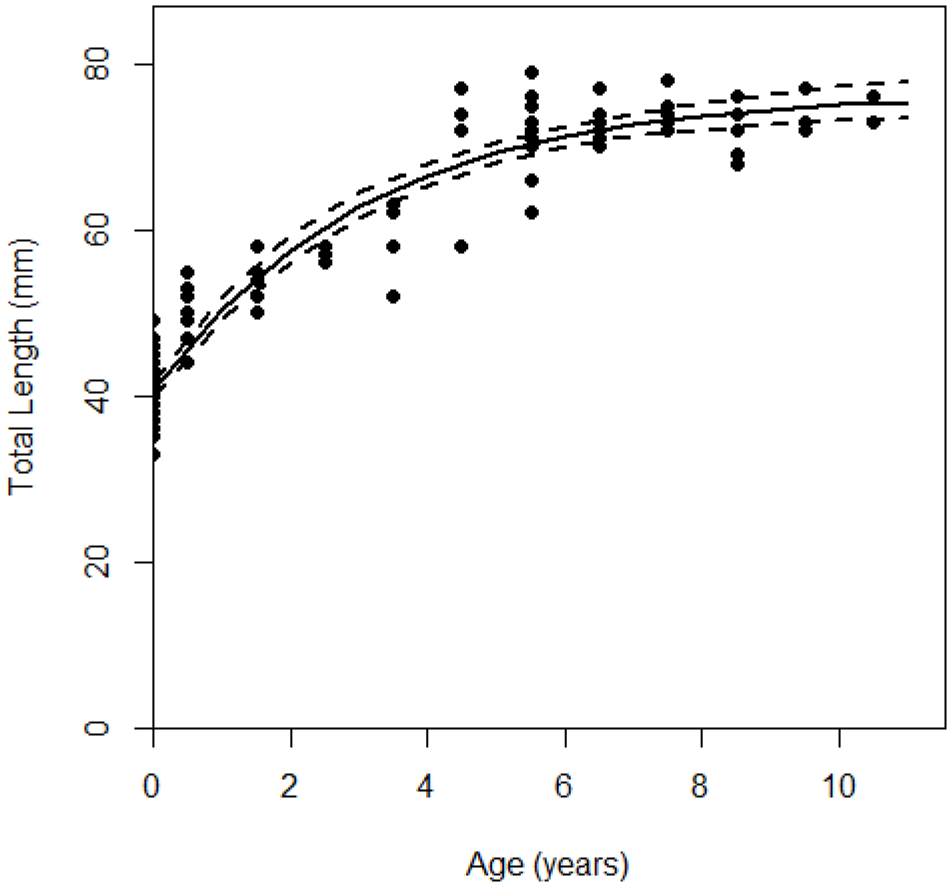
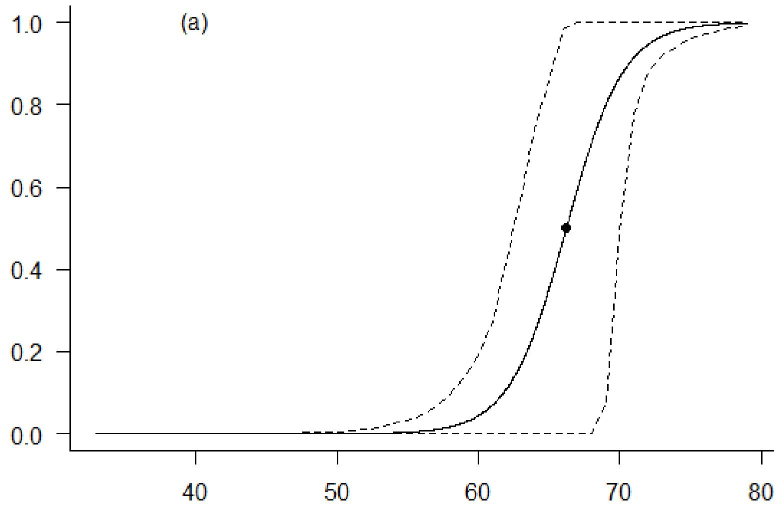


Figure 4. Length-at-age curve for *Carcharhinus coatesi* with both sexes combined from the Gulf of Papua fitted with a three-parameter von Bertalanffy growth model (solid line) and 95% bootstrapped confidence intervals (dashed line).



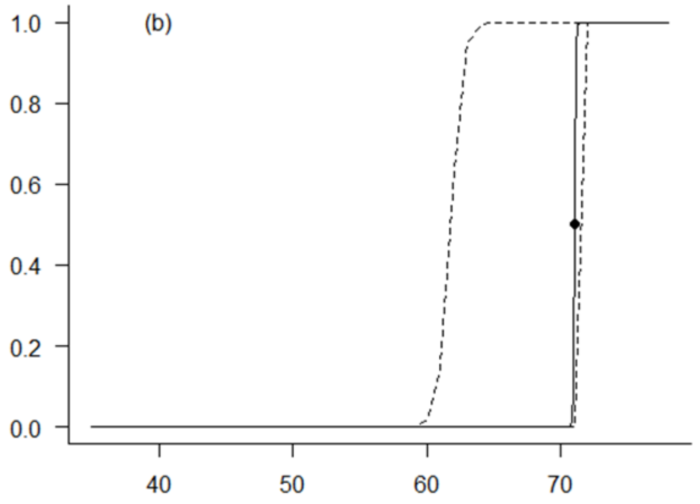
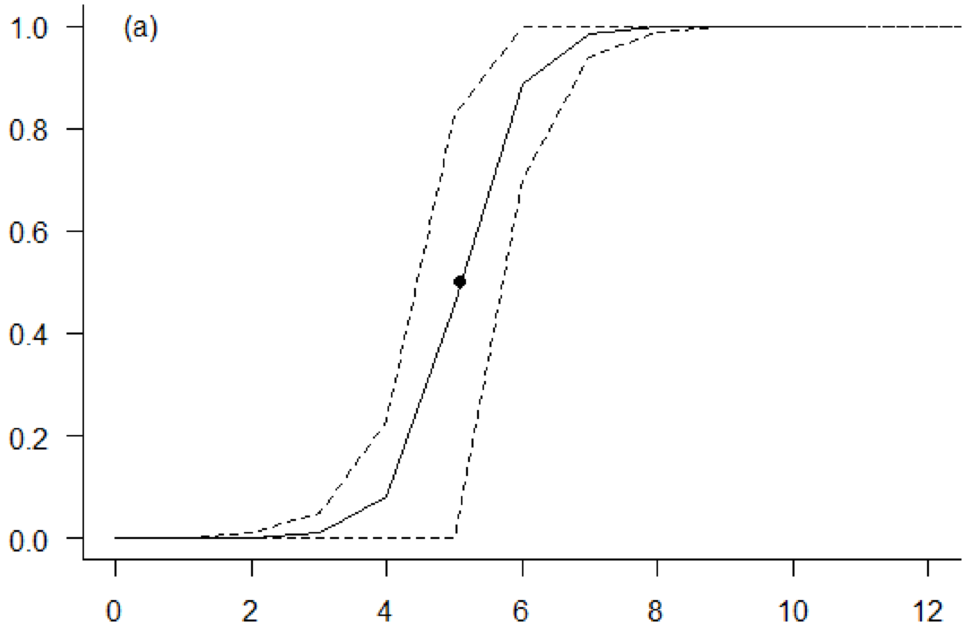


Figure 5. Length-at-maturity ogives for male (a) and female (b) *Carcharhinus coatesi* from the Gulf of Papua. The points represent the length at which 50% of population reaches maturity. 95% bootstrapped confidence intervals are indicated with dashed lines.



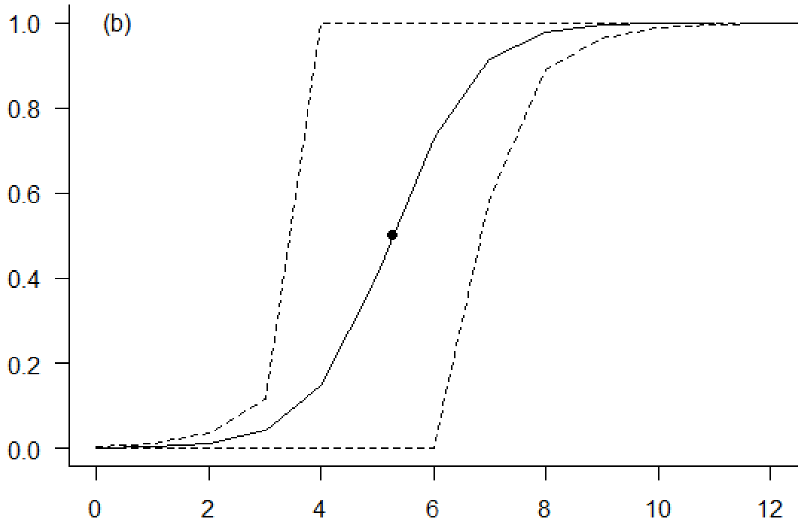


Figure 6. Age-at-maturity ogives for male (a) and female (b) *Carcharhinus coatesi* from the Gulf of Papua. The points represent the ages where 50% of the population reaches maturity. 95% bootstrapped confidence intervals are indicated with dashed lines.

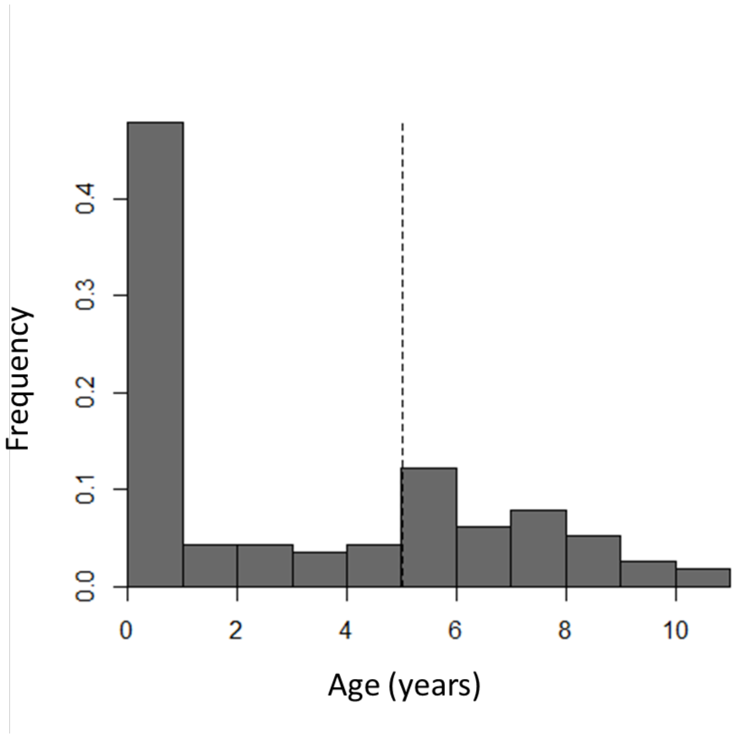


Figure 7: Age frequency of individuals sampled. The dotted line indicating age at maturity.

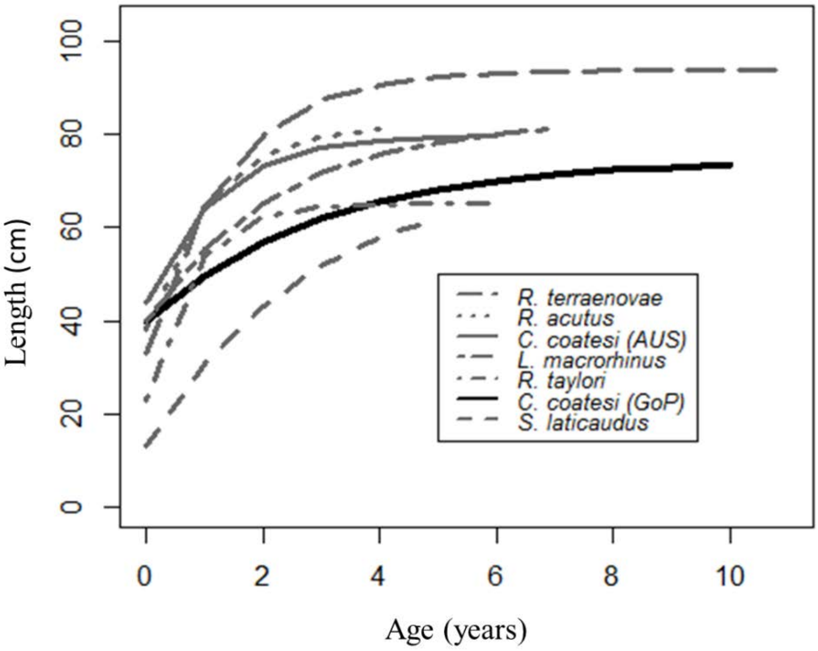


Figure 8: von Bertalanffy growth curves of small bodied carcharhinids

Tables

Table 1. The maturity of male and female samples were determined by the state of the uteri and ovaries in females, and claspers in males. Maturity stages were assigned a binary category for statistical analysis.

Female stage		**Description**	**Binary category**
1	Immature	Uteri very thin, ovaries small and without yolked eggs.	0
2	Maturing	Uteri slightly becoming enlarged at one end, ovaries becoming larger and small yolked eggs developing.	0
3	Mature	Uteri large along entire length, ovaries containing some large yolked eggs.	1
4	Pregnant	Uteri containing embryos or large eggs.	1
5	Post-partum	Uteri very large but without embryos.	1
Male stage			
NC	Not Calcified	Clasper very short not extending past the pelvic fin tip.	0
PC	Partially Calcified	Claspers longer, extending past the pelvic fin tip, not entirely hard, still flexible.	0
FC	Fully Calcified	Claspers long, hard along almost the entire length.	1

Table 2. Equations of the three growth functions used in the multi model approach

Model	Growth function
von Bertalanffy	$L(t) = L_0 + (L_\infty - L_0)(1 - exp(-kt))$
Logistic	$L(t) = \frac{L_\infty L_0 (g_{log} t)}{L_\infty + L_0(exp(g_{log} t) - 1)}$
Gompertz	$L(t) = L_\infty\, exp(-L_0\, exp(-g_{gom}\, t))$

Table 3: Summary of results from the multi model inference framework (MMI) incorporating Akaike's Information Criterion (AIC)

Sex	**Model**	**n**	**AIC_C**	**Δ**	**W (%)**	**L_0(±SE)**	**L_∞(±SE)**	**k(±SE)**	**$g_{(log)}$(±SE)**	**g**
Combined	VBGM	115	729.84	0	0.42	40.61±0.81	74.84±2.05	0.33±0.06		
	Logistic	115	730.8	0.97	0.26	40.86±0.08	73.70±1.56		0.48±0.07	
	Gompertz	115	730.31	0.47	0.33	40.74±0.81	74.17±1.75			0

n is the sample size, AIC_C is the small-sample bias adjusted from the Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_0 and L_∞ are the length-at-birth and asymptotic length in cm respectively, k is the growth completion rate in (year^{-1}) for the VBGM, $g_{(log)}$ and $g_{(gom)}$ are the growth parameters for Logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the model.

Table 1. Specifications of the five trawl vessels on which observers where deployed in this study.

Vessel	Length (m)	Gross Registered Tonnage	Main Engine (kW or HP)	Rigging
FV Ipali	21.36	138.07	388 kW	Quad
Charisma	21.36	138.07	388 kW	Quad
Lavai No. 1	27.83	150.07	420 kW	Twin
Lou Aro	27.83	150.07	420 kW	Twin
FV Siwi	29.3	113.67	540 HP	Quad

Table 2. Number of trawls, number of hours trawled, depth range fished, number of elasmobranchs recorded and catch per unit effort (CPUE, number of elasmobranchs/hour of trawling) in each of the fishing areas in the Gulf of Papua.

Fishing area	# trawls	# hours	depth range	# elasmos	CPUE (elasmos/hr)±SD
0	25	65.4	8–31	163	2.5 ± 1.9
1	6	11.2	7–36	28	2.5 ± 2.5
2	67	203.3	10–37	351	1.7 ± 1.3
3	1	3.0	16–18	10	3.3
4	3	9.5	11–34	0	0.0
5	17	40.0	6–24	51	1.3 ± 1.7
6	146	498.9	9–29	878	1.8 ± 3.0
7	97	320.9	8–26	314	1.0 ± 1.3
8	40	120.9	7–34	235	1.9 ± 1.4
Total	402	1273.1	6–37	2030	1.6 ± 2.2

Table 3. Abundance, biomass, CPUE (elasmobranchs/hr), size range recorded and maximum known size of each elasmobranch species recorded in this study.

Species	#	# (%)	Weight (kg)	Weight (%)	CPUE (#/100 hrs)	Size range (cm)	Max. known
Hemiscylliidae							
Chiloscyllium punctatum	74	3.6	34.4	0.8	5.8	TL: 18–88	TL: 132
Stegostomatidae							
Stegostoma fasciatum	10	0.5	21.0	0.5	0.8	TL: 39–186	TL: 235
***Ginglymostomatidae**							
**Nebrius ferrugineus*	-	-	-	-	-	-	
Hemigaleidae							
Hemigaleus australiensis	118	5.8	40.0	0.9	9.3	TL: 21–90	TL: 110
Carcharhinidae							
Carcharhinus amblyrhynchoides	1	<0.1	4.5	0.1	0.1	TL: 87	TL: 178
Carcharhinus amboinensis	3	0.1	15.2	0.3	0.2	TL: 89–95	TL: 280
Carcharhinus brevipinna	20	1.0	88.8	2.0	1.6	TL: 79–158	TL: 300
Carcharhinus coatesi	192	9.5	201.9	4.6	15.1	TL: 33–88	TL: 88
Carcharhinus fitzroyensis	18	0.9	94.5	2.2	1.4	TL: 66–123	TL: 135
Carcharhinus leucas	3	0.1	66.1	1.5	0.2	TL: 85–192	TL: 340
Carcharhinus limbatus	11	0.5	20.1	0.5	0.9	TL: 55–91	TL: 250
Carcharhinus macloti	19	0.9	35.2	0.8	1.5	TL: 38–90	TL: 110
Carcharhinus sorrah	3	0.1	15.6	0.4	0.2	TL: 96–100	TL: 160
Carcharhinus tilstoni	8	0.4	33.8	0.8	0.6	TL: 54–139	TL: 200
Rhizoprionodon acutus	148	7.3	117.3	2.7	11.6	TL: 31–86	TL: 100
Rhizoprionodon taylori	597	29.4	356.6	8.2	46.9	TL: 30–68	TL: 68
Sphyrnidae							
Eusphyra blochii	86	4.2	164.7	3.8	6.8	TL: 37–159	TL: 186
Sphyrna lewini	133	6.6	162.6	3.7	10.4	TL: 40–171	TL: 350
Sphyrna mokarran	2	0.1	20.3	0.5	0.2	TL: 119–150	TL: 600
Pristidae							
Anoxypristis cuspidata	11	0.5	190.3	4.4	0.9	TL: 102–215	TL: 350
Pristis pristis	1	<0.1	126.4	2.9	0.1	TL: 349	TL: 656
Rhinidae							
Rhina ancylostoma	2	0.1	52.8	1.2	0.2	TL: 120–165	TL: 270
Rhynchobatus palpebratus	60	3.0	401.9	9.2	4.7	TL: 43–234	TL: 262
Glaucostegidae							
Glaucostegus typus	5	0.2	96.5	2.2	0.4	TL: 39–240	TL: 284
Gymnuridae							
Gymnura australis	154	7.6	149.8	3.4	12.1	DW: 26–77	DW: 94
Dasyatidae							
Hemitrygon longicauda	25	1.2	9.4	0.2	2.0	DW: 12–31	DW: 31
Himantura australis	13	0.6	402.7	9.2	1.0	DW: 52–140	DW: 183
Himantura leoparda	19	0.9	180.9	4.1	1.5	DW: 38–104	DW: 140
Maculabatis astra	134	6.6	293.7	6.7	10.5	DW: 22–76	DW: 92
Megatrygon microps	1	<0.1	80.0	1.8	0.2	DW: ~180	DW: 222
Neotrygon annotata	35	1.7	15.3	0.4	2.7	DW: 12–30	DW: 30
Neotrygon picta	1	<0.1	0.1	<0.1	0.1	DW: 14	DW: 32
Pastinachus ater	3	0.1	50.6	1.2	0.2	DW: 80–100	DW: 200
Pateobatis fai	3	0.1	140.0	3.2	0.2	DW: 67–170	DW: 170

Pateobatis hortlei	32	1.6	79.6	1.8	2.5	DW: 16–112	DW: 112
Urogymnus acanthobothrium	3	0.1	84.0	1.9	0.2	DW: 100–11	DW: 161
**Urogymnus granulatus*	-	-	-	-	-	-	
unknown stingray	1	<0.1	12.0	0.3	0.1	DW: 78	-
Myliobatidae							
Aetomylaeus caeruleofasciatus	46	2.3	25.1	0.6	3.6	DW: 20–52	DW: 59
Aetobatidae							
Aetobatus ocellatus	5	0.2	45.1	1.0	0.4	DW: 66–107	DW: 300
Rhinopteridae							
Rhinoptera neglecta	29	1.4	293.2	6.7	2.3	DW: 37–140	DW: 140
Mobulidae							
Mobula alfredi	1	<0.1	145.8	3.3	0.1	DW: 220	DW: 550

Table 4. Length to weight conversion parameters, and their source, used to estimate biomass of specimens measured but not weighed.

Species	*a*	*b*	# based on	R^2	Source
Chiloscyllium punctatum	0.0043	2.9847	9	0.9942	this study
Stegostoma fasciatum	0.0089	2.7313	4	0.9965	this study
Hemigaleus australiensis	0.00348	3	425	0.982	Stevens & McLoughlin, 1991
Carcharhinus amblyrhynchoides	0.00265	3.21	67	0.975	Stevens & McLoughlin, 1991
Carcharhinus amboinensis	0.00194	3.27	104	0.986	Stevens & McLoughlin, 1991
Carcharhinus brevipinna	0.00317	3.1	507	0.874	Motta *et al.* , 2013
Carcharhinus coatesi	0.0066	2.9286	127	0.9792	this study
Carcharhinus fitzroyensis	0.00142	3.292	109	0.96	Lyle, 1987
Carcharhinus leucas	0.0111	2.923	182	0.908	www.fishbase.org (for Mexico)
Carcharhinus limbatus	0.00251	3.125	183	0.989	Castro, 1996
Carcharhinus macloti	0.000391	3.55	127	0.83	Stevens & McLoughlin, 1991
Carcharhinus sorrah	0.000545	3.51	164	0.9	Stevens & Wiley, 1986
Carcharhinus tilstoni	0.00475	3.06	311	0.91	Stevens & Wiley, 1986
Rhizoprionodon acutus	0.0055	2.9298	64	0.9886	this study
Rhizoprionodon taylori	0.0026	3.1558	185	0.9886	this study
Eusphyra blochii	0.006	2.8748	50	0.9742	this study
Sphyrna lewini	0.00399	3.03	252	0.985	Stevens & Lyle, 1989
Sphyrna mokarran	0.00123	3.24	117	0.991	Stevens & Lyle, 1989
Anoxypristis cuspidata	0.05	2.4735	45	0.8547	Salini *et al.* , 2007
Pristis pristis	0.003	2.9985	23	0.949	Salini *et al.* , 2007
Rhina ancylostoma	0.008	3.012	6	0.9988	from length and weights in: Gordon, 1992; Rajapackiam *et al* ., 2007; Uchida *et al* ., 1990; and Wallace, 1967.
Rhynchobatus palpebratus	0.0045	2.9959	21	0.987	this study
Glaucostegus typus	0.0046	2.9184	309	0.9797	W. White (unpubl. data)
Gymnura australis	0.0055	3.108	49	0.9606	this study
Hemitrygon longicauda	0.1708	2.5027	4	0.8904	this study
Himantura australis/leoparda	0.0728	2.7578	6	0.9737	this study
Maculabatis astra	0.0219	3.0471	46	0.9844	this study
Neotrygon annotata	0.0437	2.8717	26	0.8022	this study
Pateobatis hortlei	0.0765	2.174	14	0.9276	this study
Aetomylaeus caeruleofasciatus	0.007	3.1539	9	0.9766	this study
Aetobatus ocellatus	0.0276	2.87	331	0.98	Bassos-Hull *et al.* , 2014 (for *A. narinari*)
Rhinoptera neglecta	0.0487	2.6886	5	0.9976	this study

Table 4. Species identified by similarity percentages (SIMPER) as typifying fishing areas (grey shading), and those species distinguishing each pair of fishing areas (no shading). Note, the low number of samples for area 1 did not allow determination of typifying species and all pairwise comparisons were not significant based on ANOSIM results. Thus, area 1 not included in this table. Also excluded from this table is area 3 which did not have adequate trawls to include in analyses, and area 4 where no elasmobranchs were caught in the three trawls undertaken.

Fishing area	**0**	**2**	**5**	**6**	**7**	**8**
0	*C. coatesi*					
2	*C. coatesi* *R.taylori*	*R. taylori* *G. australis*				
5	*C. coatesi* *R. taylori*	*R. taylori* *C. coatesi*	*C. coatesi*			
6	*R. taylori* *C. coatesi*	*R. taylori* *E. blochii*	*R. taylori*	*R. taylori*		
7	*C. coatesi*	*R. taylori* *C. brevipinna*	*C. coatesi* *H. australiensis*	*R. taylori*	*H. australiensis* *G. australis* *R. acutus*	
8	*C. coatesi* *R. acutus*	*E. blochii* *R. taylori* *R. acutus* *G. australis*	*C. coatesi* *R. acutus* *G. australis*	*R. taylori* *R. acutus*	*R. acutus*	*G. australis* *M. astra* *R. acutus*

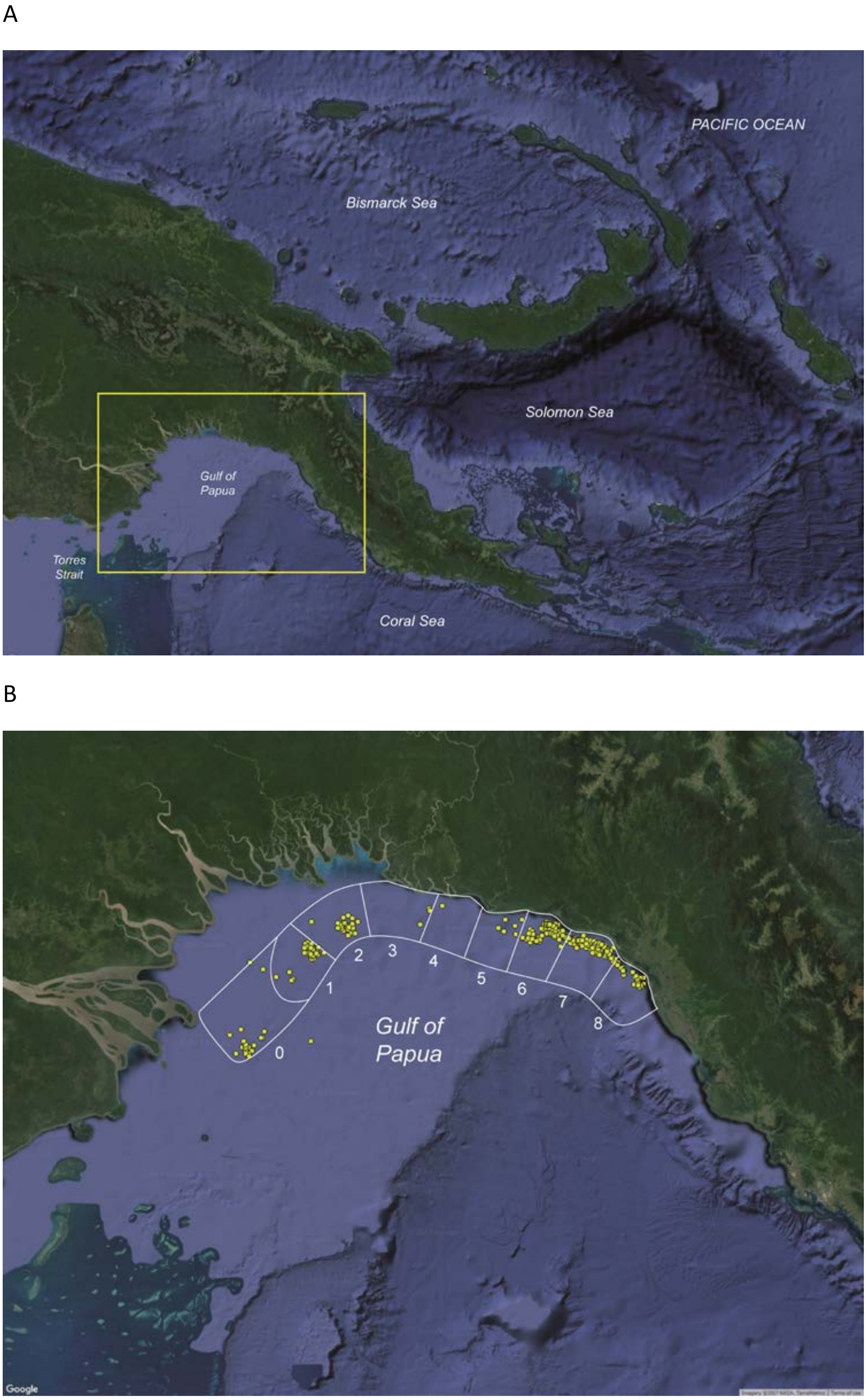

A
PACIFIC OCEAN
Bismarck Sea
Solomon Sea
Gulf of Papua
Torres Strait
Coral Sea
B
0
1
2
3
4
5
6
7
8
Gulf of Papua
Google

Fig. 1

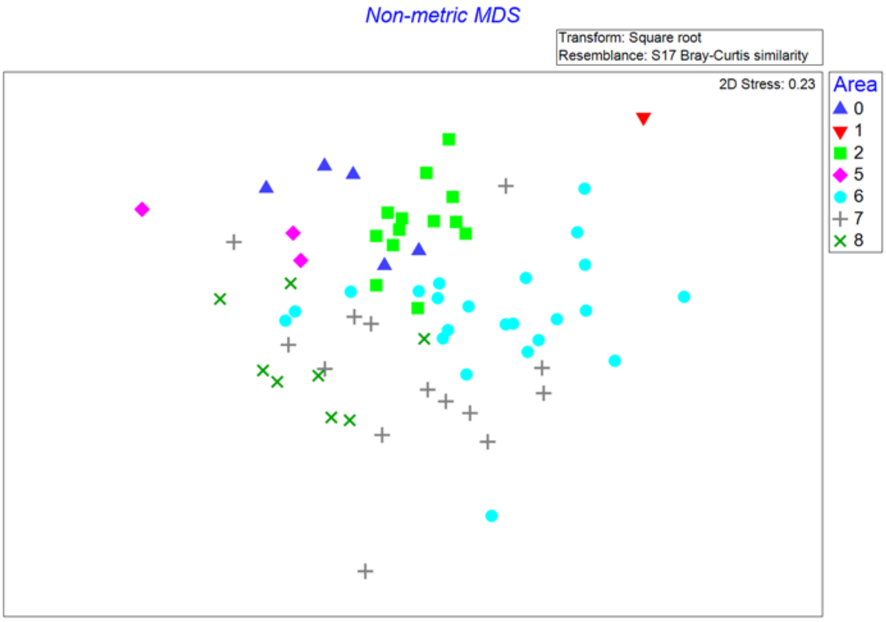

Non-metric MDS
Transform: Square root
Resemblance: S17 Bray-Curtis similarity
2D Stress: 0.23
Area
0
1
2
5
6
7
8

Figure 2

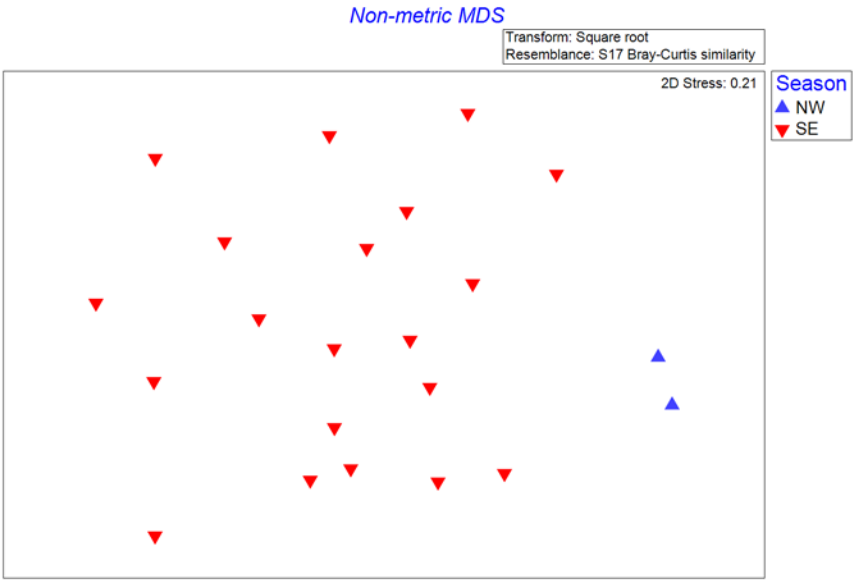

Non-metric MDS
Transform: Square root
Resemblance: S17 Bray-Curtis similarity
2D Stress: 0.21
Season
▲ NW
▼ SE

