

Age and growth of the tiger shark *Galeocerdo cuvier* off the east coast of Australia

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Total lengths (L_T) at age and growth rates for south-west Pacific *Galeocerdo cuvier* were estimated from vertebral growth-band counts of 202 sagittally sectioned centra from 112 females (71–430 cm L_T), 79 males (72–351 cm L_T) and 11 of unknown sex. Captive growth data were also examined to complement vertebral age estimations. The sexes combined modelled growth coefficient ($k=0.08$) was smaller than previously reported for *G. cuvier* populations elsewhere. Split-band and narrow banding patterns were identified as potential sources of age underestimation in this species.

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Key words: growth modelling; life history; vertebral ageing.

INTRODUCTION

The tiger shark *Galeocerdo cuvier* (Péron & LeSueur 1822) is the largest species in the family Carcharhinidae, growing to around 550 cm total length (L_T) (Holmes *et al.*, 2012; Meyer *et al.*, 2014). In the south-west Pacific Ocean, individual sharks exhibit a range of patterns of habitat use from year-round local site fidelity, to wide-ranging ocean migrations in tropical and warm temperate waters (Fitzpatrick *et al.*, 2012; Holmes *et al.*, 2014; Werry *et al.*, 2014). Off the east coast continent of Australia, *G. cuvier* are caught by the commercial, recreational and game fishing sectors, and a substantial number are also caught each year through shark control programmes in place on popular Queensland (QLD) and New South Wales (NSW) beaches (DPIF, 2006; Reid *et al.*, 2011; Holmes *et al.*, 2012). Illegal foreign fishing activity in Australian Commonwealth waters also harvests an unquantifiable number of *G. cuvier* from Australian waters each year (Griffiths *et al.*, 2008; Marshall, 2011). Recent research using data from game fishing activities and long-term shark control

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programmes has identified declining catch rates for *G. cuvier* on the east coast of Australia (Park, 2009; Reid *et al.*, 2011; Holmes *et al.*, 2012). To adequately understand the implications of these findings, examination of life-history parameters is crucial to determine the extent the species' population would be affected by fishing and the ability to recover if stocks become depleted (Branstetter, 1990; Smith *et al.*, 1998). Baseline biological information for *G. cuvier* in the south-west Pacific region, however, remains scant. The large size, semi-solitary nature and the wide-ranging movements of this species have thus far hindered a comprehensive study of its biology, which is essential for the development of appropriate management strategies. Knowledge of length at maturity, maximum age and growth rate are pre-requisites for any age-based methods of stock assessment (Wintner & Dudley, 2000).

Elasmobranch age determination typically utilizes the concentric pairs of wide opaque and narrower translucent bands found in the vertebral centra (Cailliet & Goldman, 2004). Although *G. cuvier* have a global distribution in tropical and warm temperate waters, vertebral ageing studies of the species using this method have only been conducted in Hawaii ($n=28$ individuals; De Crosta *et al.*, 1984), western North Atlantic ($n=238$; Kneebone *et al.*, 2008), Gulf of Mexico ($n=69$; Branstetter *et al.*, 1987) and off the east coast of South Africa ($n=101$; Wintner & Dudley, 2000). Moreover, backcalculation methods were often used as full size ranges for the species were not obtained. *Galeocerdo cuvier* growth has also been assessed through the use of mark-recapture methods in Hawaii ($n=37$, Meyer *et al.*, 2014), western North Atlantic ($n=42$, Natanson *et al.*, 1999; $n=217$, Kneebone *et al.*, 2008) and off Brazil ($n=2$, Afonso *et al.*, 2012). Small samples sizes, low rates of recapture and a lack of representation of the species' full size range are generally limiting features of such studies (Meyer *et al.*, 2014). Irrespective of the method used, however, modelled estimates of the growth coefficient, k , and asymptotic total length, L_{∞} , appear to be markedly different for *G. cuvier* in different regions of the world.

Previous studies have demonstrated that centrum banding patterns in elasmobranchs may be related to physiological changes induced by changes in environmental variables such as temperature and photoperiod (Cailliet *et al.*, 1986; Goldman, 2005), and evidence of subtle banding due to food shortages has been suggested in some species (Goldman, 2005). Regional differences in prey availability may also affect growth rates (Wirsing *et al.*, 2006), highlighting the need for regional assessments to be completed. Indeed, the movement capabilities of *G. cuvier*, particularly across the south-west Pacific, are seasonal and wide ranging, and encompass the use of both tropical and warm temperate waters, thus encountering a wide variety of locally abundant prey species throughout their distribution (Holmes *et al.*, 2014; Werry *et al.*, 2014). The aim of this study was to examine the age and growth of *G. cuvier* off the east coast of Australia using vertebral band-pair counts from pre- and post-natal individuals. Growth rates were compared with length and mass data from captive-reared *G. cuvier* at Sea World, Gold Coast, QLD, Australia (<http://seaworld.com.au/>). Assessment of mark-recapture *G. cuvier* data collected by citizen scientists through the NSW Game Fish Tagging Program (NSWGFTP; <http://www.dpi.nsw.gov.au/fisheries/recreational/saltwater/gamefish-tagging>) was also conducted. In addition to providing the first growth model and length and age-at-maturity estimates for *G. cuvier* in the Indo-West Pacific, pre-birth banding and split banding patterns are also identified and discussed for the first time in *G. cuvier*.

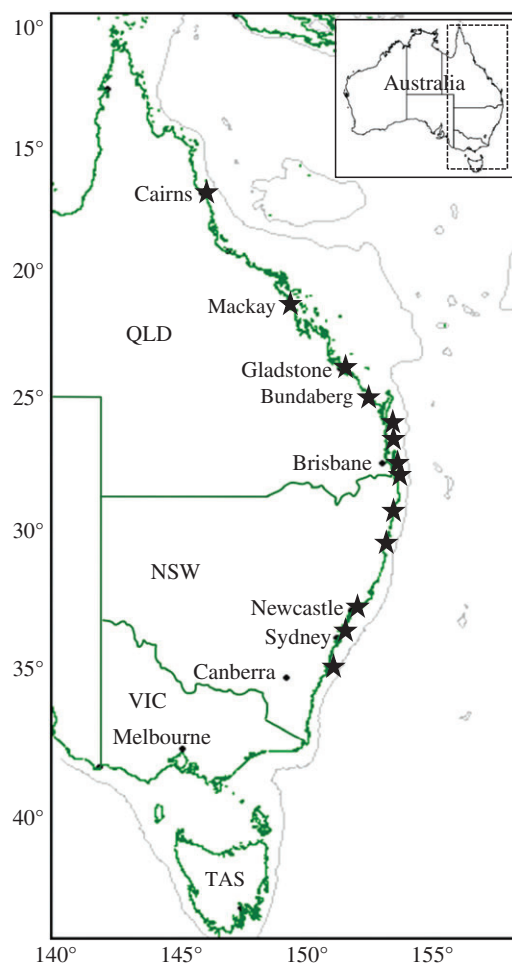


FIG. 1. Map of study area on the east coast of Australia. ★, vertebral samples were collected from locally caught *Galeocerdo cuvier*.

MATERIALS AND METHODS

SAMPLE COLLECTION

Queensland

Galeocerdo cuvier vertebrae were collected from individuals caught in the Queensland Shark Control Program (QSCP; <https://www.daf.qld.gov.au/fisheries/services/shark-control-program>) between 2008 and 2011, with the geographic range of collection from Cairns in tropical northern QLD ($16^{\circ} 55' \text{ S}$; $145^{\circ} 46' \text{ E}$) to the sub-tropical Gold Coast region ($28^{\circ} 10' \text{ S}$; $153^{\circ} 33' \text{ E}$) near the border with NSW (Fig. 1).

New South Wales

Vertebrae were collected along the NSW coast between Coffs Harbour ($30^{\circ} 18' \text{ S}$; $153^{\circ} 7' \text{ E}$) and Bermagui ($36^{\circ} 2' \text{ S}$; $150^{\circ} 4' \text{ E}$) from *G. cuvier* caught as part of recreational

game-fishing operations between 1997 and 2000. These samples were complemented by vertebrae collected by the NSW fisheries observer programme (NSWFOP), which conducted fishery-dependent sampling of commercially caught sharks north of Crowdy Head (31° 50' S; 152° 45' E) from September 2007 to July 2009. Additional vertebrae were provided from the NSW Shark Meshing (Bather Protection) Program (NSWSMP; <http://www.dpi.nsw.gov.au/fisheries/info/sharksmart/meshing/shark-meshing>) captures between Bondi (33° 53' S; 151° 15' E) and Wattamolla (34° 8' S; 152° 7' E) from 2004 to 2006 (Fig. 1).

