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Biology of Two Commercially Important Carcharhinid Sharks from Northern Australia

J. D. Stevens and P. D. Wiley[A]

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 1538, Hobart, Tas. 7001.
[A] Present address: Water Resources Commission, 201 Miller Street, North Sydney, N.S.W. 2060.

Abstract

Sharks represent 78% of the total catch by weight of a Taiwanese surface gill-net fishery off northern Australia. Two carcharhinids, *Carcharhinus tilstoni* (previously described as *C. limbatus*) and *C. sorrah*, together comprise 83% of this shark catch by number. *C. tilstoni* is distinguished from *C. limbatus* by differences in enzyme systems, vertebral counts, size data and pelvic fin coloration. Of the specimens of *C. tilstoni* and *C. sorrah* caught in the Arafura and Timor Seas from 1981 to 1983, 43% and 47%, respectively, were female; at birth these proportions were 46% and 50%, respectively. In both species, females tended to be relatively more abundant in catches of mature fish, except around March, when males predominated. In northern Australia, the usual size at maturity for *C. tilstoni* is 110 cm for males and 115 cm for females; for *C. sorrah*, it is 90 cm and 95 cm, respectively. Both species exhibit placental viviparity and have almost identical restricted reproductive cycles. Mating occurs in February–March, ovulation in March–April and the main parturition period is in January. The gestation period is 10 months and individual fish breed each year. The average litter size for both species is three. The size at birth is about 60 cm for *C. tilstoni* and 50 cm for *C. sorrah*. Stomach contents indicate that teleost fish are an important component of the diet of both species and there is some indication of a change in feeding depth with shark size.

Introduction

Carcharhinus tilstoni (Whitley) and *Carcharhinus sorrah* (Valenciennes in Müller and Henle) are the principal shark species taken by a Taiwanese surface gill-net fishery that has operated off northern Australia since the early 1970s. Before the Australian Fishing Zone (AFZ) was declared, fishing was carried out between northern Australia, Indonesia and Papua New Guinea, approximately in the area bounded by 5–20°S. and 120–145°E. (Fig. 1). Between 1975 and 1978, the total annual catch averaged 17 300 t processed weight (Walter 1981). Subsequently, fishing areas were restricted. Fig. 1 shows the permitted fishing zone in 1983, together with the area in which fishing effort was concentrated when 30 vessels were licensed to take 7000 t processed weight (about 10 000 t live weight) of combined elasmobranch and teleost fish per year.

Information on the fishery before 1980 is very limited, with even the catch composition being largely unknown. Following the introduction of the AFZ in 1979, Australia assumed management responsibilities for the fishery and initiated a research program. The present study, representing the first stage of this work, provides life-history data on *C. tilstoni* and *C. sorrah*. *C. tilstoni* was previously described as *C. limbatus* (Stevens *et al.* 1982; Lyle 1984; Stevens and Church 1984), and as *Carcharhinus* sp. (Lyle 1986).

Future papers arising from this study will report on age and growth, movements, stock structure and population dynamics of these species.

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Materials and Methods

Material Examined

From the commercial fishery

Sharks were examined from the Taiwanese gill-net fishery off northern Australia. The gill nets used in the fishery are constructed of multifilament nylon with a diagonal stretched mesh averaging 17 cm (14·5–19·0 cm). They are about 15 m deep from the headrope to the footrope. Approximately 8 km of net are set close to the surface just before dusk and hauling begins at about midnight. Hauling can take up to 10 h. Water depths in the main fishing area vary from about 46 to 82 m. The bottom is predominantly mud.

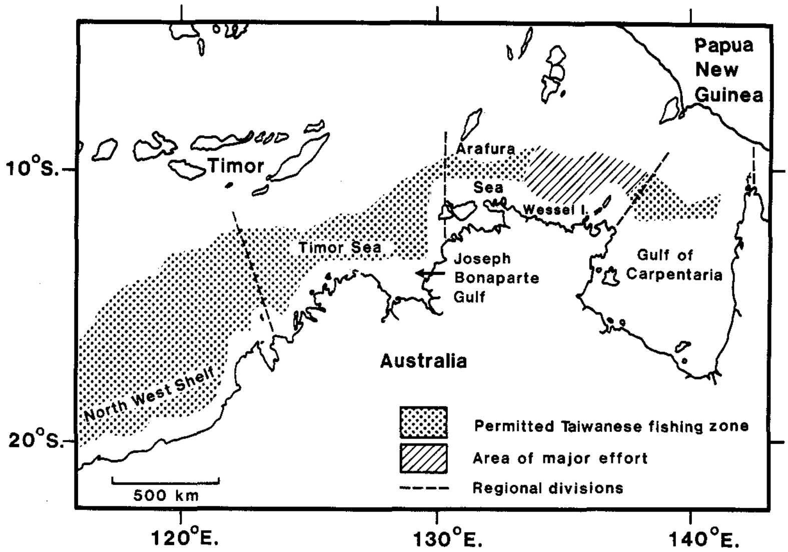

Fig. 1. Permitted Taiwanese gill-netting area off northern Australia in 1983.

Table 1. Number of *Carcharhinus tilstoni* and *C. sorrah* examined from commercial and research vessel samples taken in Australian waters from April 1981 to November 1983

Area	Sampling method	Number of *C. tilstoni* Measured	Number of *C. tilstoni* Dissected	Number of *C. sorrah* Measured	Number of *C. sorrah* Dissected
Arafura Sea	Gill net	17 401	2234	7287	1229
Arafura Sea	Demersal trawl	17	17	1	1
Timor Sea	Gill net	1305	312	251	202
Timor Sea	Demersal trawl	7	7	0	0
Gulf of Carpentaria	Demersal trawl	49	49	29	29
North West Shelf	Longline	62	62	231	231
North West Shelf	Gill net	43	22	135	0
North West Shelf	Demersal trawl	7	7	32	32
Total		18 891	2710	7966	1724

The use of a single mesh size in the commercial fishery probably affects the size distribution of fish caught and may select against the capture of *C. tilstoni* and *C. sorrah* at the extremes of their size range. However, in view of the large number of sharks examined (Table 1) it is likely that at least some specimens over the entire length range of the species would be caught if they were present in the area. Gill nets certainly captured individuals close to the size at birth. The largest specimens caught by gill net and longline were similar. Longlines presumably have no maximum size selection for these species.

The gill nets also catch other carcharhinids of a size greater than the maximum size recorded for *C. tilstoni* and *C. sorrah*.

Sharks caught by the fishery were sampled by personnel placed on board the boats from a chartered vessel. Of the charter cruises, 80% were in the main fishing area off the Wessel Islands in the eastern Arafura Sea, and the rest covered the western Arafura Sea, Timor Sea and North West Shelf (Fig. 1). Cruises lasted about 1 month and averaged about seven boardings, each boarding usually covering two nights, during which the catch was observed and sampled. In most cases, two catches were sampled each day, as vessels were usually boarded in pairs. On average, each cruise covered about 2% of the total sets made by the commercial fleet in that month. Data were collected between April 1981 and October 1983. During this period, 21 of the possible 31 months were sampled, giving an overall coverage of about 1·5% of the total sets made. The longest time between samples was from August to October 1982. Where possible, the whole catch was sampled. In cases where the catch was very large (several tonnes) a representative subsample was taken.

