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Age and Growth of Two Commercially Important Sharks (*Carcharhinus tilstoni* and *C. sorrah*) from Northern Australia

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Abstract

The age and growth of *Carcharhinus tilstoni* and *C. sorrah*, the two most abundant shark species in commercial gill-net catches off northern Australia, were investigated by the examination of vertebral rings. Corroborating evidence for age and growth estimates was obtained from length-frequency distributions and tag-recapture data. To aid validation of these estimates, tetracycline was injected into sharks at the time of tagging. Growth is relatively rapid in the first year of life: vertebral ageing indicated 17 cm growth in total length (TL) for *C. tilstoni* and about 20 cm for *C. sorrah* during the first year after birth. By the time the sharks are 5 years old, growth has declined to 8–10 cm per year in *C. tilsoni* and 5 cm per year or less in *C. sorrah*. The von Bertalanffy growth parameters for *C. tilstoni* are $L_\infty = 194\cdot2$, $K = 0\cdot14$, $t_0 = -2\cdot8$ for females, and $L_\infty = 165\cdot4$, $K = 0\cdot19$, $t_0 = -2\cdot6$ for males; for *C. sorrah* the parameters are $L_\infty = 123\cdot9$, $K = 0\cdot34$, $t_0 = -1\cdot9$ for females, and $L_\infty = 98\cdot4$, $K = 1\cdot17$, $t_0 = -0\cdot6$ for males. The greatest recorded ages for *C. tilstoni* were 12 years for females and 8 years for males, and for *C. sorrah*, 7 years for females and 5 years for males. Sexual maturity is reached early: at 3 to 4 years in *C. tilstoni* and 2 to 3 years in female *C. sorrah*.

Introduction

A Taiwanese gill-net fishery operated off northern Australia from the early 1970s until mid 1986. Between 1975 and 1978, the annual catch averaged 17 300 t processed weight (Walter 1981). This represents 24 700 t live weight, of which sharks comprised 78%. *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes in Muller & Henle) together made up 83% by number of these sharks (Stevens and Wiley 1986). With the introduction of the 200 nautical-mile Australian Fishing Zone (AFZ) in 1979, Australia assumed management responsibilities for this fishery. In the early 1980s a small Australian fishery, based on the same species, began operations in inshore waters between Napier Broome Bay and the eastern Gulf of Carpentaria (Fig. 1). This fishery caught 408 t live weight of shark in 1985 (Anon. 1986).

The population structure, reproductive biology and diet of *C. tilstoni* and *C. sorrah* from northern Australian waters were examined by Stevens and Wiley (1986). Relevant biological details from their study are summarized here. *C. tilstoni* was previously described as *C. limbatus* (Stevens *et al.* 1982; Lyle 1984; Stevens and Church 1984), but has been separated from it by differences in enzyme systems, vertebral counts, size data and pelvic fin coloration. *C. tilstoni* and *C. sorrah* have a distinctly seasonal reproductive cycle: females breed every year and parturition occurs between late November and early February, with the peak parturition period in January. The length at birth in *C. tilstoni* is 60 cm, with females maturing at 115 cm and males at 110 cm total length (TL). Females larger than

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161 cm and males larger than 143 cm TL were rarely caught by the commercial fishery. *C. sorrah* are born at 52 cm, and females mature at 95 cm and males at 90 cm TL. Few females larger than 130 cm or males larger than 112 cm TL were caught by the Taiwanese gill-net fishery during the sampling period.

Shark fisheries are particularly sensitive to overfishing (Holden 1974, 1977). Slow growth rates, low rates of reproduction and a close relationship between stock size and recruitment in shark populations typically contribute to a rapid decline in numbers soon after exploitation begins (Holden 1974). Such declines have been documented for a number of species, including the Australian school shark (Olsen 1954, 1981), the basking shark (Parker and Stott 1965; Davis 1983) and the Scottish-Norwegian stock of spiny dogfish (Holden 1968, 1974). For a fishery to be viable over the long term, it must be managed effectively. Age and growth data provide the most fundamental information for estimating mortality; they are also essential for estimating several other population parameters used in stock assessment.

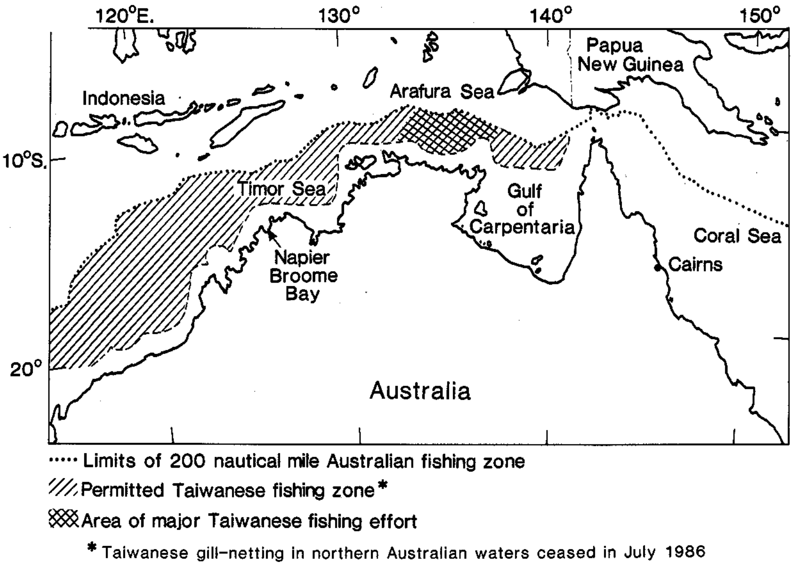

Fig. 1. Study area in northern Australian waters.

The literature on age and growth in elasmobranchs describes a variety of techniques for age determination (Prince and Pulos 1983), no single one of which is reliable for most species. To date, no studies of age and growth in *C. tilstoni* or *C. sorrah* have been published. In the present study, the age and growth of these species are investigated by the examination of vertebral rings, supported by evidence from the analysis of length-frequency and tag-recapture data.

Materials and Methods

Sharks were sampled, from 1980 to 1984, by observers on Taiwanese commercial gill-netting vessels operating inside the AFZ off northern Australia. These vessels worked multi-filament nylon gill-nets (stretched-mesh 14·5 to 19·0 cm; average 17·0 cm) that consisted of panels at least 15 m deep from headrope to footrope and 15 m long, connected to form a gill-net of 8 to 14 km in length. The nets were set close to the surface just before dusk. Hauling, which began around midnight, took up to 10 hours.

The selectivity of the gill-nets probably affects the size distribution of sharks caught by the commercial fishery, and may select against the capture of *C. tilstoni* and *C. sorrah* at the extremes of their size range. However, as Stevens and Wiley (1986) noted, gill-nets captured individuals close to the size at birth. They also noted that the largest specimens caught by longline, which presumably has no maximum size selection for these species, were a similar size to those caught by gill-net.

