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Age and growth of the common blacktip shark *Carcharhinus limbatus* from Indonesia, incorporating an improved approach to comparing regional population growth rates[§]

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Age and growth estimates from length-at-age data were produced for the common blacktip shark *Carcharhinus limbatus* from Indonesia. Back-calculation techniques were used due to a low sample size (n = 30), which was dominated by large, mature sharks. A multi-model approach incorporating Akaike's information criterion with a bias correction (AIC_c) was used to estimate growth rates, with the von Bertalanffy growth function (VBGF) providing the best fit for the separate sexes using the back-calculation data. These age and growth estimates were then compared to those of other populations of *C. limbatus* from the USA and South Africa using a combination of VBGF parameters and instantaneous (empirical) growth rates at birth (dL/dt_0) and maturity (dL/dt_{mat}). In comparison with populations from the USA, *C. limbatus* from Indonesia grow substantially larger and are more similar to South African populations. Differences in empirical growth rates were also determined between the populations, although this was not detected by the VBGF parameter k. This occurred because the parameter k is a measure of the rate at which a population reaches asymptotic length (L_∞) and is not a measure of growth. This study demonstrated that the use of dL/dt_0 and dL/dt_{mat} to measure and compare empirical growth rates can be a useful addition to life-history studies.

Keywords: Akaike's information criterion (AIC), back-calculation, Carcharhinidae, elasmobranch, life history

Introduction

Many species of elasmobranchs (sharks and rays) have circumglobal distributions and can have different regional or subregional populations (e.g. Duncan et al. 2006; Ovenden et al. 2009). Life-history theory predicts that a population's life-history traits (e.g. growth, size at maturity and fecundity) will adapt to maximise individual fitness and offspring survival due to natural selection pressures (Stearns 1992). Therefore, although different populations may belong to the same species, different regional selection pressures may alter their life histories. Consequently, the life-history information of a species in one location cannot be assumed to be representative of other populations from different regions (White and Sommerville 2010). Life-history information is an integral component of demographic models and stock assessments and the use of inaccurate age and growth information in these assessments will lead to errors in their outputs. This can potentially bias management (Cailliet and Goldman 2004) and cause population declines when the surplus production estimates of the models are erroneous (Beamish and McFarlane 1995; Musick 1999). Therefore, there is a risk of unintentional overexploitation if life-history data for a population from another region is used in lieu of data from the local population.

The common blacktip shark *Carcharhinus limbatus* (Müller & Henle, 1839) is a large-bodied carcharhinid with a circumglobal distribution in tropical and subtropical seas (Last and Stevens 2009). *Carcharhinus limbatus* is an important component of many regional shark fisheries and is targeted in many countries, including Australia (Macbeth et al. 2009; Harry et al. 2011) and the United States of America (USA) (Branstetter and Burgess 1996). It is also a common species in South Africa and, although it does not form a large component of any commercial fishery, *C. limbatus* is caught in a bather protection programme at a rate of approximately 104 ind. y^{-1} (Dudley and Simpfendorfer 2006). Growth estimates for *C. limbatus* are available from several locations and show regional variation in growth rates and maximum lengths (Branstetter 1987; Killam and Parsons 1989; Wintner and Cliff 1996; Carlson et al. 2006). In the USA, *C. limbatus* in the Gulf of Mexico attains a smaller theoretical maximum length and grows faster than in the South Atlantic Bight (Carlson et al. 2006), whereas substantially larger individuals are caught in South Africa in comparison to individuals from both of these populations (Wintner and Cliff 1996). These regional variations in life-history traits suggest that *C. limbatus* requires regional population management.

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Indonesia has one of the largest shark fisheries in the world (Blaber et al. 2009; Dharmadi et al. 2015) and *C. limbatus* was found to be the seventh-most-frequently caught species in the pelagic-longline fishery operating out of Tanjung Luar in Lombok (White 2007). While it is not a targeted species, catches of *C. limbatus* are substantial given Indonesia's high elasmobranch catch, estimated to be more than 100 000 tonnes per annum (Blaber et al. 2009). Indonesia has a high reliance on its marine resources with 60–70% of the country's protein coming from their fisheries (White and Kyne 2010). Given that Indonesia's population is in excess of 237 million people, this puts substantial pressure on these fisheries and increases the importance of effective management. Although catch and reproductive data are now available for *C. limbatus* from Indonesia (White 2007), no robust assessment of current fisheries harvests or sustainable catch levels can occur until age and growth estimates from the local population of *C. limbatus* are determined.

The aim of this study was to determine length-at-age and growth parameters for *C. limbatus* being exploited in Indonesia, to inform future fisheries management. Growth parameters were combined with the reproductive data (White 2007) to produce estimates of length- and age-at-maturity. This information was also compared with the available life-history information from other *C. limbatus* populations to examine interregional differences in life-history traits.

Material and methods

Sample collection

Samples were collected between April 2001 and August 2005 from the Tanjung Luar fish landing site in eastern Lombok, Indonesia. Although *C. limbatus* was a commonly landed species in Indonesia, most specimens were landed at sites where it was not possible to collect detailed biological data. As a result, the sample size of *C. limbatus* vertebrae collected during this study was small. All animals sampled were caught by the local longline fishery, with the exception of one individual that was caught by a demersal gillnet vessel operating out of the same location. Full details of sample collection can be found in White (2007). The total length (TL) of each individual was measured to the nearest 1 mm and a section of vertebrae was removed from below the first dorsal fin. Each section of vertebrae was stripped of soft tissue using a scalpel and stored frozen for transportation.

Vertebrae sectioning

Vertebrae were defrosted and soaked in a 5% sodium hypochlorite solution for 30 min to remove any remaining soft tissue. They were then rinsed under tap water and placed in a drying oven at 60 °C for 24 h. Vertebral centra were then sectioned longitudinally using a low-speed circular saw with two diamond-tipped blades (Beuhler, Illinois, USA). Each section was made through the centrum focus at a thickness of approximately 400 μm. After sectioning, each centrum was mounted onto a microscope slide using Crystal Bond adhesive (SPI supplies, Pennsylvania, USA).

Age determination

To determine individual ages, translucent and opaque bands were counted in the corpus calcareum of each centrum under transmitted light (Cailliet and Goldman 2004). A change in the angle of the corpus calcareum indicated the birth mark and represented an age of zero. Each set of translucent and opaque bands after the birth mark was deemed to be an individual growth band and represented one year of growth (Cailliet et al. 2006). Annual growth band deposition could not be validated in this study due to the low number of samples. However, annual growth band deposition has previously been demonstrated for *C. limbatus* through the use of marginal increment analysis (Killam and Parsons 1989) and was therefore assumed in this study as well.

Two independent readers conducted an independent count of growth bands on all centra (Cailliet and Goldman 2004). A consensus age was recorded when counts agreed between readers. Where counts differed between readers, those centra were re-examined in a second attempt at producing a consensus age. If no consensus age could be agreed then those centra were deemed as uninterpretable. Inter-reader precision was conducted on the original counts of both readers and measured using average percent error ± 1 year (APE ± 1 year) with individuals grouped by 100 mm TL classes. For long-lived species, APE ± 1 year can be variable across age classes because of the increasing difficulty of ageing older individuals. Therefore, by separating individuals into size classes rather than age classes to test precision, variability in calculating APE ± 1 year across ages was removed because length is an empirical measurement whereas age was estimated (Goldman and Musick 2006). Bowker's test of symmetry (Bowker 1948; Evans and Hoenig 1998) was used to determine if the inter-reader variability was systematically biased and was calculated using the FSA package (Ogle 2012) in the 'R' program environment (R Core Team 2013).