From research vessels

Sampling of the North West Shelf was conducted during CSIRO research cruises in the area, with most specimens being captured with a 1-km long, 60-hook surface-set longline. Longlining mainly used Mustad 10/0 tuna hooks, a size and a pattern that were designed to minimise selection by shark size. These cruises covered every month between March 1982 and November 1983, with the exception of May–July 1982 and May, July and September 1983. Some materials were also collected during CSIRO demersal trawling operations in the Timor Sea in June and July 1980, in the Arafura Sea in November 1980, and in the Gulf of Carpentaria in November and December 1980 and June and July 1981. Table 1 gives the number of specimens of *C. tilstoni* and *C. sorrah* examined from the study area and the sampling method used. All specimens caught by the research vessel were examined.

Table 2. Total length–total weight and total length–fork length relationships for *Carcharhinus tilstoni* and *C. sorrah* from northern Australian waters

TL, total length (cm); FL, fork length (cm); TW, total weight (g)

Species	Sex	Sample number	Size range (TL, cm)	Equation	r^2	P
C. tilstoni	Male and female	311	62·0–206·5	$TW = 4{\cdot}75 \times 10^{-3}\,TL^{3{\cdot}06}$ $TL = 6{\cdot}65\,TW^{0{\cdot}311}$	0·91	< 0·001
C. tilstoni	Male and female	724	57·7–197·7	$TL = 1{\cdot}235\,FL + 0{\cdot}913$ $FL = 0{\cdot}803\,TL - 0{\cdot}075$	0·99	< 0·0001
C. sorrah	Male	53	54·3–107·3	$TW = 7{\cdot}09 \times 10^{-4}\,TL^{3{\cdot}46}$ $TL = 9{\cdot}90\,TW^{0{\cdot}266}$	0·92	< 0·001
C. sorrah	Female	164	71·6–135·6	$TW = 5{\cdot}45 \times 10^{-4}\,TL^{3{\cdot}51}$ $TL = 11{\cdot}10\,TW^{0{\cdot}255}$	0·90	< 0·001
C. sorrah	Male and female	626	53·0–151·8	$TL = 1{\cdot}196\,FL + 4{\cdot}72$ $FL = 0{\cdot}828\,TL - 3{\cdot}28$	0·99	< 0·001

Data Recorded

Length measurements

Sharks were measured to the nearest centimetre either as total length (TL), the tail of the shark first being allowed to take a natural position and the top caudal lobe then being placed parallel to the body axis, or as fork length (FL). FL was converted to TL using equations derived in this study (Table 2). Sharks were weighed on calibrated spring balances reading to the nearest 500 g, except for the smaller specimens, which were weighed to the nearest 1·0 g. Lengths were converted to weights using the TL and total weight (TW) relationships shown in Table 2. The equations were obtained by fitting a power curve of the form $y = ax^b$ by the method of least squares (Snedecor and Cochran 1967).

Reproductive state

The reproductive state was determined by the method of Bass *et al.* (1973). Maturity in males was assessed on the criteria of clasper size and calcification, and in females on the development of the ovary and genital tracts. Females were judged to be virgin if a hymen still sealed the vaginal opening. Maximum ova diameters were measured on the largest egg(s) in the ovary, with calipers reading to the nearest millimetre. Gonads were excised from the surrounding epigonal organ and weighed to 0·1 g.

Stomach contents

Prey items from stomach contents, which were identified to the lowest possible taxon, were based on both intact items and remaining hard parts such as beaks, otoliths and skeletal matter. The rest of the gut was not examined. Results were expressed in terms of the number of stomachs containing a particular prey item among those stomachs that contained food.

Meristics

Tooth counts. Tooth counts refer to the number of rows, following the terminology and format of Bass *et al.* (1973), and are given in the form:

$$\frac{\text{No. of laterals} - \text{No. of centrals} - \text{No. of laterals}}{\text{No. of laterals} - \text{No. of centrals} - \text{No. of laterals}} \quad \begin{matrix}\text{(upper jaw)}\\ \text{(lower jaw)}\end{matrix}$$

Vertebral counts. Vertebral counts were obtained by dissection and are recorded as the numbers of precaudal and total vertebrae. Precaudal counts in this study include all vertebrae in front of the posterior edge of the precaudal pit.

Results and Discussion

General

The data collected during the present study indicated there were two principal groups of the species previously described as *C. limbatus*. These groups were separable on vertebral counts, size at maturity, maximum size, and pelvic fin coloration, all characters that showed considerable variation throughout the circumglobal distribution of the species (Cervigon 1966; Bass *et al.* 1973; Gubanov 1978; Garrick 1982). During final preparation of this manuscript, electrophoretic analysis, which was being carried out for studies on stock discrimination (Stevens and Church 1984), showed them to be distinct species (J. B. Shacklee, personal communication). The rarer of these two species, which occurs in the approximate proportions of 1 : 300 in the Arafura Sea (Fig. 1), is the true *C. limbatus*. The other shark was originally described from northern Australia by Whitley (1950) as *Galeolamna pleurotaenia tilstoni* before Garrick (1982) synonymised it with *C. limbatus*. Garrick (1982) stated that three syntypes of *Carcharias (Prionodon) pleurotaenia* Bleeker from Batavia, two in the Leiden Museum (RNH 7385) and one in the British Museum (BMNH 1867.11.28), were clearly *Carcharhinus limbatus*. However, only the BMNH specimen was X-rayed, confirming its vertebral count to fall within the range for the true *C. limbatus* (see section on meristics). Although the other two syntypes almost certainly have similar vertebral counts, confirmation must await X-raying of these specimens. For the present, we consider *Carcharias (Prionodon) pleurotaenia* to be synonymous with the true *Carcharhinus limbatus* and we resurrect Whitley's *tilstoni* for the Australian species (*Carcharhinus tilstoni*). We note that critical examination of *C. limbatus* material from other areas may be required.

The relationships of length to weight and total length to fork length for *C. tilstoni* and *C. sorrah* are given in Table 2. There is no significant difference between the slopes or intercepts of regressions of weight on length for male and female *C. tilstoni* (analysis of covariance: $P > 0 \cdot 05$). For *C. sorrah* there is a significant difference between the weight–length relationships for males and for females (analysis of covariance: slopes and intercepts $P < 0 \cdot 05$), females weighing more for a given TL. Since the power curves diverge noticeably above 90 cm TL, which is the size at maturity (see section on reproduction), this difference is probably due to the inclusion of pregnant females. However, there is also a significant difference between males and non-pregnant females (analysis of covariance: slopes $P > 0 \cdot 05$, intercepts $P < 0 \cdot 05$), with females above 90 cm TL being noticeably lighter for a given TL than males. Variations in the weight–length relationships may be a result of different sample sizes and unequal distribution of sizes within each data set. Alternatively, non-pregnant females may be lighter due to the inclusion of spent fish, which have a lower condition factor. Since changes in density have important implications for swimming in sharks (Bone and Roberts 1969), females might normally be lighter than males to offset subsequent weight increases due to pregnancy.

No attempt was made to separate total length–fork length relationships by sex.

Distribution

C. tilstoni is found in continental shelf waters of tropical Australia. The southern limits of its distribution are uncertain, as it has been confused with *C. limbatus*, which has been recorded as far south as Sydney (34°S.) on the east coast. On the west coast, *C. tilstoni* is known to occur as far south as Dampier (21°S.).

C. sorrah has a tropical, inshore distribution centred on the Indian Ocean and extending from the Red Sea and western Indian Ocean eastwards to the western Pacific, as far as China and Australia (Bass *et al.* 1973; Garrick 1982).

Meristics

Tooth and vertebral counts are presented because of their value as systematic characters. The usual tooth count among 12 jaws from *C. tilstoni* was $\frac{15-3\text{ or }4-15}{15-1-15}$, which is almost identical to counts reported for *C. limbatus* from northern Australia and elsewhere (Bass *et al.* 1973; Garrick 1982).