Processing of animals

For most samples, capture date and location, L_T (± 1 cm) and sex were recorded. L_T was determined by allowing the caudal fin to take a natural position, with measurements taken underneath the animal in a straight line. For whole sharks obtained from the QSCP, fork length (L_F) and pre-caudal length (L_{PC}) (± 1 cm) were also recorded. For NSW game-fishing samples, L_T was provided for all samples, with L_F and L_{PC} provided for a sub-set of samples. Where L_F or L_{PC} was not recorded, the values were calculated using a length-length conversion calculated by the regression relationships among L_T , L_F and L_{PC} from the sampled population using SigmaPlot 11.0 (Systat Software Inc.; www.systat.com). A χ^2 goodness-of-fit test was conducted to examine whether the sample was sex biased (PASW Statistics 18; www.spss.com.hk/statistics) at four life stages: pre-natal, juvenile (birth to 200 cm L_T), sub-adult (200 to 300 cm L_T) and adult (300+ cm L_T). Sex ratio by fishing method was also assessed. A Shapiro-Wilk test for normality was conducted to determine whether the size frequency distribution of either sex was skewed. Up to 10 vertebral centra were removed from the cervical region from all sharks where vertebrae are largest, facilitating more accurate age estimates than vertebrae from other regions (Officer *et al.*, 1996). Vertebral samples from *in utero* pups from three different litters were also processed to examine the presence of pre-birth banding. These pre-natal samples consisted of pups near-full term growth (>71 cm L_T) and were therefore included in the growth modelling analyses for comparison with only post-natal data, and potential to assist in anchoring the lower end of the growth curve (Silva *et al.*, 1996; White *et al.*, 2001, 2002).

Where possible reproductive state was determined from the maximum oocyte diameter (MOD), ovary and oviducal gland mass of females and from clasper length and calcification state for males (Walker, 2005; Whitney & Crow, 2007). The length and age at which 50% of the population were mature (L_{50} and A_{50}) were determined for each sex using 50 cm L_T size classes and 2 year age classes. A least-squares non-linear regression (PASW Statistics 18) using the logistic function, $P_l = 1 \left\{ 1 - e^{-\ln 19 [(l-L_{50})(L_{95}-L_{50})^{-1}]^{-1}} \right\}^{-1}$ (Walker, 2005), enabled the calculation of parameter estimates. P_l is the proportion of mature animals at L_{Ti} , and the lengths at which 50 and 95% of the population is mature are represented by L_{50} and L_{95} . For A_{50} , the proportion of mature animals in each age class (a) was substituted for l , with L_{50} and L_{95} replaced by A_{50} and A_{95} (Gutteridge *et al.*, 2013).

Captive sharks

Between June 2003 and September 2006, three *G. cuvier* were maintained for 239, 425 and 1031 days in outdoor aquaria at Sea World, Gold Coast. Data on mass (M , kg) and L_T were recorded at the time of capture and again at release. Mean growth rate was calculated for each specimen by dividing the total observed growth by their time in captivity.

Mark-recapture

As part of the NSWGFTP, 26 *G. cuvier* were tagged and recaptured between 1985 and 2014, and capture and recapture dates, L_T or L_F (m) and mass (kg) when captured and recaptured were recorded by recreational fishers. As indicated on tagging programme data sheets, initial capture data were always estimated *in situ*, and recapture data were either estimated or actually measured if the shark was killed and weighed at the wharf. Data were assessed for reliability, and found to be highly inconsistent and deemed unusable for length and mass estimates, and were subsequently discarded from the analyses.

Vertebrae preparation and ageing protocol

All vertebral samples collected from dissected individuals were stored frozen until processing. Individual centra were cleaned of soft tissue, and the neural and haemal arches were removed. For larger specimens, submersion in a 10% sodium hypochlorite solution for up to 60 min, followed by washing in distilled water, aided excess tissue removal. Cleaned centra were stored in 70% ethanol (Wintner & Cliff, 1996). For each *G. cuvier*, one vertebra was chosen at random for sectioning. Small vertebrae (<1 cm diameter) were embedded in a clear polyester resin (Diggers, Reochem; www.recochem.com.au) to facilitate sectioning. For each vertebral sample, a sagittal plane of 150 μm thick section was taken through the focus of the centrum with a LECO 801–137 diamond wafering blade (Buehler Isomet low speed saw; www.buehler.com). This thickness was chosen after conducting readability trials also using 300, 450 and 600 μm sections (Gutteridge *et al.*, 2013). Following sectioning, samples were polished with P400 grit wet emery paper for optimum resolution. Centra cross-sections were then set on glass slides using Polyplex Clear Cast 20 waxed resin (Fibre Glass International, Wacol QLD 4076, Australia) and dried overnight. Experimentation with crystal violet and silver nitrate stains was undertaken to compare with unstained vertebral band counts to determine the best preparation method (Goldman, 2005). Neither of these methods produced a marked increase in band resolution; hence, band counts were determined using natural, unstained sections.

Individual sections were viewed using transmitted and reflected light sources, with the best resolution achieved using reflected light on a dark background. A dissecting microscope (Olympus SZ; www.olympus-ims.com/microscope) fitted with a digital camera allowed photographing and reviewing of sections using ImageJ software (<http://rsb.info.nih.gov/ij/>). Most vertebral sections displayed a pattern of alternating opaque and translucent zones that consisted of both narrow and widely spaced concentric rings. Following Cailliet *et al.* (1983), each opaque and translucent pair was defined as a growth band. Age counts were assigned to vertebral sections by marking individual band pairs on the digital images along the line of the corpus calcareum from the birth band to the outer edge (Fig. 2). The birth band was identified where an angle change on the centrum was apparent (Goldman, 2005). The consistent location of this band was confirmed through comparison of the birth-band radius measurement to the centrum radius of full-term pre-natal and young-of-the-year (YOY) *G. cuvier*. Centrum radius (mm) and L_T (cm)

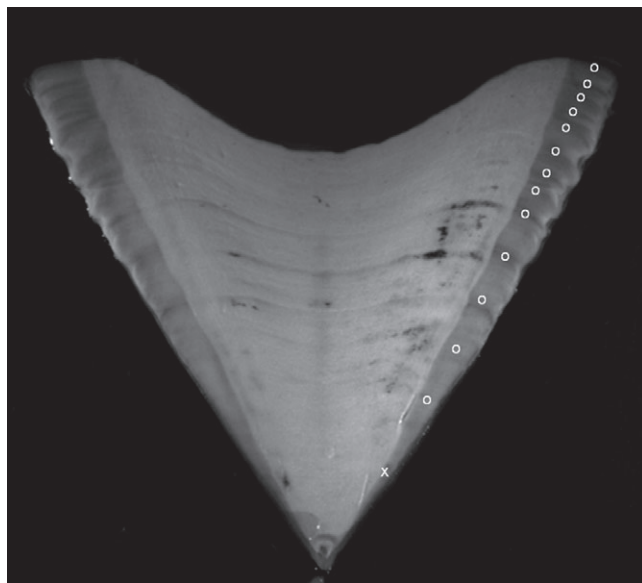


FIG. 2. Marked vertebral section from a 285 cm total length (L_T) female *Galeocerdo cuvier*, with 13 growth-band pairs visible. X on the corpus calcareum indicates the birth band.

were compared to examine linear relationships in growth. The readability of each vertebral section was given a score (1–5) according to the following definitions derived from Geraghty *et al.* (2014): (1) all growth bands well defined and visible; (2) almost all bands visible, clear interpretation possible; (3) most bands visible, interpretation reliable to within ± 1 ; (4) bands visible, majority difficult to interpret; (5) unreadable. All sections deemed to be of readability 5 were excluded from further analyses. Two training counts were performed on all centra in the first instance (Pierce & Bennett, 2009; Gutteridge *et al.*, 2013). Ages were then estimated from three independent counts conducted by both the primary author (reader 1) and secondary author (reader 2) without prior knowledge of the size, sex or date of capture for each shark. Age counts that were in agreement between readers from the third independent read were adopted as the final age count for those vertebral sections. Where agreement was not reached, the archived images of each reader's ageing interpretations were reviewed and recounted in the presence of both readers (Goldman, 2005; Piercy *et al.*, 2007). If consensus could not be reached, the sample was discarded from the analysis. Lastly, age estimates were assessed for precision and bias between readers. The precision between the final counts of both readers was tested by percentage agreement (PA; Goldman, 2005; Cailliet *et al.*, 2006), the c.v. (Chang, 1982) and the average percentage error (APE; Beamish & Fournier, 1981). An age-bias plot was also constructed to test for bias between the third counts of the two readers (Cailliet *et al.*, 2006).

