



Original Article

Age and growth parameters for three heavily exploited shark species off temperate eastern Australia

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The removal of large predatory sharks from the world's oceans poses profound threats to marine community structure and species conservation. Effective management of exploited shark stocks requires a sound understanding of the life histories of target species. Here we provide the first assessment of age and growth for *Carcharhinus brevipinna* in Australian waters, and for *C. obscurus* and *C. plumbeus* in eastern Australian waters, based on interpretations of vertebral growth bands. In doing so, we provide arguably among the most robust growth parameters to date for the abovementioned taxa on the bases of genetic validation and sample size and distribution, but acknowledge equally a range of limitations—most notably those associated with vertebral ageing and our lack of age validation. Comparatively, the three species displayed both contrasts and consistencies in their growth characteristics off Australia's southeast coast. For all three sharks, rates of growth were greatest in the years immediately after birth, males grew more rapidly than females in the juvenile phase, and females were observed to grow larger, live longer and were generally larger at any given age. Longevity and all modelled growth parameters (L_{∞} , k and L_0), however, differed among the three species, and appeared to challenge the findings for conspecific populations in other parts of the world. The validity of these latter comparisons is, however, compromised by a range of confounding factors. Nevertheless, we provide the least conservative k estimates for *C. obscurus* and *C. plumbeus* of those previously reported, and extend maximum age estimates for *C. brevipinna*. In this way, our results have important implications for the assessment of natural mortality, productivity, and hence resilience to stock depletion, in these species in southeastern Australian waters.

Keywords: asymptotic growth models, Carcharhinidae, dusky shark, fishery management, sandbar shark, spinner shark, vertebral ageing.

Introduction

Apex predators play a fundamental role in regulating species abundance and community structure in ecosystems (Ritchie and Johnson, 2009). The removal of such organisms, via natural or anthropogenic causes, can induce profound and complicated cascading impacts on lower trophic levels—as has been demonstrated in terrestrial (Moreno *et al.*, 2006; Beschta and Ripple, 2009; Wallach *et al.*, 2010) and marine environments (Myers *et al.*, 2007; Baum and Worm, 2009). Biological traits such as slow growth rate, long lifespan, late onset of maturity and low reproductive output render many apex predators vulnerable to rapid population decline and slow rates

of recovery (Musick, 1999; Purvis *et al.*, 2000; Webb *et al.*, 2002; Field *et al.*, 2009). This is exemplified in oceanic species such as sharks, where continued overexploitation has led to the depletion of virgin stocks in many parts of the world (e.g. Baum *et al.*, 2003; Ferretti *et al.*, 2008). While levels of decline are highly debatable (Burgess *et al.*, 2005), there is nevertheless widespread consensus regarding the need for effective shark fishery management and conservation (Barker and Schluessel, 2005).

Dusky (*Carcharhinus obscurus*), spinner (*Carcharhinus brevipinna*) and sandbar (*Carcharhinus plumbeus*) sharks are three large-medium carcharhinid shark species found throughout much of the world's

tropical and warm-temperate coastal and continental shelf waters (Last and Stevens, 2009). Highly sought-after for their fins (Clarke et al., 2006), all three species are important components of commercial and artisanal catches in multispecies shark fisheries across the globe (e.g. Amorim et al., 1998; Castillo-Géniz et al., 1998; McVean et al., 2006; Henderson et al., 2007; White, 2007; Morgan et al., 2009; Manojkumar et al., 2012). Recreational catches and rates of bycatch in non-target fisheries are also suspected to be substantial but, as for most shark species, they remain largely unquantified (Bonfil, 1994).

Carcharhinus obscurus, *C. brevipinna* and *C. plumbeus* are highly vulnerable to overfishing and human-induced habitat alteration due to their life-history traits (e.g. Simpfendorfer et al., 2002; Capapé et al., 2003; Carlson and Baremore, 2005; Dudley et al., 2005; McAuley et al., 2006; Baremore and Hale, 2012), susceptibility to multiple harvest methods, and utilization of inshore nursery habitat for neonate and juvenile development (e.g. Thorpe et al., 2004; Conrath and Musick, 2007; Taylor and Bennett, 2013). Consequently, the sustainability of targeted fishing activities exploiting *C. obscurus* and *C. plumbeus* in particular has been subject to considerable scrutiny in recent years (e.g. Sminkey and Musick, 1996; McAuley et al., 2005, 2007a; Cortés et al., 2006; Romine et al., 2009; Anon., 2011a, b), resulting in global IUCN classifications of “vulnerable” for both species (Musick et al., 2009a, b). Some populations have experienced greater levels of fishing mortality than others. In the Northwest Atlantic, for example, *C. obscurus* is regionally listed as “endangered” (Musick et al., 2009a), and declines of up to 64–99% in *C. obscurus* and *C. plumbeus* stocks are purported (Cortés et al., 2006; Myers et al., 2007; Baum and Blanchard, 2010). Comparatively, *C. brevipinna* is considered of less conservation concern in spite of similar life-history traits, and is globally IUCN listed as “near threatened” (Burgess, 2009).

In Australian waters, the three study species are actively targeted along the eastern, northern and western coastlines, as well as the southern coastline in the case of *C. obscurus*, with capture typically via demersal longlines, demersal and pelagic gillnets, and handlines (Simpfendorfer and Donohue, 1998; Macbeth et al., 2009; Harry et al., 2011a; Tillett et al., 2012; Rogers et al., 2013). Dramatic increases in commercial catches of these species have been reported from Australia over recent decades. For example, a sixfold increase in landings of *C. obscurus* (~100–600 tonnes (t)) and a fourfold increase in landings of *C. plumbeus* (~100–415 t) were reported from Western Australian waters between 1980 and 1990, and 1995 and 2004, respectively (McAuley et al., 2007a, b). Despite extensive management measures having been implemented in this region (Simpfendorfer and Donohue, 1998), underestimation of both species’ vulnerability to fishing mortality has failed to halt unsustainable fishing levels and declining stocks (McAuley et al., 2007a). Off Australia’s southeastern seaboard, a threefold increase in total shark catch (152 to 457 t) was recorded between 2005 and 2007 by the New South Wales Ocean Trap and Line Fishery (NSW OTLF), where *C. plumbeus*, *C. obscurus* and *C. brevipinna* were the three most abundantly caught species, respectively (Macbeth et al., 2009). During this time, shark fishing associated with the NSW OTLF was managed by input controls limiting the number of potential participants but was not subject to restrictions on the volume of catch able to be taken, highlighting the urgent need for assessment of shark exploitation and management arrangements off Australia’s southeast coast.

Effective management of exploited shark populations requires a sound understanding of the life history of target species. For example, robust estimates of age provide a basis for determining

other pertinent parameters such as longevity, growth rate, natural mortality, and hence resilience to various levels of fishing pressure (Goldman, 2004). Cosmopolitan distributions and commercial importance have led to numerous vertebral-ageing studies on *C. obscurus*, *C. brevipinna* and *C. plumbeus*. Age and growth parameters are available for all three species from the Indian Ocean and Northwest Atlantic (Casey et al., 1985; Branstetter, 1987; Casey and Natanson, 1992; Natanson et al., 1995; Sminkey and Musick, 1995; Natanson and Kohler, 1996; Allen and Wintner, 2002; Carlson and Baremore, 2005; McAuley et al., 2006; Hale and Baremore, 2010) as well as from the western Pacific for *C. brevipinna* and *C. plumbeus* (Joung et al., 2004, 2005), and the central Pacific for *C. plumbeus* (Romine et al., 2006). In Australian waters, validated age and growth studies have been conducted on *C. obscurus* (Simpfendorfer et al., 2002) and *C. plumbeus* (McAuley et al., 2006) off the west coast. While the propensity for vertebrae to underestimate age in large adult sharks is purported (Francis et al., 2007; Andrews et al., 2011), the above-mentioned studies revealed all three to be long-lived species, exhibiting generally slow rates of growth and conforming to the patterns outlined by Cortés (2000)—i.e. initially faster growth in males than females, females growing older and to larger sizes than males, and growth rates for both sexes being fastest during the juvenile stage.

Although the growth dynamics of *C. obscurus*, *C. plumbeus* and *C. brevipinna* have been widely documented across much of their respective distribution ranges, many such studies report biologically unrealistic growth parameters. Most notably, estimates of theoretical asymptotic length (L_{∞}) are typically overestimated, translating to underestimates of the growth coefficient (k). Inaccuracies such as these have profound implications for demographic analyses and population models, and generally stem from sampling biases. Nonetheless, life-history characteristics have been reported to vary among conspecific shark populations (Lombardi-Carlson et al., 2003; Driggers et al., 2004; Cope 2006; Harry et al., 2011b). Accurate age and growth parameters specific to both geographically and genetically distinct populations, therefore, are critical for informed regional fishery management.