Fig. 3

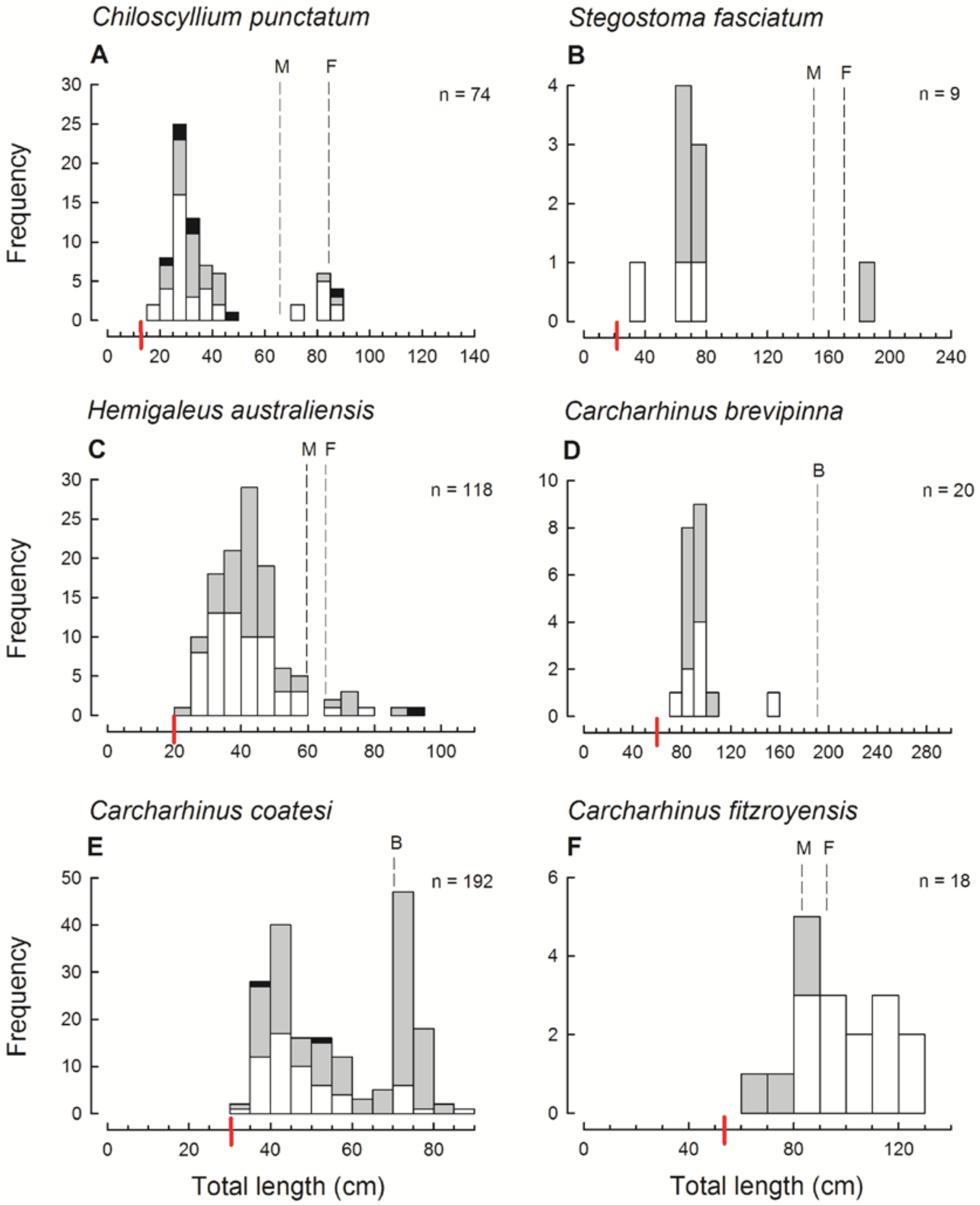
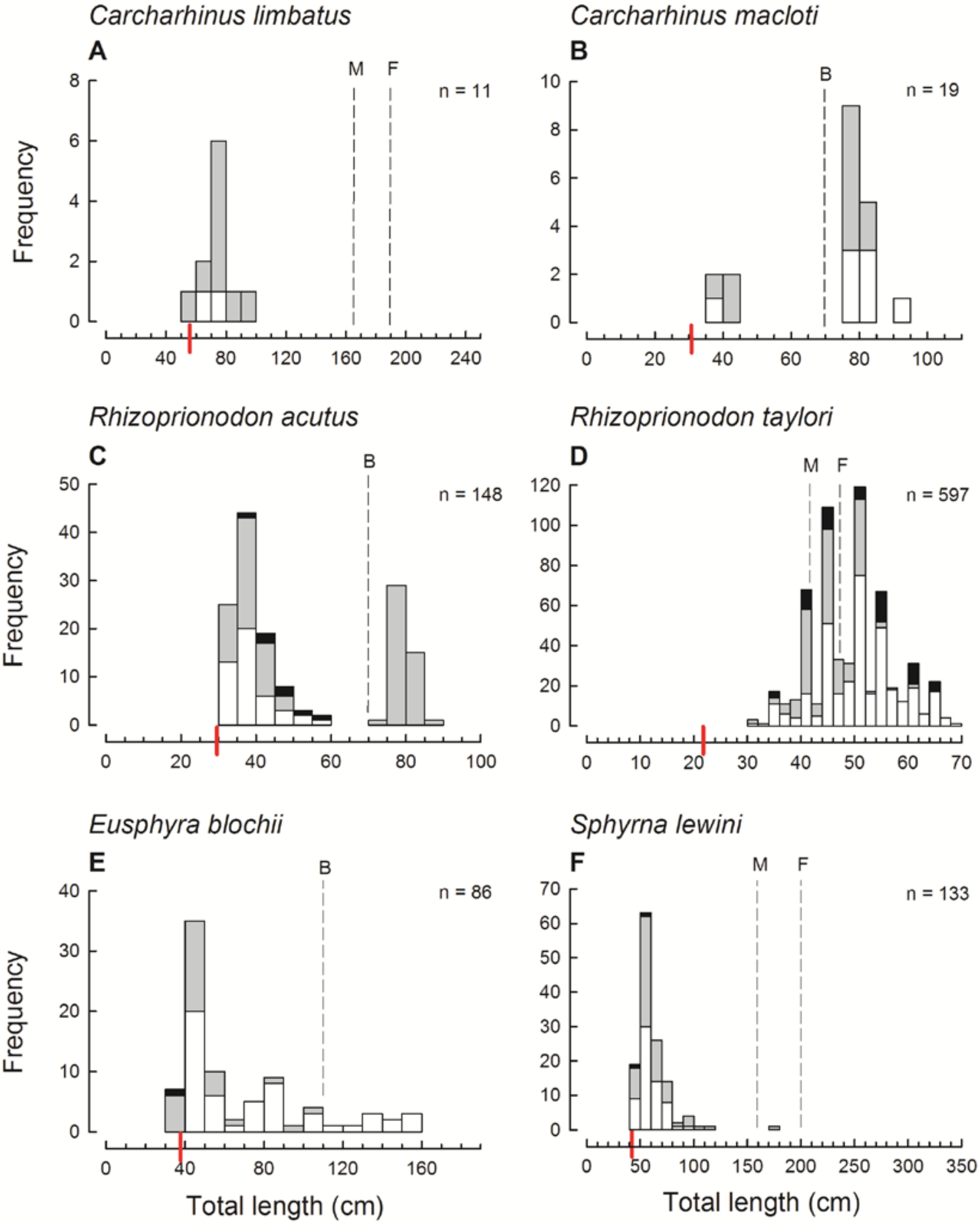

Chiloscyllium punctatum
A
M
F
n = 74
Frequency
30
25
20
15
10
5
0
0
20
40
60
80
100
120
140
Stegostoma fasciatum
B
M
F
n = 9
4
3
2
1
0
0
40
80
120
160
200
240
Hemigaleus australiensis
C
M
F
n = 118
Frequency
30
25
20
15
10
5
0
0
20
40
60
80
100
Carcharhinus brevipinna
D
B
n = 20
10
8
6
4
2
0
0
40
80
120
160
200
240
280
Carcharhinus coatesi
E
B
n = 192
Frequency
50
40
30
20
10
0
0
20
40
60
80
Total length (cm)
Carcharhinus fitzroyensis
F
M
F
n = 18
6
4
2
0
0
40
80
120
Total length (cm)

Fig. 4



Carcharhinus limbatus
A
M
F
n = 11
Frequency
0
2
4
6
8
0
40
80
120
160
200
240
Carcharhinus macloti
B
B
n = 19
0
2
4
6
8
10
0
20
40
60
80
100
Rhizoprionodon acutus
C
B
n = 148
Frequency
0
10
20
30
40
50
0
20
40
60
80
100
Rhizoprionodon taylori
D
M
F
n = 597
0
20
40
60
80
100
120
0
10
20
30
40
50
60
70
Eusphyra blochii
E
B
n = 86
Frequency
0
10
20
30
40
0
40
80
120
160
Total length (cm)
Sphyrna lewini
F
M
F
n = 133
0
10
20
30
40
50
60
70
0
50
100
150
200
250
300
350
Total length (cm)

Fig. 5

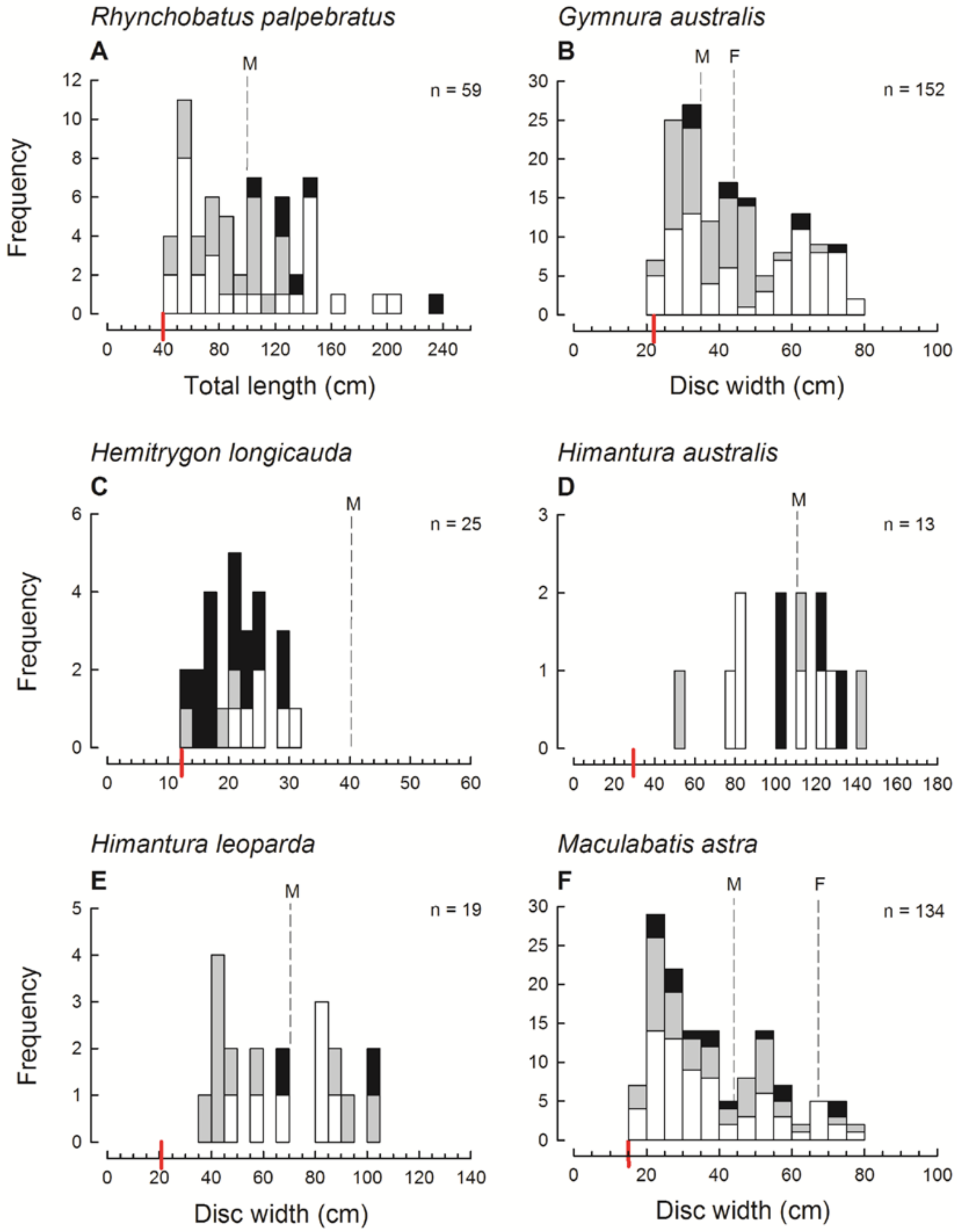

Rhynchobatus palpebratus
A
M
n = 59
Frequency
Total length (cm)
0
2
4
6
8
10
12
0
40
80
120
160
200
240
Gymnura australis
B
M
F
n = 152
0
5
10
15
20
25
30
0
20
40
60
80
100
Disc width (cm)
Hemitrygon longicauda
C
M
n = 25
Frequency
0
2
4
6
0
10
20
30
40
50
60
Himantura australis
D
M
n = 13
0
1
2
3
0
20
40
60
80
100
120
140
160
180
Himantura leoparda
E
M
n = 19
Frequency
0
1
2
3
4
5
0
20
40
60
80
100
120
140
Disc width (cm)
Maculabatis astra
F
M
F
n = 134
0
5
10
15
20
25
30
0
20
40
60
80
100
Disc width (cm)

Fig. 6

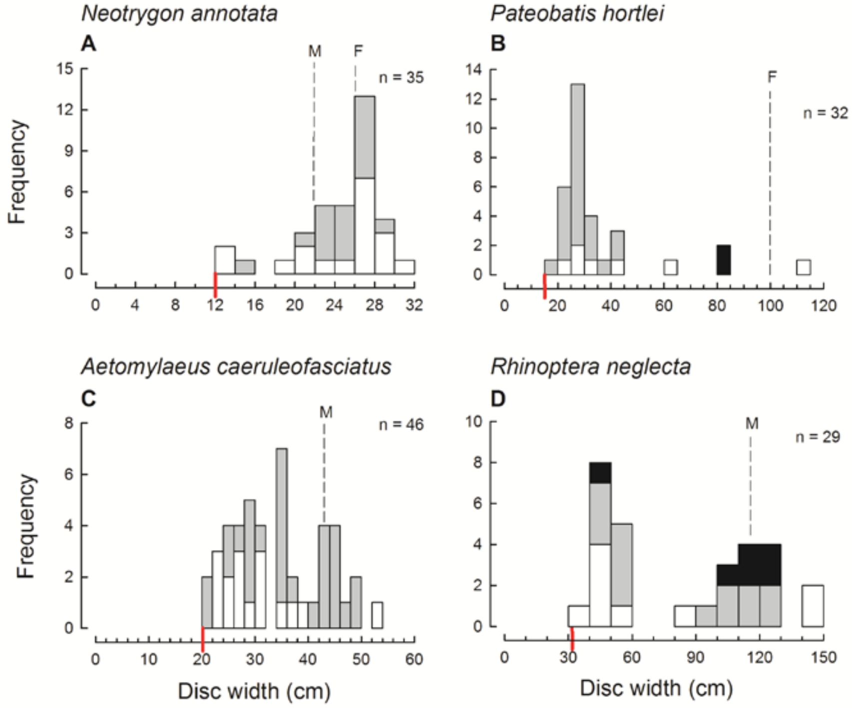

Neotrygon annotata
A
M
F
n = 35
Frequency
15
12
9
6
3
0
0
4
8
12
16
20
24
28
32
Pateobatis hortlei
B
F
n = 32
14
12
10
8
6
4
2
0
0
20
40
60
80
100
120
Aetomylaeus caeruleofasciatus
C
M
n = 46
Frequency
8
6
4
2
0
0
10
20
30
40
50
60
Disc width (cm)
Rhinoptera neglecta
D
M
n = 29
10
8
6
4
2
0
0
30
60
90
120
150
Disc width (cm)

Fig. 7

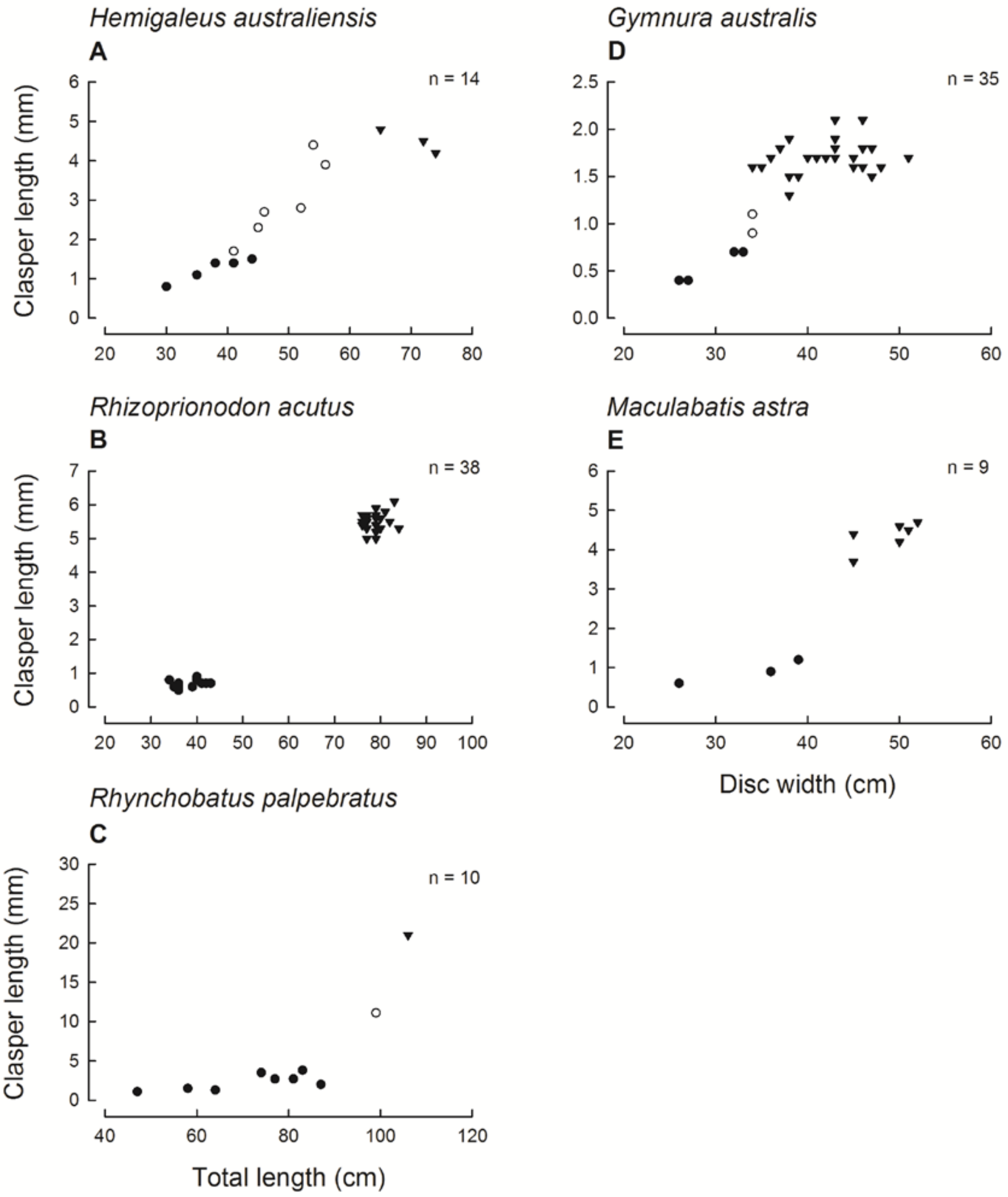

Hemigaleus australiensis
A
n = 14
Rhizoprionodon acutus
B
n = 38
Rhynchobatus palpebratus
C
n = 10
Gymnura australis
D
n = 35
Maculabatis astra
E
n = 9
Clasper length (mm)
Total length (cm)
Disc width (cm)

Fig. 8

PLOS | ONE

RESEARCH ARTICLE

Rediscovery of the Threatened River Sharks, *Glyphis garricki* and *G*. *glyphis*, in Papua New Guinea

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Abstract

Recent surveys of the shark and ray catches of artisanal fishers in the Western Province of Papua New Guinea (PNG) resulted in the rediscovery of the threatened river sharks, *Glyphis garricki* and *Glyphis glyphis*. These represent the first records of both species in PNG since the 1960s and 1970s and highlight the lack of studies of shark biodiversity in PNG. Two individuals of *G*. *garricki* and three individuals of *G*. *glyphis* were recorded from coastal marine waters of the Daru region of PNG in October and November 2014. The two *G*. *garricki* specimens were small individuals estimated to be 100–105 cm and ~113 cm total length (TL). The three *G*. *glyphis* specimens were all mature, one a pregnant female and two adult males. These are the first adults of *G*. *glyphis* recorded to date providing a more accurate maximum size for this species, i.e. ~260 cm TL. A single pup which was released from the pregnant female *G*. *glyphis*, was estimated to be ~65 cm TL. Anecdotal information from the fishers of pregnant females of *G*. *glyphis* containing 6 or 7 pups provides the first estimate of litter size for this species. The jaws of the pregnant female *G*. *glyphis* were retained and a detailed description of the dentition is provided, since adult dentition has not been previously documented for this species. Genetic analyses confirmed the two species cluster well within samples from these species collected in northern Australia.

Introduction

Papua New Guinea (PNG) sits within the Coral Triangle, a region of exceptional marine biodiversity. Despite being key components of this biodiversity and marine ecosystems more

gov) grant (Jaws and Backbone: Chondrichthyan Phylogeny and a Spine for the Vertebrate Tree of Life; DEB-01132229).

Competing Interests: The authors have declared that no competing interests exist.

broadly, there is a paucity of information on sharks in PNG waters with much of our knowledge coming from historical, rather than contemporary, records scattered across a wide range of scientific publications and expedition reports (e.g. [1–3]). The lack of even the most fundamental biodiversity information hinders a proper assessment of the impacts of the various pressures exerted on sharks in the region, e.g. fishing, pollution from mining, habitat loss. In recognition of this lack of detailed data on the shark and ray resources of PNG, the National Fisheries Authority in Port Moresby has initiated a large-scale project to obtain detailed data on the biodiversity and utilisation of elasmobranchs (sharks and rays) in its national waters.

The river sharks (Carcharhinidae: *Glyphis*) are a relatively poorly known group of sharks with patchy distributions in tropical rivers and coastal regions of the Indo-West Pacific. Two species with sympatric distributions are known from the Australian-New Guinea region; the relatively recently described Northern River Shark *Glyphis garricki* Compagno, White & Last and the Speartooth Shark *Glyphis glyphis* (Müller & Henle) [4]. In PNG waters, both species are known from very few records. *Glyphis garricki* records are based on jaws collected from the Gulf of Papua off Port Romilly (07°40′ S, 144°50′ E) in 1966 and Baimuru (07°33′ S, 144°51′ E) in 1974. *Glyphis glyphis* records are also based on jaws collected from the Gulf of Papua off Port Romilly (07°40′ S, 144°50′ E) in 1966 and Alligator Island (07°19′ S, 141°11′ E), date unknown.

In northern Australia, *G*. *glyphis* has been recorded from nine tidal rivers and estuaries, all of which are highly turbid with fine muddy substrates in salinities of 0.8–28.0 [5]. In the Adelaide River of the Northern Territory, individuals have been found up to 100 km inland with larger individuals occurring closer to the river mouth and smaller juveniles 80–100 km upstream during the late dry season [5]. No adult specimens of this species have been previously reported. *Glyphis garricki* has been recorded in several large tidal tropical river systems and coastal habitats also characterised by fine muddy substrates and high turbidity [5]. Juveniles and subadults are found in freshwater, estuarine and marine environments (salinities 2–36), whilst adults have only been recorded from marine areas [5]. In northern Australia, the presence of free-swimming neonates in October suggests that both *G*. *glyphis* and *G*. *garricki* give birth in October [5].

During surveys of shark and ray catches of artisanal fishing activities in the Daru region of PNG, two individuals of *G*. *garricki* and three individuals of *G*. *glyphis* were recorded. These represent the first confirmed records of *Glyphis* species in PNG waters since the 1960s and 1970s. The *G*. *glyphis* specimens were all adults, one a pregnant female from which only the jaws and fins were observed and two adult males based on images taken by fishers from Katatai. This represents the first adult specimens of *G*. *glyphis* recorded. The dentition of the adult female *G*. *glyphis* specimen is described in detail and insights into the ecology of the species are discussed, including a first account of litter size of *G*. *glyphis*. The two *G*. *garricki* were juvenile specimens. Species identification of the *Glyphis* specimens was confirmed using molecular analyses.

Materials and Methods

Ethics Statement

The adult female *Glyphis glyphis* examined in this study, consisting of its jaws and most fins, was captured by artisanal gillnet fishers from the village of Katatai (9°01'15" S, 143°20'31" E) in October 2014. The fins and jaws were brought to Daru the following morning for sale. The gill nets used are ~2 m high and ~100 m long and have up to 9 inch mesh size, and at this time of the year were set relatively close to shore in shallow water. The target species for this fishery at this time of the year (October) is the Barramundi *Lates calcarifer* (Bloch). The two adult male

G. glyphis and one specimen of *G. garricki* were caught by the same fishers in the following month (November 2014) and images were supplied to the project team from the village chairman (J. Page). A second specimen of *G. garricki*, consisting of only the dried first dorsal fin, was observed at the fish buyer company Philo Marine Ltd. in Daru where dried shark fin and fish swim bladders are exported. For all specimens recorded, death occurred following entanglement in the gillnet and each were dead when the nets were retrieved by the fishers.

Permission was obtained from Philo Marine Ltd. to examine their dried shark fins, which included the *G. garricki* fin. Permission was obtained to examine the female *G. glyphis* fins and jaw, the latter of which was subsequently purchased from the Katatai village chairman to be retained as a museum specimen. Although *G. garricki* and *G. glyphis* are listed as Endangered and Critically Endangered, respectively, on the Australian *Environment Protection and Biodiversity Conservation Act*, and Critically Endangered [6] and Endangered [7], respectively, on the IUCN Red List of Threatened Species, there is currently no regulation against taking of these species in PNG waters. Approval from CSIRO or National Fisheries Authority for research using moribund bycatch from fishers is not required.

The artisanal gillnet fishers are permitted to fish in the Daru region by the National Fisheries Authority. The commercial fish buyer (Philo Marine Ltd.) is certified to export dried fish products from Daru under the Independent State of Papua New Guinea's *Companies Act 1997*.

Specimens Examined

During a field trip to the island of Daru (9°03'55" S, 143°12'35" E) in the Western Province of PNG (Fig 1) in October 2014, a number of fishing villages and camps were visited along the mainland coast. At each of these villages or camps, the local chairman was informed of our study and asked to bring any captured sharks and rays to the market area in Daru over the week of the survey trip. On the 23rd October 2014, the chairman from the village of Katatai (9° 01'15" S, 143°20'31" E, Fig 1) brought several shark and ray specimens to Daru. Included in these specimens were the lower caudal lobe, dorsal fins, pectoral fins, one pelvic fin, and jaw of a large *G. glyphis* specimen that was caught in a gillnet set about 3 km offshore from the fishing village of Katatai in marine waters (Fig 1). The fins were photographed and the pectoral and first dorsal fin measured (Fig 2). The jaw was retained and is deposited in the Australian National Fish Collection in Hobart (accession number CSIRO H 7670–01; Fig 3). A muscle tissue sample was taken from the jaws and stored in 100% ethanol. The majority of the flesh and connective tissue was removed from the jaws and which was then dried completely in a fume cupboard.

A batch of dried shark fins present at the fish buyer company Philo Marine Ltd. in Daru was examined on the 25th October 2014. In order to determine the number of shark specimens present in the batch of dried fins, all first dorsal fins were separated from the remaining fins. For sawfish, guitarfish and wedgefish which have two similar-sized dorsal fins, the caudal fin was used to prevent duplication of specimens. It was determined that 66 specimens of sharks and rays were present in the batch of dried fins. For each of the selected first dorsal fins, an image, fin measurements and a small piece of tissue from the free rear tip were taken. Subsequent DNA barcoding techniques revealed that one of the 66 fins was *G. garricki* (see molecular section below; Fig 4).

The village chairman at Katatai was left with a camera to record any other sharks caught over the month of November 2014. In April 2015, images of three additional *Glyphis* specimens were sent through to the National Fisheries Authority in Port Moresby. These consisted of two adult male specimens of *G. glyphis* (Fig 5) and one unsexed specimen of *G. garricki* (Fig 6). Genetic samples on Whatman FTA Elute™ cards were also received for these specimens.

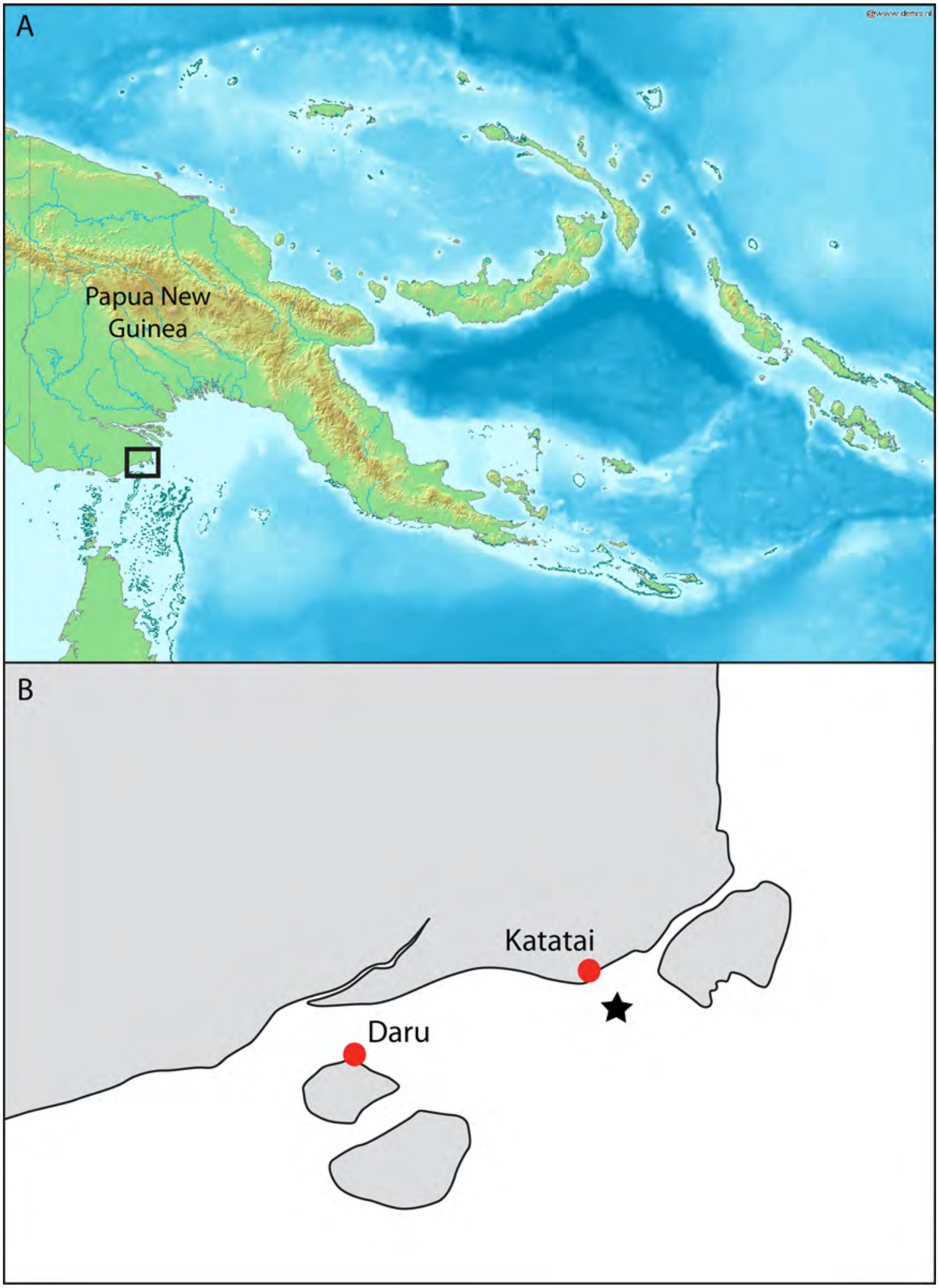

Fig 1. Map of Papua New Guinea and the Daru region. (A) Papua New Guinea with the black box indicating the Daru region; (B) Inset of the Daru region from where the five *Glyphis* specimens were caught by fishers from the village of Katatai. Black star indicates the approximate capture location of the pregnant female *Glyphis glyphis*.

doi:10.1371/journal.pone.0140075.g001

Fig 2. Fresh fins of the adult female *Glyphis glyphis*. Field code 220348, estimated length 237–260 cm: (A) first dorsal fin; (B) right pelvic fin; (C) second dorsal fin; (D) lower caudal-fin lobe; (E) left pectoral fin; (F) right pectoral fin. Tape measure is set at 47 cm.

doi:10.1371/journal.pone.0140075.g002

Morphology

The first dorsal fin of the first *G*. *garricki* specimen (Fig 4) and the adult female *G*. *glyphis* (Fig 2A), and the left pectoral fin of the adult female *G*. *glyphis* (Fig 2E) were measured. For both pectoral and first dorsal fins, their length, anterior margin length, posterior margin length, height, and base length, were measured. One of the adult male *G*. *glyphis* (Fig 5B) and the *G*. *garricki* images supplied by the Katatai village chairman included the tape measure allowing total length to be estimated. For the second adult male *G*. *glyphis* (Fig 5A), the tape measure was only shown in the pectoral fin images. For both adult male specimens, the pectoral-fin length, anterior margin and posterior margin were photographed with the tape measure allowing an accurate size to be recorded for each. Fin measurement methodology follows [8]. In order to estimate a total length for the individual *G*. *garricki* for which only the dried dorsal fin was available, and for the adult female and one adult male of *G*. *glyphis*, the measurements provided in [4] for individuals of known total length were used. For *G*. *glyphis*, the dried type specimen measurements were excluded due to its poor condition. The estimated lengths obtained for *G*. *glyphis* using this data were compared with estimates based on the photographed adult male specimen supplied by the Katatai village chairman from which a total length and three pectoral fin measurements were obtained.

