



Age, growth and maturity of the Australian blackspot shark (*Carcharhinus coatesi*) in the Gulf of Papua

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Abstract. Small-bodied coastal sharks are often caught as by-catch 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 an information-theoretic multimodel approach, the von Bertalanffy growth model fit the data best; parameters were $L_0 = 40.6 \text{ cm} \pm 0.8$, $L_\infty = 74.8 \text{ cm} \pm 2.1$, $k = 0.33 \text{ year}^{-1} \pm 0.06$. Length-at-maturity analysis indicated that males reach maturity at $L_{50} = 66.3 \text{ cm}$ (CI: 63.8, 71.4) and $L_{95} = 71.6 \text{ cm}$ (CI: 64.6, 74.2) cm while females matured at $L_{50} = 71.4 \text{ cm}$ (CI: 61.5, 72.01) and $L_{95} = 72.5 \text{ cm}$ (CI: 62.7, 74.0). Age-at-maturity estimates showed that both males ($A_{50} = 5.1 \text{ years}$ (CI: 4.6, 7.1), $A_{95} = 6.4 \text{ years}$ (CI: 5.1, 7.2)) and females ($A_{50} = 5.3 \text{ years}$ (CI: 3.5, 8.7), $A_{95} = 7.4 \text{ years}$ (CI: 3.6, 8.8)) reach maturity at about the same 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 but in need of ongoing improvements to fisheries management.

Additional keywords: elasmobranch, by-catch, fisheries, Papua New Guinea.

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Introduction

In recent years many species of chondrichthyans have faced large declines in population size leading to concerns about their conservation status (Dulvy *et al.* 2014). The main causes of declines are the effects of harvesting through various fishing practices, as well as habitat degradation, pollution and other factors (Stevens *et al.* 2000; Dulvy *et al.* 2017). The need to make fishing more sustainable and less ecologically damaging is urgent given the widespread declines, but these efforts are 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 (Simpfendorfer *et al.* 2011).

Small-bodied sharks that typically grow to a maximum length of less than 1 m are commonly caught in coastal areas

by a range of fishing gears, including gill-nets and trawls that target other species (Cortés 2002; Stobutzki *et al.* 2002; Harry *et al.* 2011). Sharks of this group 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 (White 2007; Taylor *et al.* 2016). Region- or population-specific information is therefore required to produce more accurate stock assessments (Smart *et al.* 2015) and improve fisheries management.

The Australian blackspot shark (*Carcharhinus coatesi*) is a common small-bodied carcharhinid shark found throughout northern Australia and Papua New Guinea (White *et al.* 2017). Taxonomic uncertainty led to earlier misidentification of this species in Australia as *Carcharhinus dussumieri* (white cheek shark) (Stevens and McLoughlin 1991; Stobutzki *et al.* 2002; Last and Stevens 2009). However, recent taxonomic work combined with molecular techniques distinguished *C. coatesi*