As growth is more accurately modelled using partial ages (Smart et al. 2013), and samples were collected from different months, ages were estimated in monthly time-steps. *Carcharhinus limbatus* reproduces seasonally in Indonesian waters, with parturition occurring between October and December (White 2007). Thus, December was nominated as the birth month because this was when the largest embryos were recorded (White 2007) and the partial age was calculated based on the month the sample was collected, because specific catch dates were not available. For example, an individual with nine growth bands that was caught in August was assigned a partial age of 9.75 years (Harry et al. 2013; Smart et al. 2013).

Back-calculation techniques

Back-calculation techniques were used in an attempt to compensate for the limited sample size ($n = 30$) and the small number of juveniles (immature individuals) in the sample (Cailliet and Goldman 2004). Centra were photographed during age determination using a compound video microscope and the distances between growth bands were measured using an image-analysis system (Image Pro Plus version 6.2 for Windows, Media Cybernetics).

The centrum radius (CR) was measured as a straight line from the centrum focus to the centrum edge. The distance from the focus to the birth mark and each subsequent growth-band pair was measured to the nearest 0.001 mm along this straight line. A Dahl Lea direct-proportions back-calculation technique (Carlander 1969) was then applied to the data using the equation:

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

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'. A length-at-birth modified Fraser Lee back-calculation technique was also applied to the data as an alternative to the Dahl Lea direct-proportions method. However, on visual inspection, it was determined that the Dahl Lea direct-proportions method provided more reasonable estimates when compared to the observed length-at-age data available for the older age classes and it was therefore used in all further analysis.

Fitting of growth models

A multi-model approach incorporating Akaike's information criterion (AIC) was used to model growth. This approach was applied to both the observed length-at-age data and back-calculated data for *C. limbatus* for the separate sexes and the sexes combined. The use of multiple models is recommended over the use of a single-model approach (Cailliet et al. 2006; Katsanevakis and Maravelias 2008) and is now standard practice in modelling elasmobranch growth. Three candidate growth models were chosen *a priori* and their fit for both sets of data was assessed using a bias-corrected AIC (AIC$_c$) (Katsanevakis 2006; Zhu et al. 2009). The growth models were the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938), the logistic function (Ricker 1979) and the Gompertz function (Gompertz 1825; Ricker 1975) (Table 1). All three models were fitted using a length-at-birth parameter (L_0) rather than a time-at-size-zero parameter (t_0), as L_0 can be compared directly between models whereas t_0 cannot. The asymptotic length (L_∞) can also be compared directly between models. However, the respective growth-completion parameters of each of the models (k [VGBF], G [Gompertz] and g [logistic]) are not comparable as they are measures of different processes. As L_∞ was not one of the fitted parameters for the Gompertz function, it was calculated upon completion of the model-fitting process as:

$$L_\infty = L_0 \exp^G$$

where L_∞ is the asymptotic length, L_0 is the length at birth and G is the instantaneous growth rate at L_0 (Ricker 1979).

Best-fit parameter estimates for each model were calculated using the nonlinear-least-squares (nls) function in the 'R' program environment (R Core Team 2013) and their performance was evaluated by using AIC$_c$ (Katsanevakis 2006; Zhu et al. 2009). The AIC$_c$ was calculated as:

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

Table 1: The equations of the three *a priori* model candidates used in the multi-model AIC$_c$ analysis, where L_t is length at age t, L_0 is length at age 0, L_∞ is asymptotic length and k, g and G are the different growth coefficients of the respective models

Model	Growth function equation
von Bertalanffy growth function (VBGF)	$L_t = L_0 + (L_\infty - L_0)\,(1 - \exp(-kt))$
Gompertz function	$L_t = L_0\,(\exp^{G(1 - \exp(-gt))})$
Logistic function	$L_t = \dfrac{L_\infty L_0\,(\exp(gt))}{L_\infty + L_0\,(\exp(gt) - 1)}$

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 with the lowest AIC$_c$ value (AIC$_{min}$) was chosen as the most appropriate. Each remaining model was 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 no support (Burnham and Anderson 2001). AIC differences were also used to calculate AIC weights (w) which represent the probability of choosing the correct model from the candidates (Burnham and Anderson 2001; Braccini et al. 2007). The weights were calculated as:

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

To determine whether the models for the separate sexes should be used over the model for the combined sexes in further analyses, likelihood ratio tests were used to determine whether the curves of each sex were coincident (Kimura 1980). These tests were conducted on both the observed length-at-age and the back-calculated data using Microsoft Excel according to the method outlined by Haddon (2001). One of the assumptions of the likelihood ratio test was that the two age ranges are equivalent. Therefore, the observed length-at-age data were truncated by omitting individuals less than 6 years old from the analyses, thereby ensuring that the age ranges of both sexes were comparable (Haddon 2001).

Regional growth rate comparison

In order to compare the instantaneous growth rates of *C. limbatus* between regions, the VBGF fits for other populations were reproduced using the parameter estimates from previously published length-at-age studies from populations in the Gulf of Mexico (Branstetter 1987; Carlson et al. 2006), Florida/South Atlantic Bight (Killam and Parsons 1989; Carlson et al. 2006) and South Africa (Wintner and Cliff 1996). In instances where TL was not the length measurement used in the model, length conversions from published studies were used to calculate TL model

length-at-age and parameter estimates (Wintner and Cliff 1996; Carlson et al. 2006). Instantaneous rates of growth at birth and maturity were then calculated as:

$$\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{L(t + \Delta t) - L(t)}{\Delta t}$$

where dL/dt is the instantaneous rate of growth at time t, $L(t)$ is length at time t from the respective model estimates and Δt is a period of time over which the growth rate is to be calculated, where $\Delta t = 1$ is equal to 1 year (Sparre and Venema 1998). In this instance it was set to $\Delta t = 0.00001$ to provide an instantaneous rate of growth. The growth rate at birth (dL/dt$_0$) was calculated using $t = 0$ and the growth rate at maturity (dL/dt$_{mat}$) was calculated by setting t as the age-at-maturity from estimates sourced from each respective study. Where an age-at-maturity range was given (e.g. 4–5 years) rather than a discrete age-at-maturity in any respective study, the mid-point of this range was used in all calculations.

Influence of juvenile exclusion on growth estimation
Since only a small number of juveniles were included in the sample ($n = 5$), additional analysis was undertaken to determine the influence that these individuals had in determining the shape of the model. This was performed using the best-fitting model for the sexes combined from the observed length-at-age data only. Five hypothetical sampling scenarios were created with different numbers of juveniles omitted from the model estimation process. The number of juveniles included in these five hypothetical scenarios started at zero (mature individuals only) and increased one juvenile at a time until they had all been re-introduced. Each juvenile was re-introduced in order of youngest to oldest and a new model fit was estimated for each scenario. The fits of each scenario (n of juveniles = 0–4) were then compared back to the complete model (n of juveniles = 5) by calculating the proportional difference between the length-at-age estimates of each scenario's model to that of the complete model.