Dentition

The dentition of the *G*. *glyphis* specimen was described and compared with the species redescription [4] which was based on specimens less than 1.8 m TL. During preparation of the jaw, a number of fish and stingray spines were removed. The dentition of two adult specimens of *G*. *garricki* (CSIRO H 6173–01 and CSIRO H 6635–01) was used for comparative purposes. The

Fig 3. Whole jaw of *Glyphis glyphis*. Adult female (CSIRO H 7670–01).

doi:10.1371/journal.pone.0140075.g003

description of the adult female *G. glyphis* dentition and comparison with adult *G. garricki* are provided in S1 Appendix.

Genetic analyses

Mitochondrial (mtDNA) genes are routinely used for species delineation [9,10]. Here we used three mtDNA genes, alongside morphological and dentition investigations for species determination. DNA barcoding enables the recognition and/or discrimination of an individual's species identity based on short, relatively conserved gene fragments. Here we chose to use 16S

Fig 4. Dried first dorsal fin of *Glyphis garricki*. Field code 220358, estimated length 100–105 cm.

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rRNA (*16S*), cytochrome c oxidase subunit I (*COI*) and NADH dehydrogenase subunit 2 (*NADH2*) as DNA barcodes. *COI* is one of the most commonly accepted fragments for metazoan species discrimination [11]. There are a large number of *16S* sequences in GenBank and, due to its relatively slow rate of evolution, *16S* is often used for phylogenetic reconstructions and comparative purposes. Additionally, an ongoing Chondrichthyan Tree of Life (CToL) project led by one of us (GN) at the College of Charleston has primarily used the *NADH2* gene for species delineation as a first step towards collecting genomic scale information. The molecular analyses and barcoding were undertaken in two laboratories—the CSIRO marine laboratories in Australia (*16S* and *COI*) and the Hollings Marine Laboratory in Charleston, USA (*NADH2*). The specific methodology for the *16S* and *COI* analyses are provided in S1 Text.

Results

Genetic analyses

The *G. garricki* partial *16S* gene sequence (Accession number KR703623) was 547 base pairs (bp) in length while 562 bp (Accession number KR703625) of the *COI* gene was sequenced from the same individual. In the *G. glyphis* individual, 562 bp (Accession number KR703622) and 631 bp (Accession number KR703624) of the *16S* and *COI* genes respectively were successfully sequenced. When blasted against sequences in GenBank, there was 100% pairwise identity of the *G. garricki* sequences to Accession Number KF646786 (*Glyphis garricki* complete mitochondrial genome, [12]). Additionally, we observed 100% pairwise identity of the *G. glyphis* sequences to Accession Number KF006312 (*Glyphis glyphis* complete mitochondrial genome, [13]) and to the 93 *G. glyphis* whole mitochondrial genomes from Australia (Accession Numbers KM100613–KM100704) that were recently sequenced by [14].

Each of the three gene fragments (*COI*, *16S* and *NADH2*) yielded concordant identification of the two species. The tree resulting from the neighbour-joining analysis of the *NADH2* data derived from two of the three PNG *G. glyphis* specimens and one of the PNG *G. garricki* specimens, together with previously available sequences of other representatives of *G. glyphis* and *G. garricki*, another nominal congener *G. gangeticus* and an outgroup species *Lamiopsis tephrodes*,

Fig 5. Freshly caught adult males of *Glyphis glyphis*. (A) estimated length 251–256 cm, caught 3rd Nov. 2014; (B) ~228 cm TL, caught 13 November 2014.

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is shown in Fig 7. The two PNG specimens of *G. glyphis* (labelled GN15749 and GN16686 in Fig 7) cluster within the clade of *G. glyphis* sequences derived from individuals sampled in Australia. The PNG *G. garricki* specimen (labelled GN16684 in Fig 7) clusters within a separate clade comprised of *G. garricki* sequences that were also derived from Australian specimens.

Additionally, following FTA Elute extraction (SA pers. comm.) and gene sequencing using the same mtDNA genes as outlined above, the three FTA Elute genetic samples of the

Fig 6. Freshly caught specimen of *Glyphis garricki*. Estimated length 100–105 cm, caught 6 November 2014.

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specimens caught by the Katatai village in November 2014 were identified as *Glyphis*; two adult male *G*. *glyphis* and a *G*. *garricki*.

Estimation of total length

Using the first dorsal fin measurements of the types of *G*. *garricki* with known total lengths (see [4]), the dried *G*. *garricki* first dorsal fin was from a specimen estimated to be between 100 and 127 cm total length (TL). The total fin length, anterior margin length and base length produced estimates of 100, 102 and 105 cm TL, respectively, while the height and posterior margin produced estimates of 119 and 127 cm TL, respectively. The second *G*. *garricki* specimen, photographed by the Katatai village chairman, was ~113 cm TL.

Using the pectoral fin measurements of the measured specimens of *G*. *glyphis* in [4] with known total lengths, the size of the adult female *G*. *glyphis* specimen from Katatai was estimated to be between 282 and 389 cm TL. Using the first dorsal fin measurements, its size was estimated to be between 237 and 304 cm TL. The larger estimates produced using the pectoral fin measurements is likely the result of the ontogenetic changes in relative pectoral fin sizes in *Glyphis* species. The pectoral fins of *Glyphis* species become proportionally larger as they grow. Since the morphometric data for *G*. *glyphis* in [4] is based on eight whole specimens between 59 and 145 cm TL, estimating total length of a far larger specimen from these measurements is difficult. Using the total length and corresponding pectoral-fin measurements for one of the photographed adult males from Katatai overcomes this problem as they are similar in size. This produced estimates of 256, 260 and 304 cm TL for the adult female, based on pectoral-fin length, anterior margin and posterior margin, respectively.

One of the adult male *G*. *glyphis* specimens photographed by the Katatai village chairman had a total length of ~228 cm, based on a tape measure included in the image provided. The second adult male, for which only pectoral-fin length, anterior margin and posterior margin were recorded, was estimated to have a total length of 251, 256 and 292 cm, respectively.

The estimates of total length from the first dorsal fin measurements of the adult female *G*. *glyphis* followed a similar pattern to those for *G*. *garricki*. The total fin length, anterior margin

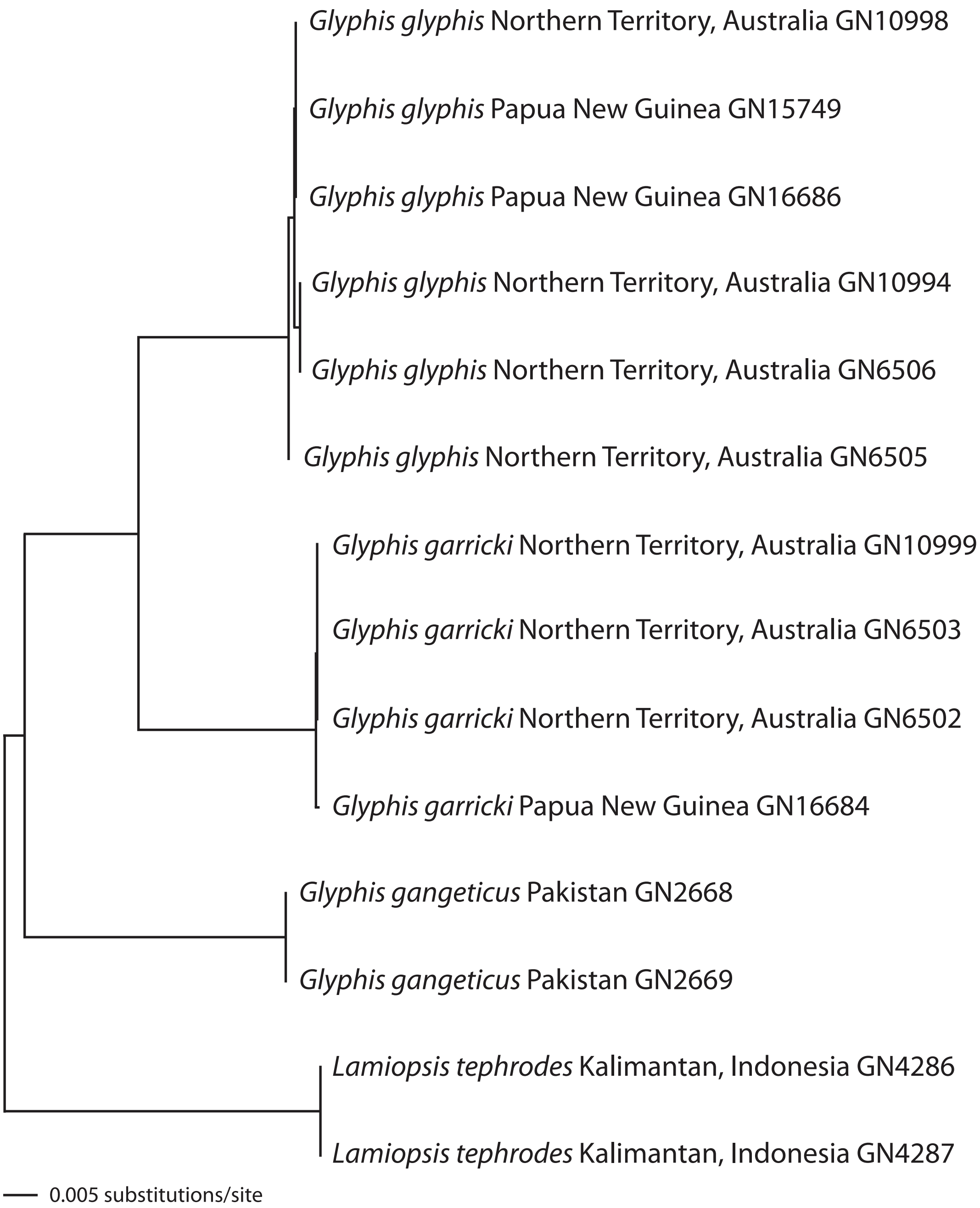

Fig 7. Molecular species identification using the mitochondrial *NADH2* gene. Neighbour-joining tree of *NADH2* sequences, estimated using the Kimura 2 parameter distance model of molecular evolution, of *Glyphis garricki*, *Glyphis glyphis*, *Glyphis gangeticus* and *Lamiopsis tephrodes*. The species identifications of samples GN15749 and GN16686 are confirmed as *G*. *glyphis* and sample GN16684 is confirmed as *G*. *garricki*.

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length and base length produced estimates of 241, 237 and 242 cm TL, respectively, while the height and posterior margin produced larger estimates of 268 and 304 cm TL, respectively. Similarly, estimates obtained from the pectoral-fin posterior margin measurements yielded far higher estimates. Since for the two *Glyphis* species, the first dorsal-fin length, anterior margin length and base length produced more consistent estimates of total length, these measurements are considered better estimates of total length than the height and posterior margin length. In

Table 1. Summary information on the five Papua New Guinea *Glyphis* specimens. Date of observation, genetic sample id, location, sex, total length (TL; lengths estimated from fin measurements in parantheses), and key measurements of the first dorsal and pectoral fins (in cm) of the *Glyphis* specimens recorded from the Daru region.

	Date	Location and part	Genetic id	sex	TL (cm)	D1L	D1A	D1B	P1L	P1A
G. garricki										
1	25 Oct 2014	Daru—dried dorsal fin (field code 220358)	KR703623 (16S); KR703625 (COI)	unknown	(100–105)	18	15	12.6	–	–
2	6 Nov 2014	Katatai observer—whole	GN16684 (NADH2)	unknown	~113	–	–	–	–	–
G. glyphis										
1	23 Oct 2014	Katatai—jaws[a] and fins (field code 220348)	KR703622 (16S); KR703624 (COI); GN15749 (NADH2)	pregnant female	(237–260)	44.2	33.8	31	37.1	55.3
2	3 Nov 2014	Katatai observer—whole		adult male	(251–256)	–	–	–	33	48.5
3	13 Nov 2014	Katatai observer—whole	GN16686 (NADH2)	adult male	~228	–	–	–	30.2	44

Date of observation, genetic sample id, location, sex, total length (TL; lengths estimated from fin measurements in parantheses), and key measurements of the first dorsal and pectoral fins (in cm) of the *Glyphis* specimens recorded from the Daru region.

[a] jaws cleaned, dried and retained in the Australian National Fish Collection (CSIRO H 7670–01)

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addition for *G. glyphis*, pectoral-fin length and anterior margin produced better estimates of total length. Table 1 summarises the sizes and estimated sizes for the five *Glyphis* specimens using the five fin measurements considered to be the most informative. Following this, the estimated size of the one *G. garricki* and two *G. glyphis* specimens from which a total length was not obtained were 100–105, 237–260, and 251–256 cm TL, respectively.

Reproductive insights

The female *G. glyphis* specimen was a pregnant female. The fishers who caught the shark reported that it contained one fully developed pup (~65 cm TL) which was released alive. It is likely that more pups were present in the litter but were aborted whilst tangled in the gill net. The fishers reported that they have caught pregnant females (containing either six or seven pups) of this species previously, including in May and June.

Dietary insights

Although the fishers reported that the stomach of the *G. glyphis* specimen was empty, some insights into the diet of this species can be ascertained from spines present in the jaw. A single stingray spine (Fig 8A) and a large number of bony fish spines (e.g. Fig 8B and 8C) were found when removing connective tissue around the jaw. The majority of fish spines were well embedded in the cartilage. This suggests that bony fish and probably stingrays are likely to be important dietary items for adult *G. glyphis*. Attempts to extract DNA from the spines was successful, but when sequenced (*16S*) only the predator (*G. glyphis*) and not prey DNA was recovered.

Discussion

Genetic analyses

Mitochondrial markers have previously been used to discriminate between *G. garricki* and *G. glyphis* in northern Australia [15], and in the current study, the morphological and dentition

Fig 8. Spines from the connective tissue of the *Glyphis glyphis* jaw. Examples of spines found during dissection of the adult female jaw: (A) a stingray spine; (B) and (C), bony fish spines.

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studies are strongly supported by the sequencing results of the three genetic markers. The mtDNA sequences from *16S*, *COI* and *NADH2* confirm that the fin sample obtained from Philo Marine Ltd. in Daru in October 2014 was from a *G. garricki* individual and the muscle sample (from the village of Katatai) collected in the same month was from a *G. glyphis* individual. Three further individuals of *Glyphis* recorded by the Katatai fishers in November 2014 were confirmed to consist of two *G. glyphis* and one *G. garricki*.

Life history implications

The biology of *Glyphis* species remains very poorly known [5], which is of concern given the conservation status of these species. Life history data such as fecundity and age is essential in understanding a species' biological productivity and hence ability to sustain exploitation or to recover from over-exploitation [16,17]. The records of *G. garricki* and *G. glyphis* documented in this study represent the first confirmed records of these two species in PNG since the 1960s and 1970s. Despite the limited material available from the PNG specimens, these surveys have resulted in important information allowing more of the life history of these rare species to be pieced together, particularly that of *G. glyphis*. Of significance is the fact that the PNG specimens represent the first records of adult male and female *G. glyphis* anywhere within the species range. The previously reported maximum size for *G. glyphis* (175 cm TL; [5]) has been greatly surpassed here with a best estimate of 260 cm TL based on conversion of fin measurements. As previously postulated [4,5], *G. glyphis* is here confirmed as a large carcharhinid species, similar to *G. garricki*, which has been recorded to 251 cm TL in Australia [5].

Across all *Glyphis* species, there is only a single previously examined pregnant individual, a *G. garricki* from northern Australia with 9 pups [5]. Anecdotal reports from the Katatai village fishers of pregnant *G. glyphis* containing 6–7 pups provides the first estimate of litter size in that species. This highlights a probable low productivity, especially given that the reproductive cycle may be biennial as suggested for *G. garricki* [5], and which is regularly the case for medium-large sized carcharhinids [18]. The reported size of a fully-developed *G. glyphis* pup from the captured female (~65 cm TL) is consistent with the size at birth from northern Australia (50–65 cm TL; [5]). The capture of this pregnant female in October is also consistent with the timing of parturition in the Adelaide River, Australia [5]. It would thus appear that in both PNG and northern Australia parturition precedes the onset of the monsoonal wet season. The transition between the dry and wet seasons is a period of re-connectivity of aquatic environments enabling the movement of biota [19], potentially increasing prey availability for neonate sharks.

The capture of the adult *G. glyphis* specimens in coastal marine waters also provides important insights into the habitat use of this species. Records of *G. glyphis* from northern Australia are restricted to juveniles and subadults from tidal rivers, typically in fresh and brackish water. These records from marine water provide strong circumstantial evidence that coastal marine waters are an important habitat for adult *G. glyphis*.

A limited number of *G. glyphis* stomachs examined from Queensland, Australia contained teleost fish remains (particularly catfishes) as well as freshwater prawns (*Macrobrachium rosenbergii*) [20]. All previously examined sharks have been juveniles, and the presence of a stingray spine and many bony fish spines in the jaws of the adult female *G. glyphis* from PNG suggests that its diet is probably fish dominated. This also supports the benthic feeding habits of *G. glyphis* as suggested by the above-mentioned prey items [20].

Conservation implications

These are the first documented records of *Glyphis* species in PNG waters since the 1960s and 1970s. Documenting their persistence in PNG improves our understanding of the contemporary distributions of these species that are of high conservation concern. Analysis of the genetic population structure of *G. glyphis* in northern Australia based on the whole mitochondrial genome showed a high degree of population separation between the three river drainages in which it occurs, suggesting strong female philopatry [14]. It is therefore possible that a New Guinean population(s) could be genetically distinct from the Australia populations. Limited exchange of individuals between these regions could indicate reduced resilience for depleted populations. It can be noted that the *NADH2* sequences (obtained from specific mtDNA genes) in this study cluster within the Australian sequences already obtained, although sequencing the whole mitogenome could provide more resolution of genetic structure [14].

The fact that adult *G. glyphis*, a large apex predator, have thus far gone unnoticed highlights the rarity of river sharks which combined with their occurrence in remote, poorly-surveyed regions, have resulted in *Glyphis* species being some of the least known sharks. Knowledge from artisanal fishers, together with the adult specimens documented here, can form the basis of surveys to document the occurrence and habitat of adults, a basic requirement for considering which management options may be appropriate in PNG for these rare species of high conservation concern.

Supporting Information

S1 Appendix. Dentition of adult *Glyphis glyphis*.
(PDF)

S1 Text. Genetic methodology.
(DOCX)

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Author Contributions

Conceived and designed the experiments: WTW SAA BS TU JJS. Performed the experiments: WTW SAA BS RL LB MH GJPN LY SC. Analyzed the data: WTW SAA MH PMK GJPN LY SC. Contributed reagents/materials/analysis tools: WTW SAA LB GJPN SC LY. Wrote the paper: WTW SAA BS LB GJPN SC LY PMK MH.

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Contribution to the Theme Section 'Biology and ecology of sawfishes'

OPEN ACCESS

Sawfishes in Papua New Guinea: a preliminary investigation into their status and level of exploitation

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ABSTRACT: The status of sawfishes (family Pristidae), and indeed most sharks and rays, in Papua New Guinea (PNG) is largely unknown due to the paucity of detailed catch and observational records available, both historic and contemporary. This paper provides the first comprehensive review of the published and unpublished literature on sawfish records in PNG. It also collates information for all sawfish specimens in the holdings of museum and fisheries collections, dating back to the late 1800s. Opportunistic sampling during a shark and ray biodiversity project in PNG has resulted in contemporary records for all 4 sawfish species known to occur in the region (i.e. *Anoxypristis cuspidata*, *Pristis clavata*, *P. pristis* and *P. zijsron*) and identification of suitable habitat for the species across PNG. A review of the literature shows that declines in sawfish populations have occurred in a number of locations. Detailed surveys of the key areas highlighted in this study are urgently required to assess the current status of sawfish in PNG. This information is crucial for developing a global strategy for sawfish conservation and fisheries management, given the apparent persistence of all 4 Indo-Pacific species in PNG.

KEY WORDS: Pristidae · Sawfish · Fisheries · Research needs

INTRODUCTION

Papua New Guinea (PNG) lies within the megadiverse region of the Indo-West Pacific known as the Coral Triangle. Elasmobranchs (sharks and rays) are key biota contributing to biodiversity in the Coral Triangle, but our understanding of the fauna of PNG is still in its infancy. Most of our knowledge of sharks and rays in PNG comes from historical records from small-scale biodiversity surveys and expedition reports (e.g. Herre 1936, Roberts 1978, Allen & Coates 1990) and there is no detailed biodiversity information. It is thus difficult to assess the current status of the sharks and rays present in PNG, and how they are impacted by various anthropogenic activities such as mining, pollution and fishing.

An example of the paucity of information available for sharks and rays in PNG was the recent 'rediscovery' of 2 species of river sharks (*Glyphis* spp.) in the Western Province of PNG (White et al. 2015). These species, which are listed as Endangered and Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2016), had not been recorded from PNG since the 1960s and 1970s. However, during a short field survey to Daru and Katatai in PNG in October 2014, both species were confirmed in the catches of local gillnet fishers, with the fishers report-

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ing that they are regularly caught in low numbers throughout the year at those locations (White et al. 2015). That finding highlighted that the 'rediscovery' reflected a lack of information available for sharks in PNG, rather than the outcome of a directed study to find an elusive and rare species.

During recent surveys of the Western Province in 2014, which aimed to broadly survey sharks and rays, another key finding from the fisheries catches were records of sawfishes. Sawfish are considered the most threatened family of elasmobranchs, with all species listed as Critically Endangered or Endangered on the IUCN Red List (Dulvy et al. 2014, IUCN 2016). It has been suggested by Dulvy et al. (2016) that sawfish are now extinct in at least 20 countries, with the dwarf sawfish *Pristis clavata* considered Possibly Extinct in PNG. The status of sawfish in PNG is largely unknown, both in a historical and contemporary sense, due to the paucity of detailed information on shark and ray catches and observations in PNG. New Guinea has, however, been suggested as possibly being a regionally significant area for sawfishes, and the need to determine local status has been previously highlighted (Kyne & Simpfendorfer 2014).

The area surveyed in Western Province near the mouth of the Fly River is prime sawfish habitat, consisting of mangrove-lined shores with numerous freshwater outflows and high turbidity (Last & Stevens 2009). However, it was surprising to find records of all 4 sawfish species known to occur in this region from the fisheries catches in only a 1 wk survey. The 4 species known to occur in the Australasian region, and more widely the Indo-Pacific, are narrow sawfish *Anoxypristis cuspidata*, dwarf sawfish *Pristis clavata*, largetooth sawfish *P. pristis*, and green sawfish *P. zijsron* (Last & Stevens 2009).

This paper provides a comprehensive review of published and unpublished literature on sawfish records in PNG and holdings in museum and fisheries collections. It also provides data on opportunistic records of sawfish obtained as part of a 4 yr project investigating shark and ray fisheries and biodiversity in PNG.

MATERIALS AND METHODS

Literature records

A comprehensive literature review was undertaken, based on unpublished reports and surveys, to find as many records of sawfish in PNG waters as possible. All literature that included a reference to sawfish in PNG are summarised in Table 1. Note that in most cases, the identity of the species could not be accurately determined based on the information available. Identification of species in particular regions is only as accurate as the literature available to researchers.

In PNG, the main faunal guide available to researchers in the 1960s through the 1980s was Munro's (1967) 'Fishes of New Guinea'. In this book, 2 species of sawfish are listed: *Pristiopsis microdon* and *P. leichhardti*, both of which are synonyms of *Pristis pristis*. Thus, the 3 other sawfish species were not represented in this guide. As a result, subsequent literature typically only makes reference to these 2 species, with most literature sources (that provide a species name) only listing *P. microdon*. A number of literature sources simply list the common name of 'sawfish' or 'sawshark', which are all considered to refer to pristids since no species of sawsharks (family Pristiophoridae) occur in PNG waters. As a result, it is not possible to accurately determine which sawfish species were represented in most of the literature sources. Filewood (1973) provided the first comprehensive key to the sharks and rays occurring in PNG, but this was never published. This key included 3 sawfish species, *Platypristis cuspidatus* (= *Anoxypristis cuspidata*), *Pristis zijaron* (= *Pristis zijsron*) and *P. microdon* (= *P. pristis*).

In addition to literature records, attempts were made to contact authors of publications with brief mention of sawfish records, along with those who visit areas of likely sawfish occurrence, e.g. fishing lodges.

Specimen records

Some literature sources also relate to specimens collected and deposited in museum collections, e.g. Herre (1936), Roberts (1978) and Allen et al. (1992). These records are particularly important in that the species involved can be confirmed. A comprehensive list of all sawfish specimens collected from PNG waters and deposited in the various museum collections around the world was established, and is summarised in Table 2. Where possible, images and measurements were obtained from the specimens (whole or rostrum) to verify their identity. A few records could be accurately linked to a specific literature source. One of the museum collections, the Kanudi Fisheries Research Station (KFRS), deserves a specific mention due to its complicated history. It is estimated that more than 80% of the shark and ray specimens housed in the original collection in Kanudi

Table 1. Literature, electronic resource and personal communication records of sawfish from Papua New Guinea. Arranged in chronological order with personal communication records at bottom. Location contains a map reference number (where possible) which refers to localities in Fig. 1. TL: total length; (–) not measured. When species could not be determined, a question mark is used. USNM: United States National Museum

Source	Location [map reference]	Notes	Size (TL; mm)	Species
Herre (1936)	Korogu, Sepik River [45]	*Pristis perotteti* common in Sepik, very well known, many rostra seen (CAS SU 41013 and 41014)	–	*Pristis pristis*
Munro (1958)	Korogu, Sepik River [45]	*Pristis microdon* based on Herre (1936) records	–	*P. pristis*
Munro (1964)	Northern and southern New Guinea	Only 2 sawfish treated in guide: *Pristiopsis leichhardti* (southern) and *P. microdon* (northern)	–	*P. pristis*
Hinton (1967)	Kapogere, Kemp Welch River [38]	Gillnet catch (8 Sep 1967): 1 *P. microdon* caught in clear water	967	?
Munro (1967)	Laloki River [35] and other southern rivers	*P. leichhardti*	–	*P. pristis*
	Sepik River [44–46]	*P. microdon*	–	*P. pristis*
Glucksman (1969)	Baboa mission, Lake Murray [8 or 9]	Gillnet catch (28 Nov 1969): a *Pristlepis microdon* caught	–	*P. pristis*
Aufenanger (1970)	Sepik River [44–46]	‘Occasionally even huge saw fishes and sharks swim up and down this great watercourse’	–	?
Rapson & McIntosh (1971)	Iokea to Orokolo Bay, Gulf of Papua [31]	Sawfish recorded in prawn trawl surveys in Feb 1963	–	?
Dept of Agriculture, Stock and Fisheries (1972)	New Bosnean Camp, Ramu River [43]	Gillnet catch (18 Aug 1972): 1 sawfish	1400	?
	Asau village, Ramu River [42]	Gillnet catch (19 Aug 1972): 1 sawfish	550	?
	Jubin village, Ramu River [42]	Gillnet catch (21–22 Aug 1972): 3 sawfish	550 and 2200	?
	Akurea village, Ramu River [42]	Gillnet catch (23 Aug 1972): 1 sawfish	800	?
	Bangapela village, Ramu River [41]	Gillnet catch (28 Aug 1972): 1 sawfish	1425	?
	Bulna or Borewa village, Ramu River [41]	Gillnet catch (31 Aug 1972): 9 sawfish	1200–1400	?
Anonymous (1973)	Mouth of Morehead River [20]	Gillnet catches (12–14 Mar 1973): 1 *P. microdon* and many *P. clavata*	–	*P. pristis*, *P. clavata*
	Mouth of Bensbach River [18]	Gillnet catches (12–14 Mar 1973): 11 *Pristis clavata* caught	–	*P. clavata*
Filewood (1973)	Papua New Guinea	*Platypristis cuspidatus* common		*Anoxypristis cuspidata*
		Pristis zijaron rare		*Pristis zijsron*
		Pristis microdon present		*P. pristis*
Berra et al. (1975)	Laloki River [35]	Gillnet catches (29 May to 11 Jun 1970): 5 *P. microdon* caught	830–1635	*P. pristis*
Haines (1977)	Purari River and delta [25–28]	*P. microdon* present	–	?
Roberts (1978)	Middle Fly River [2, 4–5, 8, 11–12]	*P. microdon* common in Middle Fly (USNM 217001 and 217002); likely reproduces in Middle Fly due to presence of neonate	809 and 916	?
Haines (1978/1979)	Purari delta [25–28]	See Haines & Stevens (1983)	–	?
Haines (1979)	Purari River and delta [25–28]	*P. microdon* common (5–10 catch^{-1}) in coastal areas [28], rarer in upstream waters [25, 26]	500–3540 (n = 50)	?
	Kikori River [23, 24]	*P. microdon* common (1–4 catch^{-1}) in coastal areas and side branches of river		?
Haines & Stevens (1983)	Purari–Kikori delta area [24, 27–30]	Survey of fishing villages Feb 1976: grouped category with sharks	–	?
Chapau & Opnai (1983)	Western Gulf of Papua [22]	Taiwanese drift gillnet surveys (Oct, Dec 1976 and Jan 1977): *Pristiopsis microdon* 2.8% of catch by number, 30% by weight; 57 ind. in Dec and 189 in Jan	–	?
		Commercial data in 1981 and 1982: *P. microdon* 5% of catch by weight	–	?
Coates (1983a)	Sepik River upstream to at least Ambunti [44]	Not caught but no doubt occurs in river channels with rostra seen in many villages		*P. pristis*
Coates (1983b)	Magendo and Imbuando, Sepik River [46]	Villagers sometimes catch in bottom gillnets in shallow waters	–	?
Frielink (1983)	Delta of the Gulf Province [23–30]	One of top 11 species groups in fisheries catches	–	?

