Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia

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Synopsis

Age and growth were studied in *Rhizoprionodon taylori* using specimens caught in Cleveland Bay, North Queensland, Australia. Von Bertalanffy growth parameters were estimated using three different techniques: vertebral ageing, back calculation and length frequency. Vertebrae from 138 specimens were sectioned and narrow circuli counted to estimate age. Marginal increment analysis verified that circuli were produced annually in late summer, probably as a result of stress during the mating season. The oldest female was 7 and male 6 years old. Von Bertalanffy growth parameters estimated from vertebral ageing data for males were $t_O = 0.410$ yr, $K = 1.337$, $L_\infty = 652.2$ mm, and for females $t_O = 0.455$ yr, $K = 1.013$ and $L_\infty = 732.5$ mm. Growth parameters determined by length frequency and back calculation techniques concurred with those from vertebral ageing. Growth of the 0 + age class was very rapid, averaging 140% of the size at birth in the first year. Males and females matured after only one year, the lowest age at maturity reported in the family Carcharhinidae. Annual growth increments decreased rapidly after maturity, and little growth occurred after three years.

Introduction

The Australian sharpnose shark, *Rhizoprionodon taylori* (Ogilby, 1915), is a small species of shark of the family Carcharhinidae. It is endemic to the inshore waters of northern Australia (Compagno 1984) where it is one of the most common small sharks in coastal waters of Queensland. Mating occurs annually from late January to early February and is followed by a 11.5 month gestation period. This species has a unique reproductive style which involves a higher fecundity than other small carcharhinid species and a seven month period of embryonic diapause (Simpfendorfer 1992).

R. *taylori* is commonly caught by gillnet fisherman in coastal waters throughout its range. Information on its feeding and reproduction is available (Stevens & McLoughlin 1991, Simpfendorfer 1992 unpublished data), however, there is currently no information on its age and growth. Given the unique reproductive biology of this species, and the importance of it in commercial catches, the determination of age and growth information will provide an insight into the life-history of this species and its ability to withstand fishing pressure.

This paper presents age and growth data obtained from R. *taylori* caught in North Queensland. Vertebral ageing, using counts of narrow circuli present on sections of centra, was the primary method of determining age. Back calculation and length frequency techniques were also utilised as a comparison to the vertebral ageing results.
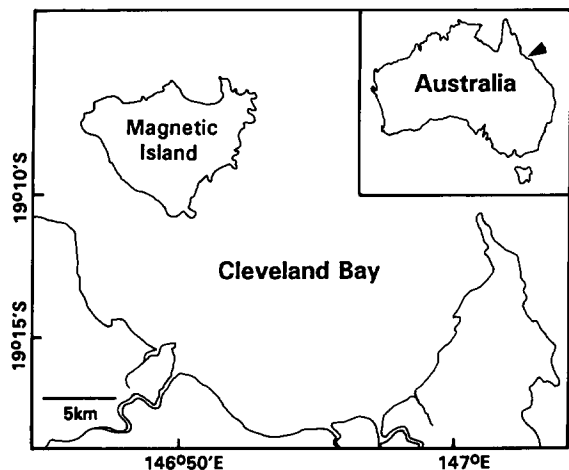
Fig. 1. Map showing the location of the study area.

Materials and methods

Four hundred and sixty five *Rhizoprionodon taylori* specimens were caught between May 1986 and January 1990 in Cleveland Bay, Queensland (Fig. 1) using 5 and 10 cm monofilament gillnets, and otter trawls. The total length (TL, the distance from the tip of the snout along the body to a point perpendicular to the tip of the tail, with the tail in its natural position) and fork length (FL, distance from the tip of the snout to the posterior fork of the tail) of all specimens were measured to the nearest millimetre. A significant linear relationship existed between TL and FL ($r^2 = 0.8502$, d.f. = 453, p < 0.001):

