

Validated age and growth of the sandbar shark, *Carcharhinus plumbeus* (Nardo 1827) in the waters off Western Australia

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Abstract Sandbar sharks, *Carcharhinus plumbeus*, collected from commercial shark fisheries in Western Australia were aged by examination of sectioned vertebrae and analysis of tag-recapture data. Growth curves were derived from consensus counts of growth bands from the vertebrae of 238 individuals ranging in size between 47 and 154 cm fork length (FL). The annual periodicity of growth band formation was validated using vertebrae from tagged sharks, which were injected with oxytetracycline ($n = 9$) and calcein ($n = 23$) and were at liberty for up to 8.1 years. The oldest female was estimated to be 25 years of age and the oldest male was 19 years. The ages at which 50% of female and male sharks were mature were

estimated to be 16.2 and 13.8 years, respectively. Growth increment data from 104 tagged *C. plumbeus*, which were at liberty for up to 7.4 years, were used to construct growth curves for comparison with those derived from vertebral analysis. The two methods yielded noticeably different results. Based on a known size at birth of 42.5 cm FL, von Bertalanffy parameters estimated using length at age data from vertebral analysis were: $K = 0.039 \text{ year}^{-1}$ and $L_{\infty} = 245.8 \text{ cm}$; $K = 0.044 \text{ year}^{-1}$ and $L_{\infty} = 226.3 \text{ cm}$; and $K = 0.040 \text{ year}^{-1}$ and $L_{\infty} = 239.6 \text{ cm}$ for females, males and both sexes combined. The von Bertalanffy parameters derived from tag-recapture data were: $K = 0.153 \text{ year}^{-1}$ and $L_{\infty} = 142.0 \text{ cm}$ for combined sexes. However, as sharks longer than 142.0 cm were commonly encountered during sampling, these estimates appear to be biologically unrealistic. Also, given the high variability in growth rates of tagged sharks, compared to those derived from the larger vertebral analysis dataset, vertebral ageing was concluded to provide a better description of age and growth in this study. These results confirm that *C. plumbeus* is a slow-growing and late maturing species and thus recovery times from periods of overexploitation would be considerable.

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Introduction

The sandbar shark, *Carcharhinus plumbeus* (Nardo 1827), is a medium-sized carcharhinid shark, which occurs globally in tropical and temperate coastal waters (Compagno 1984). Due to their cosmopolitan distribution, abundance in coastal waters, vulnerability to multiple gear-types, high quality flesh and large fins, *C. plumbeus* stocks support significant commercial target fisheries throughout the species' range, particularly on the east coast of the United States¹ (Sminkey and Musick 1996), east coast of Mexico (Bonfil 1994), East China Sea (Taniuchi 1971; Joung and Chen 1995) and on the west coast of Australia^{2,3,4}. However, due to their slow growth, late onset of maturity, small litter sizes and long reproductive cycle, sandbar sharks are highly susceptible to overfishing and the effects of commercial exploitation need to be well understood and carefully managed to avoid overfishing¹ (Sminkey and Musick 1996; Smith et al. 1998; Castro et al. 1999; Brewster-Geisz and Miller 2000). Furthermore, where overfishing of *C. plumbeus* stocks has occurred, e.g. in the north-west Atlantic Ocean (Sminkey and Musick 1995, 1996; Castro et al. 1999), stock restoration is likely to take many years (Bonfil 1994; Musick et al. 2000). Reliable age and growth estimates can provide important information for assessing the status of exploited stocks and for predicting their capacity for recovering from periods of overfishing.

¹ Hoff TB (1990) Conservation and management of the western North Atlantic shark resource based on the life history strategy limitation of sandbar harks. PhD dissertation, University of Delaware, Newark, 149 pp.

² McAuley R, Simpfendorfer C (2003) Catch composition of the Western Australian temperate demersal gillnet and demersal longline fisheries, 1994–1999. Fisheries Research Report No. 146. Department of Fisheries, Western Australia, 78 pp.

³ Gaughan D, Chidlow J (2005) Demersal gillnet and longline fisheries status report. In: Penn JW, Fletcher WJ, Head F (eds) State of the Fisheries Report 2003/04. Department of Fisheries, Western Australia, pp.186–191.

⁴ Gaughan D, Chidlow J (2005b) Northern shark fisheries status report. In: Penn JW, Fletcher WJ, Head F (eds) State of the Fisheries Report 2003/04. Department of Fisheries, Western Australia, pp.146–150.

In Australia, *C. plumbeus* occurs off both the east and west coasts and to a lesser extent off the north and south coasts (Last and Stevens 1994). In Western Australia, sandbar sharks are primarily distributed between Cape Leveque (16°30'S, 123°E) on the north coast and Albany (118°E) on the south coast. Throughout this range, they are caught by a number of fisheries that take sharks as both targeted catch and by-catch. Between 1995 and 2004, reported catches of *C. plumbeus* in Western Australia increased nearly fivefold, from 83 to 402 tonnes live weight^{3,4} (R.B. McAuley, unpublished data). Sandbar sharks are now the main component of the catch in the west coast region of the temperate shark fishery (between latitudes 26°30'S and 33°S), where they are primarily caught by demersal gillnets. The developing northern shark fishery (which operates north and east of 22°78'S, 114°06'E) also targets *C. plumbeus* using demersal longlines. Both the temperate and northern shark fisheries are limited entry, with effort in the temperate fishery controlled by restrictions on the amount of gear that can be used^{3,4} (Simpfendorfer and Donohue 1998).

There are currently no published age and growth data for *C. plumbeus* from Australian waters and age and growth estimates for other populations vary considerably between studies (Springer 1960; Wass 1973; Casey et al. 1985; Casey and Natanson 1992; Sminkey and Musick 1995; Joung et al. 2004). Although separate *C. plumbeus* populations do exhibit markedly different biological characteristics (Springer 1960; Bass et al. 1973; Wass 1973; Cliff et al. 1988; Joung and Chen 1995; Sminkey and Musick 1995; Joung et al. 2004), the magnitude of the differences in previously reported growth curves are too large to confidently be attributed to either population density or environmental effects. An alternative explanation for some of these differences is that tagging data, which have previously been used to estimate growth rates and verify the annual formation of vertebral growth bands (Casey et al. 1985; Casey and Natanson 1992), can provide an unreliable basis for growth rate analyses. Because the periodicity of vertebral growth band formation has never been comprehensively validated for this species, it is difficult to resolve whether the

reported differences in growth indicate real variability within and between *C. plumbeus* populations or whether they were caused by different ageing methods or inconsistent interpretation of growth bands between studies.