Observers sampled about 1·5% of the sets made by Taiwanese gill-netters in the AFZ between April 1981 and October 1983 (Stevens and Wiley 1986). Length-frequency data on 18 201 *C. tilstoni* and 7748 *C. sorrah* were collected between June 1981 and December 1983, with all months of the year, except May, represented. The sharks were measured to the nearest centimetre either as total lengths (TL), for which the tail was allowed to take a natural position and the top caudal lobe was then placed parallel to the body axis, or as fork lengths (FL). Fork lengths were converted to total lengths using the relationships derived by Stevens and Wiley (1986): for *C. tilstoni*, TL = 0·913 + 1·235 FL; for *C. sorrah*, TL = 4·715 + 1·196 FL.

Vertebral Ageing

Vertebral samples were collected over the full size range of the sharks from commercial catches in the Arafura Sea between 1980 and 1984, with the greatest number of samples collected in 1982 and 1983. A block of several vertebrae was taken from the vertebral column below the origin of the first dorsal fin, and was either frozen or stored in 70% ethyl alcohol until processed.

Initially, various techniques were assessed for the enhancement of the concentric rings on the cone surface of the vertebrae: whole vertebrae were stained with silver nitrate (Stevens 1975; Cailliet *et al.* 1983*a*, 1983*b*), alizarin red S (LaMarca 1966; Gruber and Stout 1983), crystal violet (Schwartz 1983), cobalt nitrate and ammonium sulphide (Hoenig 1979). All these stains have an affinity for calcium. The protein stains mercurochrome and ninhydrin (Schneppenheim and Freytag 1980) were also tested, as were xylene impregnation (Daiber 1960), histology (Tanaka and Mizue 1979; Casey *et al.* 1985), radiography (Cailliet and Bedford 1983; Cailliet *et al.* 1983*a*, 1983*b*), X-ray spectrometry (Jones and Geen 1977), image analysis and examination of sectioned vertebrae under transmitted, reflected, interference and polarized light.

Of all these methods, ninhydrin staining of whole vertebrae was chosen for its ease of use, good and consistent results on the species in this study, and relatively low cost. Before staining, the vertebrae were separated and trimmed of excess tissue. The remaining connective tissue was removed from the cone surface by soaking the vertebrae in a 5·25% sodium hypochlorite solution (Schwartz 1983) for up to an hour, depending on the size of the vertebrae. Care was taken to avoid 'over-bleaching', which interferes with subsequent absorption of the stain. The vertebrae were then washed thoroughly in tap water and stained in a 1% ninhydrin-in-ethanol (98%) solution. Immersion for at least 6 h was usually required for effective staining.

The two largest vertebrae in each block were selected for examination under a dissecting microscope with an ocular micrometer. Measurements and readings were carried out at ×10 magnification under reflected light. After examination, vertebrae were stored in 70% alcohol. The cone surfaces of treated centra showed a pattern of alternating violet-stained and white, unstained bands. Since ninhydrin is a protein stain, the stained bands were assumed to be the organically rich areas, and the unstained bands, the more heavily mineralized zones. As ninhydrin penetrates deeply, cone surfaces could be scraped gently if necessary, to clarify any obscure patterns.

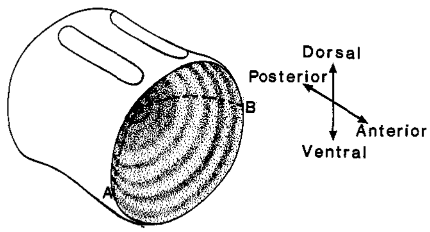

Fig. 2. Representation of shark vertebra. Measurements of vertebral radius and radii of unstained bands were taken along the line A–B.

The vertebral radius and the radii of all unstained bands were measured along the plane at right angles to the dorso-ventral axis of the vertebra (Fig. 2). The bands were assigned ages based on the assumptions that a birth ring is formed soon after birth (discussed later) and thereafter one unstained band is laid down annually. Thus, sharks captured in January were considered to be 13 months old if the first unstained band outside the birth ring was visible. Accordingly, an age in months was assigned to each shark, based on the number of bands visible and the month of capture (relative to the arbitrary birthday of 1 January). Growth parameters were calculated using these age–length values and a von Bertalanffy computer program (Kirkwood 1983). This program was chosen for two reasons: the von

Bertalanffy parameters were required for subsequent mortality estimates, and the curve provided a reasonable fit to the data.

Back-calculations of lengths-at-age were performed on measurements of the radii of all unstained bands on the vertebral centra (except the birth ring), using Fraser's (1916) formula $L = a + bR$, where L is the total length; a and b are constants derived from the shark length/vertebral radius regression, and R is the vertebral radius. Average length-at-age values were obtained using a von Bertalanffy computer program (Kirkwood 1983) and the back-calculated length–age values. Back-calculations were used to check for Lee's phenomenon of apparent change in growth rate, where the older the fish, the smaller the back-calculated lengths for a particular age group (Lee 1912; Bagenal and Tesch 1978), and for consistency in reading the same structures in young and old sharks.

Length-frequency Data

Length-frequency data for each month sampled between June 1981 and December 1983 were plotted in 1 cm FL intervals. Fork lengths rather than total lengths were used, since most of the length-frequency data were recorded in that form and conversion to total length would have decreased the precision. The data were examined separately by sex using Macdonald and Pitcher's (1979) computer program for modal analysis of distribution mixtures (Macdonald 1980). The modes identified were assumed to represent age-classes.

For *C. tilstoni*, means for the first three modes derived by the Macdonald-Pitcher method were treated as age–length values and fitted to a von Bertalanffy program (Kirkwood 1983) to give average length-at-age values. Only those means where the χ^2 value indicated a good fit to the data were used. The *C. sorrah* data were not similarly treated because the modes in the length-frequency data are less clearly discernible.

Tag-recapture

Between February 1983 and May 1985, 4839 *C. tilstoni* and 2926 *C. sorrah* individuals were tagged off northern Australia, between Napier Broome Bay and Cairns, but mainly in the Arafura Sea and Gulf of Carpentaria (Fig. 1). Cattle ear-tags [Rototags or Jumbo Rototags (Davies and Joubert 1967)] were inserted in the first dorsal fin. By October 1985, a total of 177 *C. tilstoni* (86 females and 91 males) and 48 *C. sorrah* (21 females and 27 males) individuals has been recaptured, mostly by commercial fishermen.