$$TL = 1.1632(FL) + 15.2. \tag{1}$$

Several vertebrae anterior to the first dorsal fin were removed from a sub-sample of 138 specimens. This sub-sample was selected to represent the full size range of this species (230–780 mm). The vertebrae were frozen until prepared for ageing. Vertebrae were prepared by separating them, removing excess tissue and soaking in 5% sodium hypochlorite for 30 minutes. Following their immersion in sodium hypochlorite the vertebrae were thoroughly washed and then allowed to dry. Dry vertebrae were mounted horizontally on glass micro-scope slides and ground using 120–360 grit wet and dry abrasive paper to just above the centre of the centrum. They were then remounted on the flat surface and the other side ground to produce a thin (200–400 micrometers) horizontal section.

Narrow translucent circuli were observed in the corpus calcareum of sectioned vertebrae (Fig. 2). The narrow width of the circuli suggested that they were check marks, rather than growth bands that have been observed by many other authors (for examples see review by Cailliet et al. 1986). The circuli were counted in two vertebrae from each specimen. Counts were made without knowledge of the size or sex of the specimen. If the counts varied between the two vertebrae a third was sectioned and counted. If the count of the third vertebra matched either of the previous two it was taken as the count. If there was no agreement between any of the three samples then that specimen was excluded from the analysis. This counting procedure was repeated and the estimated ages between readings compared. Errors in the counting of the circuli in the vertebrae were estimated using the Index of Average Percentage Error (IAPE) described by Beamish & Fournier (1981):

$$IAPE = \frac{1}{N} \sum_{j=1}^{N} \left(\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right) \times 100, \tag{2}$$

where N is the number of fish aged, R is the number of readings done, X_{ij} the age of the jth fish at the ith reading, and X_j the mean age of the jth fish.

The periodicity of the formation of circuli was determined by marginal increment analysis. Marginal increments were calculated by measuring the distance between the last circulus and the edge of the centrum using an optical micrometer on a high power microscope.

Back calculation analysis was undertaken using a method described by Francis (1990). The length of a specimen when the ith band was laid down (L_i) was calculated using the equation:

$$L_i = (S_i/S_c)^v L_c, \tag{3}$$

where S_i is the radius of the ith band, S_c is the radius of the vertebra at capture, L_c the length of the
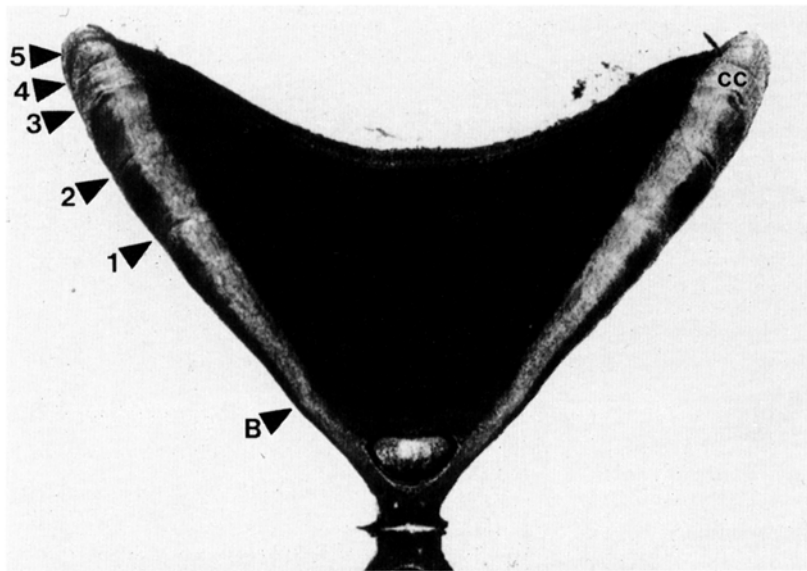
Fig. 2. Section of a centrum from a 738 mm TL female caught in January and estimated to be 5 + years. Arrows indicate circuli; B = circulus formed at birth; 1–5 = circuli formed after 1–5 years; cc = corpus calcareum.

specimen at capture, and v is a constant derived from the power equation:

$$L = uS^v. \tag{4}$$

Equation (4) describes the relationship between the radius of the vertebra (S) and the length (L), with u being a constant. When the relationship between L and S is isometric, u equals one, and equation (3) reverts to the Dahl-Lea equation (Francis 1990).