DATA ANALYSIS

Evidence of annual band-pair deposition (up to 20 years) has been validated for *G. cuvier* in the north-west Atlantic Ocean using bomb-radiocarbon techniques (Kneebone *et al.*, 2008). Partial verification has also been obtained through marginal increment analysis in the north-west Atlantic Ocean (Branstetter *et al.*, 1987) and the Indian Ocean (Wintner & Dudley, 2000). Due to the extremely low number of mark-recaptures of *G. cuvier* off the east coast of Australia (c. 2.4%; NSW DPI, unpubl. data), marginal increment analysis was conducted to qualitatively verify the timing of band deposition by observing the translucency or opacity of the centrum edge (Cailliet & Goldman, 2004). Only sections from post-natal individuals displaying clearly defined growth bands on the centrum outer margin were included (readability 1–3; $n = 142$). Marginal increment ratios (R_{MI}) were then calculated using the following equation, with means \pm s.d. subsequently plotted by month of capture: $R_{MI} = W_M W_{PB}^{-1}$ (Conrath *et al.*, 2002), where W_M = margin width and W_{PB} = previous band-pair width. A one-way ANOVA and Tukey *post hoc* test was conducted to observe significant differences between mean monthly R_{MI} .

Growth modelling

Growth studies on elasmobranchs, including *G. cuvier*, have typically been modelled using the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938). Studies in recent years using a multiple model approach have, however, established that alternative models may be more appropriate in some shark species (Natanson *et al.*, 2006; Barreto *et al.*, 2011; Geraghty *et al.*, 2014). Therefore, an information-theoretic, multi-model inference (MMI) approach was used (Burnham & Anderson, 2001; Harry *et al.*, 2013) to determine the most appropriate growth model for *G. cuvier* in eastern Australian waters. Six candidate models were fitted to observed length-at-age data for both post-natal and pre- and post-natal data sets, using modified three-parameter versions of the von Bertalanffy (VB3) $L_t = L_0 + (L_\infty - L_0)(1 - e^{-(kt)})$, Gompertz (GOM3) $L_t = L_0 \left\{ e^{\ln(L_\infty L_0^{-1}) [1 - e^{-(kt)}]} \right\}$ and logistic (LOGI3) $L_t = [L_\infty L_0 e^{(kt)}] \{ L_\infty + [L_0 e^{(kt)} - 1] \}^{-1}$ growth models as given by Geraghty *et al.* (2014), where L is a function of time t , L_∞ is the theoretical asymptotic length, L_0 is length-at-birth and k is the growth coefficient.

Two-parameter versions of the same models were also computed by substituting L_0 for a fixed length-at-birth taken from the largest near-term embryo observed in this study ($L_T = 78$ cm). All models were fitted using least-squares non-linear regression in the statistical package R (R Development Core Team; www.r-project.org). To test for significant differences between the growth curves of females and males, VB3 results were tested for equality using a log-likelihood ratio test (Kimura, 1980). Model performance was evaluated using Akaike information criteria

(AIC), with the best-fit model displaying the lowest AIC value (Burnham & Anderson, 2002). AIC differences (Δ) were calculated and used to rank the support of the remaining models relative to the statistical best-fit model; models with $\Delta = 0-2$ had substantial support, $\Delta = 4-7$ moderate support and $\Delta \geq 10$ minimal support (Burnham & Anderson, 2002). Akaike weights (ω) were then calculated to determine the weight of evidence in favour of a particular model being the best fit to the data (Burnham & Anderson, 2002). The 95% C.I. around the best-fit parameter estimates were calculated from 10 000 re-sampled datasets.

RESULTS

SAMPLES COLLECTED

Vertebrae from 180 post-natal (92–430 cm L_T) and 59 pre-natal *G. cuvier* (41–78 cm L_T) were collected, totalling 239 individuals of which 138 were females, 90 were males and 11 were of unknown sex. Both female and male size frequency distributions did not conform to normality (♀: $W = 0.90$, $n = 138$, $P < 0.05$; ♂: $W = 0.94$, $n = 90$, $P < 0.05$) (Fig. 3). χ^2 analysis among life stages revealed that only the female to male sex ratio of the pre-natal sharks was significantly different (1.8:1, $\chi^2 = 4.34$, d.f. = 1, $P < 0.05$). Female to male sex ratios were not significantly different for *G. cuvier* captured by offshore gamefishing (1:1.2) or commercial operations (1.04:1); however, significantly more females than males (2.3:1) were captured on shark control gear ($\chi^2 = 12.66$, d.f. = 1, $P < 0.05$). A linear relationship was found between centrum radius (mm) and L_T (cm) (Fig. 4). Relationships among L_T , L_F , L_{PC} and M were represented by the following equations: L_T (cm) = $22.607 + 1.096 L_F$ (cm) ($r^2 = 0.99$, $P < 0.05$); L_F (cm) = $-18.812 + 0.903 L_T$ (cm) ($r^2 = 0.99$, $P < 0.05$); L_{PC} (cm) = $-16.219 + 0.795 L_T$ (cm) ($r^2 = 0.92$, $P < 0.05$); L_T (cm) = $34.321 + 1.159 L_{PC}$ (cm) ($r^2 = 0.92$, $P < 0.05$); M_b (kg) = $1.42 \cdot 10^{-7} L_T$ (cm) $^{3.669 \pm 0.063}$ ($r^2 = 0.98$, $P < 0.05$); M_b (kg) = $2.748 \times 10^{-6} L_F$ (cm) $^{3.245 \pm 0.042}$ ($r^2 = 0.99$, $P < 0.05$).

AGE VALIDATION

Marginal increment analysis provided evidence for annual band-pair deposition in *G. cuvier* off the east coast of Australia. Formation of the translucent narrow band (annuli) was observed in the austral winter (June to August) when R_{MI} was lowest, with full band-pair deposition correlating with the maximum values observed in the austral spring and summer months (September to February; Fig. 5). One-way ANOVA was significant ($P < 0.01$), with a Tukey *post hoc* test indicating that the January mean was significantly different from April, June and August means ($P < 0.05$).

PRE-BIRTH MARKS

Pre-birth marks were observed in all the 59 pre-natal sharks specimens examined. In one litter, sourced from a 380 cm L_T female in October (austral spring), 32 of the 33 individuals (size range: 69–75.5 cm L_T) had already developed the birth band, indicating that these pups were probably nearing parturition [Fig. 6(a)]. This litter also contained one runt (41 cm L_T), probably deceased, which had one pre-birth mark just formed near the edge of the centrum. Although pre-birth marks were obvious in pre-natal and YOY samples [Fig. 6(b)], they became considerably more difficult to identify in older individuals.

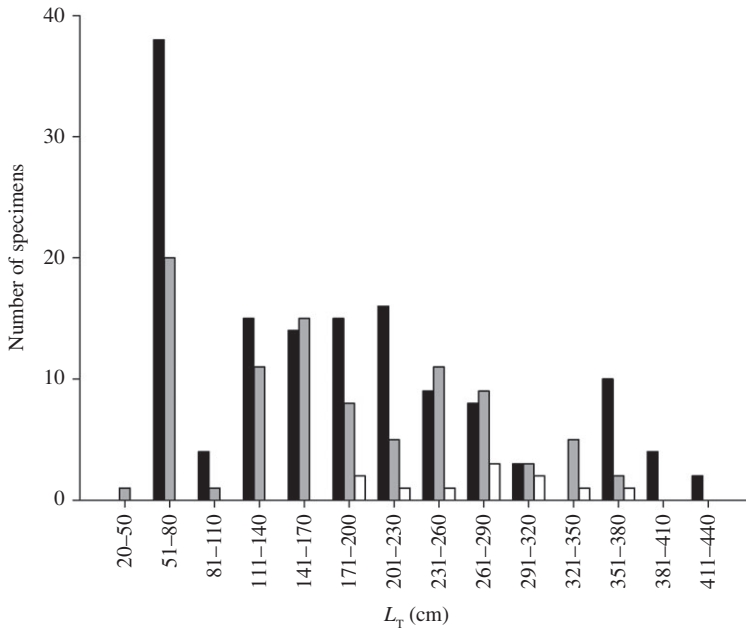


FIG. 3. Total length (L_T)–frequency distributions of female (■), male (▒) and unsexed (□) *Galeocerdo cuvier* samples used in this study.