Table 3. Distribution of total vertebral counts in *Carcharhinus limbatus* and *C. tilstoni*
Total vertebral counts should be read as follows: 170's 4 ≡ 174; 180's 0 ≡ 180, etc.

Species	No. of fish with total vertebral count of:																												
	170's						180's										190's										200's		
	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
C. limbatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		1	2	0	1	2	0	2	0	4	0	1	1
C. tilstoni	3	3	1	3	0	1	0	0	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Precaudal vertebral counts on 23 specimens of *C. tilstoni* ranged from 84 to 91 (average 87·6) and total vertebral counts on 12 specimens varied from 174 to 182 (average 176·3) (Table 3). By comparison, precaudal counts on 14 specimens of *C. limbatus* from northern Australia averaged 97·6 (range 94–101), while total counts averaged 196·5 (range 191–202) (Table 3). The large variation in precaudal counts of *C. limbatus* reported by Garrick (1982) is almost certainly due to the inclusion of some specimens of *C. tilstoni* in his sample.

The total tooth count based on six jaws of *C. sorrah* was $\frac{12-1-12}{11\text{ or }12-1-11\text{ or }12}$, which is almost identical to counts reported on this species from other areas. The average precaudal count for 10 specimens of *C. sorrah* was 70·9 (range 69–72) and the average total count was 156·4 (eight specimens ranging from 153 to 159). Vertebral numbers of *C. sorrah* from different regions vary, but counts in this study fall within the overall range given by Garrick (1982).

Size

The size distributions of male and female *C. tilstoni* taken by the commercial gill-net fishery in the Arafura and Timor Seas are given in Fig. 2*a*. Both sexes recruit to the fishery at about 63 cm TL, which is approximately the size at birth. Few females over 160 cm TL, and few males over 140 cm TL, have been caught. The maximum size is uncertain, because of confusion with *C. limbatus*, but appears to be about 180 cm TL. In northern Australia, *C. limbatus* appears to grow considerably larger: four males captured by hook and line off New South Wales measured 183·5, 213·8, 220·5 and 229·5 cm TL, while the largest specimen captured by longline from the North West Shelf was a 231-cm TL fish of unrecorded sex.

The size distribution, separated by sex, of *C. sorrah* from the Arafura and Timor Seas are shown in Fig. 2*b*. The smallest fish taken by the gill-net fishery were about 65 cm TL, the usual size at birth being 52 cm TL. Few females above 130 cm TL, and few males above 110 cm TL were caught. Of 231 specimens of *C. sorrah* on the North West Shelf, the smallest were about 70 cm TL, while most males were between 90 and 104 cm TL and most females between 100 and 130 cm TL. The largest male recorded was 131·0 cm and the largest female was 151·8 cm TL, both these fish coming from the Arafura and Timor Seas. Similar maximum sizes of 150–160 cm TL have been recorded from the eastern Indian Ocean (Wheeler 1953; Fourmanoir 1961) and western Pacific (Fourmanoir 1976).

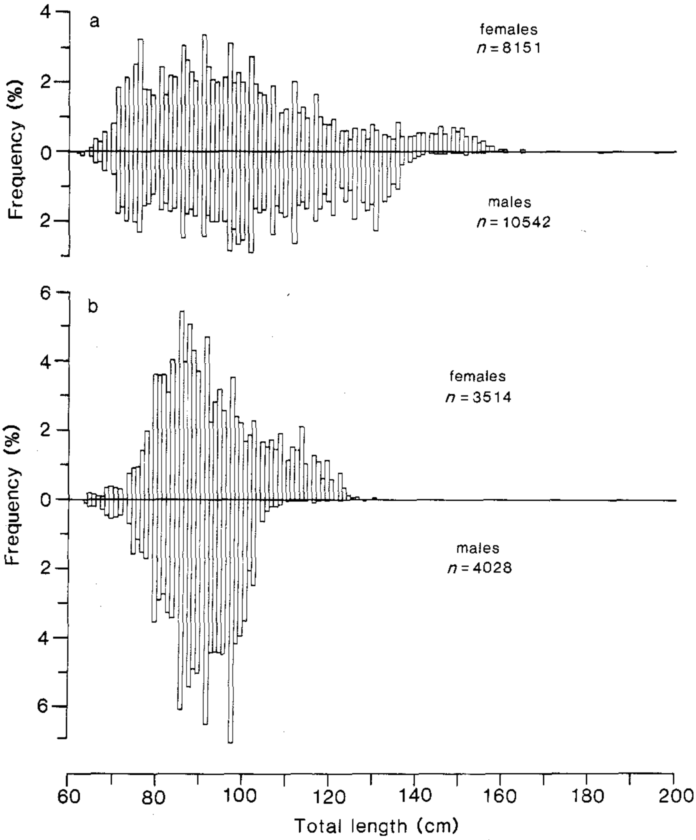

Fig. 2. Length-frequency distributions for *C. tilstoni* (*a*) and for *C. sorrah* (*b*) taken by the Taiwanese gill-net fishery in the Arafura and Timor Seas (1981-1983).

Monthly length-frequency distributions from the Arafura and Timor Seas were analysed to determine whether any seasonal trend was apparent in the proportion of mature *C. tilstoni* (>120 cm TL) or *C. sorrah* (>100 cm TL) (see section on reproduction) in the samples. Although large fluctuations occurred, no distinct seasonal pattern was evident (Figs 3*a* and 3*c*). In 1982 and 1983, the proportion of mature males in both species was high during March. Almost no mature *C. tilstoni* of either sex were present in July 1982 and 1983, however, in July 1981 mature fish occurred in considerable numbers (Fig. 3*a*). On average, mature *C. tilstoni* and *C. sorrah* comprised 18·4% and 21·1% of the population over the sampling period, respectively.

Sex Ratio

Of the 734 embryos of *C. tilstoni* examined from the Arafura Sea, 46·2% were female. The proportion of females after birth was 43·3%, based on examination of 18 732 specimens from the Arafura and Timor Seas. When these post-partum fish were split into immatures and matures, 44.1% and 40·1%, respectively, were female. All these proportions are significantly different from a 1:1 sex ratio (χ^2 test, embryos $P < 0{\cdot}05$; post-partum $P < 0{\cdot}001$). This suggests that more male than female *C. tilstoni* are born in the Arafura and Timor Seas, and that this uneven sex ratio increases through maturity. On the North West Shelf, the proportions of the sexes before birth (46·2% female among 86 embryos) and after birth (62 specimens, 56·0% female) were not significantly different from a 1:1 sex ratio. This may be due to the small sample sizes.