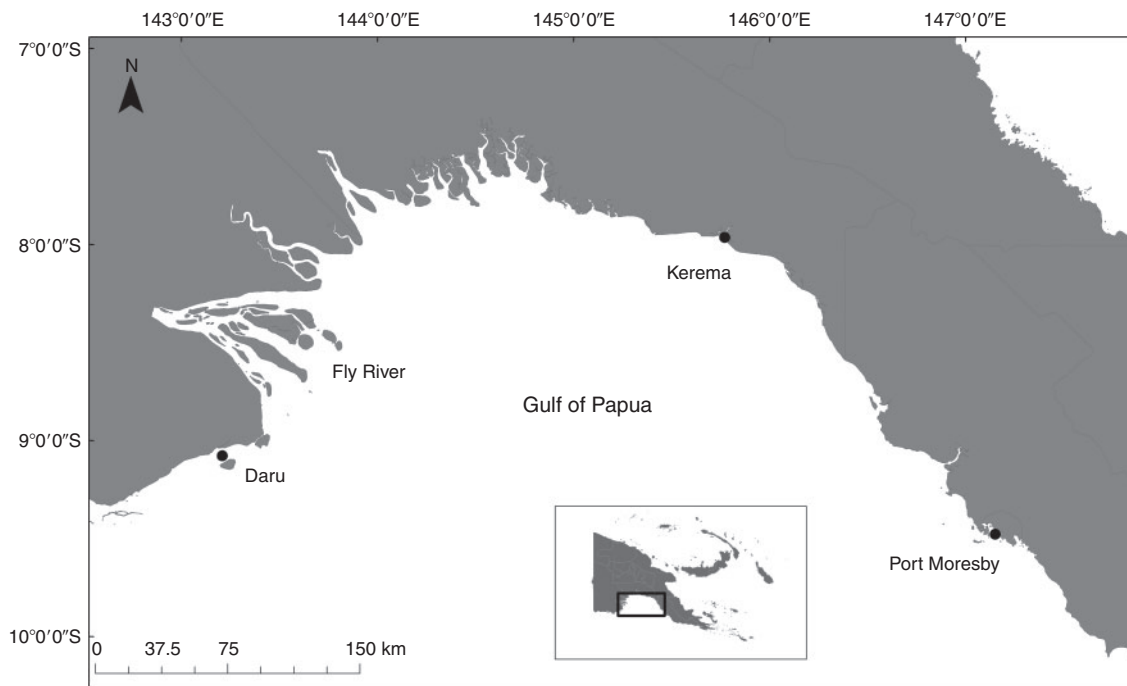


Fig. 1. Gulf of Papua situated along the southern coastline of Papua New Guinea.

as a separate species (White 2012). Stevens and McLoughlin (1991) established biological information for this species in Australia and 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 studies of *C. coatesi* in Papua New Guinea despite it being a common by-catch in commercial trawl fishing.

The Gulf of Papua prawn trawl fishery (GoPPF) has been in existence for over four decades and total levels of by-catch of all species (including sharks) varies between 60 and 85% by weight of the overall catch (Matsuoka and Kan 1991; Evans *et al.* 1995). Despite the large composition of by-catch there has been little research to identify, quantify and determine the biology and life history of by-catch species in order to understand the broader ecological 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 aimed 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 north-eastern Australia to investigate any regional variation in life history.

Materials and methods

The GoP is a semi-enclosed body of water on the southern side of Papua New Guinea covering an area of over 50 000 km² (Wolanski *et al.* 1995). Several major rivers flowing from the interior of Papua New Guinea converge onto the gulf. The larger Fly River is located in the north-west and several other rivers occur eastward (Fig. 1). Extensive mangrove swamps and estuarine areas line the coastline, providing important habitat and nursery areas that support a diverse array of aquatic life (Pernetta and Hill 1981). Several commercially valuable

crustacean species (mostly penaeid prawns) occur in the region and are harvested via the GoPPF (Gwyther 1982).

Fishery observers were deployed on seven prawn trawl fishing trips between June 2014 and August 2015 to collect shark by-catch samples and data. Sharks that had suffered fishing mortality were kept whole, frozen on board and brought back to shore. In the 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), which categorises five reproductive stages ranging from immature to postparturition in females and three stages in males. A binary category was assigned to each maturity stage (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.