VERTEBRAL FEATURES

Vertebral growth-band readability in large *G. cuvier* was difficult due to the clustering of annuli along the centrum edge. Anomalies such as split and subtle banding were also observed in a range of samples along the corpus calcareum, intermedialia or both, and were not counted as true annuli (Goldman, 2005; Goldman *et al.*, 2012) (Fig. 7). Patterns of narrow and wide band-pair deposition were observed in many individuals, which are characteristics of elasmobranch centrum (Cailliet *et al.*, 1983). Consistent identification of the birth band was verified through comparison of the centrum radius of YOY and full-term (>70 cm L_T) pre-natal *G. cuvier*. The birth-band radius of post-natal samples ($n=200$) ranged between 2.42 and 5.49 mm, with a mean \pm s.d. = 3.73 ± 0.51 mm. The centrum radius of pre-natal *G. cuvier* (70–78 cm L_T , $n=57$) ranged from 2.74 to 4.10 mm (mean \pm s.d. = 3.54 ± 0.31 mm). Early YOY sharks (92–111 cm L_T , $n=4$) had centrum radius measurements ranging from 5.35 to 6.46 mm (mean \pm s.d. = 5.80 ± 0.48 mm). Since the mean birth-band radius for post-natal sharks fell between the mean centrum radii of pre-natal and YOY *G. cuvier*, consistent identification of the birth band was achieved (Kneebone *et al.*, 2008). Vertebral sections that were assigned a readability score of 5 were discarded from the growth modelling (37 samples). To avoid pseudo-replication of pre-natal samples due to large litter sizes, a sub-sample of four males and four females from each of the three litters were randomly selected ($n=24$) and combined with the post-natal data. Final ages were therefore determined from 178 post-natal (100 females, 67 males and 11 unsexed) and 24 pre-natal (12 females and 12 males) centra. The smallest pre-natal female and male included in the modelling analyses were of 71 and 72 cm L_T .

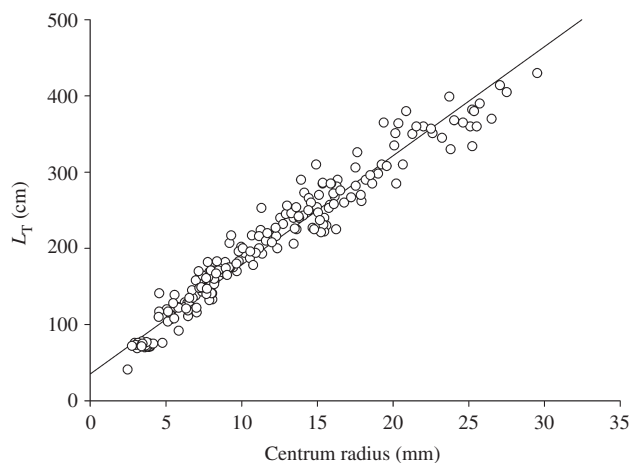


FIG. 4. Relationship between centrum radii and total length (L_T) for *Galeocerdo cuvier* on the east coast of Australia. The curve was fitted by $y = 14.314x + 35.293$ ($r^2 = 0.957$).

AGE ESTIMATION AND GROWTH RATES

For all counts, between-reader APE and c.v. were 16 and 23%, respectively. PA between the primary and secondary readers indicated that 85% of all counts differed by two or fewer bands, and 65% by one or none. The age-bias plot showed that the secondary reader assigned higher age estimates for specimens up to 12 years, and that the highest variability came from age estimates derived from older sharks (Fig. 8).

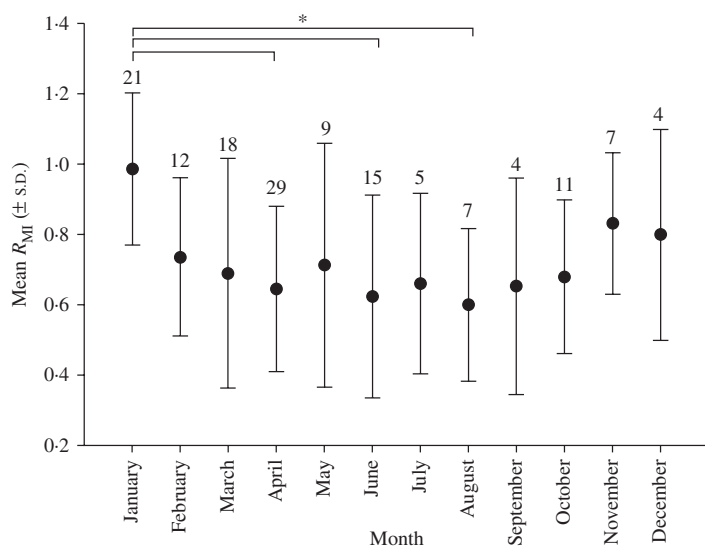


FIG. 5. Monthly mean \pm S.D. marginal increment ratios (R_M) and sample size per month for *Galeocerdo cuvier* in east coast Australian waters. Readability scores 1–3 only, $n = 142$; *, significantly different ($P < 0.05$) monthly means.

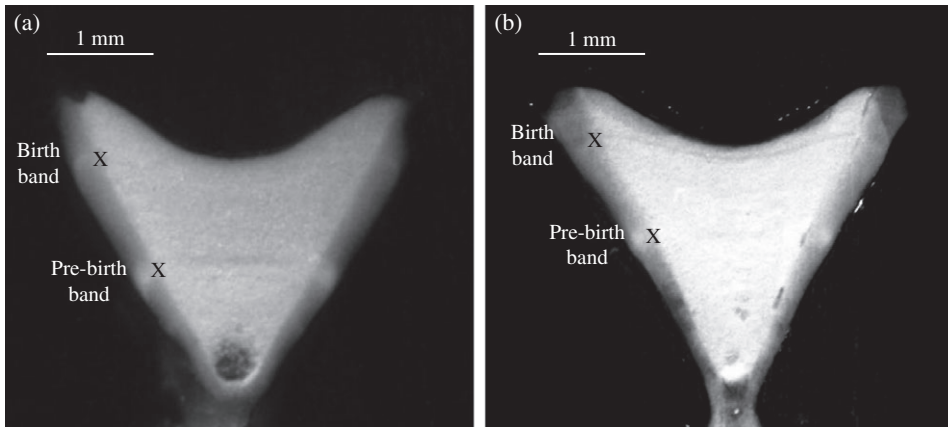


FIG. 6. Pre-birth and birth bands visible in (a) pre-natal pup (female, 71 cm total length, L_T) and (b) young-of-the-year (female, 92 cm L_T).

Of the six candidate growth functions fitted, the VB3 model attracted the strongest statistical support in describing *G. cuvier* growth for all available post-natal length-at-age data sets (Table I), but produced higher than expected estimates of L_0 . When the models were re-run on combined pre and post-natal data, the VB3 growth function again had the strongest statistical support for both sexes individually and combined sexes data (Table I; $\omega = 99.31-100$) and produced somewhat more realistic estimates of L_0 . The two-parameter models, incorporating a fixed size at birth, attracted the least statistical support of the six models. Modelled pre- and post-natal male and female growth curves indicated that after the first year males grew slightly faster until around 8–10 year of age, at which point male growth decreased at a faster

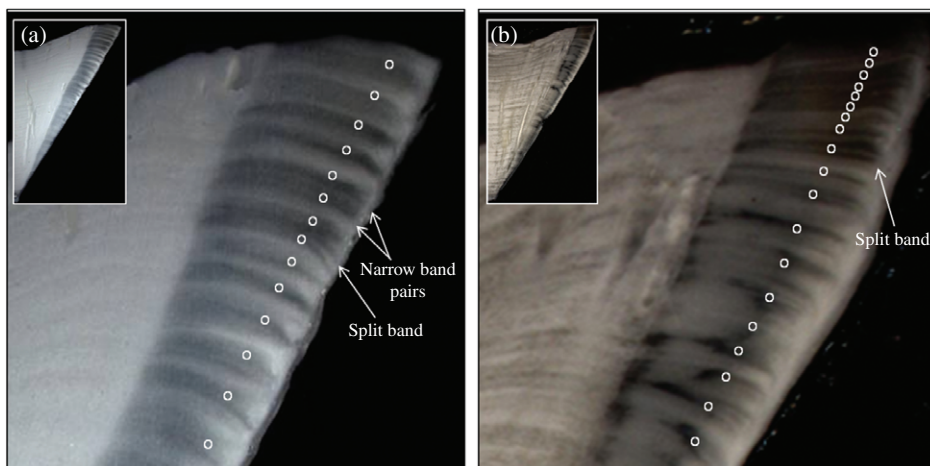


FIG. 7. Age estimation where split or narrow band pairs were evident on large *Galeocерdo cuvier* vertebra. Images of upper corpus calcareum are from (a) a 360 cm total length (L_T) female (age estimated at 22 years) and (b) a 345 cm L_T male (age estimated at 28 years).