Scientists participating in the programme measured the length of the sharks at both the time of tagging and recapture. The fishermen usually froze the sharks for subsequent examination by fisheries officers. There was no apparent relationship between the amount of shrinkage due to freezing and either the length of the shark (*C. tilstoni*; $n = 62$, $r = 0{\cdot}047$, $P > 0{\cdot}05$, *C. sorrah*; $n = 57$, $r = 0{\cdot}252$, $P > 0{\cdot}05$) or the period of freezing. The lengths of these sharks were, therefore, adjusted for freezer shrinkage by adding a mean correction factor, of 1·4 cm FL for *C. tilstoni* and 1·1 cm FL for *C. sorrah*. Growth data on sharks that had been at liberty for less than 1 month were not included, because measurement errors are magnified when growth increments from short-term recaptures are converted to growth per year (Casey *et al.* 1985). Growth data were grouped in 10 cm length intervals and examined for differences in growth rates. Growth increment and period-at-liberty data for all recaptured sharks that had been at liberty for a month or longer were analysed by a von Bertalanffy computer program (Kirkwood 1983) to obtain the parameters L_∞ and K.

Tetracycline

To validate the results of vertebral ageing, 358 *C. tilstoni* and 183 *C. sorrah* individuals were injected with oxytetracycline hydrochloride (OTC) at the time of tagging. Tetracycline is laid down in areas of active calcification, and can subsequently be detected as a yellow fluorescence under ultraviolet radiation. Sharks were injected between January and May 1985 (late summer/autumn). Tetracycline was mixed with sea-water and administered as a peritoneal injection at a dose rate of 25 mg kg^{-1} body weight (Holden and Vince 1973; Gruber and Stout 1983; Smith 1984).

The vertebrae removed from recaptured sharks that had been injected with tetracycline were viewed under ultraviolet (u.v.) radiation to confirm the presence of fluorescence. They were then cleaned of connective tissue, stained with ninhydrin and examined under u.v. radiation.

Results

Vertebral Ageing

A regression of total length on vertebral radius showed a linear relationship for both male and female *C. tilstoni*. As there was a significant difference between the sexes (*F*-test: $0 \cdot 01 < P < 0 \cdot 05$), the data were treated separately. Similarly, in *C. sorrah* there was a linear relationship between total length and vertebral radius. Data for males and females were combined, as there was no significant difference between the sexes (*F*-test: $P > 0 \cdot 05$). The regression estimates are shown in Table 1.

Table 1. Relationship between total length (cm) and vertebral radius (mm) in *Carcharhinus tilstoni* and *C. sorrah*

a, *b*, Constants in Fraser's (1916) formula $L = a + bR$, where L is total length and R is the vertebral radius

Species	*a* (s.e.)	*b* (s.e.)	*n*	R^2
C. tilstoni females	17·39 (1·30)	15·98 (0·19)	258	0·966
C. tilstoni males	12·93 (2·55)	16·97 (0·46)	132	0·912
C. sorrah sexes combined	19·90 (1·70)	15·99 (0·37)	214	0·899

Of the 395 vertebral samples collected from *C. tilstoni*, 98% were 'readable': 257 females (57 to 176 cm TL) and 132 males (66 to 142 cm TL). Of the vertebral samples from *C. sorrah*, 93% were 'readable': 133 females (51 to 123 cm TL) and 80 males (49 to 118 cm TL). For both species, therefore, the sharks that we sampled for vertebrae covered the length range of sharks normally caught by the fishery.

Table 2. Von Bertalanffy growth parameters and their standard errors for *Carcharhinus tilstoni* and *C. sorrah* from ring counts on vertebrae, modal analysis and tag-recapture data

	Von Bertalanffy growth parameters	From vertebral ring counts		From modal analysis		From tag-recapture	
		Females	Males	Females	Males	Females	Males
C. tilstoni		($n = 257$)	($n = 132$)	($n = 28$)[A]	($n = 32$)[A]	($n = 86$)	($n = 91$)
	L_∞ (cm TL)	194·2	165·4	181·4	156·8	218·2	139·5
		(7·9)	(11·9)	(38·9)	(15·2)	(28·8)	(4·6)
	K (yearly)	0·14	0·19	0·19	0·25	0·08	0·20
		(0·02)	(0·03)	(0·08)	(0·06)	(0·02)	(0·02)
	t_0 (years)	−2·8	−2·6	−2·1	−1·9	–	–
		(0·3)	(0·4)	(0·5)	(0·3)		
C. sorrah		($n = 133$)	($n = 80$)			($n = 20$)[A]	($n = 27$)[A]
	L_∞ (cm TL)	123·9	98·4			122·4	97·3
		(3·4)	(1·8)			(11·9)	(4·0)
	K (yearly)	0·34	1·17			0·12	0·44
		(0·05)	(0·18)			(0·06)	(0·22)
	t_0 (years)	−1·9	−0·6			–	–
		(0·2)	(0·1)				

[A]n = number of mean modal lengths derived from length frequency data using Macdonald–Pitcher method.

The ninhydrin-treated vertebrae of near-term embryos showed a stained area around the primordial notochord. In some new-born and young sharks, there were stained bands on the portion of the cone surface formed prior to birth. These bands are presumably formed *in utero*, perhaps in response to changes in nutrient sources during embryonic development (cf. Casey *et al.* 1985). The average vertebral radius for the new-born sharks was 3·0 mm for *C. tilstoni* (n = 3) and 2·3 mm for *C. sorrah* (n = 3). Outside the stained area on the vertebrae of some new-born and young sharks is a broad unstained area. In larger sharks, the position of this unstained area coincides with a marked change in the topography across the cone surface. Since this first, unstained band on the vertebra appears at or just after the time of birth, it is referred to as the 'birth ring'. Subsequent bands appear as alternating violet, ninhydrin-stained and white, unstained bands.

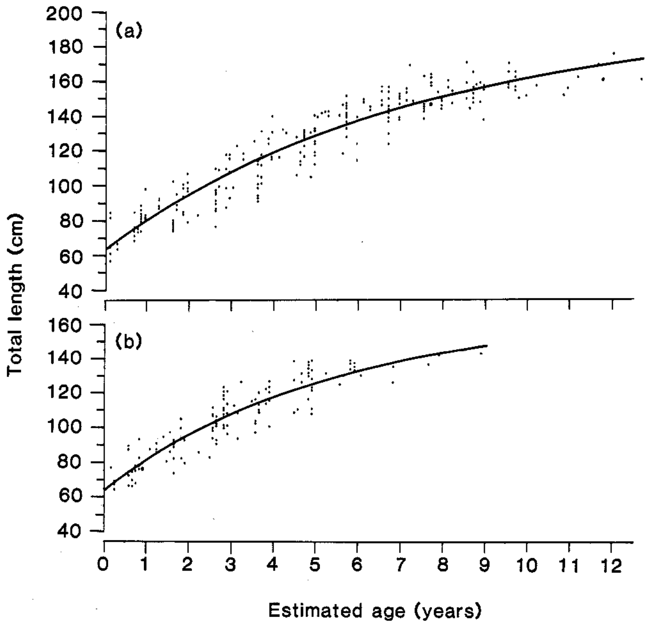

Fig. 3. Von Bertalanffy growth curves for *C. tilstoni* derived from vertebral ageing: (*a*) females, (*b*) males.