In southeastern Australian waters, life-history information on the three study species (and all exploited carcharhinids for that matter) is currently undefined. The objective of the present study, therefore, was to provide the first detailed assessment of the age and growth of *C. brevipinna* in Australian waters, and of *C. obscurus* and *C. plumbeus* in eastern Australian waters, based on interpretations of vertebral growth bands.

Methods

Sample collection and genetic validation

Samples of vertebrae were collected between November 2007 and September 2010 by scientific observers on board commercial shark-fishing vessels operating off Australia’s New South Wales (NSW) coast between Tweed Heads (28°4’S) and Sydney (34°3’S) (Figure 1). All animals were sexed and recorded for total (L_T), fork (L_F) and precaudal lengths (L_{PC}) to the nearest centimetre.

Owing to the morphological similarities among carcharhinids, a small quantity (<2 g) of white muscle tissue was collected from each individual and tested, using mitochondrial DNA, to validate species identity. Vertebrae and data associated with misidentified individuals were excluded from analyses.

Morphometric relationships between L_T , L_F and L_{PC} were determined using linear regression analyses, with male and female relationships statistically compared using analyses of covariance (ANCOVA) (Table 1).

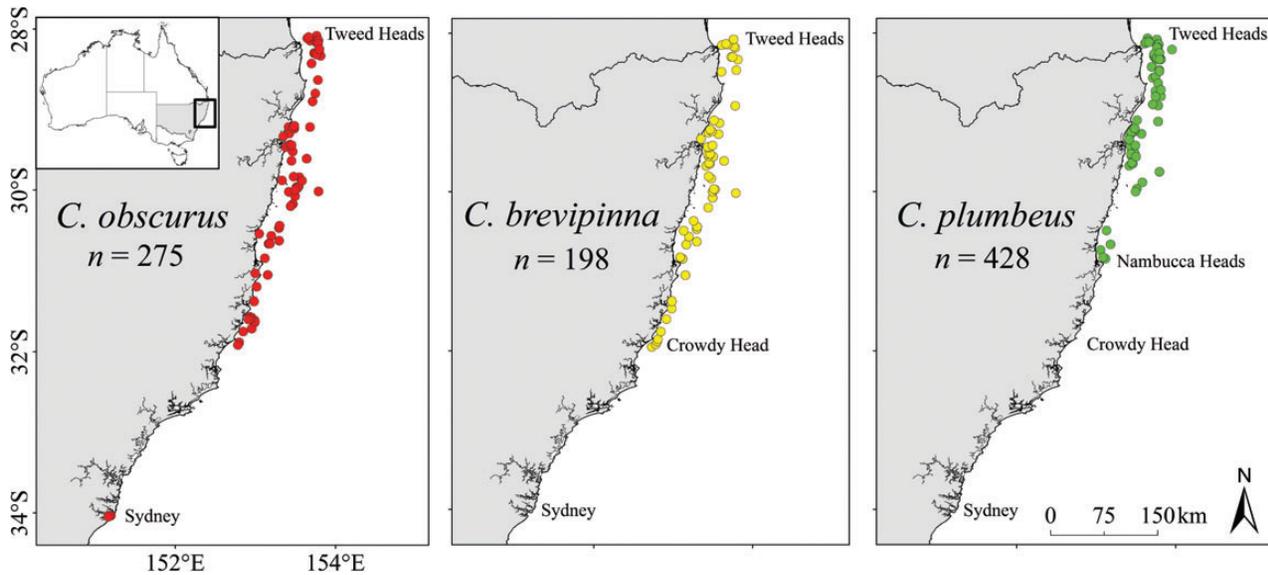


Figure 1. Study area and capture location for individual sharks aged.

Table 1. Morphometric relationships (cm) for *Carcharhinus obscurus*, *C. brevipinna* and *C. plumbeus* in New South Wales waters.

Species	Equation	n	r ²	ANCOVA		
				F	d.f.	p
<i>C. obscurus</i>	$L_T = 1.305 \cdot (L_{PC}) + 8.021$	255	0.99	0.086	253	0.770
	$L_T = 1.203 \cdot (L_F) + 4.226$	236	0.99	0.004	234	0.951
<i>C. brevipinna</i>	$L_T = 1.286 \cdot (L_{PC}) + 6.208$	183	0.99	0.668	181	0.415
	$L_T = 1.188 \cdot (L_F) + 3.519$	191	0.99	1.178	189	0.279
<i>C. plumbeus</i>	$L_T = 1.316 \cdot (L_{PC}) + 4.566$	424	0.98	0.406	422	0.525
	$L_T = 1.206 \cdot (L_F) + 2.747$	427	0.98	0.820	425	0.366

ANCOVA revealed no statistical difference between male and female length relationships for any of the species, hence regression equations represent combined sexes. All relationships were linear and highly significant ($p < 0.001$). L_T , L_F and L_{PC} denote total, fork and precaudal lengths, respectively.

Vertebrae preparation and ageing protocol

A section of 3–5 vertebrae was sampled from the cervical region of the vertebral column (i.e. anterior to the first dorsal fin) of each shark, stored on ice, and frozen upon return to the laboratory. In preparation for ageing, vertebrae samples were thawed, manually cleaned of excess soft tissue, separated into individual centra, and soaked in a 5% sodium hypochlorite solution (bleach) until all remaining soft tissue had been removed. Soak time varied from 15–45 min depending on the size of the centra. Cleaned vertebrae were rinsed thoroughly in tap water and stored in 70% ethanol. One vertebra from each shark was chosen at random, removed from the alcohol and air-dried in preparation for sectioning. Centra were sagittally sectioned through the focus to 0.5–0.6 mm thickness using an Isomet low-speed diamond-blade saw.

To determine the best vertebra preparation method, trials were conducted comparing unstained sections to sections stained with alizarin red and crystal violet. MicroCT scanning was also investigated as an alternative visualization technique (Geraghty *et al.*, 2012). All four methods produced comparable section readability, however neither method noticeably enhanced growth-band clarity relative to the other. For practicality, unstained sections were employed for ageing analysis.

Unstained sagittal sections were fixed to a glass slide with waxed resin, and examined under reflected light on a dark background using an Olympus SZ dissecting microscope fitted with digital camera. Growth bands were counted by two independent readers

(Reader 1 and Reader 2) without prior knowledge of the size, sex or date of capture of the subject. Reader 1 was experienced in shark ageing methods and interpretation, while Reader 2 was relatively inexperienced. Digital images were taken of each vertebral section, and growth bands were independently marked by each of the readers using ImageJ. Archived images of both readers' ageing interpretations permitted accurate review. A growth band was defined as a band-pair, comprising one opaque and one translucent band (Cailliet *et al.*, 2006). For the purpose of this study, the term *age count* is used to denote estimates of age based on annual band-pair deposition; the latter having been validated for *C. obscurus* (Simpfendorfer *et al.*, 2002) and *C. plumbeus* (McAuley *et al.*, 2006) in Australian waters, but has been assumed here for *C. brevipinna* in the absence of age validation for this species. Age counts were derived by counting fully formed translucent bands along the corpus calcareum occurring after the birth-mark, the latter being denoted by an angle change on the centrum face (Goldman, 2004) (Figure 2). The readability of each vertebral section was scored according to the following definitions: 5, all growth bands well defined and visible; 4, almost all bands visible, clear interpretation possible; 3, most bands visible, interpretation reliable to within ± 1 ; 2, bands visible, majority difficult to interpret; 1, unreadable. All sections deemed unreadable were excluded from further analyses. Age counts agreed upon between readers were adopted as the final age count for those vertebral sections. For any section where there was disagreement between readers, a final age count was decided upon by the more experienced

reader (Reader 1) following an interactive review and evaluation of both readers' interpretations.

Between-reader bias and precision

A combination of methods was used to evaluate bias and precision in age counts between readers (Cailliet and Goldman, 2004). Bias was investigated using age-bias plots and Bowker's test of symmetry to determine whether observed count differences were systematic or due to random error (Campana et al., 1995; Hoenig et al., 1995; Campana, 2001). Inter-reader precision estimates were calculated using the coefficient of variation (CV) (Chang, 1982) and percent-age agreement (PA) (Goldman, 2004).