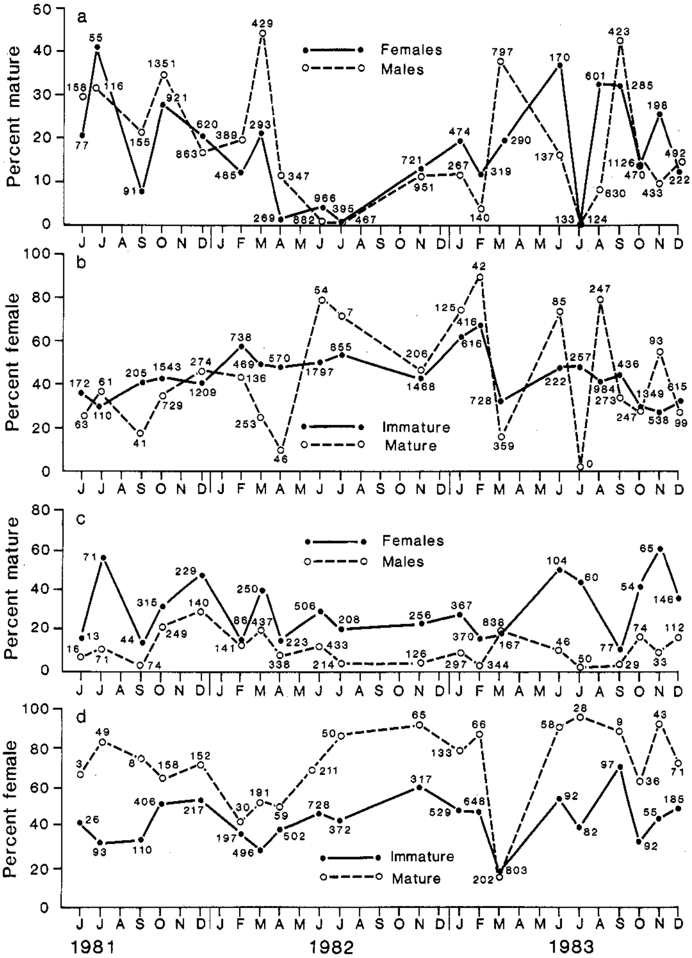

Fig. 3. Monthly proportions of mature *C. tilstoni* (*a*) and of the sexes for *C. tilstoni* (*b*) and of mature *C. sorrah* (*c*) and of the sexes for *C. sorrah* (*d*) from Taiwanese gill-net catches in the Arafura and Timor Seas. Numbers are sample size.

Of 743 embryos of *C. sorrah* examined from the Arafura Sea, 50·1% were female. After birth, this proportion was 47·1%, based on 7673 fish examined from the Arafura and Timor Seas. When the post-partum sample was separated into immature and mature fish, 42·2% and 65·4% respectively, were female. All these values, except those for the embryos, are significantly different from a 1:1 sex ratio (χ^2 test, $P < 0{\cdot}001$). Of 299 embryos examined from the North West Shelf, 47·3% were female (χ^2 test, not significant). Of 366 post-partum specimens of *C. sorrah*, 80·5% were female (χ^2 test, $P < 0{\cdot}001$). So, the sex ratio before birth in *C. sorrah* is about 1 : 1 in the Arafura Sea and on the North West Shelf. On the North West Shelf, this ratio changes dramatically after birth in favour of females, as it does to a lesser extent in mature fish from the Arafura and Timor Seas. The reason for the higher number of females of *C. sorrah* on the North West Shelf is not known. Possibly it may be due to a smaller sample size, or the sex ratio may become skewed as the southern limits of the species range is approached. No information is available in the literature on the sex ratio of *C. sorrah* populations from other areas.

Among adult sharks, a predominance of one sex is not unusual (Springer 1940; Parsons 1983) and may be a consequence of sexual segregation. Among embryos, a 1 : 1 sex ratio is usual (Suda 1953; Gubanov 1978; Francis 1980; Parsons 1983). However, Olsen (1954) found a greater ratio of males to females at birth in the school shark, *Galeorhinus galeus*. This ratio was apparently reversed after 2 years, with females being more abundant. Olsen (1954) suggested male mortality might be higher, or that fishing was more selective for females, although he discounted the latter suggestion as various fishing gears were used

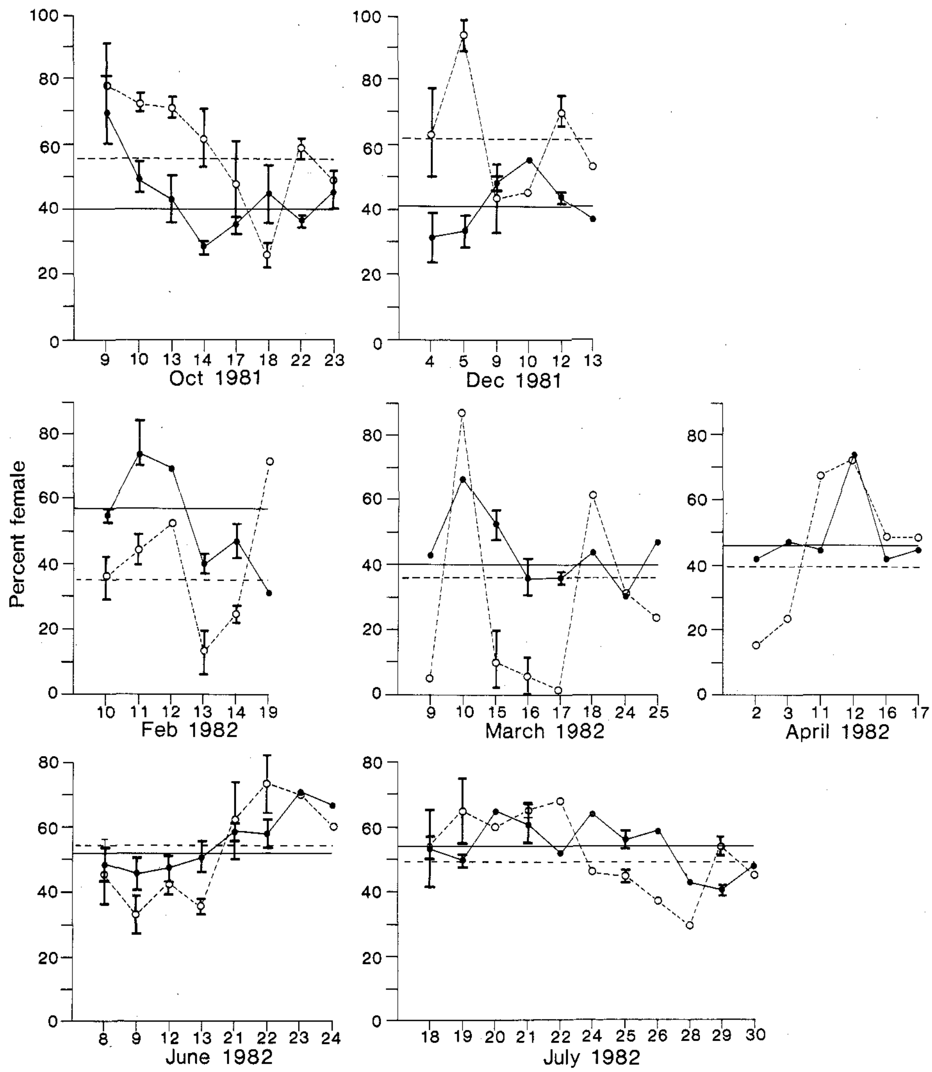

Fig. 4. Daily proportions of the sexes for *C. tilstoni* and *C. sorrah* from 7 months of Taiwanese gill-net catches in the Arafura and Timor Seas. Catches of from one to three vessels were used on any one day. *x*-Axis is day of the month; straight line is mean monthly value; bars are range of daily values. Average individual daily sample size was 108 fish, with more than 22 fish in 90% of samples. ●—— *C. tilstoni*; ○----- *C. sorrah*.

