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Biology of Tiger Sharks (*Galeocerdo cuvier*) Caught by the Queensland Shark Meshing Program off Townsville, Australia

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Abstract

The biology of 835 specimens of *Galeocerdo cuvier* caught between 1964 and 1986 off Townsville, Australia, was examined. The sharks were caught in a protective meshing programme using both large mesh gill-nets and set lines. The size at birth was estimated to be 80–90 cm total length, and females matured at approximately 287 cm total length. Litter sizes ranged from 6 to 56. Breeding and pupping both appear to occur in summer, with females not breeding every year. Mature females possibly migrate inshore during late spring and summer to give birth. The sex ratio of juveniles and adults favoured females, with few adult males being caught. Ontogenic changes in the diet were observed, with juveniles feeding predominantly on teleosts, sea snakes and birds and adults mostly consuming teleosts, sea snakes, turtles and crabs. There was no apparent decrease in the population size of *G. cuvier* in the Townsville area as a result of the long-term catching of sharks by the protective meshing programme.

Extra keywords: beach meshing, reproduction, feeding.

Introduction

The tiger shark, *Galeocerdo cuvier* (Peron & LeSueur, 1822), is one of the largest and most widespread species of tropical sharks. In Australian waters, it occurs throughout tropical and subtropical waters and also enters temperate waters (Stevens and McLoughlin 1991). Biological data on this species from Australian waters is, however, limited. The majority of information comes from studies off New South Wales (Stevens 1984) and northern Australia (Stevens and McLoughlin 1991). A few anecdotal reports have been made by Gudger (1948), Heatwole *et al.* (1974) and Lyle and Timms (1987). Further afield, the diet (Tester 1969; Bass *et al.* 1975; Rancurel and Intes 1982; Witzell 1987), reproduction and embyronic development (Sarangdhar 1943, 1949), and age and growth (Branstetter *et al.* 1987) have been examined.

G. cuvier is particularly well known for its voracious feeding habits and diverse diet (e.g. Beebe and Tee-Van 1941; Bigelow and Schroeder 1948; Gudger 1948, 1949; Springer 1963; Clark and von Schmidt 1965; Bass *et al.* 1975; Compagno 1984; Stevens and McLoughlin 1991). This, combined with the large size of this species (up to 7·2 m), makes it one of the most threatening species of shark to humans. In Australian waters, it has been positively identified in at least 19 attacks on humans, only one fewer than the great white, *Carcharodon carcharias* (John West, Australian Shark Attack File, personal communication). To combat the threat from attack by this species and other large sharks, the Queensland Government employs a protective meshing programme at popular swimming beaches. This programme is known as the Queensland Shark Meshing Program (QSMP) and was initiated in 1963. Although biological data have been recorded on all sharks caught by the

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QSMP, the usefulness of much of the information is diminished because of problems with species identification (Simpfendorfer, unpublished data). The data for *G. cuvier*, however, are considered reliable because the species is readily identified. This paper presents an analysis of the *G. cuvier* data from the beaches around Townsville, northern Queensland.

Materials and Methods

The QSMP utilizes both large mesh gill-nets and set lines (known as drumlines) to control the populations of sharks near beaches. The gill-nets are 62 m long, have 50-cm multifilament mesh, and are anchored in position off sandy beaches. Drumlines consist of a single large hook suspended from a drum and are normally anchored off rocky headlands. The gear is set at six beaches in the Townsville area (19°15′S,146°50′E) (Fig. 1). The construction of the gear and its placement at beaches was consistent between 1964 and 1986. Annual values of gill-net and drumline effort are shown in Fig. 2. Netting effort is expressed as net-days, with one net-day representing one net set for one day, and drumline effort is expressed as line-days, with one line-day being one drumline set for one day. A number of changes in the beaches fished and the amount of gear used were responsible for the variation in effort (Table 1). Prior to 1968, variation in effort also occurred because the gear was set 3 days per week, but subsequently it has been set continuously except for a 5-week annual lay-off. Gear maintenance and data collection are the responsibility of a contractor selected by the Queensland Department of Primary Industries. Except for a 2-year period in 1971–72, when two contractors were employed, a single contractor was used in the Townsville area between 1964 and 1986. The information collected from specimens by the contractor includes identity, total length, stomach contents, sex, number of pups in pregnant females, length of pups, and date and locality of capture.