Results

A sample of 30 *C. limbatus* with an even sex ratio was collected from Indonesian waters. Only five juveniles were included in the sample (741–873 mm TL), all of which were female (Figure 1a, c). These missing size classes were accounted for by back-calculation techniques (Figure 1b, d, f) which also increased the number of age-at-length data points from 30 to 294 through the inclusion of interpolated data (Table 2). The remaining 25 individuals were large and mature individuals of both sexes (1 756–2 458 mm TL) (Figure 1e). The length ranges for males and females were 1 801–2 269 mm TL and 741–2 458 mm TL, respectively. The age ranges for males and females were 5.8–16.8 years and 0.3–17 years, respectively.

The APE ± 1 year across 100 mm TL classes was 40.67% with no systematic bias detected by Bowker's test of symmetry (df = 18, $\chi^2 = 17$, $p = 0.52$). A low APE ± 1 year occurred due to the sample containing mostly older age classes. As older age classes have more growth bands that

require identification, it is these age classes where most inter-reader discrepancy typically occurs during growth-band reading, therefore decreasing the value of APE ± 1 year (Beamish and McFarlane 1995). In this study, for all individuals that were less than 1 000 mm TL, an APE ± 1 year of 100% was achieved (Figure 2). Therefore, the low APE ± 1 year was not a result of poor reader agreement but a reflection of the lack of younger age classes that are easier to read and would normally increase the APE ± 1 year. A consensus age was produced for each age disagreement and therefore no vertebrae were omitted from further analysis.

The results of the multi-model AIC$_c$ analysis showed that the VBGF produced the best model fit for the combined sexes for both the observed length-at-age data ($w = 57\%$) and the back-calculated length-at-age data ($w = 99\%$) (Table 2). The logistic and Gompertz models provided some support for the combined sexes for the observed data ($w = 10\%$ and 33%, respectively), but offered little support in comparison to the VBGF for the back-calculated data (Table 2). The VBGF also provided the best model fits for the separate sexes from the back-calculated data ($w = 99\%$ for both sexes) with the Gompertz and logistic models providing little support (Table 2). For the female observed length-at-age data, the VBGF also produced the best fit ($w = 46\%$) with some support provided by the Gompertz and logistic models ($w = 37\%$ and $w = 17\%$) (Table 2). However, for the male observed length-at-age data, equal fits were provided by the three models (Table 2). This was caused by an unrealistically high L_0 estimate (1 192.3 mm TL for the VBGF) which resulted from a lack of male juveniles in the sample (Table 2; Figure 1a).

While the VBGF parameter estimates provided an unrealistic L_0 estimate for the male observed length-at-age data, the estimates for the females were far more reasonable; $L_0 = 659.4$ mm TL, $k = 0.08$ year^{-1} and $L_\infty = 3 070.7$ mm TL (Table 2; Figure 1c). However, the VBGF parameter estimates which were most biologically realistic for the observed length-at-age data were produced for the sexes combined; $L_0 = 628.6$ mm TL, $k = 0.13$ year^{-1} and $L_\infty = 2 492.2$ mm TL (Table 2). These estimates match the known maximum length of 2 500 mm TL and the size-at-birth of 628 mm TL for the region (White et al. 2006; White 2007). The VBGF parameter estimates produced for the back-calculated data for the combined sexes and the separate sexes were similar to one another and also matched the biological parameters (Table 2; Figure 1b, d, f). The L_0 estimates for the back-calculated data suggested that males had a slightly larger length-at-birth than females ($L_0 = 688$ and 622.5 mm TL, respectively) and females had a larger L_∞ than males ($L_\infty = 2 640.4$ and 2 297.3 mm TL, respectively). The values of k were similar for the back-calculated data between the combined- and separate-sex models (Table 2).

The removal and sequential reintroduction of juveniles into the VBGF estimation process demonstrated that small numbers of juveniles, especially young-of-the-year individuals (individuals with ages less than 1 year), can have significant effects on the estimation of L_0. In the scenario where only mature individuals were included, the results resembled those of the male observed length-at-age data
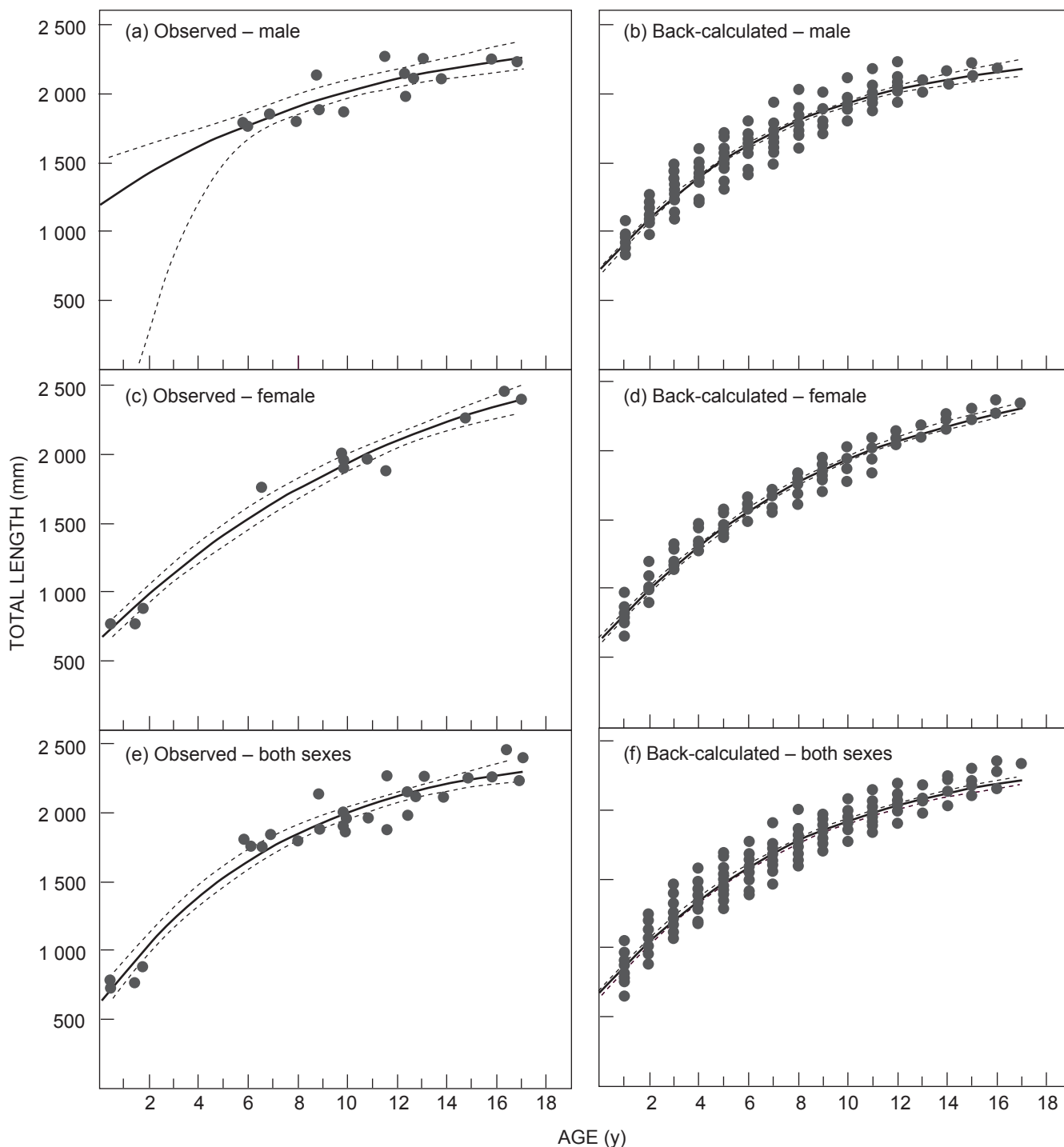
Figure 1: Length-at-age of *Carcharhinus limbatus* using observed data (a, c and e) and back-calculated data (b, d and f) with fitted VBGF models and 95% confidence intervals

where the curve was flat and the L_0 was unrealistically high (Table 3; Figure 3). The L_0 estimate that this scenario produced was 75% larger than that of the complete model (*n* of juveniles = 5; Table 3). The VBGF length-at-age estimates for this scenario did improve as age increased but did not converge with the complete model at a difference of <5% until reaching age 6 when empirical data

were available (Table 3), after which the estimates became comparable (Figure 3). Re-introducing one juvenile back into the VBGF estimation process produced an L_0 estimate of 749.8 mm TL (Table 3). This estimate fell within the range of worldwide length-at-birth estimates for *C. limbatus* (Carlson et al. 2006), indicating some biological realism. This inclusion of one juvenile reduced the L_0 estimate to a