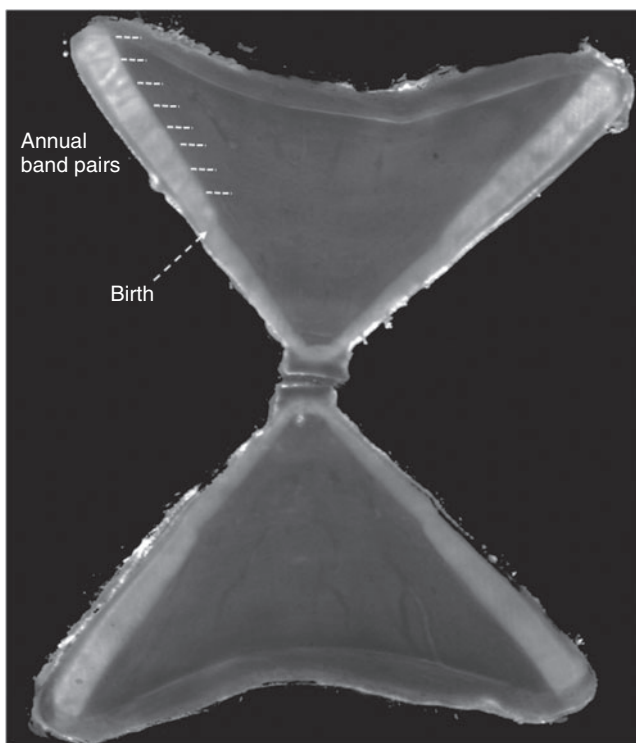
Vertebrae preparation

Protocols described by Cailliet *et al.* (2006) were used to prepare vertebrae for aging. Frozen vertebrae were thawed, 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 to remove any remaining soft tissue. Vertebrae were immersed for up to 5 min, depending on size. The centra were then rinsed with water and dried in an oven at 60°C for 24 h. Vertebrae large enough to be sectioned were mounted onto a low-speed circular saw (Beuhler, Illinois, USA) and a section ~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 adequately held by the chuck of the circular saw

Table 1. Characters used to determine the maturity of male and female specimens of *Carcharhinus coatesi*

Maturity stages were assigned a binary category for statistical analysis

	Description	Binary category
Female stage		
1	Immature	0
2	Maturing	0
3	Mature	1
4	Pregnant	1
5	Postpartum	1
Male stage		
NC	Not calcified	0
PC	Partially calcified	0
FC	Fully calcified	1

**Fig. 2.** Cross-section of a *Carcharhinus coatesi* vertebral centrum viewed under a microscope. Birthmark and annual band pairs indicate ~8 years of age.

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 band was usually opaque while the narrow band was translucent; together, they were 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. *C. coatesi* has no distinct breeding season (Stevens and McLoughlin 1991) so to account for aseasonal parturition 0.5 years was added to each individual age, following Harry *et al.* (2010). Annual growth band deposition could not be verified using marginal increment analysis because sampling was not carried out consistently in each month of the year due to logistical issues. However, it was assumed that *Carcharhinus coatesi* deposited bands annually based on evidence in the literature that supports annual growth band deposition for sharks of the family Carcharhinidae (McAuley *et al.* 2006; Barreto *et al.* 2011; Chin *et al.* 2013; Harry *et al.* 2013).

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 using 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 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 multimodel approach was used to determine the growth of *C. coatesi* by assessing the level of fit between several candidate models rather than 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 multimodel approach, which has been recommended as best practice in recent elasmobranch growth studies (Smart *et al.* 2016). The multimodel approach uses the Akaike Information Criterion (AIC) (Akaike 1973) to rank performance of each candidate model thereby indicating the model with the best fit to the length-at-age data. When all models perform similarly a multimodel inference approach calculates model-averaged parameters based on Akaike weights from each respective model (Katsanevakis and Maravelias 2008). The use of the multimodel approach minimises the risk of model-misrepresentation and associated biases (Cailliet *et al.* 2006; Thorson and Simpfendorfer 2009; Smart *et al.* 2016).

Three candidate models were used: the VBGM, the logistic model, and the 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, multimodel 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 $AIC = n \log(\sigma^2) + 2k$, 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 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 to 2 were considered to have the strongest support, less support was given to values between 2 and 10, and the least support was given to Δ values >10 (Anderson and Burnham 2002). The AIC weights were calculated by the expression:

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

To test whether 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 were 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 quasibinomial error structure and a logit-link function based on 4-cm length bins in the 'R' program environment (R Core Team 2015). Age-at-maturity was calculated using the same process as length-at-maturity by substituting length with age. The age at which 50 and 95% of the population were mature were designated as A_{50} and A_{95} respectively.

Results

A total of 115 *C. coatesi* were used in this study, 81 males and 34 females. Males ranged in size from 33 to 79 cm TL, and females from 35 to 75 cm TL. The majority of samples were smaller-sized juveniles. Only three pregnant females were observed, each having two embryos. The maximum embryo size was 12 cm, but they were not full term.

Age determination

The average percentage error was 9.93% and Chang's coefficient of variation was 14.05%, which were relatively low in comparison to other studies on small-bodied carcharhinids (Harry *et al.* 2010; Smart *et al.* 2013; Gutteridge *et al.* 2013). Percentage agreement ± 1 year between readers was 58.7%, reflecting some level of disagreement between readers. The age bias plot (Fig. 3) showed that bias was associated more with ages greater than six years. However, the Bowker's test of symmetry ($\chi = 30.13$, d.f. = 23, $P = 0.14$) indicated that bias was not significant between readers. The maximum ages were the same for both sexes at 10.5 years. The oldest male measured 76 cm TL and the oldest female was 73 cm TL.

