Age, growth and reproductive biology of the spot-tail shark, *Carcharhinus sorrah*, and the Australian blacktip shark, *C. tilstoni*, from the Great Barrier Reef World Heritage Area, north-eastern Australia

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Abstract. Understanding the life history of an exploited fish species is an integral part of successful fisheries management and this information can be used in quantitative population assessments. The present study describes the quantitative relationships among age, growth and reproductive biology of two commercially exploited sharks from the Great Barrier Reef World Heritage Area (GBRWHA), namely, the spot-tail shark, *Carcharhinus sorrah* ($n = 659$) and the Australian blacktip shark, *C. tilstoni* ($n = 512$). Longevity estimates based on vertebral ageing were 9 and 14 years for male and female *C. sorrah* and 13 and 15 years for *C. tilstoni*. However, an age-validation study failed to validate annual banding in larger individuals, suggesting that maximum age may be underestimated by vertebrae. *C. sorrah* grew to adult size relatively fast, reaching maturity at 2.3–2.4 years, whereas *C. tilstoni* grew slower, reaching maturity at 5.2–6.1 years. For both species, however, reproduction did not commence until approximately a year after maturity, at 3.4 years for *C. sorrah* and 7.2 years for *C. tilstoni*. The results of the present study suggest that in the GBRWHA, *C. tilstoni*, in particular, begins reproducing at an older age and lives longer than previously thought.

Additional keywords: shark fishery, Carcharhinidae, chondrichthyan.

Introduction

The Indo-Pacific region has an exceptionally diverse chondrichthyan fauna (sharks, rays and holocephalans) that includes high numbers of endemic species in areas such as the Coral Triangle (Last and White 2011). This high concentration of chondrichthyans is fished heavily in many areas and six of the top 10 shark-fishing nations globally are in the Indo Pacific region (Lack and Sant 2009). Sharks of the order Carcharhiniformes are particularly abundant throughout the region's continental-shelf habitat, and are often a major component of shark-fishery landings (Blaber *et al.* 2009; White and Kyne 2010; Harry *et al.* 2011*a*). Understanding the biology of these exploited chondrichthyans is integral to their successful fisheries management and conservation. For instance, if the relationships among length, age, body mass, fecundity and sexual maturity are known accurately, length- and age-structured models can then be used to model population dynamics (Punt *et al.* 2000; Aires-da-Silva and Gallucci 2007). Effective management of chondrichthyans is particularly important because many species often have biological traits (e.g. slow growth, low fecundity) that mean that only a relatively small proportion of the population can be sustainably harvested annually (Walker 1998).

In the waters surrounding northern Australia, two of the most abundant and commercially fished sharks are the Australian blacktip shark, *Carcharhinus tilstoni* (Whitley, 1950) and the spot-tail shark, *C. sorrah* (Müller & Henle 1839) (Last and Stevens 2009). Both are medium-sized sharks (1–2 m maximum total length) occupying relatively shallow waters (<150 m) on the continental shelf (Compagno *et al.* 2005). *C. tilstoni*, which closely resembles and hybridises with the more widely distributed common blacktip shark, *C. limbatus* (Müller & Henle 1839), is endemic to Australian waters (Last and Stevens 2009; Morgan *et al.* 2012). *C. sorrah* is found throughout the Indo-West Pacific and the Indian Ocean, as far as South Africa (Compagno *et al.* 2005). Both species are important components of several commercial shark fisheries operating in waters off northern Australia where they are used for their meat and fins (Bensley *et al.* 2010). In the location of the present study, the Great Barrier Reef World Heritage Area (GBRWHA) off north-eastern Australia, *C. tilstoni* and *C. sorrah* make up ~50% of the shark catch by weight in a commercial net fishery that mainly targets higher-value teleosts (Harry *et al.* 2011*a*).

Despite the commercial importance of these species, current knowledge of their life history is limited to a single study (Stevens and Davenport 1991); however, see publications by
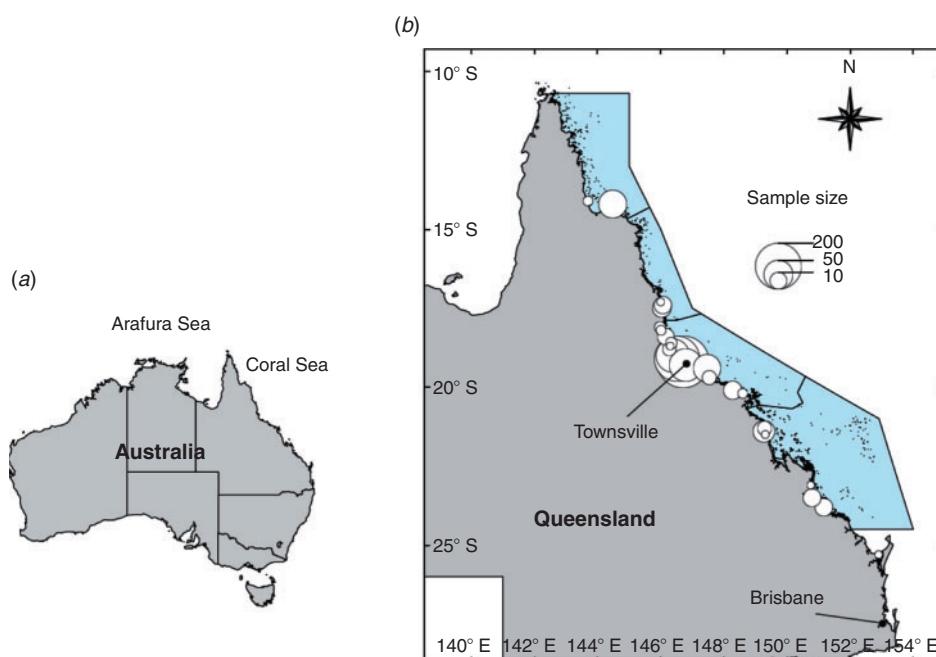
Fig. 1.   Map of Australia showing (*a*) the location of the study site in the Coral Sea relative to the Arafura Sea, where previous study on these species was carried out, and (*b*) a detailed map of the Queensland coastline with the sampling locations. The light blue area is the Great Barrier Reef World Heritage Area.

Stevens and Wiley (1986) and Davenport and Stevens (1988). This early research, carried out using samples from the Arafura Sea (Fig. 1), has served as the benchmark for managing shark fisheries across northern Australia during the past 25 years. However, because all information on these species comes from a single time and location, there is no capacity for management to factor in potential spatial and temporal variation in life-history characteristics that may exist. Spatial variation is well documented in shark populations and may extend to many facets of life history, including growth, weight, maturity, fecundity, and timing and frequency of reproduction (Yamaguchi *et al.* 2000; Walker 2007). The area these species occupy over northern Australia spans at least 18° of latitude and 40° of longitude, offering ample space for such variation to occur. Temporal differences are somewhat less well documented in sharks, but have been observed, especially in response to exploitation (Sminkey and Musick 1995; Carlson and Baremore 2003; Cassoff *et al.* 2007; Walker 2007; Taylor and Gallucci 2009). The previous study of *C. tilstoni* and *C. sorrah* was during the historically most intense period of fishing off northern Australia when both species were probably overexploited (Stevens and Davenport 1991). The effect that such high levels of fishing may have had on the life-history characteristics of these species is unknown.

The aim of the present study is to describe the life-history characteristics of *C. sorrah* and *C. tilstoni*, using samples from the Coral Sea within the GBRWHA (Fig. 1). Despite the high conservation value of the World Heritage Area, these species have not previously been studied in the region, and the purpose of the present study is to provide information suitable for quantitative population assessments. Specifically, we establish

the relationships among length, weight, fecundity and proportion of the population in mature and maternal condition. We also determine the embryonic sex ratio, and the length and duration of the reproductive cycle. To link these important components of reproductive biology to age, we also describe the relationships between length and age in *C. sorrah* and *C. tilstoni*, using a vertebral growth analysis.

Materials and methods

Sample collection and species identification

Biological samples were collected between May 2007 and January 2012 from fishery-dependent sources along the eastern coast of Queensland, from Princess Charlotte Bay (13°S) to Moreton Bay (27°S) The majority of samples were obtained between 2007 and 2009 from a fishery observer program monitoring the commercial gill-net sector of the Queensland East Coast Inshore Finfish Fishery (Harry *et al.* 2011*a*), in the inshore waters (<25-m depth) of the GBRWHA, which is between 13°S and 24°S (Fig. 1). Additional samples were also purchased or donated by commercial and recreational fishers. Further samples were collected opportunistically during fishery-independent sampling activities carried out by the James Cook University Centre for Sustainable Tropical Fisheries and Aquaculture, using multi-hook research longlines, gill-nets and rod and reel. Shark length was measured as stretched total length (STL) in millimetres (mm) following Compagno (1984), where the animal was placed ventral side down and the upper lobe of the caudal fin depressed in line with the body axis. Additional measurements of fork length (FL) and pre-caudal length (PCL) were recorded for a subsample of animals.
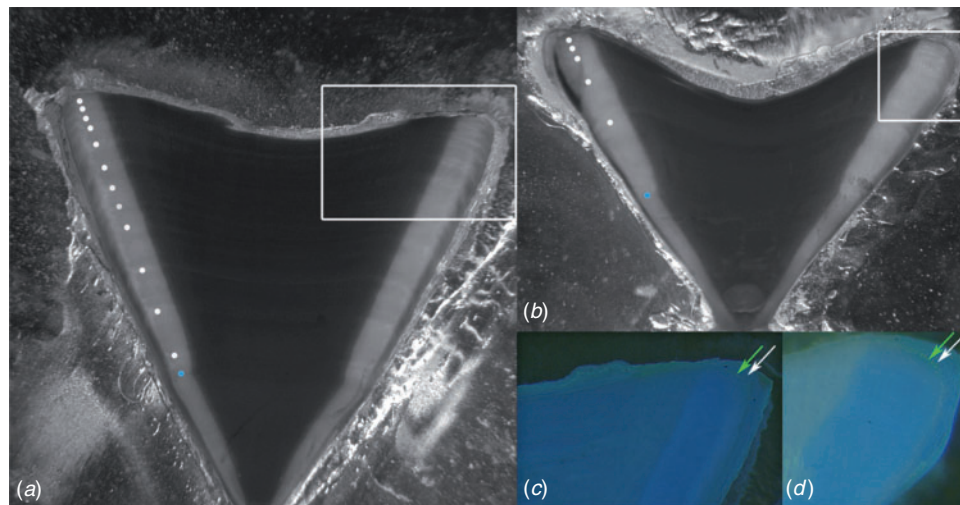
Fig. 2. Vertebral sections from (*a*) 1460-mm mature male *Carcharhinus tilstoni*, with 12 growth-band pairs visible, and (*b*) a 1025-mm mature male *C. sorrah*, with five growth-band pairs visible. Blue and white dots in the corpus calcareum denote the birth mark and completed growth-band pairs respectively. The individuals in (*a*) and (*c*) were marked with calcein and recaptured after ~3 years at liberty (see Table 3). In both individuals, the calcein mark was faintly visible (shown under ultraviolet light in *c* and *d*) near the edge of the centrum. Green and white arrows in (*c*) and (*d*) denote the calcein mark and centrum edge respectively.

