

Reproductive Strategy of the Australian Sharpnose Shark, *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay, Northern Queensland

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Abstract

Reproduction and early embryo development of *Rhizoprionodon taylori* from Cleveland Bay, Queensland, was studied on the basis of 455 specimens caught between May 1987 and February 1990. Males and females mature at sizes larger than those reported from northern Western Australia, the Northern Territory and far northern Queensland. Mating occurs annually in summer, and the gestation period is approximately 11.5 months. After development to a small blastodermic disc, the embryos enter a state of diapause that lasts approximately 7 months. *R. taylori* is the only species of shark that is known to have a period of embryonic diapause. The litter size ranges from 1 to 10 (mean 4.5), being markedly larger than that for other carcharhinid species of a similar size. The size at birth is 220-260 mm. The reproductive and developmental traits are discussed in relation to the life histories of this species and other carcharhinids.

Extra keywords: embryonic diapause, life history.

Introduction

The family Carcharhinidae contains the most abundant species of sharks that occur in tropical and subtropical inshore waters. The life histories of many of these species have been examined (e.g. Springer 1960; Teshima and Mizue 1972; Wass 1973; Bass *et al.* 1973, 1975; Randall 1977; Teshima *et al.* 1978; Parsons 1983; Stevens and Wiley 1986; Lyle 1987; Lessa 1988; Stevens and McLoughlin 1991). These studies reveal that there is a consistent pattern in the life histories of species within the family. A typical carcharhinid has an annual reproductive cycle, mates in summer, is viviparous, has a gestation period of between 10 and 12 months, has small litter sizes, and has fully developed young at birth. Not all species conform fully to this life-history pattern. For example, *Carcharhinus dussumieri* from the waters off Borneo has a nonseasonal breeding pattern (Teshima and Mizue 1972), *Galeocerdo cuvier* has ovoviviparous development (Compagno 1988), and larger species often have biennial reproductive cycles (e.g. Clark and von Schmidt 1965; Bass *et al.* 1973; Branstetter 1981).

Rhizoprionodon taylori (Ogilby, 1915) is a small species of carcharhinid shark (maximum length 78 cm) that is endemic to the waters of northern Australia (Compagno 1984). It is the most abundant species of shark caught in gill-nets in Cleveland Bay and is present throughout the year (Simpfendorfer, unpublished data). There has been little previous work on the biology of *R. taylori*. Whitley (1939) briefly described an embryo and placenta. Simpfendorfer (1986) presented results from a preliminary study on the biology of *R. taylori* from Cleveland Bay, and Stevens and McLoughlin (1991) have reported briefly on data from northern Western Australia, the Northern Territory and far northern Queensland.

In reporting the reproductive biology of this species, Simpfendorfer (1986) observed, 'Fertilised eggs were present in the uteri of mature females from all samples [May–August], however no distinct embryos were observed' (p. 55). This was the first indication that this species had an unusual development pattern and was subsequently corroborated by Stevens and McLoughlin (1991).

The present paper presents the results of a more comprehensive study on *R. taylori* in Cleveland Bay. The aims were to examine the reproductive biology, investigate the nature of the embryo development, and further investigate the lack of embryo development reported by Simpfendorfer (1986).

Materials and Methods

Samples were collected from Cleveland Bay, northern Queensland (19°15'S, 146°55'E), between May 1987 and February 1990. Specimens were caught at night with 5- and 10-cm monofilament gill-nets.

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 the fork length (FL—the distance from the tip of the snout to the posterior fork of the tail) of specimens were measured to the nearest millimetre. The relationship between fork length and total length for specimens from Cleveland Bay is given by

$$TL = 1.1632(FL) + 15.2. \quad (1)$$

This relationship is significant ($r^2 = 0.8502$, d.f. = 453, $P < 0.001$) and was used to estimate the total length of specimens with damaged caudal fins. The clasper length of male specimens was measured from the tip of the clasper to its junction with the pelvic fin. Specimens were weighed to the nearest gram with an electronic balance.