Growth model fitting

The AIC_C values were similar for all candidate models. All models (Table 3) had a Δ of <2 and w of <0.9. The length-at-birth (L_0) were 40.61 ± 0.81 (s.e.), 40.86 ± 0.08 (s.e.), 40.74 ± 0.81 (s.e.) for the VBGM, logistic and Gompertz models, respectively. The asymptotic lengths were also very similar (VBGM: 74.84 ± 2.05 (s.e.); logistic: 73.70 ± 1.56 (s.e.); Gompertz: 74.17 ± 1.75 (s.e.)) and the growth completion rates k , $g_{(\log)}$ and $g_{(\text{gom})}$ were 0.33 ± 0.06 year⁻¹, 0.48 ± 0.07 year⁻¹ and 0.40 ± 0.06 year⁻¹, respectively. Given

Table 2. Equations of the three growth functions used in the multimodel 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	$L(t) = L_\infty \exp(-L_0 \exp(-g_{\text{gom}} t))$

that all models produced almost identical growth estimates it was therefore not necessary to perform model averaging (Table 3). The VBGM (Fig. 4) model was, however, chosen to describe the growth of *C. coatesi* given its wide use in the literature. Sexes were combined because the likelihood ratio test showed no significant difference between the sexes for all three models (VBGM: $\chi^2 = 3.78$, d.f. = 3, $P = 0.29$; logistic: $\chi^2 = 4.05$, d.f. = 3, $P = 0.26$; Gompertz: $\chi^2 = 3.90$, d.f. = 3, $P = 0.27$).

Maturity

The size at which 50 and 95% of individuals became sexually mature showed that males attained maturity at $L_{50} = 66.3$ cm (CI: 63.8, 71.4) and $L_{95} = 71.6$ cm (CI: 64.6, 74.2). Females reached maturity at $L_{50} = 71.4$ cm (CI: 61.5, 72.0) and $L_{95} = 72.5$ cm (CI: 62.7, 74.0) (Fig. 5). Age-at-maturity estimates indicate that males ($A_{50} = 5.1$ years (CI: 4.6, 7.1), $A_{95} = 6.4$ years (CI: 5.1, 7.2)) and females ($A_{50} = 5.3$ years (CI: 3.5, 8.7) and $A_{95} = 7.4$ years (CI: 3.6, 8.8)) reach maturity at about five 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).

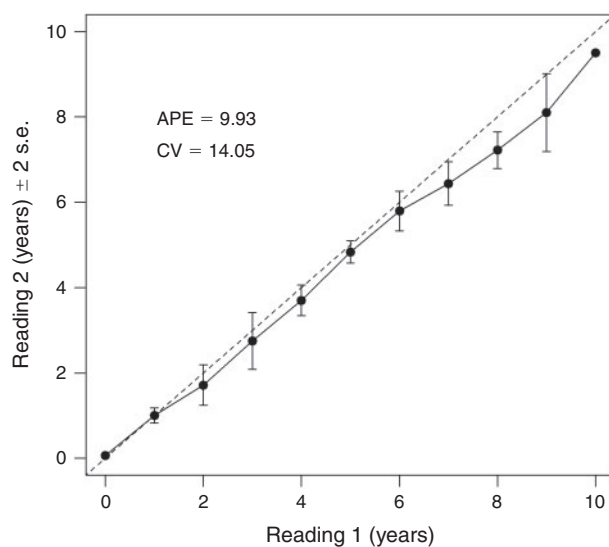


Fig. 3. Age bias plot showing agreement between two independent readers. The percentage agreement ± 1 year was 58.7%, Average Percentage Error was 9.93% and Chang's coefficient of variation was 14.05%.