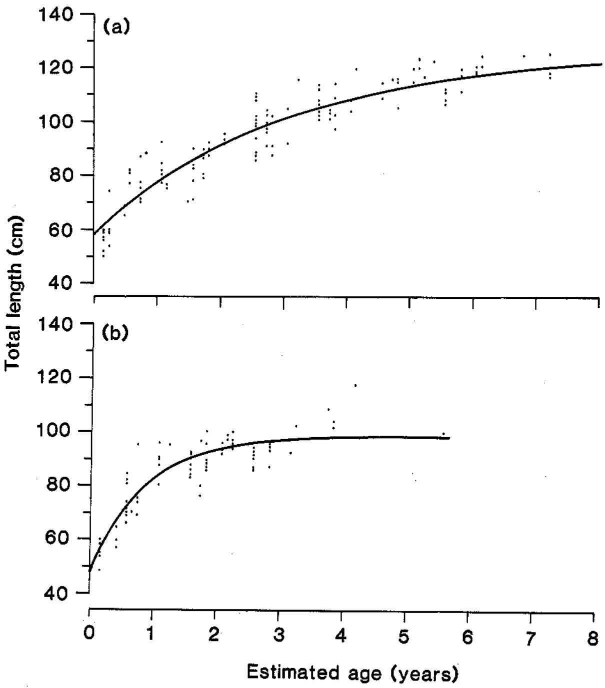

Fig. 4. Von Bertalanffy growth curves for *C. sorrah* derived from vertebral ageing: (*a*) females, (*b*) males.

The age data obtained from vertebral band counts were fitted to a von Bertalanffy growth model (Kirkwood 1983). The parameters L_∞, K and t_0 were derived (Table 2) and growth curves obtained (Figs 3 and 4).

While the size at birth and growth in the first 4 years are similar in *C. tilstoni* of both sexes, there is a significant difference (F-test: $0 \cdot 01 < P < 0 \cdot 05$) between the growth curves for males and females (Fig. 3), with females growing faster and larger than males after the fourth year. The L_∞ values of 194·2 cm for females and 165·4 cm for males (Table 2) are, respectively, similar to and lower than the largest sizes recorded during this sampling programme (a female of 196·0 cm and a male of 183·7 cm TL). The estimates of 63 cm (female) and 65 cm (male) for the length at birth (Table 3) approximate to the size at birth recorded by Stevens and Wiley (1986). The K values, 0·14 year^{-1} for females and 0·19 year^{-1} for males (Table 2), imply that the growth curve for males approaches its asymptote more quickly than does the curve for females.

Table 3. Estimates of mean length-at-age (total length, TL, cm), and growth-per-year (G, cm) for *Carcharhinus tilstoni* derived from vertebral ring counts, back-calculation and modal analysis

Age (years)	Females: Vertebral ring counts TL	G	Females: Back-calculation TL	G	Females: Modal analysis TL	G	Males: Vertebral ring counts TL	G	Males: Back-calculation TL	G	Males: Modal analysis TL	G
0	63	–	72	–	59	–	65	–	71	–	59	–
1	80	17	83	11	81	22	82	17	84	13	81	22
2	95	15	94	11	98	17	96	14	96	12	98	17
3	108	13	105	11	112	14	108	12	106	10	111	13
4	119	11	114	9			118	10	115	9		
5	129	10	123	9			126	8	122	7		
6	138	9	131	8			133	7	129	7		
7	145	7	139	8			139	6	135	6		
8	151	6	146	7			143	4	140	5		
9	157	6	152	6								
10	162	5	158	6								
11	166	4	164	6								
12	170	4	169	5								

Based on Stevens and Wiley's (1986) observed size at maturity, vertebral ageing indicates an age-at-maturity in *C. tilstoni* of 3–4 years for both sexes (at which time females have reached 59% and males 67% of their asymptotic length). The oldest *C. tilstoni* of each sex aged in this study were a female of 12 years at 168·9 cm (87·0% of asymptotic length) and a male of 8 years at 142·0 cm TL (85·9% of asymptotic length).

There was a significant difference between the growth curves for male and female *C. sorrah* (F-test: $P < 0 \cdot 01$) (Fig. 4), the male curve showing very rapid growth in the first year and reaching an early asymptote as indicated by the extremely high K value of 1·17 (Table 2). The L_∞ values of 123·9 cm for females and 98·4 cm for males (Table 2) are considerably lower than the largest sizes recorded during this programme (a female of 151·8 cm and a male of 131 cm TL). Estimates for the length at birth of 58 cm for females and 47 cm TL for males (Table 4) are, respectively, somewhat higher and lower than the 52 cm TL length at birth observed by Stevens and Wiley (1986).

In *C. sorrah* females, the age at maturity is 2–3 years; in males 1–2 years (at which time females have reached 76·7% and males 91·5% of their asymptotic length). The oldest *C. sorrah* individuals aged in this study were females of 7 years which were between 115·0 and 123·4 cm (92·8–99·6% of asymptotic length), while the oldest male was 5 years and 100 cm TL, slightly longer than the asymptotic length for males.

Results from back-calculation for both species gave length-at-age values similar to those derived from direct ageing, with the exception of size at birth (Tables 3 and 4). Lee's phenomenon was not detected in the data.

Table 4. Estimates of mean length-at-age (total length, TL, cm) and growth-per-year (G, cm) for *Carcharhinus sorrah*, derived from vertebral ring counts and back-calculation

Age (years)	Females				Males			
	Vertebral ring counts		Back-calculation		Vertebral ring counts		Back-calculation	
	TL	G	TL	G	TL	G	TL	G
0	58	–	69	–	47	–	69	–
1	77	19	79	10	83	36	80	11
2	91	14	88	9	94	11	88	8
3	101	10	95	7	97	3	94	6
4	107	6	102	7	98	2	98	4
5	112	5	109	7				
6	116	4	115	6				
7	118	2	120	5				

Modal Analysis

Monthly length-frequency histograms show clear chronological progressions of smaller (i.e. younger) size-class modes for *C. tilstoni* (Fig. 5). Early year-class modes can be tracked through the monthly length-frequency samples. *C. tilstoni* young are born at about 60 cm TL, mainly in January (Stevens and Wiley 1986) and young sharks enter the fishery soon after birth. The length-frequency data illustrated in Fig. 5 show new recruits making their appearance in the February 1982 sample at 51–55 cm FL (64–69 cm TL). These sharks have reached a modal length of about 67–70 cm FL (84–87 cm TL) by January 1983, a growth in their first year of 18 to 20 cm TL. In the January 1983 sample, the next pulse of new-born fish can be seen at 50–52 cm FL (63–65 cm TL).

For *C. tilstoni*, modal analysis using the Macdonald-Pitcher method provided the von Bertalanffy growth parameters shown in Table 2 and length-at-age values in Table 3. These results indicate a 22 cm TL growth increment in the first year, 2–4 cm more than indicated by visual assessment of one year's data in the length-frequency histograms (Fig. 5).