Due to its demonstrated vulnerability to overfishing and the rapid increases in commercial landings in Western Australia, a clear understanding of the biology and status of the *C. plumbeus* stock is essential to ensure sustainable levels of exploitation. In order to develop an age-structured population assessment of this stock, accurate and locally derived estimates of size-at-age and growth rates are necessary. The primary aim of the present study was, therefore, to determine age and growth parameters for *C. plumbeus* in Western Australian waters. Secondly, as the periodicity of growth band formation in *C. plumbeus* vertebrae has not previously been validated in wild sharks, this study also aimed to determine whether the growth bands visible in sectioned vertebrae form annually. The final aim was to examine whether growth rates derived from tagging data vary from those derived from vertebral analysis and whether the former approach could have contributed to the variation in previously reported growth rates of this species.

Materials and methods

Vertebral sample collection

Vertebral samples from 680 *C. plumbeus*, which ranged in size from 47 to 166 cm fork length (FL), were collected from both commercial and fishery-independent sources between 6 April 1999 and 28 May 2002. Sharks obtained from commercial catches were caught by demersal gillnets ($n = 379$) and longlines ($n = 263$). A smaller number of sharks were caught during fishery-independent sampling using demersal longlines ($n = 20$) and drumlines ($n = 22$). Gillnets were constructed of 0.9–1.0 mm diameter monofilament meshes of between 165 mm (6.5") and 178 mm (7") stretched mesh sizes with either a 15 or 20 mesh drop. Both commercial and fishery-independent longlines comprised size 12/0 J-shaped hooks, attached to

the main line via approximately 2 m metal snoods. Longline hooks were baited with mullet, *Mugil cephalus*, or mackerel (family Scombridae). Drumlines consisted of size 14/0 Mustad shark hooks, baited with Australian salmon, *Arripis truttaceus*, and attached to anchored 20 l plastic drums via lengths of chain, so that hooks floated approximately 1 m below the surface. Gillnets and longlines were set demersally in depth ranges of 9–121 and 14–157 m, respectively, and drumlines were fished in depths of between 54 and 100 m. Vertebral sampling was conducted between Eighty Mile Beach (20°S, 120°E) on the north coast and east of Cape Leeuwin (35°S, 115°E) in the south west of the state (Fig. 1).

Each shark was sexed and FL measured to the nearest centimetre, as a straight line from the tip of the snout to the fork of the caudal fin. For comparison with results of other studies, the relationships between FL and total length (TL) in Western Australian *C. plumbeus* are described by the equations:

$$\text{TL} = 1.118(\text{FL}) + 6.302$$

$$(n = 878, r^2 = 0.984) \text{ for males,}$$

$$\text{TL} = 1.113(\text{FL}) + 5.819$$

$$(n = 895, r^2 = 0.986)$$

for females and

$$\text{TL} = 1.122(\text{FL}) + 6.004$$

$$(n = 1,773, r^2 = 0.985)$$

for both sexes combined.

The relationships for males and females were significantly different (ANCOVA, $F = 5.53$; $df = 2, 1,769$; $P = 0.041$).

As vertebral samples were largely obtained from commercial catches, centra were removed from the vertebral column anterior to the origin of the first dorsal fin and stored frozen until being processed. Reproductive condition was also recorded for subsamples of male ($n = 65$) and female ($n = 48$) sharks, according to the following definitions. Males were defined relative to the degree of clasper calcification: immature (uncalcified, where claspers were small and could be easily bent

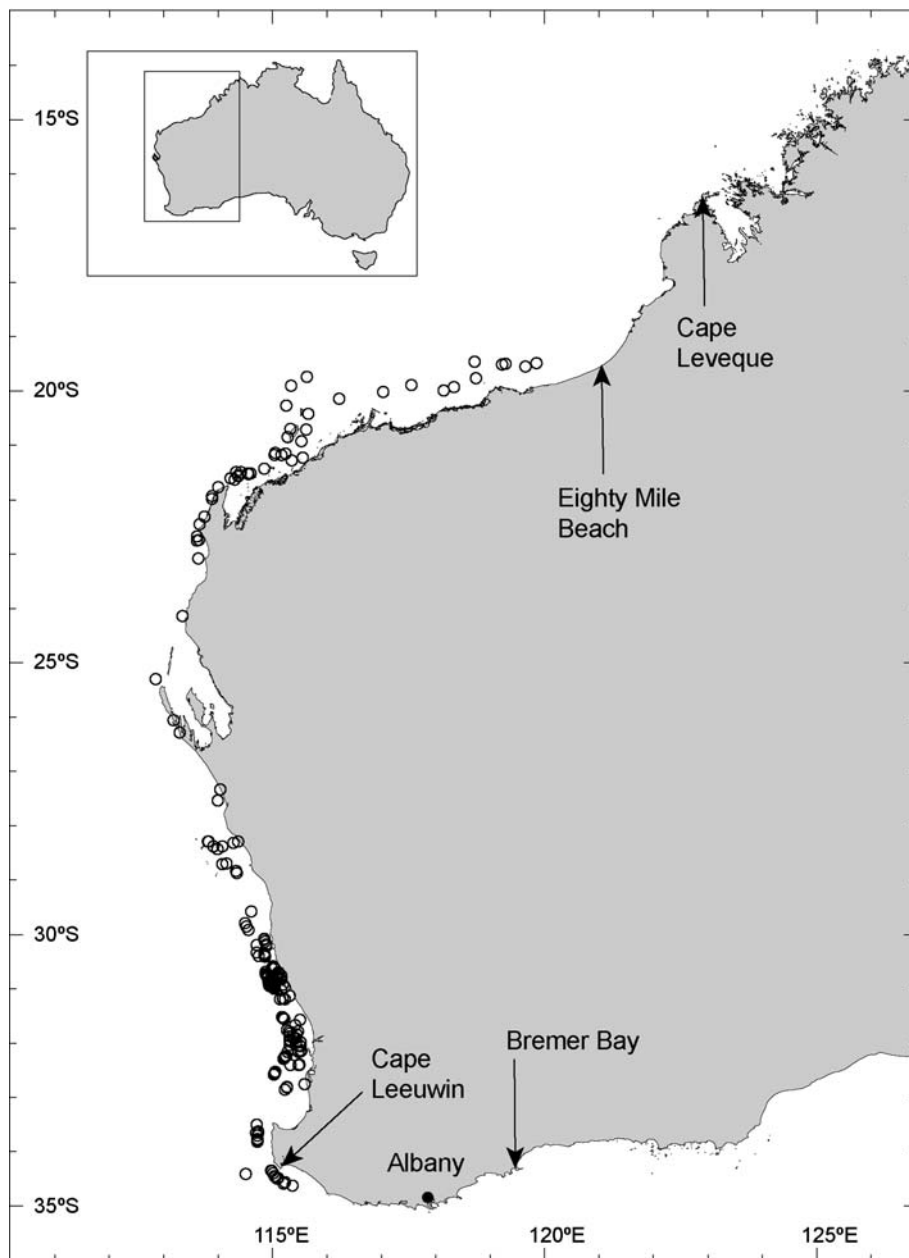


Fig. 1 Sampling locations of 680 *C. plumbeus* from waters off the west coast of Australia, which were used for vertebral analysis of age and growth