In the waters off northern Australia, *C. tilstoni* occurs sympatrically with and hybridises with *C. limbatus*, from which it is visually indistinguishable (Last and Stevens 2009; Morgan *et al.* 2012). These species can be separately identified using vertebral counts (Stevens and Wiley 1986), molecular techniques (Morgan *et al.* 2011) and life-history characteristics (Harry *et al.* 2012). Because hybridisation can result in mismatches between species identification techniques, we describe a multi-faceted identification protocol to minimise species identification errors. The protocol was used to identify *C. tilstoni* and is available in Table S1, available as Supplementary Material for this paper.

Vertebral processing and growth analysis

A section of five vertebrae was removed from the anterior region of the vertebral column between the gills and the first dorsal fin, and stored frozen. A scalpel was used to remove the neural and haemal arches and soft tissue, leaving only the vertebral centra. Centra were then soaked in a solution of 5% sodium hypochlorite (bleach) for ~30 min to remove remaining tissue, then rinsed thoroughly under tap water, and placed in a drying oven at 60°C for 24 h. One of the five centra prepared from each individual was selected for ageing. A single 400–600-μm longitudinal section was taken through the focus of the centrum using a slow-speed saw with a diamond-tipped blade (Beuhler, Lake Bluff, IL, USA) (Cailliet and Goldman 2004). Centra <10 mm in diameter were cast in a clear polyester resin before sectioning because they were too small to fit in the vice of the saw. The vertebral section was fixed to a glass slide with Crystal Bond adhesive (SPI Supplies, West Chester, PA, USA).

Sectioned centra were examined under a dissecting microscope using transmitted light (Fig. 2). The age of an animal was determined by counting the pairs of opaque and translucent (hyper- and hypomineralised) growth bands deposited on the corpus calcareum (Cailliet and Goldman 2004). The birth mark was identifiable by a change of angle on the corpus calcareum. Because both species have seasonal reproductive cycles, it was possible to assign partial ages to all individuals by using a mean population birth date of 1 December (assigned on the basis of reproductive data below). Davenport and Stevens (1988) previously found that the first growth-band pair was formed on the vertebrae approximately a year after birth in *C. sorrah* and *C. tilstoni*. As such, the first growth increment was assumed to be 1 year for both species. Prior to ageing all centra, a random subsample of vertebrae was read by two readers to ensure that a consensus was reached regarding interpretation of the banding pattern, then one of the readers read all of the centra twice. Precision between and within readers was evaluated using Chang's (1982) method of the coefficient of variation (CV) and percentage agreement following the method of Goldman and Musick (2006). Bias between and within readers was evaluated statistically using Bowker's test of symmetry (Evans and Hoenig 1998).

An information-theoretic, multi-model inference (MMI) approach was taken to modelling growth (Burnham and Anderson 2001; Katsanevakis and Maravelias 2008). A set of three candidate models was chosen and fit to length-at-age data (Table 1). These consisted of a three-parameter version of the von Bertalanffy growth function (VB), a three parameter version of the Gompertz function (GOM) and a logistic growth curve (LOG). Each model represented an alternative hypothesis for growth and, in each case, asymptotic growth was assumed (Table 1). Models were fit using the method of non-linear least-squares in the statistical package R (R Development Core Team 2011). On the basis of examination of residual diagnostic plots, additive normal error structure was assumed for *C. sorrah* and multiplicative normal error structure assumed for *C. tilstoni*.

Table 1.   Set of deterministic models fit to length-at-age data

Models describe length, L, as function of time, t. Parameter β_1, common to all models, is asymptotic length (L_∞). All other parameters are not directly comparable

Model	Potential process and parameter description	Growth function
von Bertalanffy (VB)	Growth rate decreases linearly with increasing length: β_1 is L_∞ (mm), β_2 is L_0 (mm), β_3 is k (years^{-1}), the growth constant.	$L(t) = \beta_2 + (\beta_1 - \beta_2)(1 - \exp(-\beta_3 t))$
Gompertz (GOM)	Growth rate decreases exponentially with increasing length: β_1 is L_∞ (mm), β_2 is L_0 (mm), β_3 is k (years^{-1}), the growth constant.	$L(t) = \beta_2 \exp\left(\ln\left(\dfrac{\beta_2}{\beta_1}\right)(1 - \exp(-\beta_3 t))\right)$
Logistic (LOG)	There is a sigmoidal relationship between age and length: β_1 is L_∞ (mm), β_2 is the point of inflection (mm), β_3 (years^{-1}) is the growth constant.	$L(t) = \dfrac{\beta_1 \beta_2 \exp(\beta_3 t)}{\beta_1 + \beta_2 (\exp(\beta_3 t) - 1)}$

Performance of models relative to each other was evaluated using Akaike's information criteria (AIC). The best model was the one with the lowest AIC value, AIC_{min}. AIC differences were calculated as $\Delta_{AICi} = AIC_i - AIC_{min}$, and used to rank the support of the remaining models ($i = 1–3$) relative to the best model. Models with Δ_{AIC} of 0–2 had substantial support, whereas models with Δ_{AIC} of 4–7 had considerably less support. Models with Δ_{AIC} of >10 had essentially no support (Burnham and Anderson 2001). Akaike weights (w) were calculated as the weight of evidence in favour of a model being the best model in the set of candidate models (Burnham and Anderson 2001). Approximate 95% confidence and prediction intervals for the best-fit parameter estimates and population estimates were derived from 10 000 resampled datasets.

Age validation

Davenport and Stevens (1988) previously found evidence to suggest that growth-band pairs were formed annually on the vertebral centra of *C. sorrah* and *C. tilstoni*, by using oxytetra-cycline (OTC) chemical marking, size-mode analysis and tag–recapture data. However, upper age estimates in that study were not consistent with later results from a long-term tag–recapture study (Stevens *et al.* 2000). To validate the frequency of growth-band formation in older animals, we undertook a mark, tag and recapture study in the waters of Cleveland Bay (19°12′S, 146°54′E) near Townsville. Sharks were captured using multi-hook research lines and using gear and methods aimed at catching larger individuals in the population. The lengths and sex of captured sharks were recorded and individuals were then tagged externally on the first dorsal fin with Rototags or Jumbotags (Dalton, Henley-on-Thames, Oxfordshire, UK). The vertebral centra of captured sharks were marked using the fluorescent dye calcein ($C_{30}H_{26}N_2O_{13}$). Calcein is one of several fluorescent dyes that have successfully been used to mark elasmobranch verte-brae (Officer *et al.* 1997). Calcein was chosen over other dyes such as OTC because it forms a mark that can be seen under a standard stereo microscope without the need for ultraviolet light. A pH-buffered, isotonic solution of 12.5 mg mL^{-1} calcein was injected intramuscularly behind the first dorsal fin at a dosage of 5 mg kg^{-1} (Gelsleichter *et al.* 1997; McAuley *et al.* 2006).

Reproductive biology

Quantitative analysis of reproductive biology closely followed the methods and format outlined in Walker (2005), which has been adopted in several studies, e.g. Walker (2007) and Trinnie *et al.* (2009).

Length–weight relationship

The relationship between total body mass, W, and STL, l, was determined using a power curve $W(l) = \beta_1 l^{\beta_2}$, where β_1 and β_2 are fitted parameters estimated using linear regression analysis $\ln(W(l)) = \ln(\beta_1) + \beta_2 \ln(l)$. Sex and the interaction of sex and STL were included as a factor in the linear model to establish whether there was a difference in weight-at-length between males and females. The model that included all parameters was fitted and then the best model obtained through stepwise back-ward elimination of non-significant parameters.

Maturity and maternity analysis

A single index was adopted for staging maturity in each sex, based on the descriptions of Walker (2005) (Table 2). Maturity stage of males was based on clasper condition (C = 1–3), and maturity stage of females was based on uterus condition (U = 1–6). Maturity-stage data was converted to binary form (immature = 0, mature = 1) for statistical analysis. Population estimates of length-at-maturity were established separately for males and females, using a logistic regression model (Roa *et al.* 1999), reformulated by Walker (2005) to be more biologically meaningful as

$$P(l) = P_{MAX} \cdot \left(1 + e^{-\ln(19)\left(\frac{l - \beta_1}{\beta_2 - \beta_1}\right)}\right)^{-1},$$

where $P(l)$ is the proportion of the population mature at STL, l, where β_1 and β_2 are fitted parameters corresponding to l_{50} and l_{95} respectively, and P_{MAX} is the asymptote. A generalised linear model (GLM) with a binomial error structure and logit-link function was used to estimate parameters β_1 and β_2. The overall significance of fitted models was tested by comparing the amount of deviance explained relative to the null model by using chi-squared tests.

Population estimates of age-at-maturity and length- and age-at-maternity were also computed using this method. A female was defined as in maternal condition if it would have given birth during December of the year it was caught. This included all females with U = 4–6. Female *C. sorrah* individuals for which the largest follicle diameter (LFD) in the ovary was >10 mm between January and March were also classed as in maternal condition, because they would have become pregnant and given

Table 2. Indices used for staging reproductive condition, adapted from Walker (2005)
Criteria for classing mature and immature condition

Organ	Index	Description	Maturity assumption
Female			
Uterus	U = 1	Uniformly thin tubular structure	Immature
	U = 2	Thin, tubular structure, partly enlarged posteriorly	Immature
	U = 3	Uniformly enlarged tubular structure	Mature
	U = 4	*In utero* eggs present without macroscopically visible embryos present	Mature
	U = 5	*In utero* embryos macroscopically visible	Mature
	U = 6	Enlarged tubular structure distended	Mature
Male			
Clasper	C = 1	Pliable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

birth that year. Similarly, female *C. tilstoni* individuals with LFD >15 mm between January and March were also classed as in maternal condition.

