

NORTHERN PELAGIC FISH STOCK RESEARCH

Final Report to the Fishing Industry Research and Development Council
Projects 83/49 and 86/87



A reward of \$5.00 plus market price for tagged sharks returned with information.

WHAT TO DO:-

1. Record date, position, tag colour and number.
2. Where possible freeze the shark with the tag still in place, otherwise record fork length of shark, measured as a straight line distance (see above) not over curve of body.
3. Contact local Fisheries office or CSIRO.

協助事項

- 一. 立即記下捕到魚的經度緯度深度標簽號碼及顏色, 捕獲日期
- 二. 把所捕獲的魚或魚子撒標簽進行冷凍
- 三. 在作業後檢查時應將捕獲的標識魚及其記錄資料提交檢查員並領取獎賞

Thank you 謝謝

N.T. Fisheries, crn Day and Harvey St. Darwin Ph: (089)897593
CSIRO Marine Laboratories. P.O. Box 1538, Hobart Ph: (002)206222



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Division of Fisheries

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A . INTRODUCTION

In 1982, CSIRO applied to the Fishing Industry Research Trust Account for funding of a joint biological investigation of northern Australian pelagic fish stocks. At that time these stocks supported a Taiwanese surface gill-net fishery based on sharks, tunas and Spanish mackerel.

During the 1970's the total annual catch taken by the Taiwanese fishery from the area between northern Australia and Papua New Guinea averaged about 25,000 tonnes live weight. With declaration of the Australian Fishing Zone (AFZ) in 1979 the fishery came under Australian jurisdiction and management measures were introduced. Simple yield estimating procedures based on the commercial catch data were used to derive an annual quota of 7,000 tonnes processed weight (about 10,000 tonnes live weight). The quota was assumed to be set at a conservative level of the potential yield. However, the only information available on the stocks at this time was some limited data on species composition together with preliminary data on size and sex distributions and reproduction of some of the shark species obtained by sampling the commercial catch through the AFZ observer program. Little information was available from inshore waters not fished by the Taiwanese and nothing was known about stock structure or the population dynamics of the main species that would allow a more scientifically defensible position to be adopted on the existing exploitation rate.

This study was initiated because of mounting government concern over the lack of research into the fishery, and because of increasing interest by industry in Australian exploitation of the resource. The program was a joint undertaking between CSIRO, the Commonwealth Department of Primary Industry and the State Fisheries of Queensland, Western Australia and the Northern Territory. The program aimed to provide information on the stock structure, migration, age and growth, recruitment and mortality of the principal species, and to examine the yield potential of the stocks and the potential for increased Australian participation in the fishery. It was particularly important to know whether the target species comprised single stocks or a number of discrete stocks across northern Australia. This information has implications for management of the foreign and domestic fisheries.

Twelve three-week cruises were made between January and May 1985 in northern waters between Broome and Cairns and including the Torres Strait and Gulf of Papua. Most of the work was carried out in inshore waters (within 12 nm of the coast) with relatively poor coverage of the Taiwanese zone because of bad weather and low catch rates in this area (Fig.1). The 21 m commercial gill-net vessel FV *Rachel* was chartered for the work. Fishing was carried out with gill-nets (that included a variety of mesh sizes to enable a study of gear selectivity), handlines and longlines. A large tagging program was conducted and biological studies included collection of tissues for starch gel electrophoresis, hard parts for ageing studies, and examination of reproductive cycles and stomach contents.

B. OBJECTIVES

To determine for the target species in the fishery:

- Stock structure
- Migration
- Fecundity and reproductive cycles
- Recruitment
- Age and growth
- Mortality
- Stock size and yield potential

To examine the potential for increased exploitation of the resource by the Australian fishing industry.

C. SUMMARY

Research-fishing catch, effort and catch per unit effort

A total of 17900 elasmobranchs and 1377 teleosts were caught by all methods during the program as shown below:

Species group	Number caught	Percentage of catch
Sharks	17865	93
Rays	35	0.2
Spanish mackerel	620	3.2
Longtail tuna	60	0.3
Other teleosts	697	3.6

Sharks comprised over 90% by number of gill-net and longline research catches. Although some 20 species were recorded, *Carcharhinus tilstoni* (Whitley's blacktip shark) and *C. sorrah* (the spot-tail shark) together represented about 70% of the shark component. The proportions of these two species varied with fishing method. Gill-net catches were dominated by *C. tilstoni* and longline catches by *C. sorrah*. The hardnose or milk shark *C. maclovi* was also numerous in the catches but is currently of limited commercial importance.

A considerable diversity of teleosts was caught but numbers were low. Spanish mackerel (*Scomberomorus* spp.) comprised 33% by number of the gill-net and 34% of the longline catch of teleosts while longtail tuna (*Thunnus tonggol*) represented 4% of the gill-net and 2% of the longline catch of teleosts.

The survey region was broken up into areas that roughly corresponded to north Queensland and Torres Strait (area 1), eastern Gulf of Carpentaria (area 2), western Gulf of Carpentaria (area 3), inshore Arafura Sea (area 4), offshore Arafura Sea (area 5) and Timor Sea (area 6). *C. tilstoni* and *C. sorrah* together represented 79-97% of the gill-net shark catches in area 1-4, while in areas 5 and 6 these species accounted for only 30 and 45% of the numbers respectively. Most of the area 6 sample was taken from Napier Broome Bay where *C. macloiti* and juvenile *C. tilstoni* and *C. sorrah* were prevalent.

C. tilstoni were the most abundant species caught at each depth strata examined; there is some evidence that adults favour the deeper water. *C. sorrah* were relatively more abundant at depths over 20 m.

Gill-net and longline catch rates for *C. tilstoni* and *C. sorrah* were highest in area 3 and lowest in area 5.

Biology of principal shark species

The shark component in the northern gill-net fishery is dominated by *C. tilstoni* and *C. sorrah* which together comprise about 64% of the total catch by number.

The principal shark species in the fishery was initially thought to be the blacktip shark *C. limbatus*. Size at maturity data collected prior to this study suggested the occurrence of two forms or stocks of this shark in northern waters. Electrophoretic and morphometric data obtained during this study showed that these forms were in fact separate species. The rarer of the two was the true *C. limbatus* (confirmed through electrophoretic analysis of tissue samples obtained from overseas *C. limbatus*) while the dominant species was Whitley's blacktip *C. tilstoni*.

Stock structure

Tissue samples for starch gel electrophoresis were collected from 925 *C. tilstoni* and 655 *C. sorrah* taken throughout the range of the fishery from the North West Shelf off Western Australia to north-eastern Queensland. Each species was screened for 47 enzyme loci of which 13 were found to be polymorphic ($P_{0.99}$) for at least one species; only five loci for each species showed sufficient variation ($P_{0.95}$) for analysis of population structure. Mean heterozygosity values were relatively low (0.037 for *C. tilstoni* and 0.035 for *C. sorrah*) and there was a low level of population subdivision within each species.

No difference was found between the genetic composition of inshore and offshore sharks and although there was some degree of genetic heterogeneity between areas there was insufficient evidence to suggest that there is more than one population of either species in Australian waters. This is supported by the results of tagging (see next section) which suggest that there is sufficient mixing and interbreeding to provide gene flow between widely separated areas.

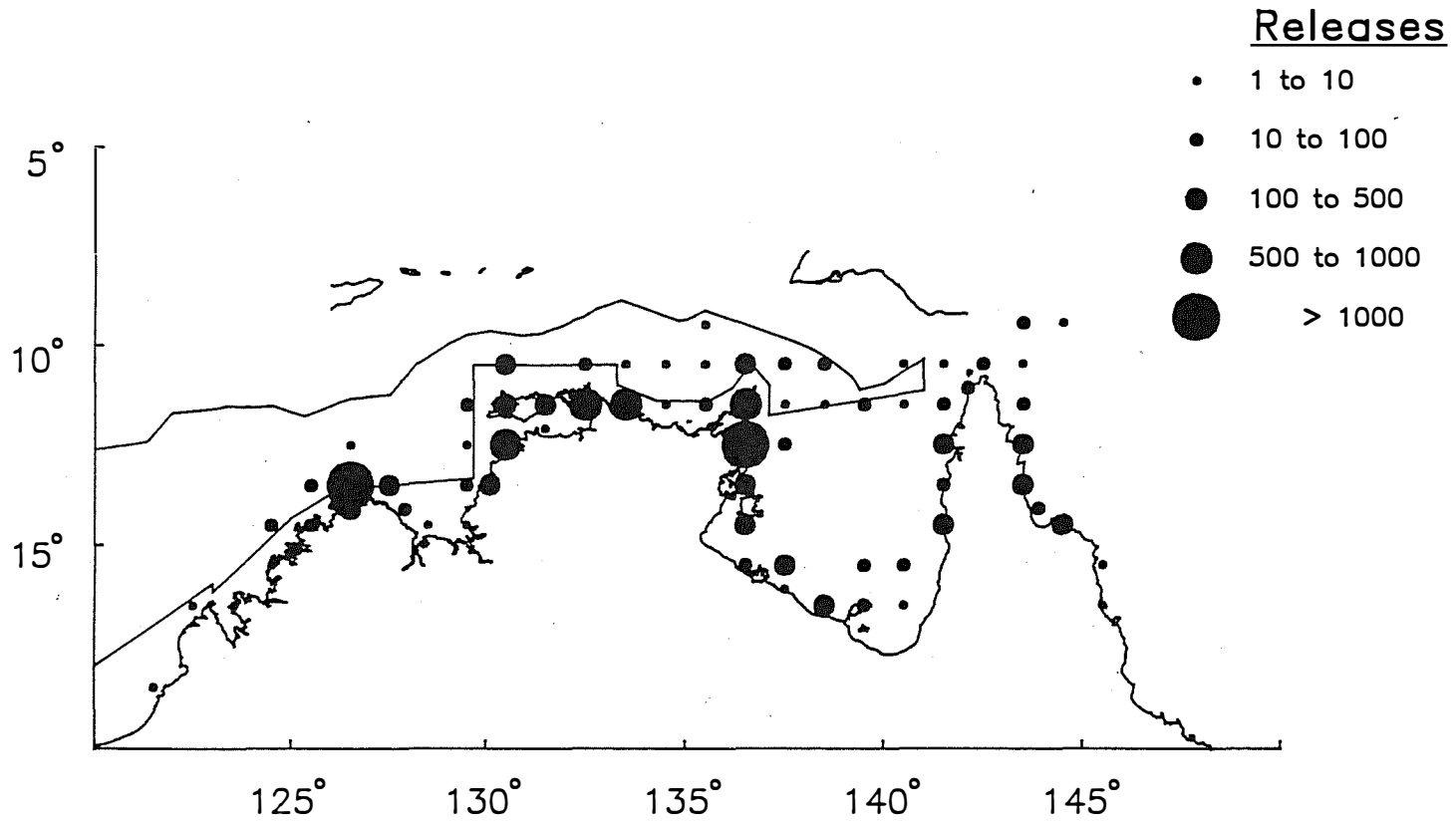


Fig. 1. Location of tag releases off northern Australia.

Migration

C. tilstoni and *C. sorrah* were tagged in northern waters between Broome and Cairns, although most releases were in inshore (< 35 km from the coast) waters of the Arafura Sea and Gulf of Carpentaria (Fig.1). The combined total of both species tagged was 7786. Movement data based on 317 recaptures of *C. tilstoni* and 75 recaptures *C. sorrah* are shown in Figs. 2 and 3 and suggest substantial migration. However, while the maximum distance travelled for both species was greater than 1000 km, the median distance travelled was only 21 km for *C. tilstoni* and 62 km for *C. sorrah*. Most sharks appeared to move very little, with 65% of *C. tilstoni* and 48% of *C. sorrah* caught within 50 km of the tagging site. Both species appear to be capable of dispersing quickly, some of the greatest distances travelled occurring about 30 days after tagging. There was no significant difference between the distances moved by males and females of either species, but there was between mature and immature *C. tilstoni* — immature fish in the 81-94 cm TL range moved greater distances. No evidence of a seasonal component to the movements of *C. tilstoni* was found (there were insufficient data for this analysis of *C. sorrah*).

Between 1984 and 1986, there were 108 combined recaptures of both species from the offshore Taiwanese gill-netters compared to 147 from inshore Australian gill-netters. However, Taiwanese fishing effort was about 60 times higher than effort in the Australian fishery. We estimate, after fishing effort is taken into account, that only about 3% of either species tagged inshore were recaptured offshore by the Taiwanese fleet.

Reproductive biology

Both *C. tilstoni* and *C. sorrah* are viviparous, the young being nourished through a yolk-sac placenta. The usual size at maturity for *C. tilstoni* is 110 cm for males and 115 cm for females; for *C. sorrah* it is 90 and 95 cm TL, respectively. Both species have an almost identical reproductive cycle; mating occurs in February-March, ovulation in March-April and the main birth period is January. The reproductive cycle is the same throughout northern Australia, although the precise timing of mating and ovulation appears to vary by about two weeks, depending on the year and specific area. Both species produce litters of three pups after a 10 month gestation; the birth size is 60 cm TL in *C. tilstoni* and 52 cm TL in *C. sorrah*. Individual females of both species breed each year.

Recruitment

C. tilstoni is born at 60 cm TL in January and recruits almost immediately to the fishery. Length-frequency data from the Taiwanese fishery illustrated in Fig.4 shows new recruits appearing in the February 1982 sample at about 64 cm. These sharks have reached a modal length of about 86 cm by January 1983, when the next pulse of neonatal fish can be seen at about 63 cm TL. At birth *C. tilstoni* are at about a third of their maximum selectivity in the commercial mesh size (15 cm); peak selectivity is at 79 cm FL (98 cm TL).

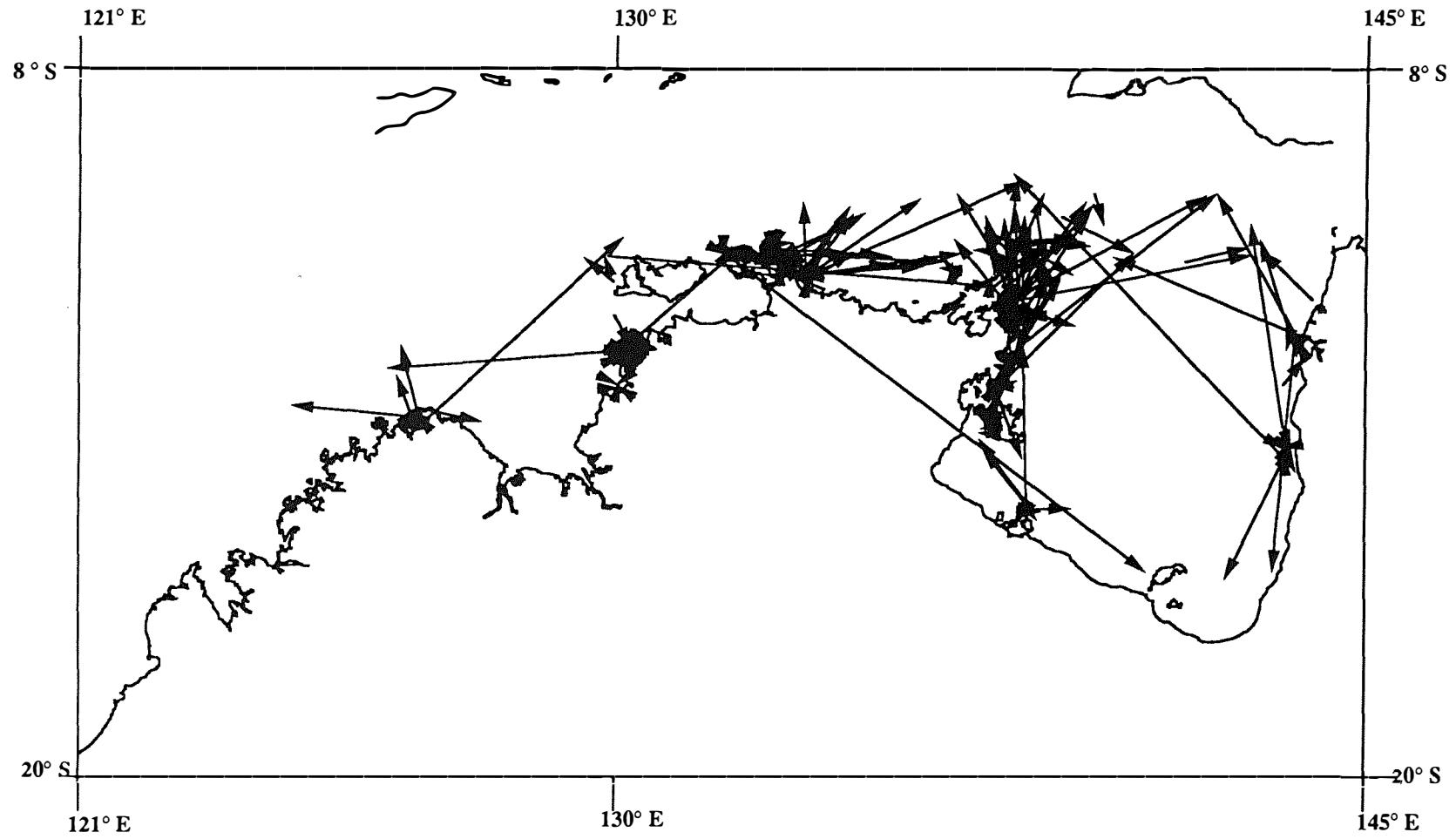


Fig. 2. Movements of tagged *Carcharhinus tilstoni*.

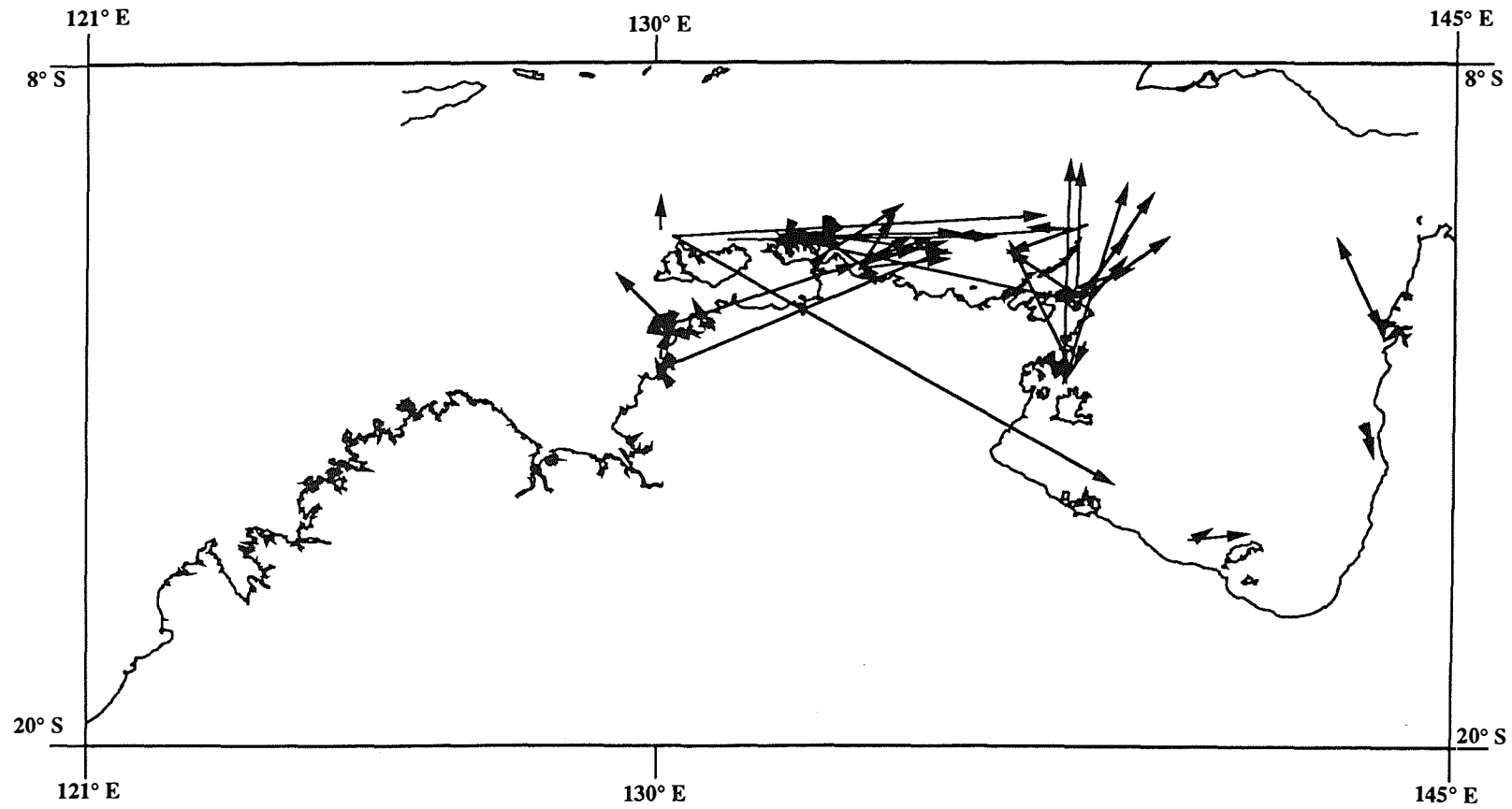


Fig. 3. Movements of tagged *Carcharhinus sorrah*.

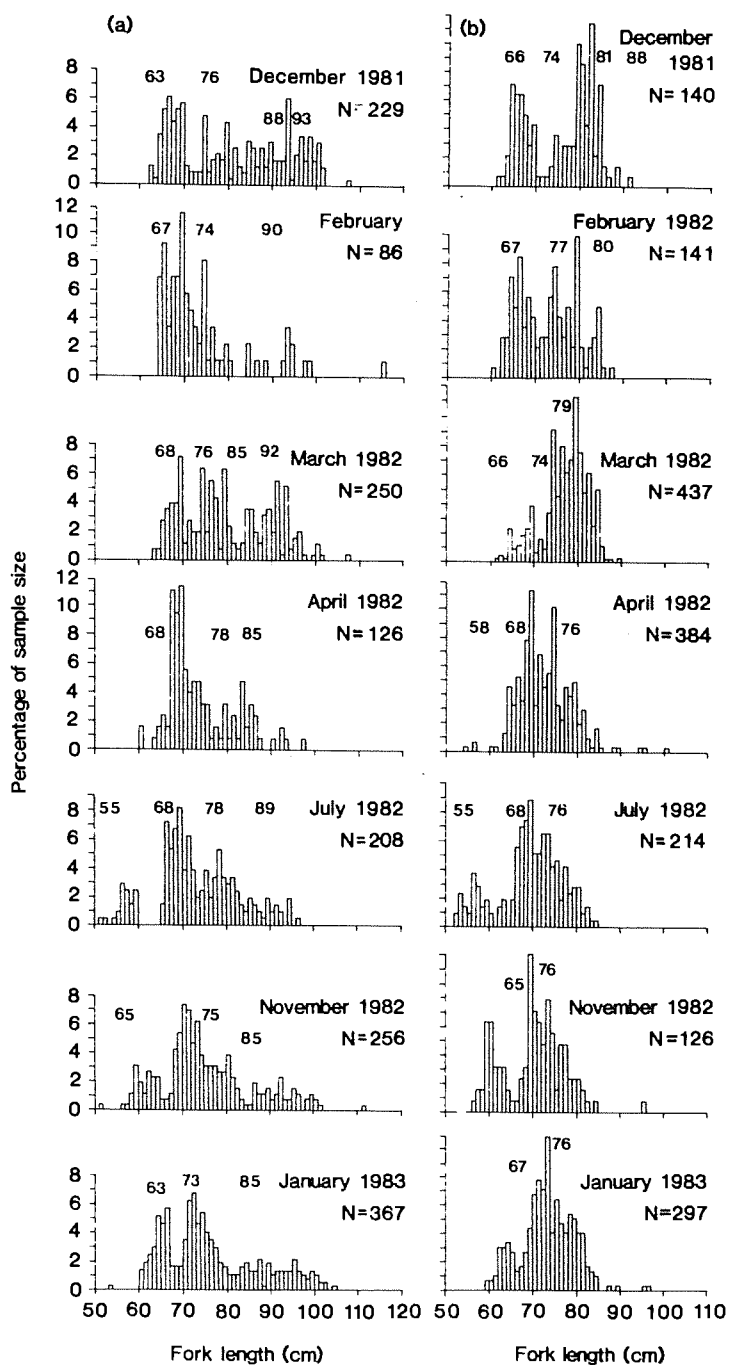


Fig. 5. Length-frequency data for *C. sorrah*, December 1981-January 1983 : (a) females, (b) males

C. sorrah are born at 52 cm TL in January but are not caught by the gill-net fishery until they are about 65 cm. The length-frequency data from the Taiwanese fishery (Fig.5) shows the young-of-the year fish appearing in the April 1982 sample at about 68 cm. At birth *C. sorrah* is only at about 0.1 of its peak selectivity in the 15 cm mesh net; maximum selectivity occurs at 74 cm TL.

Age and growth

The age and growth of *C. tilstoni* and *C. sorrah* were investigated through analysis of ring-counts on their vertebrae. A number of techniques were evaluated to enhance the clarity of the rings; ninhydrin, which stains the proteinaceous bands gave the best results. In vivo marking with oxytetracycline in conjunction with tagging confirmed that the rings were laid down annually. Corroborating evidence for age and growth estimates were obtained from analysis of length-frequency distributions and from tag-recapture information.

The age data from vertebral ring counts were fitted to a von Bertalanffy growth model. The model parameters are:

	<i>Carcharhinus tilstoni</i>		<i>Carcharhinus sorrah</i>	
	Female	Male	Female	Male
L_{∞}	194.2	165.4	123.9	98.4
K	0.14	0.19	0.34	1.17
t_0	-2.8	-2.6	-1.9	-0.6

The model does not provide a good fit to the data for male *C. sorrah*, probably because the data were concentrated over the first three year classes. There was a significant difference in the growth rate between the sexes in both species; females grow larger and faster (except in *C. sorrah* where males appear to grow faster initially). The growth curves for both species derived from vertebral ageing are shown in Figs.6 and 7.

Growth is fairly fast in the first year after birth; *C. tilstoni* grow about 17 cm and *C. sorrah* about 20 cm TL. Sexual maturity is reached relatively early; at 3-4 years in *C. tilstoni* and 2-3 years in *C. sorrah*. The greatest recorded ages for *C. tilstoni* were 12 years for females and 8 years for males, and for *C. sorrah*, 7 years for females and 5 years for males.

Growth rates and length-at-age values derived from modal analysis of length-frequency distributions show good agreement with results from vertebral ageing for the first three year classes in both species. Beyond this, the length-frequency data do not reveal clear modes. Growth rates obtained from tag-recapture data are slower, suggesting that the tag, or tagging process, may affect growth.

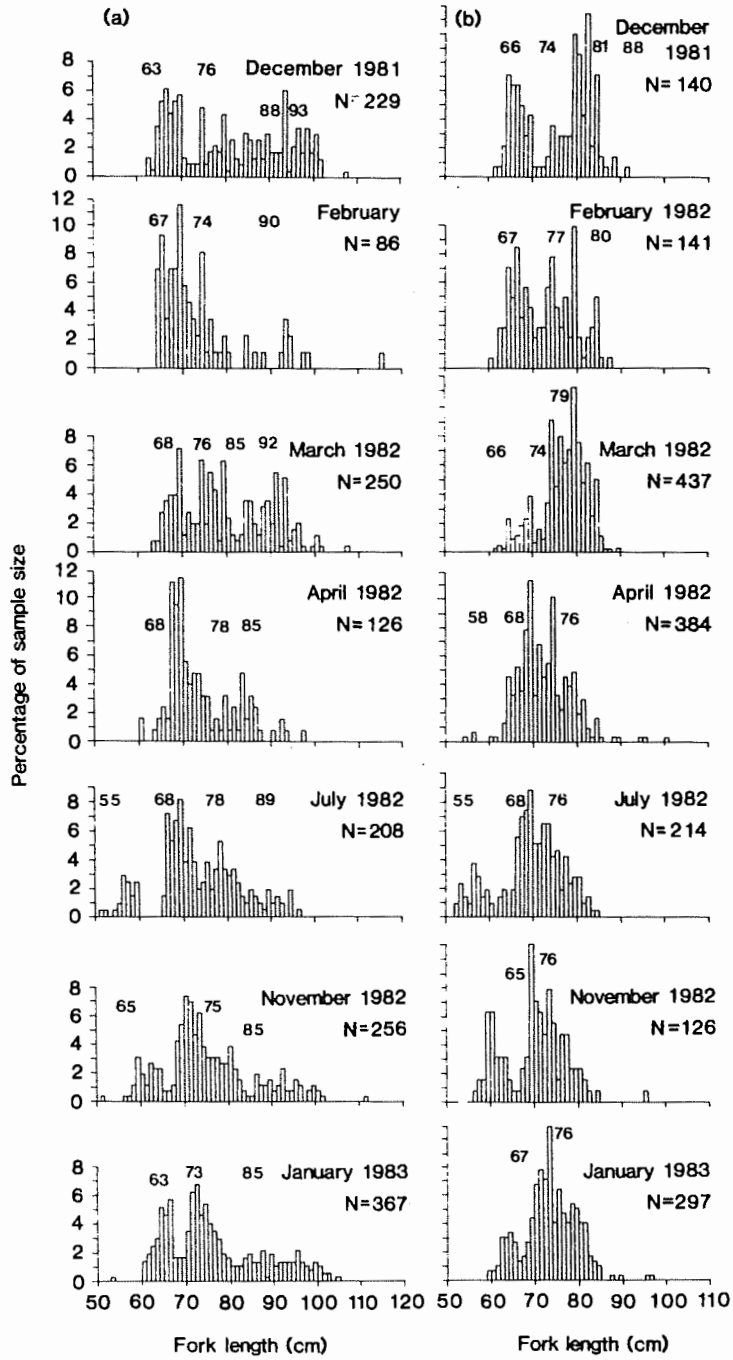


Fig. 5. Length-frequency data for *C. sorrah*, December 1981-January 1983 : (a) females, (b) males

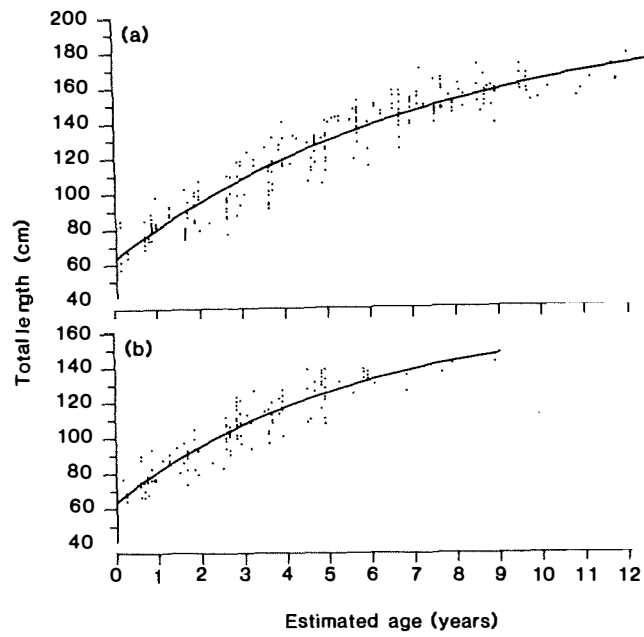


Fig. 6. Von Bertalanffy growth curves for *C. tilstoni* derived from vertebral ageing : (a) females (b) males

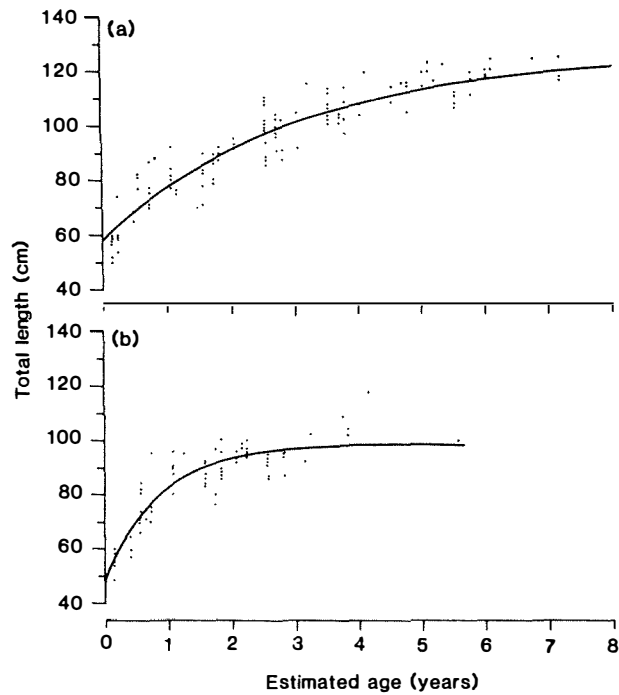


Fig. 7. Von Bertalanffy growth curves for *C. sorrah* derived from vertebral ageing : (a) females (b) males

Mortality

Total mortality (Z) was estimated from catch curves for the Taiwanese fishery and from tag-recapture data (using the decline in tag numbers with time) for the Australian fishery. Total mortality was dissected into natural mortality (M) and fishing mortality (F) from the estimating equation:

$$F/Z = n/N \quad (\text{since } F + M = Z)$$

where n = number of tag returns and N = number tagged.

Our estimate of Z for *C. tilstoni* in the Taiwanese fishery is 0.34 which is derived using all the data (ages 0–9). However, estimates varied from 0.13-0.47 depending on the age classes chosen. There is some evidence for a lower mortality field for ages 0-4 (Z = 0.13) than for ages 4-9 (Z = 0.47), but no valid explanation can be offered for this. With a Z of 0.34, F = 0.02 and M = 0.32. The estimate of Z for *C. tilstoni* in the Australian fishery is 0.46 (F = 0.02 and M = 0.44) but since this shark has been aged to 12 years, this value appears unrealistically high.

For *C. sorrah* in the Taiwanese fishery Z = 0.60, but it was not possible to get estimates of F and M as there were no tag returns from the 66 fish released in the Taiwanese zone. In the Australian fishery, Z = 0.54 (F = 0.01 and M = 0.53). *C. sorrah* has been aged to 7 years, so these mortality estimates seem much too high.

Population dynamics of sharks

An age-structured yield-per-recruit or dynamic pool model developed by T. I. Walker (Marine Science Laboratories, Queenscliff, Victoria 3225) for the southern shark fishery, was modified and adapted for use in this study. The principle of the model is that for a given mesh size and selectivity, one male and one female shark starting at age 0 are subjected to fishing and natural mortality over their life span. As a proportion of these two original fish the stock size, biomass, catch and number of pups born can be calculated for each age. The equilibrium state is determined by the fishing effort which results in the production of 2 pups over the animals' life span thus replacing the original two fish of age 0. The parameters required for the model are gill-net selectivities, age and growth, natural mortality, catchability, weight-length and fecundity.

When we set fishing effort at 0 and varied M until the simulated population achieved equilibrium, the values of M above 0.38 for *C. tilstoni* and 0.36 for *C. sorrah* were shown to be unrealistic. Consequently, we used the calculated M of 0.32 for *C. tilstoni* and because estimated mortalities for *C. sorrah* were much higher (0.5-0.6) we also used an M of 0.32 for this species.

Between 1980-84 the average annual Taiwanese fishing effort was 755,000 km hrs. The model indicated that to achieve the equilibrium state (at which point the population is neither increasing nor decreasing) Taiwanese fishing effort should not have exceeded 280,000 km hrs for *C. tilstoni* and 190,000 km hrs for *C. sorrah*. In the period 1980-84 this would have resulted in catches of 1890 and 535 tonnes live weight of *C. tilstoni* and *C. sorrah* respectively, which would have represented maximum sustainable catches at that time. The actual average annual catch taken between 1977-84 was 4,022 and 1,676 tonnes live weight of *C. tilstoni* and *C. sorrah* respectively.

Population estimates calculated using a modification of the Peterson method for tag-recapture data suggest the biomass of *C. tilstoni* in 1984 in a portion of the Taiwanese zone (35% of the area fished) was 14,750 tonnes live weight. This represents a density of 100 kg km² which is much higher than the 57 kg km² density estimate (both species combined) obtained from the Taiwanese fishery using the dynamic pool method. It is also considerably higher than the combined species density estimate of 89 kg km² from the Australian fishery. Since CPUE is four times higher in the Australian fishery than in the Taiwanese fishery, the population estimate for the Taiwanese zone based on tag-recapture data would appear to be too high (assuming differences in CPUE reflect differences in stock size).

Between 1984-89 the average annual effort in the Australian fishery was 12,000 km hrs. At this level of effort the model indicates that the populations of both shark species are underexploited. This is supported by CPUE data from the fishery which rose from 16 kg/km hr in 1984 to 45 kg/km hr in 1988. Population estimates from tagging for the period 1984-87 varied from 6,300-10,000 tonnes of *C. tilstoni* and 5,200-10,000 tonnes live weight of *C. sorrah*. This suggests that the maximum sustainable catch for both species combined should be about 1,500 tonnes. The actual catch (both species combined) has never exceeded 500 tonnes.

A comparison of yield per recruit over a range of gill-net mesh sizes (10-25 cm) showed that the most efficient mesh size was 15 cm, the size used by both the Taiwanese and Australians.

Spanish mackerel and longtail tuna

Of 620 Spanish mackerel caught during the program 335 were the main commercial species (*Scomberomorus commerson*) of which 83% were caught in the Gulf of Carpentaria and inshore Arnhem Land. *S. commerson* ranged in fork length from 57.0-134.0 cm (average 95.6 cm).

180 *S. commerson* were tagged with plastic headed dart tags but no recaptures were reported. Gonads and otoliths were retained from the remaining specimens by the Fisheries Centre of the Queensland Department of Primary Industries for studies of reproductive biology and ageing. Data obtained from these limited samples agreed with the findings of Rohan

et al. (1981) and McPherson (In preparation).

60 longtail tuna (*Thunnus tonggol*) were caught during the program ranging in fork length from 27.0-107.0 cm (average 57.6 cm). The majority (85%) were taken in the Gulf of Carpentaria and inshore and offshore Amhem Land.

13 *T. tonggol* were tagged but no recaptures were reported.

D. PRINCIPAL RECOMMENDATIONS FOR MANAGEMENT

There is no genetic evidence to suggest that *C. tilstoni* or *C. sorrah* should not be managed as single stocks in Australian waters. However, the movements of both species are relatively restricted and while they would provide sufficient gene flow to prevent genetic stock differentiation they may be insufficient to prevent heavy fishing pressure in one area reducing the local population of sharks. This suggests that the heavy fishing pressure offshore by the Taiwanese was unlikely to have had a major effect on inshore populations fished by Australian vessels.

Birth and recruitment of *C. tilstoni* and *C. sorrah* occur throughout their range and there do not appear to be major specific nursery areas that might require special protection.

The Taiwanese gill-net fishery over-exploited the shark stocks in the northern AFZ. Catch per unit effort dropped to nearly a quarter of its 1979 value by 1984. Based on shark landings and species composition data the average annual Taiwanese catch of *C. tilstoni* and *C. sorrah* from the northern AFZ between 1977-84 was 4,022 and 1,676 tonnes live weight respectively (see final FIRDC report 87/19). Average Taiwanese fishing effort between 1980-84 was 755,000 km hrs. Results from an age-structured yield per recruit model suggest that to maintain equilibrium in the fishery, effort should not have exceeded 280,000 km hrs for *C. tilstoni* and 190,000 km hrs for *C. sorrah*. The maximum sustainable catch for both species combined would have been about 2,400 tonnes live weight in 1980-84.

The Australian gill-net fishery appears to be currently under-exploiting the shark stocks in inshore northern waters. Between 1984-89 the combined catch of *C. tilstoni* and *C. sorrah* did not exceed 500 tonnes annually. Population estimates from tagging suggest that the maximum sustainable catch for both species combined should be about 1,500 tonnes live weight.

Gill-nets with a stretched mesh size of 15 cm are the most efficient in terms of maximising the yield per recruit in both the Taiwanese and Australian fishery.

E. DETAILS OF THIS STUDY

Description of fishery and research-fishing catch-effort data.

Northern pelagic fish stocks. J. D. Stevens. *CSIRO Marine Laboratories Research Report* 1981-1984.

Northern Pelagic Fish Stock Research Program: summary of catch and effort data. J. M. Lyle. *Department of Industries and Development. Fishery Report No. 16.*

Northern Pelagic Fish Stocks

J. D. Stevens

The waters between northern Australia, Indonesia and Papua New Guinea support a Taiwanese pelagic gillnet fishery for shark, tuna and Spanish mackerel. The fishery has operated since the early 1970s, and between 1975 and 1978 brought an average annual catch of about 17,000 tonnes. Although the fishery is targeted at the more valuable tuna, the bulk of the catch is shark. The fishing vessels are about 30 m long and set some eight km of 15-cm mesh net which is fished just below the surface. The net is set at dusk, and hauling starts at midnight, taking up to 12 hours to complete. The operation is labour intensive, with a crew of 16 needed to work the gear.

With the introduction of the Australian Fishing Zone (AFZ) in 1979 it became Australia's responsibility to manage the fishery. Thirty gillnetters were licensed to fish and the areas in which they could operate were progressively restricted to avoid interference with existing Australian fisheries. Inshore areas, the Gulf of Carpentaria and Joseph Bonaparte Gulf were closed and a total allowable catch (TAC) of 7,000 tonnes per year was imposed.