Growth modelling

The von Bertalanffy growth function (von Bertalanffy, 1983) has been the model most applied for describing growth in elasmobranchs (Cailliet and Goldman, 2004), however studies comparing the performance of multiple models have demonstrated others to be more appropriate in some shark species (Carlson and Baremore, 2005; Natanson et al., 2006; Barreto et al., 2011). Six candidate models, therefore, were fitted to observed length-at-age data for each species. Modified, three-parameter forms of the von Bertalanffy (VB-3), Gompertz (GOM-3) and logistic (LOGI-3) growth models were given by the following equations, where L_a is observed length at age a and L_0 (length-at-birth), L_∞ (theoretical asymptotic length) and k (growth coefficient) are fitted parameters (Simpfendorfer et al., 2000; Braccini et al., 2007; Thorson and Simpfendorfer, 2009):

$$\text{(VB-3)} L_a = L_0 + (L_\infty - L_0)(1 - e^{(-ka)})$$

$$\text{(GOM-3)} L_a = L_0 \left(e^{\ln\left(\frac{L_\infty}{L_0}\right)(1 - e^{(-ka)})} \right)$$

$$\text{(LOGI-3)} L_a = \frac{L_\infty \cdot L_0 \cdot e^{(ka)}}{L_\infty + L_0(e^{(ka)} - 1)}$$

Two-parameter versions of the above equations were also computed (VB-2, GOM-2 and LOGI-2) by substituting L_0 for a fixed length-at-birth value. Empirical L_0 values for each species were

estimated to be between the largest observed embryos and the smallest free-swimming individuals encountered during this study: 94 cm L_T for *C. obscurus*, 80.5 cm L_T for *C. brevipinna* and 71 cm L_T for *C. plumbeus* (P. Geraghty, unpublished data). Models were fitted using the method of non-linear least squares in the statistical package R (R Development Core Team, 2010).

A multimodel inference (MMI) information-theoretical approach was used to determine the most appropriate growth model for each species (Burnham and Anderson, 2001; Katsanevakis and Maravelias, 2008; Harry et al., 2011b). Model performance was evaluated using Akaike's information criteria (AIC), with the best-fit model displaying the lowest AIC value. AIC differences were calculated as $\Delta_i = y_i - x_{\min}$ and used to rank the support of the remaining models ($i = 1-6$) relative to the best model. Models with Δ of 0-2 had substantial support; models with Δ of 4-7 had considerably less support; models with $\Delta > 10$ had essentially no support (Burnham and Anderson, 2002). Akaike weights (w_i) were calculated as the weight of evidence in favour of a model being the best in the set of candidate models (Burnham and Anderson, 2002). The 95% confidence intervals (CI) around the best-fit parameter estimates were derived from 10 000 resampled datasets.

Growth-band periodicity

Verification of growth-band periodicity was achieved via marginal increment analysis. Only sections displaying clearly defined, unambiguous growth bands on the centrum outer margin were included. Marginal increment ratios (MIRs) were calculated using the following equation, with means ($\pm SE$) subsequently plotted against month: $MIR = MW/PBW$ (Conrath et al., 2002), where MW = margin width and PBW = previous band-pair width (see Figure 2).

Results

Carcharhinus obscurus

Carcharhinus obscurus was caught along the NSW coast between Tweed Heads and Sydney (Figure 1). Vertebrae from 275 genetically confirmed individuals, ranging in size from 92-386 cm L_T , were sectioned and read. Specimens sampled for both sexes were predominantly large (>270 cm L_T), although some small individuals were also obtained (Figure 3a).

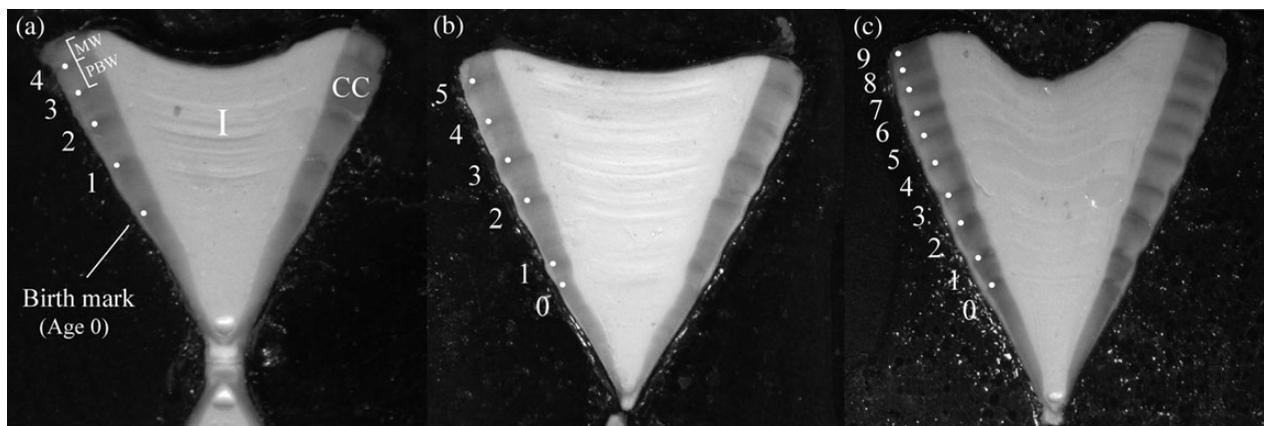


Figure 2. Unstained sagittal sections from an (a) 4+ year old, 145 cm total length (L_T) male *C. plumbeus*, (b) 5+ year old, 176 cm L_T female *C. brevipinna*, and (c) 9+ year old, 245 cm L_T female *C. obscurus*. Fully formed translucent bands occurring after the birth-mark are marked with white dots. All three sections were scored a readability of 5. I = intermedialia, CC = corpus calcareum, MW = margin width, PBW = previous band width.

Vertebral growth-band readability was generally high in individuals ≤ 270 cm L_T and comparatively low in individuals > 270 cm L_T (Figure 4a). Overall mean ($\pm SE$) readability was moderate (2.6 ± 0.05). Those sections deemed unreadable (18) were excluded from further analyses. Growth was therefore examined using observed length-at-age data from 257 individuals (126 females and 131 males), with lengths ranging from 99–386 cm L_T for females and 92–356 cm L_T for males.

An age-bias plot and Bowker’s test of symmetry identified no systematic bias in age counts between Reader 1 and Reader 2 ($\chi^2 = 80.5$, d.f. = 68, $p > 0.05$) (Figure 5a). Overall interreader precision

was high ($CV = 7.48$) (Campana, 2001), despite PA being $< 30\%$ (Figure 5a, Table S1). Agreement with the final age count was 72.4% for Reader 1 and 37.0% for Reader 2.

Marginal increment analysis provided evidence for annual band-pair deposition commencing in midwinter. Marginal increment ratios peaked in autumn (March–May) and remained high in early winter (June), but were comparatively small in late winter (August) and spring (September–November) (Figure 6a).

All six growth models provided good fits of the observed length-at-age data for both sexes (Figure 7a). Statistically, the three-

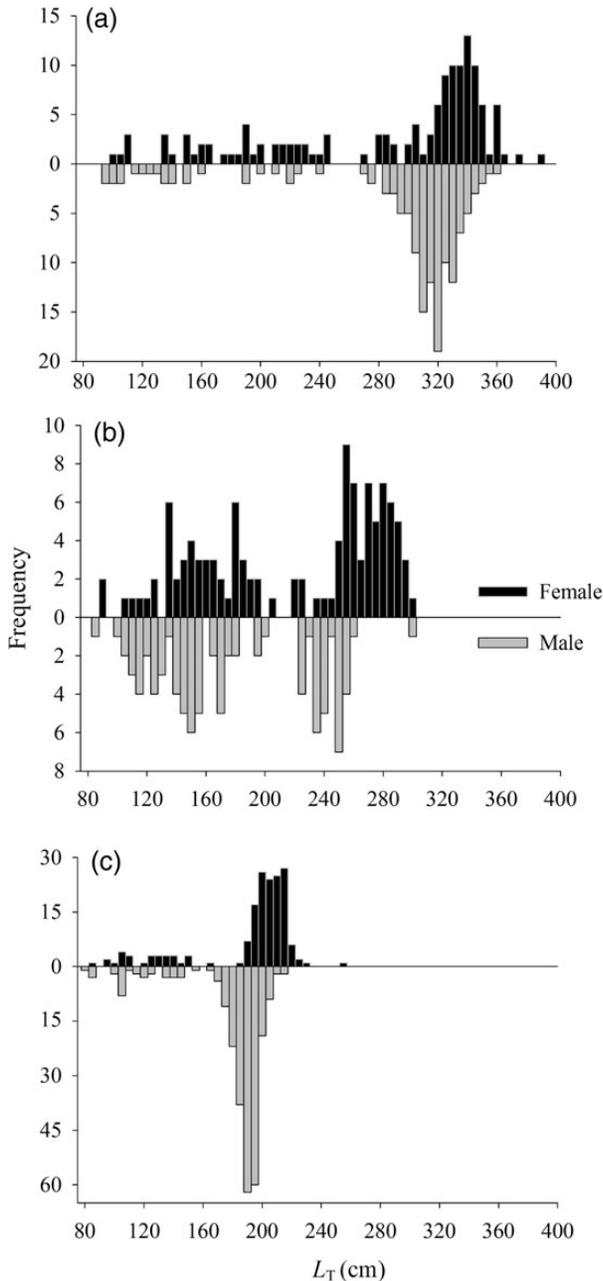


Figure 3. Length-frequency distributions, demonstrating differences in attainable size, of (a) *C. obscurus* ($n = 275$), (b) *C. brevipinna* ($n = 198$), and (c) *C. plumbeus* ($n = 428$) specimens aged via vertebral analysis.