Fecundity and embryonic sex ratio

The relationship between fecundity, F, and maternal STL, l, was established using a linear regression model $F(l) = \beta_1 + \beta_2 l$, where β_1 and β_2 are fitted parameters. A chi-squared test was used to test whether the sex ratio of all *in utero* embryos was significantly different from $1:1$.

Timing of reproduction and embryonic growth analysis

The timing of the ovarian cycle was determined by examining the ovary of mature females (U = 3–6 animals) and measuring the diameter of the largest follicles (LFD) in millimetres. LFD was then plotted against month. To examine patterns of growth in embryos, the mean STL of embryos from pregnant females (U = 4 and 5 animals) was modelled as a function of age. Where embryos were not yet macroscopically visible (U = 4 animals), the STL of embryos was taken as 0. The age of developing embryos was estimated from the time since conception, on the basis of examination of U = 3 and 4 animals between January and April. Growth was clearly not constant throughout the gestation period and appeared to be influenced by temperature. As such, the Hoenig and Hanumara variation of the von Bertalanffy growth function, which incorporates seasonal fluctuations in growth, was used to model embryonic growth (Pawlak and Hanumara 1991), as follows:

$$L(t) = \beta_1 - \beta_1 e^X, X = -\beta_2(t - \beta_3) - \frac{\beta_2\beta_4}{2\pi}\sin 2\pi(t - \beta_5) + \frac{\beta_2\beta_4}{2\pi}\sin 2\pi(\beta_3 - \beta_5),$$

where L is STL in mm, t is time in years, β_1 is asymptotic length (L_∞) in mm, β_2 is the Brody growth coefficient K in years^{-1}, β_3 is t_0 in years, β_4 is the magnitude of oscillations in growth, and β_5 is the age at which zero growth begins. Mean daily temperatures for the 10-year period before the study were obtained from the Townsville region (www.bom.gov.au/, accessed 1 February 2012). Length-at-birth was established on the basis of the length

of the largest *in utero* embryos or from measurement of neonates, which were identified by the presence of an unhealed umbilical scar in their first few weeks after birth. The relationship between total body mass (kg) and STL for *in utero* embryos was established as described for post-natal animals above.

Results

Sample collection and species identification

Samples were obtained from a total of 659 *C. sorrah* individuals, consisting of 347 males, 478–1139 mm, and 312 females, 505–1310 mm (Fig. 3a). The relationships among STL, fork length (FL) and pre-caudal length (PCL) for a subsample of individuals for sexes combined were

$$STL = 105.5 + 1.135FL\left(r^2 = 0.97, P < 0.01, \text{d.f.} = 488\right), \text{and}$$

$$STL = 91.93 + 1.275PCL\left(r^2 = 0.98, P < 0.01, \text{d.f.} = 239\right).$$

Samples were obtained from a total of 1049 'unidentified' blacktip sharks, consisting of both *C. tilstoni* and *C. limbatus*. Using the identification protocol in Table S1 of the Supplementary Material for this paper, a total of 512 individuals was identified as *C. tilstoni*, consisting of 256 males, 555–1560 mm, and 256 females 570–1800 mm (Fig. 3b). The relationships among STL, FL and PCL for a subsample of individuals for sexes combined were

$$STL = 35.03 + 1.214FL\left(r^2 = 0.99, P < 0.01, \text{d.f.} = 429\right), \text{and}$$

$$STL = 22.79 + 1.359PCL\left(r^2 = 0.99, P < 0.01, \text{d.f.} = 275\right).$$

Age validation

In all, 134 *C. sorrah* individuals were marked with calcein and released in Cleveland Bay, and eight were recaptured between 188 and 1059 days at liberty (Table 3). The mean lengths of marked males and females were 1010 mm and 1145 mm, respectively, and most individuals were likely to have been adults. Recaptured individuals included five mature, pregnant females (U = 5), one mature non-pregnant female (U = 3) and two mature males (C = 3). Uptake of calcein on the vertebrae was poor, and in five of the recaptured individuals (four U = 5 females and one C = 3 male), no mark was observed. In the
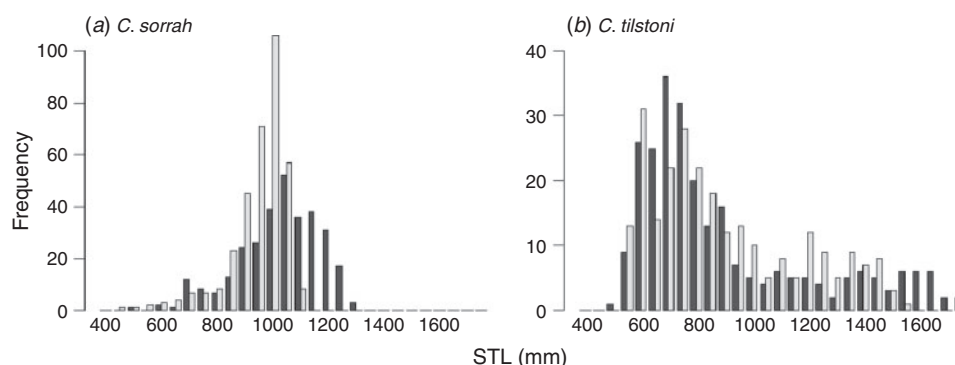
Fig. 3. Length–frequency distributions of male (light grey) and female (dark grey) samples used in the present study for (*a*) *Carcharhinus sorrah* and (*b*) *C. tilstoni*.

Table 3. Recapture details of eight calcein marked *Carcharhinus sorrah* and one *C. tilstoni*
STL, stretched total length

Species	Date of release	STL$_{Release}$ (mm)	Date recaptured	STL$_{Recap}$ (mm)	Days at liberty	Growth (mm)	Band-pairs visible after mark	Sex	Maturity stage
C. sorrah	14 May 2008	1260	18 November 2008	1245	188	−15	No mark	Female	U = 5
	18 April 2008	1240	26 November 2008	1224	222	−16	No mark	Female	U = 5
	27 May 2008	1160	21 May 2009	1157	359	−3	Unclear	Female	U = 5
	28 October 2008	1050	26 June 2009	1054	241	4	1	Female	U = 3
	4 April 2008	1110	30 June 2009	1039	452	−71	No mark	Female	U = 5
	9 September 2009	1240	22 September 2010	1264	378	24	No mark	Female	U = 5
	4 November 2009	1001	20 July 2011	1025	623	24	No mark	Male	C = 3
	7 January 2009	960	2 December 2011	1025	1059	65	0	Male	C = 3
C. tilstoni	15 December 2008	1460	27 October 2011	1460	1046	0	0	Male	C = 3

U = 3 female at liberty for ~8 months, a translucent band was visible between the calcein mark and the margin of the vertebral centra. In the U = 5 female, there was a small amount of space visible between the calcein mark and the margin; however, it was unclear whether a band had formed. In the C = 3 male at liberty for 3 years, the calcein mark was faintly visible; however, it was on the margin of the centra and no bands were visible after it (Fig. 2*d*). In all, 98 unidentified blacktips (mean length 1224 mm) were marked with calcein and released, although only a single adult male *C. tilstoni* (C = 3) was recaptured after 1046 days at liberty (Table 3). In this individual, the calcein mark was faintly visible; however, it was also on the margin of the centra and no growth bands were visible after it (Fig. 2*c*).

Although previous study of these species suggested that growth-band pairs were formed annually on the centra (Davenport and Stevens 1988), we were unable to validate that this pattern continues throughout life. Furthermore, the recapture of two individuals at liberty for 3 years without any visible bands after the calcein mark suggested that bands either do not form or become unresolvable in older animals. We proceeded with the growth analysis under the assumption that the band pairs visible did provide a record of the length-at-age in younger individuals, although that they may not provide an accurate record of age as growth begins to slow. The implications of this are treated further in the discussion.