along their entire length), maturing (partially calcified, where claspers had begun to elongate and calcify but could still be bent along most or all of their length) and mature (calcified, where claspers were elongate and could not be bent at all). Female maturity was defined by a combination of uterine and ovarian development: stage 1 (immature), uterus very thin along its entire length and empty

and ovaries indistinguishable from epigonal organ; stage 2 (maturing), uterus very thin along most of its length but enlarged posteriorly and empty, ovaries difficult to distinguish from epigonal organ; stage 3 (mature, not pregnant), uterus enlarged along its entire length but empty and functional ovary clearly distinguishable from epigonal organ, with differentiated ovarian follicles or developing

yolky ova; stage 4 (mature, ovulatory and post-ovulatory), uterus containing yolky eggs but no visible embryos on eggs; stage 5 (mature, pregnant), uterus containing visible embryos; stage 6 (mature, post-partum), uterus enlarged and flaccid, appearing to have just given birth, possibly with visible placental scars.

Vertebral processing and analysis

After defrosting, the neural arch, transverse processes and excess tissue were excised from each vertebral sample and individual centra were separated. Centra were soaked in a 5–10% sodium hypochlorite solution for up to 60 min, depending on their size and quantity and the age of the solution, until all remaining tissue had been removed. Cleaned centra were thoroughly rinsed in fresh water and dried in an oven at 50°C for periods of up to 24 h. Three centra from each shark were embedded in polyester casting resin and longitudinal cross-sections of 170 µm thickness were taken from as close to the focus of each centrum as possible, using a variable speed linear precision saw. Sections were mounted on microscope slides with casting resin and digitally photographed through a dissecting microscope under reflected light.

Images were viewed and minor adjustments to their brightness and contrast were made using Microsoft Photo Editor. Growth bands (defined as a narrow translucent band and adjacent wide opaque band pair) were independently counted by three readers, without knowledge of the size, sex or previous results for any shark. Two readers had experience in ageing sharks, while the third had no experience in ageing sharks but was experienced in ageing teleosts. Counts commenced after the birth-mark, which was identified by a change of angle on the outer edge of the corpus calcareum and an associated translucent band. The readability of each section was scored according to the following definitions: 0, unreadable; 1, bands visible but difficult to interpret; 2, bands visible but the majority difficult to interpret accurately; 3, bands visible but a minority difficult to interpret accurately; and 4, all bands unambiguous. Sections with a readability score of 0 were excluded from further analysis.

A consensus was determined for each reader's counts of the three centra from each shark using the following criteria: (i) where at least two counts matched, the matching count was adopted; (ii) where no counts matched but two counts varied by 1, the count with the higher readability was adopted; (iii) where no counts matched but two counts varied by 1 and readability was equal, the final reading was adopted, since this was made with greater experience in the interpretation of band formation. Where a consensus could not be reached, that specimen was excluded from further analysis of that reader's results. Final consensus of the number of growth bands for each specimen was determined among readers by taking the count that matched in at least two of the consensus counts from each reader.

The index of average percentage error (IAPE) was calculated for each reader's counts and for the consensus counts according to the method described by Beamish and Fournier (1981):

$$\text{IAPE} = \frac{1}{N} \sum_{j=1}^N \left(\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right) \times 100,$$

where N is the number of animals aged, R is the number of readings, X_{ij} is the count from the j th animal at the i th reading and X_j is the mean age of the j th animal from i readings.

A form of the von Bertalanffy growth equation that fits the curve to a known size at birth (Simpfendorfer et al. 2000) was fitted to the resulting length at age data:

$$L_T = L_0 + (L_\infty - L_0)(1 - e^{-KT}),$$

where L_0 is the mean size at birth (42.5 cm FL for both sexes, R.B. McAuley, unpublished data), L_T is the mean length at time T , L_∞ is the mean asymptotic length and K is the growth coefficient. The equation was fitted using the non-linear regression function of Sigmaplot 9.01 (Systat 2004). Ninety-five percent confidence intervals were estimated for von Bertalanffy parameters by re-sampling the length-at-age data from vertebral analysis, to create 1,000 new datasets (of the same size as the original data) and re-fitting the growth curve to each through the known size at birth of 42.5 cm FL. Values of t_0 were derived from each

of the resulting estimates using the standard definition of the von Bertalanffy curve:

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right].$$

Validation of growth band periodicity

A total of 2,107 sharks, caught by a variety of fishery-dependent and -independent methods, were tagged between 22 March 1994 and 15 June 2004 in waters between Cape Leveque (16°30'S, 123°E) on the north coast and Bremer Bay (34°S, 120°E) on the south coast. Prior to release, sharks were sexed, measured (FL) and tagged with Jumbo Rototags (Dalton I.D. Systems, Dalton Group Ltd, Dalton, UK) in the first dorsal fin. Subsamples of tagged sharks were injected with either oxytetracycline (OTC, prior to December 2000, $n = 151$) or calcein (post-December 2000, $n = 725$) to mark their vertebral centra for age validation. Both OTC and calcein were injected as an aqueous solution (25 mg ml⁻¹) into the dorsal musculature anterior to the first dorsal fin and adjacent to the vertebral column at doses of 25 and 3–5 mg kg⁻¹ body weight, respectively. Due to concerns about the potential toxicity of low doses of calcein in sharks (Gelsleichter et al. 1997), three calcein-injected sharks were held in captivity for observation over 12 months. The two females (69 and 72 cm FL) and one male (72 cm FL) were caught by demersal longlines during fishery-independent surveys in August 2002 and were tagged and injected following capture according to the methods described above. Captive sharks were held in a shaded circular outdoor tank of 5 m diameter and 1.5 m depth with open seawater circulation. The tank was subject to natural photoperiod and temperature regimes and sharks were fed to satiation 2–3 times weekly with pilchards *Sardinops neopilchardus*.