Length frequency data were analysed using the ELEFAN I program (Pauly 1987). Data for males and females were analysed separately, except for juveniles which were combined because of small sample sizes. Data from specimens caught within months were pooled, as were months between years, to provide sufficient data for analysis.

Maturity in males and females was judged using the criteria used by Springer (1960) and Clark & von Schmidt (1965). Males were considered mature when the claspers were elongate and fully calcified. Females were considered mature when the ovaries contained enlarged ova, or the uteri were enlarged and contained eggs or embryos. Juveniles caught just after birth were distinguished by the presence of a fresh umbilical scar between the pectoral fins.

Results

Centrum morphology

Centrum growth was not significantly different between males and females (t-test, $p > 0.05$) and was allometric (Fig. 3, $v = 0.707, 95\%$ C.I. $= 0.038$). The relationship, however, did not adequately describe the growth of centra early in life, passing above the points of the youngest individuals caught. The allometric growth of centra necessitated the use of the non-linear back calculation method given in equation 3.

All specimens were found to have at least one circulus, which was assumed to be formed at birth. This birth circulus was associated in many specimens with a change in angle of the corpus calcareum, a characteristic of marks formed at birth in other species (e.g. Casey et al. 1985, Branstetter 1987a). The mean back calculated size at which this first mark was formed was 291 mm TL.
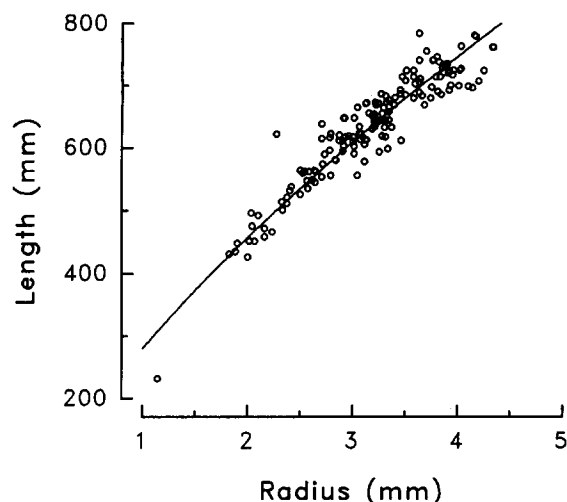
Fig. 3. Relationship between centrum radius and total length for 151 *Rhizoprionodon taylori* caught in Cleveland Bay, Queensland.

The circuli on older specimens were close together and marginal increments were calculated only for specimens that had four or less circuli (including the circulus formed at birth). The smallest of these marginal increments occurred during February, while the largest increments were present in specimens from November to January (Fig. 4). Circuli, therefore, apparently form annually in February, or possibly January.

Length at age

The pupping season of *R. taylori* in Cleveland Bay lasts only two weeks (Simpfendorfer unpublished data) and means that the age of individuals could be calculated from the number of circuli and the time since the birth date. A common birth date of January 15th was used, which corresponds to the middle of the pupping season. The oldest male specimen examined was estimated to be 5.7 years old, and the oldest female 6.9 years. The youngest individuals examined were estimated to be 9 days old and measured from 230–250 mm TL. The largest male examined was 691 and largest female 784 mm TL.