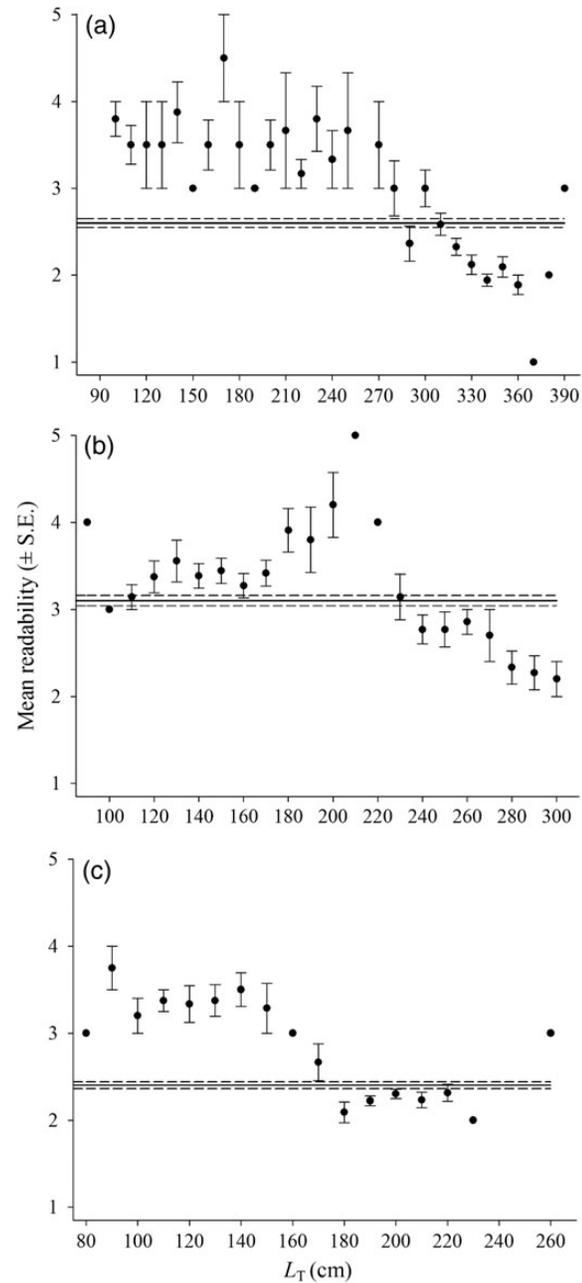


Figure 4. Mean readability ($\pm SE$) by total length (L_T) for (a) *C. obscurus* ($n = 275$); (b) *C. brevipinna* ($n = 198$); and (c) *C. plumbeus* ($n = 428$). Solid and dashed lines represent overall mean readability and upper and lower standard errors, respectively.

parameter von Bertalanffy (VB-3) growth function was the best model for describing female *C. obscurus* growth in NSW waters, with L_{∞} , k and L_0 estimated at 365.03 cm L_T , 0.083 and 107.03 cm L_T , respectively (Table 2a). The two-parameter von Bertalanffy (VB-2) model was considered the best for describing male growth, with L_0 fixed at 94 cm L_T and L_{∞} and k estimated at 336.28 cm L_T and 0.108, respectively (Table 2a).

Observed mean length-at-age varied between sexes (Table S2). At most ages, females were larger than males. Predicted length-at-age, however, suggested less contrast between males and females, with

both sexes similar in size for the first 17 years of life (Figure 8, Table S2). Females and males displayed similar longevity, with the oldest observed *C. obscurus* being a 359 cm L_T female aged at 33 years, and the oldest observed male being a 347 cm L_T individual aged at 32 years (Figures 7a and 8).

Analysis of modelled yearly growth increments suggested males grow at a faster rate than females for the first eight years of life, after which females grow faster than males (Figure 9, Table S2). For both sexes, growth was greatest in the first year following birth (Figure 9, Table S2).

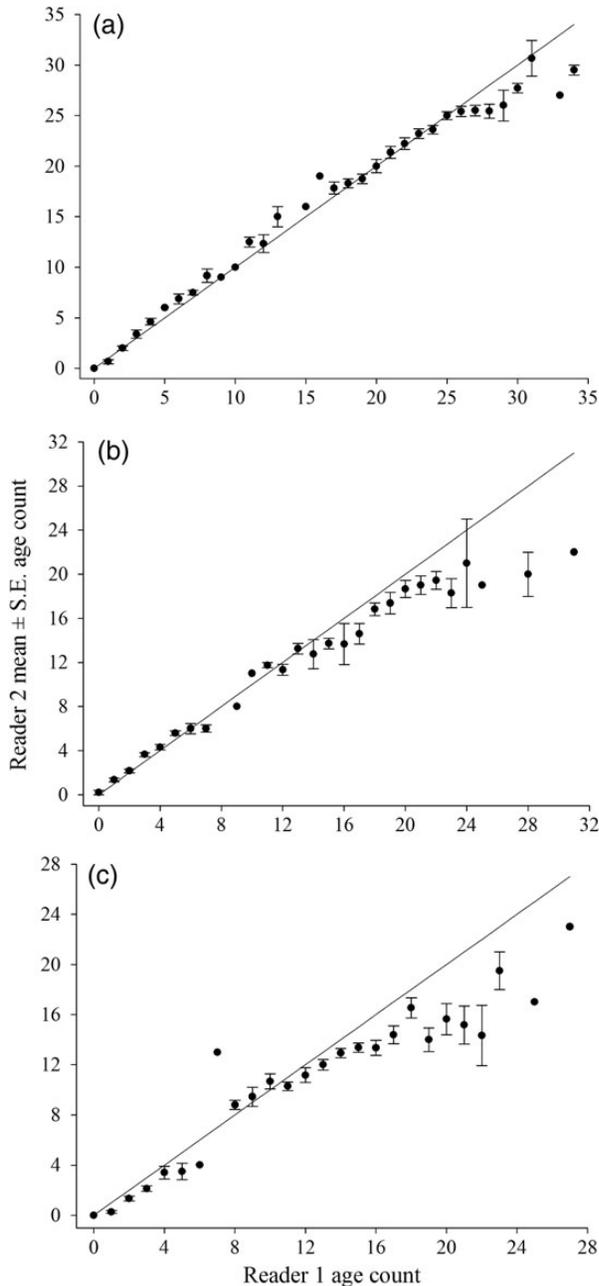


Figure 5. Between-reader age-bias plots of (a) *C. obscurus* ($n = 257$, $CV = 7.48$), (b) *C. brevipinna* ($n = 195$, $CV = 12.6$), and (c) *C. plumbeus* ($n = 393$, $CV = 19.8$) vertebral age counts. One-to-one equivalence lines are shown.

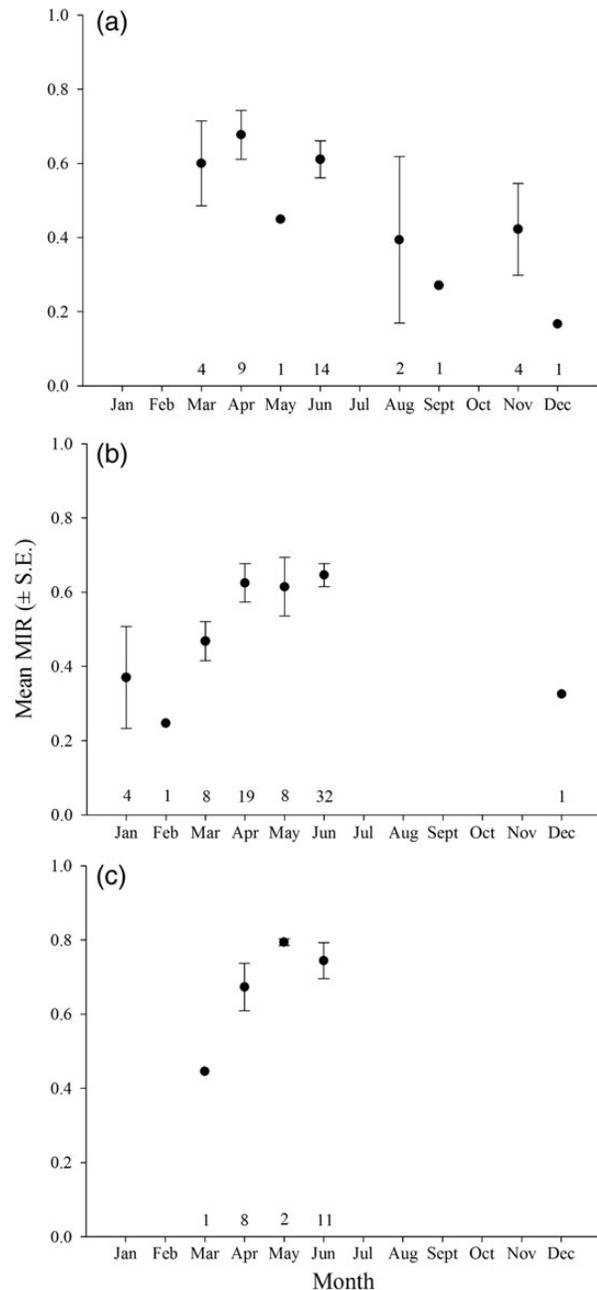


Figure 6. Monthly mean marginal increment ratios (MIR, \pm SE) for (a) *C. obscurus*, (b) *C. brevipinna*, and (c) *C. plumbeus* in NSW waters. Monthly sample sizes are shown.