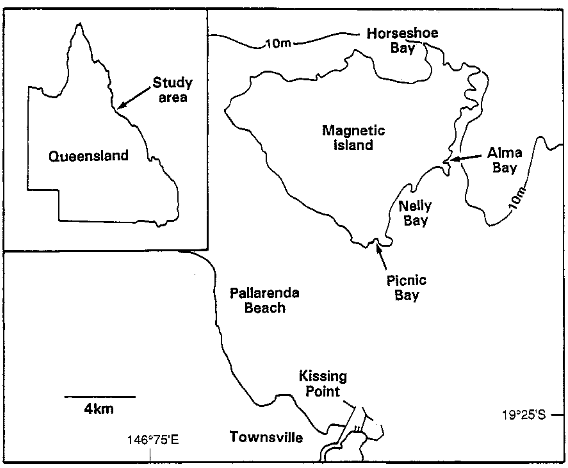

Fig. 1. Beaches protected by the Queensland Shark Meshing Program in the Townsville area.

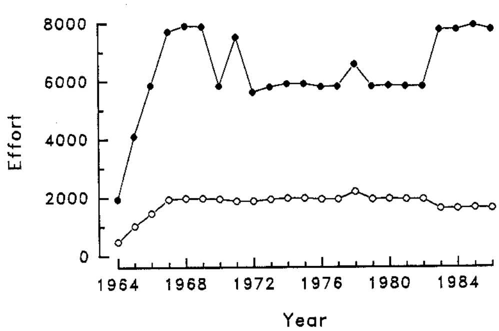

Fig. 2. Annual effort values for (○) gill-nets and (●) drumlines used by the Queensland Shark Meshing Program in the Townsville area between 1964 and 1986. Netting effort is expressed as net-days, drumline effort as line-days.

Table 1. Numbers of gill-nets and drumlines set at beaches in the Townsville area by the Queensland Shark Meshing Program between 1964 and 1986

Values of 0·5 and 1·5 indicate that nets or lines were fished alternatively at beaches, with a rotating periodicity of 1 month

Beach	Year																						
	'64	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	'76	'77	'78	'79	'80	'81	'82	'83	'84	'85	'86
											Gill-nets												
Picnic Bay	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nelly Bay	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Alma Bay	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Horseshoe Bay	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2
Kissing Point	0	0	0	0	0	0	0	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	1	1	1	1	1	1	1
Pallarenda Beach	0	0	0	0	0	0	0	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0·5	0	0	0	0	0	0	0
											Drumlines												
Picnic Bay	3	3	3	3	3	3	3	9	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Nelly Bay	9	9	9	9	9	9	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Alma Bay	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Horseshoe Bay	9	9	9	9	9	9	6	6	6	6	6	6	6	6	6	5	5	5	5	11	11	11	11
Kissing Point	0	0	0	0	0	0	1·5	1·5	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Pallarenda Beach	0	0	0	0	0	0	1·5	1·5	1	1	1	1	1	1	1	3	3	3	3	3	3	3	3

The data for the period from 1964 to 1986 were obtained from logbooks held by the Queensland Department of Primary Industries. Catch rates (either sharks net-day^{-1} or sharks line-day^{-1}) were calculated to eliminate differences in fishing effort between localities and years. Stomach contents were recorded by the contractor only as the presence of broad taxonomic groups (e.g. teleosts, crabs, lobster, squid, turtle). These data were analysed by the occurrence method (Hyslop 1980).

Results

Catch Rates

More specimens of *Galeocerdo cuvier* were caught on drumlines (653 specimens) than in gill-nets (182 specimens). The annual catch rate of the nets fluctuated between 0·0025 and 0·0075 sharks net-day^{-1} through the period examined (Fig. 3), but there were no significant differences between years (analysis of variance, $P = 0{\cdot}7418$). There were significant differences in the drumline catch rate between years (ANOVA, $P = 0{\cdot}0005$). Most annual drumline catches were between 0·002 and 0·006 sharks line-day^{-1}, with higher catch rates in 1964, 1982 and 1983 (Fig. 3).