Stevens and Wiley (1986) noted that the smallest *C. sorrah* specimens caught by the gill-net fishery are about 65 cm TL. The length-frequency data (Fig. 6) show that young-of-the-year *C. sorrah* enter the fishery in the April 1982 sample at 53–60 cm FL (68–76 cm TL). In January 1983 the modal length of these sharks is about 63–65 cm FL (80–82 cm TL). Since these sharks are born at about 52 cm TL (Stevens and Wiley 1986), this indicates a growth increment of 28–30 cm TL over the first year. In January 1983, the 2+ fish have a modal length of about 71–72 cm FL (90–91 cm TL), suggesting that growth in the second year of life has dropped to 9–10 cm TL.

Tag Recapture

By January 1986, 4·4% of all tagged *C. tilstoni* (214 of 4839) and 1·9% (56 of 2926) of tagged *C. sorrah* individuals had been returned. After the freezer correction factor was applied, 'negative growth' was recorded in 12 *C. tilstoni* specimens from a total of 181 tag returns (6·6%) and 5 *C. sorrah* specimens from 45 tag returns (11%) for which growth information was available. The number of returned sharks showing 'negative growth' decreased as the period of liberty after tagging increased. Of the sharks that had been at liberty for less than a month, 16·6% of the *C. tilstoni* and 50% of the *C. sorrah* specimens

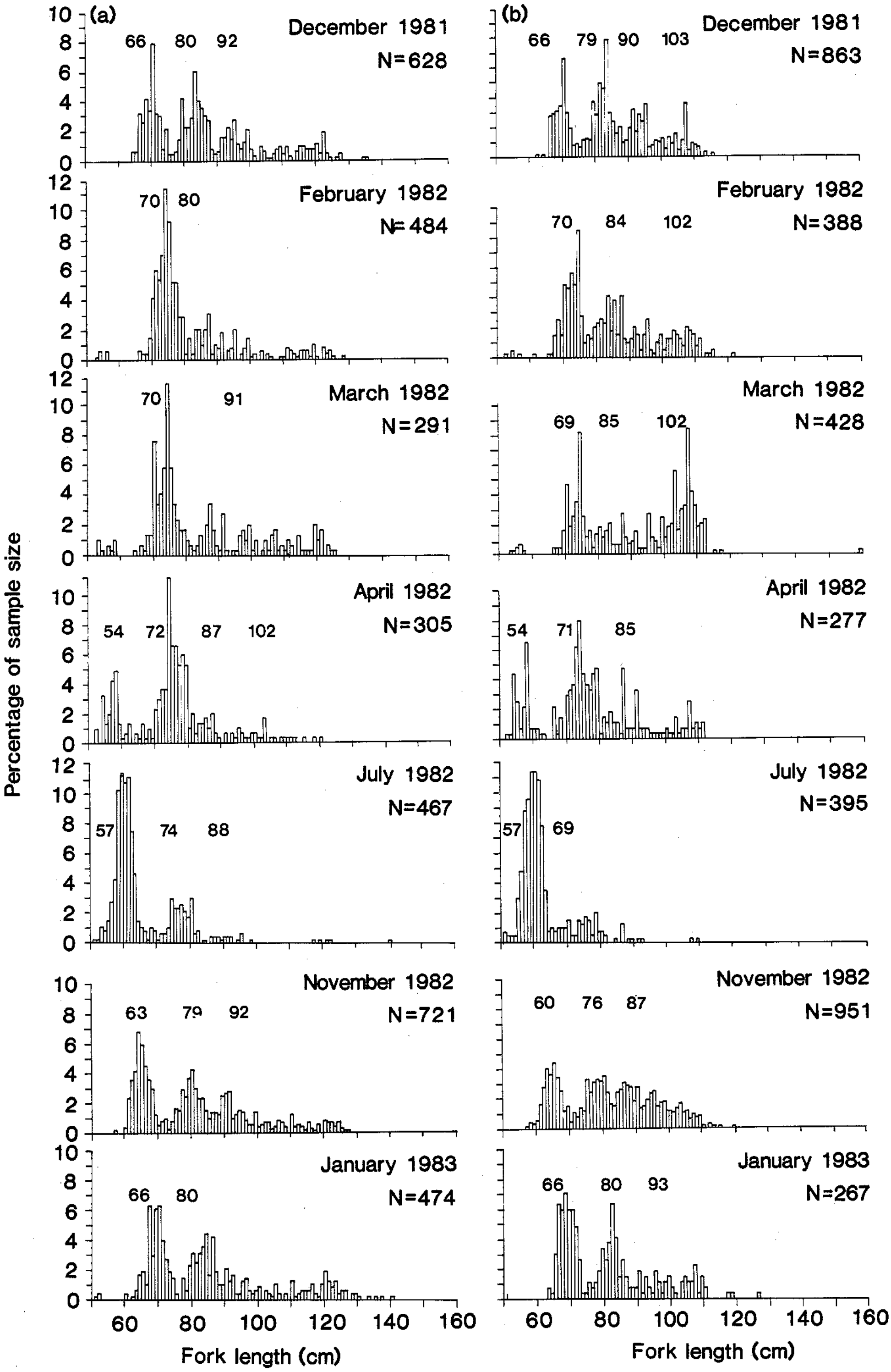

Fig. 5. Length-frequency data for *C. tilstoni*, December 1981–January 1983. Values above the histograms are means derived by the Macdonald–Pitcher method: (*a*) females, (*b*) males.

showed 'negative growth'. For sharks at liberty between 1 month and 1 year, 5·8% of the *C. tilstoni* and 8·6% of the *C. sorrah* specimens showed 'negative growth'; for sharks at liberty for more than 1 year, these values were 2·9% for *C. tilstoni* and 6·3% for *C. sorrah*.

Table 5. Estimate of mean annual growth of *Carcharhinus tilstoni* from tag-recapture data

Total length (cm)	Growth per year (cm)			
	Females	*n*	Males	*n*
⩽80	11·1	26	10·9	18
81–90	12·3	23	10·3	24
91–100	10·2	15	8·8	14
101–110	5·4	10	6·9	10
111–120	7·2	2	4·5	11
>120	7·3	10	2·2	14

When the tag return data were analysed for the 177 *C. tilstoni* individuals at liberty for a month or longer, a significant difference was apparent in the growth rate between the sexes (*F*-test: $P < 0{\cdot}001$). This difference in growth rate between the sexes is greatest in sharks over 110 cm TL (Table 5). The largest recaptured sharks of each sex were a female of 151 cm and a male of 126 cm TL.