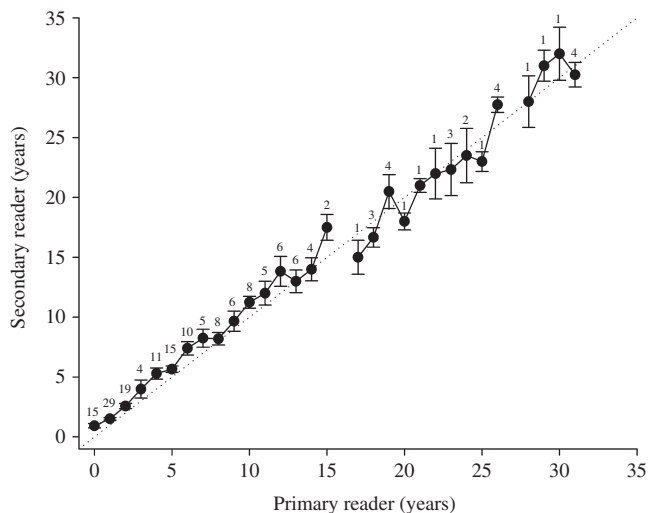


FIG. 8. Between-reader age-bias plots for *Galeocerdo cuvier* vertebral age estimates. Counts are plotted relative to a line of equivalence, with error bars representing two s.e. Numbers above data points indicate sample sizes.

rate than the female growth. Older age classes were dominated by female sharks, whose continued growth did not produce a pronounced asymptote (Fig. 9). The oldest female was estimated to be 33 years old at 430 cm L_T , and the oldest male was 351 cm L_T and 28 years old. The combined pre and post-natal VB3 data produced a growth curve similar to previous vertebral ageing studies of *G. cuvier* in the north-west Atlantic Ocean (Fig. 10).

SIZE AT MATURITY

There was some difficulty obtaining both the reproductive organs and vertebrae from larger *G. cuvier* when the whole animal could not be landed, or when processing was time-limited on board commercial fishing vessels or at weigh stations during game fishing competitions. Of the sharks where both vertebrae and reproductive organs were collected, the largest immature female (290 cm L_T) and male (285 cm L_T) were estimated to be 13 and 9 years of age. The smallest mature female (310 cm L_T) was 12 years old. The smallest mature male was 276 cm L_T , but vertebrae were not collected from this individual so no age estimate was obtained. As the vertebral samples from sharks around the size at maturation were conspicuously lacking, A_{50} could not be quantitatively determined and was estimated for both males and females between 10 and 13 years. L_{50} was calculated from all specimens assessed for maturity status ($n = 109$). For females in this population, L_{50} was calculated at 326 cm L_T and for males at 297 cm L_T .

CAPTIVE SHARKS

Growth rates of long-term captive-reared *G. cuvier* were consistent across the three individuals and ranged between 20.7 and 29.7 cm year⁻¹ (Table II). Based on the VB3

TABLE I. Growth model parameters for pre and post-natal *Galeocerdo cuvier* from the east coast of Australia. Values in bold indicate the best model fit according to Akaike information criteria (AIC)

	<i>n</i>	Model	<i>L</i> _∞ (95% C.I.)	<i>L</i> ₀ (cm) (95% C.I.)	<i>k</i> (95% C.I.)	AIC	<i>Δ</i>	<i>ω</i>	RSE
Pre and post-natal Females	112	VB3	418.3 (398.8–441.8)	101.5 (94.8–108.1)	0.07 (0.06–0.08)	992.3	0.00	99.99	19.86
	112	VB2	395.3 (379.6–412.4)	78	0.10 (0.09–0.11)	1028.4	36.04	0	23.43
	112	GOM3	394.3 (380–410.3)	108.2 (101.6–114.6)	0.12 (0.11–0.14)	1010.6	18.27	0.01	21.55
	112	GOM2	373.1 (359.6–386.9)	78	0.17 (0.16–0.19)	1070.0	77.66	0	28.22
	112	LOGI3	383.8 (370.6–397.7)	113.2 (106.5–119.7)	0.18 (0.16–0.19)	1026.6	34.30	0	23.15
	112	LOGI2	362.1 (348.2–375.5)	78	0.27 (0.25–0.29)	1102.7	110.37	0	32.66
Males	79	VB3	350.5 (328.8–380.7)	101.6 (93.6–109.5)	0.12 (0.09–0.14)	714.7	0.00	99.31	21.62
	79	VB2	327.3 (310.5–348.1)	78	0.16 (0.13–0.19)	739.0	24.23	0	25.35
	79	GOM3	337.1 (318.2–360.3)	106.7 (98.9–114.5)	0.17 (0.14–0.20)	724.7	9.98	0.68	23.02
	79	GOM2	309.1 (295.1–325.8)	78	0.28 (0.24–0.32)	759.5	44.76	0	28.87
	79	LOGI3	329.7 (312.8–349.9)	110.5 (102.8–118.5)	0.23 (0.19–0.27)	733.4	18.63	0.01	24.32
	79	LOGI2	296.5 (283.6–310.6)	78	0.43 (0.37–0.5)	775.0	60.23	0	31.84
Combined	202	VB3	403.6 (387–423.9)	103.4 (98.2–108.5)	0.08 (0.07–0.09)	1821.0	0.00	100	21.20
	202	VB2	376.2 (363.3–391)	78	0.11 (0.10–0.12)	1890.0	69.54	0	25.22
	202	GOM3	381.0 (367.9–395.2)	109.6 (104.5–114.6)	0.13 (0.11–0.14)	1852.0	30.93	0	22.87
	202	GOM2	353.2 (342.3–364.4)	78	0.19 (0.18–0.20)	1957.0	136.30	0	29.72
	202	LOGI3	370.0 (358.9–382.4)	114.3 (109.1–119.5)	0.18 (0.16–0.19)	1879.0	57.78	0	24.44
	202	LOGI2	339.8 (329.4–350.5)	78	0.29 (0.27–0.32)	2008.0	187.50	0	33.72
Post-natal only Females	100	VB3	441.1 (417.4–472.9)	116.8 (109.6–123.9)	0.06 (0.05–0.07)	859.9	0.00	96.31	17.39
	100	VB2	395.4 (379.0–414.2)	78	0.10 (0.08–0.11)	929.9	69.99	0	24.79
	100	GOM3	408.4 (393.3–427.1)	122.6 (116.2–129.2)	0.10 (0.09–0.11)	866.4	6.55	3.64	17.97
	100	GOM2	373.1 (359.1–387.7)	78	0.17 (0.16–0.19)	967.1	107.20	0	29.87
	100	LOGI3	394.1 (382.0–408.1)	127.2 (121–133.3)	0.14 (0.13–0.16)	875	15.06	0.05	18.75
	100	LOGI2	362.1 (347.7–376.2)	78	0.27 (0.25–0.30)	996.4	136.5	0	34.57

TABLE I. Continued

	<i>n</i>	Model	<i>L</i> _∞ (95% C.I.)	<i>L</i> ₀ (cm) (95% C.I.)	<i>k</i> (95% C.I.)	AIC	Δ	ω	RSE
Males	67	VB3	379.9 (353.4–420.8)	123.4 (115.6–131.2)	0.08 (0.06–0.10)	573.5	0.00	58.65	16.85
	67	VB2	327.4 (309.6–349.5)	78	0.16 (0.13–0.20)	638.3	64.74	0	27.51
	67	GOM3	359.3 (339.9–385.4)	127.2 (120.2–134.4)	0.12 (0.10–0.15)	574.7	1.14	33.23	16.99
	67	GOM2	309.4 (293.9–326.1)	78	0.20 (0.23–0.33)	655.8	82.24	0	31.35
	67	LOGI3	348.7 (332.6–369.3)	130.4 (123.6–137.2)	0.17 (0.15–0.20)	577.5	3.953	8.13	17.35
	67	LOGI2	296.6 (282.6–311.7)	78	0.43 (0.37–0.51)	668.9	95.41	0	34.59
Combined	178	VB3	433.7 (412.2–461.2)	121.5 (116.2–126.9)	0.06 (0.05–0.07)	1544.0	0.00	99.60	17.83
	178	VB2	376.2 (386.7–417.0)	78	0.11 (0.09–0.12)	1690.0	145.20	0	26.82
	178	GOM3	400.7 (386.7–417.0)	126.6 (121.6–131.5)	0.10 (0.09–0.11)	1555.0	11.060	0.39	18.39
	178	GOM2	353.2 (341.9–364.9)	78	0.19 (0.17–0.2)	1749.0	204.20	0	31.63
	178	LOGI3	385.6 (374.3–398.3)	130.7 (126.0–135.5)	0.14 (0.13–0.15)	1570.0	25.240	0	19.14
	178	LOGI2	339.8 (329–350.9)	78	0.29 (0.27–0.32)	1794.0	249.50	0	35.90

n, sample size; *L*_∞, mean age at length infinity; *L*₀, total length-at-birth; *k*, growth coefficient; Δ, Akaike score; ω, Akaike weighting; RSE, relative standard error.