Discussion

The Australian blackspot shark is a small but relatively fast growing species of shark. Studies in Australia show that on the Great Barrier Reef coast it has a growth completion rate of 0.83 year^{-1} and reaches a maximum age of 6.5 years (Smart *et al.* 2013), while the maximum length is 88 cm in the Northern Territory (Stevens and McLoughlin 1991). The results of this study demonstrate that the life history of *C. coatesi* in the waters of southern Papua New Guinea was somewhat dissimilar. The von Bertalanffy growth completion rate was lower (0.33 year^{-1}), maximum age higher (10.5 years) and maximum length smaller (79 cm). These differences occurred despite the size at birth and maximum size being similar between these areas. Such intraspecific variation in life-history traits is often reported in sharks (Lombardi-Carlson *et al.* 2003; Gutteridge *et al.* 2013; Taylor *et al.* 2016) and can be the result of a range of factors, including local selection pressures, differences in methodology, differential effects of fishing or latitudinal variation in environmental conditions.

The Carcharhinidae are the most diverse family of sharks, with over 50 species (White and Sommerville 2010), and show a

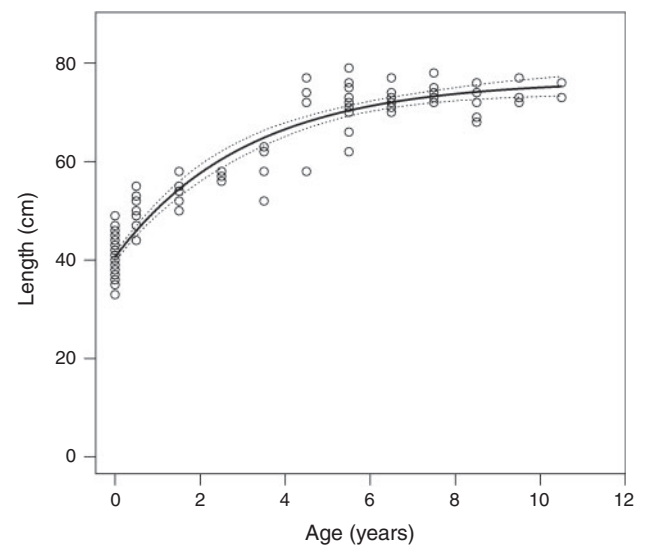


Fig. 4. Length-at-age curve for *Carcharhinus coatesi* from the Gulf of Papua with both sexes combined fitted with a three-parameter von Bertalanffy growth model (solid line) and 95% bootstrapped confidence intervals (dotted lines).

Table 3. Summary of results from the multimodel inference framework incorporating Akaike's Information Criterion (AIC)

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

Model	n	AIC_C	Δ	W (%)	L_0 (\pm s.e.)	L_∞ (\pm s.e.)	k (\pm s.e.)	$g_{(\log)}$ (\pm s.e.)	$g_{(\text{gom})}$ (\pm s.e.)	RSE
VBGM	115	729.84	0	0.42	40.61 ± 0.81	74.84 ± 2.05	0.33 ± 0.06			5.65
Logistic	115	730.8	0.97	0.26	40.86 ± 0.08	73.70 ± 1.56		0.48 ± 0.07		5.67
Gompertz	115	730.31	0.47	0.33	40.74 ± 0.81	74.17 ± 1.75			0.40 ± 0.06	5.66