Marked vertebrae were prepared according to the previously described methods and digitally photographed via a dissecting microscope under both normal reflected light and then under fluorescent light with an ultraviolet filter. Fluorescent images were superimposed on their non-fluorescent counterparts using Adobe Illustrator 10.0 software. The transparency of the fluorescent layer of the composite image was then adjusted so that the fluorescing

mark was visible while banding patterns from the non-fluorescent layer could be easily distinguished. The number of complete growth bands after the mark were then counted and plotted against time at liberty. The slope of the linear regression between post-injection band counts and time at liberty equates to the number of bands formed per year.

Growth rate estimation using tagging data

Recapture data were collected for 104 tagged *C. plumbeus*, which were at liberty for between 1 and 2,723 days (up to 7.4 years). Capture information, including date, location and FL were collected by commercial fishers and scientific observers during fishery-dependent and -independent surveys. To assist in the collection of comprehensive and accurate tag capture data, commercial fishers and observers were provided with measuring tapes, standardised tag-recapture reporting forms and training in measuring sharks and in the collection of vertebral samples.

Growth rates were calculated from tag length-increment data using the Francis (1988a) maximum likelihood method. This method estimates growth (ΔL_i) of tagged fish based on growth rates, g_α and g_β , at two arbitrary lengths of α (70 cm FL) and β (110 cm FL), which were chosen as they represented the range of most of the empirical data, so that:

$$\Delta L_i = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_i \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T_i} \right],$$

where L_i is the length at release and ΔT_i is the period at liberty.

Variability in growth rates (v), measurement error (m , s) and the probability of incorrectly recorded length data, referred to as the contamination probability (p), were estimated by maximising the likelihood function:

$$\lambda = \sum_i \log[(1-p)\lambda_i + p/R],$$

where

$$\lambda_i = \frac{\exp(-0.5(\Delta L_i - \mu_i - m)^2 / (\sigma_i^2 + s^2))}{[2\pi(\sigma_i^2 + s^2)]^{0.5}},$$

R is the range of observed growth increments and subscript i refers to the i th fish. This method assumes that v is normally distributed with a mean of μ and a standard deviation σ and that σ is proportional to μ , such that $\sigma = v\mu$. Net measurement error at release and recapture is also assumed to be normally distributed with a mean of m and a standard deviation s .

Confidence intervals of parameter estimates were calculated by refitting the model to 500 'bootstrapped' length-increments. Bootstrapped data were generated by randomly selecting (with replacement) from a normal distribution with a mean equal to the predicted growth increment and a standard deviation of $v\mu$. Bootstrapped measurement error data were generated by randomly selecting from a normal distribution with a mean equal to m and a standard deviation of s .

Resulting values of g_α and g_β were used to estimate the von Bertalanffy growth curve parameters by:

$$K = -\ln(1 + ((g_\alpha - g_\beta)/(\alpha - \beta))), \text{ and}$$

$$L_\infty = (\beta g_\alpha - \alpha g_\beta)/(g_\alpha - g_\beta).$$

Results

Validation of growth band periodicity

Apart from an orange discolouration of their teeth for a period of approximately 3 weeks, captive sharks showed no immediate or longer-term signs of being adversely affected by calcein injection or tagging. One shark (72 cm FL female) was released after 12 months due to worsening abrasions on its snout and body caused by impacts with the tank wall or circulation pipes. The remaining sharks were released 2 weeks later, suffering no apparent ill effects from their captivity.

Vertebral samples from nine OTC-injected and 26 calcein-injected sharks were either collected by researchers or returned after recapture by commercial fishers. However, one OTC-marked sample and three calcein-marked samples were returned with insufficient capture data (capture date or length) and were omitted from

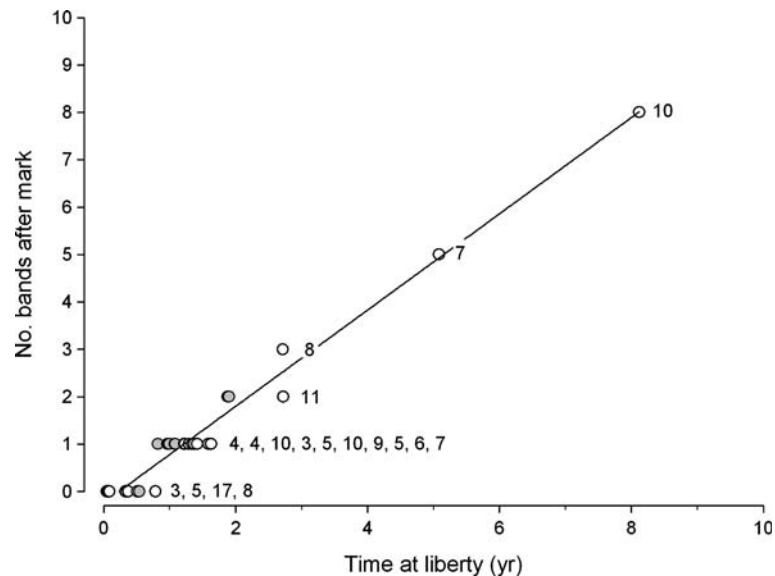
further analysis. Fluorescing marks were visible in all calcein-marked sections and in all but two sections from OTC-injected sharks. Times at liberty for the sharks from which the 29 remaining samples were collected varied between 16 and 2,963 days (up to 8.1 years). There was a significant linear relationship between the number of complete growth bands counted after the injection marks and the periods for which the corresponding sharks were at liberty (ANOVA, $r^2 = 0.972$; $F = 945$; $P < 0.0001$; Fig. 2). The slope of this regression was 1.02 (SE = 0.033), demonstrating that growth bands were formed annually.

Vertebral analysis

Vertebrae from 680 *C. plumbeus*, ranging in size between 47 and 166 cm FL (Fig. 3), were sectioned and read. Mean band counts, mean readability, IAPE and the percentage of readings by each reader that were in agreement with final consensus counts were similar for all three readers (Table 1), although readers A and B obtained slightly more individual consensus counts than reader C. Reader C provided both the highest individual growth band count (27 years) and the highest individual consensus age (26 years). Final consensus counts between readers were obtained for 238 specimens, ranging in size from 47 to 154 cm FL.