More than 66% of circuli counts from individual specimens at each reading matched, and over 93%
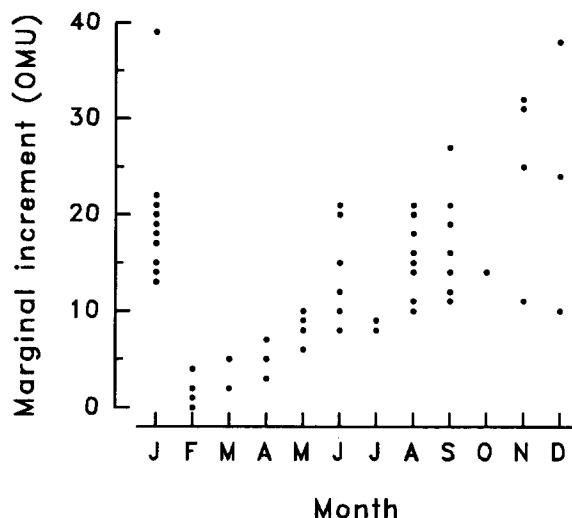

Fig. 4. Marginal increments for *Rhizoprionodon taylori* from Cleveland Bay, Queensland, based on individuals with 4, or less, circuli (including the circulus formed at birth). 1 OMU = 0.027 mm.

were within one circulus (Table 1). Agreement between readings was higher, with over 85% matching and over 99% within one circulus. The error associated with each reading was similar, while the between readings error was lower than error for individual readings.

Von Bertalanffy growth curves were fitted to length at age data for males and females separately (Fig. 5, 6) because of the large difference in the maximum sizes. Initial growth was very rapid with both males and females growing approximately 315 mm in their first year. Subsequently males on average grew 80 mm in their second year and

Table 1. Differences in the circuli counts of vertebrae from *Rhizoprionodon taylori* and errors (IAPE) for readings and between readings.

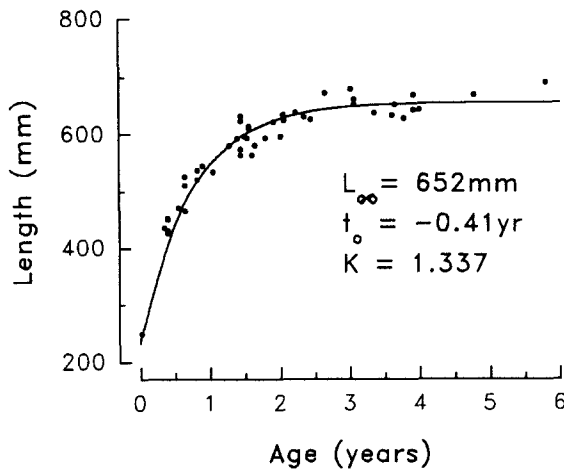| Difference in circulus counts	1st reading (%)	2nd reading (%)	Between readings (%)
0	66.7	71.2	85.9
1	30.8	22.6	13.3
2	2.5	4.8	0.8
3	0	1.4	0
IAPE	17.3	14.9	8.09

Fig. 5. Von Bertalanffy growth curve fitted to length at age data for 52 male *Rhizoprionodon taylori* caught in Cleveland Bay, Queensland.
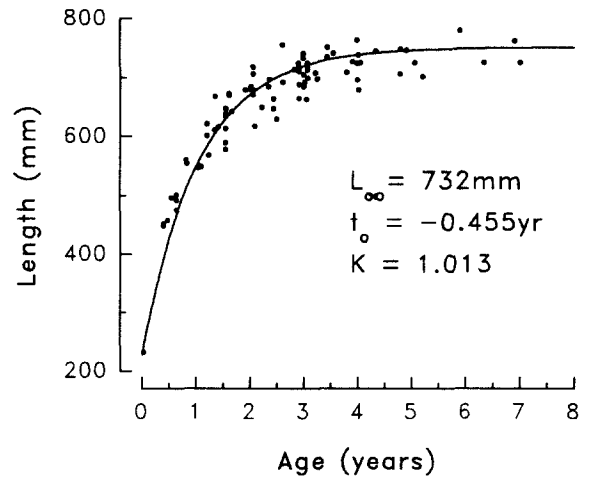

Fig. 6. Von Bertalanffy growth curve fitted to length at age data for 85 female *Rhizoprionodon taylori* caught in Cleveland Bay, Queensland.