The sex of specimens was recorded along with their state of maturity. Males were adjudged mature if the claspers were elongate and fully calcified; otherwise, they were considered juveniles. Mature females were distinguished by the presence of large yolky eggs in the ovary or uterus or by the presence of intrauterine embryos. A sub-adult category was used to differentiate females in which the ova were undergoing vitellogenesis but which had not mated as shown by the presence of a hymen. All other females were considered juveniles.

The gonads were dissected out of specimens and weighed on an electronic balance to the nearest 0.1 g. Weights of gonads were used to calculate gonadosomatic indices (GSIs) from the equation

$$GSI = \frac{\text{gonad weight}}{\text{total weight}} \times 100. \quad (2)$$

The timing of the mating period was determined for male specimens by the presence of large quantities of spermatozoa in the ductus epididymus. To examine the contents of these ducts, a transverse cut was made across the kidney region of the dorsal body wall. A large amount of milky white fluid running from the cut indicated that spermatozoa were present and was taken as an indicator that mating was soon to occur.

Two forms of uterine eggs were found in the uteri of mature females. Eggs that showed no macroscopic signs of embryo development were designated as Stage I. Eggs on which macroscopic development of embryos was visible were designated as Stage II. Stage I and II eggs were excised, weighed and preserved. Free embryos, with attached yolk sac or placenta (post Stage II), were measured to the nearest millimetre, weighed and sexed. Oviducal glands from mature females were also excised and preserved for histological examination. Mature females that had recently given birth were identified by the uteri being enlarged and flaccid but not containing embryos. Recently pupped young were distinguishable by the presence of an umbilical scar between the pectoral fins.

The preserved Stage I eggs were examined for development by histological staining of serial sections. Eggs were embedded in wax, sectioned serially at 8–10 μm , and stained with Mayer's haematoxylin and eosin, Mallory–Heidenhain trichrome, Martius Scarlet Blue (MSB) or iron haematoxylin. Best results were obtained with MSB staining. Oviducal glands were similarly prepared but sectioned at 6–8 μm .

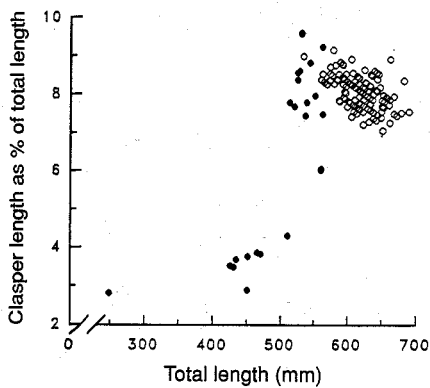


Fig. 1. Relationship of clasper length (as a percentage of total length) to total length in 165 male specimens of *Rhizoprionodon taylori* from Cleveland Bay. ● Uncalcified, ○ calcified claspers.

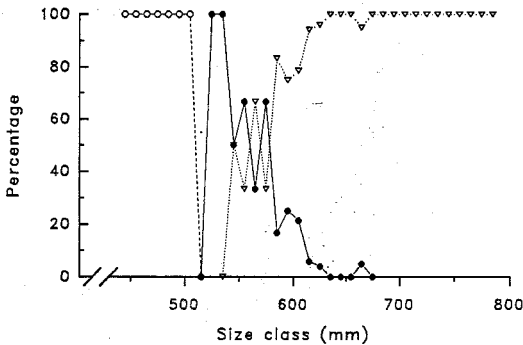


Fig. 2. Percentage of maturity groups (juvenile, subadult and adult) in 10-mm size classes of the female *Rhizoprionodon taylori* population from Cleveland Bay. ○, Juveniles; ●, sub-adults; ▽, adults. See text for description of maturity groups.