(Continued on next page)

Table 1 (continued)

Source	Location [map reference]	Notes	Size (TL; mm)	Species
Coates (1987)	Sepik River [44–46]	*P. microdon* is rare and likely breeds in the upper river	–	*P. pristis*
Osborne (1987)	Papua New Guinea	*P. microdon* widespread in all rivers	–	*P. pristis*
Allen & Coates (1990)	Sepik River [44–46]	Not caught but local fishers possessed dried rostra	–	*P. pristis*
Smith & Hortle (1991)	Fly River	*P. microdon* recorded in Fly	–	*P. pristis*
Taniuchi et al. (1991), Taniuchi & Shimizu (1991), Mizue & Hara (1991), Ishihara et al. (1991), Watabe (1991), Tanaka (1991)	Magendo 1–3 and Angoram, Sepik River [46]	Gillnet catches (3–8 Sep 1989) *P. microdon:* 8 males and 4 females caught (salinity 0–2)	778–870 (M) 794–869 (F)	*P. pristis*
	Jagita, Bobowa and Miwa in Lake Murray [8–9]	Gillnet catches (17–23 Sept 1989) *P. microdon:* 12 males and 11 females caught (salinity 0–1)	925–2473 (M) 970–1279 (F)	*P. pristis*
	Oriomo River Estuary [21]	Gillnet catches (24–25 Sep 1989): 1 male *P. microdon* and 1 male *A. cuspidata* caught (salinity 20–25)	3611 (*P. microdon*) 1182 (*A. cuspidata*)	*P. pristis*, *A. cuspidata*
Allen et al. (1992)	Bunapas, Ramu River [43]	Not caught but rostra recorded (e.g. CAS 63666)	–	*P. pristis*
Coates (1993)	Sepik and Ramu Rivers [40–46]	*P. microdon* present in both rivers	–	*P. pristis*
Smith & Bakowa (1994)	Floodplains of Upper and Middle Fly River [1–7]	*P. microdon* caught	–	*P. pristis*
Burton (1995)	Mipan village, Middle Fly [3]	*P. microdon* previously caught but listed by villagers as absent from area due to overfishing	–	*P. pristis*
	Wanga–Wanga, Middle Fly [7]	One sawfish caught at Obo in 1994, none seen recently	–	?
Hyslop (1996)	Lower Angabanga River [32–33]	*P. microdon* recorded from seine net catches in lower, non-tidal reaches	–	?
Powell & Powell (1999)	Maripora River, Bougainville [58]	*P. microdon* recorded at 2 lower reach locations between 1975 and 1988	1000–1200	*P. pristis*
Swales et al. (1999)	Fly and Strickland River [5–7, 10]	*P. microdon* recorded in gillnet catches and in one rotenone site	–	*P. pristis*
Jenkins (2000)	Lake Lalili, West New Britain [50]	Potentially unharvested populations of *P. microdon* found	–	*P. pristis*
Swales et al. (2000)	Fly River [1, 5, 7, 14–16]	*P. microdon* caught in gillnets	–	*P. pristis*
Hitchcock (2002)	Middle Bensbach River [19]	One *P. microdon* caught in gillnet	–	*P. pristis*
Swales (2002)	Upper and Middle Fly River	*P. microdon* becoming less frequent in catches in main channel sites	–	*P. pristis*
Hitchcock (2004)	Middle Bensbach River [19]	*P. microdon* caught by local fishers (see Hitchcock 2002) and fins traded with Indonesian merchants at Sota	–	*P. pristis*
Storey et al. (2009)	Middle Fly River	Once common in Middle Fly but not seen upstream of Everill Junction [7] for past 15 yr; still common downstream and in Strickland River	–	*P. pristis*
Loop (2015)	Wakunai, Bougainville [56]	A large sawfish caught in net by fishers in a canoe in June 2015	>4000	*P. pristis*
Personal communications				
Garrick Hitchcock, Arafura Consulting, Aug 2016	Balamuk village, Bensbach River [19]	Two sawfish caught in gillnet (16 Oct 1997)	–	*P. pristis*
	Wando village, Bensbach River [19]	Sawfish rostra kept as decorative items in many houses in area	–	*P. pristis*
Garry Barmby, Angling Adventures, Aug 2016	Lake Murray [8–9], Bensbach [20] Rivers	No sawfish observed in at least the last 4 yr [18–19] and Morehead	–	–
Kevin Atana, NFA provincial officer, Buka, Oct 2016	Nissan Atoll [55]	Large sawfish observed on atoll whilst free diving (~10 yr prior)	–	?
Riccard Reimann, Baia Sportfishing, Jul 2016	Mouths of Via, Pandi and Toriu Rivers, West New Britain [51–52]	Observed near mouths of rivers between May and Nov leading up to New Moon and just before whitebait enter rivers	~3000–3658 (10–12 ft)	?
Ray Moore (retired), Jul 2016	Daru region [21] and surrounds	In 1970–1980: *P. microdon* most common,	–	*P. pristis*,
	Lake Murray [8–9]	One *P. microdon* caught in 1972 Bensbach River to Gulf; *P. zijsron* rare, only in coastal waters; *Anoxypristis cuspidata* only in coastal waters	~5000 (16 ft 5 in)	*P. pristis* *P. zijsron*, *A. cuspidata*

were lost or destroyed between 1998 and 2002. The remains of the collection is now housed at the University of Papua New Guinea in Waigani, Port Moresby. A large number of sawfish specimens were among those lost or destroyed (see footnote in Table 2).

Recent records

Records of sawfish from fisheries catches were collated from data obtained during an intensive project on sharks and rays in PNG which commenced in 2014. The PNG National Fisheries Authority (NFA) deployed observers on 7 separate prawn trawl trips in the Gulf of Papua between June 2014 and September 2015. Observers recorded all sharks and rays caught during trawl activities and obtained basic data such as species, size, sex and, where possible, maturity stage. Additionally, coastal fisheries catches were examined during a series of artisanal fisheries survey trips, with sawfish recorded during surveys of Daru and Katatai (October 2014; map reference 21 in Fig. 1), Bougainville (October 2015) and Milne Bay (March 2016).

Dried fins were examined at the local fish buyers during artisanal surveys (see also White et al. 2015)

Table 2. Sawfish from Papua New Guinea in various museum collections around the world. Museum abbreviations follow the international standard codes (see Fricke & Eschmeyer 2016). Numbers in square brackets are references to locations in Fig. 1. Sizes are given in total length (TL) or standard length (SL); TRL: total rostral length; ?: unknown whether this was a whole specimen or only rostrum; –: no data available

Registration or field no.	n	Part	Date	Locality [map reference]	TRL (mm)	Size (mm)	Sex
Anoxypristis cuspidata							
FUMT–P10855	1	Whole	24 Sep 1989	Oriomo River Estuary [21]	–	TL: 1182	M
KFRS E028[a]	1	?	Oct 1963	Hall Sound [34]	–	–	–
KFRS E142[a]	1	?	Jun 1964	Yule Island [34]	–	–	–
KFRS E166[a]	3	?	Aug 1965	S of Ramu River mouth [43]	–	–	–
KFRS E191[a]	5	?	Dec 1965	Darapap area [47]	–	–	–
KFRS E238[a]	1	?		N of Yule Island [34]	–	–	–
KFRS E375[a]	1	?	29 Mar 1969	Yule Island [34]	–	–	–
KFRS E394[a]	1	?	20 Dec 1969	Panaroa River [28]	–	–	–
KFRS E404[a]	1	?	7 Apr 1970	Bootless Bay [37]	–	–	–
KFRS E427[a]	2	?		Daru [21]	–	–	–
KFRS unreg	1	Whole	–	Nigoherm Islands [48]	–	TL: 570	F
10/2000 (in Faria et al. 2013)	1	Rostrum	Oct 2000 or earlier	Gulf of Papua	–	–	–
Pristis clavata							
KFRS E205[a]	1	?	Feb 1966	Alele River mouth [30]	–	–	F
KFRS E221[a]	1	?	14 Feb 1966	Alele River [30]	–	–	–
KFRS E224[a]	3	?	13 Mar 1966	Port Romilly [27]	–	–	2F, 1M
KFRS E236[a]	1	?	12–13 Mar 1966	Port Romilly [27]	–	–	–
KFRS E237[a]	1	?	22 Mar 1966	N of Yule Island [34]	–	–	–
KFRS E372[a]	1	?	Mar 1966	Alele River [30]	–	–	–
KFRS E428	1	Rostrum	–	Daru [21]	178	TL: ~890	–
Pristis pristis							
AMS I 30207–001[a]	1	?	Aug 1988	Magendo, Sepik River [46]	–	TL: 784	–
AMS IB. 2854	1	Rostrum	6 Aug 1952	Laloki River, near Bomana [35]	–	SL: 735	–
CAS 63666	2	Rostra	18 Oct 1987	Bunapas, Ramu River [43]	–	–	–
CAS SU 41013	1	Rostrum	23 May 1929	Korogu village, Sepik River [45]	–	–	–
CAS SU 41014	1	Rostrum	23 May 1929	Korogu village, Sepik River [45]	–	–	–
FUMT–P10851	1	Whole	3 Sep 1989	Magendo 3, Sepik River [46]	–	TL: 801	M
FUMT–P10854	1	Whole	17 Sep 1989	Miwa, Lake Murray [9]	–	TL: 970	F
KFRS E024	1	Rostrum	Oct 1963	Hall Sound [34]	1270	TL: ~5292	–
KFRS E025[a]	1	?	Oct 1963	Hall Sound [34]	–	–	–
KFRS E026A	1	Rostrum	27 Jun 1964	Vanapa River [35]	194	TL: ~808	–
KFRS E026B	1	Rostrum	27 Jun 1964	Vanapa River [35]	203	TL: ~846	–
KFRS E027A	1	Rostrum	Aug 1964	Laloki River [35]	225	TL: ~938	–
KFRS E027B[a]	1	?	Aug 1964	Laloki River [35]	–	–	–
KFRS E032A	1	Rostrum	Jun 1964	Yule Island [34]	242	TL: ~1008	–

(Continued on next page)

Table 2 (continued)

Registration or field no.	No.	Part	Date	Locality [map reference]	TRL (mm)	Size (mm)	Sex
KFRS E032B	1	Rostrum	Jun 1964	Yule Island [34]	263	TL: ~1096	–
KFRS E092[a]	4	?	Dec 1962	Orangerie Bay [39]	–	–	–
KFRS E256[a]	1	?	–	Warangoi River [54]	–	–	M
KFRS E278	1	Rostrum	–	?	242	TL: ~1008	–
KFRS E380[a]	1	Embryo	Nov 1969	Kairuku [34]	–	–	–
KFRS E418[a]	1	?	19 Dec 1970	Aiome, Ramu River [40]	–	–	–
KFRS E429A	1	Rostrum	–	Oriomo River [21]	292	TL: ~1217	–
KFRS E429B	1	Rostrum	–	Oriomo River [21]	237	TL: ~988	–
KFRS unreg PNG232	1	Whole	21 Oct 2007	Sapuka, Fly River [13]	–	TL: 870	M
QM I 3686	1	Rostrum	–	?	–	–	–
QM I 3687	1	Rostrum	–	?	–	–	–
USNM 217001	1	Whole	27 Nov 1975	Wam River, swampy lagoons of the Middle Fly [6]	–	TL: 809	F
USNM 217002	1	Whole	6 Dec 1975	Side channel of Strickland 4 km downstream from Massy Bakers Junction [11]	–	TL: 916	M
ZMB 14507	1	Rostrum + parts	1896 or 1899	Ramu River [40–43]	225	TL: ~938	–
ZMB 32538	1	Rostrum	Early 1900s	Bismarck Archipelago	1030	TL: ~4292	–
ZMB 33545	1	Whole	Aug 1913	'Tschessbandai', west of Korogu, Middle Sepik [45]	–	TL: ~700	F
ZMB 33553	1	Rostrum	–	New Guinea	273	TL: ~1138	–
3/1998 (in Faria et al. 2013)	1	Rostrum	Mar 1998 or earlier	Gulf of Papua	–	–	–
12/1999 (in Faria et al. 2013)	3	Rostra	Dec 1999 or earlier	Sepik River [44–46]			
Unregistered (in Seeadler Hotel)	1	Rostrum	–	Seeadler Harbour, Manus [49] (genetic sample # 180758)	790	TL: ~3292	–
Unregistered (in Rabaul Hotel)	1	Rostrum	–	Rabaul Hotel, Rabaul [53]	~1200	TL: ~5000	–
Pristis zijsron							
CAS SU 40592	1	Rostrum	May 1929	Sepik River [44–46]	409	TL: ~1515	–
KFRS E049[a]	1	?	May 1965	Yule Island [34]			
KFRS E378	1	Rostrum	May–Jul 1968	Balimo area [17]	285	TL: ~1056	–
KFRS E411[a]	1	?	8 May 1970	Bootless Bay [37]			
KFRS unreg (200781)	1	Rostrum	–	Probably either KFRS E049 or E411 above	880	TL: ~3259	–

[a] Specimens are considered lost

and from the larger fish buyers in Port Moresby. Key standard morphological measurements of first dorsal (length, height, anterior margin) and caudal (dorsal margin) fins were taken. Tissue samples were taken from all dried fins and DNA barcoding was employed to determine the species involved. DNA barcoding using the *COI* gene follows the methodology provided in White et al. (2015). Since sawfish dorsal fins are similar in size and shape, any dorsal fins that were found to be sawfish needed to be matched into pairs and with a caudal fin (if present) to avoid duplication of numbers in the dried fin batches. For sawfish fins, morphometric measurements were used to estimate total length of the individual by using data obtained from museum specimens in the CSIRO Australian National Fish Collection and measurements in Wallace (1967) and Faria et al. (2013). The proportions used to calculate these lengths are provided in Table 3. For dorsal fins, length was considered the most accurate measurement, with dorsal fin height in particular producing much larger estimated sizes, especially for *A. cuspidata*. When only dried sawfish rostra were observed, the total rostral length (TRL) of each rostrum was taken and the total length (TL) estimated using the TRL/TL morphometric data presented in Whitty et al. (2014).

All recent sawfish records are summarised in Table 4.

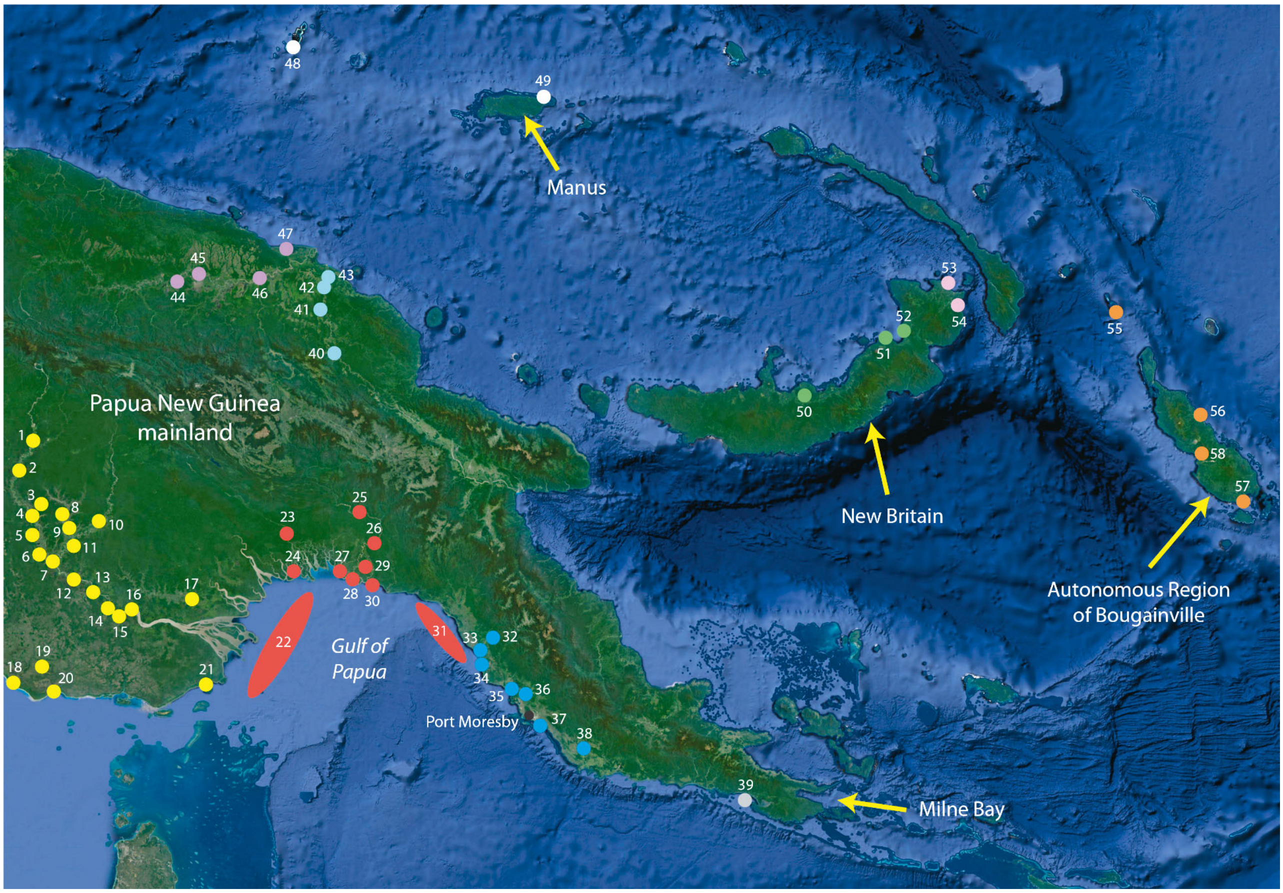

Fig. 1. Locations where sawfish have been recorded in Papua New Guinea. Each numbered reference point corresponds to the map reference in Tables 1, 2 & 4. Provinces (colour of points): Western (yellow; 1–21), Gulf (red; 22–31), Central (blue; 32–38), Milne Bay (grey; 39), Madang (cyan; 40–43), East Sepik (purple; 44–47), Manus (white; 48–49), West New Britain (green; 50–52), East New Britain (pink; 53–54) and the Autonomous Region of Bougainville (orange; 55–58). Base image © NASA, TerraMetrics, Google Earth

RESULTS

Historical records

Table 1 summarises all literature records sourced during this study, including both published and unpublished papers, reports and trip summaries. The first published records of sawfish in PNG were from Herre (1936), who recorded *Pristis perotteti* (= *P. pristis*) from the Sepik River in May 1929 during the Crane Pacific Expedition. Two *P. pristis* and 1 *P. zijsron* rostra were collected by Herre and were deposited in the Californian Academy of Sciences ichthyological collection (see Table 2). Interestingly, only the 2 *P. pristis* jaws were mentioned in Herre (1936) as having been collected from Koragu (= Ko-

Table 3. Number of sawfish specimens used (n) and mean (±SE) proportions of first dorsal fin length (D1L), first dorsal fin height (D1H), first dorsal fin anterior margin (D1A) and dorsal caudal margin (DCM) to total length (TL) for the 4 sawfish species

	D1L/TL		D1H/TL		D1A/TL		DCM/TL	
	n	Mean (±SE)	n	Mean (±SE)	n	Mean (±SE)	n	Mean (±SE)
Anoxypristis cuspidata	1	0.09	1	0.08	1	0.10	1	0.13
Pristis clavata	4	0.10 (±0.000)	5	0.06 (±0.002)	5	0.09 (±0.001)	5	0.14 (±0.001)
Pristis pristis	3	0.10 (±0.002)	13	0.07 (±0.001)	9	0.10 (±0.003)	10	0.16 (±0.003)
Pristis zijsron	1	0.08	–	–	1	0.07	1	0.13

Table 4. Records of sawfish in Papua New Guinea collected as part of an ongoing shark and ray fisheries project. Estimated total length (TL) from caudal and dorsal fins based on proportions in Table 3, where fins were genetically identified. Numbers in square brackets are references to locations in Fig. 1. TRL: total rostral length. GoP: Gulf of Papua

Registration or field no.	Notes	Date	Locality [map reference]	Depth (m)	TRL (mm)	TL (mm)	Sex
Anoxypristis cuspidata							
KFRS unreg. 100616	Whole, prawn trawl	27 Aug 2015	GoP: 8°18′39″S, 146°11′27″E [31]	12–14	–	1330	F
Not retained: 220334	Dried rostrum, gillnet	2014	Katatai village: 9°1′15.1″S, 143°20′30.6″E [21]	<5	780	~3000	–
Not retained: 220344	Dried rostrum, gillnet	Aug 2014	Oriomo River Estuary: 9°2′14.7″S, 143°11′10.6″E [21]	<5	870	~3360	–
Not retained: 100706	Whole, prawn trawl	18 Sep 2015	GoP: 8°8′48″S, 146°1′41″E [31]	11–13	–	1420	F
Not retained: 110053	Whole, prawn trawl	9 Dec 2014	GoP: 8°8′58″S, 144°27′2″E [22]	19–20	–	1020	F
Not retained: 110116	Whole, prawn trawl	14 Dec 2014	GoP: 8°2′8″S, 144°38′33″E [22]	22	–	2150	F
Not retained: 010500	Whole, prawn trawl	27 Aug 2015	GoP: 8°20′14.5″S, 146°12′31.7″E [31]	12–14	–	1280	M
Not retained: 010531	Whole, prawn trawl	29 Aug 2015	GoP: 8°15′19.5″S, 146°7′4.6″E [31]	14–16	–	1880	M
Not retained: 010779	Whole, prawn trawl	4 Sep 2015	GoP: 8°2′36.3″S, 145°43′39.9″E [31]	14–16	–	1280	M
Not retained: 010788	Whole, prawn trawl	7 Sep 2015	GoP: 8°1′12.7″S, 145°43′16″E [31]	12–14	–	1460	M
Not retained: 010843	Whole, prawn trawl	19 Sep 2015	GoP: 8°5′51.2″S, 145°55′11.2″E [31]	9–10	–	1450	F
Not retained: 100029	Whole, prawn trawl	14 Jun 2014	GoP: 8°8′19.2″S, 145°57′4.2″E [31]	14–18	–	–	–
Not retained: 100030	Whole, prawn trawl	14 Jun 2014	GoP: 8°8′19.2″S, 145°57′4.2″E [31]	14–18	–	–	–
Not retained	Dried rostrum, gillnet	2014	Dahuni village, Mullins Harbour [39]	–	730	~2960	–
Not retained: 210324	Dried rostrum, gillnet	2014	Yule Island [34]	–	770	~2810	–
Not retained: 250152, 250153	Dried dorsal fins	Jan to Mar 2016	Milne Bay Province (probably outer islands)	–	–	~3040–3300	–
Not retained (n = 14)	Dried caudal fins	Mid 2015	Unknown, probably GoP	–	–	~820–1120	–
Not retained (n = 5)	Dried caudal fins	Mid 2015	Unknown, probably GoP	–	–	~1200–1420	–
Not retained: 180650	Dried caudal fin	Mid 2015	Unknown, probably GoP	–	–	~1940	–
Not retained: 180603	Dried dorsal fin	Mid 2015	Unknown, probably GoP	–	–	~3050	–
Not retained: 220380, 220402, 220414	Dried caudal and 2 dorsal fins	Sep or Oct 2014	Daru to Katatai area [21]	–	–	~1570	–
Not retained: 220378	Dried caudal fin	Sep or Oct 2014	Daru to Katatai area [21]	–	–	~2090	–
Not retained: 220377, 220363	Dried caudal and 1 dorsal fin	Sep or Oct 2014	Daru to Katatai area [21]	–	–	~2160	–
Not retained: 220419	Dried caudal fin and 2 dorsal fins	Sep or Oct 2014	Daru to Katatai area [21]	–	–	~4100	–
Not retained: 210304	Dried caudal fin	2014	Unknown, probably GoP	–	–	~4480	–
Not retained: 210306	Dried caudal fin	2014	Unknown, probably GoP	–	–	~1040	–
Not retained: 210307	Dried caudal fin	2014	Unknown, probably GoP	–	–	~1340	–
Not retained: 210309	Dried caudal fin	2014	Unknown, probably GoP	–	–	~1630	–
Not retained: 210311	Dried caudal fin	2014	Unknown, probably GoP	–	–	~2090	–
Not retained: 210314, 210308	Dried caudal and 1 dorsal fin	2014	Unknown, probably GoP	–	–	~2390	–
Not retained: 210512	Dried caudal fin	2015	Unknown, probably GoP	–	–	~970	–
Not retained: 210525, 210527	Dried dorsal fins	2015	Unknown, probably GoP	–	–	~1840	–
Not retained: 210520	Dried dorsal fin	2015	Unknown, probably GoP	–	–	~2820–3120	–

(Continued on next page)

rogu), 346 km from the sea. Given that *P. zijsron* is normally found in coastal waters and not far into rivers (Stevens et al. 2005), the *P. zijsron* rostrum (CAS SU 40592) was possibly collected or acquired near the mouth of the Sepik River. Alternatively, it could have been collected from near Madang and Sek, the only other 2 PNG localities sampled during this expedition; however, Sepik River is hand written on the rostrum itself.

The first detailed list of the fishes of New Guinea (Munro 1958) included *Pristis microdon* based on the Korogu record of Herre (1936). Munro (1964) listed 2 species of sawfish, *Pristiopsis leichhardti* and *Pristiopsis microdon*, which occurred in southern and northern New Guinea, respectively. The comprehensive guide to fishes in Munro (1967) included treatments for these 2 species, both of which are now synonomised with *Pristis pristis*. The treatments for both species refer to the anteriorly placed first dorsal fin (relative to the pelvic fins) which confirms they both refer to *P. pristis*. The separation of the 2 'species' was originally based on the free rear tip of the second dorsal fin reaching the caudal fin in *P. leichhardti* or well separated in *P. microdon* (see Munro 1967). It is possible this observation was an artefact of comparing different size classes (with damaged free rear tips in some specimens) or intraspecific variation.

Many of the literature sources examined include records of *P. microdon* in the catches (e.g. Hinton 1967, Glucksman 1969, Haines 1979, Chapau & Opnai 1983), but the identity of the species cannot be confirmed in most cases. In other sources, the catches included only reference to sawfish without specific species being mentioned (e.g. Rapson & McIntosh 1971, Anonymous 1972, Burton 1995).

Filewood (1973) produced the first detailed key to the elasmobranchs of PNG, but unfortunately this was never published and thus only used by those who had access to the few copies available. The key included the first mention of the species *Platypristis cuspidatus* (= *A. cuspidata*) and *Pristis zijaron* (= *P. zijsron*), as well as *P. microdon* (= *P. pristis*) but did not include *P. clavata*. Confidence can be placed on the identity of *P. zijsron* in Filewood (1973) as the key difference provided is the unequal spacing of the rostral teeth (i.e. wider spacing at the base and closer together at the tip), which is the key character for this species. The records of *P. cuspidatus* and *P. microdon* can also be confirmed from the information provided, i.e. origin of first dorsal opposite or behind pelvic origin versus well before. However, there is an error in one character difference in the key, with the lack of a distinct ventral caudal lobe attributed to *P. cuspidatus*.

Table 4 (continued)

Registration or field no.	Notes	Date	Locality [map reference]	Depth (m)	TRL (mm)	TL (mm)	Sex
Pristis clavata							
Not retained: 210383	Dried caudal fin	Sep or Oct 2014	Daru to Katatai area [21]	–	–	~1730	–
Not retained: 210302	Dried caudal fin	2014	Unknown, probably GoP	–	–	~3030	–
Pristis pristis							
Unreg. 200629	Dried rostrum, gillnet	Caught in 2015	Buin [57]: stored in fisheries office in Buka	–	720	~3000	–
Not retained: 100036	Whole, prawn trawl	15 Jun 2014	GoP: 8°5′9″S, 145°40′22.2″E [31]	16–23	–	3490	M
Not retained: 220343	Dried rostrum, gillnet	Sep or Oct 2014	Oriomo River Estuary: 9°2′14.7″S, 143°11′10.6″E [21]	<5	610	~2640	–
Not retained: 220382	Dried rostrum, gillnet	Sep or Oct 2014	Daru to Katatai area [21]	–	760	~3170	–
Pristis zijsron							
Not retained: 210303	Dried caudal fin	2014	Unknown, probably GoP	–	–	~4730	–
Not retained: 180627	Dried caudal fin	2015	Unknown, probably GoP	–	–	~4850	–
Not retained: 210508	Dried caudal fin	2015	Unknown, probably GoP	–	–	~4930	–
Not retained: 210528	Dried caudal fin	2015	Unknown, probably GoP	–	–	~4930	–
Not retained: 180623	Dried caudal fin	2015	Unknown, probably GoP	–	–	~5240	–
Not retained: 210507	Dried caudal fin	2015	Unknown, probably GoP	–	–	~6420	–
Not retained: 180601, 180631	Dried dorsal fins	2015	Unknown, probably GoP	–	–	~3900	–
Not retained: 220360, 220391	Dried dorsal fins	2014	Daru to Katatai area [21]	–	–	~2270	–

Depth of Agriculture, Stock and Fisheries (1973) was the first survey report to record more than one species of sawfish, with both *P. microdon* and *P. clavata* caught during gillnet surveys at the mouth of the Morehead River in Western Province. In this survey report, only a single *P. microdon* was recorded, but *P. clavata* was abundant at this location and at the mouth of the Bensbach River. Although *P. clavata* was reported to be abundant, it is not possible to confirm the identifications of these records. As these records could also refer to *A. cuspidata* or *P. zijsron*, this identification must be treated with caution.

It is important to note that in a number of studies, sawfish were recorded as being abundant in the catches or common according to villagers in the areas visited. For example, Haines (1979) found that sawfish were common in the Purari-Kikori delta region with between 5 and 10 ind. per catch in coastal areas of the Purari and 1 to 4 ind. per catch in coastal areas and side branches of the Kikori. Likewise, Roberts (1978) reported that *P. microdon* (= *P. pristis*) was common in the Middle Fly River.

Fisheries catches

The largest catch records of sawfish in the available literature are from the trial fishery surveys, which used Taiwanese drift gillnets in the Gulf of Papua in October and December 1976 and January 1977 (Chapau & Opnai 1983). During these trial surveys, *Pristiopsis microdon* (= *P. pristis*) accounted for 30.1% by weight and 2.7% by number of the total catch. In December 1976, 57 ind. were recorded with a combined weight of 4500 kg, and in January 1977, 189 ind. were recorded with a combined weight of 12 382 kg. These equate to an average weight per individual of 69 kg. The majority of the sawfish were caught in the shallower sets (7 to 15 m depth) near the mouth of the Fly River. The gillnets used in these surveys were 3440 m long and 14 m deep with 15.2 cm mesh (Chapau & Opnai 1983), thus touching the bottom at these depths. The identity of the species of sawfish involved is not possible to determine and likely consisted of multiple species in the total catch.

Subsequent commercial fishing commenced in mid-1980 with 5 Taiwanese drift gillnet fishing vessels operating through 1981, dropping to 2 vessels in 1982. The nets used by the commercial vessels were 9000 m long, 12 m deep with 17.8 cm mesh and were suspended 5 to 6 m below the surface (Chapau & Opnai 1983). The 1981 and 1982 commercial data showed total catches of 810 and 405 t, respectively, with *Pristiopsis* spp. comprising 5% of the catch by weight. This corresponds to about 60.7 t of sawfish caught during this period, which equates to ~880 ind. based on the average weight of 69 kg from the 1976/1977 survey data. No other data is available after this period, but drift gillnetting came under increasing scrutiny in the South Pacific in 1989 (Stewart 1990) and ceased in 1993 (Anas et al. 2000).

Sawfish are currently recorded in the bycatch of the prawn trawlers operating in the Gulf of Papua (see e.g. Table 4). Surveys to assess the viability of establishing prawn trawling in PNG commenced in the mid-1950s (Rapson 1955) and surveys in the mid-1960s showed there were commercial quantities of prawns in the Gulf of Papua. Rapson & McIntosh (1971) reported sawfish present in prawn trawls between Iokea and Orokolo Bay during surveys conducted in February 1963. The commercial Gulf of Papua fishery commenced in 1969 (Evans et al. 1995), and from 1990 to 2011 the number of vessels operating in this fishery ranged from 1 to 18 (mean: 9.8) (Liviko 2012). No previous detailed surveys have been undertaken on the prawn trawl bycatch, but sawfish are likely to be regularly caught in this fishery. In the current study, observer data was collected from 7 prawn trawl fishing trips in the Gulf of Papua between June 2014 and September 2015, representing 403 trawl shots and 1273 h of trawling. Observers recorded 1 *P. pristis* of 3490 mm TL and 11 *A. cuspidata* ranging from 1020 to 2150 mm TL (Table 4).