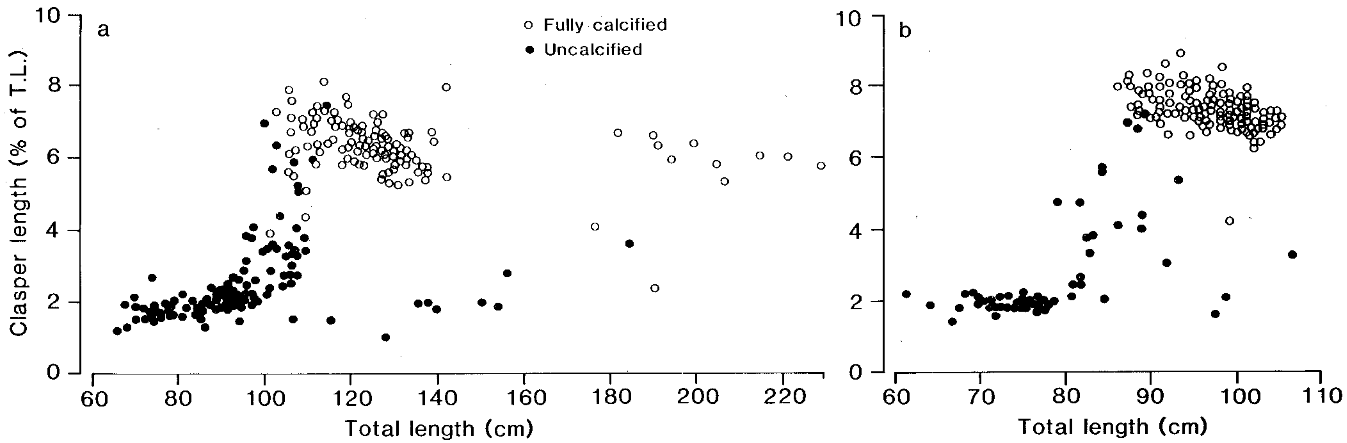

Fig. 5. Relationship between clasper length (expressed as a percentage of total body length) and total body length for *C. tilstoni* and *C. limbatus* (*a*) and for *C. sorrah* (*b*).

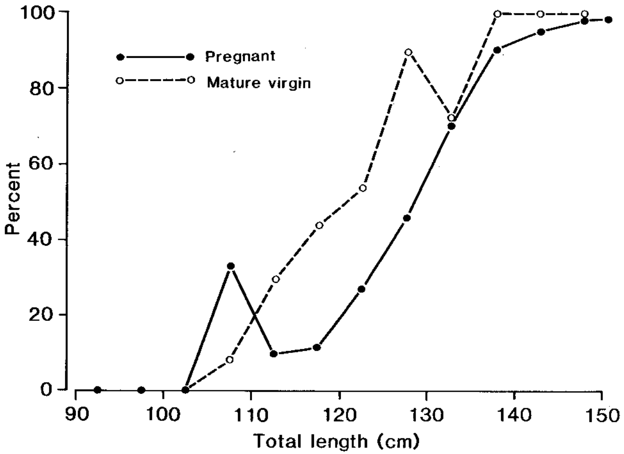

Fig. 6. Percentage of virgin *C. tilstoni* that were mature, and the percentage of *C. tilstoni* that were pregnant, by 5-cm length groups.

and there was no apparent sexual difference in body proportions. However, Grant *et al.* (1979) found no difference in mortality rates between the sexes for *G. galeus*. The reason for the greater number of male *C. tilstoni* and *C. sorrah* at birth found in this study is not known.

Samples from the Arafura and Timor Seas were used to examine changes in the proportion of the sexes, on a seasonal basis, in both the immature and mature components of the population. In the immature segment of the population, the proportion of the sexes remained relatively constant (mean 44% female in *C. tilstoni* and 42% female in *C. sorrah*). In the mature segment, the proportions fluctuated more widely (mean 40% and 65% female for *C. tilstoni* and *C. sorrah*, respectively) (Figs 3*a* and 3*c*), which would be expected if the changes are related to seasonal reproductive activity. In the mature fish, no clear seasonal pattern was evident, which might be due to insufficient sample size. However, more mature males appeared to be present around March, which coincides with the end of the mating season, whereas females were more prevalent during the remainder of the year (Figs 3*a*, 3*b*, 3*c* and 3*d*).

In the gill-net catches, both species occurred in groups that were sometimes composed predominantly of one sex or size range, sometimes with small spatial distributions. Since short time-scale variations might mask any seasonal pattern, daily catches were examined over 7 months. It was not possible to separate the mature from the immature fish, as the sample sizes were too small, but the proportions of the sexes in the total population of each day's catch varied considerably from the mean monthly values, suggesting that sample variability was high (Fig. 4).

Reproduction

The relationship between relative clasper size and body length for male *C. tilstoni* is shown in Fig. 5*a*. In immature sharks less than 100 cm TL, the claspers were short and soft and lengthened slowly with respect to body length. In sharks between 100 and 115 cm TL, elongation was rapid. Calcification of the claspers first occurred at about 105 cm; all sharks normally had calcified claspers by 120 cm TL. The size at which males attain sexual maturity is thus between 105 and 120 cm TL. Plotted to the right in Fig. 5*a* are data for *C. limbatus*, showing the larger size at maturity of this species (about 180 cm TL).

Based on the condition of the uterus and the vaginal hymen, the smallest mature virgin *C. tilstoni* from the Arafura Sea were between 105 and 110 cm TL, with 50% of virgins mature by 120 cm TL (Fig. 6). The smallest pregnant female was also in the 105–110-cm TL length group; 50% of females were pregnant by 130 cm TL (Fig. 6). The largest immature and the largest mature virgin were in the 130–135-cm and 140–145-cm length groups, respectively.

The size at maturity for *C. sorrah* given in the literature is about 105–115 cm TL, based on a limited number of specimens (Wheeler 1953; Fourmanoir 1961, 1976; Gohar and Mazhar 1964; Bass *et al.* 1973; Garrick 1982). The smallest size at which male *C. sorrah* mature in the Arafura Sea, based on clasper size and calcification, is about 87 cm TL. Most fish are mature by 92 cm TL (Fig. 5*b*). The smallest mature virgin and the smallest pregnant fish were both in the 85–90-cm size group, with 50% of virgins mature at 97 cm TL. Between 95 and 100 cm TL, 50% of *C. sorrah* females were pregnant.

Based on smaller samples, there was no apparent difference in the size at maturity of *C. tilstoni* or *C. sorrah* from the Gulf of Carpentaria, Timor Sea or North West Shelf when compared to those from the Arafura Sea.

Data on male and female gonad condition collected from the Arafura Sea, and summed by month for the period April 1981 to October 1983, demonstrated a distinct seasonal reproductive cycle in both species. In *C. tilstoni*, testes weight was low between May and December [$<0\cdot30\%$ of body weight (BW)], during December it increased rapidly, reaching a peak in February ($0\cdot96\%$ BW), after which it declined rapidly until May (Fig. 7*a*). The quantity of sperm in the seminal vesicles showed a similar annual cycle, although it was more variable. The ovary weight followed a similar pattern, reflecting an increase in ova size. Ovary weight and maximum ova diameter reached a peak in March, 1 month later than maximum testes weight, when the ovary was 0·26% BW and the ova were about 24 mm in diameter (Fig. 7*b*). This cycle suggests that mating in February is followed by ovulation in March–April.