The oldest female and male sharks for which consensus ages were agreed were 25 years (152 cm FL) and 19 years (142 cm FL), respectively. The oldest immature female and male sharks were both 12 years. Maturing females were aged at between 12 and 16 years and a single maturing male was aged at 15 years. The youngest mature female and male sharks were aged at 14 and 13 years, respectively. On the basis of these data, age at maturity is estimated to be 12–16 years for females and 12–15 years for males. Based on the known sizes at which 50% of Western Australian *C. plumbeus* are mature ($L_{0.5} = 135.9$ cm FL for females and 126.9 cm FL for males, R.B. McAuley, unpublished data), ages at maturity were calculated from these curves as 16.2 and 13.8 years for females and males,

Fig. 2 Number of complete growth bands counted after OTC or calcein mark in 29 sectioned *C. plumbeus* centra. Numbers beside datapoints are the estimated ages of sharks at capture, shown by white circles. Centra for which absolute age estimates could not be determined are shown as grey circles



respectively. These estimates concur with the ranges determined from aged sharks with known reproductive condition.

The modified form of the von Bertalanffy equation provided adequate descriptions of the male, female and combined length-at-age data derived from vertebral analysis ($r^2 = 0.92$, 0.94 and 0.93 , respectively). Although the fitted growth curves suggested that males grew slightly faster and reached a smaller asymptotic length than females (Fig. 4; Table 2), these differences were not significant (Kimura 1980; Likelihood Ratio Test, $\chi^2 = 0.350$, $df = 2$, $P = 0.839$). The growth rate for both sexes combined was predicted to slow gradually from 7.8 cm year^{-1} in the first year, to 2.4 cm year^{-1} at the projected age of 30.

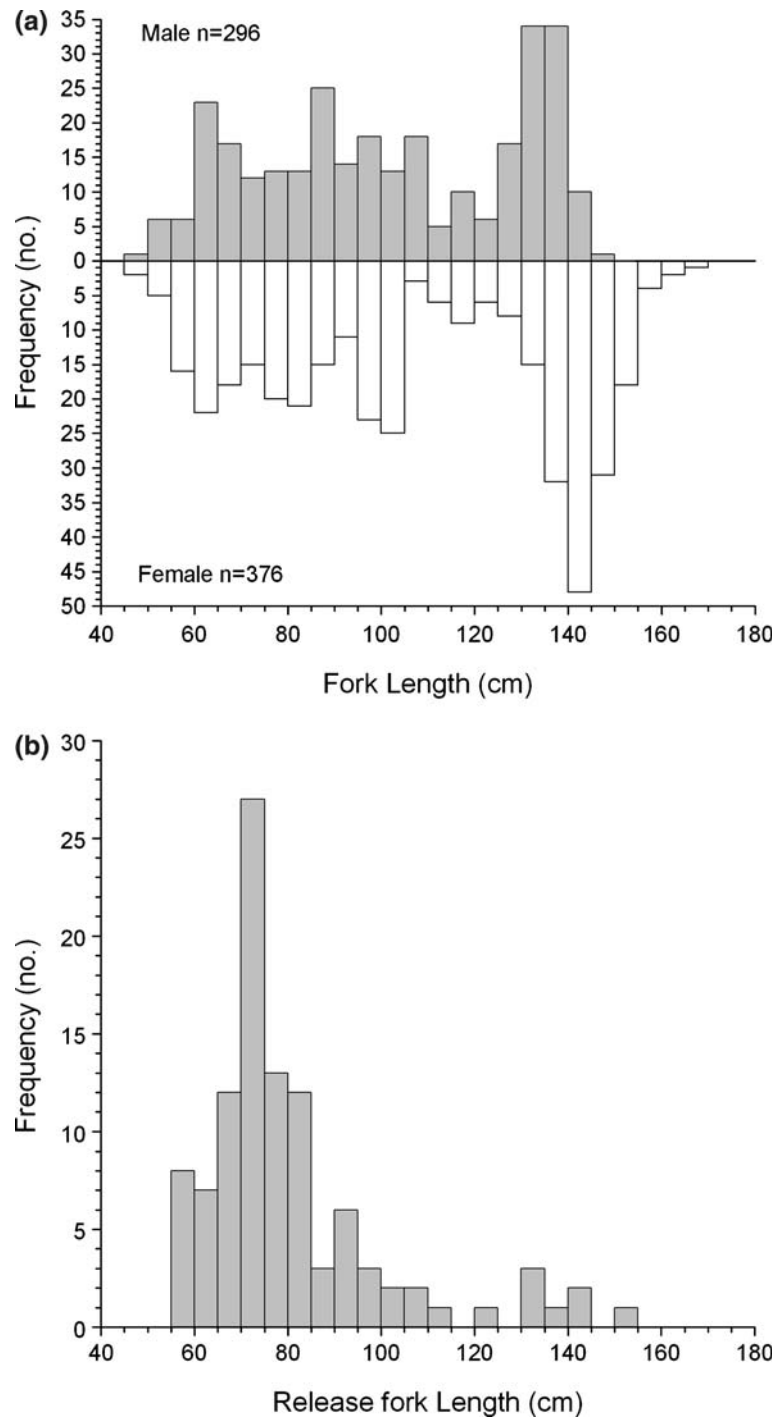
Based on the maximum observed sizes of *C. plumbeus* in Western Australia (165 cm for males and 166 cm FL for females, R.B. McAuley, unpublished data), maximum ages were estimated from these parameters to be 23.9 and 25.3 years for females and males, respectively. Using the maximum reported size of *C. plumbeus* in Australian waters [240 cm stretched TL (Last and Stevens 1994), which equals 196 cm FL, according to the relationship given in Stevens and McLoughlin (1991)], these parameters gave maximum age estimates of 36.4 and 40.9 years for females and males, respectively.

Tagging data

The von Bertalanffy parameter estimates derived from analysis of tagging data by the Francis (1988a) model were noticeably different to and less precise than those calculated from vertebral analysis (Fig. 4d; Table 3). With the observed data, the model predicted that L_∞ was considerably lower (142.0 cm) and K was higher (0.153 year^{-1}) than their values estimated by vertebral analysis. This combination of parameters indicated that initial growth was more rapid but that *C. plumbeus* reached a far lower asymptotic length than estimated by vertebral analysis. However, sharks longer than the theoretical maximum size (L_∞) estimated from tagging data were commonly encountered during sampling (Fig. 3) and this estimate was considerably less than the maximum observed size in this population (166 cm FL, R.B. McAuley, unpublished data).