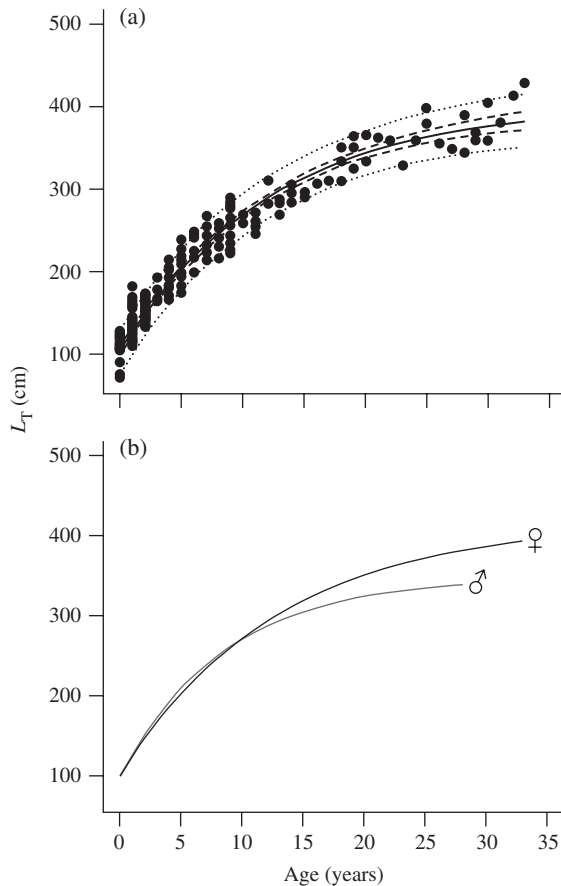


FIG. 9. Modelled growth curves of combined sexes pre and post-natal *Galeocerdo cuvier* as determined by the three-parameter von Bertalanffy growth function. Plots are (a) total length (cm) at age (—), with 95% C.I. (---), 95% prediction intervals (.....) and raw data (●), and (b) corresponding separate female and male growth curves.

modelled growth curve for *G. cuvier* on the east coast of Australia, these sharks were between *c.* 5 and 10 years of age at initial capture. These annual growth rates were slightly higher than the modelled growth estimates derived from vertebral age counts for wild Australian *G. cuvier* in the same age classes. The largest shark (SW1) had the slowest rate of growth for length, but the highest for mass as it approached maturity.

DISCUSSION

This study provides the first formal assessment of the age and growth of *G. cuvier* from the south-west Pacific region. Samples from the offshore gamefishing and commercial sectors provided similar numbers of male and female *G. cuvier*, while samples from shark control operations were biased towards female *G. cuvier* during this study period. Analysis of long-term QSCP catch data (1993–2014) indicates that a sex ratio

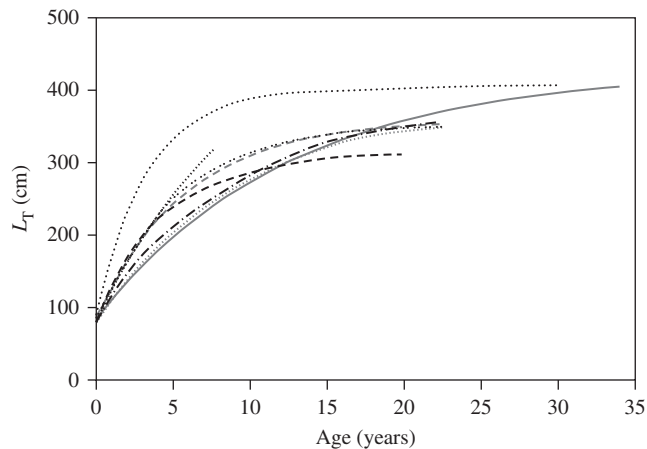


FIG. 10. Comparison of growth curves derived from *Galeocerdo cuvier* studies in different locations, using various methodologies: (.....) VB2, Kneebone *et al.* (2008); (.....) Wintner & Dudley (2000); (-.-.) Branstetter *et al.* (1987); (- - -) Natanson *et al.* (1999); (- - -) GROTAG, Kneebone *et al.* (2008); (.....) Gulland and Holt; Kneebone *et al.* (2008); (.....) Meyer *et al.* (2014). Growth curve for this study (—) is of the VB3 pre- and post-natal sexes combined.

bias of 1.51:1 females to males exists in this programme (Holmes *et al.*, 2012). A higher abundance of female *G. cuvier* catch was also reported in coastal waters of Western Australia, which was theorized to occur due to a spatial segregation of male shark size classes, with mature individuals probably occurring in deeper waters (Heithaus, 2001). Examination of large-bodied *G. cuvier* specimens from offshore gamefishing operations between 2002 and 2012 in NSW revealed that significantly more male sharks were caught (1.97:1, $\chi^2 = 12.11$, $P < 0.05$; B. Holmes, unpubl. data), indicating that spatial segregation between immature and mature males may also be occurring on the Australian east coast.

GROWTH RATES

There was some variability in model fit between the six candidate growth models applied to length-at-age data for post-natal sharks; however, the inclusion of pre-natal individuals served to anchor the growth curves and provide more realistic length-at-birth (L_0) estimates. Overall, pre and post-natal *G. cuvier* growth was statistically best described by the VB3 model. The smaller growth coefficient (k) obtained for the female and combined categories appear to be driven by the presence of five large females that were estimated >30 years old. This study is the first on *G. cuvier* to identify more than one individual over the age of 22 years, which is surprising given that *G. cuvier* are the largest of the family Carcharhinidae, and presumably amongst the longest lived (Blueweiss *et al.*, 1978; Hoenig & Gruber, 1990). Notwithstanding, longevity estimates for *G. cuvier* reported from the north-west Atlantic Ocean range from 27 to 37 years of age (Branstetter *et al.*, 1987; Natanson *et al.*, 1999; Kneebone *et al.*, 2008), indicating that a larger proportion of older sharks were sampled in this study than previously collected elsewhere, probably influencing the resultant growth coefficients for this population (for comparisons, see Table III). Recent

TABLE II. Growth rates for three long-term captive *Galeocerdo cuvier* held at Sea World (SW), Gold Coast, Australia

#	Sex	Capture information			Recapture and release information			Growth rate			
		Date	L_T (cm)	Mass (kg)	Date	L_T (cm)	Mass (kg)	Growth (cm)	Time (days)	cm year ⁻¹	kg year ⁻¹
SW1	♂	25 June 2003	290	120*	24 August 2004	314	240.5	24	425	20.7	103.4*
SW2	♀	16 December 2003	226	62.5	12 August 2004	243	102.5	17	239	26.0	61.1
SW3	♀	16 December 2003	209	47.5	28 September 2006	293	204.5	84	1031	29.7	55.6

L_T , total length.
*Estimated measurement.

mark-recapture studies utilizing the Francis maximum likelihood model (GROTAG; <http://finzi.psych.upenn.edu/library/fishmethods/html/grotag.html>) have reported considerably higher growth coefficients of between 0.26 and 0.46 for *G. cuvier* from Hawaiian and north-west Atlantic waters (Kneebone *et al.*, 2008; Meyer *et al.*, 2014), with resulting growth curves being much steeper and hence suggestive of rapid early growth and sexual maturity within the first 5 years. Moreover, growth rates of $>100 \text{ cm year}^{-1}$ for YOY were reported by Afonso *et al.* (2012) in Brazil and Meyer *et al.* (2014) in Hawaii, but these were limited to single recaptured individuals at both locations. Kneebone *et al.* (2008), however, using GROTAG on over 200 recaptured juvenile *G. cuvier* predominantly between 116 and 154 cm L_T , calculated mean growth rates of between 45.3 and 36.9 cm year^{-1} for these size ranges, respectively. Previous studies comparing age-length and length-increment (tagging) data have found that growth curves are not directly comparable as VBGF parameters derived from tagging data are noticeably higher (Francis, 1988; Skomal & Natanson, 2003). Model effects such as higher L_∞ and k values derived from mark-recapture VBGF parameters may be attributed to the absence of older recaptured sharks in the sample; therefore, comparison of growth rates at length may be more appropriate (Skomal & Natanson, 2003).