Table 2: Summary of model parameters and AIC_C results for the observed length-at-age and back-calculated data for *Carcharhinus limbatus*; 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 (%) is the AIC_C weight, L_∞ is the asymptotic length parameter in mm, L_0 is the length-at-birth parameter in mm, k is the growth rate parameter in y^{-1} for the VBGF, G and g are the growth coefficients of the Gompertz model and g is the growth rate parameter for the logistic model. Only L_0 and L_∞ are comparable between the three models

Sex	Model	n (ind.)	AIC_C	Δ	w (%)	L_∞ (mm)	L_0 (mm)	k (y^{-1})	G	g
				Observed						
Sexes combined	VBGF	30	375.96	0.00	57	2 492	629	0.13	–	–
	Logistic	30	379.46	3.50	10	2 286	701	–	–	0.29
	Gompertz	30	377.01	1.05	33	2 344	669	–	1.26	0.21
Male	VBGF	15	190.45	0.05	33	2 526	1 192	0.10	–	–
	Logistic	15	190.40	0.00	34	2 431	1 292	–	–	0.15
	Gompertz	15	190.43	0.03	33	2 471	1 251	–	0.68	0.12
Female	VBGF	15	185.67	0.00	46	3 071	659	0.08	–	–
	Logistic	15	187.71	2.04	17	2 524	709	–	–	0.22
	Gompertz	15	186.13	0.45	37	2 692	687	–	1.36	0.15
				Back-calculation						
Sexes combined	VBGF	294	3 535.04	0.00	99	2 440	659	0.13	–	–
	Logistic	294	3 605.34	70.30	<1	2 164	727	–	–	0.29
	Gompertz	294	3 569.49	34.45	<1	2 379	696	–	1.17	0.21
Male	VBGF	167	2 023.77	0.00	99	2 297	688	0.14	–	–
	Logistic	167	2 050.03	26.27	<1	2 085	750	–	–	0.31
	Gompertz	167	2 035.95	12.18	<1	2 246	721	–	1.09	0.23
Female	VBGF	127	1 478.84	0.00	99	2 640	622	0.11	–	–
	Logistic	127	1 530.54	51.70	<1	2 270	695	–	–	0.27
	Gompertz	127	1 505.05	26.21	<1	2 454	662	–	1.28	0.19
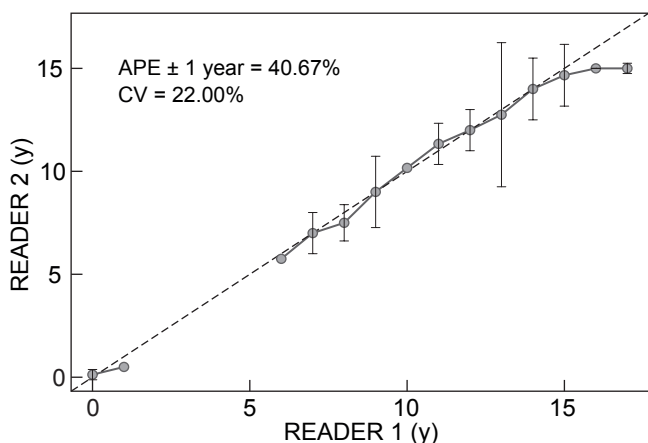
Figure 2: Age-bias plot for *Carcharhinus limbatus* incorporating the age-specific agreements between Readers 1 and 2 used for Bowker's test of symmetry. Mean age-specific agreements ±2 standard errors are plotted along a 1:1 equivalence line for comparison

difference of 19% when compared to the complete model, an improvement of 56% over the scenario which included mature individuals only (Table 3). As more juveniles were iteratively re-introduced to the data during the VBGF estimation process, the length-at-age estimates continued to improve, and once four individuals were included the model did not differ from the complete model by more than 4% at any age (Table 3; Figure 3).

No significant difference between sexes was found for the truncated observed length-at-age data using the likelihood-ratio tests (df = 3, χ^2 = 6.33, p = 0.09). However, the likelihood-ratio tests produced a significant difference between sexes for the back-calculated data (df = 3, χ^2 = 32.31, p < 0.001). Given that these results were contradictory, the most conservative conclusion was to accept the result for the back-calculated data as there have been previous suggestions that likelihood-ratio tests can be biased at low sample sizes (Cerrato 1990). This avoids the larger risk of a Type II error. Therefore the VBGF model fits for the separate sexes from the back-calculated data were considered the most appropriate for the Indonesian *C. limbatus* population.

There was a substantial difference between the growth of *C. limbatus* from Indonesia and that of other regional populations (Table 4; Figure 4). The Indonesian population has the highest maximum age (t_{max}) with males and females being 16.8 and 17 y, respectively (Table 4; Figure 4). Maximum age estimates for US populations ranged from 9.5 to 11.5 y in the Gulf of Mexico (Branstetter 1987; Carlson et al. 2006) and 9 to 15.5 y in Florida/South Atlantic Bight (Killam and Parsons 1989; Carlson et al. 2006). Maximum age estimates for *C. limbatus* from South Africa were also younger than those from this study at 10 and 11 y for males and females, respectively, despite attaining substantially larger maximum lengths than their conspecifics from the USA (Wintner and Cliff 1996). The L_∞ of *C. limbatus* in South Africa were 2 615 and 2 584 mm TL for males and females, respectively, whereas neither population from the USA attained a L_∞ larger than 1 950 mm TL (Branstetter 1987; Killam and Parsons 1989; Wintner and Cliff 1996; Carlson et al. 2006). The L_∞ of 2 640 mm TL estimated in this study for females was the largest L_∞ estimated for any

Table 3: Comparison of VBGF length estimates (mm TL) for hypothetical sampling conditions with varying numbers of juveniles ranging from 0 to 5. Proportional differences to the complete model (5 juveniles) at each age class are in parentheses