Precision and bias in age estimation

Mean inter-reader percent agreement (PA) and PA ± 1 year between the first and second read pooled into 50 mm length groupings was 46% and 75% for *C. sorrah*, whereas Chang's coefficient of variation (CV) was 27.50%. Although precision was low, there was no significant difference between the readers (Bowker's test of symmetry: $\chi^2 = 15$, d.f. = 10, $P < 0.13$) (Fig. S1*a*, available as Supplementary Material for this paper). For *C. tilstoni*, mean inter-reader PA and PA ± 1 year between the first and second read pooled into 100-mm-length groupings was 32% and 72%, whereas the CV was 34.84%. There was a highly significantly difference between the readers (Bowker's test of symmetry: $\chi^2 = 63.42$, d.f. = 22, $P < 0.01$); with Reader 2 ageing younger animals slightly older than Reader 1 did (Fig. S1*b*, available as Supplementary Material for this paper). For *C. sorrah*, mean intra-reader PA, PA ± 1 year and CV were 68%, 79% and 14.77%, respectively. There was a highly significant difference between the first and second reads (Bowker's test of symmetry: $\chi^2 = 38.75$, d.f. = 19, $P < 0.01$); individuals up to 5 years old were aged consistently between the reads, but there was systematic over-ageing of those individuals older than 5 years (Fig. S1*c*, available as Supplementary Material for this paper). For *C. tilstoni*, mean PA, PA ± 1 year and CV were 60%, 72% and 22.02%, respectively. Again, there was a highly significant difference between the first and second read (Bowker's
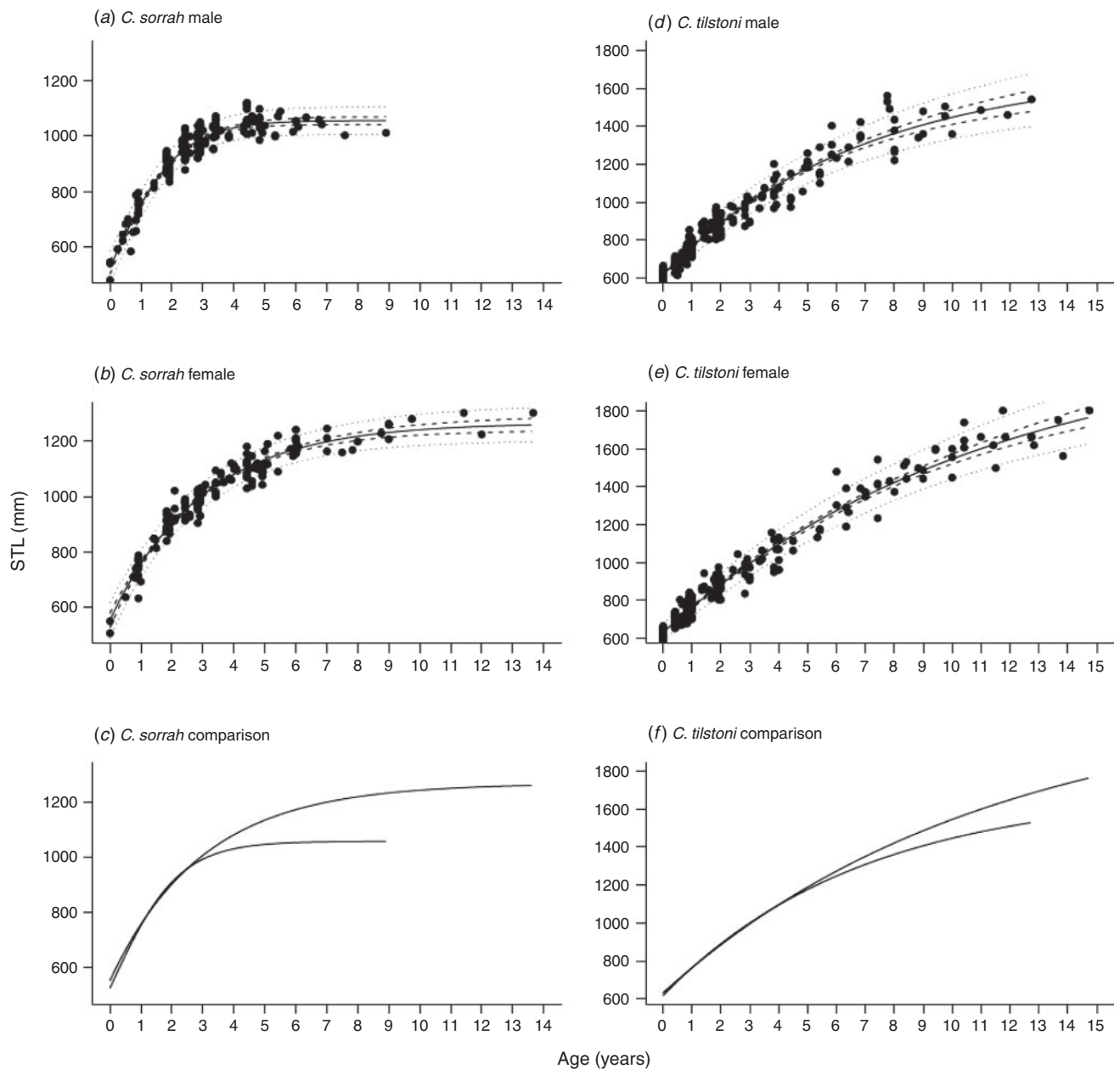
Fig. 4. Length-at-age of (*a–c*) *Carcharhinus sorrah* and (*d–f*) *C. tilstoni* as determined from vertebral growth analysis. Plots are mean stretched total length (STL) at age (—), with 95% confidence intervals (– – –), 95% prediction intervals (— -) and raw data (●), where mean values were computed using the preferred growth model selected from a candidate set of three on the basis of the values of Akaike information criterion. A comparison of male and female growth models for each species is presented in (*c*) and (*f*).

test of symmetry: $\chi^2 = 63.32$, d.f. $= 26$, $P < 0.01$); individuals up to 6 years old were aged consistently between the reads, but there was systematic under-ageing of those individuals older than 6 years (Fig. S1*d*, available as Supplementary Material for this paper). Although there was a statistically significant bias between several of the reads, in all instances the magnitude of this bias was relatively low. For both species, it was felt that an acceptable and repeatable interpretation of the vertebrae had been made and the second read in the intra-specific comparison was used as the final age.

Vertebral growth analysis

Vertebrae centra were obtained and read from 297 *C. sorrah* individuals, consisting of 153 males, 478–1120 mm, and 144 females, 505–1301 mm. The youngest male and female were zero (both had unhealed umbilical scars indicating recent birth) and were 478 and 505 mm. The oldest male was 8.9 years old and 1009 mm and the oldest female was 13.7 years old and 1310 mm. Both sexes of *C. sorrah* displayed strongly asymptotic growth, with growth rates fast during the first few years of life, and rapidly slowing thereafter (Fig. 4*a–c*, Table 4),

especially in males. The logistic model was the most parsimonious for males in the multi-model analysis of growth (Table 4, $w = 68.50\%$). The Gompertz model was also supported by the data to a lesser extent (Table 4, $\Delta_{AIC} = 1.66$, $w = 29.81\%$), whereas the von Bertalanffy had little support. Growth to asymptotic size occurred at a slower rate for females; the von Bertalanffy model was by far the best, given the data (Table 4, $w = 98.97\%$), and there was little support for either of the other two models (Table 4, $\Delta_{AIC} > 2$). Male and female growth was similar in individuals younger than 2 years of age and the slight difference between growth curves was probably due to a deficiency of the data, as few very small females (<650 mm) were sampled compared with males. At approximately 2 years of age, growth became sexually dimorphic, with male growth slowing much more rapidly than female growth.

Vertebrae centra were obtained and read from 449 *C. tilstoni* individuals, consisting of 212 males, 568–1560 mm, and 237 females, 533–1800 mm. The youngest male and female were zero (both had unhealed umbilical scars), and were 568 mm and 533 mm. The oldest male was 12.8 years and 1540 mm and the oldest female was 14.8 years and 1800 mm. Length-at-age-data fit to the candidate models showed strong support for the von Bertalanffy model (Fig. 4*d–f*, Table 4), which was convincingly best for both sexes (Table 4, $w = 97.07$–99.63%). There was little support for either the Gompertz model (Table 4, $w = 0.37$–2.91, $\Delta_{AIC} = 7.01$–11.17), or the logistic model (Table 4, $\Delta_{AIC} = 17.3$–25.13). Growth patterns between the sexes were similar until approximately the age of 5 years, at which point male growth slowed at a faster rate than did female growth. A pronounced asymptote in growth was not observed in either sex and asymptotic lengths for the von Bertalanffy model were much longer than the largest individuals observed.

Length–weight relationship

Weight-at-length data were available for 192 *C. sorrah* individuals. The largest male weighed was 8.10 kg (1139 mm), and the largest female was 14.45 kg (1260 mm). Although there was a large difference in the maximum weight between males and females, neither sex, nor the sex–length interaction was significant and removal of these terms did not result in a significantly worse fit

of the model to the data ($F = 1.608$, d.f. $= -2$ and 190, $P = 0.203$). Stepwise backward elimination of these parameters resulted in a single slope and intercept for both sexes (Fig. 5*a*). Weight-at-length data were available for 194 *C. tilstoni* individuals. The
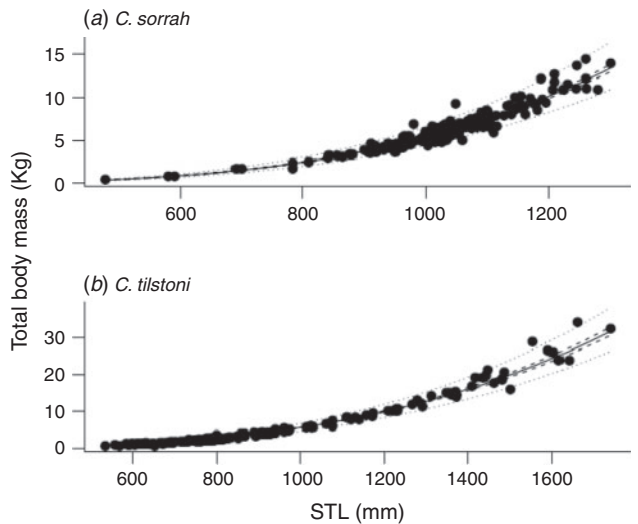

Fig. 5. Relationships between total body mass and stretched total length of sharks. Plots are mean total body mass against stretched total length (STL) (—), with 95% confidence intervals (– – –), 95% prediction intervals (— -) and raw data (•) for (*a*) *Carcharhinus sorrah* and (*b*) *C. tilstoni*. Values of parameters and statistical quantities from linear regression analysis used to derive the equation $W(1) = \beta_1 l^{\beta_2}$ re given in the following tabulation:

Species	β_1 (s.e. range) $\times 10^{-10}$	β_2 (s.e.)	n	r^2	rmse	Significance
C. sorrah	2.131 (1.439–3.156)	3.467 (0.0567)	192	0.951	0.102	***
C. tilstoni	24.57 (20.87–28.93)	3.120 (0.024)	194	0.988	0.070	***

where W is body mass, l is STL, β_1 and β_2 are parameters, n is the number of individuals, r^2 is square of correlation coefficient and rmse is root mean square error for the regression $log_e = (W(l)) = log_e(\beta_1) + \beta_2 l$. *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

Table 4. Comparison of three growth models fit to length-at-age data for two species of carcharhinid shark
The best model (in **bold**) was the one with the lowest value for Akaike's information criterion (AIC). The relative support of other models can be gauged on the basis of Akaike differences (Δ_{AIC}) and Akaike weights (w). K is the number of estimated parameters, plus one for the error term $N(0, \sigma^2)$, which was assumed to be additive for *Carcharhinus sorrah* and multiplicative for *C. tilstoni*. Best-fit estimates are given for parameters β_1–β_3 (with 95% CI) as described in Table 1

Species	Sex	Model	n	K	AIC	Δ_{AIC}	w (%)	σ^2	β_1		β_2		β_3	
C. sorrah	M	VB	153	4	1542.85	7.41	1.68	36.85	1074	(1057–1092)	494.8	(465.8–524.8)	0.6315	(0.5645–0.7025)
		GOM	153	4	1537.10	1.66	29.81	36.16	1063	(1049–1079)	510.4	(483.4–536.7)	0.7746	(0.6991–0.8520)
		LOG	**153**	**4**	**1535.44**	**0.00**	**68.50**	**35.97**	**1056**	**(1043–1070)**	**525.3**	**(500.9–548.5)**	**0.9160**	**(0.8350–1.003)**
	F	**VB**	**144**	**4**	**1455.98**	**0.00**	**98.97**	**37.31**	**1266**	**(1241–1295)**	**552.9**	**(523.6–579.6)**	**0.3360**	**(0.3000–0.3739)**
		GOM	144	4	1465.13	9.15	1.02	38.52	1247	(1224–1273)	580.9	(554.9–605.1)	0.4221	(0.3810–0.4663)
		LOG	144	4	1475.35	19.37	0.01	39.91	1234	(1212–1257)	602.6	(579.2–625.3)	0.5078	(0.4606–0.5580)
C. tilstoni	M	**VB**	**212**	**4**	**−621.43**	**0.00**	**97.07**	**5.523E−02**	**1698**	**(1588–1845)**	**616.3**	**(605.6–627.0)**	**0.1459**	**(0.1207–0.1721)**
		GOM	212	4	−614.41	7.01	2.91	5.615E−02	1548	(1479–1632)	622.7	(612.2–633.1)	0.2462	(0.2187–0.2748)
		LOG	212	4	−604.13	17.30	0.02	5.753E−02	1478	(1424–1541)	629.1	(618.9–639.4)	0.3479	(0.3169–0.3780)
	F	**VB**	**237**	**4**	**−702.36**	**0.00**	**99.63**	**5.440E−02**	**2182**	**(2005–2432)**	**631.1**	**(622.2–639.9)**	**0.0892**	**(0.0724–0.1064)**
		GOM	237	4	−691.19	11.17	0.37	5.571E−02	1860	(1769–1972)	638.2	(629.8–646.6)	0.1775	(0.1586–0.1964)
		LOG	237	4	−677.23	25.13	0.00	5.737E−02	1739	(1675–1812)	644.8	(636.2–653.0)	0.2676	(0.2472–0.2892)

largest male weighed was 20.85 kg (1485 mm), and the largest female was 34.15 kg (1660 mm). Like for *C. sorrah*, there was a weak effect of sex on the length–weight relationship and neither sex nor the sex–length interaction was significant. Stepwise backward removal of these terms did not significantly decrease the explanatory power of the model ($F = 2.369$, d.f. $= -2$ and 192, $P = 0.096$) and, as such, the final model contained a single intercept and slope for both sexes (Fig. 5*b*).