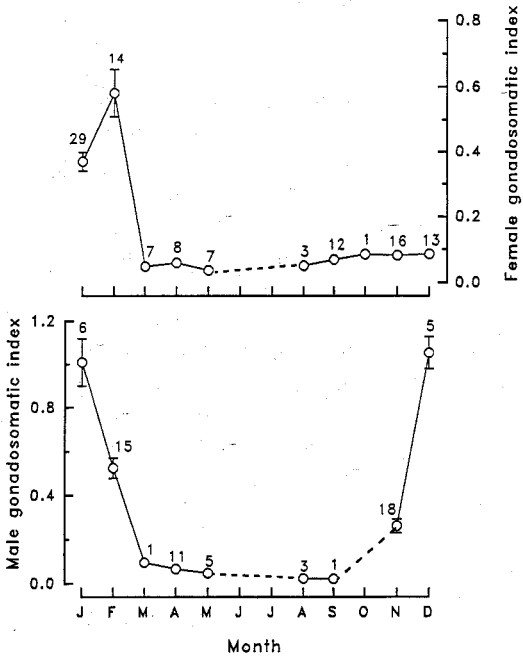


Fig. 3. Mean monthly values of gonadosomatic index for male and female specimens of *Rhizoprionodon taylori* from Cleveland Bay. Error bars, ± 1 s.e.; numbers, sample sizes.

Results

Reproductive Biology

The claspers of males of *R. taylori* become elongate at approximately 510 mm TL, and most were fully calcified at 560 mm TL (Fig. 1). Similarly, all females less than 510 mm TL are juveniles, and those between 520 and 540 mm TL are all sub-adults (Fig. 2); 50% of females are mature at approximately 575 mm TL.

The monthly mean values of GSI for both males and females are shown in Fig. 3. There is only a single peak in male and female GSI values throughout the year, indicating that *R. taylori* from Cleveland Bay mates only once each year. Male GSI values peak in December and January. Female values are highest later, in January and February.

A more accurate estimate of the timing of the mating period of *R. taylori* was determined from observations on dissected specimens. During mid-January to early February, large amounts of spermatozoa were present in the ductus epididymus of male specimens. During late January and early February, female specimens frequently had light scarring on the dorsal side consistent with the mating scars reported for other species of carcharhinid shark (Springer 1967; Pratt 1979). This evidence indicates that *R. taylori* mates from late January to early February in Cleveland Bay.

The litter sizes of *R. taylori* from Cleveland Bay range from 1 to 10, with a mean value of 4.5. There is a significant relationship between the litter size and the body size of individual females ($r^2 = 0.3062$, d.f. = 218, $P < 0.001$), with the largest females producing the largest litters. Adult females with the largest embryos were caught in early and mid-January, and those with enlarged flaccid uteri were caught in mid-January. This indicates that pupping occurs in mid-January. Full-term embryos from females caught during mid-January ranged in size from 220 to 261 mm TL. Newly pupped individuals caught in January measured between 232 and 249 mm TL. The normal size at birth of *R. taylori* in Cleveland Bay thus appears to range from 220 to 260 mm TL.

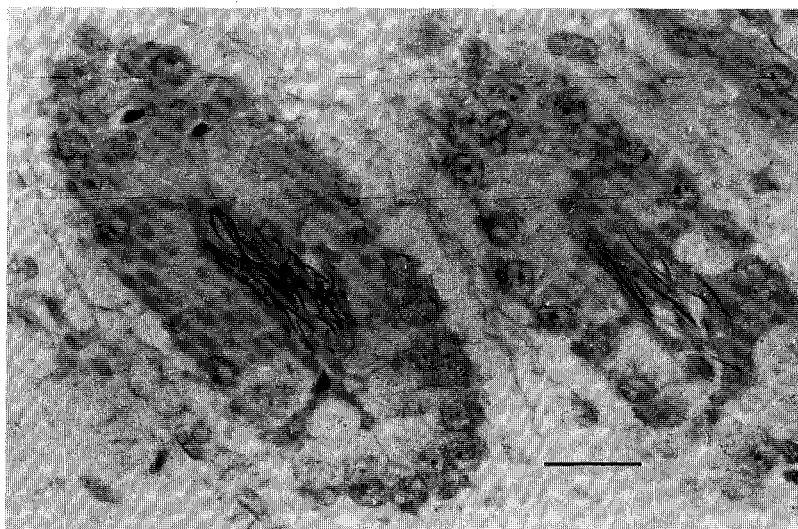


Fig. 4. Section through tubules in the oviducal gland of an adult female specimen of *Rhizoprionodon taylori* caught in early February, showing the presence of spermatozoa. Scale bar, 0.02 mm.