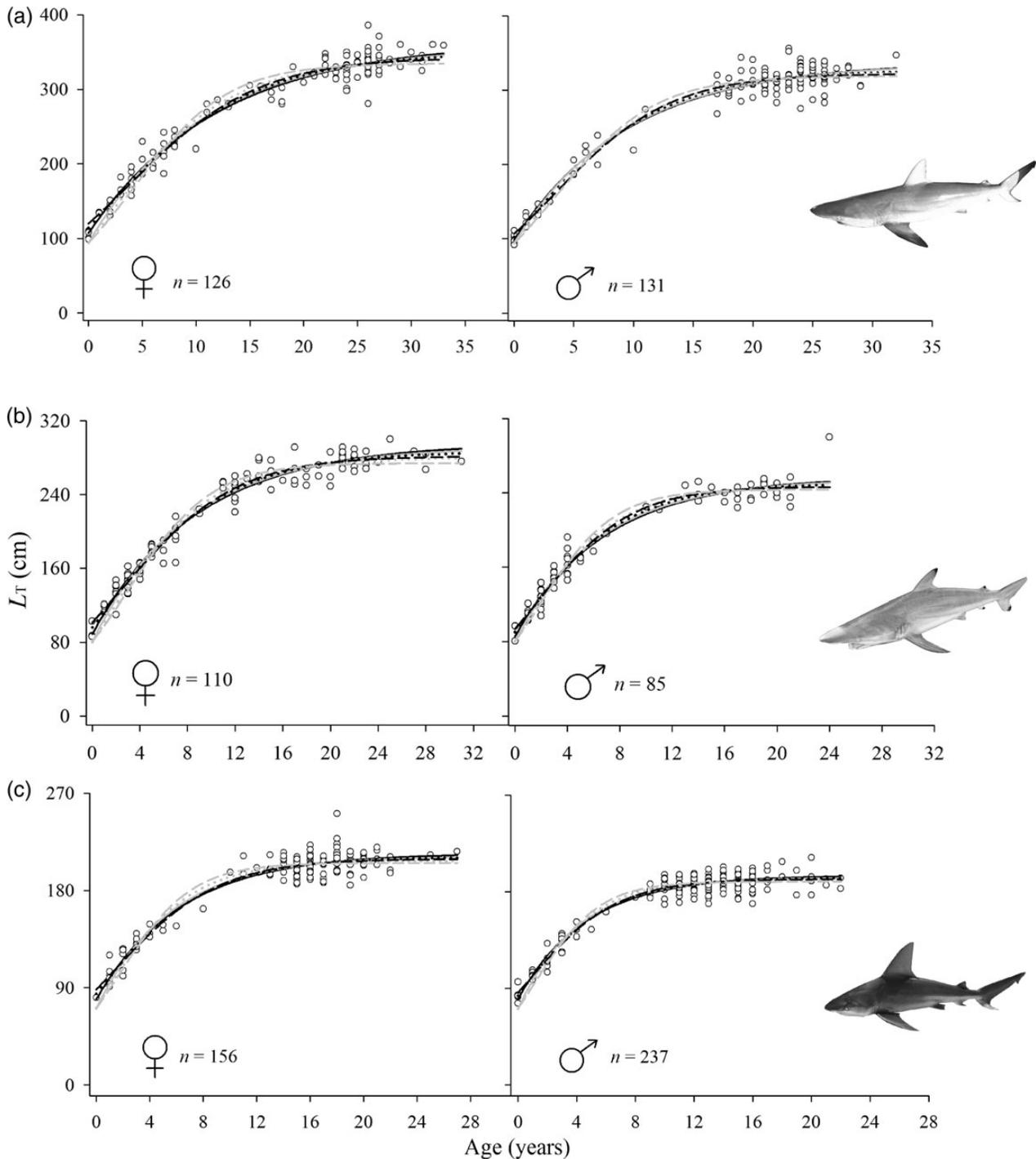


Figure 7. Observed total (L_T) length-at-age for (a) *C. obscurus*, (b) *C. brevipinna*, and (c) *C. plumbeus* in NSW waters as determined by vertebral analysis. Fitted candidate growth curves: VB-3 (black line); VB-2 (grey line); GOM-3 (dotted black line); GOM-2 (dotted grey line); LOGI-3 (dashed black line); LOGI-2 (dashed grey line).

Carcharhinus brevipinna

Carcharhinus brevipinna was caught along the NSW coast between Tweed Heads and Crowdy Head (Figure 1). Vertebrae from 198 genetically confirmed *C. brevipinna*, ranging in length from 81–300 cm L_T , were sectioned and read. Length-frequency distributions exhibited two modes for both sexes (Figure 3b).

Vertebral growth-band readability was high in individuals ≤ 230 cm L_T and lower in larger specimens (>230 cm L_T) (Figure 4b). Overall mean ($\pm SE$) readability was high (3.1 ± 0.06), although three were deemed unreadable and excluded from further analyses. Growth, therefore, was investigated using observed length-at-age data from 195 individuals (110 females and 85 males),

Table 2. Summary of fitted parameter values (with 95% CI) and Akaike's Information Criteria results from six candidate models describing (a) *Carcharhinus obscurus*; (b) *Carcharhinus brevipinna*; and, (c) *Carcharhinus plumbeus* growth in New South Wales waters.

	Model	L_{∞}	L_0	k	AIC	Δ	w	RSE
(a) <i>Carcharhinus obscurus</i>								
Females (n = 126)	VB-3	365.03 (354.99, 377.68)	107.03 (97.70, 115.98)	0.083 (0.071, 0.095)	1037.14	0.00	86.41	14.54
	VB-2	357.16 (350.02, 365.23)	94	0.095 (0.086, 0.103)	1042.92	5.78	4.80	14.94
	GOM-3	350.11 (343.50, 358.45)	114.02 (106.06, 121.73)	0.124 (0.109, 0.139)	1041.75	4.60	8.65	14.81
	GOM-2	341.64 (336.73, 346.89)	94	0.155 (0.144, 0.165)	1061.35	24.21	0.00	16.07
	LOGI-3	342.96 (337.62, 349.20)	119.94 (112.34, 127.29)	0.165 (0.148, 0.184)	1050.04	12.90	0.14	15.31
Males (n = 131)	LOGI-2	334.86 (330.49, 339.33)	94	0.226 (0.213, 0.240)	1086.03	48.89	0.00	17.72
	VB-3	338.15 (329.68, 349.89)	98.22 (89.52, 106.69)	0.104 (0.087, 0.121)	1078.36	1.04	20.92	14.56
	VB-2	336.28 (329.19, 345.50)	94	0.108 (0.095, 0.123)	1077.32	0.00	35.28	14.55
	GOM-3	327.52 (322.00, 334.77)	102.75 (94.77, 110.43)	0.153 (0.133, 0.175)	1077.54	0.22	31.59	14.51
	GOM-2	324.63 (320.31, 329.93)	94	0.168 (0.152, 0.185)	1080.28	2.96	8.05	14.72
	LOGI-3	322.23 (317.98, 327.64)	106.84 (98.97, 114.20)	0.205 (0.179, 0.233)	1081.62	4.30	4.10	14.74
	LOGI-2	319.07 (315.64, 322.96)	94	0.241 (0.220, 0.263)	1090.14	12.82	0.06	15.28
	(b) <i>Carcharhinus brevipinna</i>							
Females (n = 110)	VB-3	296.04 (288.18, 305.36)	89.06 (81.22, 96.39)	0.113 (0.098, 0.127)	858.90	9.67	0.54	11.74
	VB-2	291.70 (285.40, 298.35)	80.5	0.124 (0.115, 0.134)	861.74	12.51	0.13	11.94
	GOM-3	286.57 (280.87, 293.00)	95.97 (89.58, 102.10)	0.162 (0.145, 0.180)	850.76	1.53	31.54	11.31
	GOM-2	280.15 (275.56, 284.78)	80.5	0.198 (0.186, 0.210)	870.78	21.55	0.00	12.44
	LOGI-3	281.63 (276.85, 286.79)	101.43 (95.87, 106.76)	0.212 (0.192, 0.233)	849.23	0.00	67.79	11.23
Males (n = 85)	LOGI-2	274.12 (269.94, 278.32)	80.5	0.287 (0.271, 0.302)	893.10	43.88	0.00	13.77
	VB-3	257.24 (250.23, 266.52)	85.67 (77.78, 93.92)	0.145 (0.122, 0.170)	651.09	0.44	30.51	10.83
	VB-2	254.67 (249.07, 261.30)	80.5	0.158 (0.145, 0.172)	650.65	0.00	37.93	10.86
	GOM-3	250.31 (245.11, 256.93)	90.31 (83.84, 97.46)	0.210 (0.180, 0.241)	651.65	1.00	23.06	10.86
	GOM-2	247.01 (242.55, 252.21)	80.5	0.248 (0.232, 0.265)	656.93	6.28	1.64	11.27
	LOGI-3	246.91 (242.58, 252.31)	93.98 (87.96, 100.37)	0.277 (0.241, 0.316)	654.08	3.42	6.85	11.02
	LOGI-2	243.66 (239.46, 248.37)	80.5	0.355 (0.336, 0.377)	667.93	17.28	0.01	12.02
	(c) <i>Carcharhinus plumbeus</i>							
Females (n = 156)	VB-3	214.59 (210.24, 220.75)	79.45 (71.33, 87.33)	0.159 (0.131, 0.189)	1148.92	3.20	9.85	9.46
	VB-2	211.80 (208.87, 215.20)	71	0.182 (0.164, 0.201)	1151.21	5.49	3.13	9.56
	GOM-3	211.27 (207.85, 215.91)	84.60 (77.87, 91.16)	0.206 (0.174, 0.243)	1146.20	0.48	38.26	9.38
	GOM-2	207.54 (205.40, 209.98)	71	0.266 (0.243, 0.290)	1158.86	13.14	0.07	9.80
	LOGI-3	209.27 (206.38, 213.09)	88.42 (82.50, 94.19)	0.253 (0.216, 0.297)	1145.72	0.00	48.70	9.37
Males (n = 237)	LOGI-2	205.47 (203.64, 207.45)	71	0.369 (0.341, 0.401)	1171.18	25.46	0.00	10.20
	VB-3	195.34 (193.15, 197.99)	80.27 (75.58, 84.75)	0.214 (0.191, 0.238)	1607.72	7.51	1.37	7.12
	VB-2	193.50 (191.78, 195.38)	71	0.244 (0.226, 0.264)	1621.22	21.00	0.00	7.34
	GOM-3	193.12 (191.36, 195.12)	83.15 (79.01, 87.05)	0.273 (0.246, 0.302)	1600.96	0.74	40.28	7.02
	GOM-2	190.93 (189.62, 192.31)	71	0.337 (0.314, 0.361)	1629.97	29.75	0.00	7.47
	LOGI-3	191.74 (190.22, 193.50)	85.75 (81.88, 89.44)	0.332 (0.301, 0.367)	1600.22	0.00	58.35	7.00
	LOGI-2	189.43 (188.28, 190.63)	71	0.451 (0.422, 0.482)	1646.96	46.74	0.00	7.75