Table 6. Estimate of mean annual growth of *Carcharhinus sorrah* from tag-recapture information (sexes combined)

Total length (cm)	Growth per year (cm)	*n*
⩽80	9·8	5
81–90	2·4	16
91–100	2·2	15
101–110	2·0	9
111–120	2·6	2

For the 47 *C. sorrah* individuals at liberty for a month or longer, examination of tag return data by 10 cm length groups gave growth rates indicated in Table 6. The data for *C. sorrah* were not analysed separately by sex because of the small number of returns. More small males than females were caught (up to 100 cm), while males over 100 cm TL were not represented in the returns. The largest tagged female returned was 116 cm and the largest male, 97 cm TL.

The von Bertalanffy growth parameters L_∞ and K were obtained for both species (Table 2), but it is not possible to estimate t_0 from tag-recapture data alone (Kirkwood 1983).

Tetracycline

Of the 358 *C. tilstoni* and 183 *C. sorrah* individuals injected with tetracycline, 10 *C. tilstoni* and 1 *C. sorrah* specimens have been returned to date. Of the 10 *C. tilstoni* specimens, 9 were tagged and injected in March and one in May 1985. Eight were at liberty between 83 and 298 days, the other two for 379 and 381 days. Under ultraviolet radiation, all the vertebrae clearly displayed a fluorescent ring at the distal edge of an unstained band (formed during the Austral summer) or within the early part of a stained (winter) band.

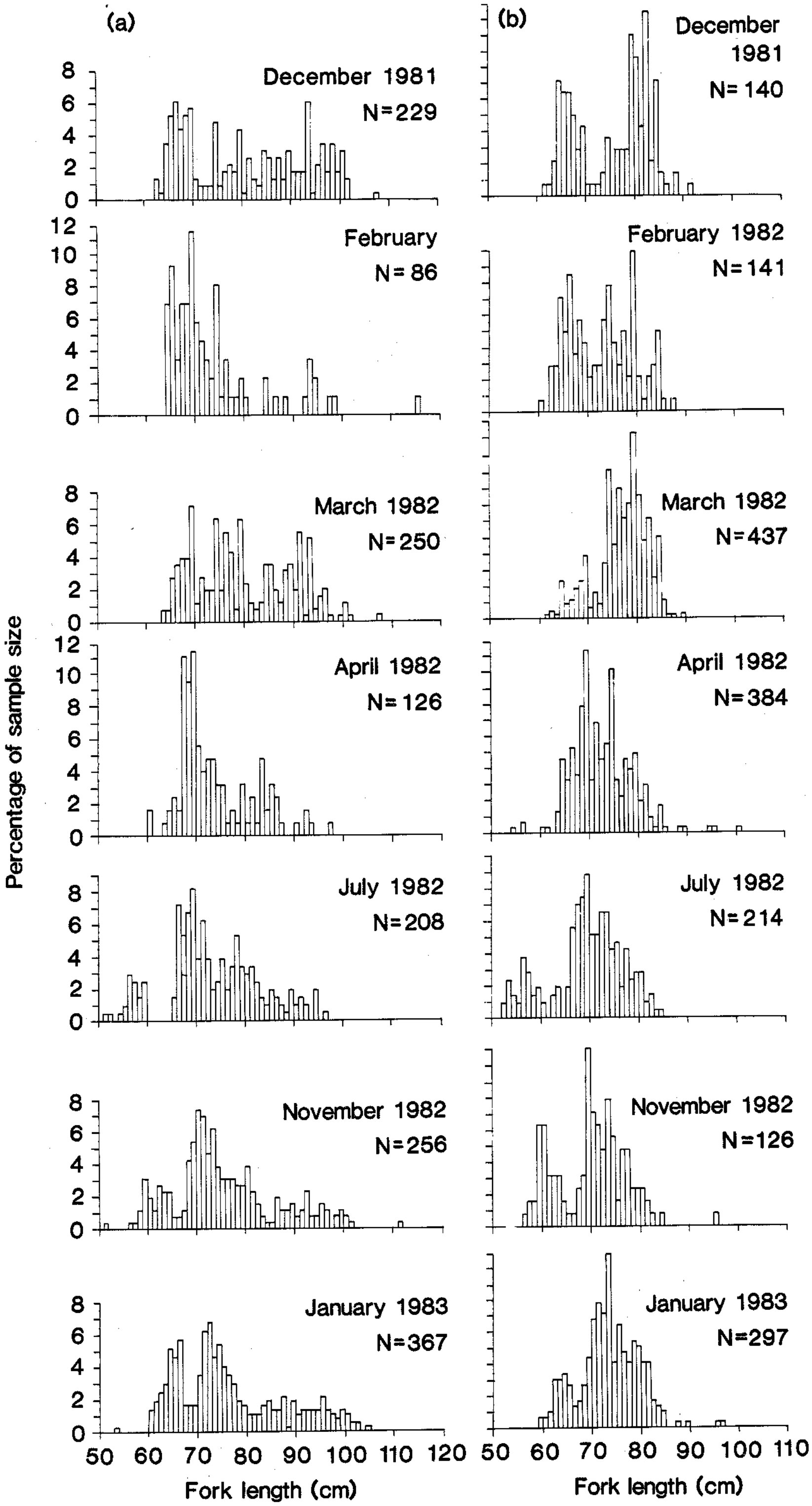

Fig. 6. Length-frequency data for *C. sorrah*, December 1981–January 1983: (*a*) females, (*b*) males.

Each vertebra bore a stained band distal to the fluorescent tetracycline ring, and, except for the shark recaptured after 83 days, part of a further unstained band was also present. On the vertebrae of two sharks at liberty for 379 and 381 days, this unstained band was complete, and distal to it was the beginning of the next stained band (Fig. 7). The single injected *C. sorrah* specimen that was returned had been at liberty for 199 days and showed a 'negative growth' of 2·5 cm. Under ultraviolet radiation, OTC fluroescence could be seen at the extreme periphery of the cone surface and in patches on the sides of the vertebra.