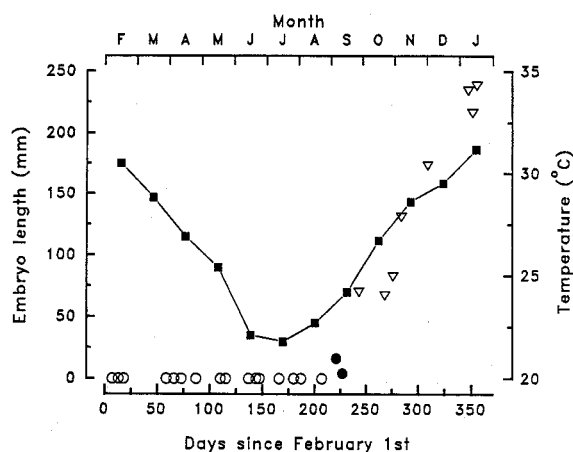


Fig. 5. Growth of *Rhizoprionodon taylori* embryos. ○, Stage I uterine eggs; ●, Stage II uterine eggs; ▽, free embryos; ■, mean monthly sea surface temperature for Townsville (from Kenny 1974).

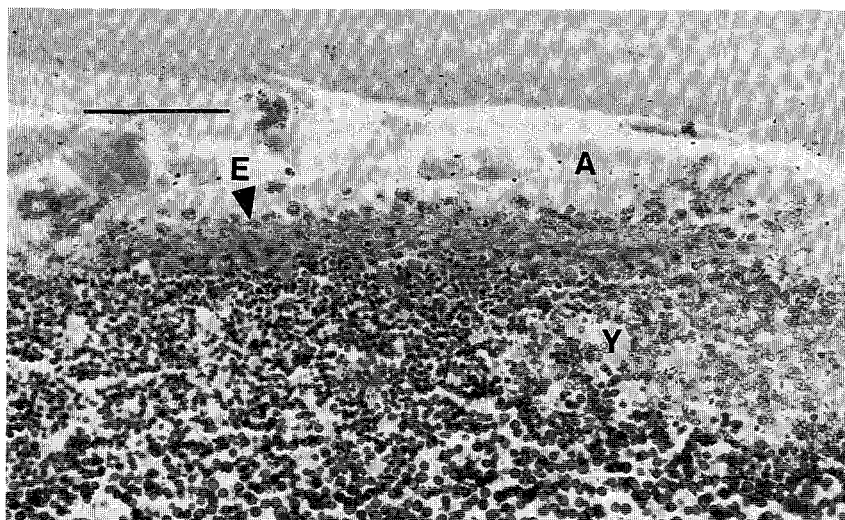


Fig. 6. Section through a Stage I uterine egg of *Rhizoprionodon taylori*, showing (E) the diapausing embryo located between (Y) the yolk and (A) the albumen. Scale bar, 0.1 mm.

Embryo Development

Ova were observed in oviducts in early February. These ovulated ova pass down the oviducts, through the oviducal gland, and into the uteri. Spermatozoa are stored in tubules in the oviducal gland (Fig. 4) between mating and ovulation but were not present during the rest of the year. The stored spermatozoa are presumed to fertilize the eggs as they pass through the oviducal gland. Also in the oviducal gland, the ova are encapsulated in a thin membranous egg case that persists until parturition.

Eggs or embryos were present in the uterus between February and the following January. Stage I eggs were recorded in the uterus from ovulation through to September, Stage II eggs only during September, and free embryos from October onwards (Fig. 5). Histological sectioning of Stage I eggs revealed that development progressed to a blastodermic disc stage (Fig. 6) that is approximately 1.9 mm in diameter, and this persisted until development

recommenced in September. The blastodisc is bilaminar and is located on the dorsal side of the oval-shaped uterine eggs. The first macroscopic evidence of embryo development occurred in September of each year during this study, when Stage II eggs were observed. The commencement of normal embryo development coincided with increasing sea temperatures after winter, and parturition occurred during the period of maximum water temperature (Fig. 5).