20 mm in their third. Females on average grew 125 mm in their second year and 50 mm in their third. Little growth occurred after three years in males or females. The variability of growth was large, with individuals of a similar age covering a wide range of sizes.

Back calculated sizes at which circuli formation occurred were also variable (Table 2). Estimates of von Bertalanffy growth parameters based on these back calculated data were similar to those from the length at age data.

Length frequency

The results of length frequency analysis using ELE-FAN I are shown in Fig. 7. The 0 + individuals show a distinct modal progression with very rapid growth from birth until May. However, modes were much less apparent in later age groups. The estimates of L_∞ and K which gave the best fit to the data are given in Table 3. ELEFAN I does not estimate values of t_0 but the growth curves produced indicate that they are between − 0.3 and − 0.4 years for males and females. The pooling of length data from juvenile males and females should not effect the results as vertebral ageing suggested that they grow at similar rates.

Table 2. Back calculated lengths at circuli formation, and von Bertalanffy growth parameters calculated from these data, for *Rhizoprionodon taylori* from Cleveland Bay. Lengths are in millimetres and are shown as range and mean (in parentheses).

Circulus	Male	Female
B (birth)	247–334 (291)	232–333 (291)
1	483–580 (530)	490–692 (544)
2	546–657 (594)	584–721 (640)
3	572–644 (617)	619–738 (685)
4	590–660 (631)	636–738 (704)
5	606–679 (653)	716–748 (726)
L_∞	630	715
t_0	− 0.519	− 0.586
K	1.20	0.894

Table 3. Estimates of von Bertalanffy growth parameters for male and female *Rhizoprionodon taylori* from ELEFAN I.