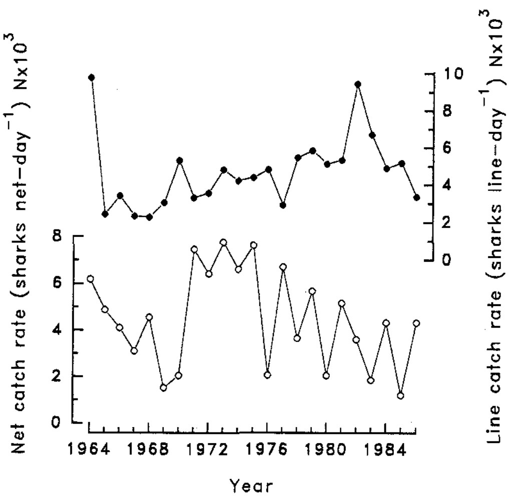

Fig. 3. Annual catch rates of *Galeocerdo cuvier* in the Townsville area between 1964 and 1986 for (○) gill-nets and (●) drumlines.

There were significant variations (ANOVA, $P = 0{\cdot}0001$ and $0{\cdot}0001$, respectively) in the catch rate of *G. cuvier* between localities for both gill-nets and drumlines (Table 2). Catch

Table 2. Catch rates of *Galeocerdo cuvier* in gill-nets and on drumlines used by the Queensland Shark Meshing Program at six beaches in the Townsville area between 1964 and 1986

Beach	Catch rate: Drumline (sharks line-day^{-1}) ($\times 10^3$)	Catch rate: Gill-net (sharks net-day^{-1}) ($\times 10^3$)
Horseshoe Bay	8·153	7·610
Alma Bay	6·849	1·427
Nelly Bay	3·444	1·000
Picnic Bay	0·427	0
Kissing Point	0·614	2·310
Pallarenda Beach	0·452	3·682

rates were highest at Horseshoe Bay for both drumlines and gill-nets. Drumline catch rates were also high at Alma Bay, moderate at Nelly Bay, and low at the three beaches closest to the mainland. Gill-net catch rates were low at Picnic, Nelly and Alma Bays and moderate at the mainland beaches.

Size

The size of *G. cuvier* specimens captured ranged from 84 to 428 cm total length (TL). Specimens caught in gill-nets were most commonly between 190 and 350 cm TL, whereas those caught on drumlines were most commonly between 170 and 280 cm TL (Fig. 4). The mean size of *G. cuvier* specimens caught in gill-nets (260·7 cm TL) was significantly larger (t-test, $P < 0·0001$) than those caught on drumlines (239·8 cm TL).

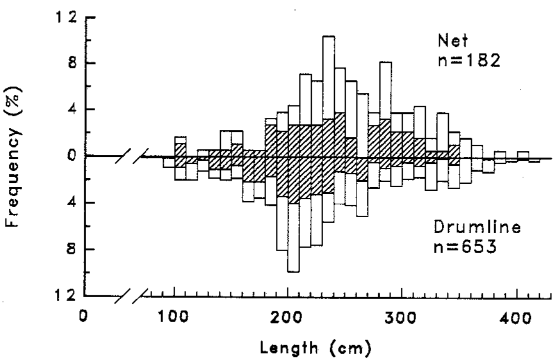

Fig. 4. Size frequency distribution of (hatched bars) males and (open bars) females of *Galeocerdo cuvier* caught in gill-nets and on drumlines in the Townsville area between 1964 and 1986.

The size frequency distributions of males and females were similar, although few males longer than 330 cm TL were caught (Fig. 4). The overall mean length of males was 228·8 cm TL, which was significantly shorter (t-test, $P < 0·0001$) than the mean length of females (254·2 cm TL). Changes in the annual mean length of males and females were examined only for drumline-caught specimens. Differences in the size selectivity of gill-nets and drumlines, and differing annual efforts for these types of gear, meant that combined data could not be analysed. The gill-net data were not analysed due to the small sample size. The annual mean length of drumline-caught males varied between 193 and 253 cm TL (Fig. 5) but did not differ significantly between years (ANOVA, $P = 0·299$). There were

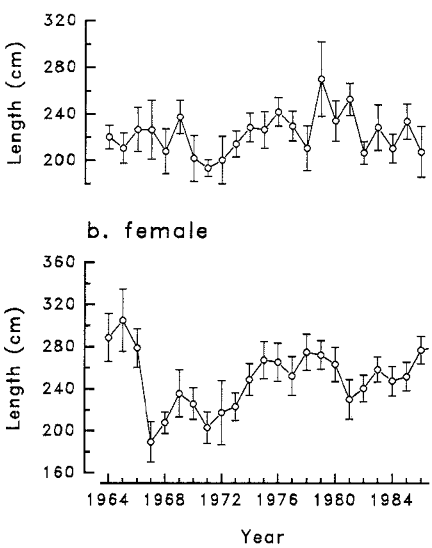

Fig. 5. Annual mean lengths of (*a*) males and (*b*) females of *Galeocerdo cuvier* caught in the Townsville area between 1964 and 1986. Error bars, ±1 s.e.