Parameters are asymptotic total length (L_{∞} , cm L_T), total length-at-birth (L_0 , cm L_T) [fixed for 2-parameter models at (a) 94 cm L_T for *C. obscurus*, (b) 80.5 cm L_T for *C. brevipinna*, and (c) 71 cm L_T for *C. plumbeus*], and growth coefficient (k). Akaike's Information Criteria values (AIC), Akaike differences (Δ) and Akaike weights (w) show the relative support for each model. RSE = residual standard error. The "best-fit" model for each sex, as determined by AIC, is bolded.

ranging in length from 86–300 cm L_T for females and 81–300 cm L_T for males.

No systematic bias in age counts was identified between Reader 1 and Reader 2 ($\chi^2 = 69.7$, d.f. = 55, $p > 0.05$) (Figure 5b). Interreader precision was acceptable ($CV = 12.6$) (Campana, 2001) and overall PA was 36.4% (Figure 5b, Table S1). Agreement with final age count was 80% for Reader 1 and 44.6% for Reader 2.

Marginal increment analysis suggested band-pair deposition commencing in midwinter. Marginal increment ratios were lowest in the summer months (December–February), increasing to a maximum value in early winter (June) (Figure 6b).

All growth models provided good fits of the observed length-at-age data for both sexes (Figure 7b). Statistically, the three-parameter logistic (LOGI-3) growth function was the best model for describing female *C. brevipinna* growth in NSW waters, with L_{∞} , k

and L_0 estimated at 281.63 cm L_T , 0.212 and 101.43 cm L_T , respectively (Table 2b). The VB-2 model was considered the best for describing male growth, with L_0 fixed at 80.5 cm L_T and L_{∞} and k estimated at 254.67 cm L_T and 0.158, respectively (Table 2b).

Observed mean, and predicted length-at-age suggested similar sizes for both sexes over the first seven years of life (Figure 8, Table S3). At all subsequent ages, females were considerably larger than males. Longevity varied between sexes, with the oldest observed *C. brevipinna* being a 276 cm L_T female aged at 31 years and the oldest observed male being a 300 cm L_T individual aged at 24 years (Figures 7b and 8).

Modelled yearly growth increments indicated males grow at a faster rate than females for the first four years of life, with growth in the first three years being substantially greater in males than females (Figure 9, Table S3). From the age of five onwards,

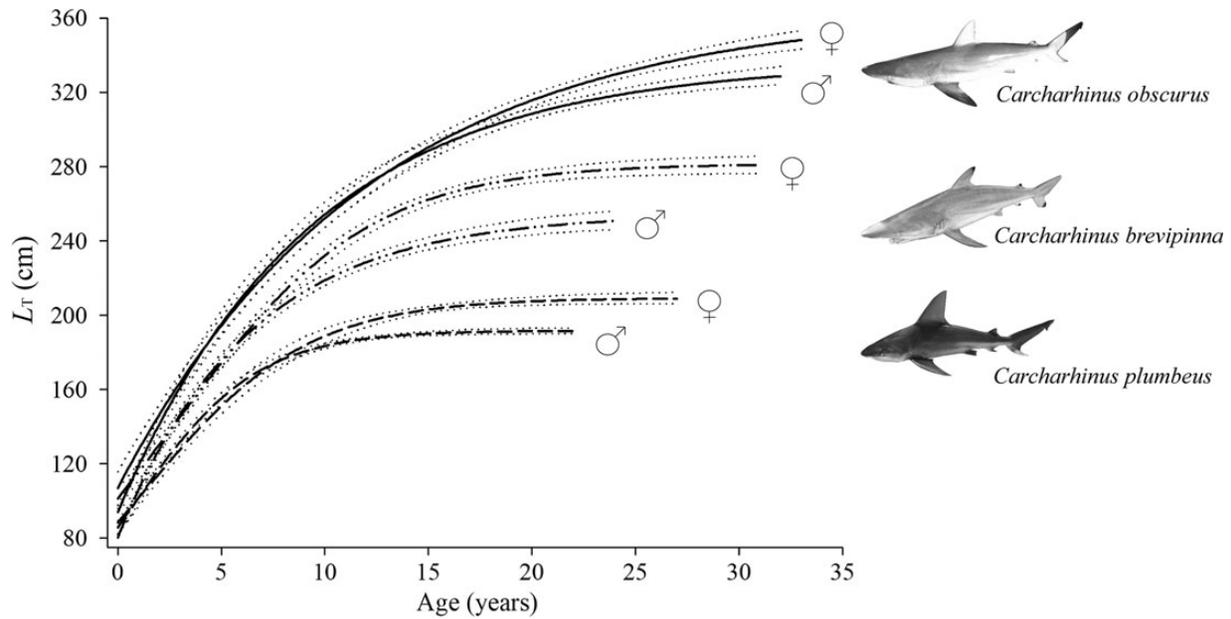


Figure 8. Comparative statistical “best-fit” growth curves, as determined by Akaike’s Information Criteria, for female and male *C. obscurus*, *C. brevipinna* and *C. plumbeus* in NSW waters. Dotted lines indicate 95% CIs based on 10 000 bootstrap iterations.

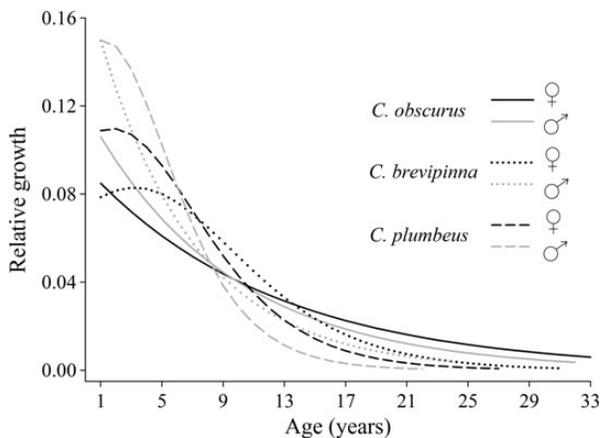


Figure 9. Relative growth (yearly growth increment/total growth) over observed lifespans of *C. obscurus*, *C. brevipinna* and *C. plumbeus* in NSW waters. Total growth (L_{∞} minus L_0) was calculated from values derived from statistical “best-fit” growth models, as determined by Akaike’s Information Criteria.

females grow at a faster rate than males. Growth was greatest in the first and third years after birth in males and females, respectively (Figure 9, Table S3).