Age (y)	Complete age range	Mature individuals only		1 juvenile		2 juveniles		3 juveniles		4 juveniles	
0	629	1 099	(0.75)	750	(0.19)	721	(0.15)	701	(0.11)	652	(0.04)
1	862	1 225	(0.42)	959	(0.11)	938	(0.09)	923	(0.07)	883	(0.02)
2	1 066	1 341	(0.26)	1 143	(0.07)	1 128	(0.06)	1 118	(0.05)	1 085	(0.02)
3	1 245	1 448	(0.16)	1 305	(0.05)	1 295	(0.04)	1 288	(0.03)	1 261	(0.01)
4	1 401	1 546	(0.10)	1 447	(0.03)	1 441	(0.03)	1 437	(0.03)	1 415	(0.01)
5	1 538	1 637	(0.06)	1 573	(0.02)	1 569	(0.02)	1 567	(0.02)	1 549	(0.01)
6	1 658	1 721	(0.04)	1 683	(0.02)	1 681	(0.01)	1 680	(0.01)	1 667	(0.01)
7	1 762	1 799	(0.02)	1 780	(0.01)	1 780	(0.01)	1 780	(0.01)	1 770	(0.00)
8	1 854	1 870	(0.01)	1 866	(0.01)	1 866	(0.01)	1 867	(0.01)	1 859	(0.00)
9	1 934	1 936	(0.00)	1 941	(0.00)	1 942	(0.00)	1 943	(0.00)	1 938	(0.00)
10	2 004	1 997	(0.00)	2 007	(0.00)	2 008	(0.00)	2 009	(0.00)	2 006	(0.00)
11	2 065	2 053	(−0.01)	2 065	(0.00)	2 066	(0.00)	2 067	(0.00)	2 066	(0.00)
12	2 118	2 104	(−0.01)	2 116	(0.00)	2 117	(0.00)	2 118	(0.00)	2 118	(0.00)
13	2 165	2 152	(−0.01)	2 161	(0.00)	2 162	(0.00)	2 162	(0.00)	2 164	(0.00)
14	2 206	2 196	(0.00)	2 201	(0.00)	2 201	(0.00)	2 201	(0.00)	2 204	(0.00)
15	2 242	2 237	(0.00)	2 236	(0.00)	2 235	(0.00)	2 235	(0.00)	2 239	(0.00)
16	2 273	2 274	(0.00)	2 267	(0.00)	2 265	(0.00)	2 264	(0.00)	2 269	(0.00)
17	2 301	2 309	(0.00)	2 294	(0.00)	2 292	(0.00)	2 290	(0.00)	2 296	(0.00)
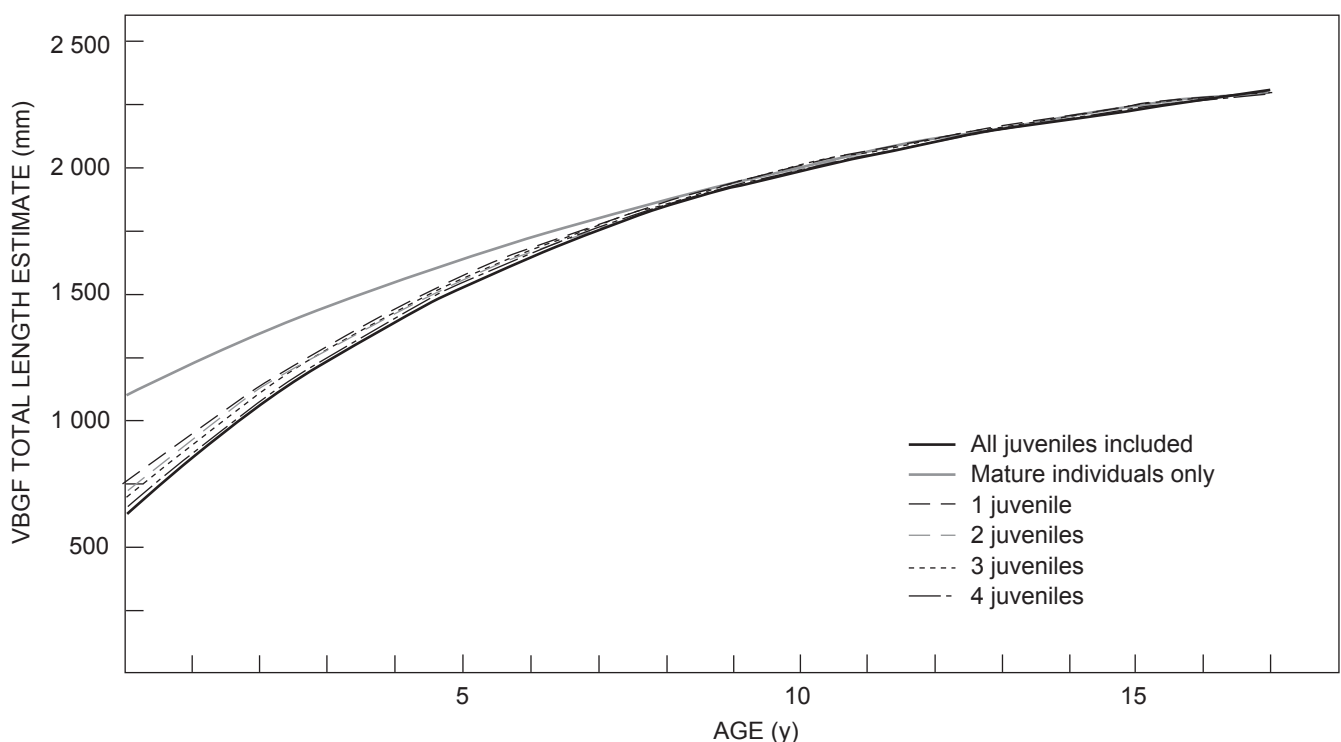
Figure 3: A comparison of VBGF length-at-age estimates with varying numbers of juveniles included (*n* of juveniles = 0–5)

population of *C. limbatus* (Table 4). The L_0 for *C. limbatus* varied between regions with Carlson et al. (2006) reporting the largest estimates for the South Atlantic Bight (750 mm TL for females), while the smallest L_0 estimate was from South Africa (516 mm TL for males) (Wintner and Cliff 1996). All of the other L_0 estimates occurred within this range (Table 4). The instantaneous growth rate at bir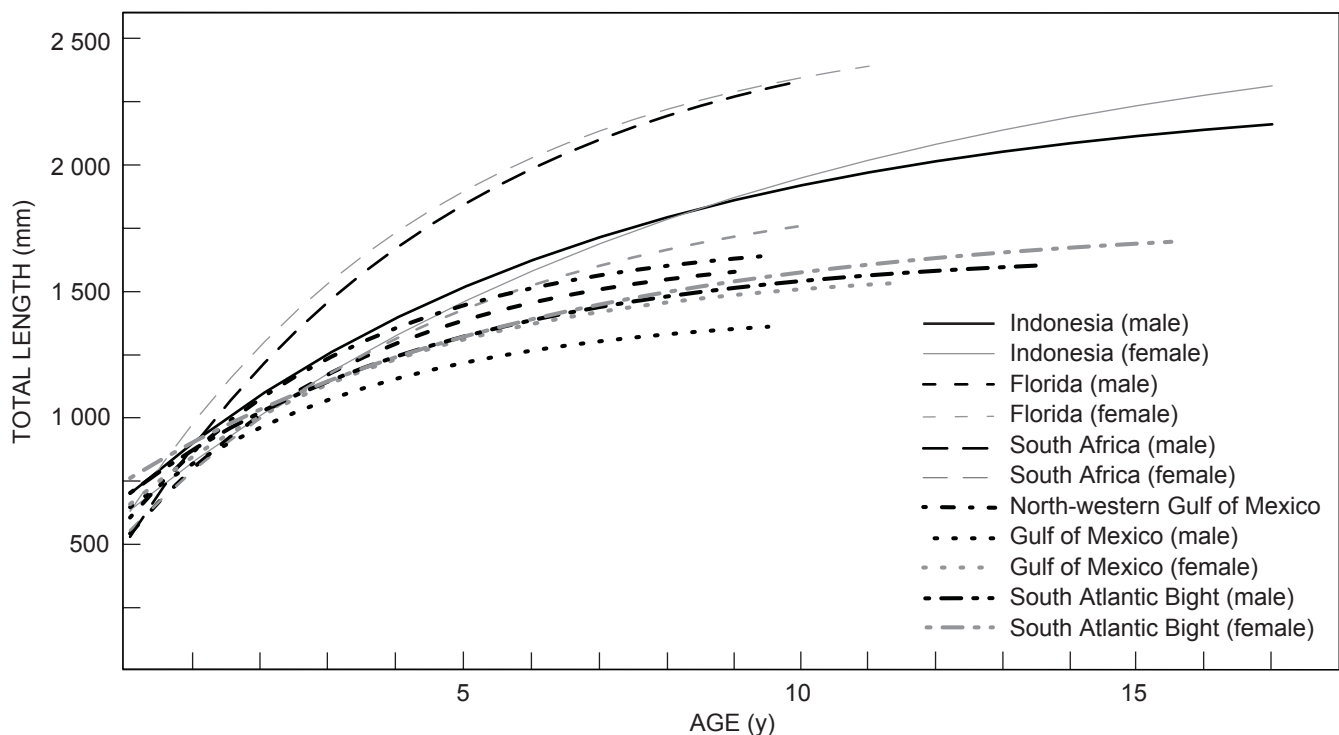th (dL/dt_0) also differed between regions and ranged from 164 mm y^{-1} in the South Atlantic Bight to far more than twice that in South Africa at 420 mm y^{-1} (Table 4).