The TAC was based essentially on reported Taiwanese catches; because of the very limited knowledge of the fishery this was one of the few forms of management then possible. At that time it was not even clear what species were involved, let alone anything of their life histories or population dynamics. This situation existed largely because the product was unloaded and marketed in Taiwan, no biological information was available from the logbooks (all foreign vessels fishing in the AFZ are required to fill out logbooks) and no sampling of the catch was carried out at sea. Although this is presently a foreign fishery industry, the Federal Government is interested in greater Australian involvement.



Figure 1. The gillnet fishery in the waters between northern Australia, Indonesia and Papua New Guinea produces shark, tuna and Spanish mackerel.

In 1980 the AFZ Committee and subsequently the Northern Pelagic Fish Seminar held in Darwin recognised the need for urgent research on the stocks because a more scientifically defensible management policy was required and because shark populations are particularly sensitive to fishing pressure.

In 1981 the Division of Fisheries Research became responsible for the research, and scientists started sampling the commercial catch from a chartered vessel. It was used to locate the commercial vessels and carry observers to be placed on board to check the logbooks and sample the catch.

The vessel made 19 one-month-long cruises between May 1981 and September 1983. It was established that sharks comprise 62% of the annual catch by weight, and teleosts 38%. The teleost component, mainly longtail tuna (*Thunnus tonggol*) and mackerel (*Scomberomorus* spp.), can constitute 60% of the catch during certain months. Some 20 species of shark are taken but 2 species of blacktip, *Carcharhinus limbatus* and *C. sorrah*, comprise 83% of the total shark catch by number, *C. limbatus* alone accounting for 60%.

Research concentrated on establishing the basic life histories of these two species. Both are viviparous and have very similar restricted breeding seasons. Mating in February is followed by ovulation and pregnancy in March/April. Three pups are produced in January of each year after a gestation period of ten months. While their



Figure 2. The Taiwanese pelagic gillnet fishery is labour-intensive, with a crew of 16 needed to work the 8 km of 15-cm mesh net.

fecundity is low, they have a fast growth rate. Interpretation of rings on the vertebral centra and analysis of length-frequency modes show that both species have an average annual growth increment of some 15 cm during the first four years of life. Rapid growth together with an early attainment of sexual maturity may endow these species with a resistance to high fishing intensity.

These results represent the first phase in obtaining information useful for management. To obtain other data vital for management needs, a new approach was required. This resulted in the Northern Pelagic Fish Stock Research Program, which is a joint undertaking of the Department of Primary Industry (DPI), CSIRO Fisheries Research and the fishery departments of Northern Territory, Queensland and Western Australia. The program is funded by the Fishing Industry Research Trust Account (FIRTA) together with contributions from the participating states. The initial objectives are to obtain information on the size, geographical distribution, mortality, recruitment and yield potential of the stocks of shark, tuna and mackerel taken by the Taiwanese gillnet fishery in the Arafura Sea. The ultimate objective is to provide the relevant information for DPI to plan and implement management strategies for the fishery.

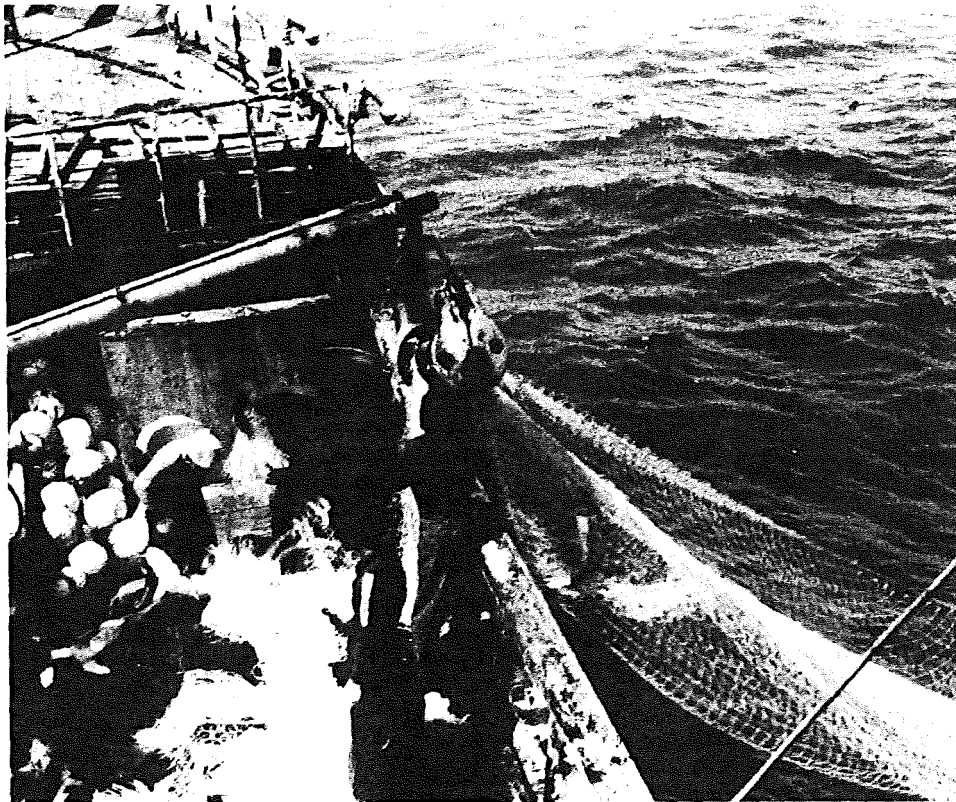


Figure 3. It can take up to 12 hours to complete the haul of the Taiwanese long net.

A gillnet vessel has been chartered for this work and a large tagging project in conjunction with exploratory fishing in areas closed to the Taiwanese has commenced. A series of eight 24-day cruises is planned, the first of which started in mid-January 1984, working the area between Joseph Bonaparte Gulf and Cape York and from close inshore to the limits of the AFZ.

Participating organisations are responsible for different sections of the work. CSIRO is concerned mainly with shark research and, in addition to tagging, stock discrimination is being examined by electrophoresis. The Northern Territory is interested in the stocks of longtail tuna and in the development of an inshore Australian shark fishery. The work includes aerial surveys for tuna and market testing, product suitability, mercury analysis and economic assessment of shark. Queensland is concerned with Spanish mackerel and has a separate tagging project off the northeast coast that links in with the cooperative program.

DEPARTMENT OF
INDUSTRIES & DEVELOPMENT

**NORTHERN PELAGIC FISH STOCK RESEARCH
PROGRAMME: SUMMARY OF CATCH
AND EFFORT DATA**

FISHERY REPORT No. 16



by J.M. LYLE

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NORTHERN PELAGIC FISH STOCK RESEARCH PROGRAMME:
SUMMARY OF CATCH AND EFFORT DATA

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FOREWORD

The pelagic species in the waters of northern Australia constitute one of Australia's most extensive fishery resources. There are however, significant gaps in knowledge about these stocks which was recognised when the Australian Fishing Zone was declared in 1979.

In 1982 a Northern Pelagic Fish Stock Research Programme was established as a joint exercise between the CSIRO and the Northern Territory, Commonwealth, Queensland and Western Australian government fisheries organizations. The objectives of the programme were broadly to obtain information on the biology and population dynamics of the pelagic fish resources off northern Australia. The breadth of the programme required considerable resources and a series of joint applications for support were made to State and Commonwealth funding authorities, including the Commonwealth Fishing Industry Research Trust Account and the Northern Territory Fishing Industry Research and Development Trust Account.

The programmes undertaken with grants provided has paved the way for a better understanding of the tropical pelagic fish resources. This will be used in the planning and implementation of improved management strategies for the fishery.

The secondary objective of the study was to undertake exploratory fishing trials and the results of these trials together with information about the resource and the potential for further utilisation are given in this report.



C J FULLER
SECRETARY

ABSTRACT

The Northern Pelagic Fish Stock Research Programme is a co-operative study between CSIRO, Department of Primary Industry, Northern Territory, Queensland and Western Australian government fisheries organizations. Its objectives are to provide information on the biology and population dynamics of the pelagic fish resources off northern Australia. Field work was undertaken between January 1984 and May 1985, and northern waters between Broome and Cairns were surveyed. A variety of fishing methods were employed but only catch and effort results for gillnet and longline fishing operations are reported here.

Sharks represented over 90% of gillnet and longline catches by number. Although some 20 species were recorded, the black-tip shark (Carcharhinus tilstoni) and sorrah shark (C. sorrah) together comprised about 70% of the shark component. The relative importance of each species did, however, vary with fishing method; black-tip sharks were dominant in the gillnet catches while sorrah sharks dominated the longline catches. Black-tip and sorrah sharks are of considerable commercial importance. Milk sharks (C. macroti) were also numerous but are presently of limited local commercial significance.

The region surveyed was broken up into areas that roughly corresponded to north Queensland (Area 1), eastern Gulf of Carpentaria (Area 2), western Gulf of Carpentaria (Area 3), inshore Arafura Sea (Area 4), offshore Arafura Sea (Area 5) and Timor Sea (Area 6). Black-tip and sorrah sharks together represented 79 - 97% of the gillnet shark catches in Areas 1 - 4 whereas in Areas 5 and 6 these species accounted for only 30 and 45% of the numbers respectively. Most of the Area 6 sample was taken from Napier Broome Bay where milk sharks and juvenile black-tip sharks were prevalent.

Black-tip sharks were the most abundant species caught at each of the depths examined with adults favouring the deeper waters. Sorrah sharks were comparatively more abundant at depths of over 20 m.

Gillnet and longline catch rates for black-tip and sorrah sharks were highest in Area 3 and lowest in Area 5. Most of the commercial gillnet effort off the Northern Territory is concentrated in Area 4. This survey suggests potential exists for shark fishing in the western Gulf of Carpentaria.

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1. INTRODUCTION

1.1 General

The presence of substantial pelagic fish resources, principally shark, mackerel and tuna off northern Australia has been known for a number of years. Taiwanese commenced gillnetting in the region in 1974 and between 1975 and 1978 annual catches averaged over 17000 t, with sharks representing up to 70% of the total weight (Walter 1981). During this period, the Taiwanese gillnetters fished areas presently within the Australian Fishing Zone (AFZ), including areas now closed to foreign fishing, and the Exclusive Economic Zone of Indonesia.

With the implementation of the AFZ in 1979 Australia assumed management responsibility for the fishery. Taiwanese fishing operations were restricted to specified offshore areas and a catch quota of 7000 t processed weight was imposed (Branford 1984). This quota represented an interim management measure in the absence of appropriate information about the biology and population dynamics of the exploited stocks. In 1985 the foreign fishing quota was reduced to 6000 t because of concern over declining catch rates particularly for sharks, and increasing catches by Australian vessels. In July 1986 the Commonwealth Government passed legislation that limited pelagic gillnets and drift nets to a maximum of 2.5 km in length (Fisheries Notice 182). This measure was intended to reduce the accidental kill of dolphins in gillnets but also resulted in the withdrawal of the Taiwanese gillnetters from the AFZ. The Taiwanese had been using up to 20 km of net prior to the introduction of this measure and the restriction rendered their operations uneconomical.

In recent years a small inshore gillnet fishery has developed off northern Australia. Landings of shark in the Northern Territory have grown from less than 20 t in the late 1970's to over 400 t in 1986.

1.2 Northern Pelagic Fish Stock Research Programme

At the sixth meeting of the Australian Fishing Zone Committee in August 1980 it was agreed that ... "Research is urgently needed to establish the condition of the stocks (of northern pelagic fish)", and the following recommendation was made to the Australian Fisheries Council (AFC):

"...investigation of the state of the stocks of the gillnet fishery off the Northern Territory be endorsed in principle and that proposals should be developed in this regard for consideration by appropriate authorities."

AFC endorsed the recommendation as follows:

"... proposals for investigation of the state of the stocks in the gillnet fishery off the Northern Territory be developed for consideration by appropriate authorities."

The Northern Pelagic Fish Stock Research Programme was established in recognition of these needs. It is a co-operative study between the CSIRO Division of Fisheries, Federal Department of Primary Industry (DPI), and the Northern Territory, Queensland and Western Australian fisheries organisations. The main objectives of the programme were to obtain information on the size, geographical distribution, stock discrimination and population dynamics of the exploited stocks (Stevens and Church 1984). This information together with data collected previously on the biology of sharks will be used in the planning and implementation of improved management strategies for the fishery. Secondary objectives were to undertake exploratory fishing trials and provide the Australian fishing industry with information about the resource and potential for further development. This report presents the results of this latter aspect.

2. MATERIALS AND METHODS

2.1 General

Fishing operations were undertaken from the 21 m gillnet fishing vessel RACHEL over the period January 1984 to May 1985. The survey consisted of 12 cruises each of about 24 days duration, cruise details are given in Appendix I. The survey was conducted in northern waters between Broome and Cairns and included the Gulf of Carpentaria, Torres Strait and the Gulf of Papua. For convenience of reporting results the region has been subdivided into the following areas:

- Area 1 - North Queensland, including Torres Strait and Gulf of Papua
- Area 2 - Eastern Gulf of Carpentaria
- Area 3 - Western Gulf of Carpentaria
- Area 4 - Arafura Sea (inshore)
- Area 5 - Arafura Sea (offshore)
- Area 6 - Timor Sea

The area breakdown is presented in Figure 1. Demarcation between the inshore and offshore Arafura Sea is based on the foreign fishing closure line. Area 5 represents the area in which the Taiwanese concentrated their gillnet fishing operations.

2.2 Fishing Gear

A gillnet consisting of two 500 m panels was fished either as a single 500 m length or with both panels combined. The net was stored on a hydraulically powered net reel positioned at the stern of the vessel. The net was constructed of green monofilament nylon (line 30), had a stretched mesh size of 15 cm (6 inch) and was 100 meshes deep. A lead-core lead line weighted the net while polystyrene floats, attached by 3 m float lines to the head rope, buoyed it (Appendix II).

The gillnet was fished just below the surface and was allowed to drift either with the vessel or free of it. During the setting operation the vessel headed down-wind and the net was fed off the reel and over the stern gunwale. Floats were attached to the float line by shark clips. When the entire net was shot away, a rope attached to the end of the net was fed forward over the bow roller and tied back onto the net reel. This allowed the vessel to turn and hang off the net by the bow. The net was hauled over a bow roller, down the length of the vessel and fed back on the net reel. Fish and floats were removed as each section of net was brought on board. The net and fishing method is similar to that used by Australian gillnet fishermen operating off northern Australia.

Longlines consisted of 1000 m (for 60 hooks) or 5000 m (for 300 hooks) of 8 mm polypropylene sink rope mainline. Snoods comprised 1-2 m of 5 mm sink rope attached by torpedo swivel to 1-2 m of 2 mm stainless steel wire trace. Shark clips were used to attach snoods to the mainline. Various hook types and sizes were used including 10/0 and 11/0 long shanked hooks and 9/0 and 10/0 Japanese tuna hooks. Hooks were baited with squid or whole or cut fish.

The longline was set over the stern gunwale and was anchored and buoyed at either end. Radar reflectors and light buoys were also positioned along the length of the mainline. Polystyrene floats were clipped directly onto the mainline and 10-15 hooks placed between each float. The longline effectively fished the upper part of the water column. The longline was retrieved over a bow roller and wound onto the net reel. Snoods and fish were generally removed on deck. With particularly large sharks, however, snoods were detached at the bow roller and the fish brought down the side of the vessel. The fish was then secured with a heavy rope and winched on board or tagged and released if alive.

In addition to the gear reported above, mesh selectivity was investigated using a gillnet that comprised four 200 m panels of different mesh size - 10, 15, 20 and 25 cm. Fish were also caught by handlining and trolling but this report is confined to the results obtained for the gillnet and longline operations only.

2.3 Fishing Strategy

A primary objective of the programme was to release a large number of tagged shark. In order to ensure that a high proportion of sharks were alive and healthy, gillnet sets were generally short in duration. The net was usually left for less than 30 minutes prior to hauling, and in most instances only 500 m of net was fished. When catch rates were low, 1000 m of net was used and sets were left for longer periods. As a general rule sharks survived longer on the longline than in the gillnet. Longlines were fished for several hours, allowing time for fish to locate the baits. Longlines were used extensively in the offshore regions where gillnets tended to yield poor catches. Fishing operations were conducted primarily between dusk and dawn.

2.4 Data Recorded

Full set details were recorded; position, depth, sea state, weather conditions and set and haul times. Fish were identified and in most cases fork length (from the tip of the snout to caudal fork) was measured to the nearest millimetre. Sharks that were still alive and healthy were tagged (plastic tag attached to the first dorsal fin, refer to Stevens and Church 1984) and released. Biological information including age, reproductive condition and stomach content data were collected from other fish and these results will be reported elsewhere.

3. RESULTS AND DISCUSSION

3.1 General

A total of 465 gillnet and 150 longline sets were completed. Full set details are presented in Appendix III. As shown in Figure 2 sampling effort was not uniformly distributed over the region surveyed, a consequence of cruise schedules and catch rates (i.e. more sets were made in the more productive areas).

Gillnet effort was most heavily concentrated around the north-western Gulf of Carpentaria and Wessel Islands. Other areas sampled extensively include the north-eastern Gulf of Carpentaria (near Weipa), Mornington Island, Goulburn Islands, Fog Bay, Anson Bay and Napier Broome Bay. Most longline sets were undertaken in the offshore waters to the north and north-east of the Wessel Islands (Fig. 2).

3.2 Catch Composition

Fishing method

Sharks accounted for 93% of the gillnet catches and 95% of the longline catches by number (Table 1). Although some 20 shark species were recorded during the survey, black-tip sharks (Carcharhinus tilstoni*) and sorrah sharks (C. sorrah) together comprised the bulk of the

* Referred to as C. limbatus in previous studies.

shark component (77% and 66% of the gillnet and longline catches respectively). The relative importance of these species did, however, vary with fishing method; black-tip sharks were the most abundant species caught by gillnet (57% by number) while sorrah sharks dominated the longline catch (47% by number). Commercially, black-tip and sorrah sharks are of greatest interest to fishermen as Australian markets have been established and the species have been favourably accepted by consumers (Welsford et al. 1984).

Size distributions for black-tip and sorrah sharks caught by the two fishing methods are shown in Figure 3. On average, larger black-tips were caught by longline, a tendency that is clearly reflected in the length-frequency histograms. Although the average size of sorrah sharks caught by both methods was very similar, there were differences in the size distributions. Longline catches included fish in the 35 - 54 cm fork length (FL) size groups which were essentially missed by the gillnet. The modal lengths also differed, 70 - 74 cm FL for the gillnet compared with 70 - 79 cm FL for the longline. It is generally recognised that longlines are less size selective than gillnets and thus represent a more accurate picture of population size structure.

Of the other shark species caught, only milk sharks (C. macloiti and Rhizoprionodon acutus) were of any numerical significance (Table 1). When compared with gillnet catches, proportionally higher numbers of grey whalers (C. amboinensis), black-spot sharks (C. dussumieri), tiger sharks (Galeocerdo cuvier) and hammerheads (Sphyrna spp. and Eusphyrna blochii) were taken by longline. Small numbers of rays, saw sharks and shovelnose sharks were also caught.

A considerable diversity of teleosts (scale fish) were caught though numbers were low (Table 1). Mackerels (Scomberomorus spp.) featured prominently in the catches; the broad-barred Spanish or grey mackerel (S. semifasciatus) being most important in gillnet and narrow-barred Spanish mackerel (S. commerson) in longline catches. Other species of significance include long tail tuna (Thunnus tonggol), mackerel tuna (Euthynnus affinis), Indian mackerel (Rastrelliger kanagurta), scad (Megalaspis cordyla) and pomfret (Apolectus niger).

Influence of area

Gillnet catch composition for sharks has been broken down by area in Table 2. Black-tip sharks accounted for 24 - 74% of the catch depending on area and were the most abundant species caught in Areas 1 - 4. Sorrah sharks were comparatively more important in the Gulf of Carpentaria (Areas 2 and 3) and inshore waters off the Northern Territory (Area 4) than elsewhere.

Milk sharks were particularly abundant in Areas 5 and 6. The sample size in Area 5 is small and therefore may not be representative of the species relative abundance in that area. Monitoring of Taiwanese gillnet catches supports this suggestion; black-tip and sorrah sharks usually comprised over 80% of the shark catch (Stevens and Wiley 1986). Almost 90% of the sharks sampled from Area 6 were taken from Napier Broome Bay where black-tip and milk sharks occurred in approximately equal proportions and together accounted for about 75% of the total shark catch. Despite comparatively good catches in Napier Broome Bay, the high proportion of milk sharks is commercially undesirable - these sharks are small and have not been readily accepted by fish buyers in Australia.

Figures 4 and 5 represent length-frequency distributions for black-tip and sorrah sharks caught by gillnet and broken down by area. The most conspicuous difference is the particularly high abundance of small black-tip sharks in Area 6; over 80% of the sample was less than 75 cm FL compared to 30 - 45% for all other areas. Black-tip sharks averaged only 66 cm FL in Area 6 compared with 82 cm FL or larger elsewhere. As noted above, most of the sharks from Area 6 were caught in Napier Broome Bay. The predominance of small fish in this bay and in Fog Bay (Lyle and Timms 1984) suggests that such areas may represent important nursery grounds for juvenile fish. Other than this difference, the average sizes and size distributions for either species varied only slightly between areas.

Influence of depth

The relationship between depth and relative catch composition was investigated by splitting gillnet catches into four depth categories (Table 3). Black-tip sharks were the most abundant species over the entire depth range considered, representing 45 - 64% of the total numbers. At depths of less than 20 m sorrah sharks represented only 10% of the catch whereas at greater depths they made up 19 - 29% of the numbers. The milk shark (C. macroti) represented an important component of the catches at all depths but in particular at depths of less than 20 m and greater than 40 m. Of the other sharks that occurred in reasonable numbers, the grey whaler (C. amblyrhynchoides) and milk shark (R. acutus) appear to favour the shallower waters.

Length-frequency histograms for black-tip and sorrah sharks caught by gillnet and split by depth are shown in Figures 6 and 7. The average size of black-tip sharks increased with depth, from about 74 cm FL at depths of less than 20 m to 90 cm FL at 40 m or deeper (Fig. 6). Length distributions indicate that

although there was little difference in the range of sizes caught at each depth, the shape of the distributions differed. The 65 - 69 cm FL mode, evident in the samples from shallow water, was replaced by one at 100 - 104 cm FL at depths greater than or equal to 40 m. These findings suggest that whilst adult black-tip sharks occur over the entire depth range they are comparatively more abundant in the deeper waters [black-tip sharks attain sexual maturity at about 90 - 95 cm FL (Stevens and Wiley 1986)]. Conversely, immature individuals appear to favour the shallower waters. The biological significance of this is not certain but may be related to reproduction and/or availability of suitable prey for the different size groups. These findings do, however, tie in with the suggestion that some shallow inshore bays may represent nursery areas.

There was little variation in the average size and length composition of sorrah sharks with depth (Fig. 7), suggesting no obvious depth preferences for the various size groups.

3.3 Effort and Catch Rates

Gillnet

As noted under Section 2.3, gillnets were generally set for short periods and either 500 or 1000 m of net was used. Commercial gillnet fishermen use up to 2.5 km of net which they fish for several hours. Such differences in fishing strategy make extrapolation of survey catch rates difficult. In an attempt to take account of this, catch rates are described as numbers of fish per kilometre of net hour (km-h). Determination of effective fishing time is complicated because from the time the net enters the water it has the capacity to catch fish and will continue to do so until it leaves the water. Fishing time consists of three components; (i) 'setting time' during which the length of net in the water is increasing (setting time is fairly constant for a given length of net), (ii) 'set duration' during which the entire net is in the water and fishing, and (iii) 'haul duration' during which the length of net in the water is decreasing (haul duration is highly variable and is dependent of the quantity of fish in the net). For the purposes of this study, effective fishing time has been defined as the time elapsed from the completion of setting the net to completion of hauling (i.e. set duration plus haul duration).

Over 50% of the gillnet effort and almost 60% of the total catch of all species was taken from Area 4 (Table 4). Overall catch per unit effort (CPUE) for sharks averaged about 37 fish/km-h, with the highest figure attained in Area 6. When considering catch rates, however, it is more relevant to consider commercial

species (i.e. black-tip and sorrah shark) rather than the entire catch. The average CPUE for commercial sharks was 28 fish/km-h, the catch rate for Area 3 being over double this figure. It is significant that the catch rate for Area 4 (the area from which the bulk of the Northern Territory shark catch is currently taken) is around half of that for Area 3. There is some commercial gillnetting in the western Gulf of Carpentaria at the present time and unconfirmed reports suggest that good catch rates have been achieved. The potential for higher catch rates in the Gulf may offset, to some degree, the increased costs of operating in that area.

CPUE for Area 6 was similar to that for Area 4 but, as indicated previously, the bulk of this sample came from a single locality (Napier Broome Bay) where most of the black-tip sharks were comparatively small fish (Fig. 4).

Although only limited data is available for Area 5, it is evident that catch rates were significantly lower than in the adjacent inshore waters (Area 4). Very little gillnetting has been attempted by Australians in these offshore waters because of the expectation of poor catches. The Taiwanese were able to maintain commercially viable operations in this area because they utilized large quantities of net (up to 20 km per set).

The low CPUE for Area 1 has been influenced by poor catches in the Torres Strait and Gulf of Papua regions. There is some shark fishing off northern Queensland where good catches have been reported.

Within each area there was considerable variation in catch rates for individual sets. About one third of all sets yielded nil catches and 40 - 50% of sets had CPUEs of less than 25 black-tip and sorrah sharks/ km-h (Fig. 8). Areas 3 and 4 appear to be exceptions with a lower proportion of nil catches and a comparatively high proportion of large catches (over 100 sharks/ km-h) in Area 3.

Details of sets with CPUEs of over 100 sharks/ km-h are presented in Table 5 and approximate positions shown in Figure 9. Localities such as Napier Broome Bay off Western Australia; Fog Bay, the Goulburn Islands, the Wessel Islands, areas adjacent to Nhulunbuy, the north-western Gulf of Carpentaria, Groote Eylandt and Vanderlin Island off the Northern Territory; and Mornington Island and Claremont Isles off Queensland appear to represent areas with potential for commercial gillnet fishing. There are, however, reports of many other localities within the region studied that have produced commercial quantities of shark.

Reports from commercial fishermen and previous surveys (e.g. Lyle and Timms 1984) indicate that gillnet catch rates tend to be highly variable. It is probable that such variability reflects the patchy distribution of the fish. It has also been suggested that both black-tip and sorrah sharks may form aggregations or schools (Stevens and Wiley 1986), an observation supported by some of the larger catches being dominated by one species with individuals of similar size or of the same sex.

Seasonal changes in CPUE have not been considered in this analysis since the level of variability between sets masked any pattern that may have been present.

Longline

Unlike gillnets, longline catches probably do not increase significantly with time in the water. That is, once the effectiveness of the bait in attracting fish has diminished, few additional fish will be caught. The probability of a hooked fish being eaten by other predators may also increase with fishing time. For these reasons longline catch rates have been expressed as number of fish per 100 hooks rather than per hook-hour. CPUE of all shark and black-tip and sorrah sharks averaged 4.3 and 2.8 fish/ 100 hooks respectively (Table 6). In accordance with gillnet results, catch rates for the commercial species were highest in Area 3 (7.8 sharks/ 100 hooks) and lowest in Area 5 (1.0 shark/ 100 hooks).

Taiwanese longliners operated in the Arafura Sea between late 1985 and early 1986 and averaged catches of 6.9 sharks/ 100 hooks (Read and Ward 1986). The Taiwanese set the lines on the bottom in deep water (120 m) and the species composition was quite different to that for this survey (refer to Read and Ward 1986). Puffet (1969) reported catches of about 14 sharks/ 100 hooks in a survey of Northern Territory inshore waters, marginally higher than the figure for the same area considered here.

4. CONCLUSIONS

The commercially important black-tip and sorrah sharks formed the major component of both gillnet and longline catches.

Black-tip sharks were the most abundant species caught at all depths, and there was a trend for larger fish to occur in deeper water. Sorrah sharks were relatively more important in waters deeper than 20 m than at shallower depths.

Catch rates proved to be highly variable between sets, presumably reflecting the patchy distribution of the sharks. Particularly good catches were attained at a number of specific localities, these include Napier Broome Bay, Fog Bay, Goulburn Islands, Wessel Islands, north-western Gulf of Carpentaria, Groote Eylandt, Vanderlin Island and Mornington Island.

Overall CPUE for black-tip and sorrah sharks was highest in the western Gulf of Carpentaria (Area 3). This is significant given that most commercial shark fishing off the Northern Territory currently occurs outside of this area.

Longline catches were generally poor, and based on this study it is not possible to assess the commercial viability of this fishing method.

5. ACKNOWLEDGMENTS

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TABLE 1: Species composition (numbers and percentage) of all fish caught by gillnet and longline. Mean lengths and ranges for sharks are given.

SPECIES	GILLNET			LONGLINE		
	No.	%	FORK LENGTH (Mean & Range)	No.	%	FORK LENGTH (Mean & Range)
<u>SHARKS</u>						
<u>Carcharhinus tilstoni</u>	6250	56.8	81.2 (47.0-164.0)	220	18.8	94.2 (54.0-176.0)
<u>C. sorrah</u>	2234	20.3	74.2 (42.0-121.0)	548	46.8	73.4 (36.0-100.0)
<u>C. macloiti</u>	1607	14.6	64.6 (34.0- 88.0)	49	4.2	64.6 (55.0- 73.0)
<u>C. amblyrhynchoides</u>	220	2.0	83.0 (52.0-114.0)	2	0.2	88.5 (86.0- 91.0)
<u>C. fitzroyensis</u>	57	0.5	79.8 (55.0-104.0)	5	0.4	77.0 (61.0- 96.0)
<u>C. amboinensis</u>	59	0.5	97.6 (53.0-187.0)	41	3.5	112.7 (57.0-190.0)
<u>C. limbatus</u>	8	0.1	126.9 (68.0-172.0)	-	-	-
<u>C. melanopterus</u>	4	<0.1	82.3 (66.0- 93.0)	-	-	-
<u>C. amblyrhynchos</u>	2	<0.1	89.5 (63.0-116.0)	13	1.1	107.1 (58.0-139.0)
<u>C. brevipinna</u>	44	0.4	76.9 (57.0-132.0)	10	0.8	86.0 (56.0-128.0)

TABLE 1: (Continued)

SPECIES	GILLNET			LONGLINE		
	No.	%	FORK LENGTH (Mean & Range)	No.	%	FORK LENGTH (Mean & Range)
<u>C. dussumieri</u>	27	0.3	62.4 (51.0- 69.0)	29	2.5	62.3 (43.0- 71.0)
<u>C. plumbeus</u>	2	<0.1	140.5 (139.0-142.0)	4	0.3	120.5 (63.0-148.0)
<u>C. falciiformis</u>	-	-	-	1	0.1	172.0
<u>Rhizoprionodon acutus</u>	232	2.1	65.5 (41.0- 73.0)	81	6.9	64.9 (54.0- 70.0)
<u>R. oligolinx</u>	-	-	-	1	0.1	38.0 -
<u>P. taylori</u>	58	0.5	58.8 (34.0- 72.0)	27	2.3	62.9 (42.0- 71.0)
<u>Hemipristis elongatus</u>	5	0.1	98.4 (84.0-119.0)	1	0.1	140.0 -
<u>Loxodon macrorhinus</u>	1	<0.1	59.0	1	0.1	47.0 -
<u>Galeocerdo cuvier</u>	1	<0.1	83.0	71	6.1	170.0 (62.0-307.0)
<u>Sphyrna lewini</u>	88	0.8	93.1 (50.0-143.0)	31	2.6	114.1 (65.0-200.0)

TABLE 1: (Continued)

SPECIES	GILLNET			LONGLINE		
	No.	%	FORK LENGTH (Mean & Range)	No.	%	FORK LENGTH (Mean & Range)
<u>S. mokarran</u>	37	0.3	129.9 (54.0-237.0)	22	1.9	164.0 (104.0-230.0)
<u>Eusphyrna blochii</u>	62	0.6	90.2 (53.0-125.0)	6	0.5	105.2 (97.0-112.0)
<u>Stegastoma fasciatus</u>	-	-	-	2	0.2	136.5 (110.0-163.0)
<u>Nebrius ferrugineus</u>	-	-	-	5	0.4	217.6 (148.0-250.0)
TOTAL SHARKS	10998			1170		
<u>RAYS, SAWSHARKS, SHOVEL NOSE SHARKS</u>						
<u>Rhynchobatus</u> spp.	-			2		
<u>Pristis</u> spp.	13			-		
Myliobatididae	2			-		
Mobulidae	3			-		

TABLE 1: (Continued)

SPECIES	GILLNET		LONGLINE	
	No.	%	No.	%
<u>TELEOSTS</u>				
<u>Scomberomorus commerson</u>	51	6.3	18	27.7
<u>S. semifasciatus</u>	188	23.3	-	-
<u>S. munroi</u>	21	2.6	3	4.6
<u>S. queenslandicus</u>	5	0.6	1	1.5
<u>S. guttatus</u>	2	0.2	-	-
<u>Grammatocynus bicarinatus</u>	1	0.1	-	-
<u>Thunnus tonggol</u>	30	3.7	1	1.5
<u>Euthynnus affinis</u>	76	9.4	-	-
<u>Rastrelliger kanagurta</u>	144	17.9	-	-
<u>Cybiosarda elegans</u>	32	4.0	-	-
<u>Auxis thazard</u>	7	0.9	-	-
Scombridae	1	0.1	-	-
<u>Istiophorus platypterus</u>	6	0.7	1	1.5
<u>Makaira indica</u>	2	0.2	6	9.2
Ariidae	7	0.9	10	15.4

TABLE 1: (Continued)

SPECIES	GILLNET		LONGLINE	
	No.	%	No.	%
Lutjanidae	-	-	3	4.6
<u>Apolectus niger</u>	96	11.9	-	-
<u>Megalaspis cordyla</u>	52	6.4	-	-
<u>Scomberoides</u> spp.	39	4.8	-	-
Carangidae	11	1.4	-	-
<u>Rachycentron canadus</u>	4	0.5	3	4.6
Polynemidae	25	3.1	-	-
<u>Coryphaena hippurus</u>	-	-	9	13.8
Sphyraenidae	1	0.1	2	3.1
<u>Mene maculata</u>	4	0.5	-	-
Echeneidae	-	-	8	12.3
TOTAL TELEOSTS	805	100	65	100

TABLE 2: Relative numbers (percentage) by area for sharks caught by gillnet (+ denotes less than 0.1%).

SPECIES	AREA					
	1 %	2 %	3 %	4 %	5 %	6 %
<u>Carcharhinus tilstoni</u>	69.8	60.7	73.5	56.8	23.6	35.4
<u>C. sorrah</u>	14.5	25.2	23.6	22.3	6.6	10.6
<u>C. macroti</u>	8.8	2.2	0.7	13.8	64.2	36.2
<u>C. amblyrhynchoides</u>	-	-	0.8	1.2	-	6.5
<u>C. fitzroyensis</u>	0.1	-	0.2	0.6	-	1.0
<u>C. amboinensis</u>	0.8	0.6	-	0.4	-	1.7
<u>C. limbatus</u>	0.8	-	-	+	-	+
<u>C. melanopterus</u>	-	-	-	0.1	-	-
<u>C. amblyrhynchos</u>	-	-	0.1	-	-	+
<u>C. brevipinna</u>	-	1.5	0.2	0.3	0.9	0.6
<u>C. dussumieri</u>	-	0.6	-	0.3	-	0.3
<u>C. plumbeus</u>	-	-	-	-	-	0.1
<u>Rhizoprionodon acutus</u>	3.8	1.4	0.1	2.0	1.9	4.3
<u>R. taylori</u>	-	6.1	0.1	0.1	0.9	0.6
<u>Hemipristis elongatus</u>	-	-	0.1	0.1	-	-
<u>Loxodon macrorhinus</u>	-	-	-	+	-	-
<u>Galeocerdo cuvier</u>	0.1	-	-	-	-	-
<u>Sphyrna lewini</u>	0.7	0.9	0.4	0.8	1.9	1.3
<u>S. mokarran</u>	0.4	0.8	0.1	0.4	-	0.3
<u>Eusphyrna blochii</u>	0.1	-	0.1	0.7	-	0.8
TOTAL NUMBER	718	654	1519	6457	106	1544

TABLE 3: Relative numbers (percentage) by depth category for sharks caught by gillnet (+ denotes less than 0.1%).

SPECIES	DEPTH RANGE			
	< 20m %	20 - 29m %	30 - 39m %	> 40m %
<u>Carcharhinus tilstoni</u>	47.6	59.2	64.2	44.8
<u>C. sorrah</u>	9.9	24.6	18.6	28.5
<u>C. macloti</u>	23.7	9.2	13.2	24.5
<u>C. amblyrhynchoides</u>	6.8	1.2	0.2	-
<u>C. fitzroyensis</u>	1.0	0.4	0.5	-
<u>C. amboinensis</u>	1.3	0.4	0.2	0.3
<u>C. limbatus</u>	-	0.2	+	-
<u>C. melanopterus</u>	0.1	-	0.1	-
<u>C. amblyrhynchos</u>	-	+	-	-
<u>C. brevipinna</u>	0.5	0.5	0.2	0.4
<u>C. dussumieri</u>	0.5	0.3	0.1	-
<u>C. plumbeus</u>	-	+	+	-
<u>Rhizoprionodon acutus</u>	5.0	1.5	1.3	0.7
<u>R. taylori</u>	1.2	0.6	0.1	0.1
<u>Hemipristis elongatus</u>	+	+	0.1	-
<u>Loxodon macrorhinus</u>	-	+	-	-
<u>Galeocerdo cuvier</u>	+	-	-	-
<u>Sphyrna lewini</u>	1.3	0.9	0.5	0.4
<u>S. mokarran</u>	0.4	0.5	0.1	0.1
<u>Eusphyrna blochii</u>	0.7	0.6	0.5	0.2
TOTAL NUMBER	2278	4815	2903	983

TABLE 4: Summary of effort, catch and catch per unit effort (CPUE) for gillnet by area.

AREA	EFFORT		CATCH (No.)			CPUE (No./km-h)	
	NO. OF SETS	TOTAL (km-h)	ALL SHARKS	BLACK-TIP & SORRAH SHARKS	OTHER	ALL SHARKS	BLACK-TIP & SORRAH SHARKS
1	56	39.9	718	486	32	18.0	12.2
2	69	28.1	654	562	68	23.3	20.0
3	49	23.1	1519	1474	122	65.8	63.8
4	208	158.5	6457	5100	489	40.7	32.2
5	24	26.2	106	32	53	4.0	1.2
6	59	20.3	1544	711	60	76.0	35.0
TOTAL	465	295.9	10998	8484	824	37.2	28.7

TABLE 5: Set and catch details for gillnet sets with catch per unit effort (CPUE) for black-tip and sorrah sharks of greater than 100 sharks/km-h (500 m of gillnet was used unless otherwise specified).

AREA	DATE	SET/ CRUISE	POSITION		DEPTH (m)	FISHING TIME (min)	CATCH (No.)			CPUE (No./km-h)	
			LAT	LONG			ALL SHARKS	BLACK-TIP & SORRAH SHARKS	OTHER SHARKS	BLACK-TIP & SORRAH SHARKS	
1	15.4.85	46/11	13° 44.5S	143° 39.6E	17	90	172	171	0	228.0	
2	27.2.84	73/2	13° 04.4S	136° 37.6E	29	81	81	80	1	118.5	
	2.3.84	101/2	12° 22.2S	136° 29.4E	25	100	132	129	1	154.8	
	3.3.84	105/2	12° 41.8S	136° 50.5E	38	96	90	89	4	111.3	
	3.3.84	106/2	12° 41.5S	136° 50.0E	36	70	73	71	0	121.7	
	7.6.84	24/5	14° 00.0S	136° 18.3E	26	31	101	100	0	387.1	
	7.6.84	25/5	13° 56.7S	136° 19.0E	28	25	34	34	0	163.2	
	8.6.84	33/5	14° 04.2S	136° 20.3E	21	60	98	97	4	194.0	
	23.6.84	69/5	15° 30.5S	137° 03.1E	24	44	83	83	0	226.4	
	23.6.84	70/5	15° 29.2S	137° 02.8E	24	29	45	43	0	177.9	
	23.6.84	71/5	15° 27.9S	136° 59.4E	24	24	55	54	0	270.0	
	24.6.84	72/5	15° 28.7S	137° 05.0E	26	30	85	85	0	340.0	
3	6.7.84	6/6	16° 19.8S	138° 40.7E	26	77	69	65	7	101.3	
	7.7.84	14/6	16° 16.5S	138° 33.0E	26	72	88	88	0	146.7	
4	8.2.84	87/1**	12° 02.3S	136° 42.4E	20	285	944	828	4	174.3	
	27.3.84	47/3	11° 28.3S	132° 14.4E	31	100	138	136	0	163.2	

TABLE 5: (Continued)

AREA	DATE	SET/ CRUISE	POSITION		DEPTH (m)	FISHING TIME (min)	CATCH (No.)			CPUE (No./km-h)	
			LAT	LONG			ALL SHARKS	BLACK-TIP & SORRAH SHARKS	OTHER	BLACK-TIP & SORRAH SHARKS	
4	27.3.84	52/3	11° 29.6S	133° 14.7E	30	77	110	107	1	166.8	
	25.4.84	1/4	12° 34.4S	130° 14.0E	22	20	58	53	0	318.0	
	25.4.84	2/4	12° 35.3S	130° 14.3E	21	20	28	27	0	162.0	
	3.6.84	9/5	12° 07.7S	136° 43.2E	25	28	56	38	2	162.9	
	3.6.84	10/5	12° 07.7S	136° 42.6E	26	25	42	29	1	139.2	
	4.6.84	16/5	12° 08.7S	136° 44.6E	21	27	32	27	3	120.0	
	31.1.85	14/9	12° 00.4S	136° 46.5E	31	80	105	100	1	150.0	
	3.3.85	26/10	12° 02.2S	136° 44.0E	23	111	269	255	0	275.7	
	16.3.85	57/10	10° 54.4S	136° 39.9E	32	52	66	61	0	140.8	
	16.3.85	58/10	10° 54.0S	136° 40.7E	33	98	221	200	0	244.9	
6	8.5.84	72/4	13° 51.0S	126° 41.7E	18	30	89	40	0	160.0	
	11.5.84	88/4	13° 51.7S	126° 42.0E	19	29	93	37	0	153.1	
	12.5.84	92/4	13° 51.7S	126° 41.9E	19	25	39	32	0	153.6	
	28.9.84	47/8	13° 44.0S	126° 40.7E	17	112	553	299	7	320.4	

** NET LENGTH 1000 m

TABLE 6: Summary of effort, catch and catch per unit effort (CPUE) for longline by area.