Carcharhinus plumbeus

Carcharhinus plumbeus was caught along the NSW coast between Tweed Heads and Nambucca Heads (Figure 1). Vertebrae from 428 genetically confirmed *C. plumbeus*, ranging in length from 76–251 cm L_T , were sectioned and read. Specimens were predominantly large (>170 cm L_T) individuals for both sexes (Figure 3c).

Vertebral growth-band readability was moderately high in individuals ≤ 160 cm L_T , but generally poor in larger specimens (>160 cm L_T) (Figure 4c). Overall mean (\pm SE) readability was

quite low (2.4 ± 0.04). Following the exclusion of 35 vertebral sections deemed unreadable, growth was examined using observed length-at-age data from 393 individuals (156 females and 237 males), with lengths ranging from 81–251 cm L_T for females and 76–212 cm L_T for males.

Between-reader bias in age counts was identified for this species ($\chi^2 = 165.2$, d.f. = 97, $p < 0.001$); Reader 2 systematically under-aged vertebrae relative to Reader 1 (Figure 5c). Consequently, overall interreader precision was low ($CV = 19.8$, $PA = 15.3\%$) (Campana, 2001) (Figure 5c, Table S1). Agreement with final age count was 63.4% for Reader 1 and 25.2% for Reader 2.

Marginal increment analysis provided limited information, but was suggestive of increasing ratios throughout the autumn months, peaking in May and remaining high in early winter (June) (Figure 6c). This supports, albeit tentatively, band-pair deposition from midwinter onwards.

All candidate growth models provided good fits of the observed length-at-age data for both sexes (Figure 7c). Statistically, the LOGI-3 growth function was the best model for describing both female and male *C. plumbeus* growth in NSW waters (Table 2c). Asymptotic growth (L_{∞}) and L_0 estimates were larger for females (209.27 and 88.42 cm L_T) compared with males (191.74 and 85.75 cm L_T). In contrast, k was higher for males (0.332) than females (0.253) (Table 2c).

Observed mean length-at-age reported similar sizes for both sexes over the first five years of life; predicted length-at-age suggested similar sizes over the first nine years of life (Figure 8, Table S4). At all subsequent ages, females were considerably larger than males. Longevity varied between sexes; the oldest observed *C. plumbeus* being a 216 cm L_T female aged at 27 years, and the oldest observed males being two individuals measuring 183 and 193 cm L_T and aged at 22 years (Figures 7c and 8).

Analysis of modelled yearly growth increments indicated that males grow at a faster rate than females for the first four years of life, after which females grow faster than males (Figure 9, Table

S4). Rate of growth was greatest in the first and second years after birth for males and females, respectively (Figure 9, Table S4).

Discussion

This study marks the first assessment of the age and growth of *C. brevipinna* in Australian waters, and of *C. obscurus* and *C. plumbeus* off Australia's east coast, where all three were demonstrated to be long-lived. The six candidate growth models fitted the observed length-at-age data well for all three species. Nevertheless, growth parameters varied markedly among models. Statistically, female growth was best described by the three-parameter von Bertalanffy function for *C. obscurus*, and by the three-parameter logistic model for *C. brevipinna* and *C. plumbeus*. Male growth was best modelled by the two-parameter von Bertalanffy function for *C. obscurus* and *C. brevipinna*, and by the three-parameter logistic curve for *C. plumbeus*. Based on criteria outlined by Branstetter (1987) and Musick (1999), our best-fit growth coefficients (k values) suggest that in southeastern Australian waters *C. obscurus* is a slow-growing species, *C. brevipinna* has a slow to moderate rate of growth, and *C. plumbeus* is a moderate to rapidly growing species.

Statistical “best-fit” ranking, however, doesn't necessarily convey biological reality (Wang and Milton, 2000; Romine et al., 2006; Bubley et al., 2012). Growth-model goodness-of-fit and resultant parameter estimates can be highly influenced by sampling biases, such as those imparted by gear selectivity or historic length-selective fishing mortality (Thorson and Simpfendorfer, 2009; Harry et al., 2013). In the present study, a general under-representation of small-to-medium individuals resulted in three-parameter models overestimating length-at-birth (L_0) for all three species (Table 2). In addition, the von Bertalanffy functions produced the most realistic estimates of theoretical asymptotic length (L_∞), while the logistic and Gompertz models underestimated L_∞ in all cases (Table 2). Given that L_∞ and k are negatively correlated, an underestimate in the former causes an overestimate in the latter. Statistical output, therefore, must be considered in conjunction with observed biological data when determining the most suitable model (Cailliet et al., 2006).

With this in mind, we propose the two-parameter von Bertalanffy (VB-2) function to be the most appropriate for describing the growth of both sexes of all three species off the southeast coast of Australia. Despite a lack of statistical support in most cases (Table 2), the VB-2 model provided the most biologically accurate fit to each dataset given the incorporation of empirical lengths-at-birth and realistic L_∞ output, and are referred to henceforth. However, while models with fixed L_0 are highly applicable where small individuals are inadequately sampled, they are limited by a failure to account for variable length-at-birth or rapid early growth (Neer et al., 2005; Cailliet et al., 2006; Thorson and Simpfendorfer, 2009), and are vulnerable to biased parameter estimates with slight variations in L_0 (Pardo et al., 2013).

Carcharhinus obscurus, *C. brevipinna* and *C. plumbeus* displayed both contrasts and consistencies in their growth characteristics in southeastern Australian waters. With respect to attributes common to all three species: growth rates were greatest in the years immediately after birth and decreased progressively over time, males grew more rapidly than females in the juvenile phase (hence displaying greater k estimates) after which their growth rate slowed below that of females, and females were observed to grow larger, live longer and were generally larger at any given age. These growth patterns are typical of sharks (Cortés, 2000) and

corroborate the findings of previous work on these species from other parts of the world (refer to literature cited in Table 3). In addition, vertebral band-pair deposition appeared to occur annually in all three sharks commencing in the midwinter months, although our marginal increment analyses were severely limited in their sample size and monthly cover.

Longevity, however, varied among *C. obscurus*, *C. brevipinna* and *C. plumbeus* in the study area. Maximum observed ages for females and males respectively were 33 and 32 for *C. obscurus*, 27 and 22 for *C. plumbeus*, and 31 and 24 for *C. brevipinna*. In the case of the former two species, these estimates are consistent with those reported from other oceanic regions where comparable methodologies were employed (Table 3). In contrast, our maximum age estimates for *C. brevipinna* are considerably higher than those previously reported for this species (Table 3)—such discrepancies between NSW and other geographic regions, however, may be the result of a range of confounding factors, such as variations in technique of preparation and reading of vertebrae, reader accuracy and precision, as well as sample size and distribution (Cailliet et al., 1990; Carlson et al., 2006).

The parameters L_∞ and k , and hence rates of incremental and relative growth, also varied considerably among the study species in NSW waters. Yearly growth increments were largest in *C. obscurus* and smallest in *C. plumbeus* at any given age (Tables S2–S4)—not an unexpected result given the difference in maximum size attained by these species (Figure 3; Last and Stevens, 2009). Taking these differences into account, however, the reverse pattern was observed in the juvenile phase, where relative growth rates were highest in *C. plumbeus* and lowest in *C. obscurus* (Figure 9).

Our estimates of L_∞ and k did not necessarily agree with previous estimates for the same species in other areas. Similarly, rates of incremental growth were also observed to vary. Comparisons based solely on annual growth increments, however, are of limited value given that maximum attainable size within a species can vary among geographically distinct locations (Last and Stevens, 2009). We therefore recommend that measures of relative growth, as calculated in our study, be reported in conjunction with incremental growth so that more robust population (and species) comparisons can be drawn.

For *C. brevipinna*, our estimates of L_∞ and k are generally within the range of those reported for this species from other oceanic basins (Table 3). In contrast, our parameters for *C. obscurus* and *C. plumbeus* are markedly different from those reported by most other studies; our L_∞ and k estimates being comparatively low and high, respectively (Table 3). This implies that juvenile and adolescent *C. obscurus* and *C. plumbeus* are not as slow growing in NSW waters as has been reported in other parts of the world. However, rather than reflecting true conspecific differences, we propose that these discrepancies are driven by differences in sample size and length-distribution—in most cases highlighting the shortcomings of previous studies. All published works describing the growth of *C. obscurus* have grossly overestimated L_∞ (and hence underestimated k) relative to biological reality; the same can be said for *C. plumbeus*, but with notable exceptions (Table 3). These inaccuracies stem from either small sample sizes (Natanson et al., 1995; Natanson and Kohler, 1996) or a comparative overrepresentation of small individuals, resulting in poorly defined growth curve asymptotes (e.g. Casey et al., 1985; Sminkey and Musick, 1995; Simpfendorfer et al., 2002; McAuley et al., 2006). While the present study also displayed generally poor balance among size classes, the contrasting bias towards large individuals of *C. obscurus* and *C. plumbeus* translated to pronounced growth asymptotes and hence lower (more realistic) L_∞ and higher

Table 3. Comparative growth-model parameters based on vertebral analysis.