Discussion

Reproductive Biology

Stevens and McLoughlin (1991), using similar criteria for determining maturity, reported that *R. taylori* from northern Western Australia, the Northern Territory and far northern Queensland matures at 400 and 450 mm TL for males and females, respectively. This is significantly smaller than the lengths observed from Cleveland Bay. The maximum size of *R. taylori* observed in Cleveland Bay (males 691 mm TL, females 784 mm TL) also was larger than that reported by Stevens and McLoughlin (1991) (males 550 mm TL, females 660 mm TL). Therefore, the size at maturity, relative to the maximum size, in each area is similar (82 versus 72% for males, 73 versus 68% for females). Growth differences thus occur between these two areas. The size at birth observed in specimens from Cleveland Bay is smaller than that estimated by Stevens and McLoughlin (1991). However, these authors were not able to obtain juvenile specimens and used a literature value for the smallest free-swimming juveniles. Other reproductive traits (timing of the reproductive cycle, litter size, relationship between litter size and female length, and timing of the reproductive cycle) in *R. taylori* from Cleveland Bay are similar to those reported by Stevens and McLoughlin (1991).

Compagno (1988) recognized that, in viviparous species of the families Carcharhinidae, Hemigaleidae and Sphyrnidae, there was a correlation between the maximum length of a species and the maximum litter size it will produce. Compagno used the equation

$$\text{litter size} = -2.2 + (0.061 \times \text{maximum length}) \quad (3)$$

to describe this relationship, with the maximum length expressed in centimetres. Fig. 7 illustrates this relationship for the family Carcharhinidae and includes two values for *R. taylori*: one given by Compagno (1984) on the basis of a single observation by Whitley (1939), and the other from the present study. Although most carcharhinid species fit the relationship described by Eqn 3, *R. taylori* (from this study) and two other species do not. The other species that do not fit the relationship are *Scoliodon laticaudus* and *Prionace glauca*. In all three species, the litter size is larger than is predicted by Eqn 3.

Both small species that deviate from the typical carcharhinid maximum size–litter size relationship have small sizes at birth: 14 cm for *S. laticaudus* (Teshima *et al.* 1978) and 22–26 cm for *R. taylori*. These are the smallest sizes at birth recorded for the family. Given that development in carcharhinid sharks is internal, and thus that space within the mother is limited, there is a direct trade-off between litter size and the size of the young. The small size at birth and the larger than normal size of litters indicate that *R. taylori* has evolved a reproductive strategy that differs from most others occurring in the family Carcharhinidae.

Embryo Development

The lack of development beyond the blastodermic disc stage from February to September indicates that Stage I uterine eggs of *R. taylori* contain embryos in a state of diapause that persists for approximately 7 months. In other species of carcharhinid sharks, Stage I eggs persist for only a few hours or days (TeWinkel 1963). The report by Stevens and