significant annual differences in the mean length of drumline-caught females (ANOVA, $P < 0 \cdot 002$). The annual mean length of drumline-caught females was longest during the first 3 years of the programme and shortest during the late 1960s and early 1970s, subsequently stabilizing between 240 and 280 cm TL (Fig. 5).

Reproduction

The size at maturity of females of *G. cuvier* from the Townsville area, based on the length of the smallest pregnant female, was 287 cm TL. The size at maturity of males could not be determined from the logbook data. It was not possible to estimate directly the proportion of mature individuals caught because the state of maturity was not recorded by the contractor. However, this was achieved indirectly by calculating the number of individuals over the estimated size at maturity. Since the male size at maturity could not be estimated in this study, Randall's (1986) value of 290 cm TL was used. In all, 29·6% of females and 11·6% of males were over the estimated sizes at maturity, indicating that juveniles were more abundant in the catches. Only 25 of the 150 females over the estimated size at maturity were pregnant. Litter sizes ranged from 6 to 56 (mean 31·5) and were most commonly 31–35 (Fig. 6). There was a significant relationship between litter size and maternal length ($r^2 = 0 \cdot 41$, $P = 0 \cdot 0007$). On the basis of embryo size, reproduction appears to be seasonal. Small embryos were recorded only between January and April, and large embryos commonly occurred between October and December (although some large embryos occurred until May) (Fig. 7). The largest embryos were 89 cm TL and the smallest free-living individual caught was 84 cm TL, indicating that the size at birth is approximately 80–90 cm TL.

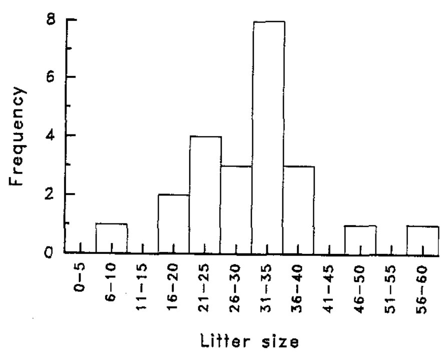

Fig. 6. Frequency distribution of litter sizes of *Galeocerdo cuvier* caught in the Townsville area between 1964 and 1986.

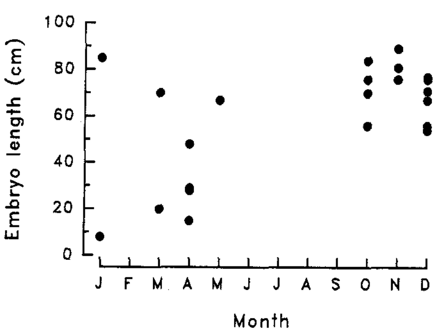

Fig. 7. Mean embryo lengths of litters of *Galeocerdo cuvier* caught in the Townsville area between 1964 and 1986.

Females comprised 61·3% of the total catch. The monthly sex ratio of immature specimens varied between approximately 50 and 65% females, with the highest proportions of females normally occurring in summer months (Fig. 8). The proportion of mature females caught normally ranged from 70 to 100% but was as low as 48% in September (Fig. 8).

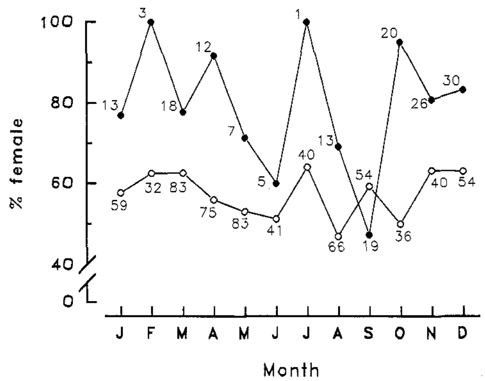

Fig. 8. Monthly sex ratios of (○) juveniles and (●) adults of *Galeocerdo cuvier* caught in the Townsville area between 1964 and 1986. Numbers indicate sample sizes.