AREA	EFFORT		CATCH (No.)			CPUE (No./100 hooks)	
	NO. OF SETS	NO. OF HOOKS	ALL SHARKS	BLACK-TIP & SORRAH SHARKS	OTHER	ALL SHARKS	BLACK-TIP & SORRAH SHARKS
1	9	2689	143	97	20	5.3	3.6
2	15	1139	131	77	3	11.5	6.8
3	10	576	65	45	1	11.3	7.8
4	48	7055	492	335	17	7.0	4.8
5	54	14871	236	142	26	1.6	1.0
6	14	836	103	51	0	12.3	6.1
TOTAL	150	27166	1170	768	67	4.3	2.8

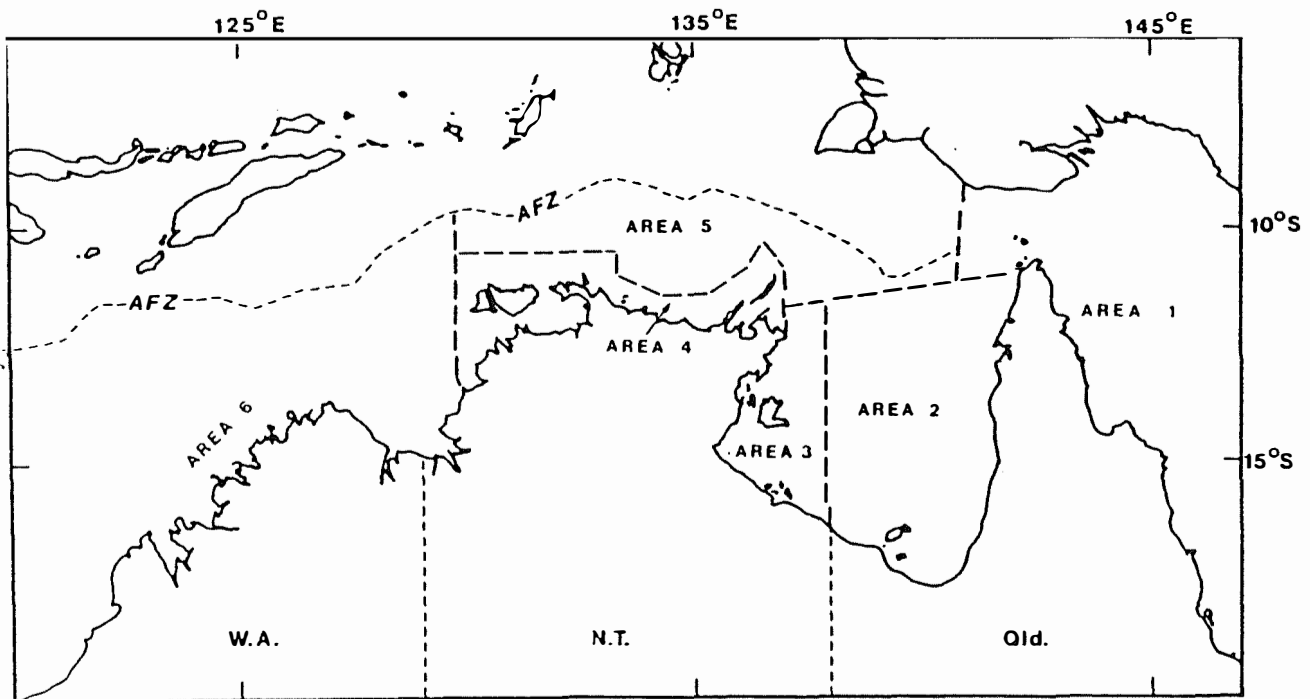


Figure 1

Map of Northern Australia showing study areas [Australian Fishing Zone (AFZ) line denoted].

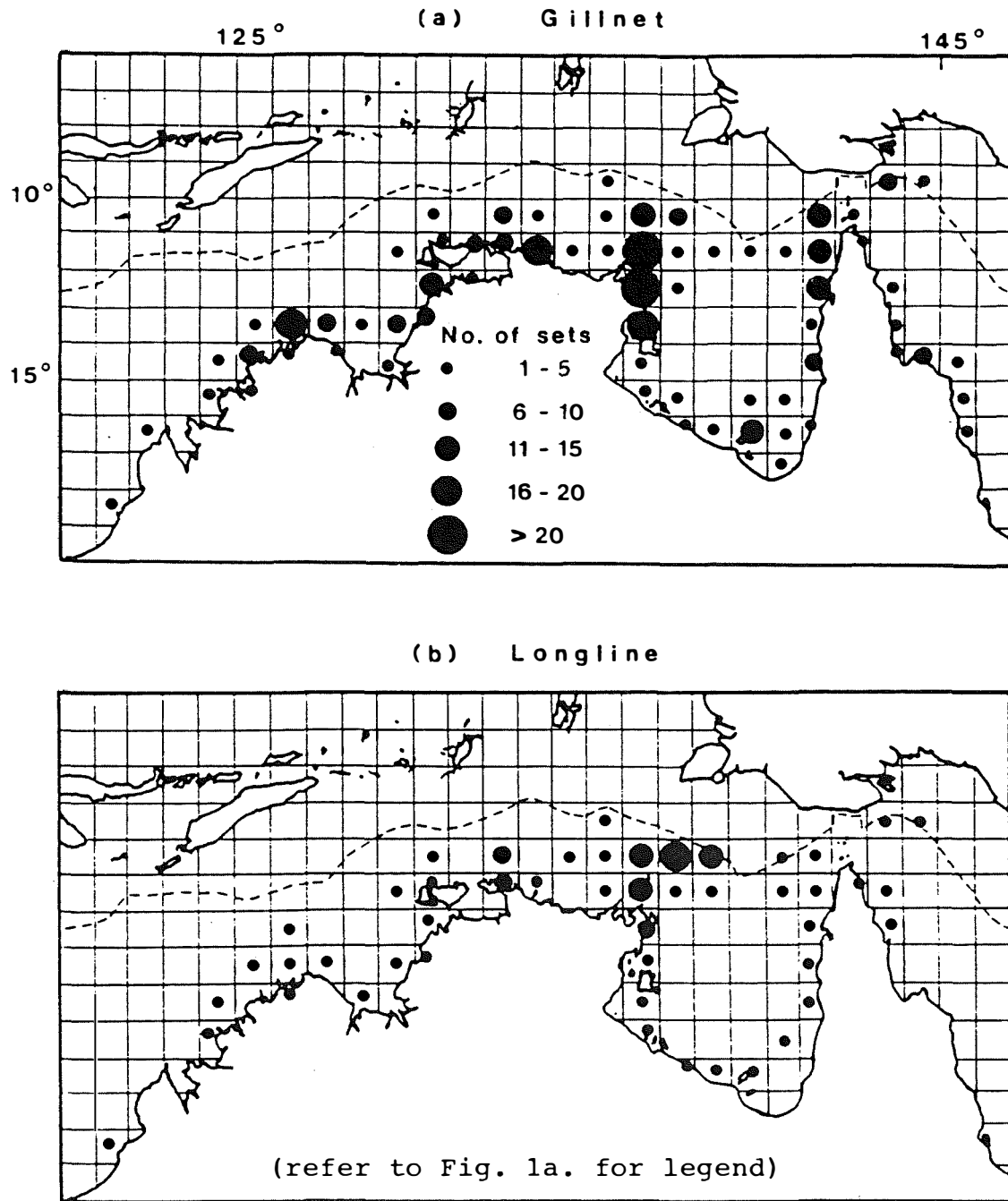


Figure 2

Distribution of Fishing Effort - Number of sets per one-degree squares [Dashed lines represent the Australian Fishing Zone (AFZ) line].

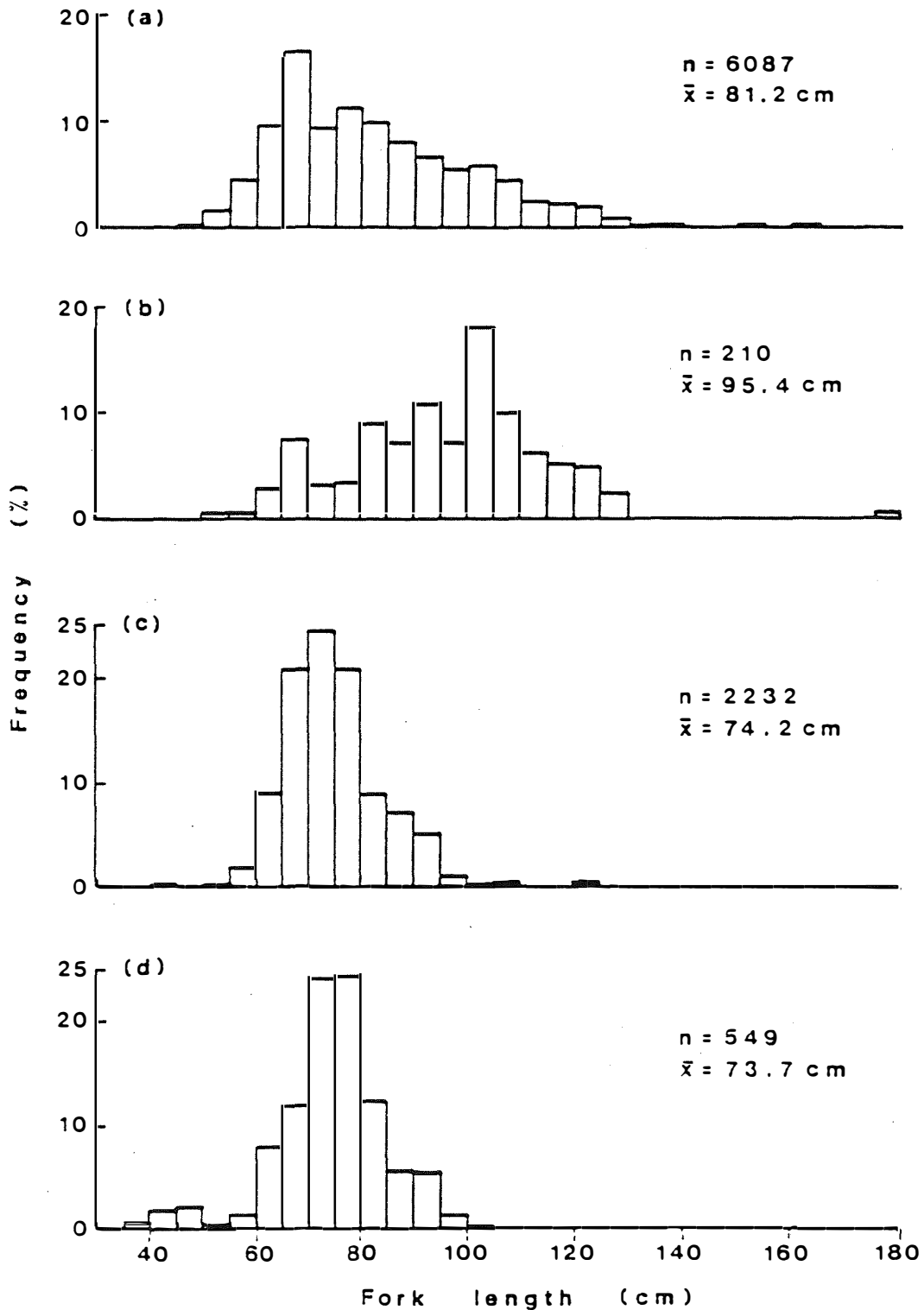


Figure 3

Size frequency distributions for black-tip sharks caught by (a) gillnet and (b) longline; and sorrah sharks caught by (c) gillnet and (d) longline (n is sample size and \bar{x} is mean length).

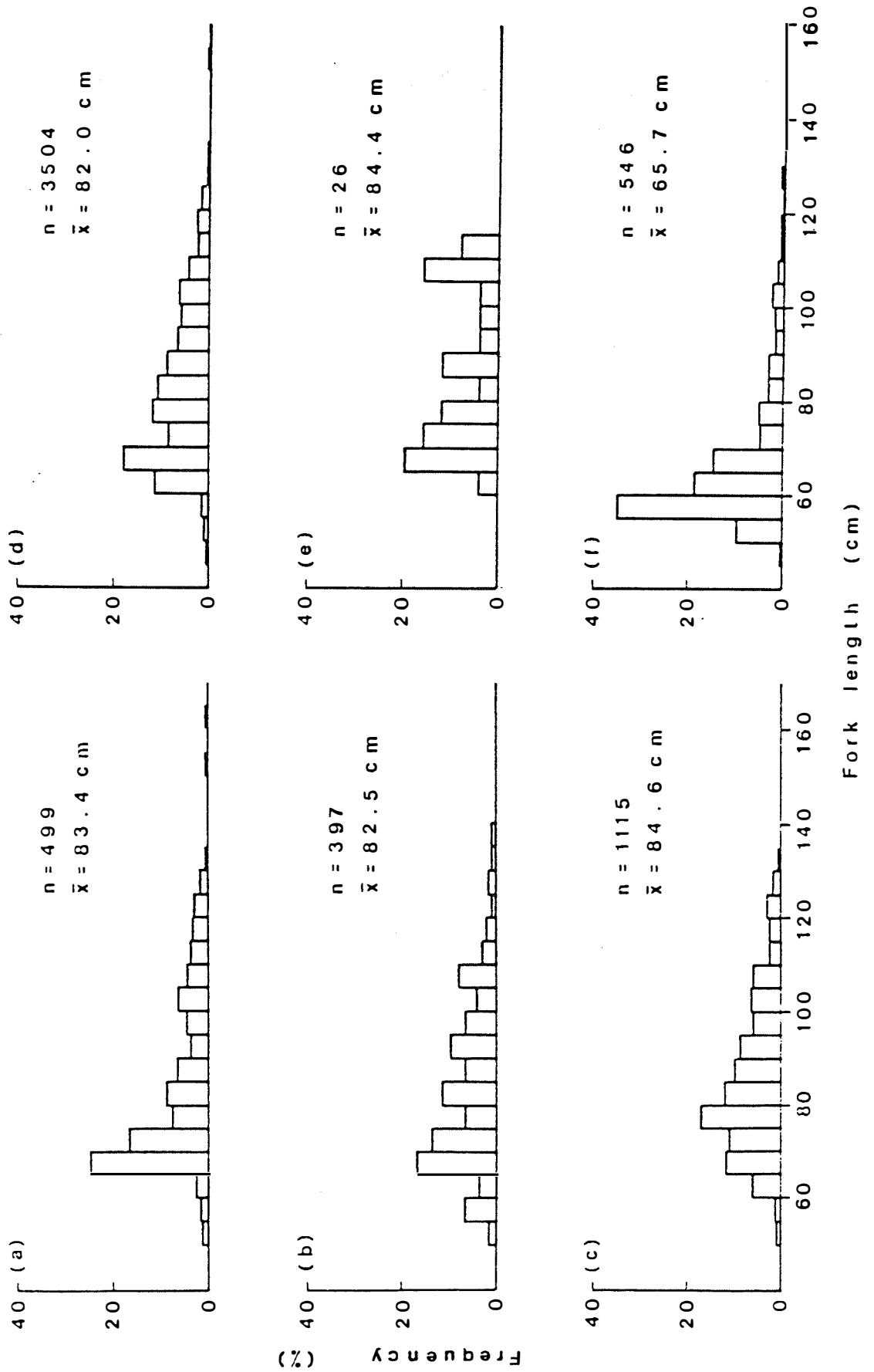


Figure 4

Size frequency distributions by area for black-tip sharks caught by gillnet - (a) Area 1; (b) Area 2; (c) Area 3; (d) Area 4; (e) Area 5; and (f) Area 6.

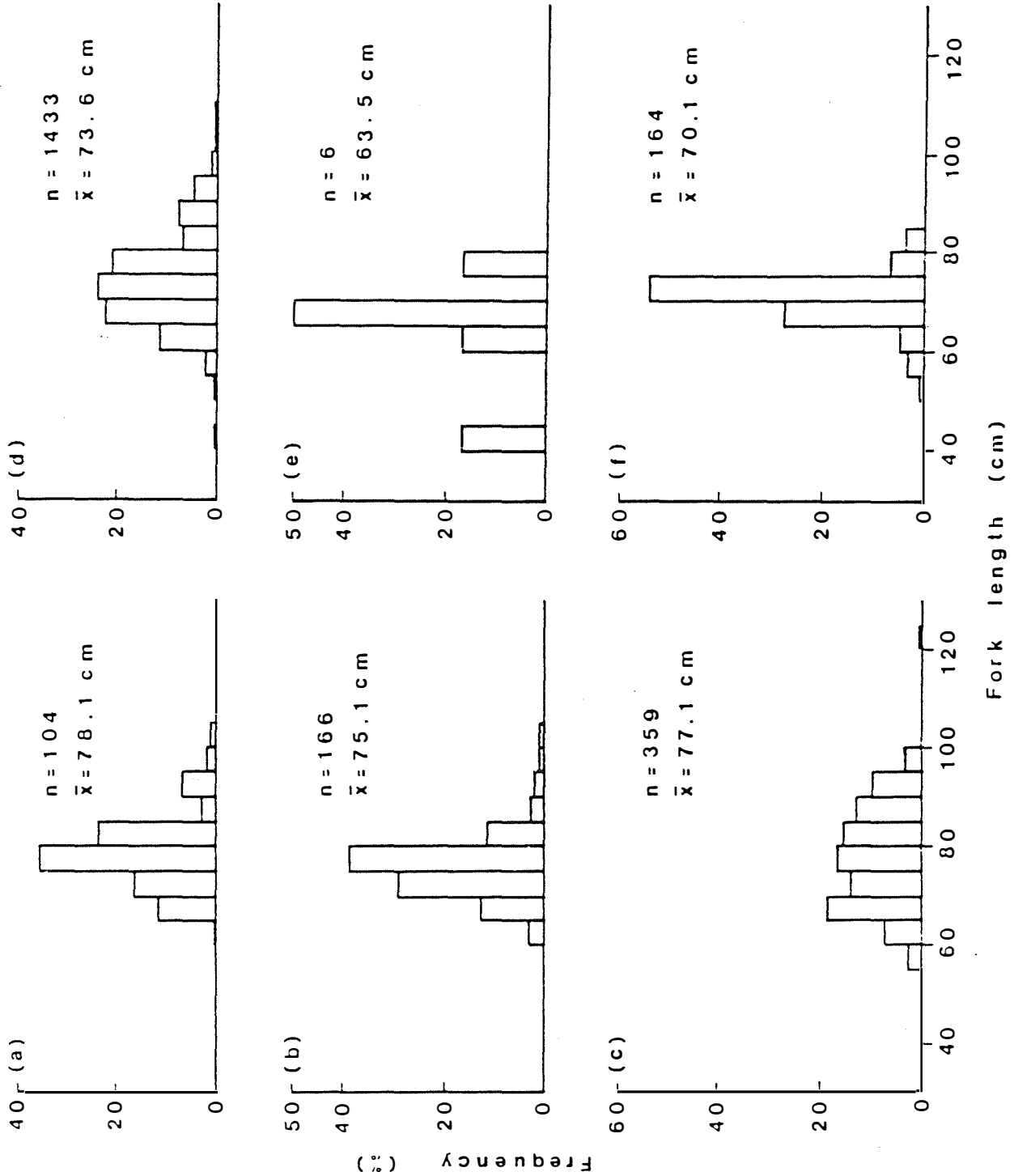


Figure 5

Size frequency distributions by area for sorrah sharks caught by gillnet - (a) Area 1; (b) Area 2; (c) Area 3; (d) Area 4; (e) Area 5; and (f) Area 6.

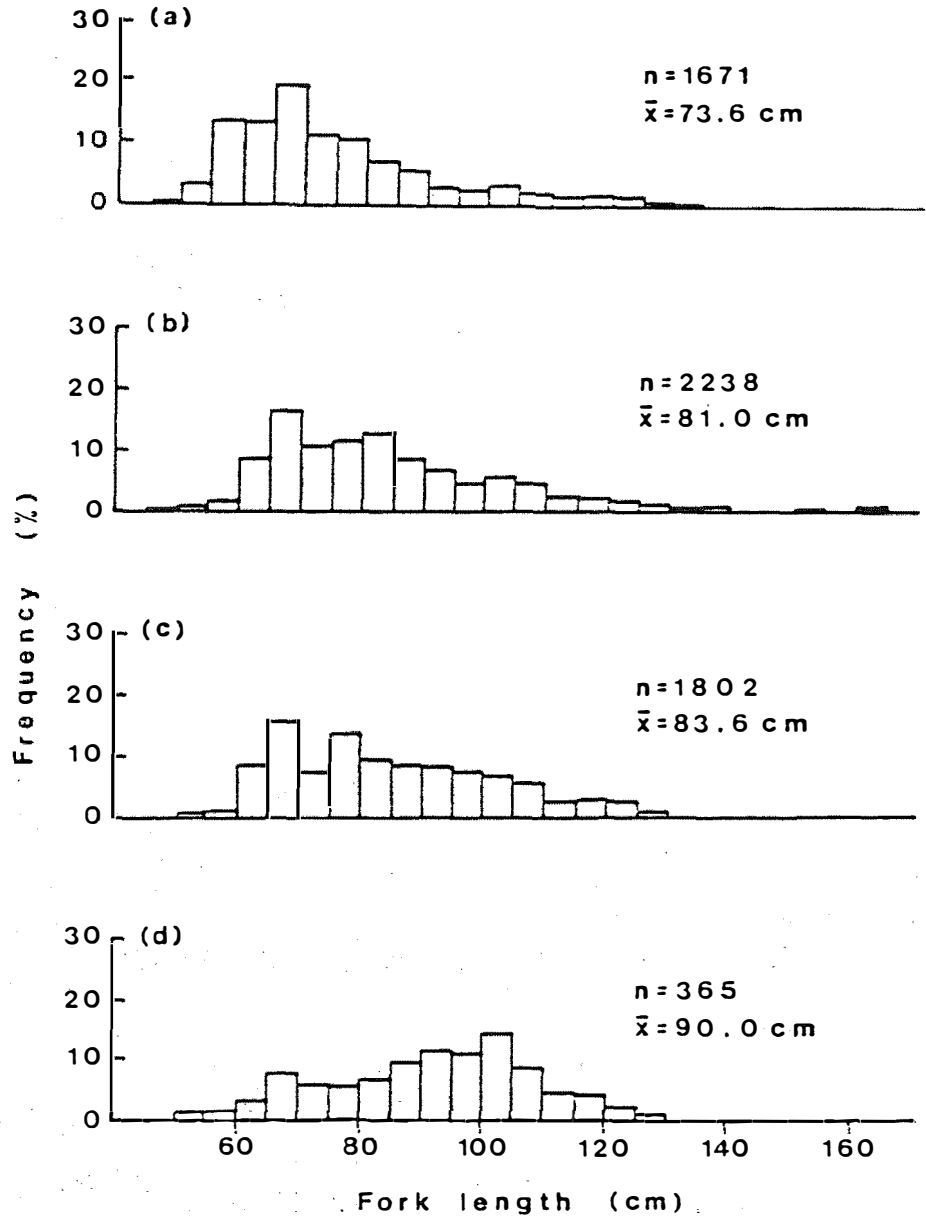


Figure 6

Size frequency distributions by depth for black-tip sharks caught by gillnet - (a) <20 m; (b) 20 - 29 m; (c) 30 - 39 m; and (d) ≥ 40 m.

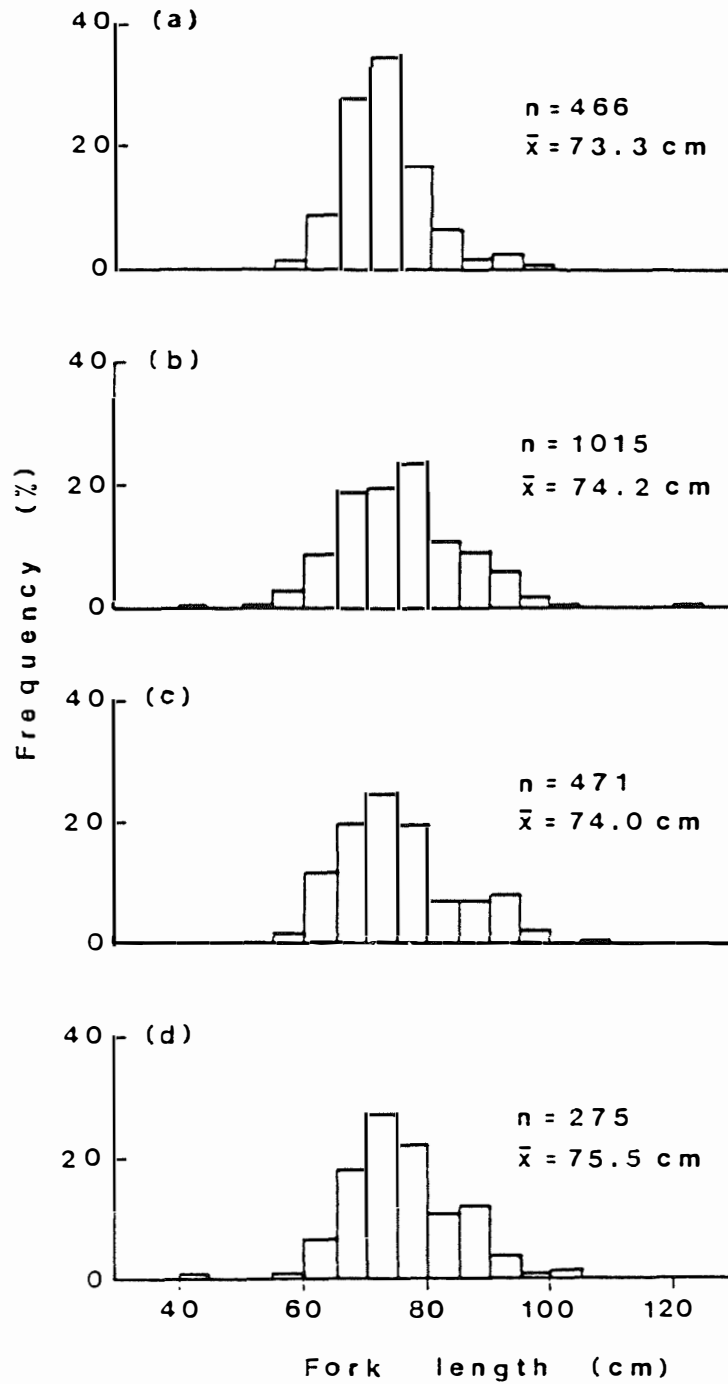


Figure 7

Size frequency distributions by depth for sorrah sharks caught by gillnet - (a) <20 m; (b) 20 - 29 m; (c) 30 - 30 m; and (d) ≥ 40 m.

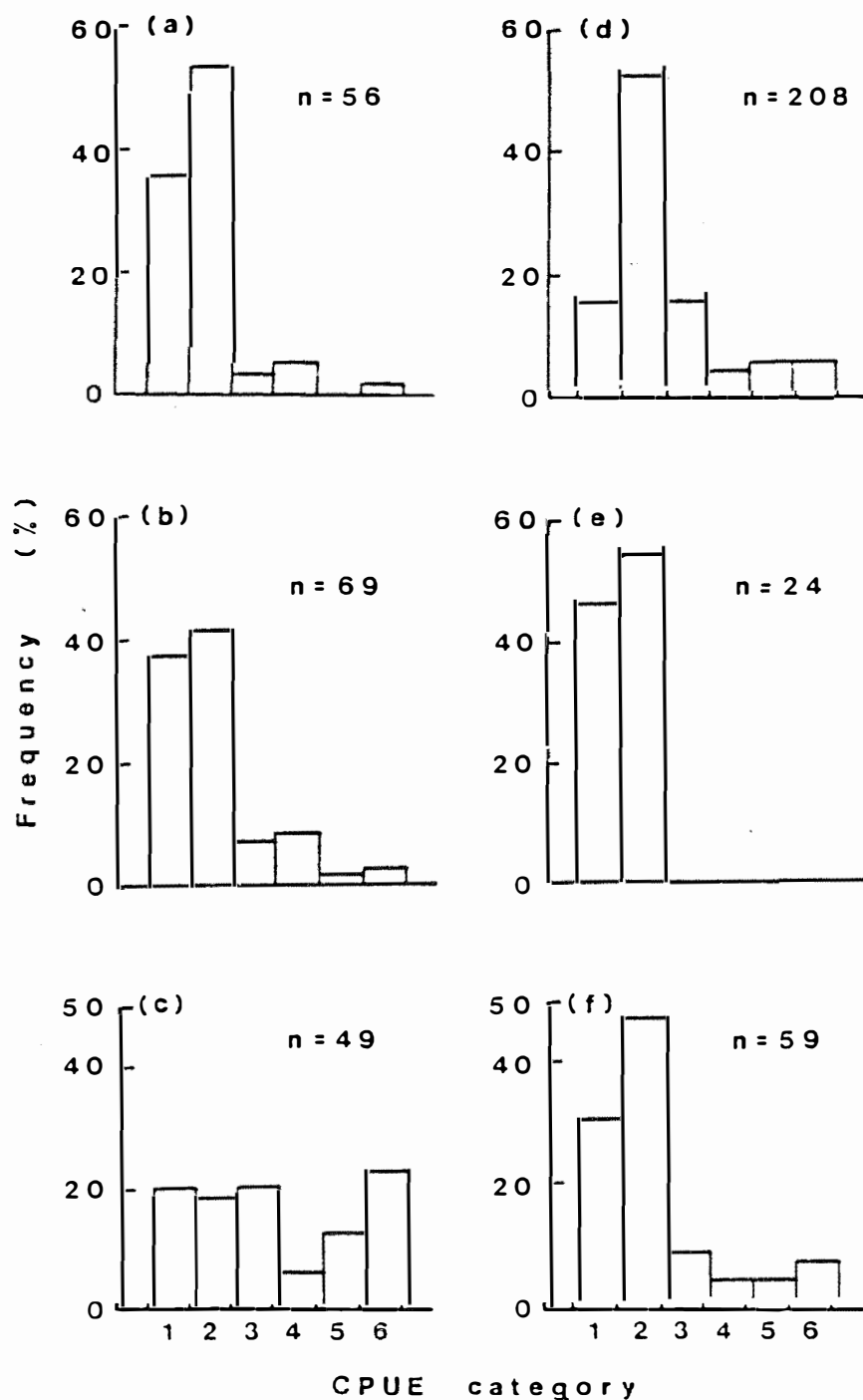


Figure 8

Distribution of catch per unit effort (CPUE) by area for black-tip and sorrah sharks - (a) Area 1; (b) Area 2; (c) Area 3; (d) Area 4; (d) Area 5; and (f) Area 6. CPUE categories: (1) nil catch, (2) 0.1 to 24.9 sharks/km-h, (3) 25 to 49.9 sharks/km-h, (4) 50 to 74.9 sharks/km-h, (5) 75 to 99.9 sharks/km-h, and (6) ≥ 100 sharks/km-h.

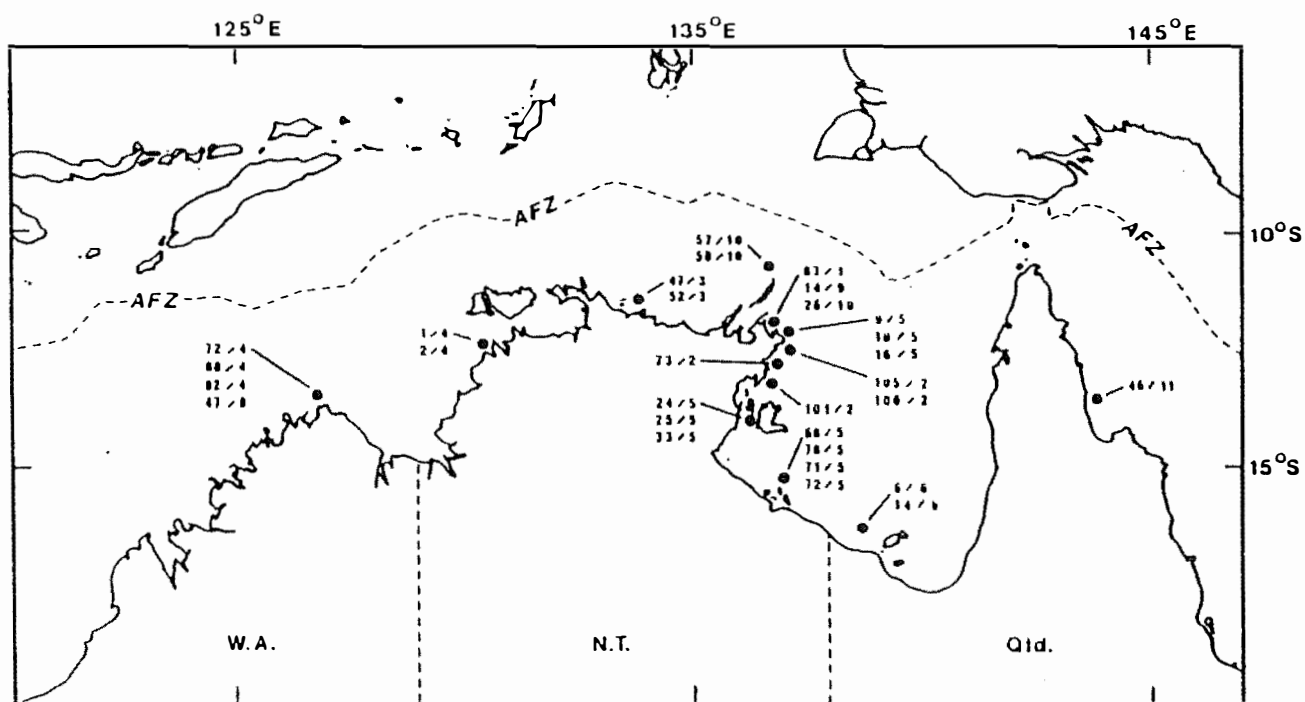


Figure 9

Map showing approximate locations of gillnet sets with catch per unit effort (CPUE) for black-tip and sorrah sharks of greater than 100 sharks/km-h (numbers represent set number/cruise number).

APPENDIX I

Summary of cruise details.

CRUISE	DATES		PORTS		AREA * FISHED
	DEPARTURE	RETURN	DEPARTURE	RETURN	
R01/84	17/01/84	09/12/84	Darwin	Gove	4
R02/84	16/02/84	11/03/84	Gove	Gove	3,4,5
R03/84	18/03/84	10/04/84	Gove	Darwin	4
R04/84	25/04/84	18/05/84	Darwin	Darwin	4,6
R05/84	02/06/84	28/06/84	Gove	Karumba	2,3,4
R06/84	05/07/84	28/07/84	Karumba	Weipa	2
R07/84	04/08/84	27/08/84	Weipa	Gove	1,2,4,5
R08/84	19/09/84	12/10/84	Darwin	Broome	4,6
R09/85	23/01/85	15/02/85	Darwin	Gove	4,5
R10/85	22/02/85	17/04/85	Gove	Gove	4,5
R11/85	29/03/85	21/04/85	Gove	Cairns	1,2,4,5
R12/85	07/05/85	30/05/85	Cairns	Gove	1,4

* Refer to Figure 1 for details.

APPENDIX II

Details of gillnet.

Stretched mesh size	-	15 cm
Drop	-	100 meshes
Hanging coefficient	-	0.63 (4 meshes in 38 cm)
Hung length	-	2 x 500 m (separated by approximately 100 m of rope)
Hung depth	-	11.6 m
Monofilament gauge	-	30
Head rope diameter	-	16 mm
Lead rope diameter	-	8 mm
Length of float lines	-	3 m
Spacing between floats	-	20 m

APPENDIX III

Summary of set and catch details.

Explanatory notes

Set duration: Timed from the completion of setting to the commencement of hauling.

Haul duration: Timed from the start of hauling to its completion.

Catch: Expressed as numbers of fish. The following categories have been distinguished:

- (i) shark (all species)
- (ii) mackerel
- (iii) other (teleosts other than mackerel).

Dominant species: Where the shark catch was greater than 30 individuals the dominant species (by number not weight) in the catch are noted. Black-tip and sorrah sharks (tilstoni and sorrah) are of particular interest to commercial fishermen.

Appendix III (A) – Gillnet*

Cruise No. R01/84: Darwin to Gove, incl. Pt. Essington, Croker Island, Goulburn Island and Melville Bay

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	17.01.84	12°19.1S	130°45.0E	20	1000	35	35	0	0	1	
2	17.01.84	12°11.2S	130°41.4E	26	1000	25	45	14	4	0	
4	18.01.84	12°01.0S	131°34.0E	22	1000	65	70	37	0	15	<i>blochii</i>
6	20.01.84	11°06.4S	131°53.8E	28	1000	45	90	138	11	0	<i>tilstoni / sorrah</i>
7	20.01.84	11°05.2S	131°58.4E	30	1000	30	145	217	2	2	<i>sorrah</i>
14	21.01.84	11°01.1S	132°07.3E	26	1000	20	70	81	1	0	<i>tilstoni / sorrah</i>
26	23.01.84	10°58.0S	132°28.5E	13	1000	30	50	22	5	0	
27	23.01.84	10°58.5S	132°30.0E	13	1000	120	105	114	8	3	<i>amblyrhynchoides</i>
35	25.01.84	11°01.5S	132°39.5E	44	1000	45	130	149	2	12	<i>sorrah</i>
36	25.01.84	11°01.5S	132°39.5E	44	1000	20	123	125	1	5	<i>tilstoni / sorrah / macloti</i>
43	27.01.84	11°10.6S	132°45.5E	47	1000	4	170	128	3	0	<i>tilstoni</i>
45	27.01.84	11°14.6S	132°48.0E	34	1000	5	150	107	0	10	<i>tilstoni</i>
46	28.01.84	11°32.0S	133°16.4E	26	1000	60	105	84	0	4	<i>tilstoni</i>
55	30.01.84	11°34.6S	133°40.0E	28	1000	20	110	102	2	0	<i>tilstoni</i>
56	31.01.84	11°38.6S	134°09.9E	31	1000	85	55	19	2	1	
57	31.01.84	11°40.5S	134°14.6E	29	1000	25	40	0	2	1	
58	01.02.84	11°26.4S	135°12.0E	37	1000	60	35	7	0	0	
59	01.02.84	11°46.2S	135°33.5E	23	1000	60	120	10	1	1	
60	02.02.84	11°55.8S	136°43.2E	33	1000	15	70	43	2	3	<i>tilstoni</i>
61	02.02.84	11°56.0S	136°42.5E	32	1000	5	70	31	1	1	<i>tilstoni</i>
63	03.02.84	12°09.6S	136°55.0E	33	1000	15	55	28	0	1	
64	03.02.84	12°09.8S	136°56.5E	37	1000	5	195	270	0	2	<i>tilstoni</i>
79	07.02.84	11°56.0S	136°42.2E	31	1000	30	105	38	0	0	<i>tilstoni</i>
85	08.02.84	11°55.3S	136°45.2E	33	1000	5	35	1	0	0	
87	08.02.84	12°02.2S	136°43.4E	20	1000	5	280	945	1	2	<i>tilstoni</i>

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* The original table was difficult to read and has been retyped. Some errors may have been introduced.