Maturity and maternity ogives

Male and female *C. sorrah* matured at similar lengths and ages. Maximum-likelihood estimates of length-at-50% maturity (l_{50}) and age-at-50% maturity (a_{50}) predicted by the binomial logit GLM were 929 mm and 2.4 years, respectively, for males (Fig. 6*a, d*, Table 5). Female l_{50} and a_{50} were 951 mm and 2.3 years, respectively (Fig. 6*b, e*, Table 5). All larger females in the population were in maternal condition, indicating that females
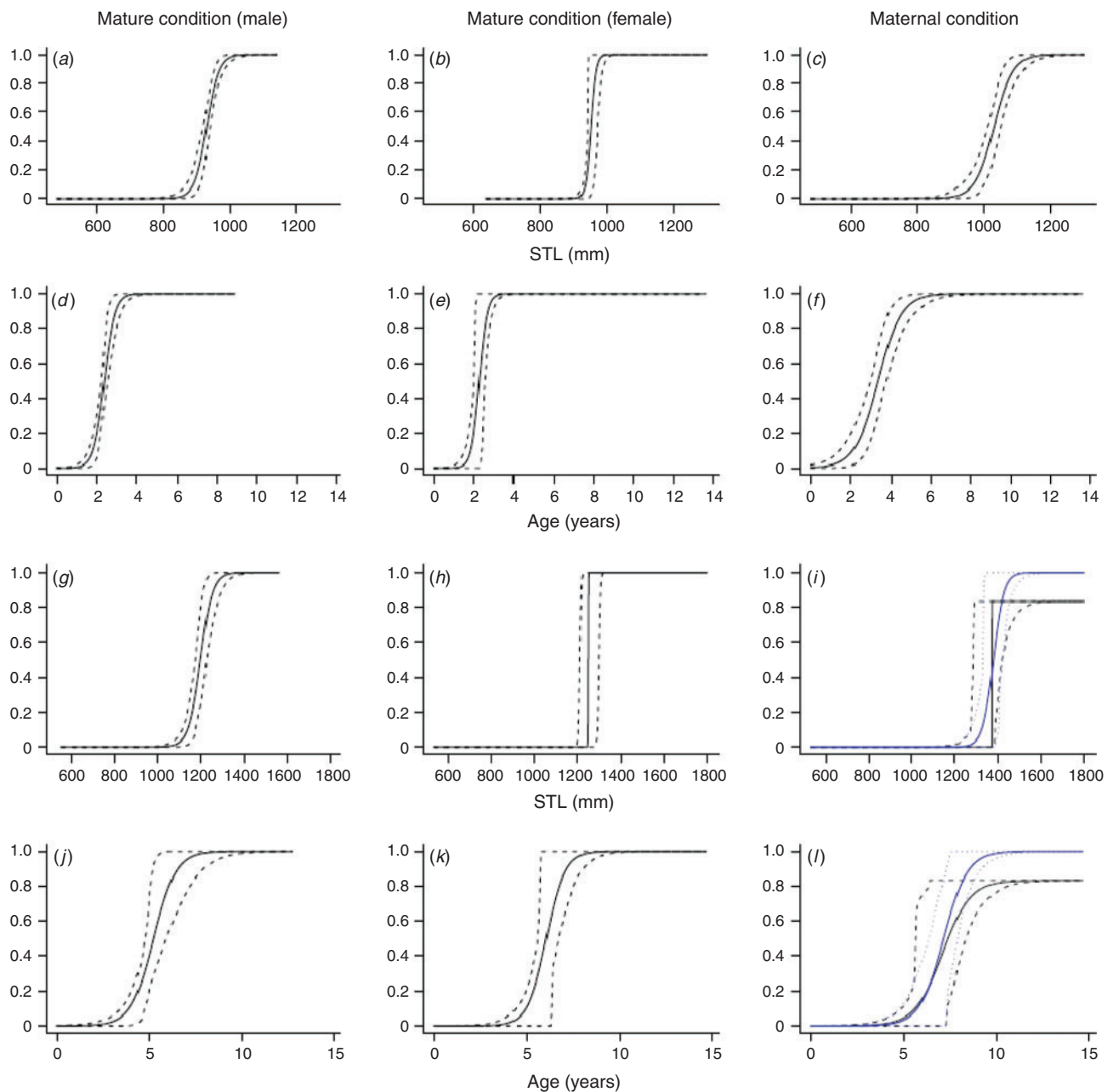

Fig. 6. Length- and age-at-maturity and -maternity for (*a–f*) *Carcharhinus sorrah* and (*g–l*) *C. tilstoni*. Proportion of both sexes mature or females in maternal condition against stretched total length (STL) (—), with 95% confidence intervals (—). Values of parameters and statistical quantities for the equations $P(l) = P_{MAX}(1 + \exp(-\ln(19)((l - \beta_1)/(\beta_2 - \beta_1)))^{-1}$ and $P(a) = P_{MAX}(1 + \exp(-\ln(19)((a - \beta_1)/(\beta_2 - \beta_1)))^{-1}$ are given in Table 5. *l* is STL (mm) and *a* is age (years), and *P* is the proportion of both sexes mature or females maternal at STL or age, P_{MAX} is the maximum proportion in mature or maternal condition, β_1 and β_2 are parameters corresponding to l_{50} and l_{95} or a_{50} and a_{95} respectively.

reproduced every year (see Table S2, available as Supplementary Material for this paper). As such, computation of maternity ogives was straightforward and the asymptote (P_{MAX}) was fixed at one. Maternity ogives were shifted to the right of maturity ogives and females appeared to start reproducing in the year after they matured; length-at-50%-maternity ($l_{50\ Maternity}$) was 1029 mm (Fig. 6*c*, Table 5) and age-at-50%-maternity ($a_{50\ Maternity}$) was 3.4 years (Fig. 6*f*, Table 5). All analyses were highly significant when tested against the null model.

Female *C. tilstoni* matured at a larger length and older age than did the male; l_{50} and a_{50} were 1199 mm and 5.2 years, respectively, in males (Fig. 6*g, j*, Table 5) and 1247 mm and 6.1 years in females (Fig. 6*h, k*, Table 5). Although females reached maturity at ~6 years of age, like *C. sorrah*, most had not begun reproducing by this age. Analysis and interpretation of maternity ogives for *C. tilstoni* were more complicated because not all larger females in the population were in maternal condition (see Table S3, available as Supplementary Material for this paper). Although the majority of females did appear to reproduce annually, 16.7% of females >1400 mm (5 of 30 animals) were recorded as mature (U = 3) but in a non-maternal condition (see Table S3). When all females in the population do not reproduce annually, using an asymptote of one in the maturity ogive is inappropriate (Walker 2005). In the absence of more detailed knowledge about reproductive frequency, the asymptote for the maternity analysis was fixed at 0.833. The reason why all females were not in maternal condition was not known; however, it was hypothesised that it could be related to either hybridisation or misidentification with the sympatric *C. limbatus*. In the case of misidentification, fixing the asymptote at a lower value could give an overly cautious estimate of the number of births in the population. Therefore, a second maternal analysis was carried out, with four 'outlying' U = 3 females >1500 mm removed from the analysis. In this analysis, P_{MAX} was fixed at one. Both sets of maternity ogives were similar in shape and shifted to the right of maturity ogives; $l_{50\ Maternity}$ was

1370–1378 mm and $a_{50\ Maternity}$ was 7.1–7.2 years (Fig. 6*i, l*, Table 5). This indicated that females typically start reproducing a year after they mature. All analyses were highly significant when tested against the null model.