Coastal artisanal fisheries also catch sawfish. In the Middle Bensbach River, sawfish are caught by the Wartha people. The flesh is eaten locally and fins are sold to Indonesian merchants at Sota in West Papua (Hitchcock 2002). Customary cross-border trade is allowed under a treaty between PNG and Indonesia as long as traded goods are not prohibited in either country (Hitchcock 2002). However, according to Government Regulation of the Republic of Indonesia (Number 7) 'Concerning the Conservation of Plant and Animal Species' (www.profauna.net/id/regulasi/pp-7-1999-tentang-pengawetan-jenis-tumbuhan-dan-satwa), all species of the genus *Pristis* have been protected in Indonesia since 1999. Sawfish have also been reported to have been caught by villagers in the Sepik River (e.g. Coates 1983b), Ramu River (e.g. Allen & Coates 1990), the Purari-Kikori delta (e.g. Haines & Stevens 1983) and Bougainville (Loop 2015). During surveys of fishing villages in Daru and Katatai (Western Province) conducted in late 2014, all 4 species of sawfish were observed from gillnet catches (see Table 4). Examination of dried fins from fish buyers in Port Moresby found that sawfish fins were commonly present (see Table 4; based on genetic identifications), but catch details were not available and thus the records could have been from either trawl or coastal artisanal fisheries. Most recently, dorsal fins from a single *A. cuspidata* of ~3 m TL were recorded from a batch of dried fins examined in Alotau, Milne Bay Province (Table 4). These fins come into Alotau from across the Milne Bay Province so no precise location data could be obtained.

In total, 56 *A. cuspidata* were recorded in the current study, ranging in length from ~970 to ~4480 mm TL (Table 4). Two *P. clavata* were recorded with estimated lengths of ~1730 and ~3030 mm TL. Four *P. pristis* were recorded with lengths between ~2640 and 3490 mm TL and 10 *P. zijsron* were recorded with estimated lengths between ~2270 and ~6420 mm TL (Table 4). The largest individuals recorded for *A. cuspidata* and *P. zijsron* were based on dried fins, and the proportions used to estimate their total lengths (Table 3) were based on a single juvenile individual for each species. Thus, ontogenetic differences have not been taken into account and the estimates could be over- or underestimates.

Sawfish in collections

Specimens of sawfish collected from PNG deposited in the various biological collections around the world are compiled in Table 2. The oldest collected sawfish specimen from PNG is ZMB 14507; this record consists of the rostrum and cranium (jaw attached), stomach, and gills and scapulocoracoid of a ~938 mm TL *P. pristis*. The collector was Dr. Carl Adolf Georg Lauterbach, a famous botanist who led several expeditions to German New Guinea (northern PNG). He visited the Ramu River in both 1896 and 1899 (van Steenis Kruseman 1959), which is likely when this specimen was collected.

The majority of the KFRS sawfish specimens (i.e. 35 out of 48 presumed rostra) are no longer present in this collection and must be considered lost. They are still included in Table 2 as they represent important geographical and temporal records. Although the identification of the lost specimens cannot be confirmed, much of the collection was either collected or examined by W. Filewood in the 1960s and 1970s and thus identifications can be considered relatively accurate. Excluding the lost specimens, a total of 3 *A. cuspidata*, 1 *P. clavata*, 32 *P. pristis* and 3 *P. zijsron* were recorded in collections (Table 2). A number of the specimens were collected from locations where sawfish had not been previously recorded, e.g. Nigoherm Islands (Manus Province), Warangoi River (East New Britain), Aiome (Ramu River), Seeadler Harbour (Manus Island) and Balimo (Fly River delta).

DISCUSSION

Cultural significance

Sawfish hold cultural significance in various parts of PNG. Villagers along the Sepik River are said to believe that sawfish spirits 'will punish people who break fishing taboos by unleashing destructive rainstorms' (McDavitt 1996). Some Iatmul clans in the Middle Sepik River use sawfish rostra as a totem and decorated rostra form part of dance costumes. One such example of a decorated rostrum, deposited in Museum Victoria in Australia (Item X 32276), is a painted *Pristis pristis* rostrum collected from the Middle Sepik River in 1920 (Fig. 2). Another example is a

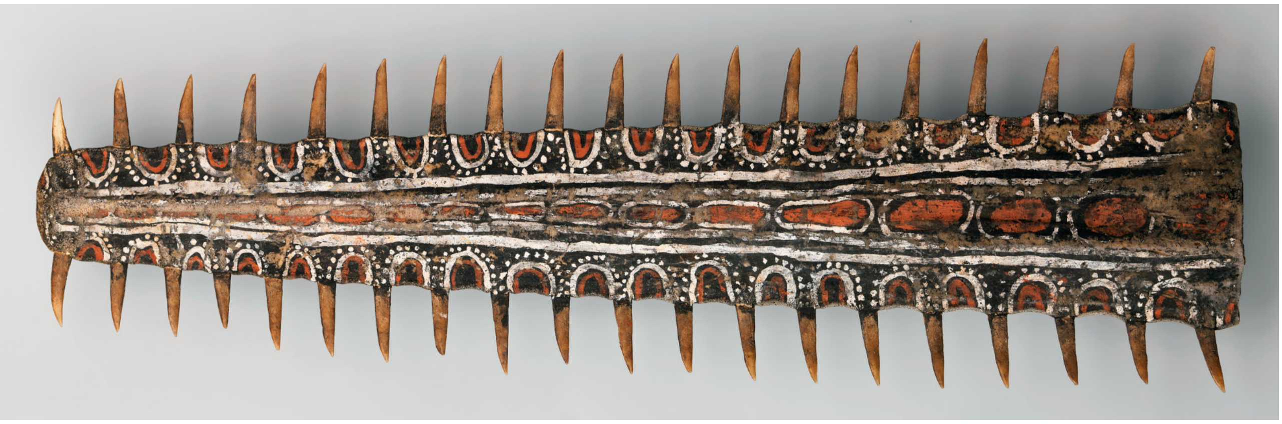

Fig. 2. Painted sawfish rostrum; part of a mask costume. Iatmul, Middle Sepik, Papua New Guinea. Acquired between 1915 and 1920. Australian War Museum Collection, on loan. Source Museum Victoria (X32276). Photograph by Jon Augier

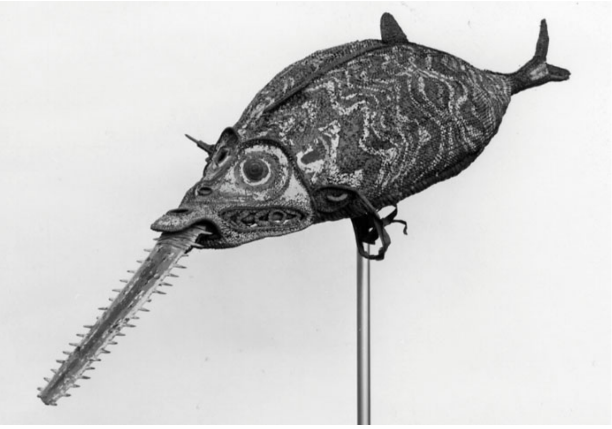

Fig. 3. Decorated rostrum which has been incorporated into a dance mask, deposited in the Ethnologisches Museum der Staatlichen Museen zu Berlin (Tanzmaske - Ident. Nr. VI 48057). Photo: Ethnologisches Museum Staatliche Museen zu Berlin

decorated rostrum which has been incorporated into a dance mask, housed at the Ethnologisches Museum der Staatlichen Museen zu Berlin (Tanzmaske – Ident. Nr. VI 48057) (Fig. 3). Sawfish are depicted on carvings in some locations, particularly in the Sepik River where sawfish heads are sometimes carved on shields (e.g. www.art-pacific.com/artifacts/nuguinea/shields/shieldso.htm) and masks (e.g. www.art-pacific.com/artifacts/nuguinea/sepikriv/sepiklow/sepiklow.htm). Sawfish rostra have also been used as weapons in PNG (McDavitt 1996). There are several records of swords made out of sawfish rostra where the base is cut down to form a handle (see Fig. 162 in Cowper 1906). Two similar such swords are also in the McGregor collection of the University of Aberdeen's Human Culture Collection (registration ABDUA 57939).

Evidence of declines in sawfish populations in PNG

The first indication of declines in sawfish in PNG was documented in Burton (1995), during an interview with the Mipan villagers in the Middle Fly River in March 1994. The interviewees stated that sawfish (local name 'katoga') are now absent from the area, which they attributed to overfishing, possibly from cross-border fishers. Swales (2002) reported that *P. pristis* is less frequently caught in main channel sites of the Upper and Middle Fly River. Storey et al. (2009) reported that although *P. pristis* was once common in the Middle Fly, it has not been seen upstream of Everill Junction for at least 15 yr. In contrast, it was still common downstream of Everill Junction and also in the Strickland River. Everill Junction is a major point of dilution for the mining run-off coming from the Ok Tedi mine site (see below), thus it is possible that sawfish are avoiding the areas upstream in the Middle Fly (Storey et al. 2009). However, increased gillnetting in the Middle Fly by local villagers and possibly Indonesian refugees is likely a major reason for these declines.

The Ok Tedi mine is one of the largest copper mines in the world and commenced operations in 1984. Due to the high rainfall in the area of operation, it is not possible to construct tailings dams; thus tailings and waste rock are discharged into the local waterways which feed into the Fly River system (Swales et al. 2000). This has led to increased riverbed aggradation resulting in the loss of habitat for fish. This, combined with elevated levels of dissolved and particulate copper from mining activities, has possibly affected sawfish in the Upper and Middle Fly River. Increase aggradation of the riverbed of up to 3 m in the Middle Fly River has likely also affected the prey items of *P. pristis*, including freshwater prawns *Macrobrachium* spp. (Storey et al. 2000).

In Lake Murray, Taniuchi et al. (1991) caught 23 *P. pristis* over a week-long period in 1989, but the species has not been seen in that area for at least the last 4 yr (G. Barmby pers. comm.). In the Sepik River, Herre (1936) reported sawfish as being common, but despite rostra seen in many villages, Coates (1983a) did not record sawfish in their survey catches and Coates (1987) considered sawfish rare in the Sepik River. However, it is not possible to determine whether there has been a decline in the Sepik River given the lack of substantiated data. Both of these river systems lack an estuary in contrast to the southern PNG rivers, thus limiting critical habitat for sawfish. One of the authors of this paper (R. R. Mana) observed many rostra, some over 1 m in length, at Marienburg (a Catholic mission close to Imbuando village) in the 1970s, but they have rarely been seen there since the 1980s.

The historical data presented in this study are thus important for highlighting the pre-mining range of sawfish in the Fly and other systems in PNG.

Size information

Last & Stevens (2009) reported that *A. cuspidata* attains lengths of 3500 mm TL, with records of 6000 mm TL doubtful. Two specimens were recorded in this study with estimated lengths exceeding 4000 mm TL (~4100 and ~4480 mm TL). Likewise, Last & Stevens (2009) stated that *P. zijsron* can attain lengths of at least 5300 mm TL, but was reported to have reached at least 7300 mm TL. Thus, the record of a ~6420 mm TL individual in this study represents one of the largest specimens recorded for this species. *Pristis clavata* was reported to attain lengths of 3100 mm TL (Last & Stevens 2009), close to the ~3030 mm TL individual recorded in this study. Although these estimates must be treated with caution (as they are based on fin measurements), it is interesting to note that for 3 of the 4 species of sawfish, very large individuals close to the maximum known sizes are still present in PNG waters.

Positive news for sawfish in PNG

Although there appear to have been documented declines of sawfish in some parts of PNG, it is not all bad news. The huge delta regions in the Gulf of Papua, e.g. Purari-Kikori and Fly, provide an expansive area of suitable habitat for sawfish in combination with a relatively low human population, and thus low overall fishing pressure. The recording of all 4 species of sawfish in artisanal catches during a week-long survey to Daru and Katatai (Western Province) in October 2014 provides evidence that the species are still common in that area, despite this being more heavily fished than much of the Gulf of Papua inshore region. Recent surveys also highlighted that *P. clavata* is still present, even though it had been considered possibly extinct from PNG (Dulvy et al. 2016). While that species once had a wide range in the Indo-West Pacific (Dulvy et al. 2016), the PNG observations in fact represent the only recent records of the species outside of Australia.

Jenkins (2000) reported possibly unharvested populations of *P. pristis* in Lake Lalili in West New Britain. They could also be distributed widely throughout the rivers of West New Britain. Sport fishers from the Baia Lodge in West New Britain reported seeing sawfish near river mouths leading up to the new moon between May and November, just before baitfish enter the rivers (R. Reimann pers. comm.). The southern coast of New Britain is poorly surveyed and could also represent an important area for sawfish.

Northern Australia is considered to be the last stronghold for the 4 species of sawfish that occur in the Indo-Pacific (Phillips et al. 2011, Dulvy et al. 2016). A detailed investigation into the current status of sawfish in PNG is urgently required to determine whether PNG may also be a stronghold for one or more sawfish species, not only regionally, but globally.

CONCLUSIONS

The information compiled and produced in this study provides a strong baseline from which more detailed studies of the status of sawfish in PNG can be undertaken. This study highlighted a number of critical areas for sawfish in PNG, in particular the Purari-Kikori delta system, Fly and Strickland Rivers (including Lake Murray), Western Province coastal areas (Katatai to mouth of Bensbach), Sepik and Ramu Rivers, Bougainville and West New Britain. These critical areas need to be thoroughly surveyed to determine the abundance and exploitation of sawfish in those areas. Obtaining detailed information on the cultural and socioeconomic value of sawfish to local communities is also paramount. Furthermore, improving the capacity for PNG researchers to develop and maintain a focused research effort on sawfishes will be crucial. Realising these aims will benefit the implementation of a global strategy for sawfish conservation (Harrison & Dulvy 2014).

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Artisanal shark fishing in Milne Bay Province, Papua New Guinea: biomass estimation from genetically identified shark and ray fins

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Our study is the first detailed examination of species composition using DNA COI barcoding of elasmobranchs from an artisanal fishery of Papua New Guinea. The study is the first in the region to provide biomass estimates based on species confirmation following examination of dried fins. Over 20 species of elasmobranchs were identified from 623 fins from the artisanal fishery in Milne Bay Province of PNG, with *Carcharhinus amblyrhynchos* and *Carcharhinus melanopterus* the most abundant species in the catches. Of concern, 21% of fins examined were from IUCN listed threatened species (Vulnerable or Endangered) with 8% of fins from the Endangered scalloped hammerhead (*Sphyrna lewini*). Following species identifications and use of species-specific length and weight extrapolations, we estimated over 9 t of elasmobranchs contributed to the fin batch. Importantly, the vast majority of the elasmobranchs in this batch were from immature animals. Genetic identification has an important role to play in the ongoing sustainable management of elasmobranchs in artisanal fisheries in PNG and more widely. However in the absence of ongoing genetic testing, recording the species (if known) at the time of catch is more achievable and would provide more robust data for fisheries managers in PNG over the longer term.

As apex predators which serve important and unique roles in the marine ecosystem[1–3], many elasmobranch species (i.e. Class Chondrichthyes, sharks and rays) and populations are under significant pressure from fisheries-driven declines[4]. Much of this decline is linked to the demand for shark fins[5–10]. Shark fin imports to Asia have been reported at up to 20 000 t per year[11] with Hong Kong previously considered the global centre of shark fin trade[5,9,10]. Recently, Hong Kong was surpassed by Thailand (from 2007 to 2011) as the world's largest exporter of shark fins[12] and currently, Indonesia is now considered the world's largest shark producer. Despite the increase in shark products, there is limited capacity to assess the sustainability of the shark landings and species compositions in these fin products[8,9,13]. This shark fin demand, coupled with the intrinsic biological attributes of some sharks and rays (i.e., including slow growth rates, low fecundity, late maturity and long gestation leading to relative lower productivity)[5,14,15] and increasingly high prices being paid for fins[16] puts significant pressure on elasmobranch species. As a result, a number of elasmobranch species are now subject to international trade restrictions under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)[17,18] (as at https://www.cites.org/eng/app/appendices.php, 28 March 2018). As of 2017, the sawfishes (Family Pristidae) are listed on CITES Appendix I, and 12 other elasmobranch species are listed in CITES Appendix II. Additionally, regional fisheries management organisations (e.g., Western & Central Pacific Fisheries Commission (WCPFC)) recently established conservation and management measures for several shark species, e.g., silky sharks *Carcharhinus falciformis* (https://www.wcpfc.int/doc/cmm-2013-08/conservation-and-management-measure-silky-sharks).

World-wide, stock assessments of elasmobranch species are severely hampered by the lack of species specific catch and trade data[3,5,6,12,19] compounded further by catches of sharks from illegal, unregulated and unreported (IUU) fisheries[5,20]. In developing countries, the stock assessments of elasmobranchs is further exacerbated

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when accurate morphological and species identifications of individuals (and shark products) are not attainable. Insufficient monitoring of landings, and fisheries (that are not well regulated) that target elasmobranch species, results in unknown or highly underestimated rates in west Pacific and Pacific countries[16,21]. The shark fin industry further compounds these aspects as most detached dried fins are difficult to identify to species level, they often lack diagnostic features[5,8,12,22] and there is generally no information kept with regards to the harvested species (even if known).

In the west Pacific country of Papua New Guinea (PNG), limited government resourcing and relatively large fishing territories, coupled with lack of species identification tools for elasmobranchs makes it challenging to quantify shark landings and fin catches more explicitly[16]. Furthermore, the combination of various shark fishing activities, including both managed larger scale fisheries (where sharks are taken as bycatch[23,24]) and localised, coastal (herein referred to as artisanal) small scale fishing activities that use small vessels, are largely unmanaged and are not well understood[16]) makes it difficult to quantify shark landings. The management of large scale shark fishing in PNG was previously governed by the National Shark Longline Management Plan, however following the WCPFC 2014 ban on the retention of silky shark, the shark fishery ceased operating[16]. In contrast, there are currently no national management arrangements in place for the artisanal fishery[16].

While FAO statistics demonstrate that PNG shark harvests are low when compared to other countries' estimates, based on official in-country data (informed by Local Level Government (LLG) information which provides some indication of locality), harvests are likely to be underestimated with shark fishing increasing dramatically over the last three decades[16,24,25]. Adding to this[16], while several shark species are vulnerable in PNG, local fishers also depend on shark fin for income. Information from the artisanal sector suggests that the Milne Bay Province of PNG, which is at the south eastern tip of mainland PNG, is a focal point for artisanal shark fishing activities[16] (although the province is not known as a nursery area). Artisanal fishers in the area are based primarily at the Louisiade Rural LLG of the Milne Bay Province and while species catches from this region of PNG have not previously been analysed in any detail, relatively high quantities of dried fins have been noted from this Province (i.e., between 2.1 t and 3.9 t per year in 2010–2014)[16]. Despite this, no national management arrangements exist for the capture and utilisation of shark in the province[16]. An opportunity therefore exists to provide better informed baseline data on the species compositions and catches of elasmobranch harvests in the Milne Bay Province through the application of accurate species identification and delineation of fins (from the artisanal fishery) to provincial shark fin buyers.

There are a number of tools and classification categories that can be used to help identify the species of origin of shark fins. In the Hong Kong and China markets, shark fins are delineated on the quality of the fin rays/needles and through distinguishing features of the dried fin (with up to eleven market categories in place for describing shark fins[5,12]). However, these product categories are market specific and not generally applicable for taxonomic species identifications or determination of species compositions. Stable isotope, infrared spectroscopy and electron microscopy analyses have also been used to examine the authenticity of dried shark fins (i.e., real dried fins, fake dried fins and artificially dried fins) although the species of origin of the fins cannot be determined with these methods[26]. There are now also various qualitative and analytical tools described in the literature[12,22] and from online websites (https://cites.org/eng/node/16695; https://cites.org/eng/prog/shark/isharkfin; http://www.sharkfinid.com/p/online-identification.html) that can be used for the morphological/taxonomic identification of shark fins. Nonetheless, in our PNG study, we found that these analytical tools were not 100% reliable for taxonomic species identifications, were not ideal or suitable for our use in some field circumstances and the morphological identification tools are often limited to certain species. We therefore infer the most accurate and robust method for species identification of elasmobranch fins (irrespective of source location) is DNA barcoding.

DNA barcoding of shark fins and/or the use of species-specific PCR primers for shark species identifications has been undertaken previously[3,5,8,27]. Barcoding utilises a highly reproducible automated DNA based identification method[28–33] which sequences the nucleotide composition of relatively short mitochondrial DNA (mtDNA) fragments. Typically, the cytochrome c oxidase subunit I (COI) gene (and other genes such as 16 S ribosomal RNA (16 S rRNA); mtDNA encoded NADH dehydrogenase 2 (ND2)) are used. Success depends on within species DNA sequences being more similar to those between species[31]. By matching a COI barcode sequence from a fin clip against a reference library (e.g., public repository of the Consortium for the Barcode of Life (BOLD, www.boldsystems.org32)), we can determine the shark species from which the fin was taken (based on low intra- but high inter-species diversity[28]). Given that several shark species have similar fins with respect to morphology, colour and size, DNA barcoding provides us with the only means to accurately identify the constituent species.

Accurate species identification of elasmobranch fins enables us to understand which species are being caught in the artisanal fishery in the Milne Bay Province and to what extent, as well as improving our knowledge of the biodiversity in the region. As part of a Commonwealth Scientific and Industrial Research Organisation (CSIRO)/Australian Centre for International Agricultural Research (ACIAR)/Papua New Guinea National Fisheries Authority (PNG NFA) research, we are utilising molecular technologies to provide fisheries managers with biodiversity information (and in many instances, baseline biological data) on various shark and ray species in PNG. In the CSIRO/ACIAR/PNG NFA research, we developed a barcode library for known elasmobranch species in the region. Herein we use this library to accurately identify the genetic species composition of elasmobranch fins from the artisanal fishery in the Milne Bay Province of PNG. While a number of recent shark fin papers have examined species characterisation and distribution in the region (e.g. from illegal fishing in Australian waters[27]; the Indonesian shark fishery[8]; Taiwan's ports, markets and customs detention[3,19]), this is the first barcoding study of any kind in PNG. This study is also one of the first to utilise genetic species identifications of fins to extrapolate to elasmobranch catch/biomass from an artisanal fishery.

Results

Out of the 623 individuals recorded in the artisanal sourced batch of fins from Asiapac (one of two licensed fish buyers in the Milne Bay Province), 557 fin samples were extracted and genetically analysed. The other 66 fins were identified to species based on morphology (from images) and colouration. While we ran some of our shark fin images through the iSharkFin application (https://cites.org/eng/prog/shark/isharkfin), we were not able to generate reliable species identifications and deemed it not fit for purpose for the PNG fins. Thus genetic species identification was undertaken on the bulk of the fins.

Genetic identifications. Amplification at the COI gene in 557 fins resulted in 55 samples not amplifying successfully in the first instance. As we were sequencing 96 samples per plate, DNAs had been normalised and we were aiming for moderate-throughput identifications, it was not cost effective to 'cherry pick' or repeat samples that did not amplify in the first instance. We did not further troubleshoot the DNA or PCR amplifications of those samples. Based on re-examination of images with subsequent genetic identifications obtained (see below), all but 7 of the 55 samples that did not amplify could be identified to species level; the remaining 7 were only identified as belonging to the family Carcharhinidae.

Following consensus sequence generation, BLAST comparisons and sequence quality control, elasmobranch species identifications based on COI sequences were obtained for 470 fins. In total, 22 species across eight genera and six families (Hemigaleidae, Carcharhinidae, Sphyrnidae, Pristidae, Rhinidae and Glaucostegidae) were genetically identified from the fins. Nineteen shark species and three ray species were recorded (Table 1). The Jukes-Cantor distance among the 22 species observed within PNG regional waters was 0.061 (se = 0.006), while the within species distance ranged from 0.000 ± 0.000 (e.g., *Galeocerdo cuvier*, *Carcharhinus sorrah*) to 0.009 ± 0.002 (*Negaprion acutidens*) (see Table 1).

There was a low level of genetic divergence observed in the Hemigaleidae, Carcharhinidae, Pristidae and Rhinidae individuals (0.000–0.002) while for the Sphyrnidae, only fins from *S. lewini* showed genetic variation (genetic divergence = 0.003). There were no genetic differences detected at the COI fragment screened in the *Sphyrna mokarran* or *Sphyrna zygaena* individuals in this study. The five Glaucostegidae individuals also showed genetic divergence (0.003).

Species compositions. Of the 22 species, the most commonly observed species (based on number of individuals) represented in the full sample of fins was the grey reef shark (*C. amblyrhynchos*) followed by blacktip reef shark (*C. melanopterus*), silky shark (*C. falciformis*), scalloped hammerhead (*S. lewini*) and blacktip shark (*Carcharhinus limbatus*) (Fig. 1). Fins from the smooth hammerhead shark (*S. zygaena*), narrow sawfish (*Anoxypristis cuspidata*) and several other carcharhinid species (e.g., *Carcharhinus altimus* and *Carcharhinus plumbeus*) were rarely observed. Individuals from species in the IUCN threatened categories (VU, EN and CR) accounted for 21% of the genetically identified dried shark fins. The endangered hammerhead species (*S. lewini* and *S. mokarran*) accounted for approximately 8% of the fins.

Total catch estimations based on fins. Following species assignment of fins, the fin measurements were used to estimate total lengths and weights for each individual (see Table 2). The estimated total length of elasmobranchs from which fins had been taken ranged from 40–325 cm representing an extrapolated total catch of over 9 t (as estimated from this fin batch). Estimated biomass per species that contributed to this batch of 150 kg of dried fins from the Milne Bay Province, ranged from 11 kg of *Rhynchobatus australiae* to 2 323 kg of *C. amblyrhynchos*. Additionally, we estimated over 1 000 kg of IUCN listed Endangered shark species have recently been taken out of the artisanal waters in the Milne Bay Province, with over 10% of this shark biomass coming from hammerhead sharks.

The length frequency histograms for all species (represented by more than 10 individuals, see Figs 2 and 3) showed that a vast majority of sharks that contributed to this batch of artisanal sourced fins were immature. For all species, catches included individuals close to the size at birth, mostly through to the size at maturity. For some species, e.g., *C. albimarginatus*, *C. amblyrhynchos*, *C. limbatus*, *C. sorrah*, *G. cuvier* and *S. lewini*, only a small percentage of the individuals present in the catch were possibly adult. Furthermore, no adults of *N. acutidens* were recorded, with all 14 individuals much smaller than the known size at maturity for this species.

Discussion

Our study is the first detailed examination of species composition based on DNA barcoding of elasmobranchs in an artisanal fishery of PNG. The identification of unknown elasmobranch fins from the PNG fin buyer, through a combination of fin images and genetic identifications enabled a very high degree of species identification. In our study and following unsuccessful attempts to use online shark fin identification resources, fin images (from either juveniles or adults) alone were not able to identify species. DNA barcoding was required when few other species-specific morphology/distinguishing characteristics were available. Our DNA COI barcoding successfully enabled delineation of the elasmobranchs observed in this survey (approximately 94% of the fins were identified to species level). For the remainder, a lack of preservation or poor storage conditions may have affected a small number of fins in the batch as bacterial contamination was noted (as evidenced from the sequencing). Additionally for some samples, while a PCR product was produced, the bi-directional sequencing did not pass quality control.

The COI sequencing successfully enabled the identification of the carcharhinids that had contributed to this batch of fins including *Carcharhinus limbatus*, *Carcharhinus tilstoni* and *Carcharhinus amblyrhynchoides*. These three species have previously been shown to be difficult to identify in the field and are often grouped together in a 'blacktip shark complex'[19,34–36]. In our study, a relatively high level of species resolution between these three species was possible using mtDNA sequencing – particularly when multiple barcoding regions were examined.

Species$^{IUCN\ status*}$	Genetic sample size	COI	nucleotide	composition**			Average divergence within species (± se)	Representative GenBank Accession Numbers
		T	C	A	G	bp		
Hemipristis elongata^{VU}	2	35.7	23.8	24.8	15.7	587.5	0.002 (0.002)	MF508658, MF508659
Carcharhinus albimarginatus^{VU}	20	34.9	23.5	26.6	15.1	631	0.000 (0.000)	MF508660
Carcharhinus altimus^{DD}	2	35.7	22.6	26.9	14.7	631	0.002 (0.002)	MF508661, MF508662
Carcharhinus amblyrhynchoides^{NT}	15	35.8	22.7	26.5	15	630.9	0.001 (0.000)	MF508663, MF508664
Carcharhinus amblyrhynchos^{NT}	219	36.4	22	26.6	14.9	618.4	0.002 (0.001)	MF508665, MF508666, MF508667, MF508668, MF508669, MF508670
Carcharhinus amboinensis^{DD}	3	35.2	23.5	26.8	14.5	573.7	0.001 (0.001)	MF508671, MF508672
Carcharhinus brevipinna^{NT}	5	34.2	24.6	26.2	15	630.8	0.000 (0.000)	MF508673
Carcharhinus falciformis^{NT}	19	35.8	22.7	26.3	15.2	631	0.002 (0.001)	MF508674, MF508675, MF508676, MF508677
Carcharhinus leucas^{NT}	6	35.4	23.4	26.6	15.1	630.9	0.001 (0.001)	MF508678, MF508679
Carcharhinus limbatus^{NT}	34	35.7	22.8	26.3	15.2	630.9	0.000 (0.000)	MF508680
Carcharhinus melanopterus^{NT}	13	34.8	23.5	26.6	15.1	630.9	0.000 (0.000)	MF508681
Carcharhinus plumbeus^{VU}	2	35.5	22.8	27	14.7	631	0.000 (0.000)	MF508682
Carcharhinus sorrah^{NT}	18	35.3	23	26.8	14.9	631	0.000 (0.000)	MF508683
Carcharhinus tilstoni^{LC}	18	36	22.5	26.4	15.1	631	0.000 (0.000)	MF508684
Galeocerdo cuvier^{NT}	22	34.9	23.1	27.1	14.9	631	0.000 (0.000)	MF508685
Negaprion acutidens^{VU}	22	35.3	23.3	25.8	15.5	631	0.009 (0.002)	MF508686, MF508687
Sphyrna lewini^{EN}	32	33.7	24.5	26.3	15.5	631	0.003 (0.001)	MF508688, MF508689, MF508690, MF508691, MF508692
Sphyrna mokarran^{EN}	6	33.9	24.4	26.8	14.9	631	0.000 (0.000)	MF508693
Sphyrna zygaena^{VU}	4	34.5	23.6	26.5	15.4	631	0.000 (0.000)	MF508694
Anoxypristis cuspidata^{EN}	2	31.9	26.3	26.3	15.5	631	0.000 (0.000)	MF508695
Rhynchobatus australiae^{VU}	2	31.9	22.8	26.5	15.1	631	0.000 (0.000)	MF508696
Glaucostegus typus^{VU}	5	33.1	24.7	24.8	17.3	631	0.003 (0.001)	MF508697, MF508698
Average	21.4	34.8	23.5	26.4	15.2	625.8		

Table 1. Species of sharks and rays genetically identified from dried PNG shark fins including: genetic sample size (number of individuals' barcoded), COI genetic information (nucleotide composition, fragment length and GenBank information) and IUCN species status *as at 27 April 2017, www.iucnredlist.org, vers 3.1 IUCN 2001, categories Near Threatened (NT), Vulnerable (VU), Endangered (EN); Data Deficient (DD); Least Concern (LC); **COI sequence lengths ranged from 574 bp to 631 bp with an average of 625.8 bp with an average nucleotide composition of T: 34.8%, C: 23.5%, A: 26.4% and G: 15.2%.

While *C. limbatus* and *C. tilstoni* have previously been shown in other studies to have low COI divergence[33,34], in this study, the COI sequencing results (which delineated *C. limbatus*, *C. tilstoni* and *C. amblyrhynchoides*) were concordant with those from the ND2 gene. Furthermore, several fins that were morphologically identified in the field as being putative silvertip sharks (*Carcharhinus albimarginatus*), were genetically identified as belonging to grey reef sharks (*C. amblyrhynchos*) that had white tip fins. In addition to describing the species composition of the fins, our study also demonstrated that several species displayed intra-specific variation, albeit at low levels (e.g., *S. lewini*, *C. amblyrhynchos*, *C. altimus*). Given the use of the COI gene here for species identification, rather than a more variable gene fragment (e.g., mtDNA D-loop) for intra-specific genetic diversity assessment, this is not unexpected.