Cruise No. R02/84: Gove to Gove, incl. Melville Bay, NW Gulf of Carpentaria, offshore Wessel Islands

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	16.02.84	12°01.7S	136°43.8E	23	1000	18	25	14	0	1	
10	17.02.84	11°59.2S	136°14.9E	29	500	19	54	97	0	0	<i>macloti</i>
11	17.02.84	11°58.7S	136°41.9E	31	500	12	25	13	0	1	
12	17.02.84	11°57.6S	136°43.6E	32	500	9	17	2	0	0	
15	18.02.84	12°00.7S	136°45.7E	25	500	24	17	5	0	0	
16	18.02.84	11°58.0S	136°41.6E	28	500	30	15	4	0	0	
18	18.02.84	12°00.8S	136°44.5E	26	500	25	16	5	0	0	
25	19.02.84	11°41.5S	136°20.3E	28	500	30	17	4	0	4	
26	19.02.84	11°44.2S	136°19.5E	29	1000	95	63	49	3	49	<i>sorrah</i>
29	20.02.84	11°37.0S	136°30.0E	30	500	24	16	0	1	1	
30	20.02.84	11°40.2S	136°23.2E	25	1000	121	39	10	0	6	
31	21.02.84	11°56.7S	136°07.0E	29	500	122	12	0	0	0	
32	21.02.84	11°41.2S	136°33.0E	32	500	28	19	7	0	0	
33	21.02.84	11°40.0S	136°36.7E	37	1000	74	38	10	5	18	
36	22.02.84	12°09.8S	136°56.4E	31	500	13	15	2	0	0	
37	22.02.84	12°11.2S	136°56.1E	30	1000	67	53	8	0	4	
38	22.02.84	12°14.0S	136°57.5E	35	500	40	45	44	0	0	<i>tilstoni</i>
39	23.02.84	12°14.0S	136°58.0E	37	500	30	34	23	0	0	<i>tilstoni</i>
40	23.02.84	12°15.0S	136°58.9E	39	500	6	32	15	0	0	<i>tilstoni</i>
42	23.02.84	12°27.2S	136°57.5E	37	500	36	66	76	0	0	<i>tilstoni/sorrah</i>
43	23.02.84	12°27.0S	136°58.5E	49	500	8	24	11	0	13	
44	23.02.84	12°27.7S	136°58.0E	46	500	19	19	0	0	0	
45	23.02.84	12°26.7S	136°57.5E	39	500	22	13	0	0	0	
46	23.02.84	12°24.8S	136°58.5E	55	500	41	31	29	0	4	<i>tilstoni</i>
47	24.02.84	12°36.5S	136°50.3E	29	1000	31	100	13	0	1	
49	24.02.84	12°39.5S	136°50.5E	27	500	38	20	4	0	0	
54	25.02.84	12°41.0S	136°49.0E	30	500	10	17	3	0	0	
56	25.02.84	12°42.5S	136°53.0E	41	1000	38	25	2	0	0	
58	25.02.84	12°47.2S	136°46.7E	30	500	24	25	41	0	1	<i>tilstoni/sorrah</i>
59	25.02.84	12°46.8S	136°46.1E	32	500	21	33	0	0	0	
60	25.02.84	12°56.0S	136°47.6E	32	500	24	48	55	2	7	<i>tilstoni/sorrah</i>

Cruise No. R02/84 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
61	25.02.84	12°54.9S	136°48.5E	33	500	22	52	50	0	0	<i>tilstoni / sorrah</i>
62	25.02.84	12°53.9S	136°44.8E	39	500	25	25	21	0	0	
65	26.02.84	12°53.5S	136°50.4E	42	500	39	19	10	0	0	
66	26.02.84	12°55.7S	136°48.8E	34	500	32	25	17	0	1	
73	27.02.84	13°04.5S	136°36.2E	24	500	33	35	28	0	4	
74	27.02.84	13°04.4S	136°37.6E	29	500	22	59	81	1	0	<i>tilstoni</i>
75	27.02.84	13°04.4S	136°40.0E	32	500	20	43	37	2	2	<i>tilstoni</i>
81	28.02.84	13°04.8S	136°38.0E	29	500	30	14	1	0	0	
82	28.02.84	13°04.1S	136°40.0E	32	500	31	30	18	0	0	
83	28.02.84	13°04.6S	136°42.7E	36	500	20	18	4	0	19	
84	01.03.84	13°02.3S	136°36.2E	19	500	21	12	0	0	1	
88	01.03.84	13°16.0S	136°33.5E	33	500	24	17	8	0	1	
89	01.03.84	13°17.8S	136°32.0E	30	500	12	33	20	2	5	
90	01.03.84	13°22.2S	136°28.4E	26	500	26	27	15	1	1	
91	01.03.84	13°24.2S	136°26.3E	25	500	28	52	63	0	3	<i>tilstoni</i>
92	01.03.84	13°24.0S	136°27.5E	25	500	17	24	17	0	2	
101	02.03.84	13°22.2S	136°29.4E	26	500	28	72	132	0	1	<i>tilstoni</i>
102	02.03.84	13°22.2S	136°23.5E	27	500	16	22	13	0	0	
103	02.03.84	13°22.6S	136°27.8E	28	500	23	34	31	0	3	<i>tilstoni</i>
104	03.03.84	12°41.7S	136°51.3E	38	500	17	55	19	0	0	
105	03.03.84	12°41.8S	136°50.5E	38	500	30	66	90	1	3	<i>tilstoni / sorrah</i>
106	03.03.84	12°41.5S	136°50.0E	36	500	32	38	73	0	0	<i>tilstoni</i>
107	06.03.84	11°49.1S	136°46.2E	45	500	29	19	7	0	0	
113	07.03.84	10°46.4S	137°07.5E	52	500	42	18	1	0	0	
120	08.03.84	10°47.8S	137°14.5E	54	1000	128	34	1	0	1	
122	09.03.84	11°41.9S	136°25.1E	30	500	53	61	1	2	0	
123	09.03.84	11°40.5S	136°25.6E	30	500	39	30	9	1	1	
124	09.03.84	11°39.6S	136°29.6E	29	500	65	18	2	3	0	
126	10.03.84	11°49.4S	136°49.2E	47	500	114	21	13	0	1	
127	11.03.84	11°53.2S	136°45.4E	38	500	34	30	41	0	1	<i>tilstoni</i>

Cruise No. R03/84: Gove to Darwin, Melville Bay, Wessel Islands, Croker Island, Bathurst Island and Melville Island

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	18.03.84	12°09.8S	136°54.6E	33	500	39	33	49	0	0	<i>tilstoni / sorrah</i>
2	18.03.84	12°09.0S	136°53.4E	32	500	26	40	55	1	0	<i>tilstoni</i>
3	18.03.84	12°08.6S	136°55.4E	32	500	25	45	49	0	0	<i>tilstoni / sorrah</i>
6	19.03.84	12°10.2S	136°56.4E	34	500	20	21	10	1	1	
7	19.03.84	12°08.8S	136°55.8E	38	500	35	23	11	1	1	
15	20.03.84	12°10.2S	136°56.5E	35	500	19	14	2	0	1	
17	20.03.84	12°11.2S	136°55.2E	35	500	95	33	24	0	2	
18	21.03.84	12°10.3S	136°53.7E	35	500	29	29	13	0	0	
19	21.03.84	12°04.9S	136°43.9E	22	500	13	26	21	0	0	
20	21.03.84	11°55.2S	136°41.3E	34	500	24	29	25	0	0	
21	21.03.84	11°54.9S	136°42.2E	35	500	13	28	26	0	1	
23	23.03.84	11°15.7S	136°42.5E	50	500	30	62	4	0	0	
24	23.03.84	11°19.4S	136°39.9E	41	500	26	13	0	0	0	
25	23.03.84	11°22.6S	136°37.4E	36	500	38	36	0	0	0	
27	23.03.84	11°34.6S	136°27.2E	28	1000	16	37	5	0	0	
35	25.03.84	11°33.2S	133°21.2E	16	500	21	13	0	0	0	
36	25.03.84	11°30.5S	133°18.8E	27	500	26	32	20	1	0	
37	25.03.84	11°26.6S	133°24.5E	20	500	21	27	9	2	0	
38	26.03.84	11°28.5S	133°16.8E	30	500	24	41	47	0	0	<i>tilstoni</i>
42	26.03.84	11°28.0S	133°18.5E	28	500	22	37	7	0	0	
43	26.03.84	11°27.0S	133°17.1E	29	500	15	22	13	0	0	
44	26.03.84	11°27.7S	133°17.3E	28	500	17	54	59	1	0	<i>tilstoni</i>
45	26.03.84	11°27.6S	133°17.0E	29	500	16	29	25	0	0	
46	26.03.84	11°27.3S	133°18.5E	28	500	16	20	6	0	1	
47	27.03.84	11°28.3S	133°14.4E	31	500	20	80	138	0	0	<i>tilstoni</i>
51	27.03.84	11°27.6S	133°15.4E	31	500	18	34	1	0	0	
52	27.03.84	11°29.6S	133°14.7E	30	500	17	60	110	1	0	<i>tilstoni / sorrah</i>
53	27.03.84	11°28.6S	133°13.7E	30	500	16	40	35	0	0	<i>tilstoni</i>
54	28.03.84	11°29.6S	133°15.7E	29	500	16	22	15	0	0	
55	28.03.84	11°29.0S	133°15.5E	31	500	16	17	2	0	1	
59	28.03.84	11°17.0S	132°46.9E	18	500	18	45	48	6	0	<i>tilstoni / sorrah</i>

Cruise No. R03/84 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
65	29.03.84	11°04.5S	132°43.2E	43	500	19	22	4	0	0	
71	30.03.84	10°51.1S	132°51.7E	40	500	15	20	0	0	0	
81	02.04.84	11°02.9S	132°01.3E	32	500	17	31	0	0	0	
82	02.04.84	11°03.6S	131°51.3E	39	500	15	14	4	0	0	
83	02.04.84	11°04.8S	131°54.3E	45	500	20	13	1	0	0	
84	02.04.84	11°07.1S	131°54.0E	24	500	17	11	0	0	0	
85	03.04.84	11°07.5S	131°55.3E	19	500	18	14	2	0	0	
87	03.04.84	11°10.1S	131°20.0E	31	500	21	20	2	0	0	
90	03.04.84	11°06.3S	131°09.0E	25	500	21	13	4	0	0	
91	03.04.84	11°04.3S	131°08.6E	30	500	19	19	7	0	0	
92	03.04.84	11°01.8S	131°01.9E	34	500	19	39	35	0	3	<i>macloti</i>
93	03.04.84	11°00.2S	130°54.8E	36	500	15	25	16	0	0	
94	04.04.84	11°00.4S	130°51.9E	38	500	17	21	12	0	0	
100	04.04.84	11°02.0S	130°15.4E	25	500	26	28	27	1	1	
101	04.04.84	11°00.7S	130°15.5E	29	500	27	43	91	0	0	<i>macloti</i>
115	06.04.84	10°57.2S	130°08.8E	53	500	35	45	30	0	2	<i>tilstoni</i>
124	07.04.84	11°12.3S	129°52.2E	87	500	25	36	27	0	1	
131	08.04.84	11°28.5S	129°52.0E	77	500	56	11	5	0	13	

Cruise No. R04/84: Darwin return Darwin, incl. Fog Bay, Anson Bay, Napier-Broome Bay and Admiralty Gulf

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	25.04.84	12°34.4S	130°14.0E	22	500	14	33	58	0	0	<i>sorrah</i>
2	25.04.84	12°35.3S	130°14.3E	21	500	13	30	28	0	0	
8	26.04.84	12°46.6S	130°11.7E	17	500	17	13	3	1	0	
9	26.04.84	12°46.0S	130°13.5E	16	500	16	14	2	0	0	
14	27.04.84	13°17.0S	129°55.4E	23	500	20	11	0	0	0	
15	27.04.84	13°16.8S	129°57.2E	24	500	17	10	0	0	0	
16	27.04.84	13°19.5S	130°02.7E	20	500	19	37	34	0	1	<i>tilstoni / sorrah</i>
17	27.04.84	13°19.3S	130°02.7E	20	500	18	19	6	0	0	
20	28.04.84	13°20.2S	130°05.7E	16	500	18	14	2	0	0	
25	28.04.84	13°21.3S	130°05.5E	15	500	21	15	4	0	0	
27	29.04.84	13°23.4S	130°03.5E	21	500	24	14	3	1	2	
28	29.04.84	13°24.5S	130°01.5E	18	500	20	25	16	0	1	
29	29.04.84	13°24.4S	130°00.0E	18	500	24	16	1	1	0	
32	30.04.84	13°31.4S	129°42.8E	26	500	21	17	2	0	1	
38	01.05.84	14°19.2S	127°51.2E	35	500	21	19	7	1	0	
39	01.05.84	14°16.7S	127°48.0E	31	500	21	27	9	0	5	
41	01.05.84	14°08.0S	127°41.0E	42	500	29	8	5	0	0	
46	02.05.84	13°54.5S	127°29.5E	44	500	19	13	2	0	0	
47	02.05.84	13°53.3S	127°29.5S	55	500	20	18	11	0	0	
54	03.05.84	13°51.2S	127°24.7E	66	500	21	12	2	0	0	
55	03.05.84	13°50.5S	127°23.3E	66	500	22	15	8	1	0	
56	03.05.84	13°48.8S	127°20.5E	66	500	18	11	0	0	0	
57	03.05.84	13°51.8S	127°17.3E	44	500	28	14	2	0	0	
60	06.05.84	14°01.3S	126°37.3E	16	500	20	25	17	0	0	
61	06.05.84	14°00.8S	126°37.9E	16	500	17	32	37	1	6	<i>acutus / macloti</i>
65	07.05.84	13°50.7S	126°41.4E	19	500	19	42	45	0	0	<i>macloti</i>
66	07.05.84	13°50.3S	126°41.4E	19	500	18	22	19	0	0	
72	08.05.84	13°51.0S	126°41.7E	18	500	24	51	89	0	0	<i>macloti / tilstoni</i>
73	08.05.84	13°50.5S	126°42.3E	18	500	19	25	33	0	0	<i>macloti</i>
74	08.05.84	13°49.3S	126°42.8E	18	500	37	15	6	0	0	
75	09.05.84	14°08.7S	125°55.3E	48	500	21	38	1	0	0	

Cruise No. R04/84 (cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
76	09.05.84	14°20.0S	125°53.3E	42	500			4	0	0	
77	09.05.84	14°23.9S	125°53.7E	30	500	19	12	1	0	0	
82	11.05.84	13°51.3S	126°44.7E	20	500	14	17	17	0	1	
83	11.05.84	13°51.7S	126°44.1E	20	500	19	16	14	0	0	
84	11.05.84	13°51.9S	126°42.7E	19	500	19	19	25	0	0	
85	11.05.84	13°51.7S	126°42.0E	19	500	22	41	93	0	0	<i>macloti</i>
86	11.05.84	13°51.3S	126°42.4E	20	500	12	18	13	0	0	
89	12.05.84	13°51.7S	126°41.9E	19	500	20	34	39	0	0	<i>sorrah / tilstoni</i>
95	13.05.84	13°44.6S	127°02.8E	26	500	21	22	2	0	0	
105	16.05.84	14°13.3S	129°21.8E	27	500	20	9	0	0	0	
106	16.05.84	14°10.5S	129°20.0E	29	500	18	10	0	0	0	

Cruise No. R05/84: Gove to Karumba, incl. Melville Bay, Groote Eylandt, Vanderlin Islands and Mornington Island

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
3	02.06.84	12°09.4S	136°33.5E	20	500	24	25	6	0	0	<i>sorrah</i>
4	02.06.84	12°08.4S	136°42.5E	23	500	21	33	25	3	1	
5	02.06.84	12°08.4S	136°41.0E	26	500	21	24	10	0	0	
6	02.06.84	12°07.9S	136°44.7E	21	500	21	24	12	0	0	
8	03.06.84	12°08.5S	136°40.6E	24	500	27	19	4	0	0	
9	03.06.84	12°07.7S	136°43.2E	25	500	21	51	56	2	0	<i>sorrah / tilstoni</i>
10	03.06.84	12°07.7S	136°42.6E	26	500	18	44	42	1	0	<i>tilstoni</i>
11	04.06.84	12°07.3S	136°43.0E	26	500	24	23	12	1	1	
12	04.06.84	12°05.1S	136°46.8E	20	500	36	15	1	0	0	
13	04.06.84	12°04.5S	136°46.0E	23	500	22	19	4	0	0	
14	04.06.84	12°05.9S	136°46.8E	19	500	22	17	6	0	0	
15	04.06.84	12°08.7S	136°44.2E	22	500	23	40	27	0	0	
16	04.06.84	12°08.7S	136°44.6E	21	500	20	40	30	0	2	<i>tilstoni</i>
18	05.06.84	12°08.2S	136°43.4E	22	500	27	12	1	0	0	
19	05.06.84	12°07.9S	136°43.5E	24	500	19	20	7	0	0	
20	05.06.84	12°08.4S	136°42.1E	24	500	21	14	5	0	0	
21	05.06.84	12°08.2S	136°43.4E	24	500	21	15	3	0	0	
23	07.06.84	13°56.3S	136°19.2E	32	500	27	12	0	0	0	
24	07.06.84	14°00.0S	136°18.3E	27	500	24	68	101	0	0	<i>sorrah / tilstoni</i>
25	07.06.84	13°56.7S	136°19.0E	29	500	19	31	34	0	0	<i>sorrah / tilstoni</i>
26	08.06.84	13°56.1S	136°18.3E	28	500	19	29	22	0	0	
32	08.06.84	14°04.2S	136°20.3E	22	500	30	60	98	3	1	<i>sorrah / tilstoni</i>
60	20.06.84	15°29.4S	136°46.7E	15	500	33	12	0	0	0	
61	20.06.84	15°26.3S	136°48.5E	17	500	30	18	3	1	0	
63	21.06.84	15°29.5S	136°47.3E	13	500	38	14	2	0	1	
64	21.06.84	15°29.2S	136°46.1E	15	500	34	13	1	0	1	
68	23.06.84	15°30.5S	137°03.1E	25	500	37	54	93	0	0	<i>tilstoni</i>
69	23.06.84	15°29.2S	137°02.8E	25	500	21	57	45	0	0	<i>tilstoni</i>
70	23.06.84	15°27.9S	136°59.4E	25	500	18	57	55	0	0	<i>tilstoni</i>
71	24.06.84	15°28.7S	137°05.0E	27	500	22	63	85	0	0	<i>tilstoni</i>
73	24.06.84	16°02.8S	137°54.4E	21	500	27	12	0	0	0	

Cruise No. R05/84 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
74	24.06.84	16°02.7S	137°52.4E	22	500	20	11	0	0	0	
75	25.06.84	16°30.1S	139°01.0E	20	500	23	10	0	0	2	
76	25.06.84	16°23.8S	139°03.5E	21	500	22	15	3	0	0	
77	25.06.84	16°20.1S	139°07.7E	23	500	25	44	25	0	0	
78	25.06.84	16°20.5S	139°09.0E	23	500	24	15	2	0	0	
80	26.06.84	16°23.7S	139°17.6E	18	500	33	12	0	0	0	
81	26.06.84	16°20.5S	139°21.7E	19	500	17	10	0	0	0	
82	26.06.84	16°18.0S	139°27.2E	21	500	18	11	0	0	0	
83	26.06.84	16°15.5S	139°35.0E	21	500	19	12	0	0	0	
84	27.06.84	16°17.7S	139°42.7E	32	500	19	16	0	0	0	

Cruise No. R06/84: Karumba to Weipa, incl. Mornington Island, Karumba, eastern Gulf of Carpentaria, Weipa

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	05.07.84	16°46.0S	140°04.5E	22	500	19	11	1	0	0	
2	05.07.84	16°45.0S	139°59.0E	24	500	17	13	1	1	0	
3	05.07.84	16°35.5S	139°56.3E	26	500	19	11	0	0	0	
5	06.07.84	16°20.6S	138°40.0E	27	500	29	28	25	0	0	
6	06.07.84	16°09.8S	138°40.7E	26	500	22	55	69	0	7	<i>sorrah / tilstoni</i>
13	07.07.84	16°20.8S	138°32.5E	27	500	25	35	32	0	0	<i>sorrah</i>
14	07.07.84	16°16.5S	138°33.0E	26	500	21	51	88	0	0	<i>sorrah / tilstoni</i>
20	08.07.84	16°07.0S	139°01.4E	35	500	25	145	34	0	0	<i>tilstoni</i>
26	08.07.84	16°02.0S	139°13.0E	27	500	28	13	2	0	0	
27	08.07.84	16°01.0S	139°18.5E	26	500	25	13	1	0	0	
29	09.07.84	15°46.9S	139°47.3E	42	500	29	24	11	0	0	
30	09.07.84	15°46.0S	139°48.0E	42	500	24	16	4	0	0	
31	09.07.84	15°38.8S	139°56.5E	44	500	26	15	2	0	0	
36	10.07.84	15°30.3S	140°06.0E	44	500	25	10	0	0	0	
37	10.07.84	15°31.8S	140°07.0E	46	500	24	12	1	0	0	
42	12.07.84	17°07.2S	140°39.0E	15	500	26	8	0	0	0	
43	12.07.84	17°03.2S	140°38.6E	26	500	30	9	0	0	0	
44	13.07.84	16°08.5S	141°04.5E	13	500	29	59	0	0	0	
48	14.07.84	14°35.0S	141°19.4E	22	500	23	39	50	2	0	<i>tilstoni</i>
49	14.07.84	14°33.3S	141°19.7E	20	500	24	26	32	0	0	<i>tilstoni</i>
50	14.07.84	14°32.5S	141°18.5E	21	500	23	18	8	0	1	
52	15.07.84	14°23.9S	141°18.6E	16	500	25	12	2	0	0	
53	15.07.84	14°21.0S	141°18.1E	16	500	26	47	9	0	2	
55	16.07.84	14°02.8S	141°17.5E	24	500	27	25	19	0	0	
56	16.07.84	14°01.3S	141°19.3E	22	500	23	21	12	0	0	
63	18.07.84	13°27.2S	141°17.5E	16	500	27	25	21	0	1	
64	18.07.84	13°25.6S	141°17.5E	13	500	21	12	0	1	2	
71	19.07.84	12°59.0S	141°30.0E	23	500	24	19	5	3	0	
72	19.07.84	12°57.0S	141°28.0E	26	500	20	17	6	0	0	
73	19.07.84	12°52.5S	141°30.5E	26	500	23	46	36	0	30	<i>tilstoni</i>
74	19.07.84	12°49.0S	141°30.5E	24	500	24	31	13	0	1	

Cruise No. R06/84 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
77	21.07.84	12°40.9S	141°36.3E	14	500	24	26	11	1	0	
78	21.07.84	12°39.1S	141°35.3E	15	500	26	19	10	0	1	
85	22.07.84	12°28.7S	141°29.3E	27	500	24	27	25	0	0	
91	23.07.84	11°51.4S	141°42.2E	21	500	32	12	0	0	0	
92	23.07.84	11°53.6S	141°45.8E	18	500	27	24	16	0	2	
94	23.07.84	11°52.0S	141°43.9E	18	500	25	11	0	0	0	
95	24.07.84	11°24.8S	141°42.9E	20	500	26	13	0	0	0	
96	24.07.84	11°34.5S	141°55.1E	18	500	47	11	0	0	0	
97	24.07.84	11°40.5S	141°51.6E	20	500	33	8	0	0	0	

Cruise No. R07/84: Weipa to Gove, incl. Weipa, NE Gulf of Carpentaria, Thursday Island and Wessel Islands.

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
4	04.08.84	12°35.5S	141°31.4E	18	500	20	22	6	0	0	
5	04.08.84	12°32.1S	141°29.8E	23	500	20	17	7	0	0	
13	05.08.84	12°30.2S	141°24.5E	35	500	33	12	0	0	0	
14	05.08.84	12°29.4S	141°26.8E	34	500	25	15	4	0	1	
22	06.08.84	12°19.4S	141°24.7E	38	500	32	28	36	0	0	<i>tilstoni</i>
23	06.08.84	12°18.7S	141°24.6E	38	500	30	22	6	0	0	
24	06.08.84	12°22.2S	141°22.8E	40	500	24	23	5	0	0	
25	06.08.84	12°22.5S	141°25.2E	37	500	23	15	1	0	0	
28	07.08.84	11°40.9S	141°31.0E	33	500	22	16	1	0	0	
29	07.08.84	11°45.6S	141°28.2E	35	500	27	13	0	0	0	
35	08.08.84	11°13.5S	141°15.0E	36	500	24	31	0	0	4	
36	08.08.84	10°59.5S	141°07.5E	38	500	20	14	0	0	0	
37	09.08.84	10°44.3S	141°27.9E	19	500	34	12	0	0	0	
39	09.08.84	10°44.5S	141°32.5E	19	500	19	11	0	0	0	
43	10.08.84	10°20.0S	141°29.5E	20	500	29	16	0	0	0	
44	10.08.84	10°20.0S	141°27.0E	20	500	26	15	0	0	0	
45	10.08.84	10°20.0S	141°25.0E	20	500	25	18	0	0	0	
47	11.08.84	10°21.7S	141°46.7E	15	500	22	14	1	0	0	
48	11.08.84	10°21.7S	141°46.7E	15	500	20	10	0	0	0	
49	11.08.84	10°25.5S	141°46.5E	15	500	19	14	0	0	0	
50	13.08.84	10°29.0S	141°47.0E	15	500	20	13	0	0	0	
52	14.08.84	11°14.0S	142°01.7E	13	500	44	18	3	0	4	
53	14.08.84	11°15.0S	142°00.5E	15	500	33	15	2	0	0	
54	14.08.84	11°16.0S	142°00.5E	13	500	50	23	4	1	0	
55	14.08.84	11°15.5S	141°58.0E	15	500	28	15	1	0	0	
58	15.08.84	11°23.7S	141°49.0E	19	500	30	14	0	0	0	
59	15.08.84	11°25.0S	141°52.2E	18	500	44	12	0	0	1	
61	16.08.84	11°19.0S	141°55.0E	16	500	23	13	0	0	0	
62	16.08.84	11°18.0S	141°47.0E	20	500	28	11	0	0	0	
65	17.08.84	11°15.5S	140°33.1E	56	1000	32	25	2	0	0	
73	18.08.84	11°15.0S	139°41.2E	61	1000	39	36	9	0	1	

Cruise No. R07/84 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
74	18.08.84	11°15.1S	139°39.0E	61	1000	46	32	1	0	1	
75	18.08.84	11°14.0S	139°37.0E	60	500	37	17	4	0	0	
76	19.08.84	11°09.5S	138°26.5E	54	1000	34	28	2	0	0	
78	19.08.84	11°03.0S	138°23.0E	56	1000	31	27	0	0	0	
80	20.08.84	11°08.0S	137°19.0E	50	1000	54	26	1	0	4	
81	20.08.84	11°02.0S	137°17.5E	50	1000	51	24	0	0	2	
83	21.08.84	10°23.0S	137°06.5E	54	1000	40	25	3	0	0	
84	21.08.84	10°29.0S	137°05.0E	54	1000	37	20	1	0	0	
86	22.08.84	10°59.7S	136°39.0E	43	1000	43	24	6	0	1	
87	22.08.84	11°02.0S	136°39.5E	40	1000	43	53	77	0	9	<i>tilstoni</i>
88	22.08.84	11°04.7S	136°38.2E	40	500	30	16	2	0	0	
92	24.08.84	11°04.0S	136°38.6E	31	1000	23	55	48	1	7	<i>macloti</i>
99	25.08.84	10°58.5S	136°40.2E	43	500	32	10	0	0	0	
100	02.09.84	11°02.5S	136°41.4E	43	500	43	10	0	0	0	
101	02.09.84	11°02.0S	136°41.5E	31	500	22	86	259	15	3	<i>macloti</i>

Cruise No. R08/84: Darwin to Broome, incl. Fog Bay, Anson Bay, Napier-Broom Bay, NW coast Western Australia.

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	19.09.84	12°39.0S	130°13.5E	20	500	16	17	5	0	1	
2	19.09.84	12°40.0S	130°12.2E	21	500	16	17	6	0	1	
3	19.09.84	12°44.2S	130°13.2E	19	500	35	9	3	0	3	
4	19.09.84	12°44.2S	130°15.0E	17	500	22	17	7	0	0	
8	20.09.84	12°46.5S	130°12.2E	15	500	32	16	14	1	0	
9	20.09.84	12°46.5S	130°12.7E	15	500	28	16	10	0	0	
14	21.09.84	13°09.0S	129°53.0E	22	500	23	12	0	0	0	
15	21.09.84	13°11.4S	129°50.2E	22	500	23	11	0	0	14	
16	21.09.84	13°17.0S	129°53.6E	26	500	49	13	1	0	6	
17	22.09.84	13°22.6S	130°02.7E	17	500	28	10	3	0	0	
21	22.09.84	13°38.0S	129°30.0E	29	500	28	9	0	0	0	
26	24.09.84	12°19.2S	130°28.2E	32	500	36	14	7	0	0	
27	24.09.84	12°17.2S	130°19.8E	36	500	32	12	4	0	0	
28	24.09.84	12°20.9S	130°11.7E	35	500	30	11	2	0	0	
29	25.09.84	13°11.9S	128°06.2E	38	500	30	13	0	0	0	
30	25.09.84	13°21.0S	127°58.7E	31	500	9	12	0	0	0	
32	26.09.84	13°50.1S	126°43.0E	15	500	39	73	212	2	1	<i>macloti / tilstoni</i>
33	26.09.84	13°52.6S	126°42.5E	15	500	18	30	44	1	0	<i>macloti / tilstoni</i>
34	26.09.84	13°51.1S	126°42.6E	17	500	15	22	16	1	0	
37	27.09.84	13°50.0S	126°43.2E	17	500	24	21	17	1	3	
38	27.09.84	13°51.7S	126°43.2E	17	500	34	25	25	3	0	
44	28.09.84	13°52.4S	126°45.0E	16	500	36	14	3	0	0	
45	28.09.84	13°51.2S	126°42.3E	15	500	22	21	13	0	1	
46	28.09.84	13°50.5S	126°41.2E	18	500	20	44	55	2	2	<i>macloti / acutus</i>
47	28.09.84	13°44.0S	126°40.7E	17	500			545	2	5	<i>tilstoni / macloti</i>
53	30.09.84	13°18.6S	125°45.4E		500	65	37	6	0	0	
54	01.10.84	14°17.2S	125°32.0E	29	500	35	15	5	0	0	
55	01.10.84	14°17.4S	125°31.2E	29	500	31	14	5	0	1	
56	01.10.84	14°19.1S	125°31.0E	29	500	33	9	1	0	1	
57	01.10.84	14°19.2S	125°32.2E	26	500			0	0	0	
59	02.10.84	14°15.1S	124°57.1E		500	30	16	5	0	0	

Cruise No. R08/84 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
60	02.10.84	14°50.0S	125°59.0E		500	28	10	1	0	0	
66	03.10.84	15°24.2S	125°00.0E	20	500	33	10	0	0	0	
67	03.10.84	15°24.2S	125°00.0E	20	500	65	18	12	0	0	
68	03.10.84	15°24.2S	125°00.0E	20	500	56	38	42	1	0	<i>sorrah</i>
69	05.10.84	15°05.0S	124°12.0E	51	500	26	9	0	0	0	
75	06.10.84	16°25.5S	122°50.0E	31	500	30	12	0	0	0	
76	06.10.84	16°27.8S	122°47.4E	31	500	66	15	2	0	0	
78	09.10.84	18°11.8S	122°47.0E	31	500	37	22	1	3	11	
79	09.10.84	18°14.5S	121°45.7E	29	500	31	10	1	0	0	
80	09.10.84	18°14.2S	121°45.6E		500	41	10	0	0	0	
83	10.10.84	18°24.2S	121°36.5E	28	500	36	11	0	0	0	
84	10.10.84	18°49.7S	121°33.2E	29	500	38	8	0	0	0	

Cruise No. R09/85: Darwin to Gove, incl. offshore region to the north of Arnhem Land.

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	25.01.85	10°33.5S	132°41.7E	61	1000	37	30	3	0	0	
4	26.01.85	10°34.0S	132°49.0E	61	1000	30	45	3	1	0	
7	27.01.85	10°22.5S	132°38.5E	65	1000	37	24	0	0	0	
9	28.01.85	10°42.0S	132°56.0E	59	1000	58**		0	0	2	
11	29.01.85	10°50.0S	133°26.5E	63	1000	11	50	0	0	0	
14	31.01.85	12°00.4S	136°46.5E	31	500	15	65	105	0	1	<i>sorrah / tilstoni</i>
15	31.01.85	11°59.6S	136°46.2E	32	500	13	22	12	0	0	
16	31.01.85	12°00.7S	136°46.0E	31	500	10	20	6	1	2	
17	01.02.85	12°02.6S	136°44.9E	20	500	22	24	14	0	0	
18	01.02.85	12°02.2S	136°44.4E	20	500	22	20	12	0	2	
19	01.02.85	12°01.5S	136°44.5E	22	500	23	25	9	0	0	
20	01.02.85	12°00.0S	136°43.7E	29	500	18	18	3	0	1	
22	02.02.85	10°48.5S	137°01.0E	58	1000	28	25	0	0	0	
25	03.02.85	10°24.4S	136°38.5E	61	1000	37	38	63	0	1	<i>macloti</i>
26	03.02.85	10°25.5S	136°38.0E	59	1000	23	30	3	0	2	
28	04.02.85	09°56.1S	135°58.3E	59	1000	31	22	0	0	0	
31	05.02.85	10°46.3S	135°46.0E	50	1000	25	27	2	1	0	
34	06.02.85	11°24.0S	135°34.5E	40	1000	23	24	0	0	2	
37	07.02.85	11°19.3S	135°33.4E	40	1000	21	20	3	0	2	
41	08.02.85	11°17.6S	135°41.8E	41	1000	27	26	2	0	10	
44	09.02.85	10°55.0S	136°15.0E	43	1000	36	27	4	0	26	
47	10.02.85	11°04.8S	136°47.5E	58	1000	25	28	1	0	0	
52	13.02.85	12°02.2S	136°45.6E	14	1000	17	49	7	11	1	
53	13.02.85	12°02.0S	136°45.0E	20	1000	23	59	28	13	4	
54	13.02.85	12°02.0S	136°42.9E	23	1000	25	30	3	1	1	
56	14.02.85	12°02.5S	136°45.4E	16	500	24	14	2	2	1	
57	14.02.85	12°05.0S	136°41.2E	25	1000	20	29	8	0	0	
58	14.02.85	12°05.5S	136°39.8E	27	1000	19	2	2	0	1	

** Fishing time (set and haul duration combined)

Cruise No. R10/85: Gove return Gove, incl. Melville Bay and offshore region to the north of the Wessel Islands.

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
26	03.03.85	12°02.2S	136°44.0E	23	500	31	80	269	0	0	<i>tilstoni</i>
27	04.03.85	12°04.3S	136°42.8E	23	500	17	16	5	0	0	
28	04.03.85	12°04.2S	136°42.7E	23	500	17	11	2	0	0	
29	04.03.85	12°03.2S	136°45.3E	14	500	16	11	2	0	0	
30	04.03.85	12°07.8S	136°42.8E	21	500	18	15	6	0	0	
36	09.03.85	10°58.5S	136°39.7E	41	1000	24	28	4	4	0	
37	09.03.85	10°56.0S	136°40.7E	43	1000	21	46	2	48	1	
40	10.03.85	10°28.4S	136°46.4E	56	1000	7	142	0	0	0	
46	12.03.85	10°08.8S	137°03.2E	50	1000	25	17	0	0	0	
53	15.03.85	11°59.8S	136°46.4E	29	500	21	16	3	0	0	
54	15.03.85	11°57.8S	136°43.3E		500	21	15	7	0	0	
55	15.03.85	11°55.4S	136°41.1E	29	500	19	44	41	0	0	<i>tilstoni</i>
57	16.03.85	10°54.4S	136°39.9E	32	500	13	39	66	0	0	<i>tilstoni</i>
58	16.03.85	10°54.0S	136°40.7E	33	500	7	36	221	0	0	<i>tilstoni</i>
59	16.03.85	10°54.0S	136°42.2E	32	500	7	36	41	0	0	<i>tilstoni</i>

Cruise No. R11/85: Gove to Cairns, incl. Melville Bay, northern Gulf of Carpentaria, Torres Strait, Gulf of Papua and North Eastern Queensland.

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
1	29.03.85	11°56.2S	136°39.4E	29	500	15	15	6	0	0	
2	29.03.85	11°54.0S	136°40.5E	31	500	15	15	4	0	0	
3	29.03.85	11°52.5S	136°42.4E	32	500	25	15	1	0	0	
6	30.03.85	12°09.6S	136°53.0E	32	500	20	10	1	0	0	
7	30.03.85	12°06.2S	136°58.6E	47	1000	25	55	57	3	4	<i>macloti</i>
8	30.03.85	12°07.1S	137°01.0E	47	1000	18	55	78	2	2	<i>macloti</i>
12	01.04.85	10°49.2S	141°09.0E	54	500	25	15	1	0	0	
14	02.04.85	10°28.3S	142°35.0E	19	1000	20	40	9	1	0	
15	02.04.85	10°28.2S	142°32.0E	19	1000	25	30	2	2	0	
18	03.04.85	09°55.6S	143°09.1E	27	1000	25	25	4	0	0	
19	03.04.85	09°54.4S	143°08.5E	27	1000	20	25	2	0	0	
20	04.03.85	09°41.0S	143°12.8E	24	1000	30	40	29	4	0	
21	04.04.85	09°41.5S	143°12.7E	24	1000	20	50	29	0	0	<i>tilstoni</i>
23	05.04.85	09°26.2S	143°25.0E	23	1000	30	35	7	2	0	
24	05.04.85	09°27.0S	143°22.3E	24	1000	20	25	2	0	0	
25	06.04.85	09°07.9S	144°07.3E	54	1000	20	45	3	0	0	
26	06.04.85	09°05.0S	144°16.3E	56	1000	25	25	4	0	0	
27	06.04.85	09°03.0S	144°10.8E	72	1000	25	25	2	0	0	
31	08.04.85	09°36.7S	143°15.7E	23	500	28	80	3	0	0	
32	08.04.85	09°40.0S	143°15.0E	22	1000	25	35	3	0	0	
34	09.04.85	09°38.5S	143°15.5E	18	1000	30	85	16	0	0	
35	09.04.85	09°39.2S	143°16.3E	20	1000	25	60	5	3	2	
37	11.04.85	10°33.4S	142°39.5E	27	1000	25	25	0	0	0	
38	11.04.85	10°34.4S	142°38.6E	23	1000	25	25	0	0	0	
39	13.04.85	12°43.5S	143°28.5E	16	1000	25	105	123	0	0	<i>tilstoni</i>
40	13.04.85	12°43.8S	143°28.8E	16	500	20	10	4	0	0	
43	14.04.85	12°42.0S	143°28.3E	18	1000	15	45	13	0	1	
44	14.04.85	12°41.4S	143°27.5E	18	1000	15	55	59	1	0	<i>tilstoni</i>
46	15.04.85	13°44.5S	143°39.6E	17	500	25	65	172	0	0	<i>tilstoni</i>
47	15.04.85	13°39.0S	143°42.9E	15	500	20	15	4	0	0	

Cruise No. R11/85 (Cont.)

Set No.	Date	Position		Depth (M)	Net Length (M)	Set Duration (Min)	Haul Duration (Min)	Catch (No.)			Dominant Species
								Shark	Mackerel	Other	
49	16.04.85	14°09.7S	143°50.3E	16	1000	25	25	6	0	0	
50	16.04.85	14°09.7S	143°54.8E	14	500	90**		0	0	0	
51	16.04.85	14°11.8S	144°01.1E	20	500	40	15	2	0	1	
53	17.04.85	14°14.9S	143°59.5E	17	1000	20	43	31	0	0	
54	17.04.85	14°13.0S	143°57.8E	16	1000	25	35	13	2	0	
55	17.04.85	14°12.9S	143°59.7E	18	1000	20	50	20	8	0	
58	18.04.85	14°08.3S	144°20.5E	20	500	25	35	11	1	1	
59	18.04.85	14°07.6S	144°21.1E	20	1000	25	50	48	0	0	<i>tilstoni</i>
60	19.04.85	14°35.9S	145°24.2E	28	1000	20	30	0	0	2	
61	19.04.85	14°35.6S	145°24.2E	20	1000	25	20	0	0	0	
62	20.04.85	15°26.8S	145°20.2E	18	1000	20	25	1	0	0	

** Fishing time (set and haul duration combined).

Cruise No. R12/85: Cairns to Gove, incl. north eastern Queensland (Cairns to Cape York), Torres Strait, offshore Wessel Islands and Melville Bay.