The observed growth rates of tagged sharks were highly variable, especially for those sharks captured after less than 3 months at liberty (Fig. 5). The model estimated that growth rate variability (v) amounted to 26.4% of the annual growth predicted by the model (with 95% confidence intervals of 1.6–38.4%). Although the mean net measurement error estimate ($m = -0.322 \text{ cm}$) was reasonably low, the standard

Fig. 3 Size frequency distributions of **a** 672 sexed *C. plumbeus* specimens used for vertebral analysis (NB. vertebrae from a further eight unsexed specimens were also aged) and **b** release lengths of 104 tagged *C. plumbeus* used for analysis of growth increment data

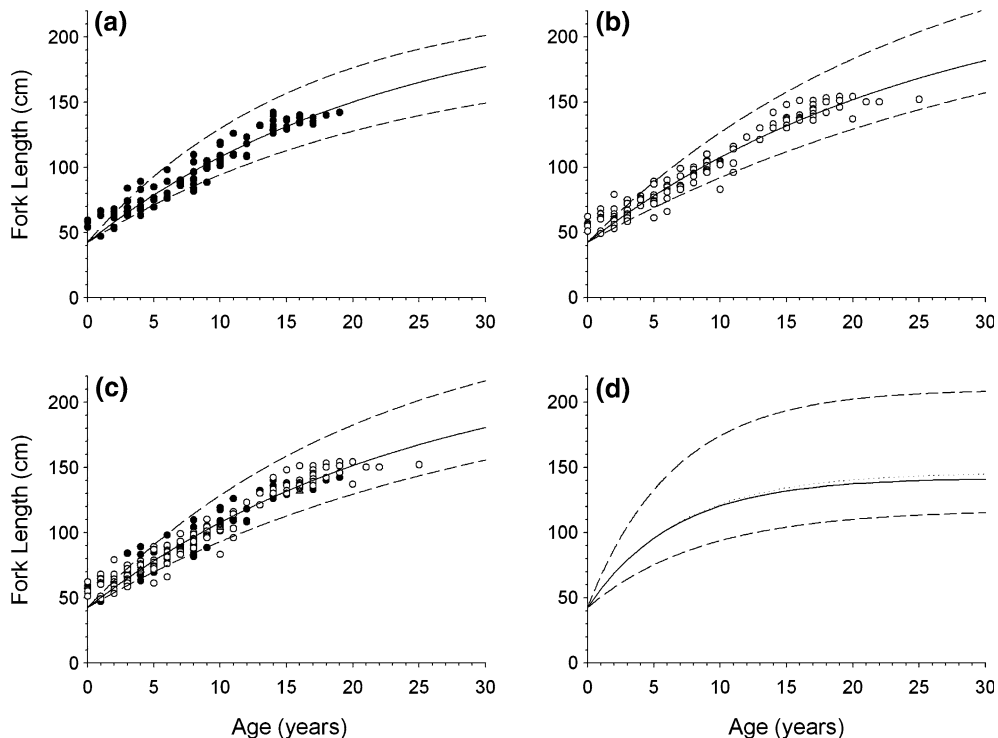


deviation of measurement error ($s = 2.510$ cm) was high, accounting for ± 24.6 and $\pm 55.8\%$ of the predicted annual growth at lengths α (70 cm) and β (110 cm), respectively. The bootstrapped

data suggested that the range of measurement error was even higher with a median estimate of $s = 3.643$ cm and 95% confidence intervals of 2.383–5.162 cm (i.e. 23.4–50.6% of predicted

Table 1 Growth band count statistics from the vertebrae of 680 *C. plumbeus* from waters off the west coast of Australia, for three readers and for final consensus count

Reader	Mean readability	Mean band count	IAPE	No individual consensus counts	Agreement with final band count (%)
A	1.8	10.9	10.0	528	49.8
B	2.1	10.2	14.0	522	44.8
C	1.9	10.6	12.6	482	47.3
Final	–	8.7	11.7	238	–

**Fig. 4** Length at age of *C. plumbeus*, determined by: vertebral analysis of **a** males ($n = 105$, filled circles), **b** females ($n = 130$, open circles), **c** sexes combined ($n = 238$, unknown sexes shown as grey triangles) and **d** growth increments of tagged sharks ($n = 104$). Solid lines are the

fitted von Bertalanffy growth curves for each dataset, dashed lines indicate 95% confidence intervals and in **(d)** dotted line is the growth curve derived from median estimates of von Bertalanffy growth parameters

Table 2 Summary of von Bertalanffy parameters, estimated by fitting the growth curve to length-at-age data derived from vertebral analysis of 238 *C. plumbeus* from waters off the west coast of Australia

Sex	N	K (year ⁻¹)	L_{∞} (cm FL)	t_0	r^2
Male	105	0.044 (0.044, 0.063)	226.3 (188.6, 229.2)	-4.7 (-4.0, -4.7)	0.925
Female	130	0.039 (0.029, 0.040)	245.8 (241.3, 297.9)	-4.9 (-4.8, -5.4)	0.940
Combined	238	0.040 (0.033, 0.047)	239.6 (222.2, 273.0)	-4.9 (-4.5, -5.1)	0.934

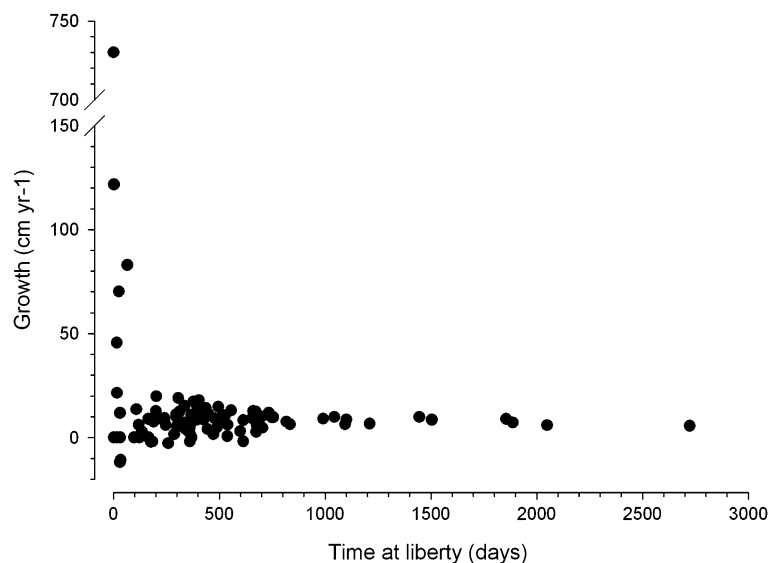
Values in parentheses are 95% confidence intervals of bootstrapped estimates

annual growth at length α and 53.0–114.7% of growth at length β). The model also estimated a contamination probability of 6.4% in the

observed data, which increased to 8.9% in the bootstrapped data (with 95% confidence limits of 1.9–22.7%), indicating that data from between