The age at maturity (t_{mat}) for *C. limbatus* in Indonesia was 8.8 y for males and 7.6 y for females (Table 4) based on the lengths at which 50% of individuals are mature (L_{t50}), i.e. 1 894 mm TL for males and 1 796 mm TL for females (White 2007). These are the oldest ages at maturity estimated for any population of *C. limbatus*, with other

Table 4: A summary of VGBF parameters, maximum age (t_{max}), age at maturity (t_{mat}), growth rate at birth (dL/dt_0) and growth rate at maturity (dL/dL_{mat}) for *Carcharhinus limbatus* from different regions. L_∞ and L_0 are given in measurements of TL. Total lengths for *C. limbatus* from Wintner and Cliff (1996) and Carlson et al. (2006) were converted from precaudal length (PCL) and fork length (FL), respectively, using the length relationships given in these studies. Age at maturity was estimated in this study using length-at-50%-mature (L_{t50}) estimates from White (2007)

Study	Location	Sex	L_∞ (mm)	k (y^{-1})	L_0 (mm)	t_0 (y)	Maximum age (t_{max}) (y)	Age at maturity (t_{mat}) (y)	Growth rate at birth dL/dt_0 (mm y^{-1})	Growth rate at maturity dL/dt_{mat} (mm y^{-1})
Branstetter (1987)	Northern Gulf of Mexico	Both	1 710	0.28	593	−1.50	9.5	4–5 (males)	317	88
								7–8 (females)	317	38
Killam and Parsons (1989)	Florida	Male	1 665	0.28	530	−0.88	9.0	4–5	314	90
		Female	1 950	0.20	542	−1.15	10.0	6–7	278	77
Wintner and Cliff (1996)	South Africa	Male	2 615	0.20	516	−1.10	10.0	6.0	420	126
		Female	2 584	0.21	617	−1.30	11.0	7.0	413	95
Carlson et al. (2006)	Gulf of Mexico	Male	1 412	0.27	635	−2.21	9.5	4.5	210	62
		Female	1 587	0.24	647	−2.18	11.5	5.7	226	57
	South Atlantic Bight	Male	1 652	0.21	691	−2.58	13.5	6.7	202	49
		Female	1 776	0.16	750	−3.43	15.5	5.0	164	74
This study	Indonesia	Male	2 297	0.14	688	−	16.8	8.8	225	66
		Female	2 640	0.11	622	−	17.0	7.6	222	96

Figure 4: A comparison between the growth curves of *Carcharhinus limbatus* from Indonesia to previously published growth rates from other regions (Branstetter 1987; Killam and Parsons 1989; Wintner and Cliff 1996; Carlson et al. 2006). Growth curves for both sexes are included for the studies that separated them

populations maturing at between 4 and 8 y (Branstetter 1987; Killam and Parsons 1989; Wintner and Cliff 1996; Carlson et al. 2006). The instantaneous growth rate at maturity (dL/dt_{mat}) varied between regions and ranged from 49 mm y^{-1} for males in the South Atlantic Bight ($t_{mat} = 6.7$ y) to 126 mm y^{-1} for males in South Africa ($t_{mat} = 6$ y).

Discussion

Regional variation in life-history traits exists for several species of wide-ranging elasmobranchs (Driggers et al. 2004; Neer and Thompson 2005). The results of this study demonstrate that *C. limbatus* is one such species as its growth characteristics differ substantially on a circum-global scale. In comparison with length-at-age studies from other regions, *C. limbatus* from Indonesia matures later and attains older ages than its conspecifics. There is also an obvious difference in the maximum lengths of the different populations, with *C. limbatus* from Indonesia growing larger than populations from the USA (Branstetter 1987; Killam and Parsons 1989; Carlson et al. 2006) but being more comparable with those from South Africa (Wintner and Cliff 1996). The L_∞ estimates of *C. limbatus* from Indonesia and South Africa are similar although the maximum ages differ substantially (Wintner and Cliff 1996). Consequently there are large differences between the two populations in dL/dt_0 and the VBGF growth completion parameter (k) as *C. limbatus* from South Africa reaches L_∞ faster than *C. limbatus* from Indonesia. As the age-and-growth estimates of *C. limbatus* in this study are substantially different to those of populations from the USA and South Africa it is apparent that using these existing estimates as surrogate data would significantly compromise demographic analyses or stock assessments of the Indonesian population. Therefore, producing age and growth data using individuals from the local Indonesian population is necessary to support fisheries management and conservation of this population.

The model estimates produced by the VBGF provided the best fit for both the observed and back-calculated data for *C. limbatus*. Back-calculation techniques were included in the study because longline fisheries can result in length selectivity, which is biased towards catching larger individuals (White et al. 2008). Indeed this may have occurred in this study as individuals between 900 and 1 750 mm TL were missing. The VBGF (as well as other growth models) is particularly sensitive to missing data points at either end of the length range because two of its parameters (L_∞ and L_0) are strongly influenced by these data (Haddon 2001). Therefore, a typical consequence when juveniles are missing from length-at-age data is an inflated L_0 estimate, which occurred in this study for male *C. limbatus* when using only the observed length-at-age data. This in turn biases the remaining VBGF parameters (k and L_∞) because a strong correlation exists between the three parameters during the non-linear estimation process (Pilling et al. 2002). Therefore, when the L_0 estimate is inflated in this manner, estimates of k will be underestimated (Pardo et al. 2013). However, in the current study the inclusion of a small number of juveniles corrected the VBGF model for the

females, producing an L_0 estimate which was biologically realistic (White 2007). The same results occurred through the experimental removal and sequential reintroduction of juveniles, the inclusion of a small number of 0+ age-class individuals correcting the VBGF model so that it more closely matched the fit of the complete model. This emphasises the sensitivity of the VBGF to the omission of juveniles and highlights that their inclusion will improve the accuracy of the growth models, producing more biologically reasonable results in the same manner as back-calculation. Therefore, in sampling situations where juveniles are not captured due to gear selectivity or other factors, targeted sampling of these individuals outside of the regular sampling methodology, such as in nursery areas, could be highly beneficial.