The monthly catch rates of mature specimens of *G. cuvier* for both gill-nets and drumlines increased during spring (Fig. 9). The catch rates of immature specimens, however, showed different patterns between gill-nets and drumlines. The monthly catch rates of immature specimens on drumlines varied seasonally, with the highest catch rates occurring in autumn (March–May) and the lowest in spring (Fig. 9). The monthly catch rates of gill-nets were more variable, with the highest peak occurring in March (Fig. 9).

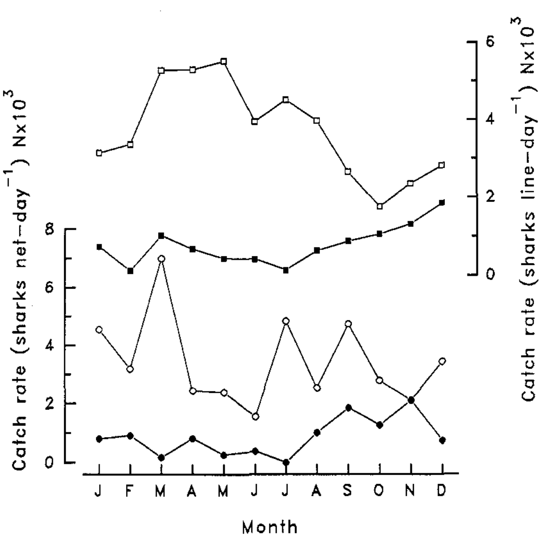

Fig. 9. Monthly catch rates of (open symbols) juveniles and (solid symbols) adults of *Galeocerdo cuvier* caught in (circles) gill-nets and (squares) drumlines in the Townsville area between 1964 and 1986.

Feeding

The stomach contents of 811 specimens of *G. cuvier* caught in the Townsville area were examined. Of these, 31·2% were empty. The percentage occurrence of prey items in the stomachs that contained food are given in Table 3. The main prey groups were teleosts and sea snakes, but crabs, turtles and birds were also important. Other prey groups included dolphins, dugongs, sharks, rays and squids. A number of items of garbage were also recorded, including plastic bags, aluminium foil, clothing, a sugar bag, prawn netting and kitchen scraps.

Table 3. Stomach contents of 558 specimens of *Galeocerdo cuvier* caught in the Townsville area between 1964 and 1986 by the Queensland Shark Meshing Program

Food item	*n*	Occurrence (%)
Teleost	353	63·3
Sea snake	279	50·0
Crab	76	13·6
Bird	58	10·4
Turtle	58	10·4
Ray	12	2·2
Squid	11	2·0
Shark	9	1·6
Dugong	8	1·4
Dolphin	7	1·3
Lobster	3	0·6
Other molluscs	2	0·4
Prawn	2	0·4
Flying fox	2	0·4
Unidentified	4	0·7

Examination of the diet of *G. cuvier* from three size groups (<1·5, 1·5–3·0 and >3·0 m) reveals ontogenic changes in the diet (Fig. 10). Teleosts and sea snakes were the dominant food types in all size groups. However, the proportion of teleosts in the diet decreased with increasing shark size. Other food groups that decreased with increasing shark size were squids and birds. Concomitant with the decrease in these groups was an increase in the occurrence of turtles, crabs and sharks in larger individuals.

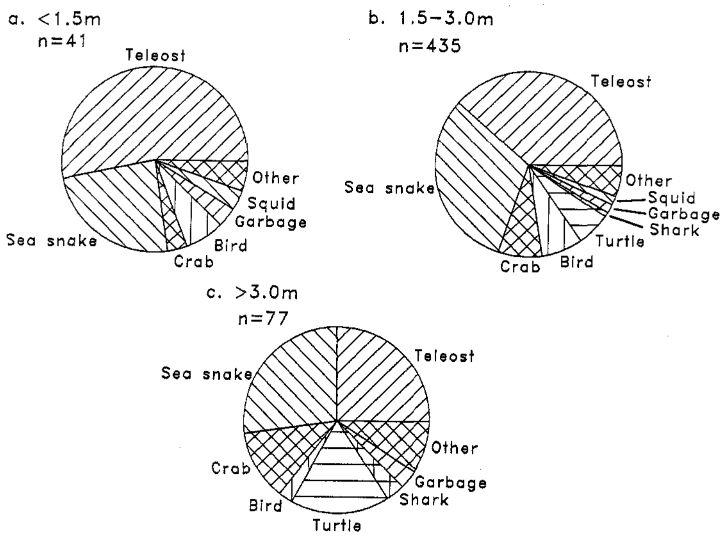

Fig. 10. Percentage occurrences of prey groups in the stomach contents of three size groups of *Galeocerdo cuvier* caught in the Townsville area between 1964 and 1986.