Fecundity and sex ratio

Macroscopically visible *in utero* embryos were examined from 71 pregnant (U = 5) *C. sorrah* individuals, 1010–1301 mm STL. The litter size of U = 5 animals ranged from one to six, with a mean (±s.d.) of 3.042 (±0.985). The only U = 4 pregnant female examined had three *in utero* eggs. There was a significant linear relationship between increasing maternal STL and fecundity (Fig. 7*a*), such that the largest individuals were the most fecund. Of 161 embryos from 52 litters where the sex could be established for all individuals, 75 were females and 86 were males. The sex ratio of embryos was not significantly different from 1 : 1 ($\chi^2 = 0.7516$, d.f. = 1, $P = 0.386$). Macroscopically visible *in utero* embryos were examined from 24 pregnant *C. tilstoni* individuals, 1410–1800 mm. The litter size of U = 5 animals ranged from one to seven, with a mean (±s.d.) of 3.667 (±1.341). No U = 4 pregnant females were examined. Like for *C. sorrah*, there was a significant linear relationship between increasing maternal STL and fecundity (Fig. 7*b*). Among 49 retained embryos, 29 were male and 20 were female. Although there was a strong bias towards males in this sample, it was not statistically significant at the 0.05 level ($\chi^2 = 1.6351$, d.f. = 1, $P = 0.1985$). The mean (±s.d.) proportion of females in 13 litters was 0.39 ± 0.27 and ranged from 0 to 0.75

Timing of reproduction and embryonic growth analysis

The timing and periodicity of the ovarian cycle of *C. sorrah* was established from examining the ovarian follicles of 75 mature females. Females were examined during 9 months of the year and consisted of 10 U = 3 animals, one U = 4 animal, 61 U = 5 animals and three U = 6 animals (Fig. 8*a*). The LFD of mature

Table 5.   Values of parameters and statistical quantities for maturity and maternity ogives in Fig. 6

P_{MAX} is the maximum proportion in mature or maternal condition, β_1 and β_2 are parameters corresponding to l_{50} and l_{95} or a_{50} and a_{95}, respectively, n is the number of individuals in mature or maternal condition, N is the total number of individuals examined, ML is maximum likelihood. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Species	Fig. 6	Sex	Analysis	P_{MAX}	β_1 (CI)	β_2 (CI)	n	N	ML	Significance
C. sorrah	a	Male	STL-at-maturity	1	929.2 (918.6, 939.0)	982.7 (960.2, 1002)	244	312	−43.08	***
	b	Female	STL-at-maturity	1	950.9 (939.8, 967.1)	973.4 (942.1, 993.2)	96	117	−3.783	***
	c		STL-at-maternity	1	1029 (1012, 1048)	1112 (1066, 1152)	78	117	−25.71	***
	d	Male	Age-at-maturity	1	2.367 (2.227, 2.536)	3.129 (2.655, 3.540)	83	126	−27.59	***
	e	Female	Age-at-maturity	1	2.267 (2.001, 2.526)	2.836 (2.101, 3.133)	70	85	−6.815	***
	f		Age-at-maternity	1	3.355 (2.911, 3.789)	5.068 (4.185, 5.811)	57	85	−23.80	***
C. tilstoni	g	Male	STL-at-maturity	1	1199 (1175, 1227)	1280 (1218, 1324)	46	287	−13.50	***
	h	Female	STL-at-maturity	1	1247 (1207, 1300)	1250 (1215, 1311)	36	119	−1.225E-10	***
	i		STL-at-maternity	0.833	1370.026 (1277, 1415)	1370.031 (1280, 1549)	27	119	−13.88	***
	i		STL-at-maternity[A]	1	1378 (1331, 1423)	1450 (1337, 1505)	27	115	−5.05	***
	j	Male	Age-at-maturity	1	5.215 (4.769, 6.022)	6.980 (5.328, 8.669)	27	153	−16.99	***
	k	Female	Age-at-maturity	1	6.065 (5.536, 6785)	7.534 (5.718, 8.590)	35	118	−6.92	***
	l		Age-at-maternity	0.833	7.102 (5.851, 8.132)	9.293 (6.631, 10.43)	26	118	−19.31	***
	l		Age-at-maternity[A]	1	7.158 (6.333, 7.915)	9.053 (7.445, 9.846)	26	114	−9.55	***

[A]P_{MAX} was fixed at both 0.833 and 1 in maternity ogives for *C. tilstoni* because there was some evidence to suggest that not all females reproduced every year.

individuals was 3–30 mm. Although *C. sorrah* has an annual reproductive cycle, follicle development did not occur synchronously with the gestation period. As such, ovulation did not coincide with parturition. Between May and October follicle growth was negligible, increasing from a mean of 5 mm to
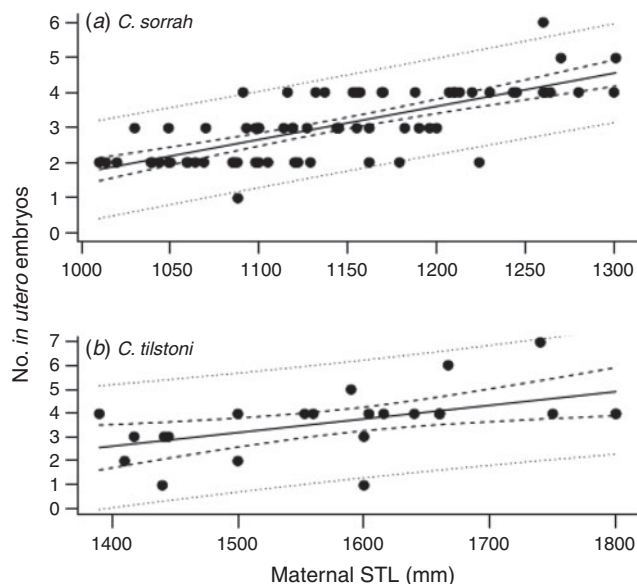

Fig. 7. Number of *in utero* embryos against maternal stretched total length (STL). Plots are mean number of embryos against STL (—), with 95% confidence intervals (– – –), 95% prediction intervals (— -) and raw data (●) for (*a*) *Carcharhinus sorrah* and (*b*) *C. tilstoni*. Values of parameters and statistical quantities for the linear regression $F(l) = \beta_1 + \beta_2 l$ are given in the following tabulation:

Species	β_1 (s.e. range)	β_2 (s.e.) $\times 10^{-3}$	n	r^2	rmse	Significance
C. sorrah	−7.751 (−8.986 to −6.515)	9.463 (8.383–10.54)	71	0.520	0.682	***
C. tilstoni	−5.408 (−8.564 to −2.253)	5.725 (3.740–7.710)	24	0.241	1.168	**

where l is STL (mm), and F is fecundity, β_1 and β_2 are parameters, n is the number of individuals, r^2 is square of correlation coefficient and rmse is root mean square error. *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

8 mm. Follicle growth increased after October; however, the mean LFD of three U = 6 females examined in December was still only 10 mm. This is ~30% of the diameter of the largest post-ovulatory follicle measured in a U = 5 female in April. Although no mature females were examined between January and March, it is evident that the majority of follicle growth and yolk accumulation occurs during this unobserved period. On the basis of the examination of U = 5 females in early April (Day 92), it appears that, for the majority of the population, ovulation occurs during mid-March and that the diameter of mature follicles is ~25–30 mm (Fig. 8*a*). A single U = 4 female examined during early April (Day 100) appeared to be an outlier.

The timing and periodicity of the ovarian cycle of *C. tilstoni* was difficult to infer because follicles were measured in only 21 mature females from 5 months of the year. In total, five U = 3 females, 13 U = 5 females and three U = 6 females were examined (Fig. 8*b*). The ovarian cycle in *C. tilstoni* appears to commence earlier than in *C. sorrah*; by late November (Days 325–335), the mean LFD of seven females (including two U = 6 females) was 17 mm, being ~60% of the diameter of the largest pre-ovulatory follicle measured. Follicles had begun accumulating yolk in November, but were not mature, indicating that parturition and ovulation are not synchronous. On the basis of the examination of a U = 3 female in mid-March (Day = 71), with pre-ovulatory follicles of 30-mm-diameter, it seems likely that ovulation occurs around this time. This was further supported by the examination of several U = 5 females in early April (Days 91–94). In four of the five females >1400 mm that were in non-maternal condition (see Table S3), the ovary was not examined; so, no inferences could be made on their stage of ovarian development. The only large non-maternal female where the ovary was examined was a 1510-mm U = 3 individual caught in March, with a LFD of 12 mm.

The timing and period of pregnancy of *C. sorrah* was inferred from 66 U = 5 females, two U = 6 females and three neonates with unhealed umbilical scars. On the basis of the assumption of mid-March ovulation (15 March, Day 75) and the examination of U = 6 females and neonates in late November to early January (Days 335, 348, 354 and 8), a period of pregnancy of ~260–298 days, or 9–10 months, is suggested. Embryonic growth did not occur evenly throughout pregnancy and appeared to be influenced by seasonal fluctuations in temperature. This process was modelled by the Hoenig and Hanumara version of the von
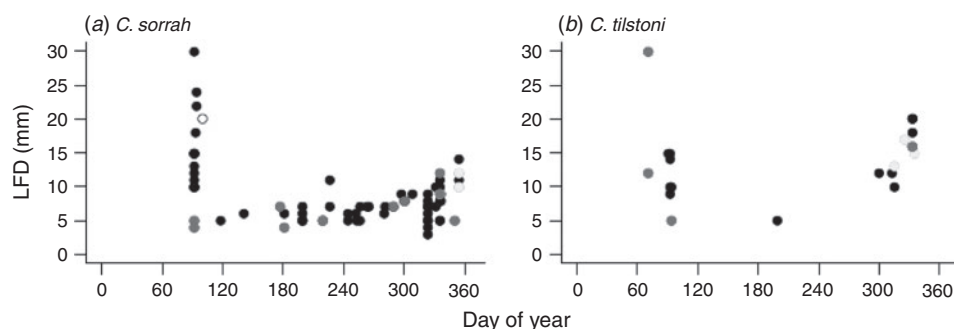

Fig. 8. Largest follicle diameter (LFD) against day of year for (*a*) *Carcharhinus sorrah* and (*b*) *C. tilstoni*. Plots are raw data for each of the four adult female uterus stages, as follows: U = 3 (●), U = 4 (○), U = 5 (●) and U = 6 (●).

Bertalanffy growth model fit to the embryo length-at-age data (Fig. 9a). Embryonic growth rate was rapid at the beginning of the gestation period, but slowed during winter months (July–September) (Fig. 9c). Embryos grew most slowly during August, approximately a month after the lowest daily temperatures, and growth rates increased with rising temperature until parturition. The largest and heaviest embryos measured in late November (Day 335) were 524 mm and 0.689 kg (Fig. S2a). The mean (±s.d.) length of five neonates with unhealed umbilical scars was 523.6 (±31.0) mm. All neonates were collected in shallow (<2 m) coastal areas, suggesting that this species gives birth in coastal nursery areas.