The mating season of *C. tilstoni* was confirmed by the presence of females with mating scars, which were observed only during February and March of each year over the period from April 1981 to October 1983. However, quantitative data were obtained only in March, when 43% of mature females were bitten. Fish with ova in their uteri were recorded in March (12% of 73 mature females) and April (69% of 16 mature females). Data were available from all other months except August, but none of the 437 fish examined had ova in their uteri. More detailed observations were made during 1983, when a particular area was sampled

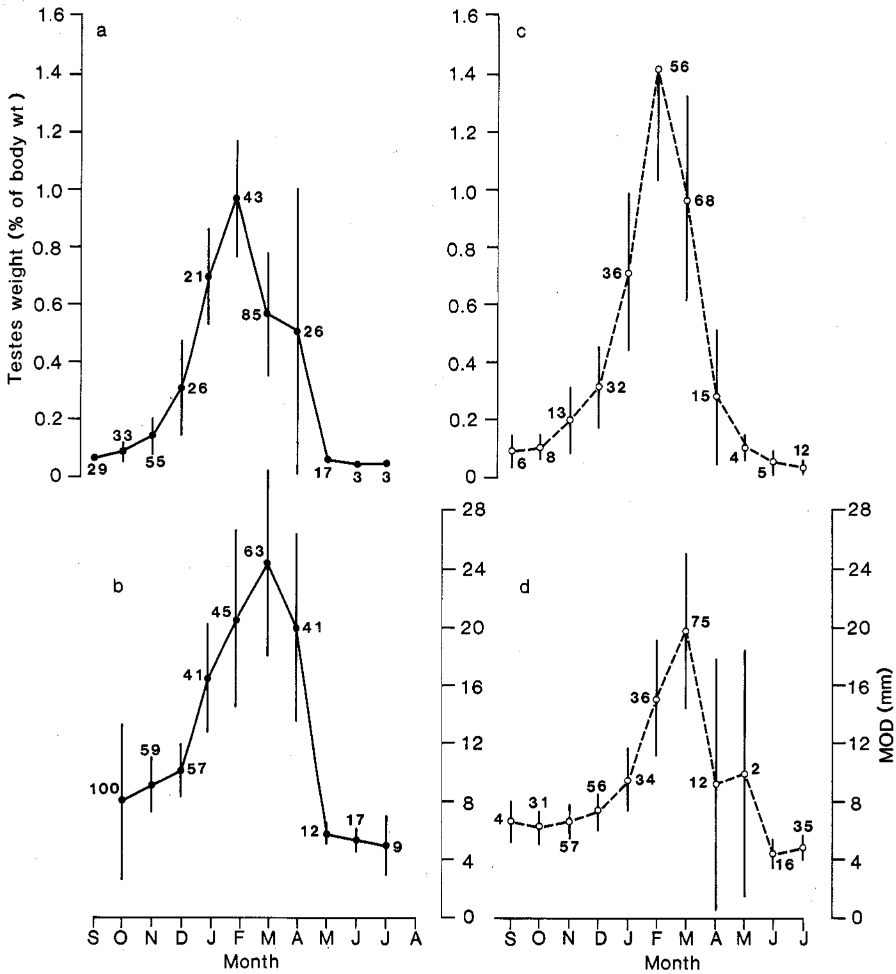

Fig. 7. Seasonal cycle of testes weight (expressed as a percentage of total body weight) for *C. tilstoni* (*a*) and for *C. sorrah* (*c*) and maximum ova diameter for *C. tilstoni* (*b*) and for *C. sorrah* (*d*) from the Arafura Sea. 1981–1983 data combined. Bars are standard deviation; numbers are sample size.

three times over 7 weeks. From early to late February, few fish had mating scars; from late February to early March, numerous fish bore fresh mating scars and some males had engorged claspers, indicative of recent copulation. All females examined from early February to early

March were in a pre-ovulatory condition. When the area was revisited from 18 to 21 March, all mature females had ovulated and contained ova in their uteri. These data show that mating occurred in late February to early March, and that ovulation was 2–4 weeks later. The time lag between mating and ovulation suggests that *C. tilstoni* stores sperm in the oviducal gland, as do certain other sharks (Pratt 1979). The precise timing of mating and ovulation appears to vary by about 2 weeks, depending on the year and specific area.

The reproductive cycle and gestation period for *C. sorrah* in northern Australian waters is virtually identical to that of *C. tilstoni*. Testes weight increased from a resting level of about 0·1% BW in the May to October period to a peak of 1·4% BW in February (Fig. 7*c*). Maximum ovary weight (0·28% BW) and maximum ova diameter (20 mm) occurred in March (Fig. 7*d*). No observation on the presence of mating scars was conducted in February, but of 60 mature females examined in March, 62% were bitten. Females with eggs in utero were recorded only in March (25% of 64 fish) and April (3·2% of 95 fish); a total of 547 individuals were examined, from all months except August. These data show that mating occurs in February and ovulation in March–April.

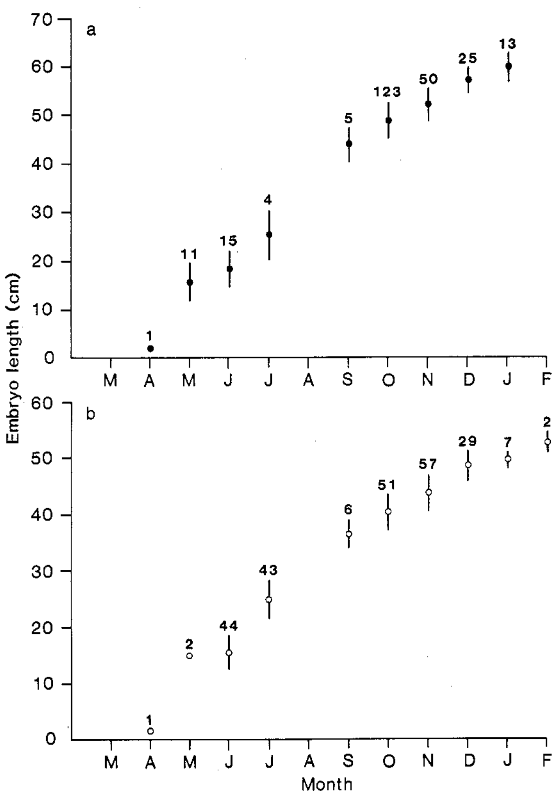

Fig. 8. Relationship between embryo length (TL) and time of year for *C. tilstoni* (*a*) and for *C. sorrah* (*b*) from the Arafura Sea. 1981–1983 data combined. Bars are standard deviation; sample sizes are numbers of litters.

Reproductive information on *C. sorrah* from other regions is limited. Bass *et al.* (1973) examined one litter containing three embryos. They noted that the size at birth is 50–60 cm and that the young are probably born during the summer. Wheeler (1953) recorded two pregnant females from the Seychelles area, each with two pups, and two litters from the Red Sea contained five and six pups (Gohar and Mazhar 1964).

Both species are viviparous, with a well-developed yolk-sac placenta. Early embryos were visible on the ova by April; in *C. tilstoni* embryo length increased through the year until January, the parturition period, when the mean length was 59·5 cm TL (Fig. 8*a*). The smallest free-swimming specimen of *C. tilstoni* captured was 57·7 cm TL, which suggests that the size at birth is about 60 cm TL. Monthly examination of the percentage of mature females that were pregnant or spent provided further evidence that January is the main parturition period. In December, 83% were pregnant and 17% spent (sample size, 30), whereas in January, 35% were pregnant and 65% spent (sample size, 37). No pregnant fish were recorded in February, but 96% were pregnant in November.

Pup size in *C. sorrah* increased monthly until February, when the mean size was 52 cm TL (Fig. 8*b*). This appears to be the usual size at birth, as the smallest free-living specimen of *C. sorrah* captured was 53 cm TL. In December, 81% of mature females were pregnant and 19% were spent (sample size, 36) and in January, 30% were pregnant and 70% were spent (sample size, 23). This indicates that the peak of parturition for *C. sorrah* occurs in January. The gestation period in both species, measured from the time when fertilised ova are present in the uteri until parturition, is thus 10 months.