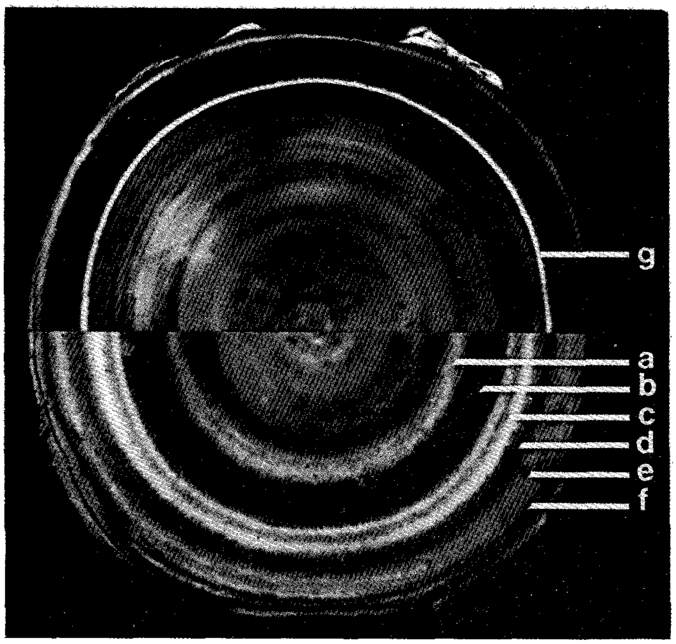

Fig. 7. Vertebra of a *C. tilstoni* specimen (total length 95·8 cm), tagged and injected with tetracycline on 16 March 1985 at the end of the Austral summer, recaptured on 1 April 1986 after 379 days of liberty. The lower half of the illustration was photographed under daylight to show the pattern of ninhydrin staining; the upper half under u.v. radiation. The tetracycline appears under u.v. illumination as a bright, narrow ring. Its position corresponds to the start of the 1985 dark-stained 'winter' band on the daylight photograph. *a*, Birth ring formed early in 1984; *b*, 1984 'winter' band; *c*, 1984/85 'summer' band, Age I; *d*, 1985 'winter' band; *e*, 1985/86 'summer' band, Age II; *f*, start of 1986 'winter' band; *g*, tetracycline ring.

Discussion

Annual Nature of the Growth Bands

Initial comparisons of vertebral ageing results with visual inspection of length-frequency data suggested that bands on the vertebrae of both species were laid down annually. This indication was supported by evidence from modal analysis, tag returns and, for *C. tilstoni*, tetracycline labelling. Results from back-calculation confirmed that the position of the bands on the vertebrae did not alter with age and that the same early bands were being read in older sharks as in younger sharks.

Evidence that bands in young *C. tilstoni* are annual was provided by the examination of tetracycline-labelled vertebrae from ten recaptured sharks. These *C. tilstoni* specimens were from 84 to 96 cm TL, at which size vertebral ageing puts them at between 1 and 2 years of age. Eight of these sharks were injected at the end of the 1984/85 Austral summer and, except for one, were caught early the following summer in November and December. All vertebrae bore a stained band distal to the fluorescent unstained band, and except for one shark caught in June, part of the next unstained band was visible. These observations suggest that the tetracycline-labelled unstained band was formed during the 1984/85 Austral summer and that the subsequent stained band was laid down during the following winter. The presence of part of the next unstained band on the vertebrae of the seven sharks captured in November and December provides reasonable evidence that its formation is well under way by November. The other two sharks were injected in March 1985 and recaptured in April 1986. The vertebrae of these sharks (Fig. 7) display a tetracycline ring at the start of the 1985 stained (winter) band. Distal to this stained band is an unstained band, presumably formed during the 1985/86 Austral summer, and the start of the next stained band (1986 winter), suggesting that the winter bands begin to appear on the vertebrae around March. To date, the results do not indicate how long it takes for the tetracycline to be deposited in the vertebral tissues, but do indicate that the dosage and administration of tetracycline were sufficient for its inclusion into the vertebral tissues of both species. The incorporation of the tetracycline ring within an unstained (summer) band on the vertebral centrum of summer-injected sharks verifies the ninhydrin-staining technique, in which the organically rich, rather than the heavily calcified, bands are stained.

Growth and Length-at-age

Von Bertalanffy growth curves derived from vertebral aging give a good fit to the observed data for *C. tilstoni*, assuming bands are annual. The results in Table 3 show that, for the first three year-classes, except for a disparity in the estimates of lengths at birth, vertebral readings are well supported by the results from modal analysis.

Analysis of tag-recapture data (Table 5) indicates a somewhat slower growth rate; 9–12 cm per year for *C. tilstoni* of up to 100 cm TL compared with 13–17 cm annual growth from vertebral ageing of similar-sized sharks. For sharks between 100 and 120 cm TL, annual growth estimated from tag data has declined to 5–7 cm while vertebral ageing suggests 10–14 cm a year for fish of this size.

When the von Bertalanffy growth curve is fitted to the vertebral ageing data for *C. sorrah* females (Fig. 4), the curve provides a reasonable fit to the data, except for sharks less than 1 year old. The von Bertalanffy growth curve is not a good fit to the vertebral ageing data for males, particularly for sharks less than a year old and more than 3 years old. The relatively low L_∞ value of 98·4 cm TL, derived from the vertebral ageing of males, is probably influenced by the concentration of vertebral samples over the first three year-classes. Only a few samples of older fish could be obtained, so the growth curve derived by vertebral ageing is tentative.

Because the von Bertalanffy growth curve does not describe well the early growth in this species, the derived lengths at birth (Table 4) show some variation from the observed size at birth of 52 cm TL (Stevens and Wiley 1986).

Results from vertebral ageing suggest average total lengths for 1-year-old sharks of 77 cm (females) and 83 cm (males). This is supported by the length-frequency data (Fig. 6), which, for January 1983, shows the first mode at 65 cm FL (82 cm TL) for females and 63 cm FL (80 cm TL) for males. For 2-year-old sharks, vertebral ageing indicates lengths of 91 cm for females and 94 cm TL for males. Equivalent modal lengths for January 1983 are 71 cm FL (90 cm TL) for females and 72 cm FL (91 cm TL) for males. Thus, for the first two year-classes, there is good agreement between vertebral ageing and length-frequency data. Beyond this, the length-frequency data for *C. sorrah* do not reveal clear modes.

Analysis of tag-recapture data (sexes combined) (Table 6) suggests an annual growth of about 10 cm for sharks up to 80 cm TL whereas vertebral ageing indicates a growth increment of 19 cm for *C. sorrah* females of a similar size. For sharks between 110 and 120 cm TL, the annual growth rate estimated from tag data is 2·0–2·6 cm while that from vertebral ageing is 2–5 cm per year.

Differences in growth rates and length-at-age values derived by modal analysis and from length-frequency data can be attributed in part to the sampling for vertebral ageing representing up to twelve year-classes, whereas modal analysis concentrates on the first few discernible year classes in the length-frequency data. The length-frequency data may also reflect a gill-net selectivity that favours the capture of faster-growing fish in their first year.

Tag returns for both species indicate a slower growth rate than is suggested by the other methods. Negative and zero growth in tagged sharks have been reported previously (Ketchen 1975; Casey *et al.* 1985). Gruber (1981) noted a slower rate of growth in tagged than in untagged lemon sharks, *Negaprion brevirostris*, held under semi-natural conditions. Possibly the stress of capture is reflected in a disrupted growth pattern. The vertebrae of the one tetracycline-injected *C. sorrah* specimen recaptured after 199 days at liberty fluoresced only at the periphery of the cone surface and in patches along the sides of the vertebra. This indicated that there had probably been no deposition of skeletal tissue since injection. The shark 'grew' a negative 2·5 cm during this period.