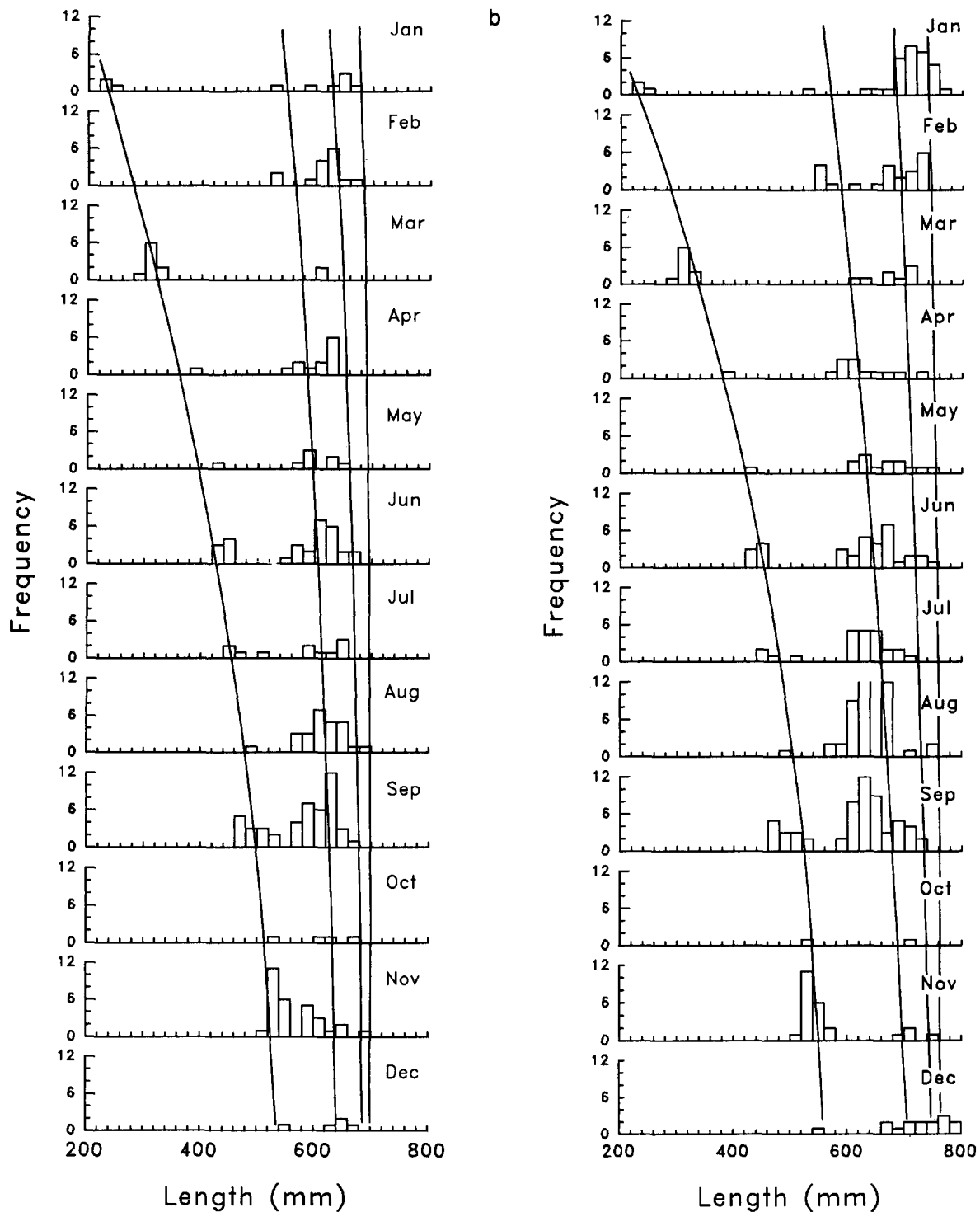| Sex	Parameter	
	L_∞ (mm)	K
Male	685	1.3
Female	775	1.0

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Fig. 7. Length frequency data for (a) male and (b) female *Rhizoprionodon taylori* caught in Cleveland Bay, Queensland. The von Bertalanffy growth curves calculated using ELEFAN I for the first four years are shown. Data for juvenile males and females (< 580 mm TL) are combined.

Size and age at maturity

Based on length at age data, male and female *R. taylori* matured after a single year's growth, at a size of approximately 550 mm TL. Both 0 + males and females began to mature in September or October at approximately 500 mm TL, but were not fully mature until just prior to mating.

Discussion

Beamish & McFarlane (1983) pointed out that for length at age data to be meaningful the periodicity with which the bands or circuli within the centrum are produced needs to be verified. The results of the marginal increment analysis, as well as the similarity of von Bertalanffy parameters between length at age, back calculation and length frequency techniques indicate that the periodicity of the circuli in *R. taylori* in Cleveland Bay is annual. Annual production of bands or circuli have been reported in a number of carcharhinid species (Cailliet 1990). The production of circuli in January or February coincides with the mating season and may result from stress during this period. During mating the hepatosomatic index and condition factor of both male and female *R. taylori* are low, indicating that individuals are probably stressed (Simpfendorfer unpublished data).

The accuracy of the von Bertalanffy growth parameters determined from the vertebral ageing technique is corroborated by the similarity of parameters determined from back calculation and length frequency data. Although useful as a check for vertebral ageing techniques the back calculation and length frequency techniques had limitations. As Cailliet (1990) observed, 'When . . back-calculated curves are compared with those from other methods, they provide only a check on the growth model used, and are actually more useful for providing data on sizes of missing age classes' (p. 159). The use of length frequency analysis in *R. taylori* was limited because of the rapid decline in annual growth increments and variability in growth. Analysis was only possible due to the distinct 0 + age class. Analysis of the data without the 0 + age class failed to yield comparable results as later age classes were not distinct. Length frequency techniques were also limited because of the need to pool samples within months and between years.