Set No.	Date	Position	Depth (m)	Net Length (m)	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
1	07.05.85	16°45.0S	145°49.8E	18	500	23	8	1	0	0	
2	07.05.85	16°41.5S	145°46.0E	22	500	23	10	0	0	0	
3	07.05.85	16°35.8S	145°39.5E	21	500	22	8	0	0	0	
8	09.05.85	14°08.2S	144°25.5E	16	500	24	18	13	0	0	
9	09.05.85	14°09.2S	144°22.5E	15	1000	21	39	18	0	1	
10	09.05.85	14°08.6S	144°21.6E	17	500	28	13	3	0	0	
14	10.05.85	14°16.1S	144°03.2E	14	500	18	21	21	0	0	
15	10.05.85	14°16.0S	144°02.4E	16	500	19	21	23	0	0	
16	10.05.85	14°15.9S	144°01.2E	16	500	19	12	5	0	0	
17	10.05.85	14°17.2S	144°00.4E	14	500	20	14	5	0	0	
29	19.05.85	12°08.2S	136°44.4E	22	500	21	11	2	2	0	
30	19.05.85	12°06.5S	136°44.6E	20	500	23	12	2	0	0	
31	19.05.85	12°05.8S	136°39.8E	23	500	21	11	1	0	0	
34	22.05.85	11°44.8S	136°32.5E	32	500	23	8	0	0	0	
35	22.05.85	11°42.8S	136°31.6E	31	1000	22	24	0	0	1	
37	23.05.85	11°26.2S	136°25.0E	25	1000	22	51	31	3	0	<i>tilstoni</i>
38	23.05.85	11°22.6S	136°25.8E	25	1000	21	26	4	0	0	
39	23.05.85	11°16.9S	136°31.0E	27	1000	19	27	7	0	0	
42	25.05.85	11°04.2S	136°25.8E	31	500	24	21	13	1	2	
43	25.05.85	11°02.6S	136°40.2E	34	1000	24	65	52	0	16	<i>macloti/fitzroyensis</i>
44	25.05.85	11°06.2S	136°39.0E	27	1000	16	63	37	0	5	<i>macloti</i>
45	26.05.85	11°32.5S	136°18.8E	18	500	21	10	2	0	0	
46	26.05.85	11°31.0S	136°18.2E	21	1000	23	91	90	0	0	<i>tilstoni</i>
47	26.05.85	11°31.5S	136°16.2E	23	500	18	12	0	0	0	
48	27.05.85	12°05.5S	136°42.8E	25	1000	20	51	37	0	0	<i>tilstoni</i>
50	28.05.85	12°05.4S	136°44.5E	22	1000	126	156	8	0	0	
51	28.05.85	12°05.1S	136°41.0E	29	500	23	15	2	0	0	
52	28.05.85	12°06.3S	136°42.2E	25	500	24	27	12	0	0	
53	28.05.85	12°09.6S	136°42.0E	22	500	7	13	1	0	0	
55	29.05.85	12°06.3S	136°40.2E	25	500	21	14	3	0	0	
56	29.05.85	12°04.8S	136°39.6E	25	500	21	27	19	0	0	
57	29.05.85	12°04.5S	136°40.0E	25	500	22	13	3	0	0	

Appendix III (B) – Longline*

Cruise No. R01/84: Darwin to Gove, incl. Pt. Essington, Croker Island, Goulburn Island and Melville Bay.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
9	21.01.84	11°04.6S	132°03.5E	26	59	208	37	14	0	0	
16	22.01.84	11°03.2S	132°09.8E	26	60	310	25	8	0	0	
29	24.01.84	11°02.2S	132°42.3E	42	59	320	35	7	0	0	
38	26.01.84	11°07.7S	132°45.3E		58	490	37	6	0	0	
48	29.01.84	11°33.0S	133°18.5E	26	60	265	35	12	0	0	
54	30.01.84	11°35.0S	133°37.0E	27	59	330	50	5	0	0	
69	04.02.84	12°09.2S	136°54.3E	32	53	220	70	6	0	0	
74	06.02.84	11°45.8S	136°52.4E	40	60	295	50	7	0	0	
80	07.02.84	11°56.4S	136°43.2E	33	60	420	55	2	0	0	
86	08.02.84	12°01.0S	136°43.4E	23	58	370	40	4	0	0	

Cruise No. R02/84: Gove return Gove, incl. Melville Bay, NW Gulf of Carpentaria, offshore Wessel Islands.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
2	16.02.84	12°02.0S	136°43.6E	23	56	250	60	11	0	0	
9	17.02.84	11°59.2S	136°39.0E	29	60	358	37	12	0	0	
17	18.02.84	11°59.6S	136°42.4E	28	59	360	28	5	0	0	
24	19.02.84	11°39.5S	136°20.2E	27	59	419**		5	0	0	
48	24.02.84	12°38.0S	136°49.5E	31	58	382	21	1	0	0	
67	27.02.84	13°03.4S	136°36.2E	22	54	346	21	10	0	0	
94	02.03.84	13°22.0S	136°29.5E	25	57	252	18	4	0	0	
108	06.03.84	11°44.6S	136°46.6E	48	55	206	35	6	0	0	
114	07.03.84	10°44.4S	137°07.0E	54	55	239	18	0	0	0	
119	08.03.84	10°40.0S	137°16.3E	56	54	205	16	0	0	0	

* The original table was difficult to read and has been retyped. Some errors may have been introduced.

** Fishing time (set and haul durations combined).

Cruise No. R03/84: Gove to Darwin, incl. Melville Bay, Wessel Islands, Croker Island, Bathurst Island and Melville Island.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species
							Shark	Mackerel	Other	
5	19.03.84	12°09.4S	136°54.0E	37	60	462**	20	0	0	
26	23.03.84	11°33.8S	136°26.4E	27	58	408**	10	0	0	
58	28.03.84	11°14.5S	132°48.6E	34	60	270**	13	0	0	
64	29.03.84	11°03.7S	132°45.1E	33	59	377**	12	0	0	
73	01.04.84	10°59.2S	132°47.3E	20	60	299**	5	0	0	
99	04.04.84	11°02.7S	130°16.0E	22	59	502**	16	0	0	
107	05.04.84	10°53.7S	130°06.5E	51	60	288**	4	0	0	
114	06.04.84	10°57.5S	130°07.8E	53	60	268**	7	0	0	
123	07.04.84	11°10.6S	129°51.8E	84	60	287**	11	0	0	
130	08.04.84	11°27.7S	129°53.0E	55	60	230**	2	0	0	
136	09.04.84	11°47.5S	129°58.0E	51	60	237**	9	0	0	

** Fishing time (set and haul durations combined).

Cruise No. R04/84: Darwin return Darwin, incl. Fog Bay, Anson Bay, Napier-Broome Bay and Admiralty Gulf.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species
							Shark	Mackerel	Other	
7	26.04.84	12°47.6S	130°12.8E	17	56	303	7	0	0	
19	28.04.84	13°20.9S	130°05.0E	17	60	268	9	1	0	
31	30.04.84	13°33.8S	129°42.1E	26	60	295	8	0	0	
45	02.05.84	13°57.1S	127°29.0E	33	60	402	1	0	0	
59	06.05.84	14°04.4S	126°37.3E	15	60	279	7	0	0	
64	07.05.84	13°54.8S	126°39.0E	22	60	368	10	0	0	
79	10.05.84	13°18.4S	125°45.4E	25	60	282	21	0	0	
91	12.05.84	13°51.7S	126°39.4E	26	60	526	4	0	0	
97	13.05.84	13°44.6S	127°04.4E	31	60	283	10	0	0	
103	15.05.84	14°09.3S	128°14.5E	55	60	210	2	0	0	

Cruise No. R05/84: Gove to Karumba, incl. Melville Bay, Groote Eylandt, Vanderlin Islands and Mornington Island.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
32	08.06.84	14°04.7S	136°22.9E	19	45	475	21	17	0	1	
38	10.06.84	14°09.0S	136°23.2E	11	62	300	32	9	0	0	
43	11.06.84	14°11.6S	136°20.3E	13	61	433	24	9	0	1	
49	11.06.84	14°11.4S	136°19.9E	16	57	300	241	6	0	0	
54	12.06.84	13°42.0S	136°21.2E	27	61	156	16	1	0	0	
60	20.06.84	15°31.3S	136°45.8E	12	60	238	16	2	0	0	
73	24.06.84	16°03.5S	137°55.4E	20	61	341	40	4	0	1	

Cruise No. R06/84: Karumba to Weipa, incl. Mornington Island, Karumba, eastern Gulf of Carpentaria, Weipa.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
7	06.07.84	16°19.5S	138°39.0E	26	60	349	38	32	0	0	<i>sorrah</i>
21	08.07.84	16°05.2S	139°02.3E	26	60	153	22	2	0	0	
35	10.07.84	15°31.0S	140°06.9E	29	60	323	125	13	0	0	
57	16.07.84	14°01.5S	141°18.2E	22	60	199	39	5	0	0	
65	18.07.84	13°20.8S	141°18.0E	16	59	306	30	8	0	0	
79	21.07.84	12°38.7S	141°33.6E	15	60	269	30	21	0	0	
86	22.07.84	12°27.4S	141°30.0E	27	60	310	25	6	0	0	
93	23.07.84	11°53.1S	141°45.8E	18	60	162	38	6	0	0	

Cruise No. R07/84: Weipa to Gove, incl. Weipa, NE Gulf of Carpentaria, Thursday Island and Wessel Islands.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
6	04.08.84	12°33.8S	141°28.5E	29	60	230	25	14	0	0	
15	05.08.84	12°30.0S	141°27.4E	32	60	240	30	8	0	0	
30	07.08.84	11°43.4S	141°26.1E	40	60	275	15	4	1	0	
57	15.08.84	11°22.0S	141°29.0E	19	60	290	20	2	2	0	
60	16.08.84	11°22.0S	142°05.0E	11	60	430	50	3	0	1	
66	17.08.84	11°15.0S	140°30.0E	60	60	160	40	3	0	0	
77	19.08.84	11°08.5S	138°25.0E	53	60	162	22	0	0	0	
79	20.08.84	11°03.4S	137°21.0E	50	54	315	40	1	0	0	
82	21.08.84	10°24.9S	137°07.0E	54	60	305	30	1	0	0	
93	24.08.84	11°02.7S	136°39.3E	40	60	210	30	3	0	0	

Cruise No. R08/84: Darwin to Broome, incl. Fog Bay, Anson Bay, Napier-Broome Bay, NW coast Western Australia.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
7	20.09.84	12°49.5S	130°11.6E	15	57	395	17	4	0	0	
20	22.09.84	13°37.7S	129°29.2E	29	60	366	20	1	0	0	
36	27.09.84	13°49.1S	126°43.0E	20	56	323	20	12	0	0	
48	29.09.84	12°38.5S	126°24.7E	28	60	130	86	6	0	0	
61	02.10.84	14°50.0S	124°59.2E		60	213	21	14	0	0	
70	05.10.84	15°04.5S	124°13.0E	53	60	167	17	3	0	0	
82	10.10.84	18°24.8S	121°37.0E	30	60	401	53	4	0	0	

Cruise No. R09/85: Darwin to Gove, incl. offshore region to the north of Arnhem Land.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
2	26.01.85	10°39.1S	132°46.5E	59	276	155	80	5	0	1	
3	26.01.85	10°36.1S	132°46.5E	59	276	130	85	12	0	1	
5	27.01.85	10°40.8S	132°50.4E	59	276	195	100	13	0	1	
6	27.01.85	10°23.2S	132°37.4E	63	278	134	83	2	0	3	
8	28.01.85	10°22.0S	132°27.0E	67	300	138	110	10	0	1	
10	29.01.85	10°45.0S	132°57.5E	54	300	139	103	9	0	0	
12	30.01.85	10°43.8S	134°42.4E	52	300	127	47	6	0	1	
21	02.02.85	11°04.9S	136°54.3E	54	298	127	60	2	1	3	
23	03.02.85	10°39.2S	136°58.1E	56	298	133	82	1	0	1	
24	03.02.85	10°23.6S	136°38.2E	59	284	157	83	1	0	1	
27	04.02.85	10°04.0S	136°08.0E	59	297	125	75	2	0	1	
29	05.02.85	09°54.0S	135°58.5E	68	297	139	81	2	0	0	
30	05.02.85	10°34.3S	135°51.6E	50	288	95	65	1	0	0	
32	06.02.85	10°46.1S	135°44.8E	45	295	136	90	7	0	0	
33	06.02.85	11°16.6S	135°38.0E	40	295	128	82	2	0	2	
35	07.02.85	11°25.0S	135°39.8E	40	296	125	94	32	0	0	
38	08.02.85	11°23.8S	135°40.0E	40	299	109	86	15	0	2	
40	08.02.85	11°21.0S	135°40.5E	40	300	103	76	6	0	1	
42	09.02.85	11°17.9S	135°44.4E	40	299	101	77	6	0	1	
45	10.02.85	11°04.2S	136°18.1E	40	300	102	96	30	0	0	sorrah
46	10.02.85	10°58.0S	136°52.2E	58	298	126	77	13	0	0	
49	12.02.85	11°13.0S	136°59.5E	52	297	91	75	1	0	1	
50	13.02.85	11°10.5S	137°13.5E	52	297	95	86	7	0	1	
55	14.02.85	12°04.0S	136°41.9E	23	297	114	100	28	0	0	sorrah

Cruise No. R10/85: Gove return Gove, incl. Melville Bay and offshore region to the north of the Wessel Islands

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
6	24.02.85	10°54.1S	137°16.0E	50	300	98	70	2	0	2	
7	24.02.85	10°47.8S	137°27.1E	50	300	105	90	3	0	0	
8	25.02.85	10°36.1S	137°32.1E	50	300	99	71	4	0	0	
9	25.02.85	10°29.8S	137°33.8E	52	300	114	64	3	0	0	
10	25.02.85	10°22.8S	137°33.5E	50	300	105	70	0	0	0	
11	26.02.85	10°11.7S	137°41.2E	49	300	90	80	1	0	0	
12	26.02.85	10°05.2S	137°45.6E	47	300	126	74	12	0	2	
13	26.02.85	10°05.3S	137°49.3E	47	300	175	77	7	0	0	
14	27.02.85	10°06.4S	138°04.2E	47	300	108	74	7	0	0	
15	27.02.85	10°06.1S	138°06.8E	50	300	93	76	13	0	0	
16	27.02.85	10°05.5S	138°11.1E	50	300	108	70	4	0	0	
17	28.02.85	10°09.5S	138°24.5E	50	300	108	65	5	0	0	
18	28.02.85	10°13.2S	138°29.7E	50	300	85	82	7	0	0	
19	28.02.85	10°16.3S	138°33.7E	50	300	103	71	3	0	0	
20	01.03.85	10°30.0S	138°30.4E	54	300	98	64	2	0	0	
21	01.03.85	10°33.2S	138°33.4E	54	300	95	69	7	0	0	
22	01.03.85	10°36.8S	138°36.7E	54	300	97	70	4	0	1	
23	02.03.85	10°50.6S	138°31.8E	56	300	104	73	7	0	0	
24	02.03.85	10°53.0S	138°38.1E	56	300	108	56	1	0	0	
25	02.03.85	10°56.0S	138°35.1E	54	300	102	69	4	0	0	
31	06.03.85	10°49.2S	136°51.1E	56	295	106	72	10	0	0	
32	06.03.85	10°39.1S	136°53.9E	56	295	91	79	1	0	0	
33	07.03.85	10°32.4S	136°58.4E	54	295	99	69	4	0	0	
34	07.03.85	10°33.4S	137°03.8E	54	295	102	63	5	0	0	
35	07.03.85	10°37.9S	137°01.7E	54	295	90	66	2	0	0	
38	10.03.85	10°48.8S	136°45.1E	50	290	105	71	6	0	1	
39	10.03.85	10°42.9S	136°44.3E	56	300	97	71	3	0	0	
41	11.03.85	10°14.9S	136°46.5E	54	300	95	69	11	0	2	
42	11.03.85	10°35.5S	136°48.8E	55	300	92	60	3	0	0	
43	11.03.85	10°11.1S	136°49.2E		300	100	63	9	0	0	
44	12.03.85	10°06.8S	136°55.0E	52	300	93	68	10	0	4	
45	12.03.85	10°08.3S	136°57.7E	52	300	102	70	8	0	0	

Cruise No. R10/85 (Cont.)

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species
							Shark	Mackerel	Other	
47	13.03.85	10°13.6S 137°11.8E	50	300	94	68	4	0	0	
48	13.03.85	10°13.9S 137°06.5E		295	95	66	7	0	1	
49	13.03.85	10°19.4S 137°07.4E	32	300	92	69	7	0	1	
50	14.03.85	10°27.3S 137°20.0E	50	295	91	66	4	0	0	
51	14.03.85	10°30.2S 137°16.1E	50	295	93	66	4	0	0	
52	14.03.85	10°33.7S 137°14.9E	52	295	107	67	3	0	1	

Cruise No. R11/85: Gove to Cairns, incl. Melville Bay, northern Gulf of Carpentaria, Torres Strait, Gulf of Papua and north eastern Queensland.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
9	31.03.85	11°41.9S	138°22.3E	54	300	100	70	3	0	0	
10	01.04.85	10°51.8S	140°32.3E	52	300	95	80	3	0	0	
22	05.04.85	09°42.0S	143°12.5E	22	300	105	75	12	0	0	
28	07.04.85	09°00.8S	144°07.5E	54	300	110	75	4	0	2	
30	08.04.85	09°36.0S	143°13.7E	41	300	105	105	22	1	1	
33	09.04.85	09°37.0S	143°13.0E	20	300	95	80	10	3	0	

Cruise No. R12/85: Cairns to Gove, incl. north eastern Queensland (Cairns to Cape York), Torres Strait, offshore Wessel Islands and Melville Bay.

Set No.	Date	Position	Depth (m)	No. of hooks	Set Duration (min)	Haul Duration (min)	Catch (No.)			Dominant species	
							Shark	Mackerel	Other		
11	13.05.85	12°27.2S	143°20.0E	16	300	107	72	24	1	1	<i>sorrah</i>
23	14.05.85	11°48.5S	143°02.8E	18	300	96	83	37	4	1	<i>sorrah</i>
24	14.05.85	11°48.8S	143°03.6E	18	300	106	86	19	3	1	
26	15.05.85	11°39.5S	142°58.2E	22	296	95	75	10	1	1	
27	17.05.85	10°37.0S	141°44.0E	14	293	95	73	2	2	1	
33	22.05.85	11°44.0S	136°31.4E	29	300	94	84	7	2	0	
40	24.05.85	11°04.3S	136°30.4E	32	295	82	96	21	0	1	
41	25.05.85	11°07.8S	136°36.5E	29	300	114	72	18	0	2	
58	30.05.85	12°05.0S	136°41.5E	25	298	97	78	24	0	0	<i>sorrah</i>

Shark stock structure

Genetic evidence for separation of two sharks, *Carcharhinus limbatus* and *C. tilstoni*, from northern Australia. S. Lavery and J. B. Shaklee.
(In preparation)

Population genetics of two tropical sharks, *Carcharhinus tilstoni* and *C. sorrah*, in northern Australia. S. Lavery and J.B. Shaklee. *Australian Journal of Marine and Freshwater Research*, 1989, **40**, 541–557.

Genetic Evidence for Separation of Two Sharks, *Carcharhinus limbatus* and *C. tilstoni*, from Northern Australia

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Abstract

Allozyme electrophoresis was used to show that the two morphologically different groups of *Carcharhinus limbatus* co-existing in waters to the north of Australia were distinct species. Forty-seven loci were examined in 967 specimens of the normal form and 20 specimens of the dark pelvic form. Two loci exhibited nearly fixed allelic differences between the two forms, indicating that they must be considered as two distinct species. Further genetic analysis of *C. limbatus* specimens from South Africa and the West Indies (the type locality) showed that the rare dark pelvic form is the true *C. limbatus*, while the normal form in Australian waters is *C. tilstoni*.

Introduction

The dominant species of shark in the commercial shark fishery of northern Australia was formerly recognised as *Carcharhinus limbatus* (Valenciennes). Compagno (1984) describes *C. limbatus* as having a circumglobal distribution, being widespread in all tropical and subtropical continental waters. During a research program into the population biology of *C. limbatus* in Australian waters, it became apparent from morphological characters that two groups of *C. limbatus* co-existed in northern Australian waters (Lyle 1986, Stevens and Wiley 1986). One of these (the dark pelvic form) occurred only rarely, in the frequency of about 1 in 300 normal *C. limbatus*. Stevens and Wiley (1986) separated the two groups on

vertebral counts, size at maturity, maximum size and pelvic fin colouration. However, all these characters showed considerable variation throughout the distribution of the species (Garrick 1982). Stevens and Wiley (1986) noted that in a personal communication from J. B. Shaklee, allozyme electrophoresis (which was being carried out for studies on population discrimination (Lavery and Shaklee 1989)) showed the two groups to be distinct species. The present paper documents that evidence, along with additional comparisons with overseas specimens which show that the rare dark pelvic form is the true *C. limbatus*.

Materials and Methods

Sharks from Australian waters were collected between 1982 and 1985 from locations ranging from the North-West Shelf (off Western Australia) to the north-east coast of Queensland (see Lavery and Shaklee (1989) for details of collections). Of a total of 987 individuals collected, only 20 of these were of the dark pelvic form. The dark pelvic individuals were caught throughout the entire range of sampling, with the majority from two particular collections: a group of 8 caught near Darwin, and a group of 6 taken in Torres Strait (Fig. 1). The sharks were caught by gillnet, longline and handline from both research and commercial vessels. For comparison with *C. limbatus* from other locations throughout its range, additional sampling was arranged from both Natal, South Africa (9 sharks) and the Bimini Islands in the Bahamas (11 sharks). The type locality for *C. limbatus* is the West Indies (Garrick 1982).

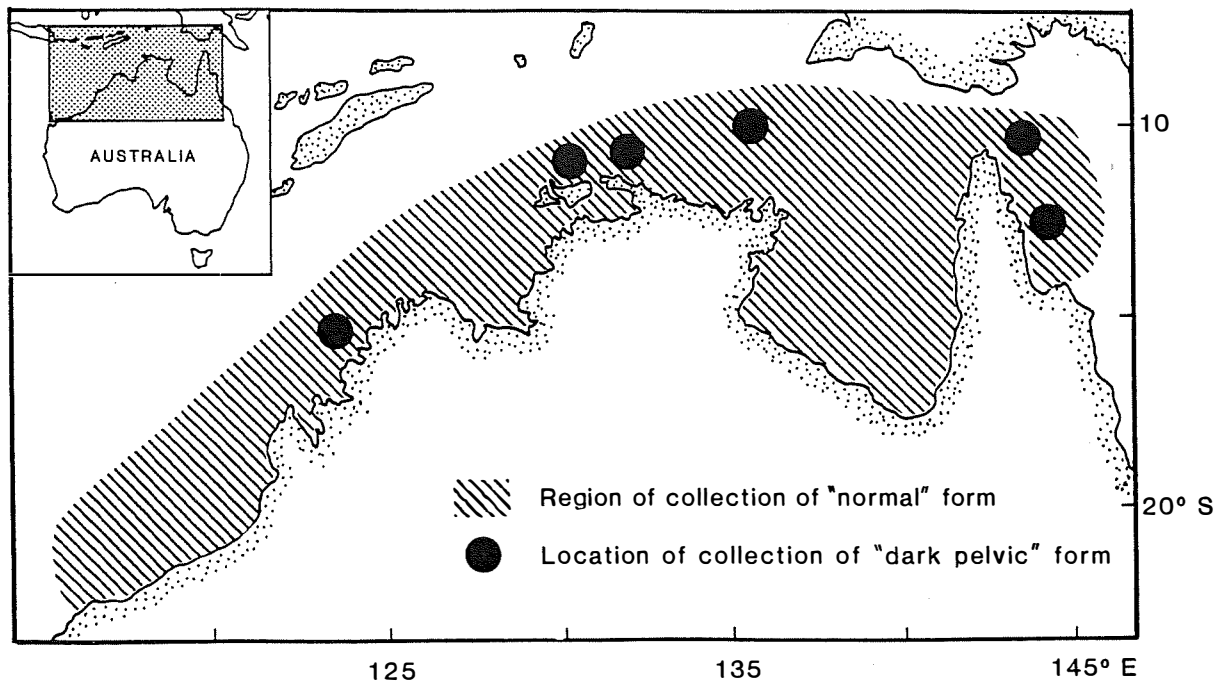


Fig. 1. *Carcharhinus limbatus*. Study region.

Allozyme electrophoresis is an extremely useful technique in population genetics (Shaklee 1983) and is particularly powerful in identifying cryptic species which are difficult to distinguish morphologically (Shaklee *et al.* 1982, SolÇ-Cava *et. al.* 1983, Richardson *et al.* 1986, Lavery and Staples 1990). This technique was used to determine the genetic relationship between the two forms of *C. limbatus*.

Tissue samples of muscle, heart, eye and liver were taken from individuals as soon as possible after capture and frozen at -20°C for transport to the laboratory. There, tissue extracts were prepared by homogenisation and centrifugation (at 20 000 x g) and stored at -70°C until used. Horizontal starch-gel electrophoresis was used to resolve all isozymes and allozymes, which were visualised using a variety of histochemical enzyme stains. The specific electrophoretic conditions used in the analysis of each variable enzyme system are given in Lavery and Shaklee (1989). We have followed the AFS fish gene nomenclature system of Shaklee *et al.* (1989). Alleles are identified by their electrophoretic mobilities relative to that of the most common allele (=100) at each locus.

Results

In the initial electrophoretic analysis, 76 enzyme stains were used. Of these, 40 enzymes encoded by 47 loci gave clear, interpretable results. These loci are listed in Table 1. In the normal form of *C. limbatus*, there was little genetic difference between geographic areas in tropical Australia ($F_{ST} = 0.0094$; Lavery and Shaklee, 1989).

Two loci, PEP-S and GPI, exhibited dramatic and highly significant differences in allele frequencies between the two forms of *C. limbatus* (Table 2) in Australia. The probability of obtaining the observed genotype frequencies from a population of one randomly-mating species is extremely low ($G=57.7$, $p = 10^{-14}$, 1df). At four other loci, AH, CK-A, EST-1 and FH, the allele frequencies differed significantly between the two forms (Table 3) (AH: $G = 9.14$, 2df, $p < .025$; CK-A: $G = 5.42$, 1df, $p < .025$; EST-1: $G = 4.50$, 1df, $p < .05$; FH: $G = 27.01$, 1df, $p \ll .001$). The dark pelvic form also expressed an additional esterase isozyme in all individuals that was not observed in the normal specimens. Genotypes for all loci were in Hardy-Weinberg equilibrium when the normal and dark pelvic forms were tested separately. The value of Nei's (1978) standard genetic distance, D , (using all 47 loci) between the two forms is 0.045.

Evidence of a genetic basis for the allozyme differences in PEP-S and GPI was provided by inheritance studies (Lavery, unpublished data). Two dark pelvic family groups (pregnant mother plus pups) were analysed electrophoretically. Both mothers had a genotype of: *114/114 at PEP-S and *-86/-86 at GPI. All eight pups (2 litters of 4) possessed this same genotype. This result is consistent with a simple Mendelian basis for the observed electrophoretic variation. Furthermore, this outcome indicates that the matings had occurred with males of the same genotype and thus of the same dark pelvic form (cf. Table 2). Although these data are limited, they provide direct evidence of reproductive isolation

Table 1. *Carcharhinus limbatus* . Enzyme loci analysed

Locus	Abbrev	Enzyme No	Tissue ^a
acid phosphatase		3.1.3.2	L
aconitate hydratase	AH	4.2.1.3	L
adenylate kinase		2.7.4.3	M
alanine aminotransferase		2.6.1.2	L
alcohol dehydrogenase		1.1.1.1	L
alpha-mannosidase		3.2.1.24	L
aspartate aminotransferase		2.6.1.1	L
beta-galactosidase		3.2.1.23	L
creatine kinase-A	CK-A	2.7.3.2	M
creatine kinase-C		2.7.3.2	H
dihydrolipoamide dehydrogenase-like enzyme		1.6.-.-	H
enolase		4.2.1.11	M
esterase-1,-2 & -4	EST	3.1.1.-	L
esterase-D		3.1.1.-	M
fructose bisphosphate aldolase		4.1.2.13	M
fumarate hydratase	FH	4.2.1.2	L
glucose-6-phosphate isomerase	GPI	5.3.1.9	M
glutamate dehydrogenase		1.4.1.2	L
glyceraldehyde-3-phosphate dehydrogenase -1 & -2		1.2.1.12	L
glycerol-3-phosphate dehydrogenase		1.1.1.8	M
hydroxyacylglutathione hydrolase		3.1.2.6	L
isocitrate dehydrogenase		1.1.1.42	L
L-idoitol dehydrogenase		1.1.1.14	H
L-lactate dehydrogenase-A & -B		1.1.1.27	L
lactoylglutathione lyase		4.4.1.5	H
malate dehydrogenase -2 & -3		1.1.1.37	M
malic enzyme -1 & -2	MEP	1.1.1.40	M
mannose-6-phosphate isomerase	MPI	5.3.1.8	L
N-acetyl-beta-glucosaminidase		3.2.1.30	L
octanol dehydrogenase		1.1.1.73	L
peptidase-B (leucyl-glycyl-glycine)		3.4.11.4	L
peptidase-C (prolyl-leucine)		3.4.-.-	L
peptidase-D (leucyl-proline)		3.4.13.9	M
peptidase-E (tri-phenylalanine)		3.4.-.-	L
peptidase-S (leucyl-tyrosine)	PEPS	3.4.11.1	L
phosphoglucomutase	PGM	2.7.5.1	M
phosphoglycerate kinase		2.7.2.3	M
purine-nucleoside phosphorylase	PNP	2.4.2.1	L
pyruvate kinase		2.7.1.40	L
superoxide dismutase -1 & -2	SOD	1.15.1.1	L
xanthine dehydrogenase	XDH	1.2.1.37	L

^a : M = muscle, H = heart, L = liver

Table 2 . *Carcharhinus limbatus* . Allele frequencies for the two diagnostic loci for all collections.

Locus	Allele	Collections			
		Australian normal form	Australian dark pelvic form	West Indies	South Africa
PEPS	100	1.000	0.053	-	-
	114	-	0.947	1.000	1.000
	(n)	(963)	(19)	(6)	(6)
GPI	100	1.000	0.071	-	nd ^a
	-86	-	0.929	1.000	nd
	(n)	(856)	(14)	(6.0)	(0)

nd ^a = no data (see text)

Table 3 . *Carcharhinus limbatus* . Allele frequencies for five non-diagnostic polymorphic loci for the Australian shark collections.

Locus	Allele	Normal Form	Dark Pelvic Form
AH	10	0.505	0.208
	-12	0.230	0.417
	79	0.265	0.375
	(n)	(703)	(12)
CK-A	100	0.934	1.000
	-180	0.066	-
	(n)	(960)	(20)
EST	100	0.868	1.000
	105	0.132	-
	(n)	(884)	(8)
FH	100	0.634	1.000
	80	0.366	-
	(n)	(827)	(15)
PGM	100	0.922	0.868
	-177	0.078	0.132
	(n)	(924)	(19)

between the two forms. Furthermore, the presence of these two pregnant females suggests that the dark pelvic form is a distinct species actively and selectively breeding in Australian waters, rather than a stray immigrant from a distant population.

Samples of known *C. limbatus* from the West Indies (the type locality of this species) and from South Africa were obtained for comparison with the normal and dark pelvic forms from Australia. Twelve loci were scored in these known *C. limbatus* samples. All specimens from the West Indies and South Africa expressed only the *114 allele at PEP-S. Because this allele was never observed in the normal form in Australia (963 fish screened) but was the predominant allele in the dark pelvic form, the dark pelvic form is almost certainly *C. limbatus*. The fact that the specimens from the West Indies expressed only the *-86 allele of GPI, an allele that was common in the dark pelvic form but completely absent in the normal form in Australia (856 individuals screened), establishes the dark pelvic form as the true *C. limbatus* beyond any doubt. The South African specimens were unscorable for this locus; presumably because they had been dead in the nets for some time before tissue collection and this relatively unstable enzyme had broken down. All specimens examined (dark pelvic and normal forms from Australia as well as the reference *C. limbatus* from the West Indies and South Africa) expressed the same invariant patterns at the other ten loci screened in all samples: EST-1, EST-2, EST-4, MEP-1, MEP-2, MPI, PNP, SOD-1, SOD-2, and XDH. Because several of these loci are fixed for different alleles in Australian *C. limbatus* compared to other carcharhinid species (Lavery, unpublished data), they were screened to provide additional evidence that the specimens from the West Indies and South Africa were actually *C. limbatus*.

Discussion

The existence of nearly fixed allelic differences in two loci between the two sympatric forms of *C. limbatus* in Australian waters is clear evidence that reproductive isolation occurs between the forms. Therefore they must be considered two distinct species. The further evidence that known *C. limbatus* from the West Indies (the origin of the holotype for *C. limbatus*) and South Africa share the same alleles for these two definitive loci with the Australian dark pelvic form shows that this form is the true *C. limbatus*, while the normal *C. limbatus* from Australian waters is, in fact, a previously unrecognised species, named *C. tilstoni* by Stevens and Wiley (1986).

It would seem that *C. tilstoni* has a relatively restricted distribution, based on previous records of vertebral counts. In Garrick's (1982) revision of the genus, it is clear that the total vertebral counts in *C. limbatus* exhibit a distinct non-overlapping bimodal distribution corresponding to the two ranges reported for *C. tilstoni* and *C. limbatus* by Stevens and Wiley (1986). Of 125 specimens which Garrick analysed from around the world, only 6 specimens fall into the range for *C. tilstoni*. These specimens came from Australia, Java, Borneo, the Gulf of Thailand and Hong Kong (Garrick 1982).

Although these two forms of carcharhinid shark should be recognised as separate species,

it is clear that they are very closely related. Apart from being morphologically almost indistinguishable, their genetic similarity is high for distinct species (cf. Solç-Cava *et al.* 1983). The Nei's D value of 0.045 suggests that these two species have undergone a relatively recent evolutionary divergence (ca. 200 000 years using Nei's 1987 calculations). On the other hand, it has been found in other genetic studies on sharks (Smith 1986; MacDonald 1988; Lavery and Shaklee 1989) that this group generally exhibits low levels of genetic variation. Such apparent genetic conservatism and the known morphological conservatism of sharks may suggest a much earlier divergence of the two species.

The separation of *C. limbatus* and *C. tilstoni* exemplifies the complex taxonomy and phylogeny of the genus *Carcharhinus*. A study currently in progress aims to examine the phylogenetic relationships among all the carcharhinid sharks found in northern Australia using allozyme electrophoresis (Lavery, unpublished data).

Major fisheries can impact, and even be directed at, species other than those presumed to be the targets of exploitation. In the present case, a major fishery (up to 8000 tonnes harvested per year) existed for several years in the territorial waters of northern Australia exploiting what was thought to be a single species, *Carcharhinus limbatus* (plus a second recognised target species, *C. sorrah*). It is now clear that two species (*C. limbatus* and *C. tilstoni*) were being exploited and that the latter, in fact, supported the fishery since it apparently accounted for over 90% of the harvest.

This study emphasises that our understanding of even major fisheries is often inadequate; not only with regard to possible contributions by multiple genetic stocks but fundamental taxonomic identity of the target species as well. Electrophoretic investigations can provide considerable insight, concerning both stock-specific contributions in mixed-stock fisheries (Shaklee *et al.* 1990) and the basic species status of the organisms harvested. Because effective long-term fisheries management is not possible unless the fundamental reproductive units (stocks and species) are identified and characterised, we strongly recommend that careful electrophoretic assessments of species subjected to substantial fisheries be conducted to provide or substantiate this critical information.

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Population Genetics of Two Tropical Sharks, *Carcharhinus tilstoni* and *C. sorrah*, in Northern Australia

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Abstract

The genetic structure of the Australian populations of *Carcharhinus tilstoni* and *C. sorrah* was investigated by starch gel electrophoresis. Tissue samples were taken from 1580 sharks from throughout the fishery, which extends from the North-West Shelf (off Western Australia) to the north-eastern coast of Queensland. From a total of 47 enzyme loci screened in each species, 13 proved to be polymorphic ($P_{0.99}$) for at least one species, with only 5 loci for each species showing sufficient variation ($P_{0.95}$) to be of use in the analysis of population structure. Mean heterozygosity values were relatively low: 0.037 for *C. tilstoni* and 0.035 for *C. sorrah*. A low level of population subdivision was found within each species, with F_{ST} values of 0.0094 for *C. tilstoni* and 0.0076 for *C. sorrah*. There was insufficient evidence to suggest that there is more than one population of either species of shark in Australian waters.

Introduction

A Taiwanese gill-net fishery has harvested significant pelagic fish resources off the coast of northern Australia since the early 1970s. Before being restricted to offshore areas by the declaration of the Australian Fishing Zone in 1979, the Taiwanese were catching as much as 17 000 tonnes in one year in this fishery (Walter 1981). Approximately 80% of this catch was composed of sharks. The two species examined in this study, *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes in Müller and Henle), represent about 58% and 25%, respectively, of the shark catch by number (Stevens and Wiley 1986). In recent years, Australian fishermen have become increasingly interested in the tropical shark resource. There are indications that tropical sharks could become the basis of an important fishery in inshore waters of northern Australia (Lyle and Timms 1984).

Management of such a fishery requires some knowledge of the population structure of the species, including the possible existence of genetically distinct subpopulations (MacLean and Evans 1981; Allendorf *et al.* 1987). For example, in this shark fishery it would be of considerable interest to determine whether the sharks taken by the Taiwanese in the offshore regions are from the same population fished close inshore by the Australians. As the geographical range of these sharks includes waters controlled by the State Fisheries of Queensland, Northern Territory and Western Australia, it is important to know whether they are managing separate populations or should be co-operatively managing one population.

The management problems of a shark fishery differ in some respects from those of other species. Sharks generally appear to grow very slowly and to be long-lived (Grant *et al.* 1979; Gruber 1981). Heavy fishing pressure may therefore severely affect a population. Furthermore, as very little research on the population structure of sharks has been undertaken anywhere, little is known about population subdivision in these primitive fishes.

There is some indication from the biology of the two species in this study that their populations could have subdivisions. Both species of shark exhibit placental viviparity (Stevens and Wiley 1986). Thus, there is no planktonic stage of the life cycle to facilitate substantial dispersal and mixing of the entire population. On the other hand, the adults of both species are strong swimmers and could cover long distances [cf. Olsen 1954].

Carcharhinus tilstoni was regarded as a synonym for the world-wide species *C. limbatus* (Garrick 1982) until electrophoretic analysis of protein variation revealed that '*C. limbatus*' in Australian waters actually comprises two very similar, but distinct, sympatric species (Lavery and Shaklee, unpublished data). The species dominating the Australian catch (by approximately 300 to 1) has proved to be a currently unrecognized, although previously named species—*C. tilstoni* (Whitley 1950; Lyle 1986; Stevens and Wiley 1986). It is not known whether this species occurs beyond Australian waters; however, *C. sorrah* is found throughout the Indian and western Pacific Oceans.

Electrophoretic analysis of genetically determined protein variation has been used to define the population structure of many commercial fish species (for reviews see Berst and Simon 1981; Shaklee 1983), but there have been very few electrophoretic studies of elasmobranch general proteins (Peterson and Smith 1969; Peterson 1970; Fyhn and Sullivan 1975; Benz 1980) or specific enzymes (Solé-Cava *et al.* 1983; Al-Hassan 1985; Smith 1986; MacDonald 1988). This study used electrophoretic protein variation to examine possible population differentiation within both *C. tilstoni* and *C. sorrah* in Australian waters. Because this is one of the first major electrophoretic studies of the population structure of elasmobranchs, the electrophoretic results are described in some detail.

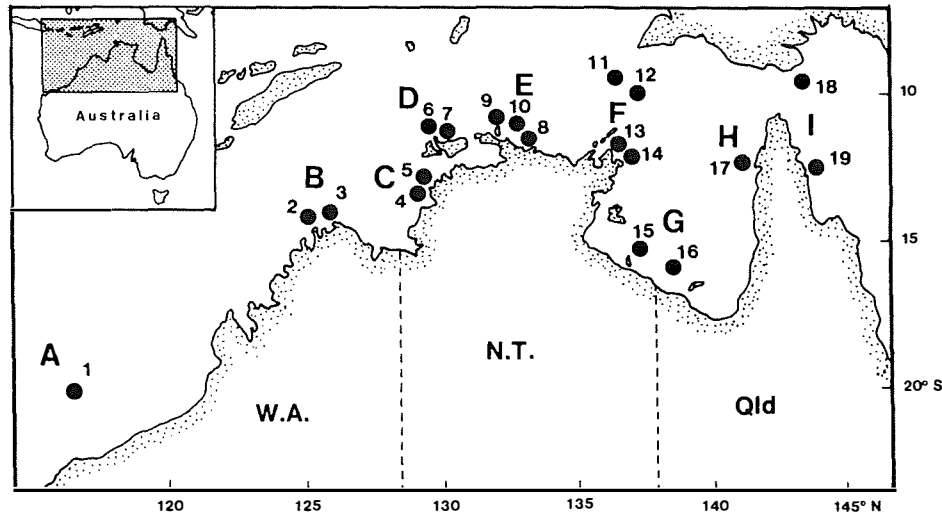


Fig. 1. Collection sites for *Carcharhinus tilstoni* and *C. sorrah*; see Table 1 for details.

Materials and Methods

Sample Collection

Tissue samples for electrophoresis were taken from sharks caught between 1982 and 1985 in locations ranging from the North-West Shelf (off Western Australia) to the north-eastern coast of Queensland (Fig. 1). The bulk of the samples came from gillnet, longline and handline catches of the fishing vessel *Rachel* during the Northern Pelagic Fish Stock Research Program. Additional samples came from gillnet catches of Northern Territory Fisheries Service cruises, the Commonwealth Department of Primary Industry 'Observer' program, and from the private vessel *Kiama*. Samples were collected from 925 *C. tilstoni* (comprising 14 collections) and 655 *C. sorrah* (15 collections), details of which appear in Table 1. The collections were grouped into the geographic areas (A–I) shown in Fig. 1.