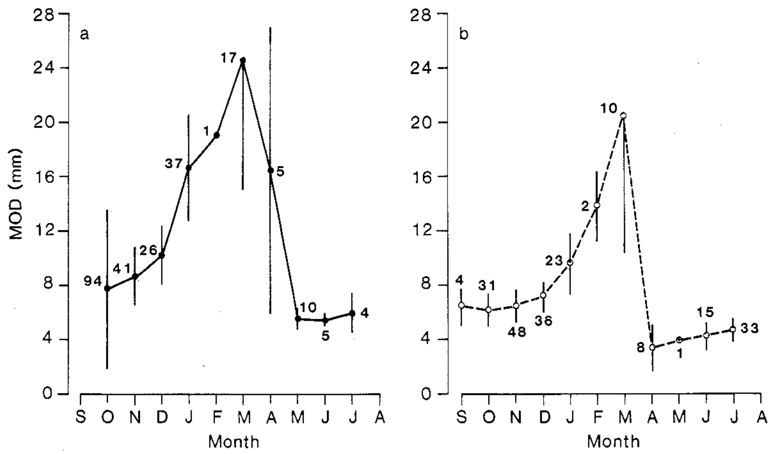

Fig. 9. Seasonal cycle of maximum ova diameter in pregnant and spent *C. tilstoni* (*a*) and *C. sorrah* (*b*) from the Arafura Sea. 1981–1983 data combined. Bars are standard deviation; numbers are sample size.

The mean litter size from a sample of 250 pregnant specimens of *C. tilstoni* was 3·0 [standard deviation (s.d.) 1·0], with a range of 1–6. The litter size of 248 pregnant specimens of *C. sorrah* ranged from 1 to 8 with a mean of 3·1 (s.d. 1·1). Although there was a significant relationship between increasing litter size and increasing maternal length (*C. tilstoni*, $r^2 = 0 \cdot 09$, $P < 0 \cdot 001$; *C. sorrah*, $r^2 = 0 \cdot 32$, $P < 0 \cdot 001$), about 90% of variation in litter size in *C. tilstoni* and 70% in *C. sorrah* was attributable to factors other than maternal length.

To determine whether females breed every year, the pregnancy rate was examined. Fig. 6 shows that 70% of *C. tilstoni* specimens in the 130–135-cm TL size range and over 90% of those above 135 cm TL were pregnant. Of mature female *C. sorrah* in the 100–105-cm TL length group, 93% were pregnant. This indicates that the females of both species breed each year. Further evidence for annual breeding was obtained by examining the gonads of pregnant females. Since ovulation occurs in March–April, pregnant females would be expected to have a new batch of ripening ova if they are to breed again the next year. Figs 9*a* and 9*b* show an increase in maximum ova diameter of pregnant and spent fish similar to that in non-pregnant specimens.

Annual breeding in males is supported by the high testes weight of males examined during the breeding season in each of the 2 years. Mean testes weight of 43 specimens of *C. tilstoni* and 56 of *C. sorrah* examined in February was 0·96% BW (s.d. 0·2) and 1·4% BW (s.d. 0·4), respectively.

More limited data on both species collected from the North West Shelf demonstrate essentially the same seasonal cycle as observed in the Arafura Sea. Mean litter size from 21 pregnant specimens of *C. tilstoni* on the North West Shelf was 4·1 (s.d. 1·6), with a range of 1–8, and from 102 pregnant specimens of *C. sorrah*, 3·4 (s.d. 1·1) with a range of 1–6. However, some observations on seasonal embryo growth made over 2 years from Joseph Bonaparte Gulf in the Timor Sea (Fig. 1) suggest that the cycle in that area may be 2 months later for *C. tilstoni*, and 1 month later for *C. sorrah*, than in the Arafura Sea or on the North West Shelf.

Diet

The body form and dentition of *C. tilstoni* suggest that it is an active surface and midwater predator. This view is supported by the observations of Carey *et al.* (1972), who recorded an elevated body temperature in *C. limbatus*, which is identical to *C. tilstoni* in body form and dentition. Bass *et al.* (1973) reported that teleost fish occurred in 93% of stomachs containing food in *C. limbatus* from South Africa. The teleosts included several fast-swimming pelagic species, although demersal prey items were also recorded. Other studies have also recorded both pelagic and bottom-dwelling prey from *C. limbatus* stomachs (Bigelow and Schroeder 1948; Clark and von Schmidt 1965; Branstetter 1981).

The stomach contents of 1943 specimens of *C. tilstoni* from the Arafura Sea sample were examined; 51·2% were empty. Of 995 specimens whose stomachs contained food, 92% had preyed on fish. The only other item of any significance in the diet was cephalopods, which occurred in 9·4% of stomachs containing food. In a limited sample of 56 specimens of *C. tilstoni* from the North West Shelf, 58·9% of stomachs were empty. Of those containing food, 89·5% contained fish and 15·8% contained cephalopods.

Table 4. Seasonal variation in the distribution of prey types amongst stomachs (percentage occurrence of major prey categories) of *Carcharhinus tilstoni* and *C. sorrah* from the commercial fishery in the Arafura Sea

Number of stomachs examined is given (no samples in May)

Month	*C. tilstoni* *n*	*C. tilstoni* % occurrence of: fish	cephalopods	crustaceans	*C. sorrah* *n*	*C. sorrah* % occurrence of: fish	cephalopods	crustaceans
January	40	82·5	15·0	5·0	39	69·2	17·9	23·1
February	43	93·0	7·0	0	62	91·9	14·5	4·8
March	69	91·3	2·9	0	57	86·0	8·8	8·8
April	87	49·4	59·8	1·1	15	53·3	26·7	13·3
June	166	97·0	4·2	2·4	164	81·7	20·7	7·3
July	20	95·0	0	5·0	42	95·2	14·3	0
August	62	98·4	0	0	2	50·0	50·0	0
September	116	96·6	3·4	0	60	80·0	26·7	10·0
October	293	98·0	4·7	1·4	123	74·8	26·0	24·4
November	71	94·4	4·2	1·4	27	100·0	7·4	3·7
December	28	89·3	10·7	7·1	13	76·9	15·4	7·7

To determine whether diet varied with body length, the percentage occurrence of major prey categories in the stomachs of sharks from the Arafura Sea was analysed separately for fish of less than 90 cm (small) and greater than 90 cm TL (large). In the large specimens, fewer stomachs contained fish (90%) and more contained cephalopods (11%) and miscellaneous items (1·3%) than did those of smaller sharks (99%, 2·8% and 0%, respectively). Other molluscs and crustaceans occurred in about equal numbers in both size groups.