The timing and length of the period of pregnancy for *C. tilstoni* was inferred from 24 U = 5 females, three U = 6 females and 58 neonates. Three U = 6 females were captured on Days 315, 325 and 335, whereas 44 neonates with unhealed umbilical scars were captured between Day 305 (late October) and Day 39 (February). The majority of neonates, however, were caught during Days 343–353 (early December). Although

some individuals gave birth as early as October or as late as February, reproduction was highly synchronous at the population level; within a given year, most females appeared to give birth within a small period of time (early December in the present study). Assuming that ovulation occurs mid-March (15 March, Day 75), this suggests that *C. tilstoni* has a period of pregnancy of ~268–278 days, or ~9 months (Fig. 9b). Like for *C. sorrah*, embryonic growth rate was influenced by seasonal fluctuations in temperature (Fig. 9c). Given the close association of embryonic growth rates with temperature in both of these species, the exact timing and length of reproduction in a given year may be affected by the conditions in that year. Full-term embryos from two U = 5 females (caught on Day 333) were between 578 and 644 mm and 1.25 and 1.55 kg (Fig. S2b). The length of 58 neonates was 533–663 mm, with a mean (±s.d.) of 617.1 (±24.0) mm. The weight of 29 neonates was 0.872–1.8 kg with a mean (±s.d.) of 1.309 (±0.198) kg. Neonates were exclusively caught in shallow coastal waters, suggesting that also this species gives birth in coastal nurseries.
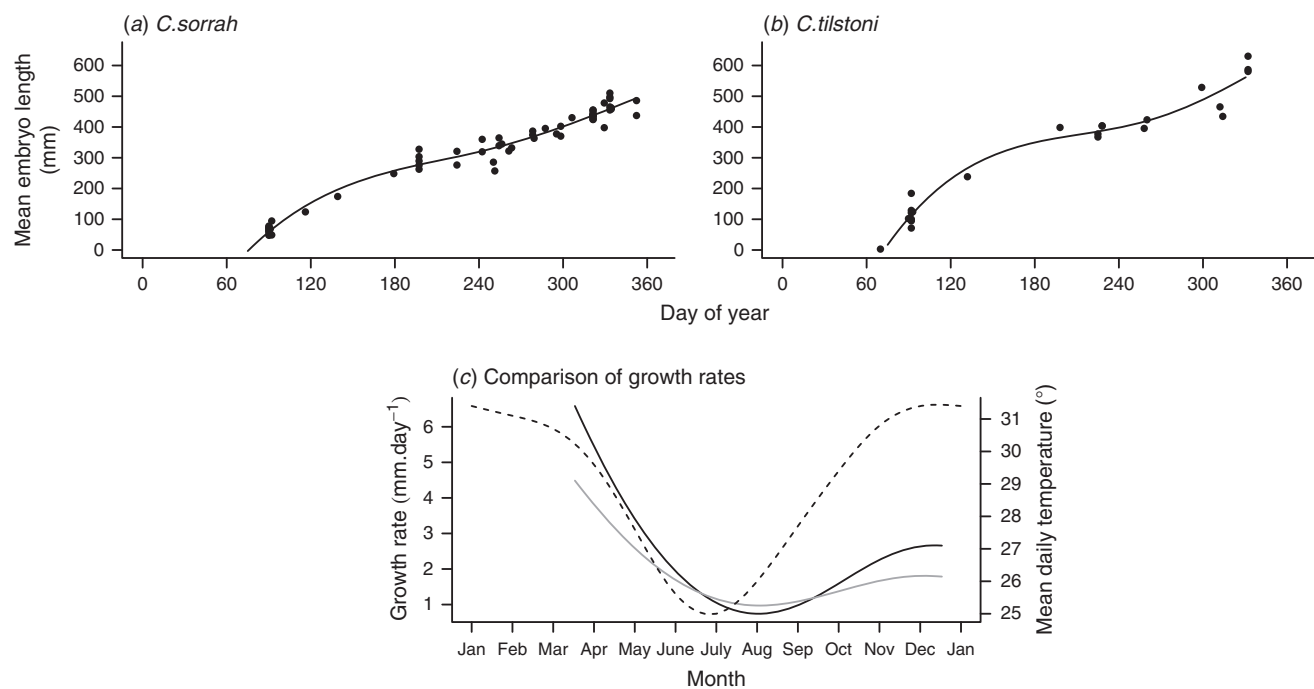

Fig. 9. Mean embryo length against day of year for (a) *Carcharhinus sorrah*, (b) *C. tilstoni* and (c) a comparison of mean embryonic growth rate and mean daily temperature in Townsville against month. Plots (a) and (b) are mean embryonic stretched total length (STL) at age (—) and raw data (●). Plot (c) is mean embryonic growth rate throughout the gestation period for *C. sorrah* (—) and *C. tilstoni* (—) and mean daily temperature (– – –). Values of parameters and statistical quantities for the non-linear regression $L(t) = \beta_1 - \beta_1 e^X$, $X = -\beta_2(t-\beta_3) - \frac{\beta_2\beta_4}{2\pi}\sin 2\pi(2-\beta_5) + \frac{\beta_2\beta_4}{2\pi}\sin 2\pi(\beta_3-\beta_5)$ used in plots (a) and (b) are given in the following tabulation:

Species	β_1	β_2	β_3	β_4	β_5	n	rse
C. sorrah	790.0	1.530	0.0020	0.5367	−0.1372	63	24.31
C. tilstoni	1000	1.575	−0.0071	−0.7331	2.372	23	39.23

where L is STL in mm, t is time in years, β_1 is asymptotic length (L_∞) in mm, β_2 is the Brody growth coefficient K in years^{-1}, β_3 is t_0 in years, β_4 is the magnitude of oscillations in growth, and β_5 is the time at which zero growth begins.

Discussion

Age validation

In the present study, we found that calcein consistently failed to mark the vertebrae of adult *C. sorrah* animals, especially those of pregnant females where a mark was observed in only one of five recaptures. Calcein marking worked successfully on a range other species marked concurrently (Harry *et al.* 2011*b*), suggesting the technique of applying the marker by intramuscular injection was suitable. The dosage injected (5 mg kg^{-1} bodyweight) has also been reported as suitable for marking vertebrae in several other elasmobranch species (Gelsleichter *et al.* 1997; McAuley *et al.* 2006; Pierce and Bennett 2009). We suspect that the failure of the calcein mark to form may have been due to the slowing or cessation of somatic growth and calcification of the vertebrae in these pregnant females, and in larger animals in general. In three of the four cases where calcein did successfully mark the vertebrae, it did not validate a pattern of annual growth-band pairs (Table 3), suggesting that the age of larger individuals was likely underestimated. The finding that maximum age may be underestimated when the estimation is based on vertebral sections is consistent with the findings of several studies, notably Francis *et al.* (2007) who found that the age of porbeagle sharks, *Lamna nasus*, may have been underestimated by as much as 50%. Similarly, Moulton *et al.* (1992) found that school shark, *Galeorhinus galeus*, could be aged to 20 by using the whole vertebrae, whereas on the basis of tag–recaptures, it lived to at least 54 (Francis *et al.* 2007). More recently, Andrews *et al.* (2011) found that age estimates of sandbar sharks, *Carcharhinus plumbeus*, based on bomb radiocarbon validation and tag–recaptures, were higher by up to 11 years than were vertebral age estimates, lending support to Casey and Natanson's (1992) earlier suggestion that growth-band pairs may not form annually in adult sharks.

Age underestimation also appears to have previously occurred for *C. sorrah* and *C. tilstoni*. Davenport and Stevens (1988) reported a maximum age of 7 and 12 years for *C. sorrah* and *C. tilstoni*, respectively, based on ageing the whole vertebrae. However, taking into account the duration of later tag–recaptures and adding on an estimated age at tagging (data available at www.cmar.csiro.au/, accessed 3 March 2010), it seems likely that *C. sorrah* lives to at least 11 and *C. tilstoni* to at least 20 (Stevens *et al.* 2000; Last and Stevens 2009). In the present study, we aged *C. sorrah* to ~14 years and *C. tilstoni* to ~15 years, suggesting that sectioned vertebrae may provide more realistic estimates of maximum longevity. However, based on the calcein marking, age underestimation still seems to be a common occurrence. These findings reaffirmed the importance of age validation in elasmobranch studies (Cailliet *et al.* 2006) and suggested that age-underestimation is not just an issue that affects long-lived species (Francis *et al.* 2007). Understanding the implications of age-underestimation may be important, especially for elasmobranchs where population assessments and demographic models are often based solely on life-history information (e.g. Tsai *et al.* 2010). Using inaccurate longevity and growth parameters in these models (such as via Hoenig's mortality equation) would presumably affect their ability to adequately assess a population.

Growth

In the present study, we were able to obtain samples across the full range of lengths for both species, although the sampled length structures of the two species were very different. The modal length of *C. sorrah* was 1000–1050 mm, in comparison to 750–800 mm for *C. tilstoni* (Fig. 3). This bias towards juveniles in the *C. tilstoni* sample probably explains why a distinct asymptote was not reached in any of the growth models, and consequently why L_∞ exceeded the maximum length of this species (females generally appear to grow to ~1600–1800 mm, whereas fitted L_∞ values were 1739–2182 mm, Table 4). A lack of distinct asymptote is a common feature of many shark growth curves (Simpfendorfer *et al.* 2002; Braccini *et al.* 2007), and computer simulation studies have indicated that it may be related to gear selectivity and the effects of length-selective fishing mortality (Walker *et al.* 1998; Thorson and Simpfendorfer 2009). If age-underestimation has also occurred, presumably this could further compound the issue. One consequence of the growth curve for *C. tilstoni* having a biased asymptote is that any extrapolation of the model to ages beyond those observed (say to the maximum age of 20 on the basis of tag-returns) will give biologically unrealistic predictions of length. This should be noted when using the models, and in such cases the logistic model may be better suited to modelling the length of older and larger animals.

Maturity and maternity ogives

The difference found between maturity and maternity ogives in the present study highlighted the importance of explicitly defining and distinguishing between these reproductive conditions (Braccini *et al.* 2006; Huveneers *et al.* 2007). In the GBRWHA, both sexes of *C. sorrah* reached maturity shortly after their second summer, at a length of 929–951 mm and at 2.3–2.4 years of age. It is important to recognise, however, that because reproduction is strongly seasonal and mating and ovulation occur during summer, reproduction does, therefore, not commence until the following summer, and neither sex reproduces until at least age three. Indeed, this is reflected in the maternity ogives for females (Fig. 6*c*, *f*, Table 5), which indicate that the age at 50% maternity is 3.4 years. Modelling maternal condition in *C. tilstoni* was also important for this reason, because reproduction does not occur until at least a year after maturity is reached (Fig. 6*i*, *l*, Table 5). In both instances, the use of a maturity ogive rather than a maternity ogive would overestimate the number of births in the population. Thus, it is important to model both mature and maternal condition, even for annually reproducing species.

Another important observation in the present study was that 5 of 30 female *C. tilstoni* individuals of >1400 mm were in non-maternal condition. This was unexpected because development of ovarian follicles was most consistent with an annual reproductive cycle (Fig. 8*b*), as has been reported for *C. tilstoni* from the Arafura Sea (Stevens and Wiley 1986). One hypothesis to explain this observation is that a small proportion of females take a resting year between pregnancies. The duration of elasmobranch reproductive cycles is not typically thought to vary among individuals of a population, although there are exceptions. Driggers and Hoffmayer (2009), for example, found both annually and biennially reproducing finetooth sharks, *Carcharhinus isodon*, in a sample of pregnant females from the Gulf of Mexico. Evidence that the frequency of reproduction varies with length or age has also been found in whiskery sharks, *Furgaleus macki* (Simpfendorfer and Unsworth 1998) and some rays (Capapé 1993; Mull *et al.* 2010).