The Milne Bay Province is a data poor region of PNG, with little known about elasmobranch utilisation. Genetic identification of the dried fins sampled from the Asiapac fin buyer provided us with substantial baseline information as to the elasmobranch species caught in the region, and the sizes of animals caught in the artisanal fishery. Some of these species (e.g., *S. zygaena*) had not previously been recorded from these provincial artisanal waters. Nevertheless, the overall species composition represented in the fin batch was not surprising given the preferred habitats of the most frequently caught species (i.e., grey reef, blacktip reef, silky, blacktip, tiger and silvertip sharks and scalloped hammerheads) varies from shallow coastal and tropical reefs to waters over insular shelf areas – all of which are presumably accessible by the artisanal fishers in this province. Our study highlighted the medium to high diversity (with over 20 different species being detected) of elasmobranchs caught in the artisanal fishery with most of this information being considered new, as species catch rates in this artisanal fishery were not previously known or retained. In contrast, the high number of *C. amblyrhynchos* shark fins is not surprising given the predominantly coral reef habitats in this province. Although this could indicate that the population of *C. amblyrhynchos* within the provincial waters of Milne Bay is part of a relatively large number of individuals, dive operators in the area state they now observe far less *C. amblyrhynchos* than in previous decades. This species was also the most frequently caught shark species in a neighbouring Indonesian study[13]. Given the geographic closeness of PNG and Indonesia (and the numbers of grey reef sharks that have been caught), the analysis of both genetic and demographic connectivity of this species is highly important.

A relatively large number (20%) of the fins in this study came from taxa that are currently IUCN listed as threatened species (i.e., Vulnerable or Endangered). Furthermore, the estimate of 2 000 kg of *C. falciformis* (that

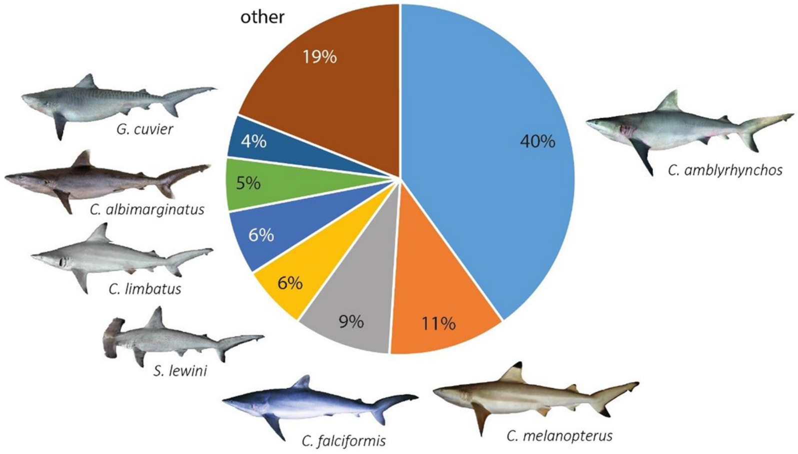

Figure 1. Composition of the most abundant species (i.e., number of individuals) as identified from the dried shark fins following morphological and genetic species identification (images ©Australian National Fish Collection).

Family			Estimated length (cm)		Estimated weight (kg)		
Common name	**Scientific name**	**#**	**Min.**	**Max.**	**Min.**	**Max.**	**Total**
Hemigaleidae							
Fossil Shark	*Hemipristis elongata*	2	102	184	4.5	30.3	34.8
Carcharhinidae							
Silvertip Shark	*Carcharhinus albimarginatus*	28	69	201	1.8	55.3	328.3
Bignose Shark	*Carcharhinus altimus*	2	169	190	29.5	43.0	72.5
Graceful Shark	*Carcharhinus amblyrhynchoides*	16	52	137	0.8	19.1	137.4
Grey Reef Shark	*Carcharhinus amblyrhynchos*	251	40	141	0.4	18.9	2322.7
Pigeye Shark	*Carcharhinus amboinensis*	5	79	220	3.1	88.2	237.0
Spinner Shark	*Carcharhinus brevipinna*	6	78	194	2.2	46.6	119.8
Silky Shark	*Carcharhinus falciformis*	54	96	303	5.1	207.3	2093.7
Bull Shark	*Carcharhinus leucas*	9	101	230	7.0	98.4	459.1
Common Blacktip Shark	*Carcharhinus limbatus*	39	66	192	1.2	34.3	224.9
Blacktip Reef Shark	*Carcharhinus melanopterus*	69	70	121	1.7	12.8	380.4
Sandbar Shark	*Carcharhinus plumbeus*	3	156	177	25.8	39.2	92.1
Spottail Shark	*Carcharhinus sorrah*	18	69	119	1.9	11.8	78.1
Australian Blacktip Shark	*Carcharhinus tilstoni*	17	51	141	0.8	17.8	139.3
Tiger Shark	*Galeocerdo cuvier*	24	98	306	3.9	159.5	976.2
Sicklefin Lemon Shark	*Negaprion acutidens*	14	59	150	0.8	17.3	118.8
unknown carcharhinid		7	86	113	3.8	9.7	50.7
Sphyrnidae							
Scalloped Hammerhead	*Sphyrna lewini*	40	76	242	2.0	67.0	756.0
Great Hammerhead	*Sphyrna mokarran*	6	128	235	8.3	59.1	165.2
Smooth Hammerhead	*Sphyrna zygaena*	4	122	152	9.2	17.0	48.2
Pristidae							
Narrow Sawfish	*Anoxypristis cuspidata*	1	325	325	81.7	81.7	81.7
Rhinidae							
Whitespotted Wedgefish	*Rhynchobatus australiae*	1	136	136	10.7	10.7	10.7
Glaucostegidae							
Giant Guitarfish	*Glaucostegus typus*	7	97	205	3.8	33.5	167.1
TOTAL		623					9094.8

Table 2. Species of sharks and rays identified from the dried shark fins including: number of individuals, ranges of estimated total length and estimated total individual weight, and total estimated weight.

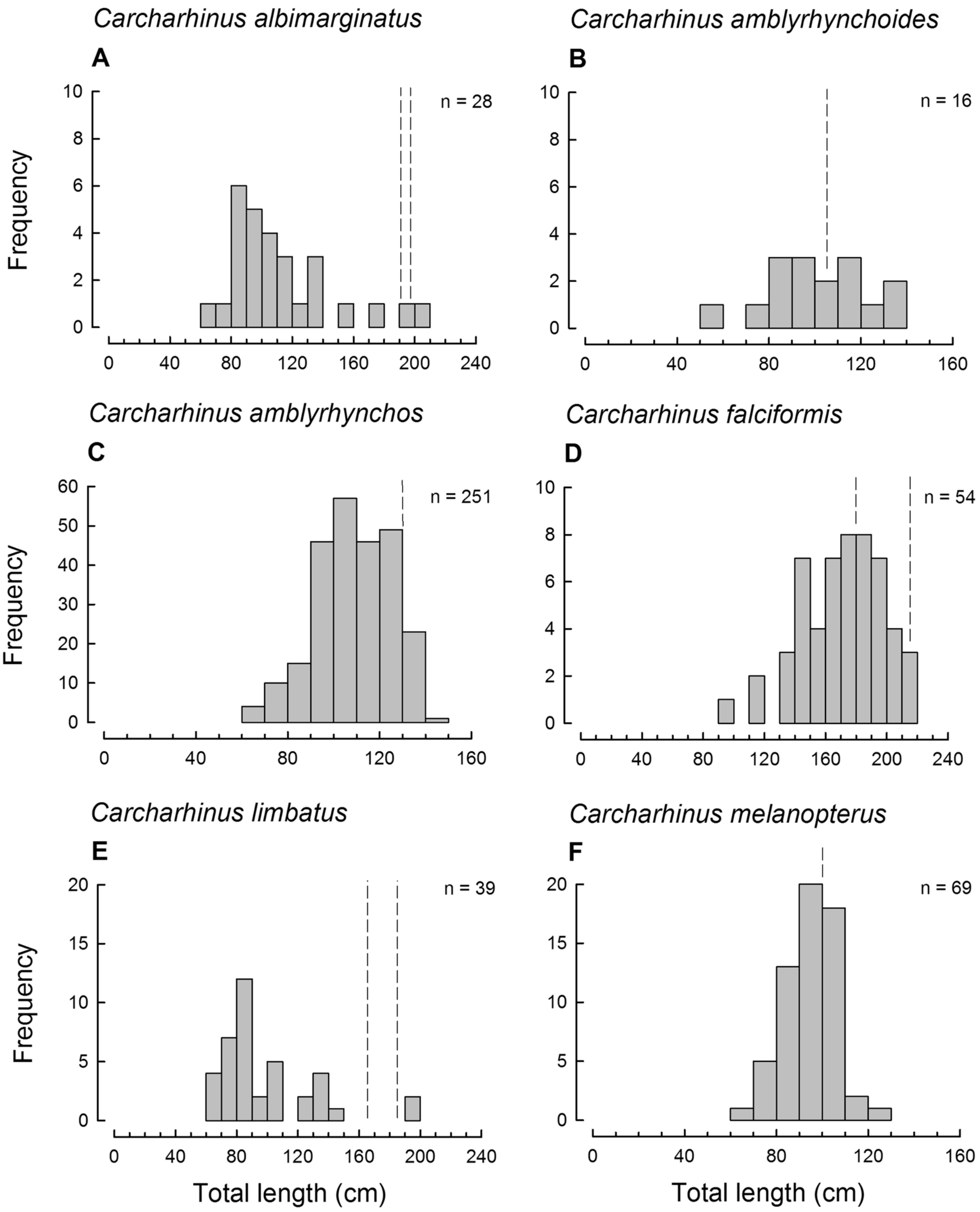

Figure 2. Length frequency histogram of six shark species represented by more than 10 individuals in the dried shark fin batch from the Milne Bay Province PNG. Total number (n) of sampled fins and length at maturity is given for each species (left dashed line denotes known length of maturity for males, right dotted line denotes known length at maturity for females; a single dashed line indicates that both sexes mature at that size; for length at maturity/species see Table 3 references).

contributed product to this single batch of fins) is despite a recent Conservation and Management Measure (CMM) for Silky Sharks 2013–08 (https://www.wcpfc.int/system/files/CMM%202013–08%20CMM%20for%20Silky%20Sharks_0.pdf) by the WCPFC. However as noted previously, while the CMM for silky sharks caused the subsequent closure of the large scale shark fishing in PNG, for small scale fishing/artisanal activities there are no national management arrangements (i.e., no regulations) in place[16]. Another significant finding from this study was that the majority of sharks recorded from the fin batch (i.e., *C. albimarginatus*, *C. amblyrhynchos*, *C. falciformis* and *S. lewini*) were also key species caught within the target longline fishery which operated prior to July 2014 (PNG NFA/CSIRO unpupl data). From a regional perspective, many of these fins come from species that are under worldwide pressure, with similarly concerning catch levels observed in neighbouring Indonesia and regional areas[3,8,13,21]. Additionally, following estimation of catches, extrapolated length frequencies and weight estimates, we identified a biological issue with individuals that are harvested from the area. As was found in

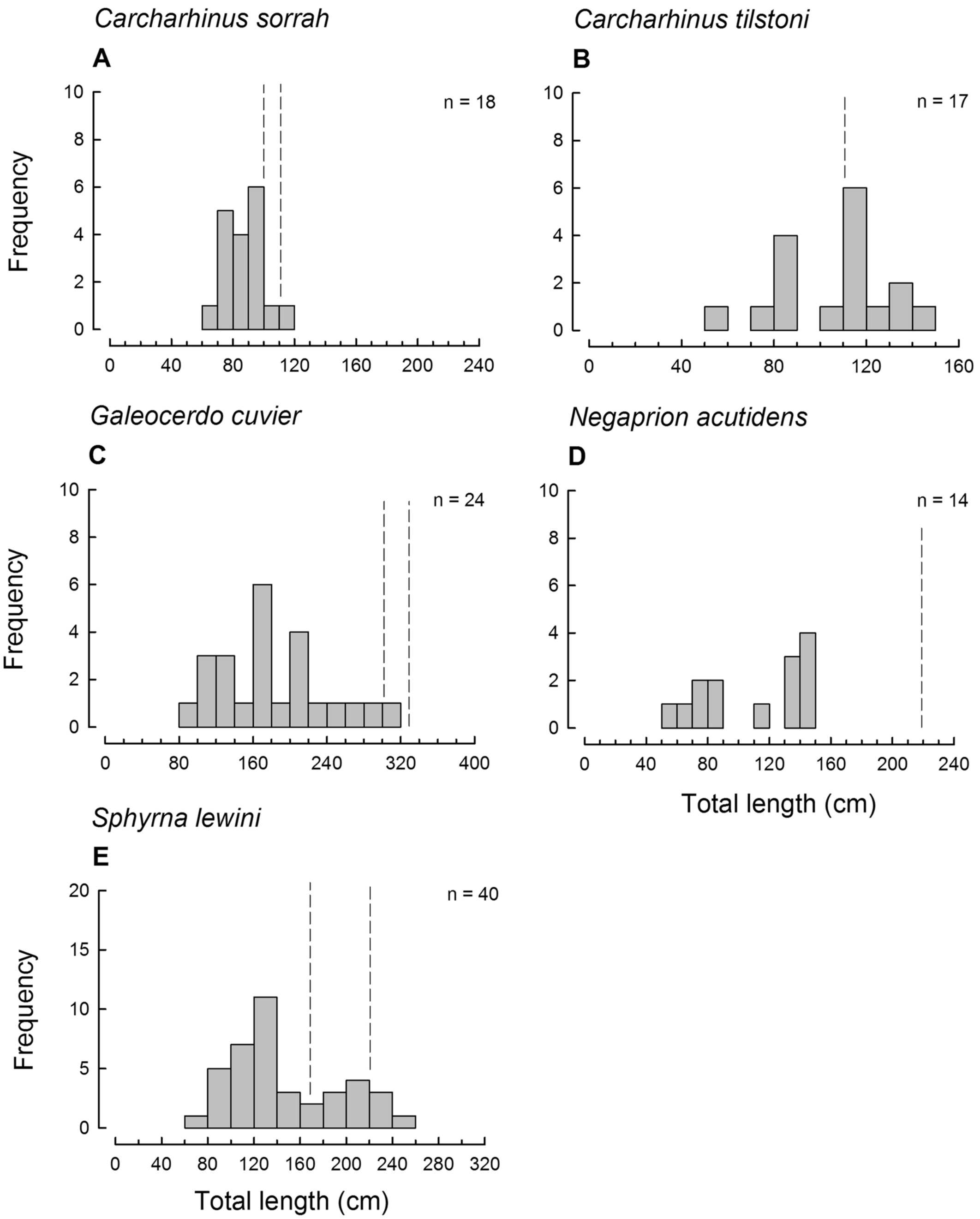

Figure 3. Length frequency histogram of five shark species represented by more than 10 individuals in the dried shark fin batch from the Milne Bay Province PNG. Total number (n) of sampled fins and length at maturity is given for each species (left dashed line denotes known length of maturity for males, right dotted line denotes known length at maturity for females; a single dashed line indicates that both sexes mature at that size; for length at maturity/species see Table 3 references).

Indonesia[13], a large proportion of the elasmobranchs in the Milne Bay artisanal fishery are caught immature or before individuals have reached their length at maturity – these individuals are not reproducing. This could be an indication of unsustainable shark populations if the harvested animals are not contributing to the next generation.

Putting our results into context, this study is a snapshot of the artisanal shark fishery which provides shark fins to the Milne Bay fin buyers. Although we do not know the precise locations where these elasmobranchs have been caught (albeit the fins going to Asiapac are artisanal sourced), our results provide first records and detailed baseline information on the artisanal fishery in this area. While all fins examined were from the Milne Bay Province, we cannot be certain if the elasmobranchs detected here are resident or transient through these local PNG waters (as fins were sampled at the processor and not directly from fishing boats). Combining this with the uncertainty surrounding connectivity of species in the region, the extent to which the Milne Bay shark fin industry is impacting on these regional (and for several, internationally listed) elasmobranch species is unknown.

	Fin to total length conversions		Length to weight conversions		
Species	**Estimated TL**	**Source**	***a***	***b***	**Source**
Hemipristis elongata	=(D1H/0.115) + 1.666	42, 43, W.White unpubl. data	0.00162	3.21	44
Carcharhinus albimarginatus	=D1H/0.097	45	0.00201	3.23	50
Carcharhinus altimus	=(D1H/0.1005) − 0.4778	47, W.White unpubl. data	0.00189	3.23	48
Carcharhinus amblyrhynchoides	=(D1H/0.133) + 1.835	47, W.White unpubl. data	0.00265	3.21	44
Carcharhinus amblyrhynchos	=D1H/0.103	45	0.00746	2.98	44
Carcharhinus amboinensis	=D1H/0.122	45	0.00194	3.27	44
Carcharhinus brevipinna	=D1H/0.094	45	0.00113	3.33	44
Carcharhinus falciformis	=(D1H/0.088) + 1.616	47, W.White unpubl. data	0.00201	3.23	50
Carcharhinus leucas	=D1H/0.102	45	0.00271	3.2	46
Carcharhinus limbatus	=D1H/0.125	45	0.00251	3.125	51
Carcharhinus melanopterus	=D1H/0.102	45	0.00325	3.649	52
Carcharhinus plumbeus	=D1H/0.152	48	0.00142	3.31	48
Carcharhinus sorrah	=(D1H/0.106) + 1.523	49, W.White unpubl. data	0.00079	3.46	53
Carcharhinus tilstoni	=D1H/0.125	using *C. limbatus* conversion	0.00475	3.06	53
Galeocerdo cuvier	=D1H/0.084	54	0.00141	3.24	55
Negaprion acutidens	=(D1H/0.129) + 5.003	54, W.White unpubl. data	0.001208	3.29	56
Sphyrna lewini	=D1H/0.132	54	0.00399	3.03	57
Sphyrna mokarran	=D1H/0.166	54	0.00123	3.24	57
Sphyrna zygaena	=D1H/0.137	54	0.0126	2.81	50
Anoxypristis cuspidata	=D1A/0.103	W.White unpubl. data	0.005	2.474	58
Rhynchobatus australiae	=(D1H/0.109) + 0.516	W.White unpubl. data	0.004	3.0145	W. White unpubl. data
Glaucostegus typus	=(D1H/0.141) + 4.729	W.White unpubl. data	0.006	2.918	W. White unpubl. data

Table 3. Fin to length conversion and length to weight conversion with the source of the parameters used for each species (where n>1 individuals observed) recorded from the dried fins (where D1H = first dorsal fin height).

The shark resources in Milne Bay are currently considered open access, with no limit on how much shark can be harvested[16]. We would expect many of these individuals from the 'local' populations to be connected to nearby regional populations (such as those in Indonesia and Australia), particularly as studies on the shark industry in Indonesia[8,13] highlighted catches of the same Vulnerable and Endangered species (e.g., *S. lewini*, *N. acutidens*). Given this, there needs to be some form of control and monitoring of the shark catch in Milne Bay Province in the near future[16]. Several input and output controls that could be considered (including allocation of community based catch allowances) have been outlined[16]. While it is beyond the scope of this current research to advocate for particular strategies or control measures, our research here further highlights a substantial biological socio-economic issue. Previous work has showed that production of shark fins is a key income source that supports the livelihood strategies of some local communities in the Milne Bay Province[16]. This is particularly the case for isolated, low-income, island communities that have few alternative income sources. Shark fins pose as an economically viable primary product given that they do not require refrigeration, are easily processed and transported[16]. Therefore any resource management intervention aimed at addressing the biological sustainability issues for elasmobranchs identified here has the potential to have localised, undesired socio-economic impacts.

Within this socio-economic framework, the question of how to improve resource management to achieve a sustainable shark fishery is one that warrants discussion - particularly given PNG's international commitments. Such commitments include its Memorandum of Understanding with the IUCN signed in 2013 (https://www.iucn.org/content/png-and-iucn-seal-environment-partnership) under which the government of PNG is to secure and manage the important biodiversity resources of the country. Papua New Guinea's commitments as a signatory to the convention on international trade CITES (https://cites.org/eng/cms/index.php/component/cp/country/PG) could also be better addressed. Currently, its' elasmobranch data is aggregated and it is not possible to identify and or monitor the trade in shark parts belonging to listed species in Class Elasmobranchii (Pristidae spp - *A. cuspidata*, *S. lewini*, *S. mokarran*, *S. zygaena*). As shown in this study, fins from these four species were part of the 150 kg of dried fins that were barcoded.

Our research in linking genetic species identification of dried fins from this PNG artisanal fishery, to species compositions and catch extrapolations will contribute to the more sustainable use of elasmobranch resources in PNG, as country specific and regional fisheries assessments rely on accurate species identifications and catch effort data. Genetic testing/barcoding of shark products is the most accurate method (particularly when whole animals are not accessible) to obtain elasmobranch species identifications irrespective of origin. Nonetheless, genetic testing and barcoding comes at a cost and large scale barcoding of elasmobranch fins (and other tissue types) in PNG is not currently viable due to budget and capacity limitations in-country. Requiring artisanal fishers to land shark whole would enable identification at the point of landing or sale (rather than harvest), but for the fishers, this would be a difficult requirement to meet[16], and may reduce the socio-economic viability[16] of shark harvesting in the PNG artisanal sector. Therefore, improving cost-effective local data collection methods, such as recording (where known) the elasmobranch species at the point of catch/harvest, would allow for better catch data to be obtained and provide a better understanding of the dynamics of the fishery over the longer term. We recommend this should be undertaken to enable the collection of species specific data rather than aggregating all species product data to just 'shark fin'. Species specific data is more valuable information for fisheries and conservation managers particularly regarding CITES listed taxa and species which share trans-country boundaries.

Methods

Processing of shark fins. In March 2016, the dried shark fins present at Asiapac (one of two licensed fish buyers in the Milne Bay Province) in the Provincial capital Alotau were examined (see Fig. 1[16]). Previous work[16,25] indicated that the majority of the dried fin traded through the two licensed buyers in Alotau are sourced from the artisanal fishing sector within the province. This sector includes specialised and targeted artisanal harvesting of shark in some areas using longlines and handlines as well as non-targeted and opportunistic harvesting[16]. At the time of the study, approximately 150 kg of dried shark fin were available for examination. This was about one month's worth of purchases from fishers within the Milne Bay Province, but does not necessarily reflect when the sharks were caught as fishers and small-scale buyers may store fins for several months before selling to a licensed buyer. Licensed buyers are required to maintain a record of the source location of fins from within the Province (down to LLG). However, once purchased and stored, there is no requirement to identify which fins have come from which LLG[16]. For this reason, locality of harvests within the province was not explored.

All suspected first dorsal fins were separated from the remaining fins, with a total of 640 fins isolated from the main batch. The height (D1H), length (D1L) and anterior margin (D1A) of each of these fins were measured[37]. Note in some circumstances, not all of these three measurements could be taken (e.g., if free rear tip was damaged), but in all cases at least one measurement was obtained. An image and a small piece of tissue was taken from the majority (n = 557) of the fins, with each of these fins allocated a unique label number to be included in all images and used as the tissue sample identifier. An image and tissue sample was not taken from all first dorsal fins identified as one of the following three species; blacktip reef shark *C. melanopterus*, silvertip shark *C. albimarginatus* and silky shark *C. falciformis* as these species could be accurately identified from the fins alone. All samples were tracked throughout the genetic laboratory analysis pipeline based on the unique label number.

Confirmation of first dorsal fins. Based on the genetic identification results (see later), all examined dorsal fins from species which possessed two similar-sized dorsal fins were reinvestigated. This was done to refine the number of individuals present in the dried fin batch and to eliminate double counting of individuals. The identified shark-like rays (i.e., narrow sawfish *A. cuspidata*, giant guitarfish *Glaucostegus typus* and whitespotted wedgefish *R. australiae*) possess similar-sized dorsal fins. For each of these species, the number of fins were sorted by their fin measurements and each pair working down the list was considered from a single individual with the larger of the pair allocated as the first dorsal fin and the smaller as the second dorsal fin. Thus, for *G. typus*, 14 fins were initially observed but this was considered to be from 7 individuals. For the sicklefin lemon shark *N. acutidens*, the first and second dorsal fins are similar in height but easily separable based on their morphology (Fig. 4), thus enabling the first dorsal fins to be separated out easily following species identification.

After second dorsal fins were eliminated from the batch of fins, a total of 623 individuals were confirmed from the 150 kg batch of dried fins examined. Images were stored in a database at CSIRO, while the fin clips were stored dried in 1.7 ml microfuge tubes at room temperature (while in the field) and were transferred to an ultra-low freezer (−80 °C) on arrival in the CSIRO marine genetics laboratory in Hobart.

Genetic identification of fins. Total genomic DNA was extracted from approximately 25 mg fin tissue using the Promega Wizard® Genomic DNA Purification kit (Promega Corporation, USA) according to the manufacturer's specification, with an overnight digestion step at 55 °C; DNA was precipitated in 160 μl water. DNA was normalised to 10 ng/μl with working stock stored at 4 °C and the bulk of the DNA stored at −80 °C.

Approximately 650 base pair (bp) segment of the 5′ end of the mtDNA COI gene was primarily amplified using the primers Fish-BCL-5′TCAACYAATCAYAAAGATATYGGCAC-3′ and Fish-BCH-5′ ACTTCYGGGTGRCCRAARAATCA-3′[38]. Where additional mtDNA information was required to confirm species validation, the NADH-2 primers ASNM 5′ AAC GCT TAG CTG TTA ATT AA 3′ and ILEM 5′-AAG GAG CAG TTT GAT AGA GT-3′[39] were also utilised. PCR amplifications were carried out in an ABI 9600 thermocycler (Applied Biosystems™, USA) performed in 25 μl reactions which consisted of 12.5 μl of GoTaq Master Mix Green (Promega), 1 μl Bovine Serum Albumin (Promega), 1.0 μl of each 10 μM primer, 7.5 μl water and 2 μl of template DNA. The PCR conditions consisted of 94 °C for 3 mins, then 35 cycles of 94 °C for 1 min, 50 °C/48 °C (for COI and ND2 respectively) for 1 min 30 s, 72 °C for 1 min and a final extension step of 72 °C for 10 min.

Amplified PCR products were cleaned using Agencourt AMPure XP magnetic particles (Beckmann Coulter Life Sciences, USA) with the quality and quantity of cleaned products checked using a Nanodrop 8000 spectrophotometer (Thermo Scientific, USA). Purified PCR products were labelled with the Big Dye Terminator v3.1 cycle sequencing ready reaction kit (Thermofisher, USA), cleaned using Agencourt CleanSEQ (Beckmann Coulter) magnetic particles and then bi-directionally sequenced at the CSIRO marine genetics laboratories on a 16 capillary ABI 3130XL DNA Autosequencer (Applied Biosystems™, USA). Forward and reverse sequences were trimmed, *denovo* assembled, sequences were checked by eye and then converted into consensus sequences using Geneious (Biomatters Ltd, New Zealand) vers R8.1.4. Consensus sequences for each sample were compared using the BOLD[32] IDS tool and GenBank BLASTn (via an internal application in Geneious) to check the similarity of sample sequences against existing database sequences. Species identification was based on a percentage of sequence identity, with homology of ≥99% as the criterion used here for species confirmation. BOLD was

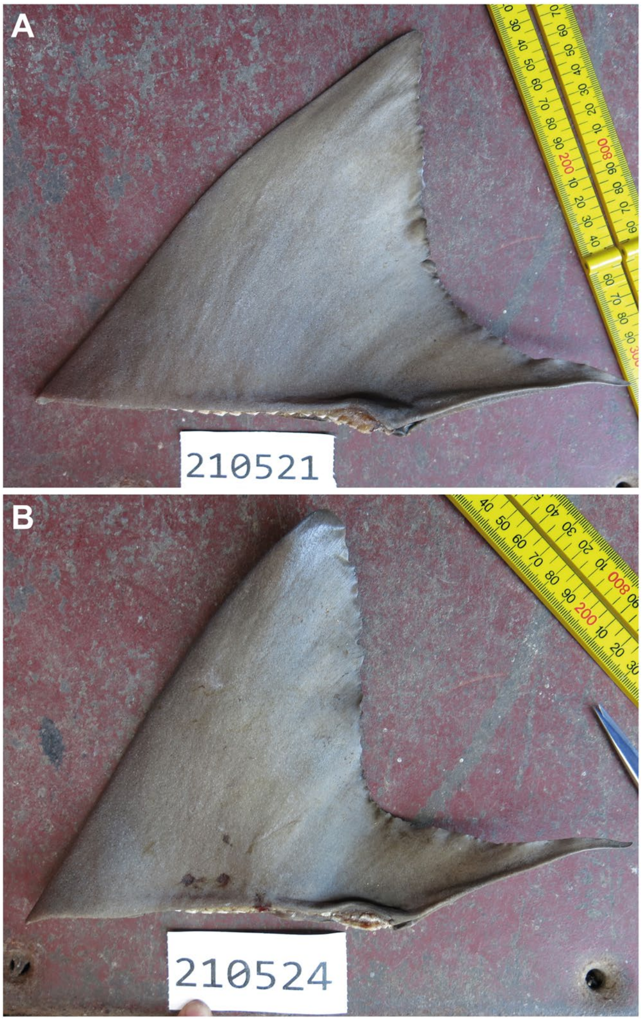

Figure 4. (**A**) First and (**B**) Second dorsal fins of *Negaprion acutidens*, highlighting the different morphology of the two fins, despite being similar in height (images ©Australian National Fish Collection).

primarily used for species identity based on the COI sequence, while both COI and ND2 sequences were compared in GenBank.

Following species confirmations, consensus sequences for all confirmed elasmobranch species were aligned in Geneious using a MUSCLE alignment. Aligned sequences were then exported into MEGA version 6.0[40]. The nucleotide composition and genetic distances between and among identified species were calculated using a Jukes-Cantor[41] model with rate variation among sites modelled with a gamma distribution, and all positions containing gaps and missing data were eliminated. As this was not a phylogenetic study, we did not produce phenograms or phylogenetic trees. Representative COI sequences from each of the species identified from the fin samples have been deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/; Accession Numbers MF508658 – MF508698).

Conversion of confirmed fins to species total lengths and weights. Fin measurements and species conversions used to estimate the total length of all individuals of each of the species identified are provided in Table 3 (along with the source of the conversion data used). Additional fin measurements from individuals of known length were taken by one of us (WW) from whole specimens examined in the field and from preserved specimens housed in the CSIRO Australian National Fish Collection. First dorsal fin height (D1H) was used for the conversion to total length for all but one of the species, as a better range of data was available than for the other two fin measurements. The model for these conversions is:

$$\mathrm{W[weight]} = \mathrm{a} \times \mathrm{TL[total\ length]}^{\wedge}\mathrm{b}$$

a and b parameters used to convert the estimated total lengths (cm) to total weight (g) are also provided in Table 1 together with their source.

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Author Contributions

Conceived, designed, analysed and prepared the manuscript: S.A., W.T.W. Provided field support: B.S. Provided background information: S.V. All authors reviewed the manuscript.

Additional Information

Competing Interests: The authors declare no competing interests.

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Artisanal shark fishing in the Louisiade Archipelago, Papua New Guinea: Socio-economic characteristics and management options

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ABSTRACT

Small-scale shark fisheries in Papua New Guinea have developed rapidly and are largely unmanaged. While shark species are vulnerable to overexploitation, local fishers who depend on shark fin for income also have limited alternative income options. This implies a difficult trade-off for policy makers between conservation and community welfare. A case study of shark fishing activities in the Louisiade Archipelago of the Milne Bay Province, a major small-scale shark fin producing region, is presented to inform such trade-offs. The region has experienced a significant reduction in available income opportunities due to the recent closure of the local sea cucumber fishery in 2009. While it had been widely assumed that shark fin production and income was likely to have escalated in the region to replace lost sea cucumber income, our model of small-scale shark fin production shows that quarterly dried fin production was in fact, on average, 68 kg higher while the sea cucumber fishery operated (holding all else constant). Furthermore, annual shark fin income is estimated to have fallen by 75% following the sea cucumber fishery closure. Falling prices and a decline in market access resulting from the closure of the sea cucumber fishery appear to be the major drivers of the fall in shark fin production. These factors have been accentuated by the geographical isolation of Louisiade communities, high fuel costs and the low economic returns associated with the sale of shark fin (relative to sea cucumber). The influence of market access on shark fin production is also reflected in the modelled increase in shark fin production (119 kg per quarter on average) that occurred with the introduction of a transport boat in the region. Market access is likely to further improve, particularly if the sea cucumber fishery is reopened and/or shark fin prices increase. Therefore, low-cost, community-based management of shark resources based on the allocation of allowable shark catches to ward communities is recommended. Such an approach takes advantage of the communal characteristics of the local island communities as well as the fishery data collection and monitoring mechanisms that are already being used by the local government.

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1. Introduction

Shark species are characterised by slow growth rates and low productivity and, as a result, are highly susceptible to overfishing (Hoenig and Gruber, 1990; Stevens et al., 2000; Walker, 1998). They also play a vital role as apex predators in the functioning of marine ecosystems (Ferretti et al., 2010). Despite this, the harvesting of shark resources internationally has been, in general, poorly managed and global shark catches have escalated dramatically (Clarke et al., 2013; Eriksson and Clarke, 2015; Lack and Sant, 2011) and international shark populations have declined as a result (Cortés, 2002). Also, as teleost target species have become less accessible, due to overfishing or catch restrictions, the fishing pressure on sharks has increased (Clarke et al., 2006; Lack and Sant, 2009).