As the VBGF parameters for the observed length-at-age data for the males are biologically unrealistic, the VBGF for the back-calculated data are considered the most accurate as their L_0 and L_∞ estimates are within range of the known length-at-birth and maximum size of *C. limbatus* from the region (White et al. 2006; White 2007). The VBGF growth estimates for the separate sexes are significantly different for Indonesian *C. limbatus*, with females growing larger than males. However, it cannot be determined whether this sexual dimorphism is an accurate representation of differences in the population, or whether it is an artefact of the small sample size used in this study. Since there were no male juveniles in the sample this could have led to the estimation of a larger L_0 than in the case of females. Furthermore, the largest individuals were female and this could have resulted in a larger L_∞ than in males. While the presence of sexual dimorphism is not definitive in this study, in previous studies it was confirmed in regions such as South Africa (Wintner and Cliff 1996) and the USA (Killam and Parsons 1989; Carlson et al. 2006), where females typically grow larger. Sexual dimorphism is also apparent for the age-at-maturity in every region. However, there is disparity as to which sex matures earliest between regions because males mature younger in some populations (Branstetter 1987; Killam and Parsons 1989; Wintner and Cliff 1996; Carlson et al. 2006), whereas females mature younger in others (Carlson et al. 2006; this study).

Given that many species of elasmobranchs have circum-global distributions, it is common to compare growth estimates among different regions (Driggers et al. 2004; Neer and Thompson 2005). Consequently, several studies have based their model choice (use of the VBGF, Gompertz, logistic or other model types) on that of previous studies in order to compare the resulting growth parameters between these populations (Neer and Cailliet 2001; Carlson et al. 2007; Piercy et al. 2007). There have also been instances where studies have performed multi-model approaches only to disregard the AIC results and choose a model used in previous studies to facilitate such comparisons (Henningsen and Leaf 2010). The primary argument for doing so is that the growth-completion parameters (k, G and g) of the different models are not comparable. However, this is a poor reason for limiting model choice because none of these parameters represents an empirical growth rate. They can more precisely be defined as curvature parameters for their

respective model types. For example, k in the VBGF is a non-biological curvature parameter that represents the rate at which the asymptotic length (L_∞) is reached (Haddon 2001). Therefore, two populations with different maximum sizes can have the same value of k despite having contrasting rates of empirical growth. This occurs because the population with the larger maximum size will grow faster than the population with the smaller maximum size to reach their L_∞ at the same rate. Previous studies on different *C. limbatus* populations demonstrate this. The highest value of k estimated for the species was 0.28 y^{-1} in Florida and in the Gulf of Mexico (Branstetter 1987; Killam and Parsons 1989). However, when the growth curves for *C. limbatus* from different regions are compared to one another it is evident that populations from Florida and the Gulf of Mexico are not the populations with the fastest growth rate, demonstrating that a higher value of k does not equate to a faster rate of empirical growth.

Instantaneous rates of growth at birth (dL/dt_0) and maturity (dL/dt_{mat}) have previously been used in addition to growth models as they provide an empirical measurement of growth (Thorson and Simpfendorfer 2009; Harry et al. 2010). In this study, the estimates of dL/dt_0 and dL/dt_{mat} were calculated for each *C. limbatus* population and used to compare the empirical growth rates. The estimates confirm that the populations in Florida and the Gulf of Mexico are not the fastest-growing for this species despite having the highest values of k. As these values are calculated from the model length-at-age estimates and not the resulting growth parameters, values of dL/dt_0 and dL/dt_{mat} can be calculated from any growth model and can subsequently be compared to other model types. This means that future studies can implement a multi-model approach without concern that the resulting model choice may restrict comparability with previous studies. Furthermore, as dL/dt_0 and dL/dt_{mat} are calculated in mm y^{-1}, they are biologically relevant values. Therefore, their use is recommended over the sole use of growth completion parameters to compare the growth of different populations.

As *C. limbatus* from Indonesia lives longer and matures later than in other regional populations, its life history is increasingly K-selected in comparison. Subsequently, the proportion of the stock that can be harvested sustainably is likely to be lower than that in populations that are less K-selected and the stock is also likely to recover more slowly from overfishing (Musick 1999). While management strategies exist that facilitate the sustainable harvest of slow-growing species such as *C. limbatus*, these involve limiting the fishing pressure on the older age classes and focusing effort on juveniles or young-of-the-year (Simpfendorfer 1999; Prince 2005). However, the Indonesian fishery predominantly uses longlines which are biased towards catching larger individuals (White et al. 2008). This observation is supported by the samples collected from Indonesia, of which 66% were mature individuals. In the event that fishing effort cannot be redirected to target more suitable and resilient size- and age classes, other management measures will need to be developed to identify and achieve sustainable fishing practices. In order to facilitate these efforts, demographic analyses and stock assessments of the Indonesian *C. limbatus* stock are

needed. This study has taken an important step towards facilitating such future assessments by producing accurate growth estimates from the local population.

References

Beamish R, McFarlane GA. 1995. A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. In: Secor D, Dean JM, Campana SE (eds), *Recent developments in fish otolith research*. Columbia: University of South Carolina Press. pp 545–565.

Blaber SJM, Dichmont CM, White W, Buckworth R, Sadiyah L, Iskandar B et al. 2009. Elasmobranchs in southern Indonesian fisheries: the fisheries, the status of the stocks and management options. *Reviews in Fish Biology and Fisheries* 19: 367–391.

Bowker AH. 1948. A test for symmetry in contingency tables. *Journal of the American Statistical Association* 43: 572–574.

Braccini JM, Gillanders BM, Walker TI, Tovar-Avila J. 2007. Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia. *Marine and Freshwater Research* 58: 24–33.

Branstetter S. 1987. Age and growth-estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. *Copeia* 1987: 964–974.

Branstetter S, Burgess GH (eds). 1996. Commercial Shark Fishery Observer Program. Characterization and comparisons of the directed commercial shark fishery in the eastern Gulf of Mexico and off North Carolina through an observer program. Final report. MARFIN Award NA47FF0008.

Burnham KP, Anderson DR. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28: 111–119.

Cailliet GM, Goldman KJ. 2004. Age determination and validation in chondrichthyan fishes. In: Musick JA, Carrier JC, Heithaus MR (eds), *Biology of sharks and their relatives*. Boca Raton, Florida: CRC Press. pp 399–447.

Cailliet GM, Smith WD, Mollet HF, Goldman KJ. 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes* 77: 211–228.

Carlander KD. 1969. *Handbook of freshwater fishery biology*, *vol. 1*. Ames: Iowa University Press.

Carlson JK, Middlemiss AM, Neer AA. 2007. A revised age and growth model for blacknose shark, *Carcharhinus acronotus* from the eastern Gulf of Mexico using X-radiography. *Gulf of Mexico Science* 25: 82–87.

Carlson JK, Sulikowski JR, Baremore IE. 2006. Do differences in life history exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico? In: Carlson JK, Goldman KJ (eds), *Special Issue. Age and growth of chondrichthyan fishes: new methods, techniques and analysis. Developments in Environmental Biology of Fishes* 25. Dordrecht: Springer. pp 279–292.