Table 1. Details of sharks, *Carcharhinus tilstoni* and *C. sorrah*, collected off northern Australia

Area	Collection	Date	<i>C. tilstoni</i>			<i>C. sorrah</i>		
			Total	Sex ratio ^A (m : f)	Mean fork length ^A (cm)	Total	Sex ratio ^A (m : f)	Mean fork length ^A (cm)
A North-West Shelf	1	Oct. 83	—	—	—	19	2 : 17	91·2
B Timor Sea	2	May 84	51	41 : 10	85·1	16	15 : 1	72·3
	3	Sept. 84	—	—	—	41	22 : 17	72·9
C Fog Bay	4	Sept. 84	41	20 : 16	64·6	43	22 : 18	72·5
	5	June 85	72	12 : 14	57·6	72	12 : 4	65·2
D Melville I.	6	Oct. 83	—	—	—	26	10 : 15	77·5
	7	Apr. 84	101	62 : 34	81·8	39	21 : 18	78·2
E Croker I.	8	Aug. 83	19	4 : 15	95·0	—	—	—
	9	Jan. 84	107	29 : 28	90·7	66	22 : 26	77·7
	10	Mar. 84	—	—	—	48	27 : 20	72·1
F Wessel Is (offshore)	11	Nov. 82	76	35 : 29	109·6	32	14 : 15	73·0
(inshore)	12	Feb. 85	70	58 : 12	78·0	—	—	—
	13	Feb. 84	—	—	—	50	5 : 8	79·8
	14	Mar. 84	100	59 : 40	86·5	53	33 : 14	75·0
G Southern Gulf	15	June 84	32	18 : 14	87·6	—	—	—
	16	July 84	64	31 : 25	82·9	56	11 : 10	76·7
H Eastern Gulf	17	July 84	54	37 : 11	81·0	39	19 : 16	80·0
I North-eastern Queensland	18	Apr. 85	22	11 : 11	90·6	—	—	—
	19	Apr. 85	116	55 : 59	84·9	55	21 : 16	80·3

^A Data on sex and length were not available for all individuals.

Electrophoresis

Tissue samples were frozen at -20°C immediately after dissection, and transported and stored at this temperature until extracts were prepared in the laboratory. The extracts were stored at -70°C until electrophoresis. Techniques of tissue preparation, horizontal starch gel electrophoresis and enzyme-specific histochemical staining largely followed those of Shaklee and Salini (1985) and Shaklee and Keenan (1986). Adequate resolution was not obtained for many enzymes. The high frequency of smeary staining or considerable sub-banding in many of the shark enzymes (despite considerable variations of the standard techniques) was in sharp contrast to the clear isozyme patterns obtained from several species of teleostean fishes examined in our laboratory.

Only the patterns of enzyme variation that were consistent with the subunit structure of the enzyme (where known) and simple models of Mendelian inheritance were scored and recorded as genotypes. Names of enzymes and Enzyme Commission numbers follow the recommendations of the IUB Nomenclature Committee (Anon. 1984), and enzyme abbreviations were derived from these recommended names. Locus designations for multi-locus enzyme systems and allelic designations follow Shaklee and Salini (1985).

Statistical Analyses

Genotype frequencies were tested (by χ^2 goodness-of-fit tests) for conformity to Hardy-Weinberg expectations of the genetic model for each locus. Contingency table analyses by the likelihood-ratio (G) statistic were used to partition effects into within-area and between-area components. The within-area components test the homogeneity of gene frequencies between collections taken at different times as well as at different localities. For all these analyses, rare alleles were pooled, when necessary, with those of closest relative electrophoretic mobility to avoid excessively low expected frequencies. In order to detect any possible cline in allele frequencies (e.g. Richardson 1983) a test for linear trend across areas was

Table 2. Enzyme loci surveyed and their level of polymorphism in *Carcharhinus tilstoni* and *C. sorrah*

Enzyme	EC number	Locus	Level of polymorphism ^A	
			<i>C. tilstoni</i>	<i>C. sorrah</i>
<i>N</i> -Acetyl- β -glucosaminidase	3.2.1.30	<i>bAga</i>	1.000	1.000
Acid phosphatase	3.1.3.2	<i>Acp</i>	1.000	1.000
Aconitate hydratase	4.2.1.3	<i>Ah</i>	0.496	0.986
Adenylate kinase	2.7.4.3	<i>Ak</i>	0.999	0.998
Alanine aminotransferase	2.6.1.2	<i>Alat</i>	1.000	1.000
Alcohol dehydrogenase	1.1.1.1	<i>Adh</i>	1.000	1.000
Aspartate aminotransferase	2.6.1.2	<i>Aat</i>	1.000	1.000
Creatine kinase	2.7.3.2	<i>Ck-A</i> ^B	0.935	0.998
		<i>Ck-C</i>	1.000	1.000
Cytosol aminopeptidase (Pep-S ^C)	3.4.11.1	<i>Capep</i>	0.999	0.694
Dihydroliipoamide dehydrogenase	1.8.1.4	<i>Dia</i>	1.000	1.000
Enolase	4.2.1.11	<i>Eno</i>	0.999	1.000
Esterase	3.1.1.-	<i>Est-1</i>	0.865	0.887
		<i>Est-2</i>	1.000	1.000
		<i>Est-4</i>	1.000	1.000
		<i>Est-D</i>	0.976	0.562
Esterase-D	3.1.1.-	<i>Est-D</i>	0.976	0.562
Fructose-bisphosphate aldolase	4.1.2.13	<i>Fbald</i>	1.000	1.000
Fumarate hydratase	4.2.1.2	<i>Fh</i>	0.636	1.000
β -Galactosidase	3.2.1.23	<i>bGal</i>	1.000	1.000
Glucose-6-phosphate isomerase	5.3.1.9	<i>Gpi-B</i> ^D	0.996	0.978
Glutamate dehydrogenase	1.4.1.2	<i>Gdh</i>	1.000	1.000
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	<i>Gapdh-1</i>	1.000	1.000
		<i>Gapdh-2</i>	1.000	1.000
Glycerol-3-phosphate dehydrogenase	1.1.1.8	<i>G3pdh</i>	1.000	0.999
Hydroxyacylglutathione hydrolase	3.1.2.6	<i>Hagh</i>	1.000	1.000
L-Iditol dehydrogenase	1.1.1.14	<i>Iddh</i>	1.000	1.000
Isocitrate dehydrogenase (NADP ⁺)	1.1.1.42	<i>Idh</i>	1.000	1.000
L-Lactate dehydrogenase	1.1.1.27	<i>Ldh-A</i> ^E	1.000	1.000
		<i>Ldh-B</i>	0.999	1.000
Lactoylglutathione lyase	4.4.1.5	<i>Lgl</i>	1.000	1.000
Malate dehydrogenase	1.1.1.37	<i>Mdh-2</i>	0.998	0.985
		<i>Mdh-3</i>	0.986	0.998
Malate dehydrogenase (NADP ⁺)	1.1.1.40	<i>Mdhp-2</i>	0.997	0.846
Mannose-6-phosphate isomerase	5.3.1.8	<i>Mpi</i>	1.000	1.000
α -Mannosidase	3.2.1.24	<i>aMan</i>	1.000	1.000
Octanol dehydrogenase	1.1.1.73	<i>Odh</i>	0.986	0.999
Peptidase-C	3.4.-.-	<i>Pep-C</i> ^C	1.000	1.000
Peptidase-E	3.4.-.-	<i>Pep-E</i> ^C	1.000	1.000
Phosphoglucomutase	5.4.2.2	<i>Pgm</i>	0.922	0.999
Phosphoglycerate kinase	2.7.2.3	<i>Pgk</i>	1.000	1.000
Proline dipeptidase (Pep-D ^C)	3.4.13.9	<i>Pdpep</i>	0.973	0.896
Purine-nucleoside phosphorylase	2.4.2.1	<i>Pnp</i>	1.000	1.000
Pyruvate kinase	2.7.1.40	<i>Pk</i>	1.000	1.000
		<i>Sod-1</i>	1.000	1.000
Superoxide dismutase	1.15.1.1	<i>Sod-2</i>	0.997	1.000
		<i>Tapep</i>	1.000	1.000
Tripeptide aminopeptidase (Pep-B ^C)	3.4.11.4	<i>Tapep</i>	1.000	1.000
Xanthine dehydrogenase	1.1.1.204	<i>Xdh</i>	1.000	1.000

^A Frequency of most common allele.^B Presumed homology with *Ck* loci of other vertebrates based on relative mobility and tissue specificity (Fisher and Whitt 1978).^C Presumed homology with peptidase loci of other fishes and vertebrates based on substrate specificity (Frick 1983). Substrates employed: *Capep*, leucyl-tyrosine; *Pep-C*, prolyl-leucine; *Pep-E*, tri-phenyl-alanine; *Pdpep*, leucyl-proline; *Tapep*, leucyl-glycyl-glycine.^D Presumed homology with *Gpi* loci of other vertebrates based on tissue specificity (Fisher *et al.* 1980).^E Presumed homology with *Ldh* loci of other vertebrates based on relative mobility and tissue specificity (Markert *et al.* 1975).

performed. This is a χ^2 test with one degree of freedom, equivalent to testing the slope of a simple linear regression, where the dependent variable is the allele frequency (Cochran 1954).

The degree of genetic heterogeneity was described with Wright's F statistics (Wright 1965, 1978; Nei 1977) at both a hierarchical and a non-hierarchical level. The simple formula for the fixation index is $F_{ST} = s^2/p(1-p)$, where s^2 is the estimated variance of allelic frequencies between areas and p is the frequency of the most common allele averaged over areas. F_{ST} values were tested for significance by the method of Workman and Niswander (1970), i.e. $\chi^2 = 2NF_{ST}$ with appropriate degrees of freedom. Rogers' measure of genetic distance (modified by Wright 1978), calculated from all polymorphic ($P_{0.99}$) loci, was used to compare sharks from different areas, and Sneath and Sokal's (1973) UPGMA clustering method was used to construct dendrograms.

For age-class comparisons (mature v. immature), sharks were considered to be mature if their fork length was greater than the average minimum fork length of mature sharks, as determined by Stevens and Wiley (1986) (i.e. 84 cm for *C. tilstoni* and 71 cm for *C. sorrah*).

The BIOSYS-1 statistical package of Swofford and Selander (1981) was used extensively. Statistical significance throughout is indicated by * for $P < 0.05$, ** for $P < 0.01$ and *** for $P < 0.001$.

Table 3. Characteristics and conditions for analysis of polymorphic enzymes from *Carcharhinus tilstoni* and *C. sorrah*
Frequency of most common allele < 0.99

Locus	Subunit structure	Tissue	Buffer ^A
<i>Ah</i>	monomer	liver	CAAPM
<i>Capep</i>	hexamer	liver	LiOH
<i>Ck-A</i>	dimer	muscle	CAAPM
<i>Est-1</i>	monomer	liver	LiOH
<i>Est-D</i>	dimer	muscle	EBT
<i>Fh</i>	tetramer	liver	TRIC
<i>Gpi</i>	dimer	muscle	CAAPM
<i>Mdh-2</i>	dimer	muscle	TRIC
<i>Mdh-3</i>	dimer	muscle	TRIC
<i>MdhP-2</i>	tetramer	muscle	TRIC
<i>Odh</i>	dimer	liver	Poulik
<i>Pdpep</i>	dimer	muscle	TRIC
<i>Pgm</i>	monomer	muscle	CAAPM

^A CAAPM: citric acid—aminopropylmorpholine pH 6.0 (Clayton and Tretiak 1972) LiOH: lithium hydroxide—boric acid; modified buffer 2 of Selander *et al.* (1971) EBT: EDTA—boric acid—tris pH 8.6 (Boyer *et al.* 1963) TRIC: triethanolamine—citric acid pH 7.2 (Clayton and Tretiak 1972) Poulik: sodium hydroxide—boric acid pH 8.7; buffer 3 of Selander *et al.* (1971) (detailed buffer recipes can be found in Shaklee and Keenan 1986).

Results

Electrophoresis

Initial electrophoretic analysis involved the use of 76 enzyme stains on extracts from six tissues, with up to 14 electrophoretic buffers. Enzymes showing uninterpretable, weak or no staining for at least 50 animals from three or more collections were eliminated from further analysis, together with tissues (eye, kidney and blood) that did not contribute additional information. The optimum tissue—enzyme—buffer combinations were then used to score the genotypes of individuals. All enzymes that were monomorphic or exhibited rare variation (Table 2) were scored for approximately 50 or more fish from each area (A–I) of Fig. 1. All individuals of a species were screened for all polymorphic enzyme loci (Table 3).

Examples of isozyme banding patterns and genotype scoring are presented in Fig. 2. Two enzymes, AH and EST-1, exhibited greatly reduced activity or partial breakdown in some collections, resulting in a relatively high proportion of unscorable individuals in these collections. As this could bias results (see Shaklee 1983), data for that locus for that particular collection were omitted from the statistical analyses.

Additional evidence of a genetic basis for the observed electrophoretic variation was collected for some loci. Inheritance data (genotype ratios) from family groups (pregnant females plus litters of pups) gave clear support to the genetic interpretation of the observed variation in the enzyme loci: creatine kinase-A (*Ck-A*), phosphoglucosmutase (*Pgm*), umbelliferyl esterase (*Est-D*), NADP⁺-dependent malate dehydrogenase (*MdhP*) and cytosolic aminopeptidase (*Ca pep*) (Lavery, unpublished data). Sufficient data were not available for the less polymorphic loci.

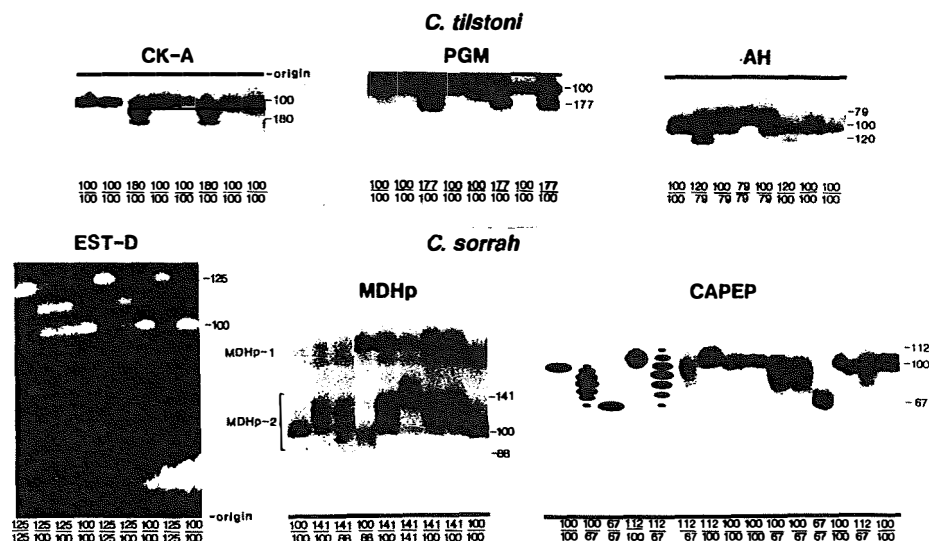


Fig. 2. Isozyme banding patterns for six polymorphic enzyme systems—three in *C. tilstoni* and three in *C. sorrah*.

Polyacrylamide gel electrophoresis was used to search for polymorphic general proteins in all tissues. All proteins visualized with the non-specific protein stains appeared as monomorphic bands, except for two proteins in heart tissue of *C. sorrah*. One slowly migrating (anodal) protein exhibited a low level of tetrameric variation (heterozygosity, $H < 0.01$) with three alleles, and a fast-migrating (anodal) protein exhibited a much higher level of monomeric variation with two alleles ($H = 0.22$). Unfortunately, the latter locus could not be resolved adequately in the majority of collections and had to be omitted from the calculations. No general protein loci were included in any statistical analyses.

Mean heterozygosity (H) was 0.037 for *C. tilstoni* and 0.035 for *C. sorrah*. Allele frequencies were calculated for all polymorphic loci for each collection and each area. As some collections had relatively few samples, only loci polymorphic at the 0.95 level (frequency of the most common allele less than 0.95) were included in the statistical analyses of population differentiation. The allele frequencies for these loci appear in Tables 4 and 5.

Population Structure

C. tilstoni

Both *Ah* and *Est-1* in two collections and *Ck-A* in one collection deviated significantly

Table 4. *C. tilstoni* allele frequencies for five polymorphic loci

Alleles are identified by the relative electrophoretic mobilities of the homomeric isozymes they encode compared with that of the most common allele (100) at each locus. Rare alleles were pooled with alleles of closest relative mobility. For all loci except *Ah*, there were two allele classes. Only the frequency of most common allele class (100) is given for these loci. The following are the allelic compositions of the allele classes for each locus. *Ah*: 100; 120+ = 120, 142, 168; 79+ = 79, 47. *Ck-A*: 100; 180+ = 180, 400. *Est-1*: 100; 105. *Fh*: 100; 80. *Pgm*: 100; 180. Asterisks indicate the degree of deviation of genotype frequencies from Hardy-Weinberg expectations within that collection (χ^2 probability: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). +, heterozygote excess; -, heterozygote deficiency

Area/ Collection	N	Locus and alleles						
		100	<i>Ah</i> 120+	79+	<i>Ck-A</i> 100	<i>Est-1</i> 100	<i>Fh</i> 100	<i>Pgm</i> 100
B 2	51	—	—	—	0.957	0.915	0.692	0.897
C	113	0.505	0.240	0.255	0.916	0.886	0.641	0.907
4	41	0.536	0.214	0.250	0.866	0.882	0.632	0.963
5	72	0.493	0.250	0.257	0.944	0.889	0.646	0.875
D 7	101	0.458	0.239	0.303	0.922(*-)	0.851(*-)	0.628	0.960
E	126	0.504	0.230	0.266	0.921	0.872	0.665	0.948
8	19	0.500	0.263	0.237	0.921	0.789	0.735	0.895
9	107	0.505	0.223	0.272	0.921	0.887	0.654	0.958
F	246	0.477	0.182	0.341(*-)	0.957	0.856(*-)	0.645	0.919
11	76	0.526	0.026	0.447	0.941	0.950	0.625	0.936
12	70	—	—	—	0.964	0.850	0.643	0.921
14	100	0.456	0.228	0.316(*-)	0.965	0.843(***-)	0.649	0.908
G	96	0.570	0.273	0.156	0.947	0.856	0.633	0.926
15	32	—	—	—	0.906	0.828	0.556	0.922
16	64	0.570	0.273	0.156	0.968	0.871	0.667	0.929
H 17	54	0.510	0.240	0.250	0.870	0.806	0.532	0.926
I	138	0.465	0.213	0.322(**+)	0.942	0.873	0.622	0.894
18	22	0.333	0.310	0.357	0.955	0.955	0.591	0.909
19	116	0.491	0.194	0.315(**+)	0.939	0.858	0.628	0.891

from Hardy-Weinberg equilibrium (Table 4). In *Ck-A*, this was primarily due to a small expected genotype frequency (< 1) where further pooling of alleles was not possible. These significant results represented 7.5% of the 67 comparisons made, and were also reflected in the tests for each area.

Likelihood-ratio (G) tests of allele frequencies were conducted to examine the pattern of variation within and between areas (Table 6). Comparisons of allele frequencies between all collections were significant for *Ck-A*, *Ah* and over all loci. When this variation was partitioned into between-area and within-area components, only *Ck-A* showed significant heterogeneity between all areas, while only *Ah* exhibited significant differences between collections within all areas. Standardized statistics (G divided by degrees of freedom) were calculated for these two components of genetic variation. Comparison of the values for between-area variation (1.51) and within-area variation (1.47) suggested that allele frequency differences between areas were not significantly greater than within areas. The pattern of within-area heterogeneity indicates that the *Ah* differences were found only in the two collections from the Wessel Islands (Fig. 1, area F). One of these collections (14) also had a significant deviation from Hardy-Weinberg equilibrium for *Ah*. No other tests, either overall or for individual loci, gave a significant result for this comparison between inshore and offshore locations in the Wessel Islands area. The two collections from Fog Bay (4 and 5) had significant allele frequency differences for two loci: *Ck-A* and *Pgm*.

Heterogeneity between areas was examined in more detail by comparing adjacent, paired areas. This was done to identify the location of possible discontinuities in allele frequencies.

Table 5. *C. sorrah* allele frequencies

Alleles are identified by the relative electrophoretic mobilities of the homomeric isozymes they encode compared with that of the most common allele (100) at each locus. Rare alleles were pooled with alleles of closest relative mobility. *Capep*: 100+ = 100, 112; 67. *Est-1*: 100; 108. *Est-D*: 100+ = 100, 72; 125+ = 125, 115. *MdhP-2*: 100+ = 100, 83; 141+ = 141, 118. *Pdpep*: 100+ = 100, 80; 117+ = 117, 157, 145, 122, 108. Asterisks indicate the degree of deviation of genotype frequencies from Hardy-Weinberg expectations within that collection (χ^2 probability: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). +, heterozygote excess; -, heterozygote deficiency

Area/ Collection	N	Locus and alleles				
		<i>Capep</i> 100+	<i>Est-1</i> 100	<i>Est-D</i> 100+	<i>MdhP-2</i> 100+	<i>Pdpep</i> 100+
A 1	19	0.711	0.789	0.474(+)	0.868	0.895
B	57	0.705	0.892(***-)	0.509	0.851	0.918(*-)
2	16	0.733	1.000	0.594	0.781	0.967
3	41	0.695	0.859(**-)	0.476	0.878	0.900(*-)
C	115	0.670	0.915	0.617	0.826	0.861
4	43	0.663(*-)	0.927(*-)	0.616	0.837	0.884
5	72	0.674(+)	0.908	0.618	0.820	0.847
D	65	0.715	0.897(***-)	0.600	0.846	0.885
6	26	0.769	0.942(***-)	0.635	0.884	0.846
7	39	0.679	0.865(*-)	0.577	0.821	0.910
E	114	0.693	0.923	0.544	0.864	0.889
9	66	0.705	0.923	0.568	0.849	0.908
10	48	0.677	-	0.510	0.885	0.865
F	135	0.692	0.891(***-)	0.559	0.860	0.940
11	32	0.617	0.941	0.594	0.891	0.969
13	50	0.700	0.870(**-)	0.540	0.850	0.959
14	53	0.726	0.896(***-)	0.557	0.849	0.906
G 16	56	0.727	0.861(***-)	0.618	0.873	0.900
H 17	39	0.713	0.863	0.610	0.914	0.878
I 19	55	0.657	0.843	0.491	0.855	0.882

Seven of these paired comparisons, from a total of 39 tests (18%), proved significant. The area contributing most to the differences in allele frequency was the north-eastern Gulf of Carpentaria (Fig. 1, area H). This area was different from all adjacent areas (F, G and I) for *Ck-A*, as well as over all loci, and different from the Wessel Islands collections (area F) for *Fh*. Other significant differences occurred between Fog Bay (area C) and Melville Island (area D) for *Pgm*, and Croker Island (area E) and Wessel Islands (area F) for *Ck-A*. Comparison of Wessel Islands (area F) and the southern Gulf (area G) proved significant for *Ah*; however, this is again associated with collection 14, which was out of Hardy-Weinberg equilibrium. For all other loci in this comparison, χ^2 values were very small and non-significant. None of the five loci exhibited a significant linear trend (cline) of allele frequencies across areas (Table 6). There was also no significant correlation between the genetic distance and minimum geographic distance separating areas.

In an attempt to isolate the observed frequency differences between areas into differences between larger regions, adjacent areas not exhibiting significant heterogeneity were pooled. This resulted in the following five regional groups: (B + C), (D + E), (F + G), (H) and (I) (refer to Fig. 1). For this purpose, the difference at *Ah* between areas F and G was not considered. This grouping was substantially supported by the clustering of areas based on their genetic distances averaged over all polymorphic loci (Fig. 3). The dendrogram also indicated that the north-eastern Gulf of Carpentaria (area H) was the most dissimilar area. Overall heterogeneity between the five regions was significant for *Ck-A* ($G = 13.44^{**}$, 4 d.f.) and *Pgm* ($G = 10.87^*$, 4 d.f.), and over all loci ($G = 40.35^*$, 24 d.f.), and was

Table 6. Tests of allele frequency heterogeneity in *C. tibroni*
* $P < 0.05$; ** $P < 0.01$

	d.f.	Ah	d.f.	Ck-A	d.f.	Est-I	d.f.	Fh	d.f.	Pgm	d.f.	Total
G statistics:												
Between areas	12	19.76	7	14.69*	7	7.02	7	6.67	7	12.06	7	60.20*
B-C	—	—	1	2.13	1	0.59	1	0.68	1	0.10	1	3.50
C-D	2	1.07	1	0.05	1	1.13	1	0.07	1	5.00*	1	7.32
D-E	2	0.86	1	0.00	1	0.39	1	0.64	1	0.39	1	2.28
E-F	2	3.16	1	4.05*	1	0.30	1	0.27	1	2.14	1	9.92
F-G	2	14.64**	1	0.29	1	0.00	1	0.06	1	0.11	1	14.70*
F-H	2	3.03	1	9.90**	1	1.58	1	3.91*	1	0.06	1	18.48*
G-H	2	3.36	1	5.37*	1	1.28	1	2.63	1	0.00	1	12.64*
H-I	2	1.86	1	4.98*	1	2.72	1	2.35	1	0.89	1	12.80*
Within areas	8	15.63*	6	8.72	6	10.88	6	3.22	6	8.58	6	47.03*
C	2	0.37	1	4.01*	1	0.03	1	0.04	1	5.53*	1	9.98
E	2	0.37	1	0.00	1	2.44	1	0.90	1	2.13	1	5.84
F	2	9.10*	2	1.39	2	3.97	2	0.07	2	0.78	2	17.33
G	—	—	1	3.06	1	0.62	1	1.98	1	0.03	1	5.69
I	2	4.20	1	0.17	1	3.80	1	0.22	1	0.13	1	8.35
Total (between all collections)	20	35.39*	13	23.41*	13	17.90	13	9.89	13	20.64	13	107.23**
χ^2 test for linear trend	1	0.07	1	0.07	1	1.55	1	1.89	1	0.80	1	4.38
F_{ST} between areas:	6	0.008	7	0.011**	7	0.007	7	0.008	7	0.007	7	0.0094**

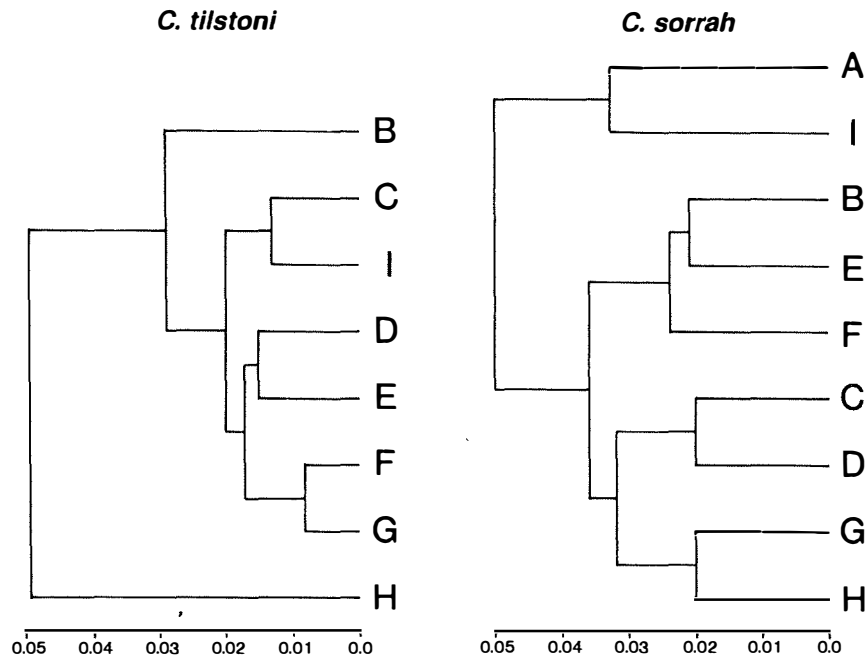


Fig. 3. Dendrograms showing results of cluster analysis of genetic distance between areas.

greatest between regions (B + C) and (D + E) (*Pgm*: $G = 7.69^{**}$, 1 d.f.), and between (F + G) and (H) (*Ck-A*: $G = 12.23^{***}$, 1 d.f.) (see Fig. 4).

Another method of analysing the variation in allele frequencies between collections is to employ Wright's F statistics (Wright 1978; Nei 1977). The fixation index, F_{ST} , estimates the degree of genetic differentiation between areas. F_{ST} values across the eight areas were calculated for all loci (Table 6). χ^2 tests of their difference from zero gave significant results for *Ck-A* and over all loci. These results are comparable with the results from the heterogeneity χ^2 tests. However, this sample F_{ST} formula takes no account of either the sample sizes or the variation between collections within areas. It is inappropriate to allow

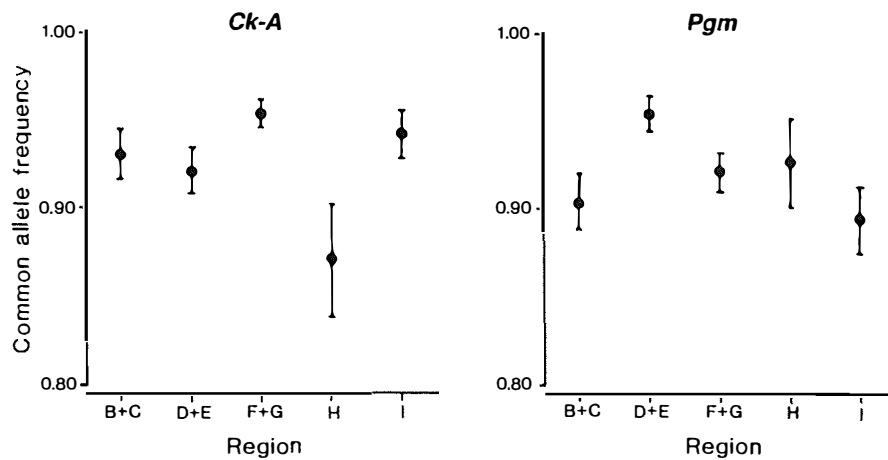


Fig. 4. *C. tilstoni* common allele frequencies for *Ck-A* and *Pgm* in each region (\pm binomial s.e.).

for sample sizes simply by weighting means and variances, as such weighting is intended for variation in population sizes – which is seldom known for fish species – as opposed to sample sizes (Nei 1977; Swofford and Selander 1981). Both sampling variances and within-area variation can be taken into consideration by Wright's application of hierarchical F statistics (Wright 1978). This method gives a series of F ratios that measure the proportion of the total genetic variation attributable to differentiation between the subpopulation units comprising each level of the hierarchy. The consideration of additional variance components in this analysis results in more conservative estimates of heterogeneity.

For the present analysis, collections were grouped into areas and then into regions in the same manner as in the contingency table analyses. The results indicated that very little of the genetic variance between collections in the total population ($F_{CT} = 0.006$) is due to between-area or between-region differences ($F_{AT} = 0.001$, $F_{RT} = 0.000$). Most of the variance between collections was due to differences within areas or regions ($F_{CA} = 0.005$, $F_{CR} = 0.006$). These results can also be expressed in terms of Nei's gene diversity (Nei 1977; Swofford and Selander 1981). Using his terminology, approximately 99.4% of all genetic variation exists within collections, while only 0.6% exists between collections, 0.1% between areas and a negligible proportion exists between regions.

Genetic variation was also examined for any effects of sex or age class. All collections with sufficient data on individual lengths and sexes were tested. Of 34 G -tests for allele frequency differences between sexes, only one (2.9%) was significant (*Est-1* in collection 19, $G = 12.20^{***}$, 1 d.f.). A test between all males and females was not significant. In a comparison of mature and immature fish, only 2 of 29 tests (6.9%) were significant. These were for *Ah* in collection 14 ($G = 7.08^*$, 2 d.f.) and *Fh* in collection 19 ($G = 6.25^*$, 1 d.f.). There was no difference between all immature and mature *C. tilstoni*.

Table 7. Tests of allele frequency heterogeneity in *C. sorrah*
* $P < 0.05$

	d.f.	<i>Capep</i>	<i>Est-1</i>	<i>Est-D</i>	<i>MdhP-2</i>	<i>Pdpep</i>	d.f.	Total
G statistics:								
Between areas	8	2.43	10.17	10.81	6.01	10.46	40	39.88
A-B	1	0.00	2.31	0.14	0.07	0.19	5	2.71
B-C	1	0.44	0.43	3.68	0.34	2.45	5	7.34
C-D	1	0.81	0.32	0.11	0.24	0.41	5	1.89
D-E	1	0.20	0.60	1.06	0.22	0.02	5	2.10
E-F	1	0.00	1.08	0.12	0.02	4.17*	5	5.39
F-G	1	0.47	0.63	1.12	0.12	1.80	5	4.14
F-H	1	0.13	0.46	0.66	1.87	1.44	5	4.56
G-H	1	0.05	0.00	0.01	0.85	0.23	5	1.14
H-I	1	0.64	0.14	2.69	1.66	0.01	5	5.14
Within areas	6	3.80	9.98	2.94	3.41	8.14	30	28.27
B	1	0.15	6.30*	1.29	1.60	1.52	5	10.86
C	1	0.03	0.23	0.00	0.12	0.61	5	0.99
D	1	1.25	2.11	0.43	1.01	1.23	5	6.03
E	1	0.20	0.32	0.75	0.66	1.03	5	2.96
F	2	2.17	1.49	0.46	0.36	3.75	10	8.23
Total (between all collections)	14	6.23	20.15	13.75	9.42	18.60	70	68.15
χ^2 test for linear trend between								
areas:	1	0.01	1.63	0.04	2.90	0.59	5	5.17
F_{ST} between areas:	8	0.002	0.014*	0.012*	0.005	0.006	40	0.0076

C. sorrah

Tests of Hardy–Weinberg equilibrium were calculated for each locus for each collection. Eleven tests (15%) gave significant deviations (Table 5). Genotype frequencies for two loci, *Pdpep* and *Est-D*, differed from the expected in only one collection each. However, these tests had low expected genotype frequencies (< 1) or a low total number of individuals ($n < 20$). *Capep* gave significant results in the two collections (4 and 5) from Fog Bay (area C). These departures from expected were, however, in opposite directions, indicating that they may simply be sampling artifacts. All other significant results occurred at *Est-I*, which had a deficiency of heterozygote genotypes for all but 1 of the 15 collections, with 7 of these being significant. In all the *Est-I* comparisons, however, the expected frequency of the alternate homozygote class was less than 1, which disproportionately increased the χ^2 values. Hardy–Weinberg tests were also performed on the pooled data for each area, where all genotype classes were sufficiently large. The only significant results here were for *Est-I*, in which there was a highly significant heterozygote deficiency in areas B, D, and F.

Results of likelihood ratio tests of allele frequencies appear in Table 7. There was no overall significant heterogeneity in frequencies between all collections. In the tests between collections within each area, only one significant difference was found (area B). Included in these tests was a comparison between an offshore collection and two inshore collections in the Wessel Islands area (area F). When collections within areas were pooled, there was again no significant genetic heterogeneity observed between areas. In the adjacent pairwise comparisons of areas for all polymorphic loci, only one test out of 45 was significant. This was the comparison between Croker Island (area E) and Wessel Islands (area F) for *Pdpep*. The North-West Shelf collection (area A) was relatively small (19 fish), which may have substantially reduced the level of significance of any differences with adjacent areas. When this collection was pooled with the adjacent ones from the Timor Sea (area B), a significant difference was found between this combined area and Fog Bay (area C) for *Est-D* ($G = 5.15^*$, 1 d.f.). All tests for a cline (linear trend) in allele frequencies across areas proved non-significant. There was also no significant correlation between the genetic distance and geographic distance separating areas.

Pairwise genetic distances were used to cluster all areas into groups based on overall genetic similarity. The dendrogram (Fig. 3) indicates that areas C to H, i.e. all but the most geographically remote areas, are genetically very similar to one another. Using these results and the significant differences found between pairs of adjacent areas, the areas could be grouped into larger regions of genetic similarity, viz. (A + B), (C + D + E), (F + G + H) and (I) to determine whether a large-scale pattern of heterogeneity exists. However, contingency table analysis of these pooled frequencies revealed no significant differences, either overall or for individual loci.

F_{ST} values (using the usual simplified formula) were calculated for all loci (see Table 7). The values for *Est-I* and *Est-D* were significantly different from zero. This is not in agreement with the contingency χ^2 values, but these F_{ST} values take no account of sample size. As with *C. tilstoni*, a hierarchical analysis of F statistics was performed to take into account sampling error and within-area variation. In the three-level hierarchical analysis, collections were grouped into areas and then into regions, in the same manner as in the contingency table analyses. As with *C. tilstoni*, the results for *C. sorrah* showed that most of the genetic variance between collections ($F_{CT} = 0.0030$) occurred within areas ($F_{CA} = 0.0028$), rather than between areas or regions ($F_{AT} = 0.0002$, $F_{RT} = 0.0001$). Expressed in terms of Nei's genetic diversity, approximately 99.70% of all genetic variation existed within collections, and 0.28% between collections, while only 0.02% was accounted for by both between-area and between-region genetic diversity.

There were no differences in allele frequencies between male and female *C. sorrah* within any individual collection, or over the total population. Comparisons between age classes (immature and mature) showed a similar homogeneity, with only one test significant (*Capep* in collection 10: $G = 6.55^{**}$, 1 d.f.) out of a total of 29 tests.

Discussion

The validity of any interpretations of genetic variation are dependent on two assumptions: firstly, that there is a genetic basis to the observed phenotypic variation; and secondly, that the subpopulations under consideration are randomly mating groups, with all alleles encountered following true Mendelian inheritance laws. Traditionally, these assumptions have been analysed by χ^2 tests of observed genotype frequencies to Hardy-Weinberg expectations. However, this χ^2 test has a low power to detect departures from the expected, particularly in sample sizes of less than 200 (Fairbairn and Roff 1980; Valenzuela 1985). As suggested by Fairbairn and Roff, it is important to try to reduce the type I error (the probability of accepting the null hypothesis of equilibrium, when in fact it is false). This has been attempted in this study by (1) using well-characterized protein systems with *a priori* genetic models of banding patterns, (2) independently testing Mendelian inheritance for the most polymorphic loci and (3) eliminating alternative hypotheses for observed phenotypic variation (e.g. relationships between isozyme phenotypes and age or sex, or secondary isozyme formation due to storage). Despite these precautions, and because of the lower power of the test, it is unwise to ignore significant deviations. Heterozygote deficiencies are often explained by hypothesizing a Wahlund effect, where more than one genetically distinct population may have been sampled in the one collection (e.g. Richardson 1982). However, this could only account for a small degree of deviation from the expected, equal to F_{ST} (Johnson *et al.* 1986). The alternative possibility—that such departures are associated with non-genetic variation—is often not even considered.

In the present study, several Hardy-Weinberg tests were significant. Some are undoubtedly statistical artifacts due to the number of tests performed, but many of the significant deviations occurred only in those enzymes subject to relatively rapid breakdown and loss of activity (AH and EST-1). Although all reasonable precautions were taken to prevent this from biasing allele frequency estimates, it is possible that loss of particular phenotypes occurred in some collections. For example, heterozygotes in general have weaker staining of each isozyme because the enzyme activity is dispersed over a larger number of isozymes. Thus, heterozygotes are more likely to be unscorable in samples having weak activity, and this may have resulted in the significant heterozygote deficiencies in these loci. Ultimately, this means that allele frequencies may be unreliable for the loci *Ah* and *Est-1* in the particular collections concerned.

The potential to identify discrete populations within each of the two species was hampered by the small size of some collections. These smaller samples had the effect of increasing the inherent sampling error in allele frequencies and also, as a consequence, reducing the number of polymorphic loci that could be confidently used to only those polymorphic at the 0.95 level. Relatively low levels of genetic variation exist in both species (*C. tilstoni*: $H = 0.037$; *C. sorrah*: $H = 0.035$), which ultimately means that only a few enzyme loci could be used to study population heterogeneity.

The degree of genetic differentiation between all collections was relatively small in both species. However, there are three major findings from the results. Firstly, there was no apparent difference between the genetic composition of inshore and offshore sharks, at least in the Wessel Islands area where this possibility was tested most rigorously. Secondly, there was no clear difference in allele frequencies between collections in any one area. That is, within each area considered in this study, allele frequencies were apparently stable over time or location of sampling. Thirdly, there was some degree of genetic heterogeneity between areas or regions for *C. tilstoni*. The locations of the most significant geographic discontinuities (apparent in Fig. 4) could be interpreted as indicating the existence of genetically differentiated populations in the western and eastern sections of the range of this species in Australian waters.

The biological significance of these results is, however, reduced by other factors. It is unwise to infer overall genetic differentiation between areas based on only one or two loci

from the species' entire genome. In this study, support from three or more of the polymorphic loci for any proposed sub-population boundaries would be far more conclusive. Further, the level of genetic variance between individual collections within areas or regions is comparable to the level of variance between areas or regions. That is, the differences between areas are not greater than those within areas. The statistical significance of between-area comparisons is primarily due to the increased sample sizes. Furthermore, although the genetic distances between areas give some indication of relative similarity, even the greatest distances are small ($D_{\text{ROGERS}} < 0.07$), particularly considering that only polymorphic loci were included in these calculations.

From the statistical results, the genetic variance between collections appears to have only a small component due to geographic isolation. Other biological factors may therefore be involved. These sharks have been found in age- and sex-specific aggregations (Lyle and Timms 1984); collections in this study show a bias towards one sex or age class (Table 1). Although the observed genetic heterogeneity between collections could conceivably be attributed to genetic differences between sexes or age classes, the results of statistical tests of this hypothesis do not support it.