Histological examination of white sharks, *Carcharodon carcharias*, that had died a few days after capture revealed diffuse myonecrosis of skeletal musculature, suggestive of capture myopathy (P. Harper, Regional Veterinary Laboratory, Glenfield, New South Wales, personal communication). Capture myopathy, caused by anaerobic respiration in the muscle tissue, apparently due to the trauma of capture, often leads to severe debilitation or death. It has been reported in a range of avian and mammalian taxa (e.g. Anderson 1981; Windingstad *et al.* 1983). Although the effects on sharks of capture and tagging are not known, the evidence suggests that growth rates should not be deduced from tag-return data alone. Ketchen (1975) noted that tag-recapture information can provide a minimum estimate of growth. It can also indicate whether growth estimates from other methods are realistic.

It has been suggested that the growth parameters of elasmobranchs can be estimated independently of age-length data, assuming that pre- and post-natal growth rates are the same Holden (1974). By substituting the relevant life-history parameters for *C. tilstoni* and *C. sorrah* into Holden's equation $[l_{t+T}/L_\infty = 1 - \exp(-KT)]$, the following K values were obtained:

C. tilstoni; females $K = 0 \cdot 45$; males $K = 0 \cdot 54$.
C. sorrah; females $K = 0 \cdot 50$; males $K = 0 \cdot 61$.

These are well outside the range of K values (0·1–0·2) derived by Holden for other elasmobranchs, and the range of most of the K values obtained in this study (Table 2). In these two species, at least, the *in utero* growth rates are far higher than the *post-partum* growth rates: 60 cm (*C. tilstoni*) and 52 cm (*C. sorrah*) in just 10 months (Stevens and Wiley 1986).

Information in the literature indicates that there is considerable variation in growth between shark species. Beamish and McFarlane (1985) aged spiny dogfish, *Squalus acanthias*, to 70 years. This species matures at, on average, 23 years in females and 14 years in males, and grows between 1·5 and 3·3 cm per year (Ketchen 1975). The Australian school shark, *Galeorhinus galeus*, lives to at least 40 years; the females mature at 10 years (Grant *et al.* 1979). In contrast to the slow growth in spiny dogfish, length-frequency information analysed by Pratt and Casey (1983) for the mako, *Isurus oxyrinchus*, indicated growth rates of 55 cm per year for ages 0–1 and 36 cm per year for ages 1–2. The oldest shark in their samples was an 11·5-year female of 354 cm TL. The blue shark, *Prionace glauca*, is another fast-growing species. Using vertebral ring counts, Stevens (1975) reported that blue sharks grew from 45 cm at birth to a length of 300 cm in just 10 years. They reach maturity at about 220 cm TL (Pratt 1979) which is, using Stevens' vertebral ageing results, between 6 and 7 years of age. *Rhizoprionodon terraenovae* is a small shark that grows rapidly in the first two years (30 cm in year 1 and 15 cm in year 2) and matures early: males mature at 2·0–2·4 years (80–85 cm TL) and females at 2·4–2·8 years (85–90 cm TL) (Parsons 1985).

Mustelus manazo is a small shark that also matures early: at 2–3 years in both sexes, when males are about 60 cm and females 62–66 cm TL (Tanaka and Mizue 1979).

The relative growth rates [yearly growth increment/(maximum size – length at birth)] of a number of shark species are plotted in Fig. 8. *C. tilstoni* and *C. sorrah* display growth characteristics that are intermediate over the range of species described here. Relative growth in *C. sorrah* is reasonably fast over the first 3 years, but decreases more rapidly than in most other species illustrated. Comparisons of the growth information for *C. tilstoni* and *C. sorrah* with similar data for other species show that these sharks mature early. This is probably due to the large size at birth relative to their size at maturity. Both species reach sexual maturity between 2 and 4 years of age, which is comparable to the early maturation of the small sharks *Rhizoprionodon terraenovae* and *Mustelus manazo*. However, there is little evidence to date of such early maturation in other sharks of the genus *Carcharhinus*.

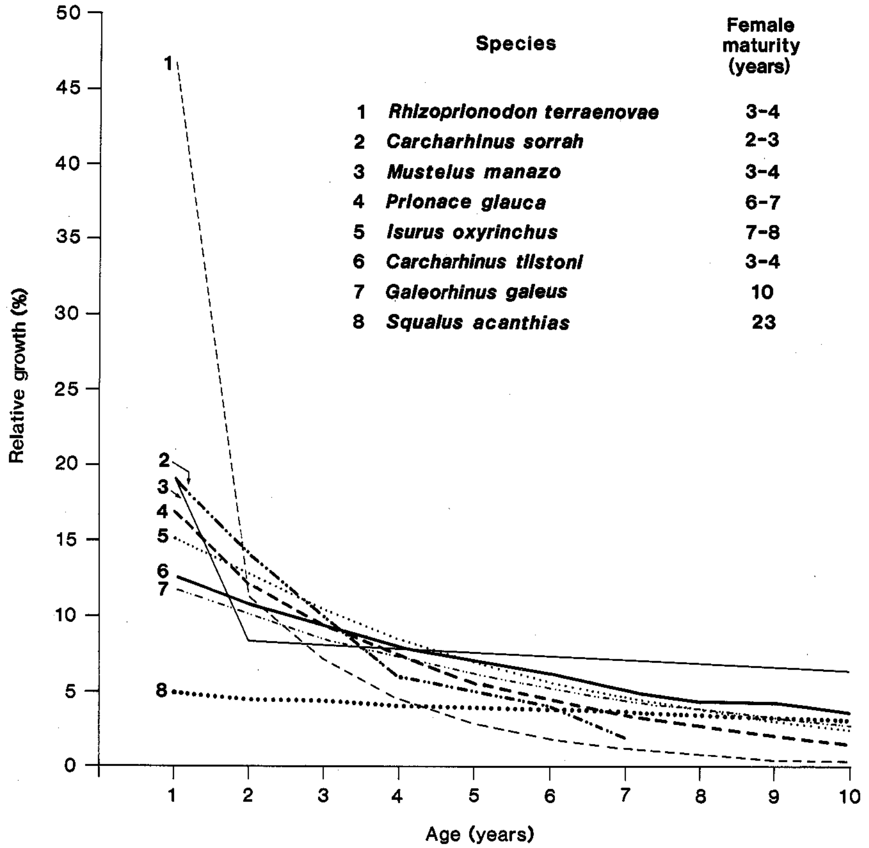

Fig. 8. Relative growth [yearly growth increment/(maximum size minus length at birth)] over the first 10 years of life in eight shark species: 1. *Rhizoprionodon terraenovae* (Parsons 1985). 2. *Carcharhinus sorrah* (this study). 3. *Mustelus manazo* (Taniuchi *et al.* 1983). 4. *Prionace glauca* (Cailliet *et al.* 1983*a*). 5. *Isurus oxyrinchus* (Pratt and Casey 1983). 6. *Carcharhinus tilstoni* (this study). 7. *Galeorhinus galeus* (Grant *et al.* 1979). 8. *Squalus acanthias* (Ketchen 1975).

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