The distribution of prey types amongst stomachs of *C. tilstoni* was examined seasonally. The only distinct variation was in April, when cephalopods, rather than fish, occurred in

Table 5. Distribution of prey in the stomachs of 995 specimens of *Carcharhinus tilstoni* and 604 specimens of *C. sorrah*

P, pelagic; PP, predominately pelagic; PD, predominately demersal; D, demersal. S, small; L, large; T, total. See text for size limits

Prey item	Prey category	Number of stomachs with prey item					
		C. tilstoni			*C. sorrah*		
		S	L	T	S	L	T
Unidentified fish		124	454	578	72	277	349
Unidentified elasmobranch		–	–	–	–	2	2
Unidentified shark		1	17	18	–	2	2
Unidentified ray		–	4	4	–	1	1
Scombridae	P	4	30	34	4	18	22
Thunnus tonggol	P	–	1	1	–	–	–
Auxis thazard	P	–	1	1	–	2	2
Euthunnus affinis	P	–	–	–	–	1	1
Rastrelliger kanagurta	P	–	4	4	–	2	2
Sarda orientalis	P	–	1	1	–	–	–
Scomberomorus spp.	P	–	4	4	–	3	3
Scomberomorus munroi	P	–	1	1	–	–	–
Coryphaena hippurus	P	–	1	1	–	–	–
Hemiramphidae	P	–	5	5	–	–	–
Exocoetidae	P	–	1	1	–	2	2
Chirocentris dorab	P	–	–	–	–	1	1
Trichiuridae	P	1	13	14	–	7	7
Megalaspis cordyla	P	–	14	14	–	–	–
Carcharhinus sorrah	PP	–	1	1	–	–	–
Hemipristis elongatus	PP	–	1	1	–	–	–
Carangoides gymnostethus	PP	–	–	1	–	–	–
Carangoides spp.	PP	3	8	11	–	3	3
Carangidae	PP	9	85	94	5	13	18
Clupeidae	PP	10	46	56	1	15	16
Apolectus niger	PP	5	14	19	1	9	10
Sphyraenidae	PP	1	–	1	–	–	–
Dactyloptena spp.	PP	–	2	2	1	–	1
Paralepididae	PP	–	1	1	–	–	–
Rhizoprionodon acutus	PD	–	1	1	–	–	–
Leiognathidae	PD	–	13	13	3	4	7
Lutjanidae	PD	–	2	2	–	–	–
Arius sp.	PD	–	4	4	–	1	1
Mene maculata	PD	–	–	–	–	2	2
Myctophidae	PD	–	1	1	–	–	–
Paramonacanthus filicauda	PD	–	2	2	1	–	1
Monocanthidae	D	3	5	8	–	12	12
Balistidae	D	4	10	14	–	4	4
Nemipteridae	D	10	22	32	1	14	15
Triglidae	D	–	1	1	–	1	1
Synodontidae	D	4	9	13	2	3	5
Saurida undosquamis	D	1	1	2	–	–	–
Eel	D	–	2	2	1	2	3
Muraenasox sp.	D	1	1	2	–	–	–
Sandeel	D	–	–	–	1	–	1
Congridae	D	–	–	–	1	–	1
Tetraodontidae	D	–	4	4	2	5	7
Diodontidae	D	–	2	2	1	5	6
Ostraciodontidae	D	–	–	–	–	10	10

Table 5 *(contd)*

Prey item	Prey category	Number of stomachs with prey item					
		C. tilstoni			*C. sorrah*		
		S	L	T	S	L	T
Lethrinidae	D	–	1	1	–	1	1
Centriscus sp.	D	–	–	–	–	1	1
Psettodes erumei	D	–	1	1	–	–	–
Bothidae	D	–	1	1	–	1	1
Platycephalidae	D	–	1	1	–	–	–
Sciaenidae	D	1	–	1	–	–	–
Triacanthidae	D	–	1	1	–	–	–
Trixiphichthys weberi	D	–	1	1	–	–	–
Mullidae	D	–	4	4	–	2	2
Fistularia sp.	D	–	–	–	–	1	1
Scaridae	D	–	1	1	1	1	2
Priacanthidae	D	–	1	1	–	1	1
Priacanthus tayenus	D	2	1	3	–	–	–
Haemulidae	D	–	1	1	–	–	–
Uranascopidae	D	–	1	1	–	–	–
Gerreidae	D	–	–	–	–	2	2
Scorpaenidae	D	–	1	1	–	–	–
Unidentified cephalopod		1	15	16	12	19	31
Unidentified squid	P	–	40	40	6	31	37
Loligo chinensis	P	1	14	15	–	–	–
Unidentified octopus	PD	1	1	2	–	2	2
Unidentified cuttlefish	PD	2	22	24	6	30	36
Bivalve shell	D	–	1	1	–	–	–
Unidentified crustacean		1	–	1	1	3	4
Unidentified decapod		–	–	–	–	1	1
Crab		1	4	5	2	34	36
Portunid	PP	–	–	–	2	11	13
Natantid	D	–	–	–	–	1	1
Prawn	D	1	5	6	4	8	12
Stomatopod	D	–	2	2	1	3	4
Isopod		–	1	1	–	–	–
Unidentified material		–	2	2	–	–	–
Cartilage		–	1	1	–	–	–
Eye lens		–	2	2	1	–	1
Seaweed		–	–	–	1	2	3
Rhizozoan		–	1	1	–	–	–
Sea snake	PP	–	1	1	–	–	–
Bird	P	–	1	1	–	–	–
Cetacean		–	2	2	–	–	–
Stone	D	–	1	1	–	–	–

the greater proportion of stomachs (Table 4). However, all but one of these stomachs containing cephalopods were recorded from one cruise in the western Arafura Sea when squid (*Loligo chinensis*) were particularly abundant in the area. Cephalopods also occurred in a greater proportion of stomachs in December and January, compared to other months (Table 4).

To obtain further information on the feeding mode of *C. tilstoni*, prey items were categorised into pelagic or demersal types, although few prey species fitted clearly into either category. Table 5 gives the stomach contents of 995 specimens of *C. tilstoni* containing food and shows to which of four categories (pelagic, predominantly pelagic, demersal and predominantly demersal) the prey items belonged. The percentage of prey in each of these four categories were summed into total pelagic (pelagic plus predominantly pelagic) and total demersal (demersal plus predominantly demersal). In small specimens of *C. tilstoni* (<90 cm TL) the number of stomachs containing pelagic and demersal prey was about equal (53% and 47%, respectively), while in the larger fish (>90 cm TL) 69% of stomachs contained pelagic and 31% contained demersal prey.

These data are based on percentage occurrence and represent the distribution of prey types amongst stomachs. They do not show the overall contribution to the diet, which would require additional data on weight and volume of prey items. However, the results show that teleost fish are an important component of the diet of *C. tilstoni* and there is some indication of a change in feeding depth with shark size.

The literature contains limited information on the diet of *C. sorrah*. Bass *et al.* (1973) examined four specimens containing food and suggested that the species feed near reefs. They noted that this shark could catch fast-swimming prey.

Of 1127 specimens of *C. sorrah* stomachs examined from the Arafura Sea, 46·4% contained food and 53·6% were empty. Fish occurred in 82% of stomachs containing food, with cephalopods and crustaceans present in 17% and 11%, respectively. In a sample of 223 specimens of *C. sorrah* from the North West Shelf, 7% had everted stomachs, 61·4% were empty and 31·6% contained food. Of the prey items, fish comprised 81%, cephalopods 20·3%, crustaceans 15·6% and other molluscs 1·6%.

Data on stomach contents of *C. sorrah* from the Arafura Sea were treated in the same way as those of *C. tilstoni*. There was little difference between the diet of fish shorter than 85 cm TL and longer than 85 cm TL. In the larger sharks (>85 cm), the percentage occurrence of major prey categories in the stomachs was fish 81%, cephalopods 16·5%, crustaceans 12·2% and miscellaneous items 0·4%. For the smaller sharks these values were 83%, 21%, 8% and 1·8%, respectively. Analysis of the distribution of prey types by month revealed noticeable differences in the proportion of major prey categories taken, but these showed no seasonal trend (Table 4). Prey items, identified to the lowest possible taxon, occurring in *C. sorrah* stomachs from the Arafura Sea are shown in Table 5. Separation of these prey items into principally pelagic and demersal types shows that in small individuals more stomachs contained demersal prey (56% compared to 44%), while in large specimens equal numbers of stomachs contained demersal and pelagic items.

These results suggest that *C. sorrah* feeds mainly on teleost fish, together with lesser numbers of cephalopods and crustaceans. As with *C. tilstoni*, there is some indication of a change in feeding depth with shark size.

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