In general, we found no compelling evidence that more than one genetically distinct population of either species of shark exists within Australian waters. Of course, a lack of detectable genetic differences between areas cannot prove that the population is not subdivided; however, the present analysis suggests that significant differentiation of populations is unlikely.

Evidently, there is sufficient interbreeding and/or mixing to provide gene flow between relatively widely separated areas. Estimates of migration can be calculated from the values of F_{ST} , the degree of subpopulation differentiation. The distribution of sharks along the northern Australian coast was considered most likely to resemble the linear stepping-stone model of migration (Kimura and Weiss 1964). This model states that

$$F_{ST} \approx 1/(4N\sqrt{2mu} + 1)$$

where N is the effective subpopulation size, m is the proportion of fish migrating into each subpopulation each generation and u is the electrophoretic mutation rate (10^{-7}). The model assumes that subpopulations are of equal size, migration is restricted to adjacent areas, and migration and genetic drift have reached equilibrium (Hartl 1980). The subpopulation sizes in each area can be roughly estimated at 1×10^6 to 1×10^7 for *C. tilstoni* and, proportionally, 7×10^5 to 7×10^6 for *C. sorrah* (based on previous total catch weights, average individual weights and estimates of exploitation rates). Using the previously determined values of F_{ST} gives estimates of migrants per generation of between 350 and 3500 for *C. tilstoni* and between 750 and 7500 for *C. sorrah*. These may be over-estimates, however, as the more conservative island model of migration (Wright 1978) would estimate the number of migrants to be much lower.

Although many assumptions and approximations are involved, the important finding is that the observed level of genetic heterogeneity may suggest considerable movement of individuals between areas. This is in contrast with many other marine species in which low levels of heterogeneity can be accounted for by the movement of only a few individuals, using the same model (e.g. Grant 1984, 1985). The difference is primarily due to the much smaller effective population sizes of the sharks relative to the other species of fishes studied.

Preliminary results of tag-recapture data lend support to the findings of this study (J. Stevens, personal communication). The tag-recapture results indicate that many individuals of both species move hundred of kilometres (up to 1000 km) between captures. *C. sorrah* apparently moves greater distances, on average, than *C. tilstoni*, which may explain *C. sorrah*'s lower level of genetic heterogeneity, and is consistent with the larger migration estimates obtained above. Although evidence for such large movements may appear to preclude any population differentiation, this need not necessarily be the case, as

demonstrated in skipjack tuna studies by Richardson (1983) and in population simulations by Allendorf and Phelps (1981).

We conclude that there is no genetic evidence to suggest that *C. tilstoni* and *C. sorrah* should not be managed as single populations within Australian waters. Furthermore, the data suggest that any impact of fishing on the abundance of tropical sharks in offshore grounds would also be felt in inshore areas and *vice versa*. However, as the unit populations have such a large geographic size, and individuals are very mobile, they may be well buffered to disturbance or perturbation. If, in the future, a high level of fishing pressure is exerted on this tropical shark resource, the total population size rather than the local population size is likely to be the limiting factor affecting production.

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Shark tagging

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Northern tagging project yields interesting results.

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Movements, recapture patterns and factors affecting the return rate of carcharhinid and sphyrnid sharks tagged off northern Australia

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Abstract

Between February 1983 and May 1985, some 10 500 sharks comprising 23 species were fin-tagged off northern Australia. Tagging concentrated on the commercially important carcharhinids *C. tilstoni* and *C. sorrah*. By May 1989, 481 tags (4.6%) had been recovered. Five years after the majority of sharks were tagged, the number of recaptures was minimal. Tag shedding was estimated to be low (0.05 yr^{-1} for *C. tilstoni*) and tagging mortality was significantly lower for sharks caught by handline than by gill-net. Australian gill-netters, Taiwanese gill-netters (fishing in the AFZ) and Australian prawn trawlers accounted for the majority of returns. The proportions in which the three main species were returned by these fisheries were different. Sharks moved distances of up to 1100 km, but the majority of returns were made within 50 km of the tagging site. Movements appeared to be random rather than seasonal and no difference was detected in distance travelled between the sexes. A size effect was detected, with immature *C. tilstoni* travelling greater distances than mature fish. Movement of sharks between inshore areas fished by Australian vessels and offshore areas fished by the Taiwanese appears to be low.

Introduction

Shark stocks off northern Australia were exploited commercially by a Taiwanese surface gill-net fishery from the early 1970s to 1986. Before declaration of the Australian Fishing Zone (AFZ) in 1979, the total annual catch of shark, tuna and spanish mackerel taken by this fishery from waters between northern Australia, Papua New Guinea and Indonesia was about 25000 tonnes live weight. In 1979, total catches from the AFZ were constrained by a quota of 7000 tonnes processed weight (about 10000 tonnes live weight), and the Taiwanese were excluded from inshore waters, the distance from shore varying from 22 to 74 km, depending on the area. A small Australian fishery (annual landings varying from about 100 to 400 tonnes), based on the same species, currently operates in inshore waters within about 22 km of the coast

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The principal shark species taken are *Carcharhinus tilstoni* (Whitley) and *Carcharhinus sorrah* (Valenciennes in Muller and Henle); some 20 additional species of mainly carcharhinid and sphyrnid shark occur in the catches.

Considerable research effort has been directed at these fisheries. The potential for Australian development was investigated by Millington and Walter (1981), Stevens *et al.* (1982), Lyle and Timms (1984), Lyle *et al.* (1984), Lyle (1987a) and Lyle and Griffin (1987). Marketing problems relating to shark were examined by Lyle (1984) and Welsford *et al.* (1984). The biology of many of the shark species was reported on by Stevens and Wiley (1986), Lyle (1987b), Stevens and Lyle (1989), and Stevens and McLoughlin (1991). In February 1983, a tagging study was started to help determine stock structure, movement patterns, growth and mortality rates of the principal shark species. Of particular interest to fisheries managers and to the local fleet was the extent of shark movements from inshore waters fished by Australian vessels into the offshore region fished (until recently) by the Taiwanese gill-netters. Some aspects of the tagging work have already been published. Davenport and Stevens (1988) reported on age and growth of *C. tilstoni* and *C. sorrah*. Preliminary results on shark movement determined from tagging (Stevens and Church 1984), together with a study of the population genetics of *C. tilstoni* and *C. sorrah*, led Lavery and Shaklee (1989) to conclude that there was only one population of either of these species in Australian waters, suggesting they should be managed as single stocks.

This paper reports on factors effecting the return rate of tags, and on the movements and recapture patterns of sharks derived from some 480 tag-recaptures made up until the end of May 1989 off northern Australia.

Materials and Methods

Capture method

Sharks were captured in a condition suitable for tagging by handlining with barbless hooks, making short sets with a gill-net and by longlining. Handlining followed attraction of the sharks to the boat by chumming with chopped fish, and was mainly carried out during the day. The surface-set gill-net consisted of 1000 m of 15 cm (stretched-mesh) monofilament which could be split and reduced to a 500 m length in areas where sharks were abundant. Gill-netting was carried out mainly at night. Hauling of the net usually commenced within 15 minutes of completing the set. Some sharks were caught in a net designed to study mesh selectivity which consisted of separate panels of 10, 15, 20 and 25 cm stretched mesh (Stevens and Church 1984). Surface set longlines employed either 60 hooks on 1 km of mainline or 300 hooks on 5 km of mainline. Snoods consisted of 1-2 m of 5 mm sink rope attached by a torpedo swivel to 1-2 m of 2 mm stainless steel wire trace. The main line was of 8 mm sink rope. Various hook types and sizes were used including 10/0 and 11/0 long shanked hooks and 9/0 and 10/0 Japanese tuna hooks. The barbs were not removed.

Tagging methods and release information

The majority of returns were expected from the Taiwanese fishery. Shark processing techniques on these vessels required the tag to be strikingly visible externally, as well as having the usual properties of good retention and minimal interference. The tags chosen were plastic cattle ear tags, Jumbo Rototags and Rototags (manufactured by Daltons of Henley-on-Thames, England). These tags compared favourably in evaluation studies carried out by Kato and Carvallo (1967) and Davies and Joubert (1967). They were used successfully in studies of blue sharks, *Prionace glauca* (Linnaeus) in the NE Atlantic and tropical reef sharks at Aldabra atoll (Stevens 1976, 1984, 1990). Two sizes were used, a 45 mm long Jumbo Rototag and a 36 mm long Rototag; Rototags were used on the smaller species such as *C. macroti* (Muller & Henle) and *Rhizoprionodon* spp. Red and yellow colours were used. The tag was applied using a special applicator, through a hole punched with a leather punch, towards the base of the leading edge of the first dorsal fin. The male half of the tag was embossed with a number and the female half with a return address (in English) and a reward message (in Mandarin). Some sharks were double tagged with a second Rototag, or occasionally a Jumbo Rototag, in the first dorsal fin above the first tag, in an attempt to estimate tag shedding rates. Fork lengths (FL) were measured to the nearest mm on a fish measuring board, by scientists participating in the programme. Only sharks judged to be in a suitable condition following removal from the net or hook were tagged. Based on any bleeding and on swimming activity following release, sharks were given a subjective condition index of 'good', 'fair' or 'poor'.

Publicity and recapture information

The tagging programme was widely publicised through the media, fishing publications, fishery offices and foreign and domestic fishing companies. Taiwanese fishing skippers were informed about the programme at pre-fishing inspections, posters (in English and Mandarin) were placed onboard the vessels and Commonwealth observers, who periodically boarded these vessels, were briefed about the project. Fishermen were requested to retain the whole shark with the tag in place, following a recapture. Returned sharks were usually frozen and subsequently thawed before measurement by scientists participating in the programme (Davenport and Stevens 1988). The distance from site of tagging to site of recapture was calculated as the minimum sea distance travelled using the Rhumbline calculation (Texas Instruments).

Tag shedding

The maximum likelihood method of Kirkwood and Walker (1984) was used to estimate tag shedding; this model was developed to analyse relatively small data sets where exact time at recapture were known. In exploratory analyses two parameters for tag loss were used. These were a constant rate of shedding with time, and the probability of tag retention immediately after release. However, the goodness of fit of the two parameter model was only marginally better than using the single parameter of constant rate of loss, and this was the model we chose.

It is described by:

$$Q(t) = e^{-Lt}$$

where $Q(t)$ is the probability of tags being retained at time t and L is the constant rate of tag shedding.

Effort corrected movement

We used a simplification of the method used by Bayliff (1979), which estimates the proportion of fish released in a particular area which are subsequently recaptured in another area. Bayliff used a 'parallel-area' method to describe inshore-offshore movements of tagged yellowfin tuna, in which he compared the number of tagged fish returned per unit of effort in various area-time strata. We reduced the areas to two, the inshore area fished by Australian gill-netters and prawn trawlers, and the offshore area fished by the Taiwanese. We considered only one time period, starting in July 1984, when consistent returns from all three fisheries commenced, to June 1986, when the Taiwanese fishery closed. Because the geographical distribution of the tag releases and the fisheries varies considerably, we restricted the comparison to the coast of Arnhem Land from $129^{\circ}00'$ to $137^{\circ}59'$ E. longitude, for latitudes up to $12^{\circ}59'$ S. Prawn trawl fishing effort data is recorded in units of days, and we converted this to the units used for the Australian gill-net fishery, hundred metre net days (HMND), based on the amount of effort required by each fishery to produce one recapture at similar times and in a similar areas. We found the equivalent of one HMND for *C. tilstoni*, *C. sorrah* and *C. maclovi* was 6.2, 14.1 and 1.8 prawn days respectively. The effort data for the Australian gill-net fishery is deficient in that the number of sets in a fishing day, and their duration, is not known. Information from observers indicated that the number of sets per day was two to three at this time. The duration of the sets is apparently about four hours. Expressed in km h, the units used for the Taiwanese fishery, 1 HMND is approximately equal to 0.8 to 1.2 km h; we used the value of 1.

The proportion of fish (P) moving offshore was estimated as follows:

$$P = \frac{R_t / E_t}{R_a / E_a + R_t / E_t}$$

where R_t = the number of Taiwanese recaptures; E_t = Taiwanese effort; R_a = the number of inshore recaptures; E_a = inshore effort.

As noted by Bayliff (1979) and Hilborn (1990), a factor which this type of analysis fails to take into account is that some of the sharks destined to move into the offshore area will be recaptured by the inshore fisheries before they have had a chance to do so. The number of recaptures on the northern periphery of the area fished by the Taiwanese were very few, and in case this reflected capture before the tagged sharks could penetrate this far, we excluded the

three recaptures and the 192190 km h of effort in the 9 ° S. latitude region of the Taiwanese fishery from the analysis.

Results

Shark tag releases

Between February 1983 and May 1985, 10 511 sharks comprising 23 species were tagged off northern Australia (Table 1). Tagging concentrated on the two principal commercial species, *C. tilstoni* and *C. sorrah*. The majority of tags were released in the Arafura Sea and Gulf of Carpentaria, but some tags were distributed throughout northern Australia between Broome and Cairns (Fig.1) . We intended to release approximately equal numbers of tags in inshore (< 35 km from the coast) and offshore (> 35 km from the coast) waters. However, low catch rates and difficult sea conditions offshore resulted in only 271 of the total of 10 511 releases being made offshore (Fig.1).

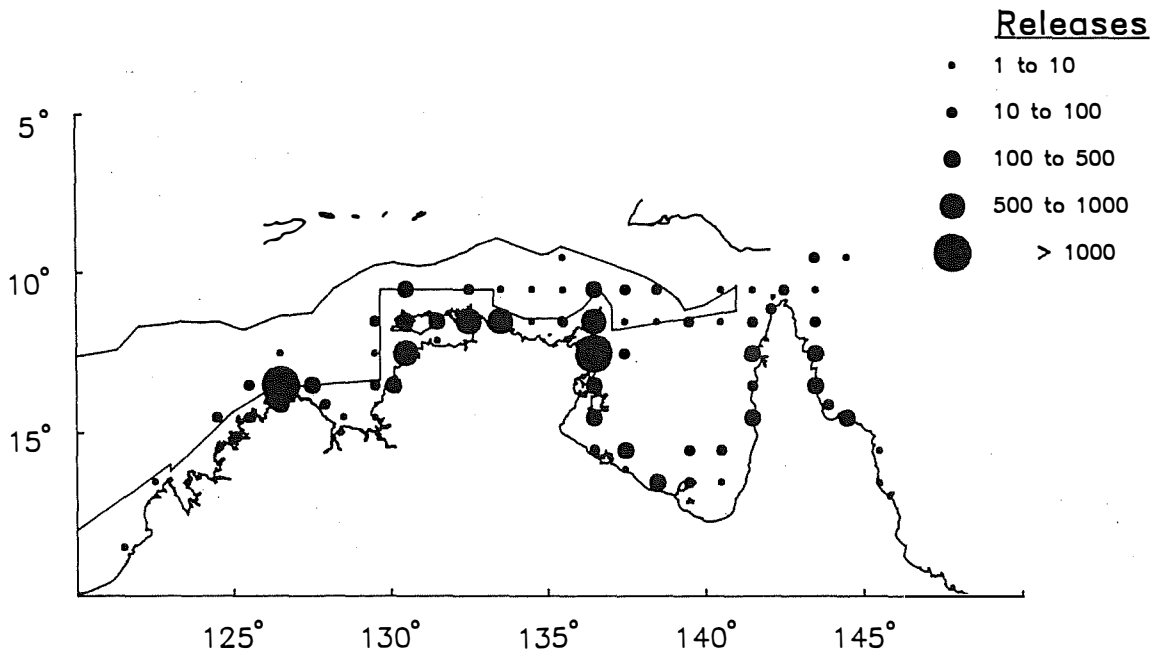


Fig. 1. Location of tag releases off northern Australia.

Gill-netting was by far the most effective method of capturing sharks for tagging, accounting for 81, 60, and 75 % of all releases for *C. tilstoni*, *C. sorrah* and *C. macloti* respectively (Table 2). The size distributions of sharks captured by the different fishing methods are shown in (Fig. 2); the only notable difference is the larger size of longline-caught *C. tilstoni*.

Tag type and colour

Chi-square tests for the effect of tag colour on the return rates of Jumbo tags for *C. tilstoni* and *C. sorrah* showed no significant association ($\chi^2 = 0.003$, 1d.f., $p = 0.96$; $\chi^2 = 0.68$,

Table 1. Numbers of sharks tagged and recaptured.

Species	Number tagged	Number recaptured	Percent recaptured
<i>C. tilstoni</i>	4862	317	6.5
<i>C. sorrah</i>	2924	75	2.6
<i>C. maclovi</i>	1611	51	3.2
<i>R. acutus</i>	277	4	1.5
<i>C. amboinensis</i>	131	13	9.9
<i>C. amblyrhynchoides</i>	122	9	7.4
<i>R. taylori</i>	119	1	0.8
<i>S. lewini</i>	93	1	1.1
<i>C. dussumieri</i>	79	1	1.3
<i>C. brevipinna</i>	59	1	1.7
<i>G. cuvier</i>	55	2	3.6
<i>C. fitzroyensis</i>	55	1	1.8
<i>S. mokarran</i>	48	2	4.2
<i>E. blochii</i>	34	1	2.9
<i>C. amblyrhynchos</i>	12	-	-
<i>C. melanopterus</i>	6	-	-
<i>C. plumbeus</i>	5	-	-
<i>C. limbatus</i>	5*	1	?
<i>H. elongatus</i>	4	-	-
<i>N. ferrugineus</i>	6	1	16.7
<i>S. varium</i>	2	-	-
<i>N. acutidens</i>	1	-	-
<i>C. falciformis</i>	1	-	-
TOTAL	10511	481	4.6

* It is possible that further specimens may have been tagged but that these were recorded as *C. tilstoni*, due to difficulty in separating these two species while alive (Stevens and Wiley 1986).

1 d.f, $p = 0.41$, respectively). A similar result was found for the smaller Rototags used on *C. macloiti* ($\chi^2 = 0.044$, 1 d.f., $p = 0.83$). However, when the colours were combined, and the effect of tag type on return rates was tested for *C. macloiti*, the only species for which there were sufficient releases of both tag types, the result was nearly significant at the 5 % level ($\chi^2 = 3.69$, 1 d.f., $p = 0.055$). The Jumbo tags were recaptured in less than expected numbers.

Table 2. Proportion of recaptures resulting from different fishing methods used to capture sharks for tagging.

Species	Fishing method	Number released	Number recaptured	Per cent. recaptured	Chi Square
<i>C. tilstoni</i>	Handline	774	78	10.1	$\chi^2 = 19.5$, 2 d.f. $p < 0.001$
	Gillnet	3935	233	5.9	
	Longline	153	6	3.9	
<i>C. sorrah</i>	Handline	914	36	3.9	$\chi^2 = 11.4$, 2 d.f. $p < 0.01$
	Gillnet	1741	36	2.1	
	Longline	268	3	1.1	
<i>C. macloiti</i>	Handline	370	19	5.1	$\chi^2 = 6.03$, 2 d.f. $p < 0.05$
	Gillnet	1211	32	2.6	
	Longline	29	0	-	

Condition of tag and tagging wound

The length of the shank of the tags where it passes through the fin is 8.3 and 7.5 mm for the Jumbo Rototag and Rototag, respectively. This was sufficient for the lobes of the tags to rotate freely at release, and to lie parallel to the fin. However, it became apparent that after considerable periods at liberty, the leading edges of many tags were becoming embedded in the fin, which apart from preventing them from rotating, also caused them to project from the fin at an angle (Fig. 3). A total of 220 fins from recaptured *C. tilstoni* were examined, and up to a year after tagging 90% of them were in the same condition as they were when released (designated 'good'). However, the proportion of fins in good condition fell sharply to about 40% for fish at liberty between one year and three and a half years (the maximum observed) (Table 3) Recoveries of double tagged sharks showed that embedding was more common in the Jumbo tags applied near the thicker base of the fin. One of the *C. tilstoni* recoveries was a double tagged fish with only the upper Rototag remaining; the tag wound

had healed completely. Fifty seven fins were examined from recaptured *C. sorrah*; 90% of fins from sharks caught again up to six months later were in good condition compared to about 70% for those at liberty between one and three years (the maximum observed) (Table 3). For *C. macroti*, 13 fins were available for examination from recaptured sharks. These had been at liberty for up to four years, and all of them were in good condition. The maximum length reached by *C. tilstoni*, *C. sorrah* and *C. macroti* is approximately 180, 150 and 110 cm total length (TL) respectively, and the extent of embedding reflects these differences in size.

Tag breakage was observed in three *C. tilstoni* returns which had been at liberty from 4.8 to 5.5 years. The lobes of the tags had broken at varying positions from close to the insertion pin to half-way along the lobe.

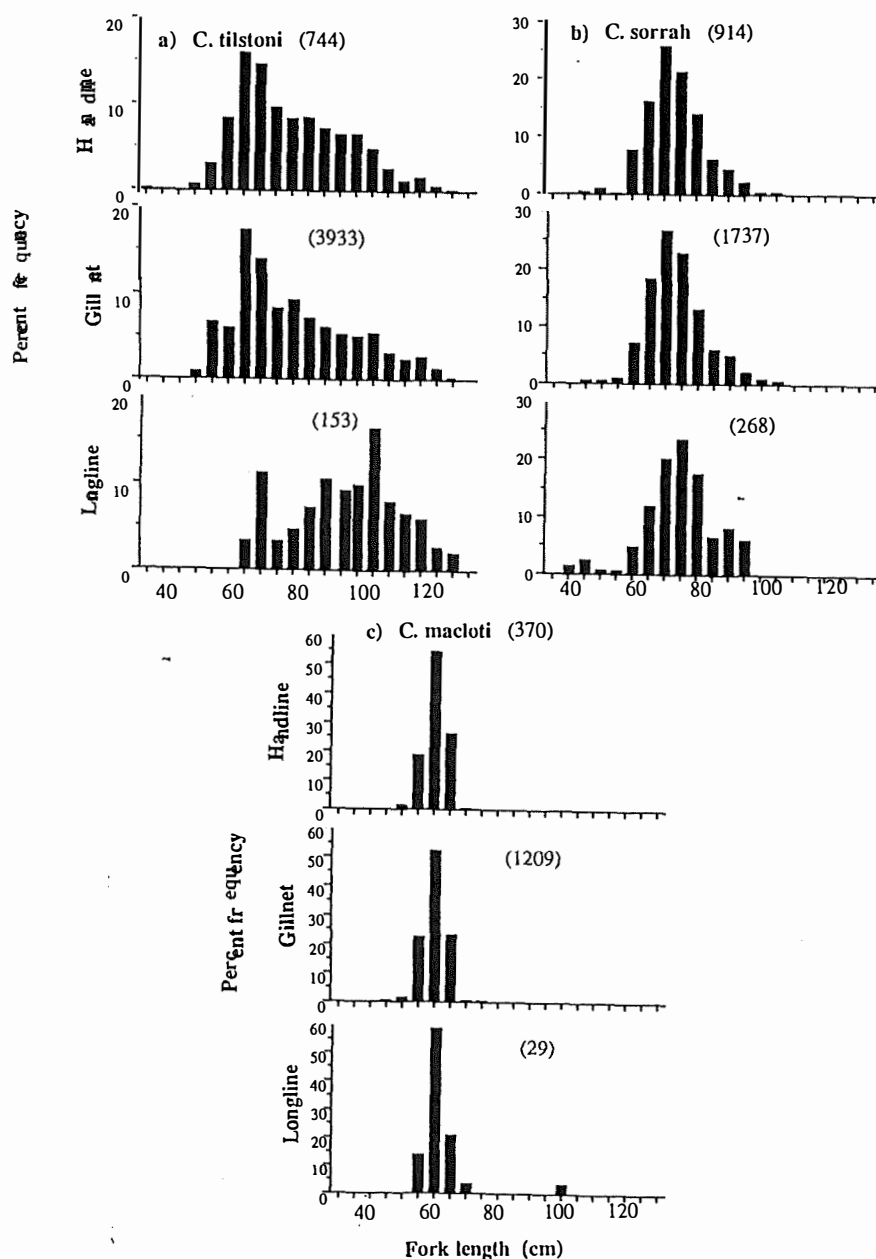


Fig. 2. Length at release for *C. tilstoni*, *C. sorrah* and *C. macroti*

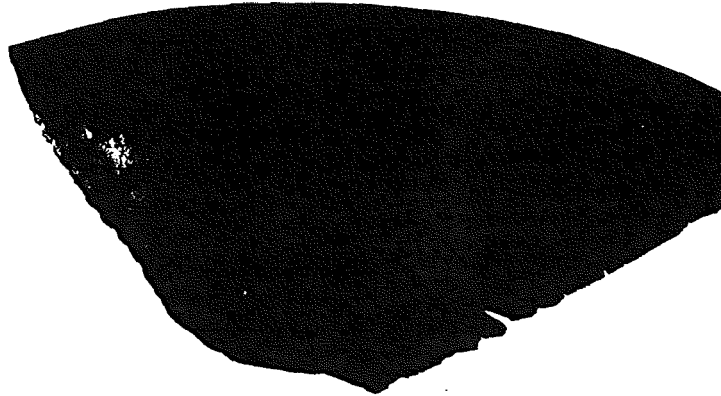


Fig. 3. First dorsal fin of *C. tilstoni* at liberty for 717 days, showing embedding of the Jumbo Rototag

Table 3. Condition of the tag wound in *C. tilstoni* and *C. sorrah*.

Years at liberty	<i>Carcharhinus tilstoni</i>				<i>Carcharhinus sorrah</i>			
	Good (%)	Fair (%)	Poor (%)	Sample size	Good (%)	Fair (%)	Poor (%)	Sample size
0 - 1	89.5	8.8	1.8	114	77.8	11.1	11.1	27
1 - 2	40.8	32.7	26.5	49	68.8	25.0	6.3	16
2 - 3	36.1	30.6	33.3	36	70.0	20.0	10.0	10
3 - 4	18.8	31.3	50.0	16	50.0	50.0	0	4
4 - 5	40.0	20.0	40.0	5	-	-	-	-

Tag shedding

Of 343 *C. tilstoni* which were double tagged, 28 were recaptured, three with only one tag remaining. Of 162 *C. sorrah* which were double tagged, four were recaptured, all with both tags present. The three *C. tilstoni* recaptured with one tag missing had been at liberty for 207, 659 and 947 days. The two earlier returns had lost the Rototag applied above the Jumbo tag, while the remaining recapture, at liberty for nearly three years, had lost the Jumbo tag. Inspection of recovered fins indicated that loss of the tags could be expected as the fins grew and thickened, and this could be expected to be more of a problem with Jumbo tags applied near the base of the fins. This can be considered as a long term tag loss. The loss of the Rototags however, especially the one at liberty for only 207 days, indicated that there are additional causes of tag loss, apart from the thickening of the fin with time. A comparison of the number of recaptures from the double tagging experiment was made with the number of recaptures from single tagging. The single tag releases were restricted to the same time and area as the double tag releases (1985, and longitudes 135° to 138°E), and resulted in 14 recaptures from 136 releases. There was no significant difference in the number of recaptures (and non-recaptures) in the double and single tagging experiments ($\chi^2 = 0.55$, 1 d.f., $p = 0.29$). This indicated that tag-shedding rates were not high, otherwise returns from double tagging would be expected to be higher than from single tagging. To estimate tag shedding rates, the Kirkwood and Walker (1984) model was used. The estimate of L, the constant rate of tag shedding was 0.047 yr^{-1} (s.e. = 0.029) with log-likelihood -9.24 (W. Hearn, CSIRO Division of Fisheries, Hobart, Tas. 7001, personal communication). It would perhaps be more realistic to have L increasing with time at liberty, in view of the embedding effect observed in recaptured sharks, but there is not sufficient data to justify it.

Condition index of released sharks

The percentage of sharks released in 'good', 'fair' or 'poor' condition, for the three principal species, is shown in Table 4. Chi-square tests for each species showed a highly significant association between capture method and condition at release for all three species. Of the handlined fish, 92-96% were in 'good' condition compared with 62-79% and 74-92% for gill-netted and longlined fish, respectively. Gill-netting resulted in the most sharks captured in 'poor' condition, although there was some variation between species, with *C. tilstoni* having the highest proportion caught in 'poor' condition. If the estimate of condition on release has any predictive value, then it might be expected that proportionately fewer recaptures would result from sharks in 'poor' or 'fair' condition. The association between condition at release and proportion of fish recaptured was tested for the three principal species by Chi-square analysis (Table 5). For *C. sorrah* and *C. macroti* the recapture rates were not related to their condition on release. However, for *C. tilstoni* there was a significant association, with fewer than expected returns of sharks released in 'fair' or 'poor' condition. When the data for *C. tilstoni* were separated into handline and gill-net caught sharks (there were insufficient data to include longlining) a significant association ($\chi^2 = 6.72$, 2 d.f., $p = 0.035$) between condition at release and subsequent recapture was found for the gill-netted sharks, but not for those caught by handlining. For *C. tilstoni* caught by gill-net fewer than expected recaptures were made from fish released in 'fair' or 'poor' condition.

Table 4 . Condition index of tagged sharks at release, by capture method.

Species	Capture method	Condition (%)			Total No. released	χ^2
		Good	Fair	Poor		
<i>C. tilstoni</i>	Handline	95	1	4	463	$\chi^2 = 222.1$
	Gillnet	62	7	30	2761	4 df
	Longline	81	13	6	139	p < 0.01
<i>C. sorrah</i>	Handline	92	1	6	637	$\chi^2 = 192.7$
	Gillnet	77	3	20	1137	4 df
	Longline	74	17	8	237	p < 0.01
<i>C. macloiti</i>	Handline	96	1	4	250	$\chi^2 = 43.5$
	Gillnet	79	4	18	617	4 df
	Longline	92	8	0	26	p < 0.01

Table 5 . Tag returns from sharks released in 'good', 'fair' or 'poor' condition, for the three main species.

Species	Condition at release	Number released	Number recaptured	Per cent recaptured	χ^2
<i>C. tilstoni</i>	Good	2274	153	6.7	$\chi^2 = 8.9$
	Fair	230	9	3.9	2 df
	Poor	859	36	4.2	p = 0.011
<i>C. sorrah</i>	Good	1645	39	2.4	$\chi^2 = 3.1$
	Fair	81	0	0	2 df
	Poor	286	4	1.4	not. sig.
<i>C. macloiti</i>	Good	748	26	3.5	$\chi^2 = 2.0$
	Fair	27	0	0	2 df
	Poor	118	6	5.1	not. sig.

Effect of capture method on subsequent recapture rates

Of the three methods used to capture sharks for tagging (gill-netting, handlining and longlining), handlining subjects the sharks to the shortest capture time, and might be expected to inflict the least stress. We investigated the proportion of returns resulting from the fishing methods used to capture them for tagging. The analysis was restricted to the three principal species and the results are shown in Table 2. For all three species the percentage of recaptures for handlined sharks was approximately two and three times higher than for gill-net and longline caught sharks, respectively. Returns from longlining may be influenced by small sample sizes. The null hypothesis that tagged fish are recaptured in proportion to the number released in each fishing method category was rejected for all three species. The additional mortality suffered by gill-net released sharks was investigated by comparing the number of recaptures by calendar year for handline and gill-net releases (there were insufficient recaptures of longline-released sharks to warrant analysis). A similar pattern of recoveries over time would indicate that the additional mortality suffered by the gill-net releases occurs shortly after release, before the sharks are available for recapture. Chi-square tests showed that this hypothesis was acceptable for *C. macloiti* ($\chi^2 = 1.29$, 3 d.f., $p = 0.73$), *C. sorrah* ($\chi^2 = 8.75$, 4 d.f., $p = 0.15$), but not for *C. tilstoni* ($\chi^2 = 11.44$, 4 d.f., $p = 0.02$). It appears that for *C. tilstoni* there is also a longer term effect on survival.

Tag return rates

Of the 10 511 sharks tagged, 89% consisted of three species, *C. tilstoni*, *C. sorrah* and *C. macloiti*. By May 1989, 480 tags (4.6%) had been returned with the same three species accounting for 92% of the recaptures. The return rate for *C. tilstoni* was 6.5%, for *C. sorrah* it was 2.6% and for *C. macloiti* it was 3.2% (Table 1). Chi-square tests carried out separately for handline and gill-net - released sharks, using the data presented in Table 2 (there were insufficient releases of longline caught sharks for this analysis) showed a significant association between the recapture numbers and the species returned ($\chi^2 = 76.0$, 2 d.f., $p < 0.001$ for gill-net releases, and $\chi^2 = 25.7$, 2 d.f., $p < 0.001$ for handline releases). In both cases *C. tilstoni* was returned in greater than expected numbers.

The distribution of recaptures for all species by fishing method are shown in Table 6. Three fisheries accounted for 92% of the recaptures. The Australian gill-net fishery returned 49%, the Taiwanese gill-net fishery 26% and the Prawn trawl fishery returned 17% of the tags. A further 2.1% of tags were returned by prawn trawlers but these sharks were caught by handline following completion of a trawl. Taiwanese gill-netting ceased in the Australian Fishing Zone in July 1986. Up to the time of the last recapture from the Taiwanese gill-net fishery, Australian and Taiwanese gill-netting had accounted for 41% and 32%, and prawn trawlers for 18% of tag returns. To test whether these three fisheries returned the same proportion of each species, a Chi-square analysis was carried out. A significant association was found ($\chi^2 = 12.2$, $df = 4$, $p < 0.025$). The prawn trawl fishery accounted for fewer *C. sorrah* and more *C. macloiti* than expected, and the Australian gill-net fishery caught

Table 6. Shark recaptures by fishing method.

Species	Fishing method						
	Australian gillnetter	Taiwanese gillnetter	Prawn trawler	Research vessel	Handline	Angler	Taiwanese pairtrawler
<i>C.tilstoni</i>	163	81	44	19	8	-	1
<i>C.sorrah</i>	36	28	6	2	2	1	-
<i>C.macloti</i>	18	15	13	5	-	-	-
<i>C.amboinensis</i>	7	-	4	1	-	-	1
<i>C.amblyrhynchoides</i>	4	-	5	-	-	-	-
<i>R.acutus</i>	3	-	1	-	-	-	-
<i>S.mokarran</i>	1	-	1	-	-	-	-
<i>N.ferrugineus</i>	-	-	1	-	-	-	-
<i>C.limbatus</i>	-	-	1	-	-	-	-
<i>C.brevipinna</i>	1	-	-	-	-	-	-
<i>C.dussumieri</i>	-	-	1	-	-	-	-
<i>C.fitzroyensis</i>	-	-	1	-	-	-	-
<i>G.cuvier</i>	-	1	-	-	-	1	-
<i>R.taylori</i>	-	-	1	-	-	-	-
<i>S.lewini</i>	-	1	-	-	-	-	-
<i>E.blochii</i>	-	-	1	-	-	-	-
TOTAL	233	126	80	27	10	2	2
%	48.9	26.4	16.8	5.7	2.1	0.4	0.2

(481 recaptures: 1 missing fishing method)

fewer *C. macloiti* than expected. However, it is apparent that it is the prawn trawl fishery which is responsible for this selectivity. When the comparison is restricted to the two gill-net fisheries, there is no association between the number of recaptures of *C. tilstoni*, *C. sorrah* and *C. macloiti*, and the recapture fishery ($\chi^2 = 5.1$, 2 d. f., $p = 0.08$).

The return rate of tags by time is given in Table 7 and shows that by 1989, five years after the majority of tagged sharks were released, the number of recaptures was minimal.

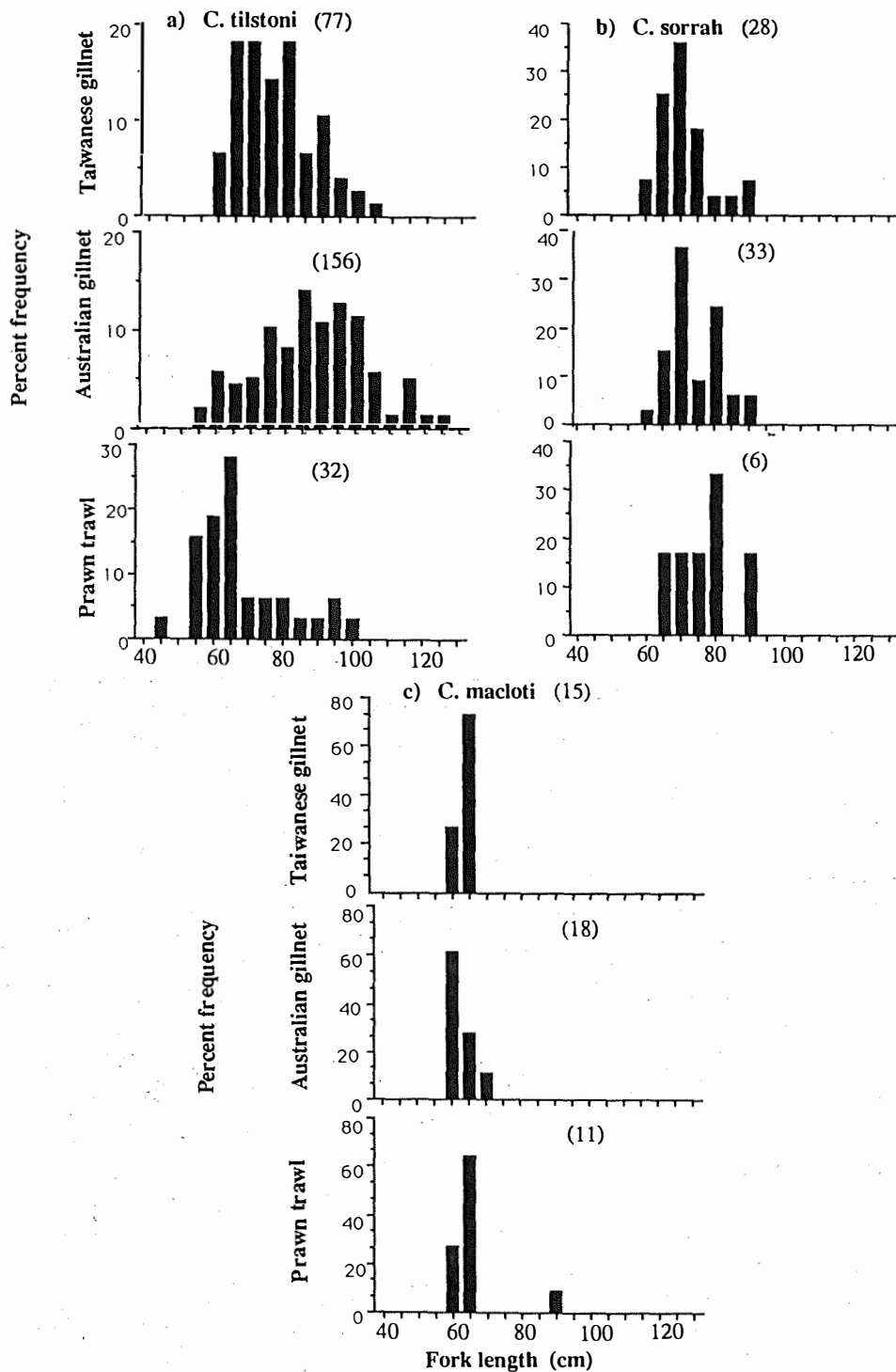
Table 7. Tag returns by year for the principle species and fishing methods.

Species	Fishing method	1983	1984	1985	1986	1987	1988	1989	Total
<i>C. tilstoni</i>	Australian gillnet	0	48	43	26	41	5	0	163
	Taiwanese gillnet	0	27	34	20	0	0	0	81
	Prawn trawl	1	30	9	0	2	2	0	44
	All methods	3	125	88	51	43	7	0	317
<i>C. sorrah</i>	Australian gillnet	0	18	9	3	6	0	0	36
	Taiwanese gillnet	1	8	12	7	0	0	0	28
	Prawn trawl	0	4	1	1	0	0	0	6
	All methods	1	33	24	11	6	0	0	75
<i>C. macloiti</i>	Australian gillnet	0	5	1	1	10	1	0	18
	Taiwanese gillnet	0	3	5	7	0	0	0	15
	Prawn trawl	0	7	2	3	1	0	0	13
	All methods	0	19	9	11	11	1	0	51
All species	Australian gillnet	0	78	58	32	58	7	0	233
	Taiwanese gillnet	1	39	52	34	0	0	0	126
	Prawn trawl	1	48	19	6	4	2	0	80
	All methods	4	192	135	77	62	9	2	481

Size composition of recaptured sharks

The length distributions of *C. tilstoni*, *C. sorrah* and *C. macloiti*, recaptured by Taiwanese gill-net, Australian gill-net and prawn trawl are shown in Fig.4. Kruskal-Wallis tests showed that the differences in length distributions between the three fisheries were highly significant for *C. tilstoni* ($H = 53.9$, 2 d.f., $p < 0.001$), but not significantly different for *C. sorrah* ($H = 4.7$, 2 d.f., $p > 0.05$) or *C. macloiti* ($H = 3.8$, 2 d.f., $p > 0.10$).

Fig.4. Recapture lengths of *C. tilstoni*, *C. sorrah* and *C. macloiti* from gillnet and prawn trawl fisheries off northern Australia.