Discussion

Beach meshing programmes are considered to be effective because they reduce populations of dangerous species of sharks (Springer and Gilbert 1963). In the Townsville region, the QSMP has reduced the populations of several groups of potentially dangerous sharks (Simpfendorfer, unpublished data). However, there is no evidence from the logbook data that there has been a significant reduction in the *G. cuvier* population. Both gill-net and drumline catch rates have remained relatively stable, except for a few years when the drumline catch rate was higher than normal. Concomitantly, there has been no reduction in the mean size of males and only a small reduction in the mean size of females. The stability of the *G. cuvier* population, despite the catches of the QSMP, disagrees with the observations of Springer (1963) and Tester (1969) that populations of this species are quickly reduced by fishing pressure. The apparent lack of decline in the population in the Townsville area suggests that tiger sharks move over a wider geographical range than that covered by the meshing programme. The stability in the catch rates also suggests that fishing pressure is light in relation to population size.

The gill-nets and drumlines had different size selectivities, with nets on average catching larger individuals. This difference restricted the comparison of data between the two methods of capture and probably accounted for the large number of juveniles caught. The predominance of juveniles in the catch may also indicate that the population is segregated. Segregation in *G. cuvier* populations has previously been reported by Bass *et al.* (1975), Stevens (1984) and Branstetter *et al.* (1987). Within the fished area, catch rates were high only at beaches close to deep water (Horseshoe and Alma Bays), possibly because tiger sharks inhabit deeper water during the day and move into shallower water at night (Tricas *et al.* 1981).

The occurrence of adult females carrying embryos longer than 80 cm TL in the Townsville area between October and January confirms the hypothesis of Stevens and McLoughlin (1991) that, in Australian waters, *G. cuvier* pups during summer. The present data suggest that adult females may migrate into inshore waters to pup, an occurrence also reported by Springer (1940). Previous reports of the litter size of *G. cuvier* have ranged between 10 and 82 (Springer 1940; Whitley 1940; Bigelow and Schroeder 1948; Clark and von Schmidt 1965; Tester 1969; Bass *et al.* 1975), with mean values around 35 (Tester 1969; Bass *et al.* 1975). The low proportion of adult females that were pregnant indicates that individual females do not produce a litter each year, a factor attributed to their long gestation period (Compagno 1984). The young are born at lengths of between 80 and 90 cm TL in the Townsville area, which is larger than other records for this species that are between 50 and 80 cm (Compagno 1984; Randall 1986).

Most reports of the diet of *G. cuvier* have commented on its diversity and suggested that these sharks are omnivorous and nonselective. Witzell (1987), however, argued that they selectively prey upon large cheloniid sea turtles. Although Witzell demonstrated that turtles do form an important component to the diet of *G. cuvier*, he did not provide explicit evidence that they were selectively preyed upon. The present data suggest that it is in fact only the larger individuals that prey on cheloniid turtles. Small tiger sharks are probably physically too small to attack and consume an adult turtle. In reviewing the literature, Witzell also observed that *G. cuvier* is the only species of shark that regularly consumes large turtles. The present study indicates two other prey groups that are commonly eaten by *G. cuvier*: sea snakes and birds. All sizes of *G. cuvier* consumed sea snakes, but it was normally small individuals that had eaten birds. Predation on sea snakes by *G. cuvier* has been reported by Gudger (1948), Day (1967), Heatwole *et al.* (1974), Rancurel and Intes (1982), Lyle and Timms (1987) and Stevens and McLoughlin (1991), and predation on birds has been reported by Bigelow and Schroeder (1948), Gudger (1948, 1949), Springer (1963), Clark and von Schmidt (1965), Tester (1969), Bass *et al.* (1975), Dodrill and Gilmore (1978), Rancurel and Intes (1982), Stevens (1984) and Stevens and McLoughlin (1991).

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