Although more than 93% of circuli counts matched, or were within one of each other, the values of IAPE were higher than previously reported for sharks. Brown & Gruber (1988), for example, reported an IAPE value of 3.4% for *Negaprion brevirostris*. High values of IAPE were obtained for *R. taylori* because its short life-span meant that even small discrepancies in counts produced a sizeable error relative to the life-span.

The size at birth estimated by back calculation is larger than that observed from neonates and full-term embryos (Simpfendorfer unpublished data). This over-estimation probably resulted from the vertebral radius-total length relationship not adequately describing growth of centra in young individuals. Additionally, if the birth mark is produced after birth then the rapid growth of the juveniles could result in it producing the over-estimate. The over-estimation of the size at birth by back calculation probably resulted in the slightly lower value of K determined by this technique as compared to vertebral ageing or length frequency techniques.

The sizes at maturity of *R. taylori* determined in this study were similar to those given by Simpfendorfer (1992) for the same area based on reproductive characters. However, the size at maturity in Cleveland Bay is larger than that reported from the Northern Territory and northern Western Australia by Stevens & McLoughlin (1991) who reported males mature at 400 mm TL and females at 450 mm TL.

The growth parameters of *R. taylori*, and the age at which they attain maturity, is not typical of the family Carcharhinidae. Most carcharhinid species studied to date have been found to have slow growth rates and to mature after several years. Normal growth of carcharhinid species during the first year is 20–60% of the birth length (BL), with the highest values previously recorded in *Rhizoprionodon terraenovae* (69% BL), *Prionace glauca* (90% BL), and *Galeocerdo cuvier* (100% BL) (Branstetter 1990). By comparison *R. taylori* grows 140% BL in its first year. Annual growth incre-

ments also decrease more rapidly in *R. taylori* than in other species.

The high initial growth and rapid decrease in annual growth increments give *R. taylori* its high values of K (females 1.01, males 1.33). Typical K values of carcharhinid species are 0.05–0.2, with some smaller species having the highest values (e.g. *R. teraenovae* 0.35–0.50 (Parsons 1983, Branstetter 1987b) and *Carcharhinus sorrah* 0.34–1.17 (Davenport & Stevens 1988)). Ages at maturity determined for other species of carcharhinid sharks vary from 2 years in *Scoliodon laticaudus* (Pratt & Casey 1990) to 18 years in *Carcharhinus leucas* (Branstetter & Stiles 1987). Maximum ages determined by vertebral analysis for carcharhinid species range from 8 years in *Rhizoprionodon terraenovae* (Parsons 1983) to 30 years in *Carcharhinus obscurus* (Hoenig & Gruber 1990).

The evolution of rapid early growth, early maturity and short life-span in *R. taylori* are probably the result of high levels of predation. Branstetter (1990) suggested that predation on sharks less than 100 cm TL was normally high since they are less proficient swimmers and a more edible size. If, as this suggests, the chances of a shark being consumed is inversely related to body size, then selection pressure will favour individuals that grow rapidly after birth and reproduce at an early age. Concomitantly, with a short life-span, selection would favour individuals that reproduced at an early age and produced as many young as possible. Simpfendorfer (1992) reported that *R. taylori* produces more young than most other carcharhinid species of a comparable size. This strategy results in large amounts of investment in reproduction, thus reducing the energy available for growth. Growth subsequent to maturity is therefore slow.

The unique life history parameters of *R. taylori* described in this study have important implications for fished stocks of this species. Rapid growth and early maturity mean that it is better placed to withstand fishing pressures than other species of carcharhinid sharks. Although fecundity is higher than other comparably sized species of carcharhinid sharks recruitment is dependent upon stock size and strict management is required to produce long-term sustainable yields.

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