Table 3 Growth and growth variability parameter estimates for *C. plumbeus* from waters off the west coast of Australia, with 95% confidence intervals, calculated from tagging data by the Francis (1988a) model

	g_{α} (cm year ⁻¹)	g_{β} (cm year ⁻¹)	v	m (cm)	s (cm)	p	L_{∞} (cm FL)	K (year ⁻¹)	t_0 (years)
Fitted	10.2	4.5	0.264	-0.322	2.510	0.064	142.0	0.153	-2.3
Median bootstrap	10.2	4.85	0.095	-0.428	3.643	0.089	146.2	0.144	2.4
95% confidence intervals	6.8, 15.2	1.1, 10.8	0.016, 0.384	-4.581, 3.017	2.383, 5.162	0.019, 0.227	117.5, 209.8	0.115, 0.155	-1.5, -3.9

Fig. 5 Growth rate versus time at liberty of 104 recaptured *C. plumbeus*, which were tagged off the west coast of Australia between March 1994 and October 2003

seven and nine sharks were likely to exert undue influence in the model fitting procedures.

Discussion

This study validated the annual nature of vertebral growth band formation in sandbar sharks up to 17 years of age, from waters off the west coast of Australia. As such, it is the first to validate the annual periodicity of growth band formation for this commercially valuable species. Although Branstetter (1987) did previously provide validation based on two captive juveniles, other age and growth studies have had to rely on the indirect methods of marginal increment analysis (Casey et al. 1985; Sminkey and Musick 1995; Joung et al. 2004) or comparison of vertebral results with growth rates of tagged sharks (Casey et al. 1985; Casey and Natanson 1992). This study is also one of only a few that

have demonstrated annual band formation in the genus *Carcharhinus* in the wild (Branstetter 1987; Brown and Gruber 1988; Simpfendorfer et al. 2002). However, unlike these previous studies, annual growth bands were validated for a relatively wide range of age classes (3–17 years), which were at liberty for periods of up to 8.1 years.

This is also believed to be the first study of elasmobranch age and growth that has used calcein to mark the centra of wild sharks. These results confirm the conclusions of Walker et al.⁵ and Gelsleichter et al. (1997), that calcein produces distinct fluorescent marks in vertebrae from

⁵ Walker TI, Officer RA, Clement JG, Brown LP (1995) Southern shark age validation: Part 1—project overview, vertebral structure and formation of growth-increment bands used for age determination. Final report to Fisheries Research and Development Corporation (FRDC Project 91/037). Department of Conservation and Natural Resources, Queenscliff, Vic., Australia.

captive sharks. Although the former study reported no deleterious effects on the health of school sharks, *Galeorhinus galeus*, or gummy sharks, *Mustelus antarcticus*, injected with calcein, the latter study found that doses of 25 mg kg^{-1} , which are typically used in validating the age and growth of teleosts (e.g. Monaghan 1993), had a toxic effect on nurse sharks, *Ginglymostoma cirratum*. Gelsleichter et al. (1997) therefore suggested administering calcein at a dose of 5 mg kg^{-1} , as this produced suitable marks for age validation without inducing mortality. The results of the current study indicate that even lower doses of calcein might be adequate for marking centra, as the $3\text{--}5 \text{ mg kg}^{-1}$ doses used in this study produced highly visible fluorescing marks in all of the 26 calcein-marked vertebrae. This was in contrast to the centra obtained from the nine OTC-injected sharks, in which no marks could be detected in centra from two sharks and could only be faintly seen in centra from one. Although previous studies have generally not reported any failure to detect OTC marks in the vertebrae of injected sharks, marks could not be detected in nearly a third of the samples in the present study. However, failure to mineralise OTC was also reported by Kusher et al. (1992), who found 'sufficient OTC uptake' in only 35% of injected leopard sharks, *Triakis semifasciata*, while Smith et al. (2002) reported a rapid decay in OTC marks in vertebrae of leopard sharks that had been at liberty for ca. 20 years. Results from the present study therefore suggest that even at low doses, calcein may be a more reliable chemical marker than OTC for age validation studies in which vertebrae from wild sharks are used.

The von Bertalanffy growth curves estimated by vertebral analysis for *C. plumbeus* in Western Australian waters were dissimilar to those previously reported from the Pacific (Wass 1973), western North Atlantic (Casey et al. 1985; Casey and Natanson 1992; Sminkey and Musick 1995) and more recently from northeastern Taiwanese waters (Joung et al. 2004; Table 4). Allowing for the fact that *C. plumbeus* in the western North Atlantic population are born at a larger size and attain a greater maximum length than those from Australia's west coast² (Springer 1960), the von Bertalanffy growth curves estimated in this study

most closely resembled those previously estimated by Sminkey and Musick (1995). Age at maturity in Western Australian sandbar sharks was similar to previous estimates of 15 for males and 13 for females by Casey et al. (1985) and 15–16 for males and females by Sminkey and Musick (1995) but was much younger than the late 20 s suggested by Casey and Natanson (1995) and much older than the 5 years derived from the results of Wass (1973) and 7.5–8.2 years reported by Joung et al. (2004). Even though Sminkey and Musick (1995) demonstrated a significant difference between growth rates of juveniles in the western North Atlantic before and after a period of stock depletion, it seems highly unlikely that even disparate populations of *C. plumbeus* that have experienced differing levels of exploitation, could realistically exhibit such dramatic differences in ages at maturity. Nor can density-dependent effects adequately account for the magnitude of the discrepancies between growth rates determined by vertebral analysis (Casey et al. 1985; Sminkey and Musick 1995) and those derived from tagging data (Casey and Natanson 1992) in the western North Atlantic stock.