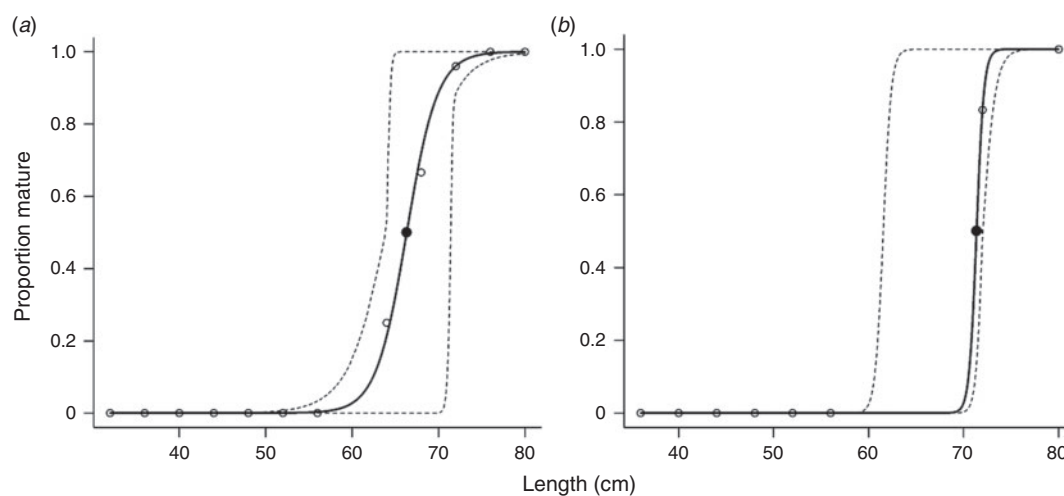


Fig. 5. Length-at-maturity ogives for (a) male and (b) female *Carcharhinus coatesi* from the Gulf of Papua. The shaded points represent the length at which 50% of the population reaches maturity. The 95% confidence intervals are indicated with dashed lines.

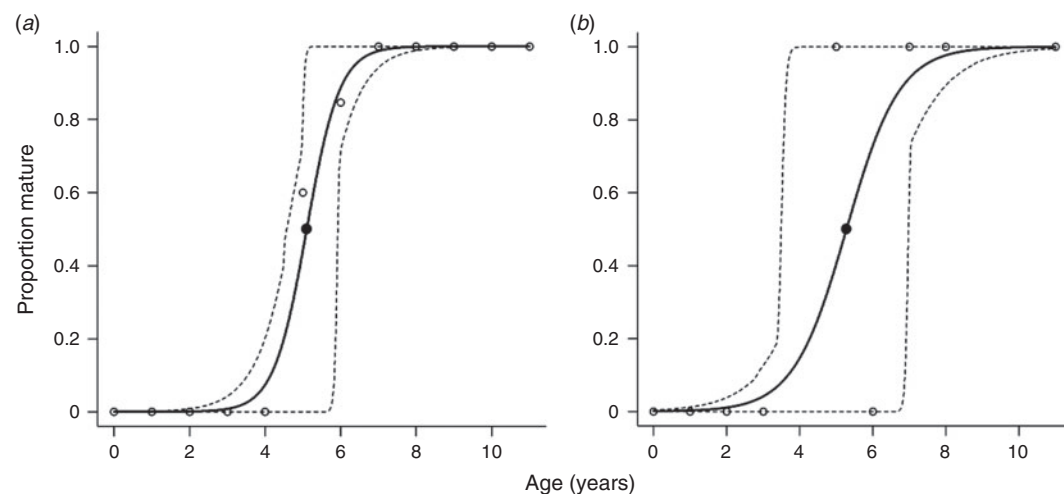


Fig. 6. Age-at-maturity ogives for (a) male and (b) female *Carcharhinus coatesi* from the Gulf of Papua. The shaded points represent the ages at which 50% of the population reach maturity. The 95% confidence intervals are indicated with dashed lines.

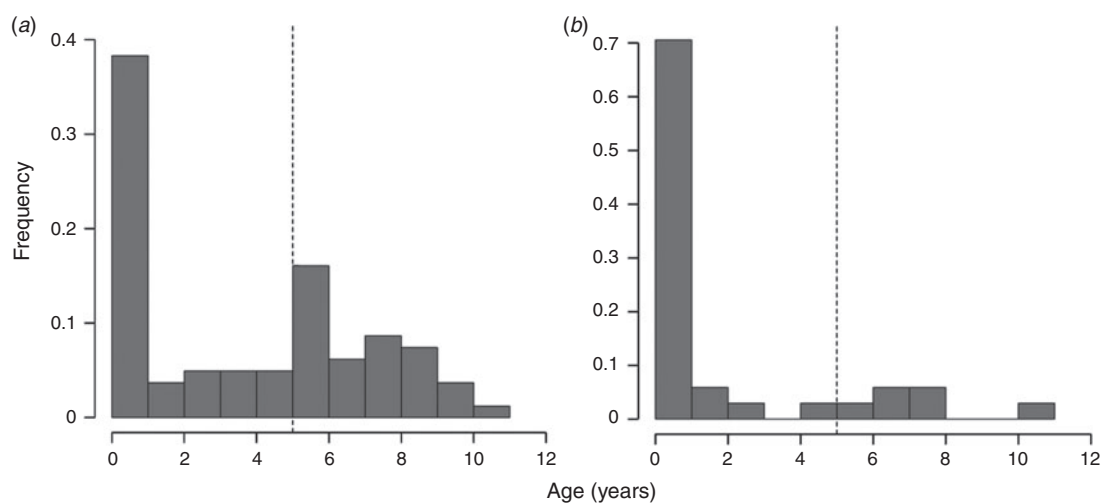


Fig. 7. Age frequency of individual *Carcharhinus coatesi* sampled. The dotted lines indicated age-at-maturity for (a) males and (b) females.