Captive animals are generally considered to undergo accelerated growth, with daily provisioning, regulated water condition and energetic savings made by neither having to hunt nor avoid predators (Branstetter & McEachran, 1986). The growth rates of the Sea World sharks (between 20.7 and 29.7 cm year^{-1}) were slightly higher than the modelled growth rate of *G. cuvier* in the same age cohorts derived from the vertebral ageing in this study (c. 12–18 cm year^{-1}). The growth rates of the captive sharks, however, were still slower than the mean annual growth rate of wild *G. cuvier* (c. 47.1 cm year^{-1}) from Hawaii in similar length classes (Meyer *et al.*, 2014). Faster linear growth in the smaller individuals (SW2 and SW3) did not correspond with a rapid increase in mass; however, as SW1 approached maturity, linear growth slowed and its mass increased considerably, which appears typical for the species based on growth rates elsewhere (Branstetter *et al.*, 1987). While food availability has been identified as a causative factor for increased growth rates in captive *Carcharhinus plumbeus* (Nardo 1827) (Wass, 1971), scalloped hammerhead *Sphyrna lewini* (Griffith & Smith 1834) (Clarke, 1971) and blacktip reef sharks *Carcharhinus melanopterus* (Quoy & Gaimard 1824) (Stevens, 1984), some smaller-bodied species, such as Atlantic sharpnose sharks *Rhizoprionodon terraenovae* (Richardson 1836) maintain growth rates that are similar to those observed in wild animals (Branstetter, 1987a). Thus, the influence of captivity on growth rates probably varies between species (Smith *et al.*, 2004). In addition, among wild conspecifics, significant differences in YOY growth rates from the same locality have been documented in north-west Atlantic *G. cuvier* (Natanson *et al.*, 1999). Natanson *et al.* (1999) concluded that wild *G. cuvier* YOY growth rates varied considerably, and that the effect of local environmental conditions probably account for the regional differences observed for this species.

Contrasting length-at-birth of *G. cuvier* at different locations may also influence YOY growth rates. Pup size is determined by the mother and her timing of parturition. Influences on parturition may include prey availability (Wirsing *et al.*, 2006), movement into areas of high productivity (Driggers *et al.*, 2008), environmental stimuli, such as calcium and phosphorus uptake (Branstetter, 1987a), and temperature, with warmer waters promoting rapid pup growth that probably reduces the risk of predation

TABLE III. Regional variation of growth model parameters for *Galeocerdo cuvier*

	De Crosta <i>et al.</i> (1984)	Branstetter <i>et al.</i> (1987)	Natanson <i>et al.</i> (1999)	Winter & Dudley (2000)	Kneebone <i>et al.</i> (2008)	Meyer <i>et al.</i> (2014)	This study
	Central Pacific (Hawaii)	Gulf of Mexico (U.S.A.)	North-west Atlantic (U.S.A.)	South-west Indian (South Africa)	North-west Atlantic (U.S.A.)	Central Pacific (Hawaii)	South-west Pacific (Australia)
Method	Vertebral ageing VBGF	Vertebral ageing VBGF	Mark-recapture VBGF	Vertebral ageing VBGF, Gompertz	Vertebral ageing VBGF, Gompertz	Mark-recapture VBGF	Vertebral ageing VBGF, Gompertz, LGF
Model							
L_{∞} (cm) L_T	434*	388	400†	400†	425‡	406	403
k (year ⁻¹)	0.155	0.184	0.178	0.202	0.102	0.31	0.08
L_T range (cm)	75–416*	91–355	99–338†	140–382†	81–412‡	96–384	72–430
n	28	25	42	90	238	37	202
Sexes	n/a	7 ♂, 10 ♀, 8 U	17 ♂, 25 ♀	26 ♂, 64 ♀	109 ♂, 126 ♀	10 ♂, 26 ♀, 1 U	79 ♂, 112 ♀, 11 U

n , sample size; L_{∞} , mean age at length infinity; k , growth coefficient. Where more than one model variation was tested, results for best fit are in bold type.

*Converted from pre-caudal length (L_{PC}) to total length (L_T) using Meyer *et al.* (2014) in Hawaii.

†Converted from L_{PC} to L_T using Bass *et al.* (1975) in South Africa.

‡Converted from fork length (L_F) to L_T using Kohler *et al.* (1995) in the north-west Atlantic Ocean.

(Branstetter, 1990; Norman & Stevens, 2007). Pre-mature birth or aborting of small pups can also be influenced by other external stressors, such as capture (Whitney & Crow, 2007). In the northwest Atlantic, length at birth has been reported to range from 45 to 50 cm L_T (Bigelow & Schroeder, 1948) to around 70 cm L_T (Clark & von Schmidt, 1965; Branstetter *et al.*, 1987). In the Caribbean, length at birth was established at 60–70 cm L_T (Rivera-López, 1970), while in Africa, estimated birth size was 70 cm L_T for *G. cuvier* off Madagascar (Fourmanior, 1961), and 85 cm L_T in South Africa (Wintner & Dudley, 2000). More recently, Whitney and Crow (2007) found that *G. cuvier* pups in Hawaii were born at 76–89 cm L_T . In Australia, *G. cuvier* length at birth has been identified as between 80 and 90 cm L_T (Simpfendorfer, 1992). These observed regional differences in birth size likely influence the respective YOY growth rates for that region, with smaller pups probably undergoing more rapid growth, particularly in tropical waters. Collectively, identification of whether inter-oceanic differences in growth rate are real, a consequence of sample collection methodology, or an artefact of statistical modelling, remains difficult to ascertain in elasmobranch age and growth studies.

LENGTH AT MATURITY

The majority of previous *G. cuvier* studies based the length-at-maturity estimates on the smallest recorded mature individual. In a Florida study, Clark & von Schmidt (1965) reported that the smallest mature female was 297 cm L_T but also found a larger 332 cm L_T female to be immature. Branstetter *et al.* (1987) found the smallest mature females were 325 cm L_T (8.8 years) and 318 cm L_T (9 years), and the smallest mature males were 310 cm L_T (8 years) and 312 cm L_T (10.1 years), in the Gulf of Mexico and the north-west Atlantic, respectively. In Africa, Wintner & Dudley (2000) reported the L_{50} and A_{50} for females at 349 cm L_T and 11 years of age, and 320 cm L_T and 8 years for males, respectively. Of the two mature females observed in their study, the youngest mature female (8 years, 380 cm L_T) was actually larger in size than the older female (13 years, 372 cm L_T). In this study, L_{50} for females (326 cm L_T) and males (297 cm L_T) was smaller than that reported in South Africa, although age at maturity was slightly higher being between 10 and 13 years for both sexes.

PRE-BIRTH BANDING

Pre-birth marks have been shown to occur in the centra of several placental shark species, with mark formation taking place when observed embryo lengths are consistent with placenta formation and attachment [*C. plumbeus*, Casey *et al.*, 1985; *C. limbatus* and spinner shark *Carcharhinus brevipinna* (Müller & Henle 1839), Branstetter, 1987b; bull shark *Carcharhinus leucas* (Müller & Henle 1839), Branstetter & Stiles, 1987], or when increases in calcium and phosphorous levels were observed, also around the time of placentation [grey reef shark *Carcharhinus amblyrhynchos* (Bleeker 1856), Radtke & Cailliet, 1984]. Pre-birth marking in aplacental species such as *G. cuvier* has been less thoroughly described and is more difficult to define. Pre-birth marks in the vertebrae of two other aplacental species, the shortfin mako *Isurus oxyrinchus* Rafinesque 1810 and the grey nurse shark *Carcharias taurus* Rafinesque 1810, were surmised to be caused by embryonic changes in nutrition associated with the switch from feeding on nutritive eggs (oophagy) to consuming

the large quantities of yolk reserves in the neonate stomach (Branstetter & Musick, 1994; Ribot-Carballal *et al.*, 2005). Information concerning the embryonic processes of *G. cuvier* is somewhat limited (Schwartz, 1994), with only one previous study documenting the presence of branchial filaments on the gills and spiracles in early embryo *G. cuvier*, presumably functioning as an absorption point for the nutritive liquid in the shell membrane sac (Sarangdhar, 1943). In the later stages, these filaments disappear and nutrition then appears to be supplied by a large external yolk sac, which, through the hepatic portal duct, is also connected to an internal yolk sac that supplies nutrients to the pup in the few days post-partum (Sarangdhar, 1943). These embryonic changes constituting a shift in nutrition may therefore cause pre-birth centrum marks in *G. cuvier*. Although previous vertebral ageing studies on *G. cuvier* have not identified pre-birth marks, these studies had few or no pre-natal or neonatal individuals [Branstetter *et al.* (1987), $n = 2$; Wintner & Dudley (2000), $n = 0$; Kneebone *et al.* (2008), $n = 8$]. Notwithstanding, all 59 pre-natal vertebrae examined in this study displayed at least one obvious embryonic mark in the centrum, with some near-full term pups also displaying an additional band near the edge of the centrum, which is consistent with the location of the birth band. Assuming a 15–16 month gestation period (Whitney & Crow, 2007) with parturition in the austral summer [December to February (Simpfendorfer, 1992)], it may be that the first pre-birth marks observed in these litters are indeed winter annuli, formed around June when pups are *c.* 35–40 cm L_T . This is consistent with the observation of a winter annulus near the edge of the centrum in the smallest examined embryo (41 cm L_T). The formation of winter annuli in *G. cuvier* was first described by Branstetter *et al.* (1987), with the first winter annulus post-partum representing *c.* 6 months of growth. Pre-birth marks became difficult to identify in the vertebrae of *G. cuvier* beyond YOY, probably due to the progressive calcification of the vertebral column that occurs through thickening of the mineralized cartilage of the intermedialia (Clement, 1992). Changes in calcification may also be linked to ontogenetic stages of progressively more mineralized tissue (Dean & Summers, 2006), which occurs post-partum.