These trends have been driven by the high prices paid for various shark products on Asian markets and in particular shark fin. Escalating prices have been caused by rising incomes and demand in China where the fin ceratotrichia (the elongated collagen fibres of the fin) are used to make shark fin soup, which is considered a prestigious dish in Chinese culture (Cheung and Chang, 2011;

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Fabinyi, 2012; Vannuccini, 1999). High shark fin prices have also led to the practice of "*shark finning*" whereby the fins of the animal are removed and the remainder of the animal is discarded (sometimes alive) given the low market value and low palatability of shark meat relative to other fishery products (Clarke et al., 2006).

International efforts to manage shark fisheries have improved more recently (Fischer et al., 2012). For example, a number of developed countries have adopted National Plans of Action (NPOAs) and have introduced new shark management measures (Fischer et al., 2012). A number of shark species are also now subject to trade restrictions under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Clarke et al., 2013; Dulvy et al., 2008) and more are likely to be listed. However, in developing countries efforts to better manage shark catches have generally not kept pace with these changes (Fischer et al., 2012). Limited government resources, substantial fishing territories, low political-will and the low value of shark relative to other fisheries are all explanatory factors. Papua New Guinea (PNG) provides an interesting example of a shark harvesting country that has such characteristics. Although FAO statistics suggest that PNG's shark harvests are low by international standards, exploration of official data indicate harvests are likely to be heavily underestimated (Vieira and Yaman, 2015). Although it is difficult to accurately quantify the changes in shark landings nationally, it is generally accepted that shark fishing activities in the country have dramatically escalated over the last two to three decades (Vieira and Yaman, 2015; Teh et al., 2014).

Shark fishing in PNG can be categorised into activities that occur in the large-scale sector, which includes a managed shark longline fishery as well as other managed large-scale fisheries where shark is taken as bycatch (Kumoru, 2003; Opu, 2007), and activities that occur in the small-scale sector. Small-scale activities include artisanal, localised fishing activities that use small vessels and relatively less developed technology and fishing gear. While information and management on shark fishing in the large scale-sector is relatively well established (Kumoru, 2003), PNG's small-scale shark fisheries are largely unmanaged and not well understood.

The available information that does exist on small-scale shark fishing activities in PNG suggests that the Milne Bay Province, which is located off the south-eastern tip of the PNG mainland, has been a focal point for such fishing activity in PNG. Recent evidence (Foale, 2006; Sabetian and Foale, 2006; Kinch, 1999) and available data indicates increasing and potentially unsustainable levels of shark fishing activity in the region. These trends are concerning not only due to the important ecological role played by shark stocks but also the international significance of the Milne Bay Province region. Its waters form part of the Coral Triangle and include one of the most diverse assemblages of coral reef fishes in the Triangle (Allen et al., 2003).

While some government intervention would likely be required to prevent these trends continuing, such action is complicated by the socio-economic vulnerability of Milne Bay island communities. Isolation, low land availability and minimal infrastructure and services all contribute to a lack of food, employment and income opportunities in many areas (Kinch, 1999, 2001, 2007; Foale, 2006). More recently, natural disasters (including cyclones and drought) and rapid population growth has made local socio-economic circumstances even more difficult. For all these reasons as well as the close proximity of communities to the marine environment, socio-economic dependence on marine resources is typically significant.

The socio-economic situation of most island communities in the area is also likely to have deteriorated in recent years following the national closure of the sea cucumber fishery in 2009 (Pomat, 2012). This fishery provided large injections of cash into island communities via the processing of sea cucumber to produce and trade beche-de-mer[1] (Foale, 2006; Kinch, 2002, 2004; Kinch et al., 2008) so the socio-economic consequences of its closure were likely to be severe. Dependence on other sources of income including shark fin is likely to have increased as a result.

Given the high levels of shark fishing in the Milne Bay Province, the vulnerability of shark stocks to overfishing and the socio-economic circumstances of the Province's island communities, there is a need for better informed management of shark fishing in the region. The current study attempts to partly address this need by providing a socio-economic evaluation of shark fishing activities in the Louisiade Rural LLG of the Milne Bay Province based on data collected during a field survey conducted in 2014. Socio-economic information and data were collected including information on fishery characteristics, management arrangements, marine commodity prices and sales, livelihood characteristics and the views and attitudes of fishery stakeholders were collected. Data on marine product sales collected by the National Fishery Authority (NFA), the agency responsible for the management of PNG's fisheries were also analysed. Using this information, the drivers of shark fishing activity and the financial dependence on shark relative to other marine commodities is evaluated for the 2007 to 2014 period to assess the changing socio-economic role of shark fishing activities pre- and post-sea cucumber moratorium. The results and observations are drawn on to discuss and highlight potential fishery management approaches to improve the status of shark fisheries in the region.

The paper provides a snapshot of the recent socio-economic situation of a relatively under-researched region of Papua New Guinea. It is the first paper to explore the interactions and relationships between marine resource based livelihoods in the area and generates an unexpected result: rather than increasing to replace lost sea cucumber based income, shark fin production has in fact declined. This finding sheds light on the importance of market access in the region and how capricious it can be. Finally, the paper also makes novel suggestions for the management of shark resources in the region that take advantage of current management processes, governance frameworks and social characteristics in the region. These suggestions could also be applied to other key marine resources in the region, including sea cucumber.

2. Background

2.1. Physical and socio-economic characteristics

The province of Milne Bay is located on the southeastern tip of the PNG mainland (Fig. 1). It includes a small part of the PNG mainland where Alotau, the provincial capital is found. The province is divided into four districts and sixteen local level government areas (LLGs). Field research focused on the Louisiade Rural LLG which is one of four LLGs in the Samarai-Murua District. It comprises the western part of the Louisiade Archipelago which extends from the PNG mainland in an east-southeasterly direction. Major islands and island groups within the Louisiade Rural LLG include Misima Island (which includes the district capital of Bwagoia), the West Calvados Chain which includes Brooker Island (also known as Utian), Motorina and Bagaman Islands; the Deboyne Island group which includes Panaeati, Panapompom and Nivani Islands; Jomard Island and the Duchateau Island Group; and Kimuta. The Louisiade Rural LLG is divided into thirty two wards, twenty three of which

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[1] As used here, the term '*sea cucumber*' refers to the harvested animal while '*beche-de-mer*' refers to the traded product that is produced from harvested sea cucumber.

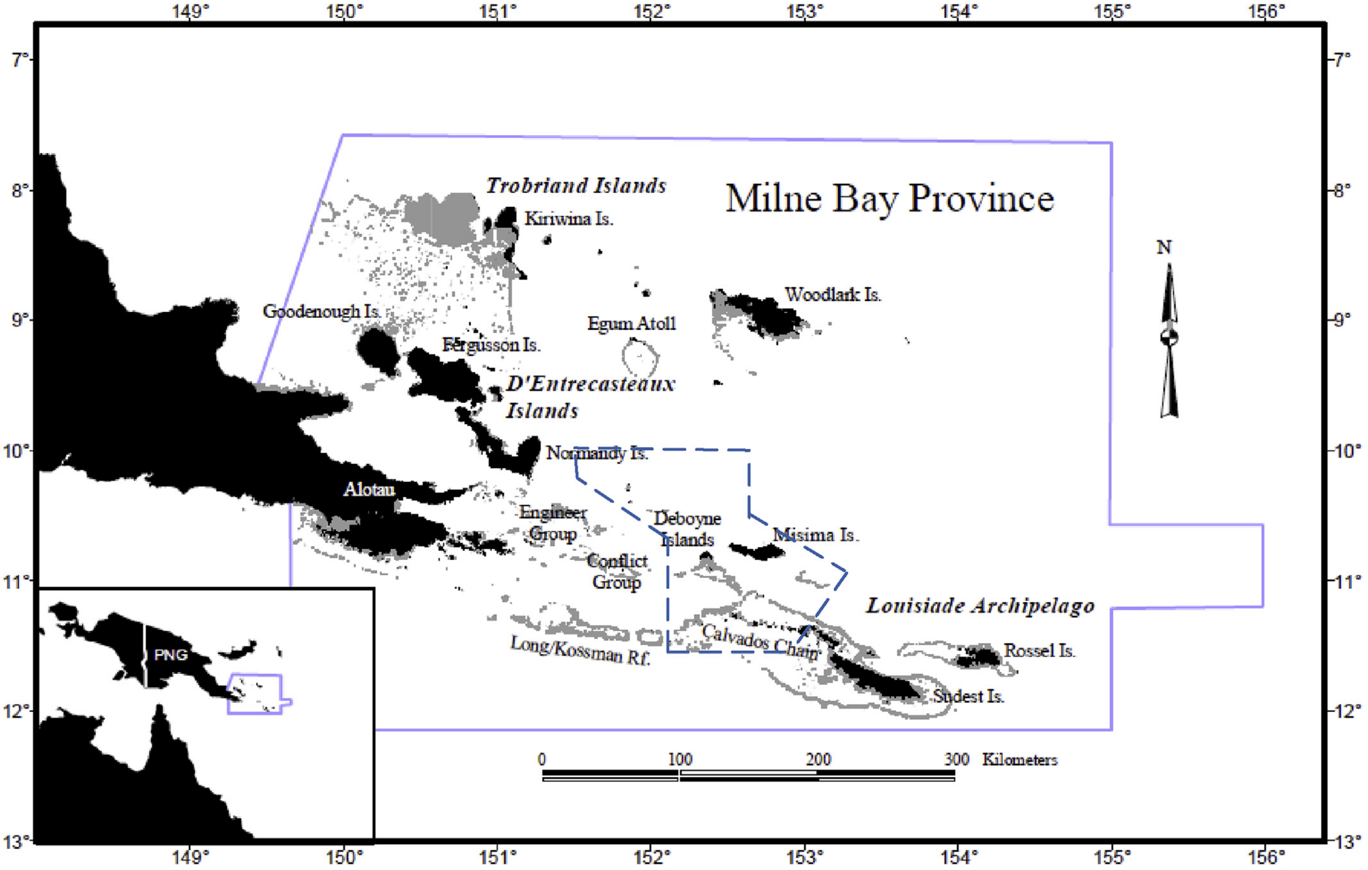

Fig. 1. Map of Milne Bay Province showing the approximate location of Louisiade rural local level government area (blue dashed line) and its major features (adapted from Skewes et al., 2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occur on Misima Island (NSO, 2002).

The Louisiade Archipelago is characterised by a sub-marine habitat mix of coral reef, sand and rubble bottom, seagrass beds and mangroves (Kinch, 1999). A tropical monsoon climate dominates the area, with north-west winds dominating the dry season (October to April) and south-east winds dominating the wet season (May to September). Calm periods occur between the seasons (Skewes et al., 2011; Kinch, 1999). Tropical cyclones can occur in the dry season, with Cyclone Yasi affecting the area recently in 2014. El Nino events also cause droughts in the region, on average, every ten years and severe droughts every thirty years (Skewes et al., 2011). A severe drought in 1997–98 was categorised as potentially life threatening in some areas, especially as it followed Cyclone Justin in 1997 (Kinch, 1999). An El Nino event was taking place in 2015–2016 at the time of writing with key indicators suggesting that it is one of the top three strongest events in the past fifty years (BOM, 2016).

In 2011, 23,225 people resided in 4542 households in the Louisiade Rural LLG (an average household size of 5.1 persons) up by 25 per cent from 18,610 in 2000 (NSO, 2014) (Table 1). In 2000, 80 per cent of the population was located on Misima Island with the remaining population located on smaller islands to the south of Misima (NSO, 2002).[2] The population is predominantly Christian and the primary language spoken in the area is Misiman, although English is also taught at schools (Kinch, 1999). Literacy and education are high relative to other regions of PNG (NSO, 2014) while health service provision is low. Malaria is the main health issue in the region (Kinch, 1999; Foale, 2006). Rates of malnutrition are generally low, although food shortages caused by drought or cyclones can create near-famine conditions (Kinch, 1999, 2001; Rayner and Rayner, 1989).

Communities within in the Louisiade Archipelago are typically communalistic, with livelihood activities undertaken in the interest of the family, clan, church and island community. On Brooker Island, for example, activities are carried out by collective work groups called '*bodas*' which include co-resident siblings, spouses and children. The boda leader mobilises the group to undertake production activities and outputs are shared (Kinch, 1999). However, Kinch, (2001) notes that the monetisation of Louisiade communities since the 1990s (driven by the sea cucumber fishery) has challenged traditional values and social arrangements.

This monetisation has seen the development of dualistic economies, with traditional subsistence and inter-island trading activities (e.g. of food, clay pots, woven baskets, mats and bags) operating alongside market-based, cash-income earning activities (Hide et al., 1994; Kinch, 2001). While subsistence and trading have historically allowed communities to be self-sufficient (Friedman et al., 2006), population growth is testing island carrying capacities (Butler et al., 2014) and cash income is becoming increasingly important. For example, Kinch (1999) notes that for Brooker Islanders, low subsistence food supplies between January and May (the traditional '*hungry time*' or '*huwalu*') sees increased reliance on cash to purchase non-traditional food such as rice, sugar and flour. In addition to food purchases, cash is also directed towards health and education (although these are now government provided), transport, Christmas celebrations, church offerings and mortuary

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[2] Ward level statistics have not yet been released for the 2011 census.

Table 1
Population of Louisiade Rural LLG and its wards in 2000 and 2011 as sourced from the 2000 (NSO, 2002) and 2011 (NSO, 2014) PNG census. Sampled column indicates whether fishers from that ward were sampled during field work.

	Estimated population		Visited	Focus groups			Interview	
	2000	2011		Fisher	Island councillor	Trade store	Fisher	Island councillor
Kimuta Ward	472	n.a.	No	–	–	–	–	–
West Panaeati Ward	607	n.a.	Yes	–	–	–	–	1
East Panaeati Ward	707	n.a.	Yes	1	–	1	–	1
Panapompom Ward	410	n.a.	Yes	–	–	–	–	1
Brooker Island Ward	427	n.a.	Yes	8	1	2	1	–
Motorina North Ward	259	n.a.	No	1	–	–	–	–
Motorina South Ward	196	n.a.	Yes	–	–	–	–	–
Bagaman Ward	201	n.a.	Yes	1	–	–	–	–
Panaumara Ward	360	n.a.	No	–	–	–	–	–
Misima Island Wards	14,971	n.a.	Yes	–	–	–	–	–
Louisiade Rural LLG	**18,610**	**23,225**	**Yes**	**11**	**1**	**3**	**1**	**3**

feasting.

Livelihood activities are dominated by agriculture and marine harvesting. Agricultural gardening has a predominantly subsistence focus and limited land and low productivity soils restrict the types of crops that can be grown with banana, cassava, coconut, sweet potato and yam being major crops (Friedman et al., 2006; Hide et al., 1994; Kinch, 1999). Increasing land scarcity due to population growth has led to more intensive use of gardening land with a reduction in fallow periods and soil overuse (Butler et al., 2014). Marine resource extraction is also widespread and provides the main source of income. Major cash commodities have included beche-de-mer (the harvesting of which has been banned since 2009), shark fin, trochus shell and fresh fish (Kinch, 1999; Friedman et al., 2006). Pearl shell and crayfish have also been minor income sources. These and other products such as turtle, turtle eggs and clam are also consumed and traded (Kinch, 1999, 2002).

An additional source of income has included copra (dried coconut meat for coconut oil extraction) although prices and production have been low in recent years (Foale, 2006). Income remittances from migrant family members have also been previously observed for Louisiade (Kinch, 1999; Friedman et al., 2006) and Milne Bay households (Foale, 2006; NFA, 2006; Hayes, 1993) but have typically been minimal. For example, Friedman et al. (2006) observed that only a few households on Panapompom and Panaeati Islands received small remittances. Similarly, Kinch (1999) noted that only 5 per cent of Brooker Island's population worked for wages in urban areas.

2.2. *Shark fishing activities and their management*

Recent shark fishing in the Louisiade Rural LLG has only been documented by Kinch (1999) who outlines the livelihood activities of Brooker Islanders. At that time, most sharks caught were bycatch and there were only two specialist fishers that targeted shark. For the specialist fishers, buoyed vertical droplines (or drum lines) with a single hook were used to target shark with turtle, moray eel, stingray and fish most frequently used as bait. Species commonly caught included blacktip reef (*Carcharhinus melanopterus*), lemon (*Negaprion acutidens*) and whitetip reef (*Triaenodon obesus*) sharks while grey reef (*Carcharhinus amblyrhynchos*), tiger (*Galeocerdo cuvier*) and hammerhead (*Sphyrna* spp.) sharks were caught less frequently (Kinch, 1999).

Kinch (1999) also presents estimates of Brooker Island income from marine commodity sales in 1999. Out of seven commodities, shark fin made the lowest income contribution accounting for less than 1 per cent of annual income. Beche-de-mer was the dominant income source (making up 47 per cent of annual income) followed by trochus shell (15 per cent), crayfish (15 per cent) and fish (14 per cent).

Other observations of shark fishing in the Louisiade LLG are limited. Indeed, Friedman's et al. (2006) survey of Panapompom and Panaeatti Islands made no mention of shark fishing, with beche-de-mer and fin fish cited as major income sources. For Milne Bay more broadly, Kinch (2001) describes shark fin production as an "*expanding income-earning opportunity*". He also notes observations by unhappy villagers of illegal shark targeting by large-scale tuna longliners, further evidenced by the grounding of a number of longliners on shallow reefs in the area (including in the Louisiade Archipelago).

Shark fishing has also been briefly described for islands in the Bwanabwana LLG, in western Milne Bay by Foale (2006) and Sabetian and Foale (2006) who focused on beche-de-mer and marine resource management more broadly. Both works describe significant increases in shark fishing driven by increased use of dinghies, purchased via debt arrangements with beche-de-mer buyers. Foale (2006) notes that although shark stocks seemed to still be abundant at the time, anecdotal reports indicated that stocks may have declined since illegal longlining began.

The management of large-scale shark fishing in PNG is governed by the *National Shark Longline Management Plan*. It was introduced in 2002 in response to the perceived increase in targeting of shark by tuna longliners. It allowed for the operation of nine shark longliners which were subject to specified limits on gear and catch. However, a ban on the retention of silky shark (the fishery's main target species) was introduced in mid-2014 in line with recommendations by the Western Central Pacific Fisheries Commission's (WCPFC) and the fishery subsequently ceased operating.

For small-scale shark fishing activities in Milne Bay and PNG more broadly, there are currently no national management arrangements. Similarly, there is no previous evidence of community-based management of shark fishing in Milne Bay and the Louisiade Archipelago. However, community tenure and access arrangements do exist and typically limit marine harvesting activities of outsiders in local territorial waters to subsistence purposes and prohibit outsider harvesting of valuable commodities such as beche-de-mer and shark fin for income (Kinch, 1999, 2004; Foale, 2006; Sabetian and Foale 2006). Such arrangements have only emerged as marine resources have become economically valuable, and their development has often been associated with community disputes and tension (Carrier, 1981; Carrier and Carrier, 1989; Akimichi, 1995; Kinch, 2003).

The lack of community management of shark and other marine resources is most likely due to a low awareness of their biological limits (Foale, 2006) and, linked to the latter, a low historical need to manage marine resources due to lower human population densities in the past. Rapid population growth and the increasing resource pressures that are resulting are now creating an increased need for government led management of these natural resources.

3. Method

3.1. Site selection

Case study sites were selected using shark fin purchase data obtained by the NFA. These data are reported to the NFA on a monthly basis by buyers that hold a licence with the NFA to export and domestically-transfer marine commodities. While the reliability of these data for all PNG provinces is being explored as part of the wider project, the current research indicates that these data are reliable for the Milne Bay Province. The province was selected as a case study area given that it accounted for a major share (35%) of reported shark fin purchases across PNG from 2004 to 2013. The majority of the province's shark fin comes from LLGs in the Samarai-Murua District: Bwanabwana Rural, Louisiade Rural, Murua Rural and Yaleyemba Rural LLGs. The Louisiade Rural LLG was selected as the focus site for the current research given its dominant share of provincial purchases (14% on average) and also given the familiarity with the area of one of us (JK).

3.2. Data collection

3.2.1. Field work

Field work occurred in the last two weeks of November 2014 and was undertaken in two stages: the first stage focused on the fishers and middle-men of the Louisiade LLG and the second stage focused on licensed large-scale buyers in Alotau.

Just under a week was spent on Brooker Island in the Calvados Chain. During this time, a number of surrounding islands were also visited including Panaeati and Panapompom Islands, Motorina Island, and Enivala and Nitabotabo Islands in the Bramble Haven Group (a major fishing area). Information was collected from shark fishers, small-scale fin buyers (trade-store owners) and community leaders. Bwagoia (the district capital) on Misima Island was also visited and the district fishery management officer was consulted there.

Data collection relied on a combination of semi-structured interviews and focus group discussions and respondents were targeted with assistance from community leaders. An individual would first be approached and requested to participate. Discussion would then be pursued with this respondent and the surrounding group which usually comprised of the respondent's family and fellow fishers. Using such an approach allowed respondents to check their answers with others in the group. Focus groups generally involved 3–15 individuals.

To guide discussions, a questionnaire was used which had four key themes:

1. **Fishery characteristics:** information on catch and income-composition, the fishing gear and methods used, and the length, frequency and location of fishing trips.
2. **Fishing costs and inputs:** estimates of key variable fishing costs, capital costs and labour use.
3. **Views and attitudes:** in relation to fishery management, the current state of the resource, future expectations and likely responses to changes in prices and catch rates.
4. **Household characteristics and livelihood strategies:** information on fisher's households and sources of income and food.

Wards in which fishers or community leaders were sampled are presented in Table 1. A total of nine focus group discussions were held with different Brooker Island fishing groups. Additional discussions were held with fishers from Motorina, Bagaman and Panaeati Islands. Community leaders on Panaeati and Panapompom Island and trade-store operators on Brooker and Panaeati Islands were also interviewed and consulted. Time constraints meant that fishers from Kimuta and Panaumara wards were not sampled while Misima Island ward was visited but no local shark fishers were encountered. Receipt data collected in the second stage of fieldwork suggests that these latter wards made minor contributions to the LLG's total shark fin production.

While an attempt was initially made to collect quantitative information about catches and income, respondents had difficulties recalling such information. Given these limitations, information on shark fin trade provided by buyers and NFA were relied upon to understand these aspects of the fishery.

The second stage of fieldwork took place in Alotau which is the main market destination for shark fin produced in the Milne Bay Province. Unstructured interviews and quantitative data collection was undertaken with the two major large-scale buyers of shark fin. Discussions focused on the characteristics of purchasing and exporting activities and their views on management and resource status. Data collected included historical price lists, purchase receipts and records and financial export reports. Two large-scale buyers of other marine commodities were also sampled. Additional data on boat, fishing gear and food costs were also opportunistically collected from trade-stores, boat dealerships and supermarkets. Discussions were also held with Provincial Fisheries Officers on issues relating to the shark fishery in the Milne Bay Province.

3.2.2. Collation of secondary data

Detailed purchase data were obtained from NFA for five commodities which were identified during field work as major income sources for the communities visited. These included shark fin (for both the Louisiade Rural LLG and Milne Bay Province), beche-de-mer, trochus shell, fresh fin-fish and black-lip pearl shell (*Pinctada margaritifera*). This data consisted of purchase quantities (in kg), date and seller and purchaser name and covered the period January 2007 to June 2014. Discussions with NFA staff and marine commodity buyers indicated that these purchases are largely sourced from the small-scale sector. Population statistics were sourced from the 2000 (NSO, 2002) and 2011 (NSO, 2014) PNG census and ward level household numbers from the 2000 census were projected to 2014.

3.3. Data analysis

NFA data on shark fin purchases from Louisiade Rural LLG fishers/sellers were analysed to explore production trends and influencing factors using an Ordinary Least Squares (OLS) econometrics approach using Eviews software. Collected price data were then applied to the shark fin purchase data to calculate and analyse the income earned by fishers from the sale of shark fin. NFA purchase data for other marine commodities and associated price data were also combined to compare shark fin sales income to sales from other marine commodities for the 2007–2014 period (which captures years prior and post sea cucumber fishery moratorium). Collected price data were converted to real 2013 PNG Kina (K) terms to adjust for inflation and matched to NFA purchase quantity data. While the NFA data includes monthly purchase quantities, collected price data related to intermittent points in time and for some commodities were specified in finer detail relative to the NFA data (e.g. by grade). Therefore, some assumptions were required to estimate the sales income earned by Louisiade Rural LLG communities. These are now outlined, first for shark fin and then for other marine commodities.

Table 2
Fin type and grade composition of shark fin purchase receipts for an Alotau buyer.

Fin type	Average proportion of monthly total	Standard deviation	Fin grade	Average proportion of monthly total	Standard deviation
Caudal	0.18	*0.02*	Grade 1	0.33	*0.16*
			Grade 2	0.19	*0.07*
			Grade 3	0.19	*0.10*
			Grade 4	0.19	*0.06*
			Grade 5	0.10	*0.03*
Dorsal	0.20	*0.03*	Grade 1	0.26	*0.17*
			Grade 2	0.22	*0.07*
			Grade 3	0.19	*0.10*
			Grade 4	0.23	*0.08*
			Grade 5	0.10	*0.04*
Pectoral	0.52	*0.05*	Grade 1	0.26	*0.10*
			Grade 2	0.18	*0.06*
			Grade 3	0.17	*0.09*
			Grade 4	0.31	*0.05*
			Grade 5	0.07	*0.04*
Belly	0.10	0.01	n.a.	n.a.	n.a.

3.3.1. Shark fin income

Shark fin prices were sourced from historical price lists provided by buyers. Prices were specified by '*fin type*' and '*grade*'. Fin type included '*belly*' (pelvic), '*caudal*', '*pectoral*' and '*dorsal*' and all fin types (except belly) were graded by size (cut fin length). NFA shark fin purchase data, however, are aggregated rather than itemised by fin type or grade. Therefore, detailed purchase receipts that were collected from buyers and which report prices and quantities by fin-type and grade per purchase were used to disaggregate the NFA data into quantities by fin-type and grade. Assumed prices could then be matched to quantities to calculate the total value of income generated.

A total of 333 purchase receipts for the periods October 2012 to January 2013 and October to November 2014 were analysed for this purpose.[3] The composition of purchases by fin type was relatively consistent, while composition by fin grade was variable (Table 2). Given a lack of alternative data, the average monthly composition by both fin type and grade was applied to disaggregate the NFA purchase data for all years into quantities by fin type and grade. Each buyers' set of reported prices could then be applied directly to the quantities to calculate income generated. Two additional companies reported purchases from Louisiade LLG fishers between 2007 and 2014 but only accounted for 4% of total purchase quantities for the period. To estimate the value of these other purchases, an average of prices from the two dominant companies was used.

While sales of shark fin by fishers to trade-stores are indirectly captured in the NFA purchase data when a trade-store sells to a large-scale buyer, they could not be separately quantified. Trade-stores capture a share of the income generated from shark fin by buying from fishers at low prices and selling to Alotau buyers at relatively high prices. While such income redistribution is not quantified here, its impacts on welfare are likely to be reduced given the communal nature of Louisiade LLG communities.

3.3.2. Other commodity income

One company's beche-de-mer price lists for 2007 and 2009 were used to estimate the income generated by beche-de-mer purchases for both years while median prices were assumed for 2008 purchases. NFA purchase data for beche-de-mer specified 31 species while the collected price data only included 15 species. Three of the NFA species missing from the price data accounted for 5 per cent of Milne Bay purchases. Prices for these species were sourced from Kinch (2004) and projected using a linear relationship (estimated using Ordinary Least Squares (OLS)) between all species common to both Kinch (2004) and the price data set. A proxy price was assumed for the remaining 12 species which only accounted for 0.1% of purchases. Prices for some species were also specified by grade but given a lack of data on grade composition, median prices across grades had to be assumed.

NFA purchase data for fin fish were in aggregated form. Fin fish purchase and price data were also provided by one company for the January 2012 to October 2014 period (this company dominates Milne Bay fish purchases) and were reported for three species groups: spanish mackerel, coral cod and other fish. Information on the species composition of purchases from the company data was applied to the aggregated NFA data to estimate quantities and values by fish species.

The estimation of value for both trochus and black-lip pearl shell was relatively straightforward with typically only one price being specified for each. Collected price data revealed that the same price prevailed for black-lip pearl shell in 2009, 2012 and 2014 and so this single price was maintained for all years analysed. Company prices for trochus shell were also available for the same years and a consistent monthly price series was assumed for the purpose of calculating income generated by trochus production.

4. Results

4.1. Fieldwork observations

4.1.1. Fishing characteristics

Fieldwork observations and discussions confirmed that shark fishing is a major livelihood activity in the Louisiade LLG. Most shark fishing occurs in calm weather months between November and February (this is also the time when cash is most needed given low crop availability).

Fishing expeditions involve extended family groups including women and children. Generally, males in the group fish, collect bait and process catch and the head male is the key decision maker, deciding when to embark and end an expedition. Women maintain the camp and cook, and sometimes may assist with fishing and drying of fins. A typical shark fishing expedition will see a family group camping on islands in the area of fishing grounds for up to a

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[3] While additional receipts were collected from island trade-stores, it was observed that these trade-store purchases were dominated by low value fin types and grades which would bias downwards the value estimates. These data were excluded from the analysis.

month, depending on weather.[4]

Traditional '*sailaus*' (wooden planked, single outrigger sailing canoes that are 4–12 m long) (Smaalders and Kinch, 2003) and/or fibreglass dinghies (5.8–7 m long, powered by 30 or 40 hp outboard motors) were most often reported as being used for shark fishing. However, minimal use of the latter was observed during fieldwork. This was likely to be due to the high cost of fuel and the low availability of cash. Small, wooden paddle canoes were also reported to be used but to a lesser extent. When fishing, larger sailaus are normally operated by 5 or 6 crew, smaller sailaus by 2 or 3 crew and dinghies by 4 crew.

Sharks are typically targeted along barrier reefs and inside lagoons within an island's territory (e.g. favoured grounds for Brooker Islanders are in the Bramble Haven, west of Brooker Island). Demersal longlines are predominately used and these vary between high quality tuna longlines (consisting of rope mainline, wire traces and stainless steel clips) and lower quality nylon monofilament longlines. Reported hook numbers ranged from 5 to 40 hooks, with greater hook numbers associated with higher quality gear. In two cases, high quality gear had been pilfered from a Taiwanese longline vessel which had grounded on a nearby reef in 2000–01 (Kinch, 2001). Interestingly, those who possessed higher quality gear also typically exhibited greater wealth and social standing within the community. Surface longlines, and to a lesser extent hand-lines, were also reported to be used (normally if fishing from a canoe given the relative ease with which such gear can be handled).

Bait is typically collected during the day using spear or line methods. Most commonly reported baits included moray eel (a preferred bait as its tough texture makes it last longer on hooks), stingray and fish. Longlines are then set in the late afternoon and pulled the following morning. Some fishers also reported setting during the day, although all fishers asserted that sharks were more readily caught at night. Calm weather, a new moon and weak ocean currents were also cited as positively impacting catch rates.

Fishing is focused on the production of dried shark fin, with sharks typically finned and the carcass dumped at sea or buried. While the meat of smaller sharks is sometimes kept and dried (to be traded or consumed), shark meat is generally considered a famine food, eaten when other protein substitutes are not available. Fishers dry the fin themselves, normally for 2 or 3 days (up to a week in cooler conditions), after which the fin can then be easily stored. Although fishers could not identify species caught, some common names were frequently referred to, such as hammerhead shark, tiger shark and white-tip shark. Other names included lemon shark, yellow shark, diamond shark, brown shark, lazy shark and black-tip shark, most of which cannot be readily attributed to species.

4.1.2. Downstream purchasing and trade

The majority of dried fin is sold to large-scale buyers in Alotau. A small amount is also sold to on-island trade-stores which operate as middle-men and have pre-established agreements with Alotau buyers, typically offering fishers lower prices. Hence, fishers indicated that they only sold fin to trade-stores when desperate for cash. Analysis of trade-store receipts revealed that trade-store transactions were dominated by low volumes of low grade fin. This suggests that fishers also selectively sell their less valuable fin to trade-stores as a means to minimising their income losses.

Currently, there are only two large-scale buyers in Alotau who buy shark fin produced in Milne Bay. They also trade in other marine commodities including trochus shell, black lip pearl shell, fin fish and crayfish (one company), and previously beche-de-mer. Both buyers previously exported shark fin although one of the companies had recently stopped given recent falls in fin prices in export markets. This company was instead sending their fin to an exporter based in Port Moresby. The other buyer had been exporting fin to Hong Kong in large shipments once or twice a year.