Whilst it was possible to estimate age at maturity in Western Australian *C. plumbeus* precisely, maximum age could not be conclusively determined due to the scarcity of samples and lack of consensus readings from the largest size classes. Although the largest aged female (25 years) equalled the maximum observed size in Western Australia, only three vertebral samples were obtained from sharks larger than 160 cm FL and a consensus age could only be agreed for one of these. The largest male shark for which a consensus age was agreed (19 years) was 23 cm smaller than the maximum observed size in this population. Although vertebrae from seven larger male sharks (143–147 cm FL) were examined, consensus ages could not be agreed for any of these. Despite extensive sampling throughout the range of *C. plumbeus* in Western Australia, it was impossible to obtain large sample sizes from the very oldest sharks due to their inherent scarcity. Furthermore, the compression of growth bands towards the margin of the corpus calcareum, which has been noted in several species (e.g. Casey et al. 1985; Simpfendorfer 1993;

Table 4 Comparison of published and derived age and growth parameters for *C. plumbeus*

Region	Female				Male				Method(s)	Reference
	L_{∞} (cm)	K (year ⁻¹)	t_0 (years)	t_{mat} (years)	t_{max} (years)	L_{∞} (cm)	K (year ⁻¹)	t_0 (years)	t_{max} (years)	t_{max} (years)
Western North Atlantic	299.0 FL	0.04	-4.9	13	21	257.0 FL	0.05	-4.5	12	15
Western North Atlantic ^a	186.0 FL	0.046	-6.5	Late 20 s	>50					
Western North Atlantic	263.3 TL	0.059	-4.8	15–16		245.9 TL	0.059	-5.4	15–16	
Western North Atlantic	220.5 TL	0.086	-3.9	15–16		221.8 TL	0.087	-3.8	15–16	
Hawaii	193.9 TL	0.001	-0.4	6.5		181.7 TL	0.001	-0.4	5.38	
East China Sea	223.0 TL	0.1	-4.5	8.2	19.8	200.0 TL	0.14	-4	7.5–8.2	20.8
Western Australia	245.8 FL (281.0 TL)	0.039	-4.9	16.2	25–36	226.3 FL (259.2 TL)	0.044	-4.7	13.8	24–41

L_{∞} , K , and t_0 are parameters of the von Bertalanffy growth curve. Natural TLs given in parentheses were derived from length relationships presented in the current study

t_{mat} indicates age at maturity; t_{max} is the maximum age

^a Denotes estimates based on growth curve for combined sexes

Natanson and Kohler 1996; Smith et al. 2002), could have caused less consistent readings of the vertebrae from older sharks. The relatively small number of length-at-age estimates for older sharks is likely to have biased the fitted von Bertalanffy growth curves and caused estimates of L_{∞} to exceed the maximum observed lengths in this population. It is therefore difficult to estimate maximum size and hence maximum age with any certainty. However, when extrapolated to the maximum reported size of *C. plumbeus* in Australia (Last and Stevens 1994), these data suggest that maximum age could be as high as 41 years for males and 36 years for females.

Francis (1988a, b) demonstrated that, because age-based growth data determined from vertebral analysis are fundamentally different to length-based growth data estimated from tagging data, growth increments of tagged fish are not comparable to and therefore should not be used to verify, length-at-age data. Nonetheless, this approach has been used for several shark species (Natanson et al. 1999; Smith et al. 2002; Wintner et al. 2002; Skomal and Natanson 2003). The von Bertalanffy growth curves derived from the tag-return data in the present study bore little resemblance to those estimated from vertebral analysis, thereby confirming some of the problems associated with such comparisons. However, the analysis of tag-recapture data using the Francis (1988a) model did provide some useful insights into and quantification of the limitations of using tagging data to describe growth rates of slow-growing species such as *C. plumbeus*. For example, although the estimated growth variability ($v = 0.26$) was lower than has been determined for other chondrichthyan species (Francis and Francis 1992; Francis 1997), including the related and co-occurring dusky shark, *Carcharhinus obscurus* ($v = 0.34$, Simpfendorfer 2000), this level of natural variability in the growth of individual sharks suggests that in some situations, tagging data provide an unreliable basis for the verification of growth rates of the population. These situations include when most of the data come from short-term recaptures (when growth-increments are most variable; Fig. 5) and when sample sizes are small relative to the amount of variation.

The growth curve derived from the tagging data was clearly unrepresentative of the larger length-at-age dataset (Fig. 4). The estimated levels of measurement error in the tagging data appear to have been sufficiently large to obscure the growth rates predicted by the model, particularly in larger sharks. This would result in unreliable estimates of the von Bertalanffy parameters. Also, despite every reasonable attempt to ensure the provision of accurate tag release and recapture information, the model predicted a 6.4% probability of data contamination. In other words, six tag returns were either misrecorded or represented observations of atypical individuals. As growth rates of tagged sharks have typically been derived from relatively small sample sizes, even at this level of contamination there is considerable potential for outliers in the data to seriously bias results. It is therefore suggested that the use of growth rates determined from the length-increments of tagged sharks should not be regarded as a substitute for the direct validation of the frequency of growth band formation in vertebrae.

The results of the present study confirm that *C. plumbeus* from waters off the west coast of Australia are slow-growing and take many years to reach maturity. In conjunction with their low fecundity (R.B. McAuley, unpublished data), this stock is likely to be particularly sensitive to exploitation pressure and consequently fishery managers need to be responsive to its intrinsic vulnerability to overharvesting. Based on these results and the known size composition of catches in the temperate Western Australian demersal gillnet fishery², *C. plumbeus* catches in the southern half of this stock's range primarily comprise all but the first few juvenile age classes and adults. In conjunction with recent increases in catches of adult-sized sharks in the Western Australian north coast shark fishery^{3,4} (R.B. McAuley, unpublished data), sandbar sharks appear to be subject to fishing at all but the very youngest and oldest ages. The highly mobile, increasingly efficient and wide ranging capacity of fishing vessels within the shark fleets of Western Australia indicate that complex management arrangements are required to maintain sustainable levels of breeding stock. It has previously been argued that limiting fishing mortality to only

a few age classes is a desirable approach to sustainable management of long-lived shark species such as this (Stevens et al. 1997; Walker 1998; Simpfendorfer and Donohue 1998; Prince 2005). Fishery managers should therefore consider low frequency or low intensity harvest strategies in conjunction with targeted spatial or temporal closures to restrict fishing mortality to a minimum of juvenile age-classes, in order to protect the breeding stock biomass of these sharks. As depletion of the breeding biomass of this stock will result in long population recovery times, the economic loss associated with recovering and rebuilding this stock may persist longer than short-term economic losses from adoption of such management strategies. To avoid such depletion, more detailed assessment of the effects of current age-specific harvest levels of the Western Australian *C. plumbeus* stock is urgently required, for which these results will be essential.

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