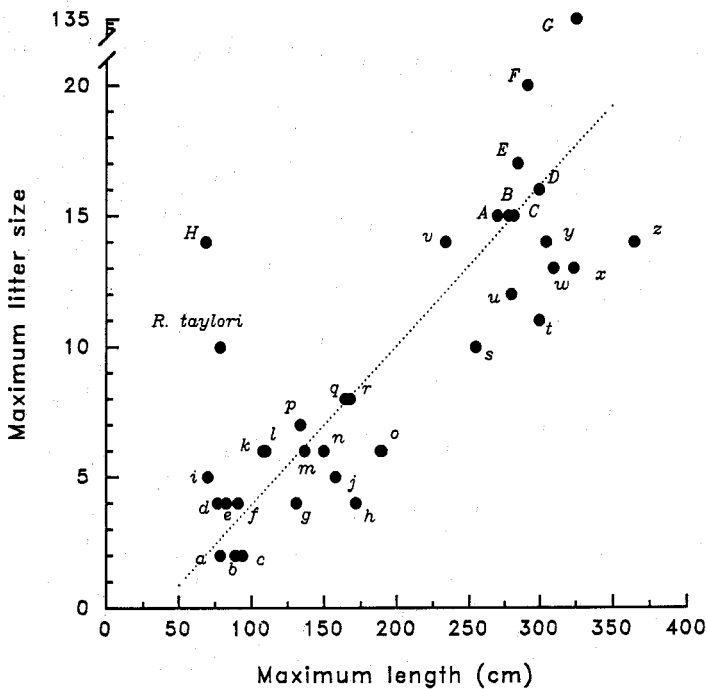


Fig. 7. Relationship between maximum length and maximum litter size for species in the family Carcharhinidae. Data for *Rhizoprionodon taylori* are from this study, all other data are from Compagno (1984). Dotted line, Eqn 3. (a) *Rhizoprionodon taylori* (Compagno's estimate), (b) *Carcharhinus macroti*, (c) *C. sealei*, (d) *R. lalandii*, (e) *C. dussumieri*, (f) *Loxodon macrorhinus*, (g) *C. melanopterus*, (h) *C. wheeleri*, (i) *R. oligolinx*, (j) *Triaenodon obesus*, (k) *R. porosus*, (l) *R. terraenovae*, (m) *C. acronotus*, (n) *C. sorrah*, (o) *C. amblyrhynchos* and *C. isodon*, (p) *C. porosus*, (q) *R. acutus*, (r) *Lamiopsis temmincki*, (s) *C. limbatus*, (t) *C. albimarginatus*, (u) *C. signatus*, (v) *C. plumbeus*, (w) *Negaprion acutidens*, (x) *C. leucas*, (y) *C. falciformis*, (z) *C. obscurus*, (A) *C. longimanus*, (B) *C. brevipinna*, (C) *C. altimus*, (D) *C. galapagensis*, (E) *N. brevisstris*, (F) *C. brachyurus*, (G) *Prionace glauca*, (H) *Scoliodon laticaudus*.

McLoughlin (1991) from northern Western Australia, the Northern Territory and far northern Queensland of a similar period during which embryo development does not proceed suggests that diapause is characteristic of this species.

Embryonic diapause in *R. taylori* possibly evolved in conjunction with the small size at birth and the large litter size. A reduction in the size at birth would permit decreased development times and so open up the possibility of a period of diapause. The reason for the evolution of diapause as opposed to functionally similar mechanisms observed in other species of viviparous sharks—reduced gestation periods (e.g. *Sphyrna tiburo*, Parsons 1987) or delayed fertilization (e.g. *Prionace glauca*, Pratt 1979)—is unknown. However, it implies an evolutionary advantage for embryonic diapause over these other mechanisms in *R. taylori*. The timing of the diapause period also enables *R. taylori* to produce its young when environmental conditions are most favourable. The young are born when the sea temperature is highest, and so higher growth rates can be achieved than if they were born during colder months. This is particularly important in species with a small size at birth, such as *R. taylori*, because rapid growth reduces the risk of predation (Branstetter 1990).

R. taylori in Cleveland Bay achieves very high growth rates during the months after birth, doubling in size in approximately 4 months (Simpfendorfer, unpublished data). Reports of embryonic diapause in other animal groups also indicate that diapause enables these groups to produce young when conditions are favourable (e.g. mammals, Renfree 1978; teleosts, Kroll 1984; insects, Braune 1973; copepods, Ianora and Santella 1991).

R. taylori is the only species of elasmobranch in which embryonic diapause has been positively identified. However, uterine eggs that do not develop immediately have been reported for two species of batoids. Lessa *et al.* (1986) reported that no development occurred in the uterine eggs of *Rhinobatus horkelli* between April and December, and Snelson *et al.* (1989) observed that 'zygote development was arrested' (p. 23) from June through to March in *Dasyatis sayi*. Aside from reporting that these species did not develop embryos immediately following ovulation, these authors did not provide any further information. However, the pattern of development in both species is similar to that observed in *R. taylori*—macroscopic development of embryos does not occur immediately after ovulation but commences more than halfway through the gestation period—suggesting that these species also have a period of diapause. The occurrence of this pattern of development in three divergent groups of elasmobranchs (Rhinobatidae, Dasyatidae and Carcharhinidae) indicates that it has evolved separately on each occasion. Further work on embryonic diapause in elasmobranchs needs to be undertaken before the full implications of this unique life-history trait are understood.

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