The geographical isolation of islands in the Louisiade Rural LLG significantly restricts access to buyers in Alotau. With the operation of the sea cucumber fishery, buyers previously sent out vessels to purchase beche-de-mer and other marine products but this has now become less viable. On Brooker Island, the recent acquisition of a work-boat (donated by the previous local Member of Parliament) has reduced these market access impediments by providing a more efficient means to transport large volumes of commodities. It is used to transport fish (in eskies) and other commodities (including shark fin) to Alotau to sell. However, it still takes over a day to reach Alotau.

4.1.3. Fishers' views and characteristics

With the closure of the sea cucumber fishery, shark fishing is viewed as being of great importance given that shark fin provides one of the few sources of income. The focus on shark fin is evidenced by all fishers suggesting that they wouldn't target shark if the fin had no value. Access to shark fishing gear and knowledge may currently be a constraint to higher levels of participation in the shark fishery. A ward councillor on Panaeati believed that more people from his island would fish for shark if it wasn't for the high cost of shark gear. Similarly, during additional fieldwork on Sariba Island in the nearby Bwanabwana LLG, a fishing group noted that their ability to fish for shark was limited by the knowledge of how to target shark.

Many fishers believed that catch rates and shark size had declined. A buyer also indicated that they now receive fewer large shark fin. While these widespread observations indicate declining stocks, the reliability of these views could not be further explored given a lack of relevant shark and fin size data. Fisher awareness of what these observations imply in terms of shark stock status was mixed, despite recent experiences in the sea cucumber fishery. Some suggested that declines were short-term and location-specific. Generally, though, there appears to be a low conservation ethic. This was evidenced by the observation of significant quantities of turtle and turtle eggs harvested during fieldwork, despite recent education efforts in the area going back over a decade.

Discussion of current management rules confirmed that there were no rules pertaining specifically to shark. There was also no evidence of community-based rules around fishing. NFA rules related to the sea cucumber ban and fin fish were typically discussed. There was no evidence of illegal sea cucumber fishing, but all fishers were interested to know when the ban would end. Most fishers indicated that fish size limits were not well followed due to low monitoring and the need for food.

4.2. Shark fin sales

4.2.1. Quantities and characteristics

Sampled receipt data suggests that the majority of fin produced in the Louisiade LLG may come from the smaller, less populated islands in the south of the LLG: 92% of observed transactions came from Brooker, Bagaman, Motorina and Panaeati Islands while only 7% came from Misima Island (1% was unidentified).

Analysis of NFA shark fin sales data, shows that a total of 3699 kg of dried shark fin were produced by Louisiade fishers between

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[4] One Brooker fishing group reported that they had been camping on the island of Enivala (typically used as a fishing camp base) for a period of about 12 months, potentially reflecting a response to population pressures on Brooker Island.

January 2007 and July 2014. Monthly production quantities averaged 41 kg, but varied considerably. Visual inspection of the data suggests that quantities are higher during the operation of the sea cucumber fishery (2007–2009) and post-2012 (Fig. 2). A striking feature of the data is the large outlier in September 2008, in which 560 kg was reported to be sold. Discussions with fishers by J. Kinch has indicated that this outlier was associated with a large quantity of fin that was obtained by a Brooker Islander from a grounded tuna longliner.

Given these observations and observations in the field, the OLS econometric model was estimated by aggregating quantities into quarterly periods and regressing on a series of dummy variables specified for the March, June and December quarters; for quarters in which the sea cucumber fishery was open; for quarters in the post 2012 period; and for the September 2008 quarter which is a positive outlier. Shark fin prices and a time trend variable were also incorporated into the model. The time trend variable, however, was shown to be insignificant and was consequently dropped. Relevant tests rejected the existence of serial correlation (Durbin-Watson) and heteroskedasticity (White test) in the final model. It explained much of the variation in shark fin production (R square of 0.88) and all coefficient signs were as expected (Table 3). Only the December quarter dummy variable was insignificant at the 5% level (but was significant at the 10% level).

The model reveals a positive relationship between prices and fin production: holding all other variables constant, production of shark fin in any quarter on average increased by 18 kg for every K10 increase in price.[5] Consistent with this, the model suggests a price elasticity of supply of 2.1 at the sample means. This indicates a strong propensity for fishers to increase their production of shark fin in response to higher prices. This result is consistent with anecdotal evidence of reduced shark fin production at the time of fieldwork due to historically low prices and suggests that reduced prices have been an important driver of shark fin production declines.

Table 3
Regression results for linear OLS estimated model of quarterly shark fin purchase quantities.

Independent variable	Coefficient
Constant	−260.84** (119.39)
Beche-de-mer	68.09** (24.8)
March quarter	62.97** (23.73)
June quarter	99.68** (23.8)
December quarter	49.84** (24.61)
September 2008 outlier	473.79** (48.53)
Price	1.8** (0.84)
Post-December 2012	119.22** (25.71)
R-squared	0.882
Adjusted R-squared	0.845
S.E. of regression	43.61
Sum squared resid	41,846
Log likelihood	−151.18
F-statistic	23.58
Prob(F-statistic)	–
Mean dependent var	120.50
S.D. dependent var	110.76
Akaike info criterion	10.61
Durbin-Watson stat	2.05
N	30

***Significant at the 1% level; **Significant at the 5% level; *Significant at the 10% level. Standard errors in parentheses.

The model also confirms some seasonality in production, with quantities in the March, June and December quarters significantly higher than in the September base quarter on average. The average quantity of fin sold in the September quarter was 115 kg. The model suggests that on average and holding all else constant, fin quantities were 55% higher in the March quarter, 87% higher in the June quarter and 43% higher in the December quarter relative to the September quarter mean. Tests of equality between quarterly dummy coefficients reveal that quantities in the June quarter are statistically greater than December quarter quantities and are only statistically different to March quarter quantities at the 10% level, while the March and December quarters are not statistically different. While most shark fishing was reported to occur in December and March quarters, fishers were observed to stockpile fin. This suggests that the lag in the sale of fin indicated in the model is possible.

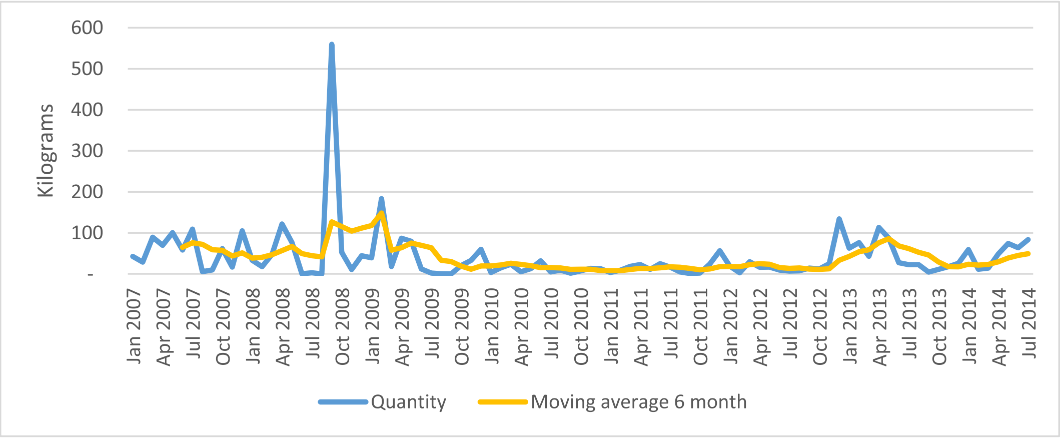

Fig. 2. Monthly quantities of dried shark fin sales by Louisiade LLG fishers, January 2007 to July 2014.

The model also confirms that the operation of the sea cucumber

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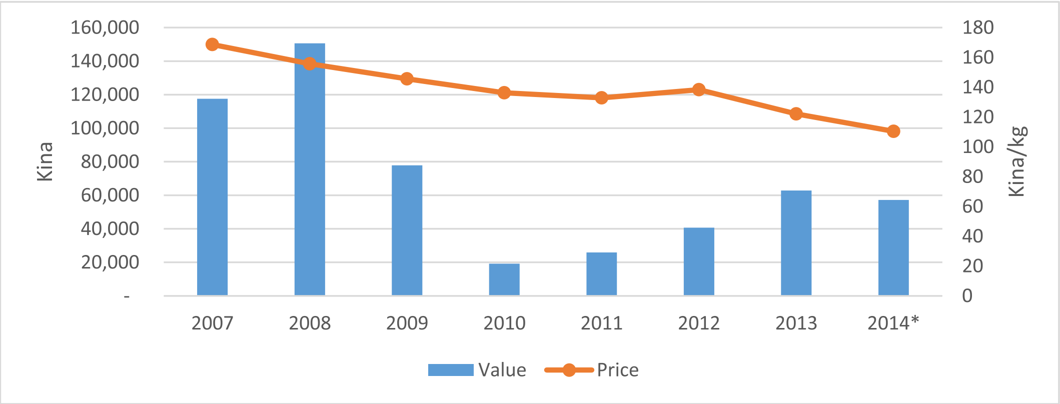
[5] In 2014, a PNG kina was equivalent to approximately $0.40 USD.



Note: * 2014 is partly predicted using the estimated model of shark fin purchases

Fig. 3. Estimated real income generated by shark fin purchases from Louisiade LLG sellers and assumed prices for shark fin in real terms (2013 kina terms), 2007 to 2014.

fishery had a positive and significant impact on shark fin quantities. Holding all else constant, production was on average 68.1 kg higher per quarter while the sea cucumber fishery was open. This runs counter to expectations that shark fin production would have increased to replace lost income. This could reflect that there was greater market access while the sea cucumber fishery was operating (with buyers sending vessels out to islands) or the fact that fishers were spending more time in fishing grounds (due to the cash returns offered by beche-de-mer production), allowing greater targeting of shark.

Holding constant all other variables, the post-December 2012 dummy variable also indicates an average elevation in shark fin production of 119.2 kg per quarter. The announced extension of the sea cucumber moratorium in 2012 may have contributed to this, with fishers increasing shark fin production to replace lost anticipated income. However, if anticipated beche-de-mer income needed to be replaced in 2013, it seems strange that the same response hadn't eventuated following the closure initially. The more likely contributing factor is the operation of the Brooker Island work boat from early 2013, with sampled receipt data for months in 2014 indicating that Brooker Islanders made a dominant contribution to shark fin production. With increased access to buyers, Brooker fishers may have had an increased incentive to produce shark fin as well as other marine commodities.

4.2.2. *Shark fin sales income*

Consistent with sales quantities, estimates of shark fin income earned by Louisiade LLG fishers were highest in the three years during which the sea cucumber fishery operated: K117,600 in 2007, K150,600 in 2008 and K77,900 in 2009 (Fig. 3). Following the beche-de-mer ban in 2009, shark fin income is estimated to have fallen by 75% to K19,200 in 2010 due to a similar fall in purchase quantities. In the three years that followed, income from shark fin followed an upward trend to K60,800 in 2013. As purchase data was only available to July 2014, shark fin income in 2014 could not be directly estimated but was predicted at K57,200 (using the estimated model and assuming unchanged prices in 2014). A 35% decline in assumed unit prices (in real terms) from K169/kg in 2007 to K110/kg in 2014 also contributed to the fall in shark fin income.

4.2.3. *Costs of shark fishing*

Fieldwork observations indicated that variable fishing costs are low. Fuel is the largest variable cost, but only if an outboard powered dinghy is used. Nearly all fishing observed during fieldwork used sailaus. This contrasts with the high level of dinghy use reported by Kinch (2001) and Foale (2006) at the height of the sea cucumber fishery. Low cash availability following the sea cucumber ban may mean that fishers were avoiding dinghy use, particularly given the high cost of fuel: up to K6.50 (2.55 USD) per litre in the southern islands (although most fishers tried to source fuel from Misima Island where it was K5.50 or Alotau at K4.00). This would also explain the recent low investment in new dinghies.

Other variable costs were minor. Gear replacement costs were reported to mainly be associated with replacing fish hooks (at a reported cost of K5–12) along with the occasional requirement to replace lost or damaged lines when required. Costs associated with food and stimulants (tobacco and betel nut) were also frequently mentioned, but once again, were low.

The calculation of capital costs is also difficult given that both dinghies and sailaus have multiple uses. Most dinghies were acquired for sea cucumber fishing (often via debt arrangements with buyers)[6] and there is currently minimal investment in new dinghies: only one new dinghy was observed on Brooker Island but it was acquired with government funding. The cost of purchasing a 19 ft dinghy fitted with a 40 hp outboard new from the single supplier in Alotau was K9,226 for the dinghy and K12,256 for the outboard (at the time of fieldwork). The usually non-cash basis for acquiring sailaus further complicates their valuation. For example, one fishing group reported paying K500, a '*bagi*' (a shell necklace), two pigs and some clay pots for their sailau and also provided food to the builders while it was being built (a custom).

While shark fin income should normally be considered net of costs to better evaluate the benefits flowing to local communities, cost estimation is difficult and in any case is likely to be low given the current characteristics of shark fishing. For this reason, gross income is focused on in the remainder of this paper.

4.3. *Comparison to other income sources*

Focus group discussions indicated that nearly all cash income was earned from marine commodities. Shark fin was consistently

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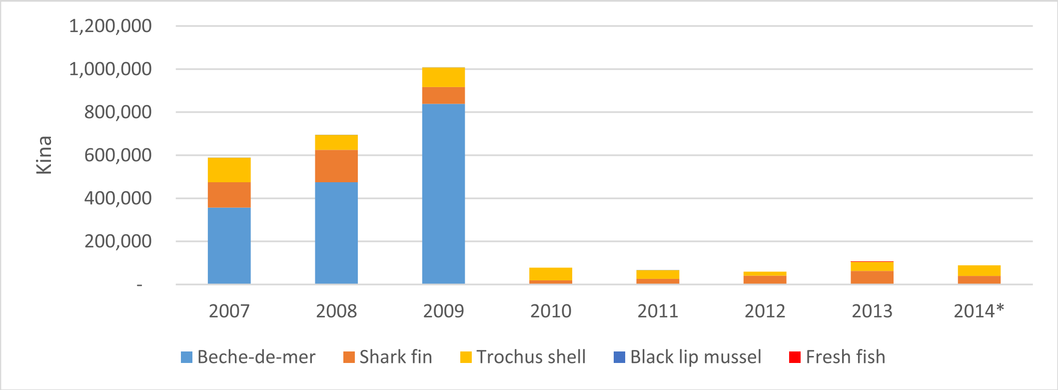
[6] Although one fisher indicated that the debt associated with his dinghy only needs to be repaid if the sea cucumber fishery reopens.



Notes: *2014 excludes data on fresh fish which were unavailable and represents a preliminary estimate for shark fin which was estimated using the model of shark fin purchases.

Fig. 4. Income in real terms from key marine resource commodities for Louisiade LLG (2013 kina terms), 2007 to 2013.

ranked as the most important source of income during focus group discussions. More often than not, trochus shell was ranked second followed by fish. Copra, crayfish[7] and black-lip pearl shell were sometimes mentioned but were typically ranked as being of low importance. Copra was typically cited as a previous income source by many respondents but low prices meant that most didn't consider this as a viable income option. Indeed many plantations in the area are now senile. Remittance income was never cited as an income source. This is consistent with observations by both Kinch (1999) and Friedman et al. (2006) of minimal amounts of remittance income in Louisiade Rural LLG island communities.

Total income earned from the sales of key marine commodities was estimated to be substantially higher in the three years in which the sea cucumber fishery was operating (Fig. 4) at K588,000 in 2007, increasing by 18% to K695,000 in 2008, before increasing again by 45% to K1.01 million in 2009. During these years, beche-de-mer was by far the dominant source of income, accounting for 61%, 68% and 83% of annual incomes, respectively. The dramatic increase in beche-de-mer income in 2009 partly reflects an increase in prices but also reflects higher quantities, potentially due to a ramp up in effort given the impending closure, with fishers given advance notice of the moratorium.

In 2009, 2010, total income is estimated to have dropped substantially by 92% to K78,000. Income from trochus shell dominates, accounting for 75% of income while shark fin makes up the remaining income. Total income remained relatively stable for the 2010 to 2012 period before increasing from K59,600 in 2012 to K106,700 in 2013. Fish sales also made a contribution to income for the first time, although this was only very small at K859, generated by two purchases from a Brooker Islander seller. Income was estimated to decline in 2014 to K88,600 in 2014 although this includes a predicted estimate for shark fin and excludes fish sales (which were not available for 2014).

Over the full period of analysis, shark fin and trochus shell make similar contributions to income. Out of the two commodities, shark fin income was most important in 2012 and 2013, accounting for 68% and 59% of total income in each year respectively. However, in 2014, income from trochus shell is estimated at K49,300 and outweighs the predicted estimate of shark fin income for the same year of K39,200.

Calculation of household level income levels provides an accuracy check for these income estimates. Using census based household numbers for wards heavily engaged in shark fishing, total household income is estimated to have averaged K653 between 2007 and 2014, with a peak of K1,945 in 2009 and a low of K108 in 2012. NFA, (2006) reported average household incomes in areas closer to Alotau for Milne Bay[8] sites (and thus excluding Louisiade LLG) of K984 kina per year (average) while the lowest estimate for a single site was K240. Kinch's (2001) estimates of income for Brooker Island fishers at a time when the beche-de-mer fishery was open equates to K877 per household. Overall, our income estimates appear reasonably consistent with previous estimates.

5. Discussion

Shark fishing and the production of shark fin has been shown to be a significant livelihood strategy for small Louisiade LLG island communities in the south of the LLG area. This is likely the result of the proximity of these islands to extensive shallow reef habitat as well as their socio-economic characteristics: geographical isolation, limited infrastructure (e.g. electricity), low market access and scarce resources. Not only do these characteristics limit food and income opportunities but they also make shark fin production an attractive livelihood activity: shark fin are economically valuable, accessible, easily processed (with low technology), easily stored (without refrigeration) and easily transported.

The sole focus of fishers on shark fin contrasts with other developing countries such as Indonesia (Blaber et al., 2009; Vieira and Tull, 2008) and India (Hanfee, 1997; Verlecar et al., 2007) where other low value shark products (i.e. meat, skin, cartilage, teeth, jaws, liver oil) are also consumed and/or sold. The contrasting situation in Louisiade communities likely reflects the underdeveloped state of local markets and market incentives; limited access to

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[7] While crayfish was mentioned, data on crayfish production was not accessed as part of the study. However, information provided by large-scale buyers indicates that it has been a relatively minor source of income for Louisiade LLG island communities.

[8] This research sampled twenty sites across the following five LLGs in Milne Bay: Alotau, Huhu, Duau, Suau and Bwanabwana.

buyers; a dominance of subsistence sourced food; and a relative abundance of alternative marine resources.

Following the closure of the sea cucumber fishery, the income from shark fin production has become central to current household consumption risk management strategies. This reflects the lack of alternative income earning options but also the timing of shark fin sales (during times of low food availability). Furthermore, the likely overfished status of trochus stocks (Foale, 2006; Kinch, 1999) and overfished status (and slow recovery) of sea cucumber stocks (Pomat, 2012) means that shark fin production is likely to remain an important income earning activity in the medium-term.

The sea cucumber fishery is focal to the current research as its operation has been shown to be associated with higher levels of shark fin production. This may reflect a combination of factors: time spent harvesting sea cucumber may provide greater opportunities to target shark; higher incomes from beche-de-mer may allow greater use of dinghies to harvest sharks more efficiently; and greater access to buyers via purchasing vessels provides a greater incentive to produce shark fin (increased fin sales since the Brooker work-boat began operating indicates that this factor may be particularly influential). Whatever the cause, the fall in shark fin production means that the moratorium may have had some positive localised impact on the status of shark stocks, further contributed to by falling prices for shark fin. For these reasons, a reopening of the sea cucumber fishery will need to be managed carefully, not only to ensure continued recovery of sea cucumber, but also to avoid overharvesting of local shark resources.

NFA's fisheries management is guided by the *PNG Fisheries Management Act's* and its objective to "*promote long-term conservation, management, and sustainable use of the marine living resources of Papua New Guinea for the people of Papua New Guinea*" (Independent State of PNG, 2015). The Act specifies a number of principles two of which are relevant here: to maintain or restore stocks to maximum sustainable yield (MSY) levels; and, to improve the welfare and livelihood of fishing communities. It also recommends a precautionary management approach.

Given the current research findings, the pursuit of two initiatives might assist in meeting NFA's management objectives for shark resources in Milne Bay: (1) implementing management of small-scale shark catches to prevent further catch increases; (2) developing community income earning capacity. These initiatives are now discussed.

5.1. *Improving the management of local shark fisheries*

Shark resources in Milne Bay can be described as being close to an open access resource. Although marine resource use and access arrangements govern where fishers can fish, there is no limit on how much shark can be harvested. Such open access inevitably leads to overexploitation. This "*tragedy of the commons*" (Hardin, 1968) outcome is linked to two characteristics of fishery resources: (1) it is difficult to exclude people from extracting fishery resources (excludability); and (2) ones' current use of the resource rivals (or subtracts from) others' future use of the resource (rivalry) (Ostrom, 1990). If these characteristics persist, individual incentives to compete and maximise one's own share of the catch overrides the collective incentive to sustain the resource for the benefit of all (Berkes, 2006).

To address these issues, some form of control of shark catch in Milne Bay is needed. Such an action would also meet the *PNG Fisheries Management Act's* requirement for MSY harvesting and precautionary management. Limited information on shark stock status in Milne Bay, the high cost of monitoring and enforcement in the area and the relatively low economic value of these small-scale fishing activities[9] require careful consideration of the options to do this. In this context, low cost management that builds on and/or makes use of current social and governance arrangements is most likely to succeed.

Government management of fishery catches typically utilises input controls (which restrict the inputs that fishers can use) and/or output controls (which directly limit the quantity that fishers can catch). For Milne Bay's shark fisheries, potential input controls could be on gear, vessel characteristics and fishing season. For example, the observed influence of gear and vessel characteristics on fisher efficiency, suggests that gear and vessel controls could initially provide an effective means to reducing or controlling catches.

There are some limitations, however, to using input controls. Under input controls, fishers have scope to increase their effort by investing in non-restricted inputs (Pascoe and Robinson, 1998; Kompas et al., 2004). For example, Milne Bay small-scale fishers typically have a low opportunity cost of time. Therefore, a marginal increase in fin prices could provide an incentive to increase their input of time into shark fishing to increase catch and income. Monitoring of compliance to input controls could also be difficult given the isolated nature of fishing activities (and given the already low level of compliance indicated by fishers). Input controls also do not address the competitive incentives to maximise one's own share of the catch previously mentioned.

Output controls which involve an allocation of catch shares in the form of individual transferrable quotas are often promoted as the best approach to reducing such negative incentives (Grafton et al., 2006). However, such an option would be too impractical and costly for the small-scale settings of Milne Bay. Foale (2006) in his discussion of shark fishing in the Bwanabwana Islands, recommended the setting of catch limits at the provincial level. However, at the provincial scale competitive incentives between island communities could in fact increase: it would give each community an incentive to race-to-fish to maximise their share of the province's allowable catch. Such incentives would lead to over investment in fishing inputs and capital (which could be put towards other productive livelihood activities) and further contribute to inter-island tensions over marine resources (Kinch, 2003).

Ward level quotas, however, might be a better option. The allocation to each ward of an excludable right to a fixed share of the Province's allowable catch would reduce competitive incentives between islands and complement current marine resource use and access arrangements.[10] Furthermore, individual fisher incentives to maximise their own share of the ward's catch would, to some degree, be overridden by the communal and co-operative characteristics that exist at the level of ward communities. Enforcement could take advantage of NFA's already existing buyer monitoring processes (although these processes may need strengthening) with buyers in many cases already recording at the ward level. Finally, allocation of community property rights over fishery resources may have the potential to improve resource stewardship incentives (Charles, 2011). The migratory nature of most shark species may limit the development of such incentives, although for more

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[9] While the focus here is the small-scale sector, the impact of illegal longlining must be better understood. Indeed, the outlying shark fin sale in the September 2008 quarter obtained from a grounded longliner indicates the potential magnitude of difference between small-scale and illegal large-scale catches. However, without better information on illegal shark fishing activity, it is difficult to evaluate the relative net benefits of management initiatives focused on better managing the small-scale sector versus large-scale activities.

[10] With the exception of Misima Island, wards within the Louisiade LLG are predominantly specified at island level.

stationary reef shark species such benefits may be more forthcoming.

Ward based quotas could also be a positive step towards community based co-management (Berkes, 2007; Johannes, 2002; Pomeroy, 1994). Greater community involvement in fishery research, monitoring and decision making often sees local socio-economic and ecological circumstances better reflected in fishery management resulting in improved compliance and harvesting practices (Berkes, 2007; Gutiérrez et al., 2011; Pomeroy, 1994). Co-management can also create learning opportunities that increase awareness of basic sustainability issues (a need previously indicated by Foale and Manele (2004) for Milne Bay) and encourage greater community support for management. Co-management while beneficial can also be associated with its own set of challenges (e.g. see Agbayani and Siar, 1994; for the PNG context Foale and Manele, 2004). Indeed, despite a desire for greater fisheries co-management in PNG, achieving it has typically been hampered by governance issues (Benson, 2012).

5.2. *Developing income earning capacity*

Any enforced reductions in shark catch will likely negatively impact the welfares of Louisiade communities (particularly with a closed sea cucumber fishery) making communities less resilient. This runs counter to NFA's principal of improving the welfare and livelihoods of fishing communities. The removal of another source of income from fishers may also negatively impact any social capital that exists between fishers and NFA, making future management of small-scale fisheries more difficult. For these reasons, government initiatives to develop both current and alternative livelihood and income sources to improve community resilience and increase community support for better resource management should be a priority if shark resource management is to be pursued.

The operation of a work-boat by Brooker Islanders to supply fresh finfish and crayfish to Alotau offers some promise. The distance to Alotau (a twenty four hour trip), fuel costs, a lack of on-board refrigeration (eskies were being used) and a limited capacity to maintain the vessel will challenge the viability of this operation. Providing direct government assistance for development of such ventures in other communities could have positive impacts on the welfare of Louisiade communities. But ensuring that such fishery development is sustainable is also a priority. Such initiatives could also allow the development of markets for already produced commodities. For example, the development of markets for other shark products (e.g. meat, jaws, oil, cartilage and skin) would reduce wasteful finning, although should only be pursued once appropriate restrictions on shark catch are in place. The potential for trochus shell to offer increased income is probably low, particularly given the likely overfished status of trochus stocks (Foale, 2006).

Projects aimed at developing alternative income sources need to be carefully tailored to the socio-economic circumstances of communities to avoid failure and unforeseen negative impacts (Cinner, 2014; Hill et al., 2012; Pomeroy et al., 2006; Sievanen et al., 2005). Mariculture has potential to take advantage of Milne Bay's abundant oceanic and labour resources, but ventures have typically failed in PNG (Uwate et al., 1984; Coates, 1989; Hambrey Consulting, 2011). Common challenges have included competition from imports, a lack of a domestic feed manufacturer, low brood-stock availability, capital constraints, low skills, low worker motivation, limited transport and storage infrastructure, poor planning and traditional user right issues (Hambrey Consulting, 2011).

The culture of Gold-lip Pearl Oyster (*Pinctada maxima*) by a foreign firm at Samarai Island in the Bwanabwana Islands provides one of the few examples of an ongoing successful mariculture venture in Milne Bay[11] (Hambrey Consulting, 2011). However, the required capital investment, skills and technology are beyond the current capabilities of local communities. The culture of giant clam (*Tridacna* spp) for restocking and income generation has also been previously discussed as a potential activity for Milne Bay communities (Kinch, 2002), though successful ventures have not eventuated. Seaweed farming has been identified as being highly suited to the physical (FAO, 2002) and socio-economic characteristics (Kinch et al., 2003) of Milne Bay and could offer some promise. Commercial ventures were established by a foreign company on the Suau coast and Trobriand Islands in Milne Bay in 2010 (Hambrey Consulting, 2011). A small-scale seaweed trial was also observed during fieldwork on Paneatti Island. Recent discussions with the local provincial fisheries officer have indicated an increased focus on seaweed culture promotion and development. .

Further development of diving tourism may have potential, with Milne Bay already being an attractive dive-tourism destination. Shark diving, specifically, has also been shown to generate substantial economic benefits in a number of developing countries (Rowat and Engelhardt, 2007; Clua et al., 2011; Cardenas-Torres et al., 2007) and has previously occurred in other parts of PNG. If shark diving tourism was developed in Milne Bay and was seen to generate benefits for specific communities, greater community incentives to conserve shark may evolve within those communities. However, current dive tourism observed in the area appears to generate minimal benefits for local communities, with dive operators capturing most of the benefits and dive tourists spending little time and money in local communities.

The viability of sport fishing eco-tourism (where fish are returned alive to sea) has also been evaluated for parts of PNG (Sheaves, 2014). While it indicated significant economic opportunities, it also highlighted a number of impediments related to information constraints (about resource status, viable business models and the social characteristics of communities) and capacity constraints.

In summary, development of alternative livelihoods in Milne Bay has been difficult and will continue to be (Kinch, 2009). Higher level government initiatives and private-public partnerships may be a key element to creating development opportunities. Provision of technical and advisory services, ensuring thorough and realistic feasibility studies, providing financing mechanisms and developing a coherent government strategy will be essential (Hambrey Consulting, 2011). In any case, the current research indicates that low cash availability is limiting shark catches (by limiting dinghy use and limiting investment in high quality longlines). Therefore, any initiatives aimed at developing income opportunities must be accompanied by appropriate management of shark resources to ensure that the benefits generated for local communities by shark resources are sustained.

6. Conclusions

The current paper has shown that a number of Louisiade LLG island communities exhibit significant dependence on shark fin for income but that the sustainability of this income source may be declining. It has done this using available fisheries data and by collecting information and sales data from various fishery stakeholders. A potentially significant source of error for the current study is the patchiness and reliability of the data used. To address

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[11] Although J. Kinch's recent discussions with company staff has indicated that they wish to cease operations and are exploring whether there is external interest in taking over the operation.

these constraints, future studies may benefit from increased resourcing (particularly in terms of fieldwork time) and increased engagement with buyers of shark fin.

Despite these issues, the paper provides some valuable insights and recommendations. It recommends a “do something” approach that aligns with legislated management objectives and takes advantage of pre-existing governance and monitoring arrangements. First, adequate restriction of shark catches is a prerequisite. To do this, allocation of allowable catches at the ward level may improve fisher incentives, limit scope for increasing catch beyond intended limits and also represent a step towards community-based management. Such an approach takes advantage of NFA's currently existing shark fin purchase monitoring processes, so would be a low cost change. However, improved rules and penalties might be required to strengthen current monitoring if it is to form the basis for a catch scheme. Determining how to best allocate catches to wards will also make the implementation of such a scheme difficult.

Second, shark restrictions should be accompanied by initiatives to increase the income earning capacity of affected communities and allow greater socio-economic resilience. Visibly linking such initiatives to government efforts to increase shark resource sustainability may increase community acceptance of shark management efforts. While some options for developing income opportunities have been outlined, any option should be pursued with care and take into account the socio-economic characteristics of local communities.

The recommendations presented here are preliminary and based on research focused on a small part of the Milne Bay Province. The authors strongly advise against extending these recommendations to both the entire Province and PNG without additional locations specific research. Any change to improve shark management in the Louisiade LLG is likely to be best implemented as part of a national, multi-sectoral approach involving communities, all fisheries sectors and provincial fisheries administrations. Further research on the species composition of shark catches and their respective stock statuses would also be required to better inform any management intervention in Milne Bay and PNG more broadly.

Focusing management effort on sectors other than the small-scale sector may be more beneficial for shark stocks in the region. For example, it was pointed out that the significant outlier in shark fin sales reported here related to the grounding of an illegal commercial longliner. The difference between this quantity and quantities typically sold by fishers from the Louisiade Rural LLG gives an indication of the relatively greater impact preventing illegal longline fishing could have for reducing shark harvests and improving stock status. Similarly, the recent closure of the shark longline fishery is also likely to have significantly benefited the status of shark stocks in PNG.

In any case, early efforts to improve shark resource management in PNG will reduce the risk of overexploitation and avoid the need for the same drastic measures that were required for PNG's sea cucumber stocks. Furthermore, the development of improved shark resource management could lay the foundations for the development of similar and improved management approaches for the more economically valuable sea cucumber fishery when it opens. Indeed, in the case of the Louisiade LLG, many of the issues that management needs to address for shark identified here, were also issues that contributed to the rapid depletion of sea cucumber stocks. Preventing history repeating should be a government priority.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2016.12.009.

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