variety of growth patterns. The largest species of this group is the tiger shark (*Galeocerdo cuvier*), which can grow to over 5 m in length, reaching maturity after 12 years of age (Holmes *et al.* 2015) and having a von Bertalanffy growth completion rate of $k = 0.08 \text{ year}^{-1}$. Another species, the silky shark (*Carcharhinus falciformis*), attains a total length over 2 m, takes over 10 years to reach maturity and grows at a rate of $k = 0.066 \text{ year}^{-1}$ (Hall *et al.* 2012). The blue shark (*Prionace glauca*) has a maximum length of $\sim 3 \text{ m}$, and fully matures after six years, growing at a rate of $k = 0.12 \text{ year}^{-1}$ (Jolly *et al.* 2013). Meanwhile, small-bodied carcharhinids that reach less than 1 m have much higher growth rates, ranging from $k = 0.18 \text{ year}^{-1}$ for *Loxodon macrorhinus* (Gutteridge *et al.* 2013) to $k = 1.33 \text{ year}^{-1}$ (Simpfendorfer 1993). Small-bodied coastal carcharhinids usually grow rapidly after birth (Fig. 8) and reach maturity within 1–2 years (Loefer and Sedberry 2003; Harry *et al.* 2010; Smart *et al.* 2013; Gutteridge *et al.* 2013). The variability in the life history of the carcharhinid sharks demonstrates that they have evolved highly diverse life histories, despite their common ancestry, to become one of the most important groups of predators in the ocean.

Validating ages, particularly in older age classes, has proven to be problematic in age and growth literature and consequently the underestimation of ages is prevalent (Harry 2018). Vertebral aging indicated that *C. coatesi* grows for more than 10 years in the GoP. Reader precision was relatively high with no significant bias detected; however, difficulty in determining ages of older individuals was evident. Bands deposited towards the edge of the vertebrae can be difficult to distinguish because of close 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 (Loefer and Sedberry 2003; Gutteridge *et al.* 2013; Huveneers *et al.* 2013). Growth band pairs are associated with seasonality in temperate waters (Cailliet and Goldman 2004). Therefore a lack of seasonality in the tropics may affect the clarity and readability of band pairs (Fig. 2) and thus the overall estimation of age. Though there is some uncertainty surrounding the correlation of band pair deposition as a reference for age, the formation of band pairs is more consistent in smaller sharks (Natanson *et al.* 2018) and therefore likely to predict age more accurately. Future work should focus on age validation of this species incorporating other datasets where possible, such as tag-recapture or length data (Harry 2018).

The slower growth completion rate of *C. coatesi* compared with other small carcharhinids may be a trade-off with the larger size at birth. The size at birth is relatively large, at about half the maximum observed size, and for individuals often $>50\%$ of the mother's length. This relatively large size at birth is uncommon in sharks, with most less than 30% of maximum size (Cortés 2000). By increasing the size at birth, survival rates of newborns will be higher (Heupel *et al.* 2007) and so the very rapid growth seen in species with very small sizes at birth is not required (Fig. 8). These very rapid growth rates in other species are believed to reduce the time that young sharks are subject to high levels of predation. A consequence of this trade-off is that litter sizes (such as those observed in *C. coatesi*: normally only