AGE ESTIMATION

The identification of narrow and split banding patterns, particularly in older *G. cuvier*, increased the difficulty associated with determining true annuli in this species. Although split banding has been described as ‘background noise’ (Goldman, 2005), and that periodic annuli deposition should have some kind of ‘consistency’ (Goldman *et al.*, 2012), it is possible that the ageing protocols used in both this and previous vertebral ageing studies have resulted in some age underestimation for *G. cuvier*. Casey *et al.* (1985) acknowledged potential underestimation of *C. plumbeus* ages by not counting the narrow rings near the outer margin of the vertebrae as annuli, because they did not fit the criteria for an annual mark as validated by the younger size classes. Casey & Natanson (1992) then revised the earlier estimates using mark–recapture data, finding that vertebral counts using conservative protocols grossly underestimated the longevity estimates for the species. Branstetter *et al.* (1987) and Kneebone *et al.* (2008) both acknowledged difficulties in counting annuli along the periphery of centra in large *G. cuvier*, but neither provided images of vertebrae that highlighted this outer edge region to allow the reader to evaluate the methodology used. Despite vertebral ageing being the most widespread method to assess shark age and growth (Cailliet,

1990), recent studies employing bomb radiocarbon analyses have found that the age of large individuals may be underestimated, predominantly due to band deposition slowing or ceasing in large, older sharks. Francis *et al.* (2007) reported that the age of porbeagle sharks *Lamna nasus* (Bonnaterre 1788) may have been underestimated by as much as 50%. More recently, Natanson & Skomal (2015) reported that white shark *Carcharodon carcharias* (L. 1758) band pairs appeared narrow, grouping together to form the broader band pairs observed on the lower portions of the centra of larger specimens. This observation is akin to the presence of both narrow band pairs and split banding observed in the *G. cuvier* vertebrae, which did not fit the criteria of an annual growth-band pair in this study, and were not counted as such. While not described in the text, evidence of split banding in *G. cuvier* vertebrae was also shown in Fig. 1 of Kneebone *et al.* (2008), who also assigned these as a single band pair representing 1 year of growth. The close association of the *G. cuvier* and reference radiocarbon chronologies in the north-west Atlantic study suggested that major under ageing (>3–6 years of absolute age) was unlikely, at least up to the age of 20 years. While this gives some confidence in the age assignment in smaller specimens, the present estimates based on band-pair counts of 18 large sharks aged >20 years in this study may still be underestimated as validation has not been achieved over the species entire size range (Hamady *et al.*, 2014; Natanson *et al.*, 2014). Notwithstanding, this study provides a reasonable estimate of maximum age (33 years) through vertebral band-pair counts, fitting with the proposed longevity estimates of between 27 and 37 years of age reported elsewhere (Branstetter *et al.*, 1987; Natanson *et al.*, 1999; Kneebone *et al.*, 2008).

Another explanation for split banding may be that differences in cartilage mineralization occur during different growth phases (Cailliet *et al.*, 1983). Jones & Geen (1977) suggest that patterns of mineralization may be strongly influenced by seasonal environmental changes therefore affecting growth rates. The cells of vertebral cartilage undergo a progressive change in shape from the flattened and fusiform cells deepest in the structure, to the ovoid cells just being incorporated into the mineralizing front. This change in shape may depend on the time and site of inclusion, and can be explained by the effect of local tissue pressure at the time of the cells' growth and incorporation (Clement, 1992). The variation in mineralization patterns, and the incorporation of these cells during growth, may contribute to the observed split banding patterns in *G. cuvier* vertebrae. To date, little is known about the interaction between the different forms of calcification in the vertebral cartilage of sharks, nor how these processes vary with age, species or feeding behaviour (Dean & Summers, 2006). These findings reinforce the importance of age validation in elasmobranch studies, particularly when population assessments and management regimes are often based on life-history information (Harry *et al.*, 2013).

VALIDATION

Validation of absolute age in elasmobranch fishes is particularly difficult; therefore, most studies attempting validation do so by focussing on validating the temporal periodicity in growth increment formation (Cailliet & Goldman, 2004). Fishes can be marked externally, or injected with chemicals so as to leave a permanent mark on the bony structures used for ageing. These approaches are not well suited to long-lived species since recapture rates of old fishes tend to be low (Campana, 2001), and failure of

chemical marking in the vertebrae of large sharks with little or no somatic growth may occur (Harry *et al.*, 2013). Moreover, the extent of movements by highly mobile shark species in some regions limits the chances of re-encountering the same individuals at a later date. For example, off the east coast of Australia *G. cuvier* have been demonstrated to move distances of up to 2000 km across the south-west Pacific in just over 1 month (Holmes *et al.*, 2014). Additionally, the NSW Game Fishing Tagging Program has tagged 1083 *G. cuvier* off the Australian coast since 1973, with only 26 recaptures up to 2014 (c. 2.4% recapture rate; NSW DPI, unpubl. data). In lieu of accurate recapture data or chemically marked individuals, R_{MI} analysis of annulus periodicity has been used as a way to verify annulus formation in *G. cuvier* ageing studies, with mixed success. Branstetter *et al.* (1987) demonstrated that one growth band, consisting of one calcified opaque zone and one less calcified translucent zone, formed annually in *G. cuvier* from the north-west Atlantic and Gulf of Mexico. Wintner & Dudley (2000), however, found no clear trend in the R_{MI} analysis conducted on *G. cuvier* in South Africa, but suggest that the larger R_{MI} range observed in spring may represent transition from one growth ring to the next, indicating annual growth-band deposition. The R_{MI} analysis undertaken in this study showed that annuli were farthest from the centrum edge in the austral summer (January), and closest during the austral winter (June to August). The R_{MI} trends indicate that *G. cuvier* off the east coast of Australia also form one growth band each year, most likely in late spring and summer. This is consistent with the austral summer pupping season in this region (Simpfendorfer, 1992). Other validation techniques to verify and validate annual band deposition in *G. cuvier* have also been used. In Hawaii, De Crosta *et al.* (1984) assumed annual periodicity based on the close agreement of growth curves derived from vertebral counts and length frequencies. Wintner & Dudley (2000) also chemically marked and recaptured three *G. cuvier* in South Africa, finding annual growth-band deposition in young age classes (<5 years). More recently, bomb radiocarbon analyses have been undertaken on *G. cuvier* in the north-west Atlantic (Kneebone *et al.*, 2008), validating annual band deposition in individuals up to age 20 years. Based on these collective findings and the results of the R_{MI} analysis of this study, it is assumed that the number of vertebral growth bands is representative of year classes for *G. cuvier* on the east coast of Australia.

Individual variation in growth is typical for *G. cuvier* across their geographic range (Natanson *et al.*, 1999; Meyer *et al.*, 2014), which partly explains the differences in the observed growth curves from different populations. These regional variations in life-history traits highlight the need to obtain local life-history information in order to determine fecundity, growth rate, mortality and subsequent susceptibility to fishing pressure before appropriate management regimes may be implemented. The south-west Pacific population of *G. cuvier* sampled in this study exhibited a slower rate of growth and slightly higher age at sexual maturity than reported elsewhere, indicating that recovery from depleted stocks may take longer in this region. This may explain why recent catch rate trends of *G. cuvier* in south-eastern Australia have shown significant declines (Park, 2009; Reid *et al.*, 2011; Holmes *et al.*, 2012), when other regions are reporting increasing abundances (Dudley & Simpfendorfer, 2006). Sample size, protocol methodology, verification and validation can also have considerable influence on regional-specific growth model results (Cailliet & Goldman, 2004; Goldman, 2005). Justification of ageing methodology will also be aided by a greater understanding of the mineralization processes associated with vertebral band deposition, which are integral in understanding the effect that anomalies such as split banding have on vertebral age

determination processes. For future studies, ongoing efforts to gain regional-specific growth estimates and promote greater transparency regarding the difficulties associated with vertebral ageing studies in elasmobranchs, particularly for larger species, are encouraged.

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