Cerrato RM. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1416–1426.

Dharmadi, Fahmi, Satria F. 2015. Fisheries management and conservation of sharks in Indonesia. In: Ebert DA, Huveneers C, Dudley SFJ (eds), *Advances in shark research. African Journal of Marine Science* 37: 249–258.

Driggers WB, Carlson JK, Cullum B, Dean JM, Oakley D, Ulrich G. 2004. Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. *Environmental Biology of Fishes* 71: 171–178.

Dudley SFJ, Simpfendorfer CA. 2006. Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978–2003. *Marine and Freshwater Research* 57: 225–240.

Duncan KM, Martin AP, Bowen BW, De Couet HG. 2006. Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). *Molecular Ecology* 15: 2239–2251.

Evans GT, Hoenig JM. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. *Biometrics* 54: 620–629.

Goldman KJ, Musick JA. 2006. Growth and maturity of salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific, and comments on back-calculation methods. *Fishery Bulletin* 104: 278–292.

Gompertz B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London* 115: 513–583.

Haddon M. 2001. *Modelling and quantitative methods in fisheries*. Boca Raton, Florida: CRC Press.

Harry AV, Simpfendorfer CA, Tobin AJ. 2010. Improving age, growth, and maturity estimates for aseasonally reproducing chondrichthyans. *Fisheries Research* 106: 393–403.

Harry AV, Tobin AJ, Simpfendorfer CA. 2013. Age, growth and reproductive biology of the spot-tail shark, *Carcharhinus sorrah,* and the Australian blacktip shark, *C. tilstoni*, from the Great Barrier Reef World Heritage Area, north-eastern Australia. *Marine and Freshwater Research* 64: 277–293.

Harry AV, Tobin AJ, Simpfendorfer CA, Welch DJ, Mapleston A, White J et al. 2011. Evaluating catch and mitigating risk in a multispecies, tropical, inshore shark fishery within the Great Barrier Reef World Heritage Area. *Marine and Freshwater Research* 62: 710–721.

Henningsen AD, Leaf RT. 2010. Observations on the captive biology of the southern stingray. *Transactions of the American Fisheries Society* 139: 783–791.

Katsanevakis S. 2006. Modelling fish growth: model selection, multi-model inference and model selection uncertainty. *Fisheries Research* 81: 229–235.

Katsanevakis S, Maravelias CD. 2008. Modelling fish growth: multi-model inference as a better alternative to *a priori* using von Bertalanffy equation. *Fish and Fisheries* 9: 178–187.

Killam KA, Parsons GR. 1989. Age and growth of the blacktip shark, *Carcharhinus limbatus*, near Tampa Bay, Florida. *Fishery Bulletin* 87: 845–857.

Kimura DK. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77: 765–776.

Last PR, Stevens JD. 2009. *Sharks and rays of Australia* (2nd edn). Collingwood, Australia: CSIRO Publishing.

Macbeth WG, Geraghty PT, Peddemors VM, Gray CA (eds). 2009. *Observer-based study of targeted commercial fishing for large shark species in waters off northern New South Wales*. Industry & Investment NSW – Fisheries Final Report Series No. 114. Cronulla: NSW Department of Primary Industries.

Musick JA. 1999. Ecology and conservation of long-lived marine animals. In: Musick JA (ed.), *Life in the slow lane: ecology and conservation of long-lived marine animals.* American Fisheries Society Symposium 23. Bethesda, Maryland: American Fisheries Society. pp 1–10.

Neer JA, Cailliet GM. 2001. Aspects of the life history of the pacific electric ray, *Torpedo californica* (Ayres). *Copeia* 2001: 842–847.

Neer JA, Thompson BA. 2005. Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environmental Biology of Fishes* 73: 321–331.

Ogle DH. 2012. FSA: fisheries stock analysis. R package version 0.3.5. Available at https://fishr.wordpress.com/fsa/ [accessed December 2013].

Ovenden J, Kashiwagi T, Broderick D, Giles J, Salini J. 2009. The extent of population genetic subdivision differs among four co-distributed shark species in the Indo-Australian archipelago. *BMC Evolutionary Biology* 9: 40.

Pardo SA, Cooper AB, Dulvy NK, Hodgson DD. 2013. Avoiding fishy growth curves. *Methods in Ecology and Evolution* 4: 353–360.

Piercy AN, Carlson JK, Sulikowski JA, Burgess GH. 2007. Age and growth of the scalloped hammerhead shark, *Sphyrna lewini*, in the north-west Atlantic Ocean and Gulf of Mexico. *Marine and Freshwater Research* 58: 34–40.

Pilling GM, Kirkwood GP, Walker SG. 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 424–432.

Prince JD. 2005. Gauntlet fisheries for elasmobranchs – the secret of sustainable shark fisheries. *Journal of Northwest Atlantic Fishery Science* 37: 407–416.

R Core Team. 2013. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* 191: 1–382.

Ricker WE. 1979. Growth rates and models. In: Hoar WS, Randall DJ, Brett JR (eds), *Fish physiology*. Vol. 8. New York: Academic Press. pp 677–743.

Simpfendorfer CA. 1999. Demographic analysis of the dusky shark fishery in southwestern Australia. In: Musick JA (ed.), *Life in the slow lane: ecology and conservation of long-lived marine animals.* American Fisheries Society Symposium 23. Bethesda, Maryland: American Fisheries Society. pp 149–160.

Smart JJ, Harry AV, Tobin AJ, Simpfendorfer CA. 2013. Overcoming the constraints of low sample sizes to produce age and growth data for rare or threatened sharks. *Aquatic Conservation-Marine and Freshwater Ecosystems* 23: 124–134.

Sparre P, Venema SC (eds). 1998. *Introduction to tropical fish stock assessment. Part 1: Manual*. FAO Fisheries Technical Paper No. 306. Rome: Food and Agriculture Organization.

Stearns S. 1992. *The evolution of life histories*. Oxford: Oxford University Press.

Thorson JT, Simpfendorfer CA. 2009. Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. *Fisheries Research* 98: 75–84.

von Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10: 181–213.

White WT. 2007. Catch composition and reproductive biology of whaler sharks (Carcharhiniformes: Carcharhinidae) caught by fisheries in Indonesia. *Journal of Fish Biology* 71: 1512–1540.

White WT, Bartron C, Potter IC. 2008. Catch composition and reproductive biology of *Sphyrna lewini* (Griffith & Smith) (Carcharhiniformes, Sphyrnidae) in Indonesian waters. *Journal of Fish Biology* 72: 1675–1689.

White WT, Kyne PM. 2010. The status of chondrichthyan

conservation in the Indo-Australasian region. *Journal of Fish Biology* 76: 2090–2117.

White WT, Last PR, Stevens JD, Yearsley GK, Fahmi, Dharmadi. 2006. *Economically important sharks and rays of Indonesia*. Canberra: ACIAR [Australian Centre for International Agricultural Research].

White WT, Sommerville E. 2010. Elasmobranchs of tropical marine ecosystems. In: Carrier JC, Musick JA, Heithaus MR (eds), *Sharks and their relatives II*. Boca Raton, Florida: CRC Press. pp 159–240.

Wintner SP, Cliff G. 1996. Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa. *Fishery Bulletin* 94: 135–144.

Zhu L, Li L, Liang Z. 2009. Comparison of six statistical approaches in the selection of appropriate fish growth models. *Chinese Journal of Oceanology and Limnology* 27: 457–467.