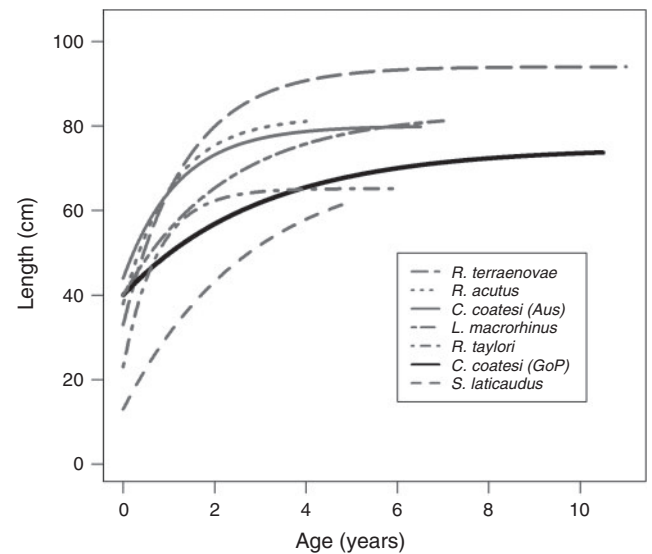


Fig. 8. von Bertalanffy growth curves of small-bodied carcharhinids. Data sources: *Rhizoprionodon terraenovae* (Loefer and Sedberry 2003), *Rhizoprionodon acutus* (Harry *et al.* 2010), *Carcharhinus coatesi* (Aus) (Smart *et al.* 2013), *Loxodon macrorhinus* (Gutteridge *et al.* 2013), *Rhizoprionodon taylori* (Simpfendorfer 1993), *Scoliodon laticaudus* (Nair 1976).

two per litter) are much smaller than these other species with smaller sizes at birth: e.g. *Rhizoprionodon taylori*: litters 1–10, size at birth 25 cm (Simpfendorfer 1993); *Rhizoprionodon terraenovae*: litters 1–8, size at birth 28 cm (Loefer and Sedberry 2003); *Scoliodon laticaudus*: litters 6–18, size at birth 14 cm (Devadoss 1979). The consequences of these trade-offs among small carcharhinids should be further investigated using demographic models to understand how these strategies may be affected by fishing and how they contribute to sustainability.

This study provides the first age-at-maturity estimates for *C. coatesi*. Whereas other small-bodied carcharhinids ($\leq 1 \text{ m}$) take 1–2 years to mature (Simpfendorfer 1993; Carlson and Baremore 2003; Harry *et al.* 2010; Gutteridge *et al.* 2013), both male and female *C. coatesi* attain sexual maturity at about five years of age. Delayed age-at-maturity combined with a small litter size (Stevens and McLoughlin 1991) suggests that this species may be less productive and less able to sustain fishing pressure than other small carcharhinids, but demographic models should be investigated to confirm this hypothesis. Length-at-maturity analysis indicated that males attain maturity at sizes smaller than females, unlike populations in northern Australia in which 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 and the confidence intervals reported for female size and age-at-maturity were wide, estimates should be treated as preliminary and be further investigated with additional sampling.

Fishing on coastal shark populations has led to several population declines (Dulvy *et al.* 2014). This could potentially cause changes in life-history parameters in heavily fished populations. Carlson and Baremore (2003) recorded a higher growth

rate and reduced age-at-maturity in *R. terraenovae* after more than a decade of intense fishing, noting increased fishing pressure and a reduction in stock size over this time as potential drivers for changing growth patterns. 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 and by-catch data over time and previous life-history information. Historical records over a 19-year period (1974–93) of the GoPPF 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) while currently only six vessels are in operation. The total amount of by-catch taken in the fishery is expected to have fluctuated in proportion with fishing effort, and in recent years total by-catch may be at lower levels given that effort appears to have decreased. The current growth and maturity information for *C. coatesi* gathered in this study implies that although it is a reasonably fast growing species, it may be more vulnerable to fishing pressure than other small carcharhinids (Baje *et al.* 2018) due to its older age-at-maturity and lower litter size. As such, increases in exploitation may differentially have greater effects on the population compared with other small carcharhinid species.

Sustainable fisheries management relies on an understanding of the biology of both targeted fish stocks for commercial markets and those that are taken as by-catch. 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 by-catch species has been overlooked, especially in the Indo-Pacific (Molina and Cooke 2012), but is 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 *C. coatesi*, which is potentially more vulnerable to population decline in the event of increased fishing pressure in the GoP due to its life-history characteristics. 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).

Conflicts of interest

The authors declare no conflict of interests.

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