Species	Oceanic region	Reference	n	Size range	Max. ages (sex)	Model	Female			Male		
							L_{∞}	k	L_0	L_{∞}	k	L_0
<i>C. obscurus</i>	SE Indian	Simpfendorfer <i>et al.</i> (2002)	305	77.7–333.9	32 (F), 25 (M)	VB (2)	418.6	0.043	92.1 ^a	397.7	0.045	92.1 ^a
	NW Atlantic	Natanson <i>et al.</i> (1995)	120	89.7–356.7	33 (F), 25 (M)	VB (3)	420.2	0.039	102.9	448.9	0.038	95.7
	SW Indian	Natanson and Kohler (1996)	42	99.1–353.6	34 (F)	VB (3)	395.7 ^b	0.047 ^b	–	–	–	–
<i>C. brevipinna</i>	SW Pacific	Present study	257	92.0–386.0	33 (F), 32 (M)	VB (2)	357.2	0.095	94.0^a	336.3	0.108	94.0^a
	SW Indian	Allen and Wintner (2002)	67	78.4–282.5	17 (F), 19 (M)	VB (3)	307.9	0.100	–	261.1	0.146	–
	NW Atlantic	Branstetter (1987)	15	67.0–208.0	11.3 (F), 8 (M)	VB (3)	214.0 ^b	0.212 ^b	72.2	–	–	–
	NW Atlantic	Carlson and Baremore (2005)	259	57.8–233.7	17.5 (F), 13.5 (M)	VB (3)	270.6	0.080	–	500.5	0.030	–
						VB (2)	242.8	0.110	64.9 ^a	333.0	0.070	64.9 ^a
						GOM (3)	263.2	0.160	75.2	239.6	0.140	74.9
	W Pacific	Joung <i>et al.</i> (2005)	208	125.0–304.0	21 (F), 17 (M)	VB (3)	288.2	0.151	75.0	257.4	0.203	75.0
SW Pacific	Present study	195	81.0–300.0	31 (F), 24 (M)	VB (2)	291.7	0.124	80.5^a	254.7	0.158	80.5^a	
<i>C. plumbeus</i>	Central Pacific	Romine <i>et al.</i> (2006)	187	46.0–147.0 ^c	23 (F), 19 (M)	VB (3)	164.9 ^c	0.080	–	151.1 ^c	0.090	–
						VB (2)	152.8 ^c	0.100	47.0 ^{ac}	138.5 ^c	0.120	47.0 ^{ac}
						GOM (2)	143.5 ^c	0.170	47.0 ^{ac}	130.4 ^c	0.190	47.0 ^{ac}
						LOGI (3)	146.4 ^c	0.170	–	134.3 ^c	0.190	–
	NW Atlantic	Hale and Baremore (2010)	1194	39.0–202.0 ^d	27 (F), 22 (M)	VB (3)	181.2 ^d	0.120	–	173.0 ^d	0.150	–
						VB (2)	178.3 ^d	0.140	46.0 ^{ad}	172.1 ^d	0.150	46.0 ^{ad}
	NW Atlantic	Casey <i>et al.</i> (1985)	475	~51.9–241.0	21 (F), 15 (M)	VB (3)	360.4	0.040	–	309.6	0.050	–
	W Pacific	Joung <i>et al.</i> (2004)	362	82.0–219.0	20.8 (F), 19.8 (M)	VB (3)	210.0 ^b	0.170 ^b	–	–	–	–
	SE Indian	McAuley <i>et al.</i> (2006)	235	58.7–178.8	25 (F), 19 (M)	VB (2)	279.4	0.039	53.7 ^a	259.3	0.044	53.7 ^a
	NW Atlantic	Sminkey and Musick (1995) ^e	188	67.7–229.8	24 (F), 20 (M)	VB (3)	263.3	0.059	–	245.9	0.059	–
	Sminkey and Musick (1995) ^f	412	57.0–215.1	22 (F), 18 (M)	VB (3)	220.5	0.086	–	221.8	0.087	–	
SW Pacific	Present study	393	76.0–251.0	27 (F), 22 (M)	VB (2)	211.8	0.182	71.0^a	193.5	0.244	71.0^a	

L_{∞} = theoretical asymptotic length, k = growth coefficient, L_0 = length-at-birth, VB = von Bertalanffy, GOM = Gompertz, LOGI = logistic, number of model parameters in parentheses. All length measurements expressed as total length (L_T , cm) unless otherwise stated, and converted where appropriate using publication-specific morphometric equations (if provided). ^afixed parameter. ^bcombined sexes. ^cPrecaudal length (L_{PC}). ^dFork length (L_F). ^e1980–1981. ^f1991–1992.

(more accurate) k values. The influence of sample length-distribution on growth parameters is further emphasized by far less variation being observed between NSW waters and other geographic regions where species-specific length-distributions more closely resembled those of the present study (e.g. Allen and Wintner, 2002; Joung *et al.*, 2004, 2005; Hale and Baremore, 2010).

Notwithstanding the abovementioned limitations, differences in growth characteristics between southeastern and western Australian waters should not be ruled out entirely for *C. obscurus*, possibly warranting further investigation. Our predicted annual growth increments for juveniles of this species were markedly larger than those reported by Simpfendorfer (2000) based on tag–recapture data, and a study by Geraghty *et al.* (unpublished data) demonstrated evidence for genetic differentiation in this species, albeit weak, between the two abovementioned regions.

On the bases of genetic validation and sample size and distribution, we propose the growth-model parameters presented herein to be among the more robust currently available for all three taxa. That said, however, due consideration must be given to the lack of age-validated longevity in the present study. Tag–recapture and bomb radiocarbon data have provided compelling evidence for vertebral-band analysis underestimating age in large adult sharks, including our study species (Casey and Natanson, 1992; Natanson *et al.*, 1995; Francis *et al.*, 2007; Andrews *et al.*, 2011)—purportedly a result of discontinued band-pair deposition coinciding with a cessation of somatic growth, and/or problems with the interpretation of growth bands on the centrum outer edge. This is particularly relevant to the present study in which most sharks aged were large adult individuals. It is worth noting too that various studies have computed maximum theoretical ages based on reported maximum sizes and modelled growth parameters, yielding greatly elevated longevity estimates (e.g. Natanson and Kohler, 1996; McAuley *et al.*, 2006)—however, such calculations are highly speculative and likely of limited value. Nevertheless, by compromising longevity estimates and growth model parameters, age underestimation has far-reaching implications for shark population modelling and assessment—highlighting the need for age validation of older age classes.

Similarly, the influence of section readability on our results also warrants some consideration. In all of the three study species, readability demonstrated a generally decreasing trend as shark size increased. This emphasizes a potential source of inaccuracy in our age counts given that the majority of sharks aged in the present study were large adults.

The results of the present study indicate that *C. obscurus*, *C. brevipinna* and *C. plumbeus* are all long-lived species displaying both contrasts and consistencies in their growth dynamics in temperate eastern Australian waters. While our results appear to challenge findings emanating from other parts of the world, confounding factors render definitive interregion conclusions potentially misleading. Nevertheless, we report the least conservative k estimates for *C. obscurus* and *C. plumbeus* of the published literature to date, which has profound implications relating to assessments of natural mortality and survival. Using k as an index of potential stock vulnerability to excessive mortality (Musick, 1999), our results suggest that these two species may in fact be somewhat more resilient to overexploitation (at least in NSW waters) than current population models would assert (Sminkey and Musick, 1996; McAuley *et al.*, 2007a; Romine *et al.*, 2009). This study also extends current estimates of maximum age for *C. brevipinna*—suggestive of greater reproductive potential. While the intrinsic

susceptibilities of the three study species to overfishing are well established (particularly for *C. obscurus* and *C. plumbeus*), our results potentially warrant some level of optimism when considering the resilience of these species to fishing pressure, at least in NSW waters. Given this, the true implications of our findings remain purely speculative in the absence of age validation (particularly of older age classes), reproductive parameters (work currently in progress), and hence demographic analyses, defined from the study region.

Supplementary data

The following supplementary data is available at *ICES Journal of Marine Science* online:

Table S1. Outlining percentage agreement between Reader 1 and Reader 2 age counts for each of the three study species.

Tables S2–S4. Reporting mean (\bar{x}) and predicted (P) length-at-age (total length, L_T , cm), and growth rates (yearly growth increment, G , $\text{cm}\cdot\text{yr}^{-1}$), for female and male *C. obscurus*, *C. brevipinna* and *C. plumbeus* in NSW waters.

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