A second hypothesis to explain the observation is observer error resulting from misidentification with *C. limbatus*. *C. limbatus* reaches maturity at ~2000 mm in Australian waters (Macbeth *et al.* 2009) and it is possible that immature *C. limbatus* (U = 1 and 2) between 1400–1800 mm may have been mistakenly staged as U = 3 on the basis of their large size. A third hypothesis is that the presence of some non-maternal females is related to the recently reported hybridisation of *C. tilstoni* and *C. limbatus* (Morgan *et al.* 2012). Because little is currently known about the effects of hybridisation (such as e.g. frequency of interspecific mating, hybrid fitness, reproductive isolating mechanisms), it is not possible to advance this hypothesis any further at present. Future research should investigate how the reproductive output of females varies with length and age, to determine whether our observations are real (e.g. Hypotheses 1 and 3) or due to observer error (Hypothesis 2). Owing to our small sample size, it is not possible to distinguish

between these competing hypotheses at present. As such, we provide length-at-age at maternity models for both situations (Table 5).

Interspecific differences; real or methodological?

Several differences in the life history of *C. sorrah* and *C. tilstoni* have been reported between the Arafura Sea (Stevens and Wiley 1986; Davenport and Stevens 1988) and the Coral Sea, most notably in maximum age and age-at-maturity (Table 6). Although there is some evidence to suggest that these differences are real, many of them may also be due to differences in methodology. For example, with the exception of male *C. sorrah*, the predicted lengths-at-age of the two species are similar between studies (Fig. 10). Thus, large differences in maximum age could be due to the use of the whole vertebrae by Davenport and Stevens (1988), rather than the sectioned

Table 6. Comparison of von Bertalanffy growth parameters and maturity parameters of *Carcharhinus sorrah* and *C. tilstoni* between the Coral Sea (present study) and the Arafura Sea (Stevens and Wiley 1986; Davenport and Stevens 1988)

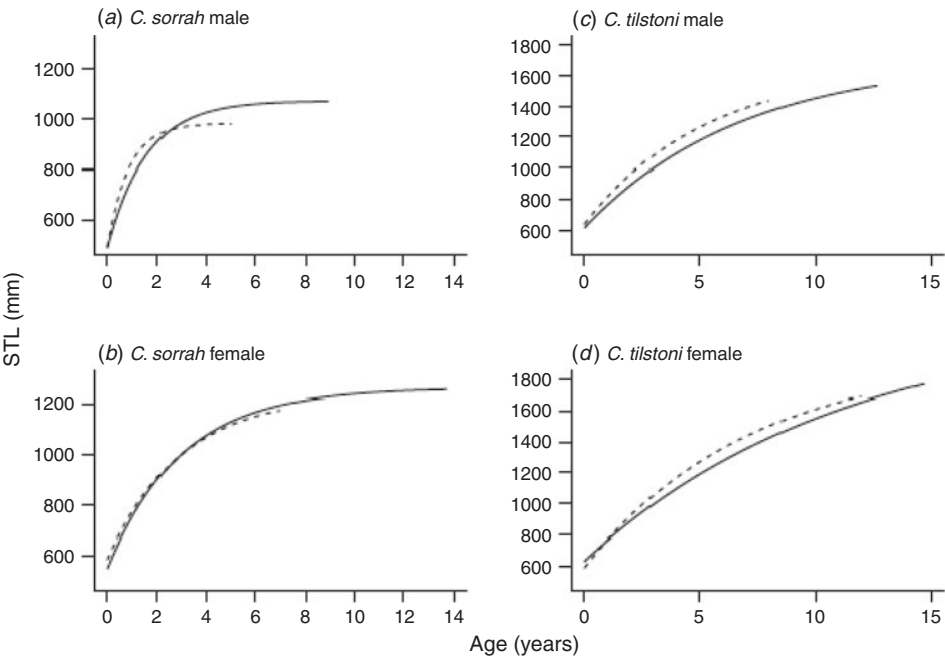| Species	Sex	Location	L_0 (mm)	k (year^{-1})	L_∞ (mm)	l_{50} (mm)	a_{50} (years)	A_{MAX} (years)
C. sorrah	M	Coral Sea	495	0.63	1074	929	2.4	8.9
	F		553	0.34	1266	951	2.3	13.7
	M	Arafura Sea	496	1.17	984	870–920	2–3	5
	F		590	0.34	1239	970	2–3	7
C. tilstoni	M	Coral Sea	616	0.15	1698	1199	5.2	12.8
	F		631	0.08	2243	1247	6.1	14.8
	M	Arafura Sea	645	0.19	1654	1050–1200	3–4	8
	F		593	0.14	1942	1200	3–4	12

Fig. 10. A comparison of deterministic growth curves derived from vertebral ageing of *Carcharhinus sorrah* and *C. tilstoni* from the Coral Sea (——) in the present study and from the Arafura Sea (– – –) by Davenport and Stevens (1988).

vertebrae. Given there was 10 years of intense commercial fishing in the Arafura Sea before the previous study (Walter 1981), growth overfishing may also explain the much younger maximum ages. Differences in maturity between these species also seem to be both real and methodological. In general, *C. sorrah* and *C. tilstoni* appear to mature at slightly larger lengths in the Coral Sea than in the Arafura Sea (Table 6), and this may be related to environmental differences between the two regions (e.g. Walker 2007). However, much of the discrepancy in age-at-maturity between the studies is probably methodological because the values in Davenport and Stevens (1988) were converted from estimates of length at first maturity.

Even though the life history of *C. sorrah* and *C. tilstoni* from the Coral Sea is similar to that in other parts of northern Australia, our interpretation of their biology suggests that some biological traits of *C. tilstoni*, in particular, may mean that it is less resilient to fishing than previously thought. Even though some individuals may mature as young as at 3 or 4 years of age, we found that most females did not begin reproducing until at ∼7 years of age. Also, it is possible that not all females in the population reproduce ever year. The potential existence of a male bias in the embryonic sex ratio (although not statistically significant) was something also previously reported by Stevens and Wiley (1986) and should be investigated further. If this combination of factors is not taken into account, then the number of female births in the population may be substantially overestimated.

Summary of key points

Fifteen summary points from the present paper are presented below.

(1) Vertebral ageing methods gave longevity estimates of 9 and 14 years, respectively, for male and female *C. sorrah* and 13 and 15 years for male and female *C. tilstoni*. These estimates are much higher than those from a previous ageing study that used whole rather than sectioned vertebrae, but are consistent with the results of a previous tagging study, which recaptured *C. sorrah* after ∼10 years at liberty and *C. tilstoni* after ∼18 years.

(2) A mark, tag and recapture study using the fluorescent dye calcein failed to validate the formation of annual growth-band pairs in larger individuals, suggesting that maximum age may be underestimated by vertebral sections. It is unclear what effect this had on the fitted growth curves.

(3) Growth in both *C. sorrah* and *C. tilstoni* was sexually monomorphic before maturity, but became dimorphic after maturity.

(4) The largest male *C. sorrah* individual measured was 1138 mm and growth was best described by a logistic growth model. The largest female measured was 1310 mm and growth was best described by a standard von Bertalanffy growth function.

(5) The largest male and female *C. tilstoni* were 1560 mm and 1800 mm, respectively. Growth was best described by a standard von Bertalanffy growth function, however all models overestimated the asymptotic length of this species.

(6) The heaviest female *C. sorrah* (14.45 kg) individual was ∼1.8 times greater in mass than the heaviest male (8.10 kg) and the heaviest female *C. tilstoni* (34.15 kg) individual was ∼1.6 times greater in mass than the heaviest male (20.85 kg). Despite these differences, a single length–weight relationship with sexes combined was adequate for both species.

(7) Computed maturity ogives indicated that 50% of male *C. sorrah* individuals were mature at 929 mm and 2.4 years, whereas 50% of females were mature at 951 mm and 2.3 years. In both sexes, maturity occurred by the end of their second summer, suggesting that individuals would be capable of reproducing during their third summer (age three). Computed maternity ogives confirmed this, indicating that 50% of females were in maternal condition at 1029 mm and 3.4 years.

(8) Fifty per cent of male *C. tilstoni* individuals were mature at 1199 mm and 5.2 years, whereas 50% of females were mature at 1247 mm and 6.1 years. Females reached maturity ∼1 year after males, and likely began reproducing the following year. Fifty per cent of females were in maternal condition at 1378 mm and 7.2 years.

(9) Both species had an annual, synchronous reproductive cycle, although there was some evidence that a small proportion of female *C. tilstoni* did not reproduce every year. More research is needed to examine whether the frequency of reproduction varies with length and age. Separate maternity ogives were computed to model a situation where a small proportion of females takes a resting year between pregnancies (or do not reproduce for some other reason).

(10) The timing of the reproductive cycle was similar for both *C. sorrah* and *C. tilstoni* in the GBRWHA. Ovulation appeared to occur during March and parturition was during early December. As such, the period of pregnancy was ∼9 months. The ovarian cycle did not occur synchronously with pregnancy, and, although not directly observed, the majority of follicle growth must occur in the months directly after birth.

(11) Embryonic growth rates were closely correlated with ambient environmental temperatures and embryonic development was slowest during winter. As such, the exact timing and duration of the reproductive cycle within a given year may vary.

(12) There was a significant linear relationship between maternal length and fecundity found for both species. The range of litter sizes observed was 1–6 for *C. sorrah* and 1–7 for *C. tilstoni*.

(13) The embryonic sex ratio of neither species was significantly different (at 0.05 level) from parity. However, in the small sample of *C. tilstoni*, there was a strong bias towards males. On the basis of previous studies, a slightly male-biased sex ratio seems possible for this species, and this may need to be incorporated into population assessments.

(14) The mean length (±s.d.) of five neonate *C. sorrah* individuals with unhealed umbilical scars was 523.6 ± 31.0 mm. The mean length of 58 neonate *C. tilstoni* individuals was 617.1 ± 24.0 mm.

(15) The results of the present study have provided the first statistically derived estimates of several important life-history parameters (e.g. maturity and maternity) that are needed for quantitative population assessment and management. *C. tilstoni*, in particular, begins reproducing at an older age and may have a lower lifetime reproductive output than was previously thought.

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