Shark movements

The movements, shown from tag returns, for *C. tilstoni*, *C. sorrah* and *C. macloiti* are shown in Figs. 5-7, and appear to be substantial. However, Fig. 8 shows that the frequency distribution of distances travelled by these three species are heavily skewed, with the smallest distance interval accounting for most of the observations. In Table 8 the distances travelled by sharks for which more than one recapture was recorded are presented in terms of the median and maximum distance travelled, as well as the maximum number of kilometres travelled per day. *C. macloiti* showed the highest median distance travelled, followed by *C. sorrah*. The remaining species showed very similar values. A one-way ANOVA carried out on the five species with five or more returns (the data was first normalised by taking log e of the distance travelled) showed significant interspecific differences in distance travelled ($F= 4.94$; 4, 449 d.f.; $p= 0.0007$). Pair-wise comparisons using the Fisher PLSD test showed four significant differences, all involving *C. macloiti*. *Carcharhinus amblyrhynchoides* (Whitley), for which there were only 9 returns, was the only species not to show a significant difference when compared with *C. macloiti*. The movements of *Carcharhinus amboinensis* (Muller & Henle), *C. amblyrhynchoides* and *Rhizoprionodon acutus* (Rüppell) are shown in Fig. 9, and Table 9 shows the distances travelled for species with only a single recapture.

To examine possible effects of a shark's sex on distance travelled, a Kruskal-Wallis test was carried out on the four species for which there were sufficient returns. The analysis showed no significant differences in distance travelled between the sexes (*C. tilstoni* $H = 0.29$, 1 d.f., $p > 0.5$; *C. sorrah* $H = 1.26$, 1 d.f., $p > 0.25$; *C. macloiti* $H = 2.31$, 1 d.f., $p > 0.1$; *C. amboinensis* $H = 0.02$, 1 d.f., $p > 0.75$)

No significant correlation (using Spearman's rank correlation) between distance travelled and time at liberty was observed for *C. tilstoni*, *C. sorrah*, *C. macloiti* or *C. amblyrhynchoides*, (Fig. 10a-d) but a significant positive correlation was observed for *C. amboinensis* ($r_s = 0.99$, $p < 0.05$). However, there are only 13 returns for *C. amboinensis* and the analysis is strongly influenced by a single recapture which had traveled over 1000 km (Fig. 10e).

The relationship between shark length and distance travelled for *C. tilstoni* and *C. sorrah* is shown in Fig. 11. The recapture data for *C. macloiti* did not warrant analysis because of the restricted range of recapture lengths. A Mood median test (Minitab statistical software), with release length classified into 10 cm intervals, showed no significant effect of shark size on distance travelled for *C. sorrah* ($\chi^2 = 0.60$, 3 d.f., $p = 0.9$), but a highly significant effect for *C. tilstoni* ($\chi^2 = 18.4$, 7 d.f., $p = 0.011$). The greatest distances travelled for *C. tilstoni* were in the 65-75 cm FL size class, which accounted for over 30% of all recaptures. Some errors in the recapture data are almost inevitable, and association of the wrong tag number with locality of capture could result in some erroneous long distance recaptures. However, nineteen of the highest distances (out of a total of 333) need to be removed before the Mood test becomes non-significant, and we conclude that we are dealing with a genuine effect of length at release on distance travelled.

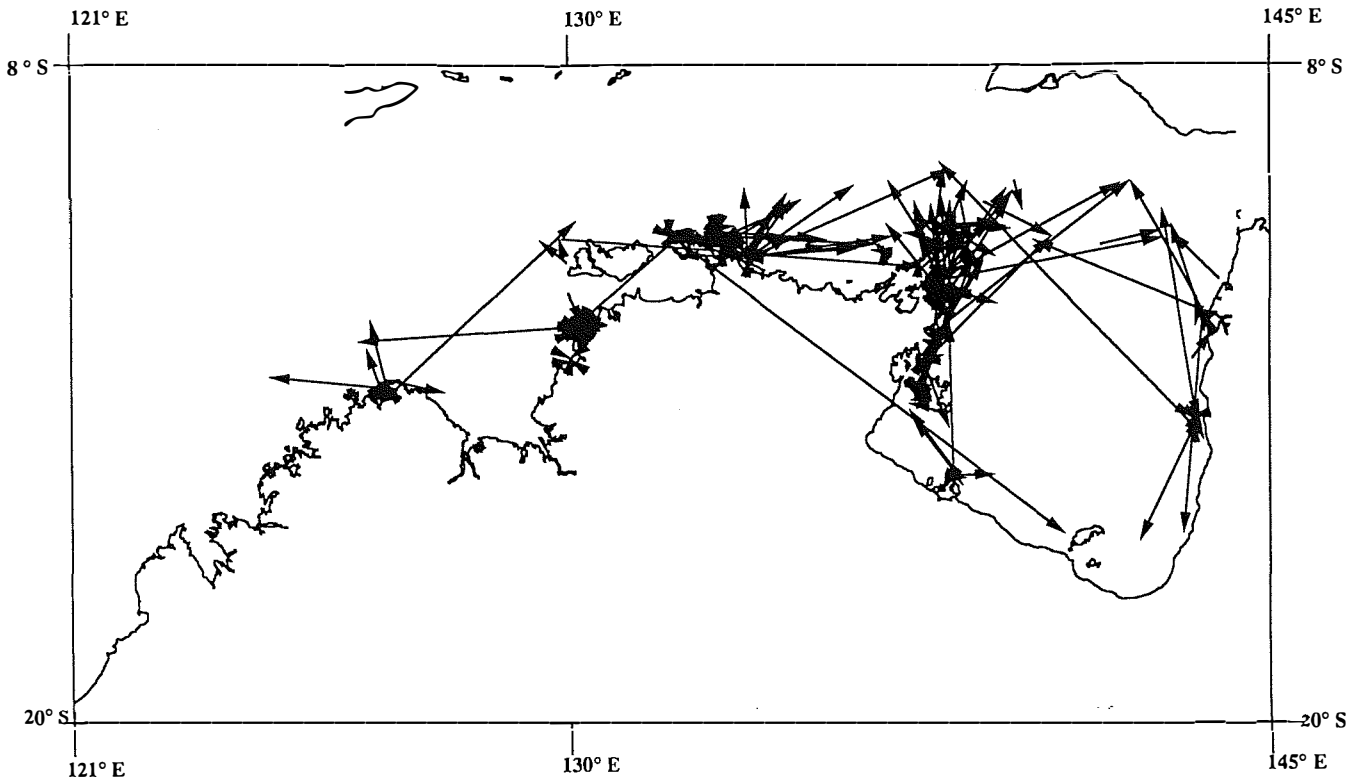


Figure 5. Movements of tagged *Carcharhinus tilstoni*.

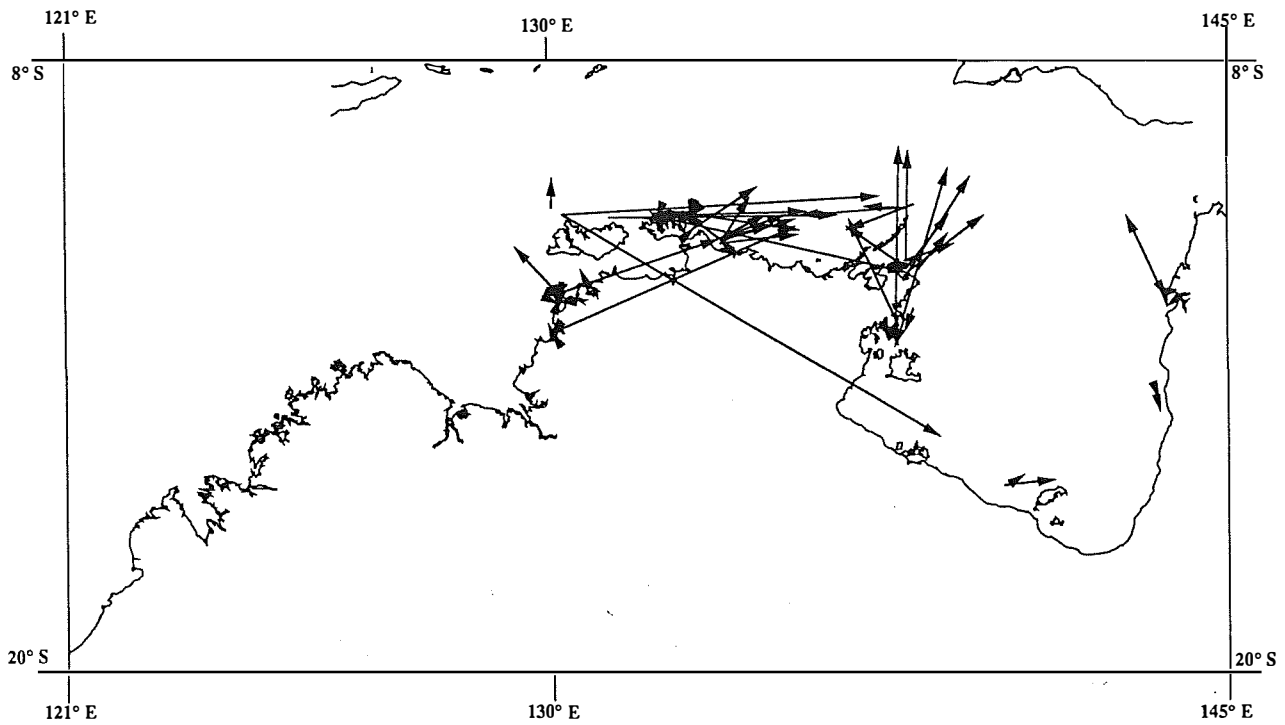


Figure 6. Movements of tagged *Carcharhinus sorrah*.

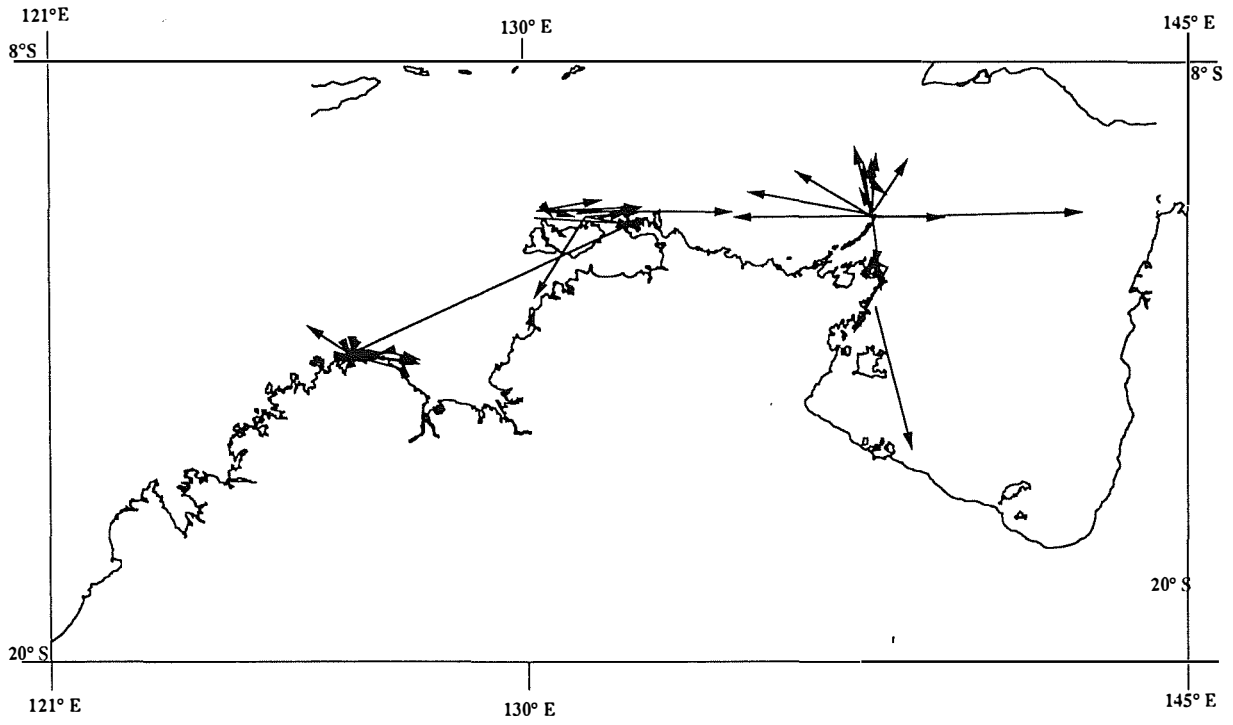


Figure 7. Movements of tagged *Carcharhinus macloiti*.

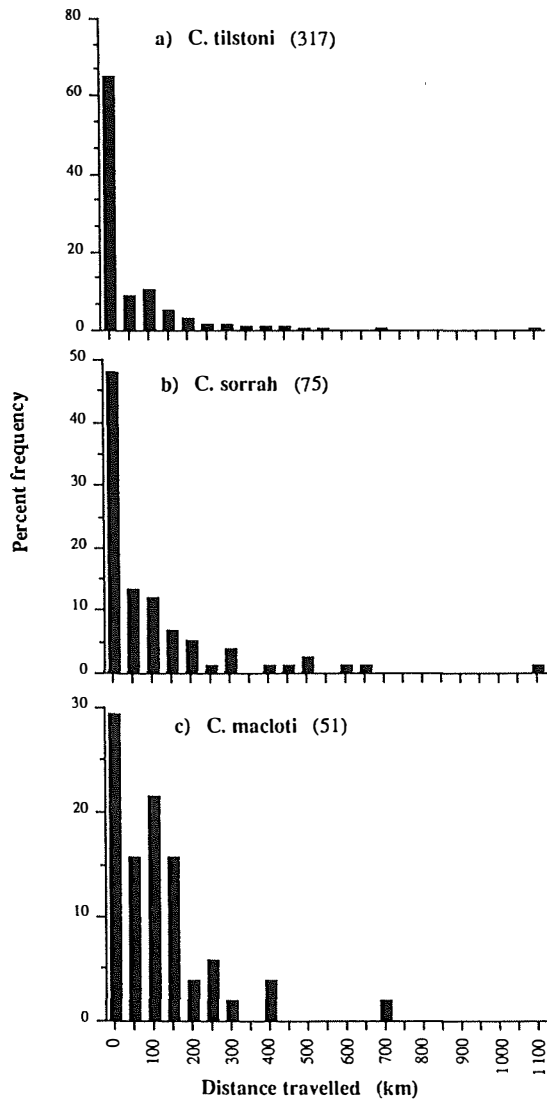


Figure 8. The proportions of *Carcharhinus tilstoni*, *C. sorrah* and *C. macloiti* moving indicated distances.

Table 8. Distances travelled (km) by eight species of shark.

Species	Number of recaptures	Maximum distance	Median distance	Max. km/day (no. days out)
<i>C. tilstoni</i>	317	1113	21	24.7 (29)
<i>C. sorrah</i>	75	1116	62	6.8 (23)
<i>C. macloiti</i>	51	711	117	18.6 (1)
<i>C. amboinensis</i>	13	1079	18	18.3 (1)
<i>C. amblyrhynchoides</i>	9	173	23	8.3 (21)
<i>R. acutus</i>	4	45	22	0.1 (417)
<i>S. mokarran</i>	2	385	-	0.8 (488)
<i>G. cuvier</i>	2	156	-	3.3 (48)

Table 9. Distance travelled and time at liberty for species represented by only a single recapture.

Species	Distance travelled (km)	Days out
<i>C. brevipinna</i>	19	616
<i>C. dussumieri</i>	4	500
<i>C. limbatus</i>	5	607
<i>C. fitzroyensis</i>	150	78
<i>R. taylori</i>	92	78
<i>S. lewini</i>	113	10
<i>E. blochii</i>	21	347
<i>N. ferrugineus</i>	43	936

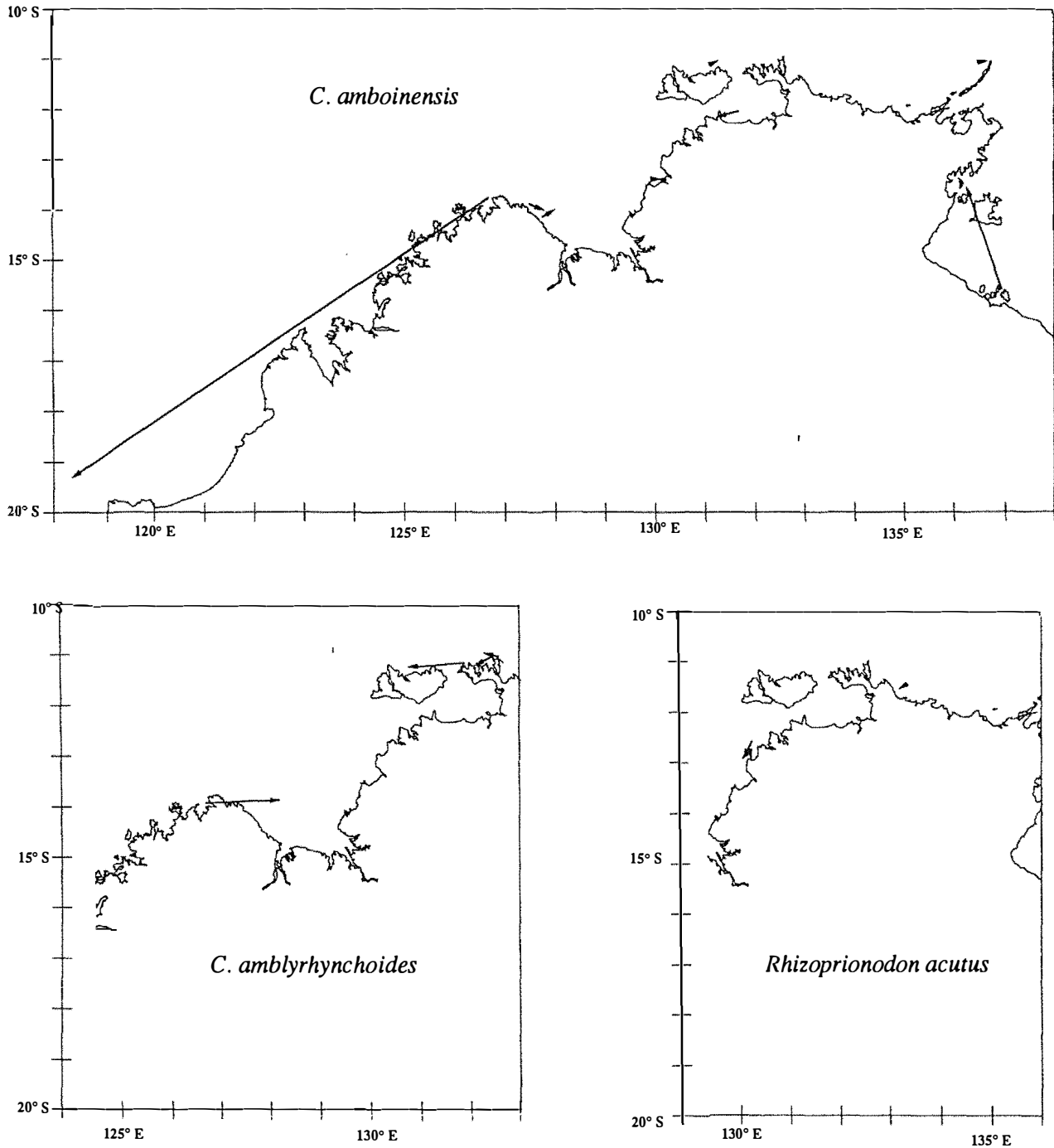


Figure 9. Movements of tagged *Carcharhinus amboinensis*, *C. amblyrhynchoides* and *Rhizoprionodon acutus*.

To examine possible interactions between time at liberty, shark size and distance travelled, a log-linear analysis was carried out. It showed that there was a complicated relationship between these three variables. Sharks recaptured early tended to be small, which may be partly due to the high proportion of them returned by prawn trawlers - prawn trawlers captured smaller *C. tilstoni* than the other two fisheries (Fig.4). Sharks which were large when released tended not to be caught early, or to travel very far. A high proportion of these were returned by the Australian gill-net fishery. Sharks travelling the greatest distances were of an intermediate size, and a high proportion of these were returned by the Taiwanese gill-

net fishery. Since nearly all the releases were inshore, any sharks caught by the Taiwanese must make an offshore movement, probably ensuring that they travel further than sharks recaptured inshore. A Kruskal-Wallis test showed significant differences between the three recapture fisheries in distance travelled by *C. tilsoni* ($p < 0.001$), with the median distance travelled by sharks recaptured by the Taiwanese gill-net fishery being much greater than for the two inshore fisheries.

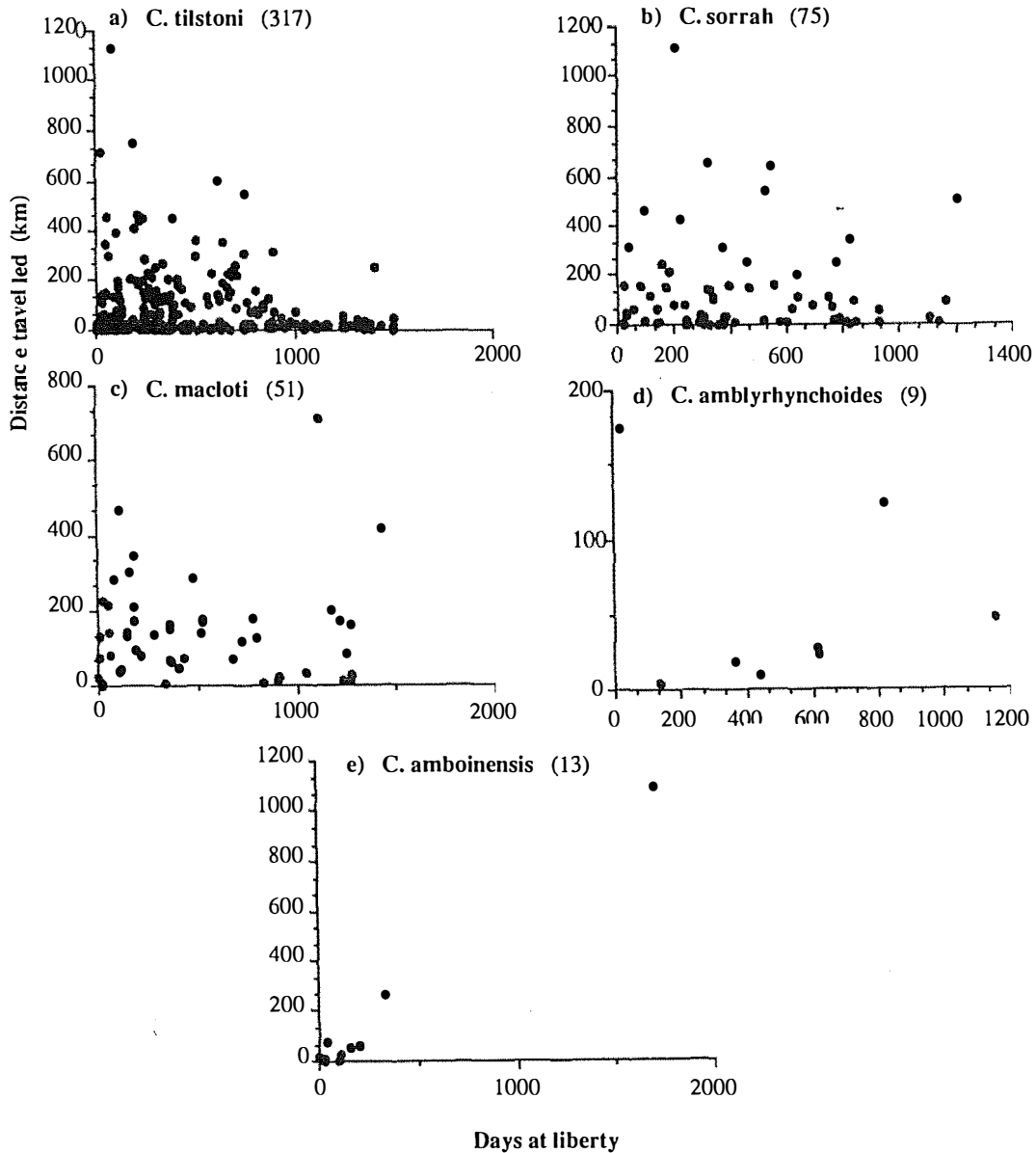


Fig. 10. Relationship between distance travelled and time at liberty for five species of shark

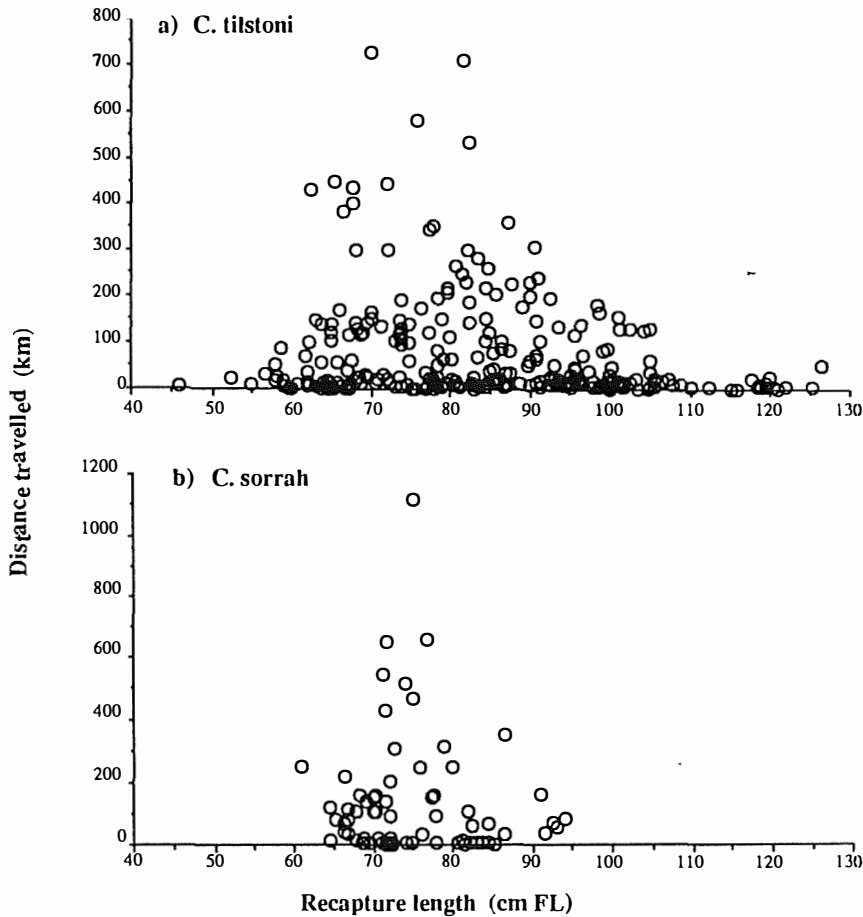


Fig. 11 . Relationship between distance travelled and shark size for tagged *Carcharhinus tilstoni* and *C. sorrah*

This raises the question of whether intermediate-size sharks tend to move further, or whether the Taiwanese fishery selectively catches this size group. Comparison of extensive length-frequency data collected from inshore research gill-netting and from the Taiwanese fleet (Fig. 12) shows only very minor differences in length composition - the research fishing used the same mesh as the Australian gill-netters (15cm stretch-mesh monofilament) while the Taiwanese fishery uses multifilament net ranging in size from 14 to 19 cm stretch-mesh. There is no indication of major differences in the length composition of *C. tilstoni* caught by gill-net inshore or offshore. The median size of the sharks caught inshore was 97 cm total length (TL) ($n = 6056$), and that from the Taiwanese fishery was 94 cm TL ($n = 47\,746$). While a Kolmogorov-Smirnov test indicated significant differences ($p < 0.001$) between the two distributions, it is unlikely that they are biologically meaningful, suggesting little selectivity difference between nets of the Australian and Taiwanese fleets. We interpret the quite different length-frequency distributions of the tagged sharks recaptured by the Australian and Taiwanese gill-netters (Fig. 4) as reflecting the greater mobility of intermediate-size *C. tilstoni*, and hence their greater probability of recapture offshore by the Taiwanese.

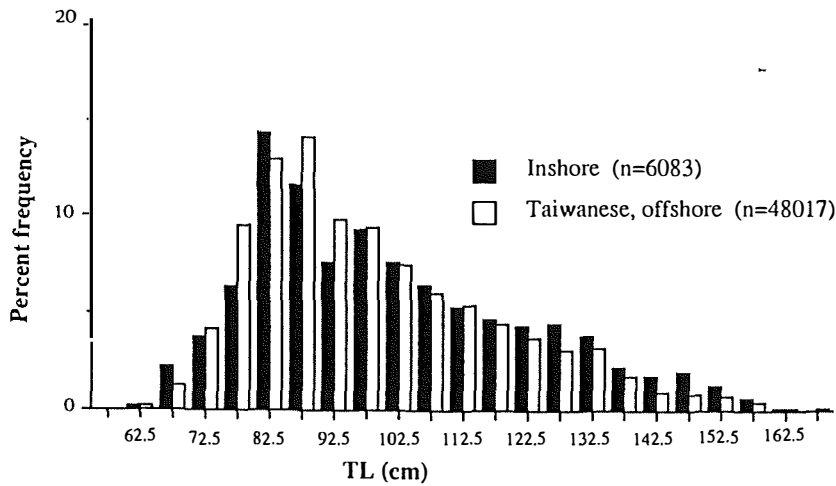


Fig 12 . Length-frequency distributions of *Carcharhinus tilstoni* captured (a) inshore by research vessels and (b) offshore by the Taiwanese fishery

Shark movements might be random with respect to time, or they may have some seasonal component. To look for seasonal effects, distance travelled was plotted against time at liberty for all the *C. tilstoni* releases in a given month. If there was any seasonal component to movements, the data might be expected to show some cyclical pattern of movements over periods of about 12 months. No pattern was apparent either when the data were examined by days at liberty following the release month, or when the data were grouped by recapture month. Seasonal movements might be related to the timing of the wet or dry seasons, the main periods of climatic change, in northern Australia. Consequently, the data for *C. tilstoni* were grouped into four categories: released and recaptured in the dry, released in the wet and recaptured in the dry, released and recaptured in the dry and released in the dry and recaptured in the wet season. For the purpose of this analysis the wet season was considered to extend from November to April and the dry season from May to October. A Kruskal-Wallis test showed no significant differences between these four groups ($H = 0.88$, 3 d.f., $p > 0.25$).

The proportion of sharks moving from the inshore Australian fishery to the offshore Taiwanese fishery was calculated using the modification of the Bayliff (1979) method together with effort and recapture data given in Table 10. For the two year period from July 1984 to June 1986. P was calculated to be 0.025 for *C. tilstoni*, 0.030 for *C. sorrah* and 0.019 for *C. maclohi*. These results were corrected for the additional mortality suffered by gill-net and longline released sharks, which increased the values slightly to 0.028, 0.031 and 0.023 for *C. tilstoni*, *C. sorrah* and *C. maclohi* respectively.

Table 10 . Shark recaptures and standardised fishing effort, by fishery.

Fishery	Number of Recaptures			Effort
	<i>C.tilstoni</i>	<i>C.sorrah</i>	<i>C.maclohi</i>	
Australian gillnet	61	18	6	21301 HMND
Australian prawn trawl	4	2	3	10983 days
Taiwanese gillnet	49	18	4	640800 kmh
Total	114	38	13	

Discussion

Suitability of tags

The long term loss rate of tags appeared to be quite low (0.05 yr^{-1} for *C. tilstoni*), and the probable major cause is growth in thickness of the fin, causing embedding and subsequent pulling through of the tags. This could be expected to vary according to whether the tag was applied nearer the thicker base of the fin, or closer to the tip. This cause of tag loss could also be expected to be less in smaller species such as *C. macloiti*. Davies and Joubert (1967) carried out tank and field tests with Jumbo Rototags applied to various carcharhinid species and, based on sharks which had been at liberty for up to 8 months, considered the tags would last for 2–3 years before shedding. They cited thickening of the fin as a probable cause of shedding but noted that designing tags with longer shafts would not necessarily solve this problem as loosely fitting tags would be likely to cause excessive movement and irritation. In tank tests they noted vertical movement of tags in the fin due to water passage over the tag blades. Davies and Joubert (1967) and Kato and Carvalho (1967) found higher tag loss with Rototags and Jumbo Rototags placed in the anal fin and second dorsal fin, than in the first dorsal fin. Davies and Joubert (1967) reported a tag shedding rate of 4% per year for *Carcharhinus obscurus* (LeSueur) and 7% for *Carcharhinus brevipinna* (Muller & Henle) which were tagged in the first dorsal fin and had been at liberty for up to 135 days. However, these rates appear to have been estimated from tags washed up on the beach, probably ripped out of the fins when sharks fouled the beach-protection set nets. In some cases, Jumbo Rototags have been retained for long periods by sharks: a *Carcharhinus plumbeus* (Nardo) was recaptured after nearly 23 years (Jack Casey, NMFS, Narragansett, Rhode Island 02882, personal communication), *Lamna nasus* (Bonnaterre) after 13 years, *Galeorhinus galeus* (Linnaeus) after 12 years and *Prionace glauca* after 11 years (Stevens 1990).

The colour of the tags made no difference to the number returned. Olsen (1952) found no difference in return rates of *G. galeus* tagged with white or grey Petersen disc tags.

Comparison of the return rates for the Jumbo tags and smaller Rototags was only possible for one species, *C. macloiti*, and the result was nearly significant ($p = 0.055$). It is possible that the larger tags applied to this relatively small shark adversely affected their survival. Tag breakage was observed in three tagged *C. tilstoni* at liberty for approximately 5 years. However, it is not clear whether they were broken while on the shark, or only after capture and freezing.

Tagging mortality

The usual methods for assessing mortality due to tagging are by keeping the fish under observation, or by comparing return rates from fish released in varying states of vigor or tagged in different ways (Ricker 1975). In the present study it was not possible to keep tagged sharks in captivity, and only one type of tag was used because it was considered to be the most suitable. However, three different capture methods were used to obtain sharks for tagging, and this proved to have an important influence on the survival of tagged sharks.

Gill-netting was the most effective method for capturing sharks. We used were either 500 or 1000 m gill-nets, and made set times as short as practical to minimize capture mortality. However, gill-net releases of tagged sharks resulted in about half the rate of recaptures as handline releases. Similarly, longline releases resulted in about one third the rate of recaptures as handline releases. Results obtained from tagging studies on sharks in which either gill-netting or longlining were the only methods used would need to be carefully assessed.

Tag return rates

The return rate for *C. tilstoni* was higher than for *C. sorrah* or *C. macloiti*. Lyle (1987a) found that while *C. tilstoni* dominated gill-net catches, *C. sorrah* dominated longline catches, suggesting that, for reasons for which we have no explanation, *C. sorrah* is less susceptible to gill-net capture than *C. tilstoni*. Because of the smaller size of *C. macloiti*, it is probably less susceptible to capture by the Australian and Taiwanese gill-netters, due to gear selectivity.

The high number of returns from Australian gill-netters which exert relatively little fishing effort in terms of the overall fishery, is a result of fishing in inshore waters where most of the sharks were released. The limited movement shown by the main species must also contribute to the high number of recaptures. In contrast, the comparable number of returns from Taiwanese vessels which fish offshore where relatively few sharks were tagged, is a result of very high fishing effort. The lower return rate from prawn trawlers probably reflects the inefficiency of this trawl gear in catching these active sharks.

There were significant differences in the proportions of the three major species returned by each fishery and it was apparent that the prawn trawl fishery was responsible for these differences. Prawn trawlers caught fewer *C. sorrah* and more *C. macloiti* than expected. These results may be partly explained by considering the size composition of sharks caught by the three fisheries (Fig. 4). The size composition of *C. macloiti* is essentially the same in each fishery, the modal length being about 60 cm FL. *C. tilstoni* caught by prawn trawlers also have a modal length of about 60 cm FL, significantly smaller than specimens caught by Australian or Taiwanese gill-netters. It appears that prawn trawlers tend to catch the smaller sharks of about 60 cm FL, larger fish probably being able to avoid the gear more easily. The size composition of *C. sorrah* caught by the three fisheries is essentially the same. It appears that the catchability of all size ranges of *C. sorrah* by prawn trawl is low; this species may be better able to avoid the net, or they may show some behavioural differences which render them less liable to capture on the bottom.

Shark movements

Even though some sharks travelled considerable distances, over 1000 km in some cases, these movements were mainly along-shore. Most sharks appeared to move very little, with 65% of *C. tilstoni* and 48% of *C. sorrah* being caught within 50 km of the tagging site.

C. macloiti appeared to be more mobile, with only 29% being caught within 50 km of the tagging site, and with a median distance travelled twice that of *C. sorrah*, and six times that of *C. tilstoni*. All three species are inshore sharks of the continental and insular shelves and might be expected to show movements intermediate between the extensive migrations of oceanic species (Casey 1985; Stevens 1990) and the restricted movements of some tropical reef-associated sharks (Randall 1977; Stevens 1984; Carrier and Luer 1990). Why *C. macloiti* should make longer movements than *C. tilstoni* or *C. sorrah* is unclear. Movements are most likely to be associated with feeding or reproduction. All three species have similar diets and reproductive cycles in northern Australia; the only difference is that *C. macloiti* gives birth in about July while the other two species give birth in about January (Stevens and McLoughlin 1991).

The fastest movements observed from our tag returns were 24.6 km/day for a *C. tilstoni* (715 km over 29 days), followed by 18.6 and 18.3 km/day (both at liberty for 1 day) for a *C. macloiti* and *C. amboinensis*. The next highest velocities were 8 km/day, with a steady decrease after this point. Francis (1988) reported a maximum velocity of 21 km/day for *Mustelus lenticulatus* (Phillips), and pointed out that estimates of velocity based on tag returns are likely to be under estimates because they are based on minimum sea distances travelled, and the sharks may have been at the recapture site for some time. When the velocities are expressed in terms of body lengths per second (bl/s) our two highest velocities are 0.35 and 0.33 bl/s for *C. tilstoni* and *C. macloiti* respectively. This is comparable to the values of 0.3-0.4 bl/s for routine activity levels in *Negaprion brevirostris* (Poey), based on theoretical, laboratory and telemetric studies (Gruber *et al.* 1988).

In this study, we found no significant difference between the distances travelled by males or females for the four shark species for which we had the most data. Francis (1988), in a tagging study of *Mustelus lenticulatus* from New Zealand, found that females travelled further than males.

Our finding that *C. tilstoni* in the 65–75 cm FL (81–94 cm TL) size range move greater distances is of some interest. These fish are immature; maturity in *C. tilstoni* is reached at 110 cm for males and 115 cm TL for females (Stevens and Wiley 1986). In the majority of shark species studied, the juveniles, which are often confined to nursery areas, tend to show more restricted movements than the adults (Olsen 1954; Casey 1976; Stevens 1976; Francis 1988; Gruber *et al.* 1988). Seasonal movement in several shark species has been demonstrated, probably associated with feeding or reproduction (Olsen 1954; Stevens 1976; Casey 1976, 1985). However, we could not detect any seasonal component to the movements of *C. tilstoni* in this study. It was evident from plots of distance travelled versus time at liberty that the majority of shark species examined are capable of dispersing very quickly from being tagged- some of the highest distances travelled occurred about 30 days after tagging.

Catch data suggests that catch per unit effort of *C. tilstoni* and *C. sorrah* is four to ten times higher in inshore areas than in offshore areas. As a result of lower catch rates and unfavourable weather conditions offshore we released only 271 of the 10511 tagged sharks

offshore. Of these offshore releases, 5.8% of *C. tilstoni*, no *C. sorrah* and 3.3% of *C. maclovi* were recaptured offshore; no fish released offshore were recaptured inshore. Consequently we could only estimate movement from inshore to offshore. We found, after fishing effort is taken into account, that only about 2.8 % of *C. tilstoni* and 3.1% of *C. sorrah* were recaptured offshore by the Taiwanese fleet during the period July 1984 to June 1986. These estimates are not affected by tag shedding or non-reporting of tags, provided these factors are the same for the inshore and offshore fisheries.

Lavery and Shacklœ (1989) found no compelling evidence to suggest that genetically distinct populations of *C. tilstoni* or *C. sorrah* existed in Australian waters. They found relatively low levels of genetic variation in both species and estimated the number of migrants per generation as between 350 and 3500 for *C. tilstoni* and between 750 and 7500 for *C. sorrah*. They noted that lower levels of heterogeneity observed in *C. sorrah* (relative to *C. tilstoni*) were consistent with their higher migration estimates for this species. Lavery and Shacklee (1989) stated that the observed levels of heterogeneity in both species suggested considerable movement of individuals between areas citing preliminary tagging results in support of this theory. The more extensive tag recapture data presented in this study support the idea that *C. sorrah* is more mobile than *C. tilstoni* but suggest that the movements of both species are more restricted than was first thought. While the movements would provide sufficient gene flow to prevent genetic stock differentiation they may be insufficient to prevent heavy fishing pressure in one area reducing the local population of sharks. This suggests that the heavy fishing pressure offshore by the Taiwanese was unlikely to have had a major effect on inshore populations fished by Australian vessels.

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Northern tagging project yields interesting results

A RESEARCH program concentrating on sharks, tuna and macerels off northern Australia is beginning to produce some interesting results.

Four cruises in this Northern Pelagic Fish Stock Research Program (NPFSSRP) have been completed since it began in January 1984. (See *Australian Fisheries* December 1983.)

A total of 5247 sharks have been tagged and 53 recaptured. Several sharks have made substantial movements across northern Australia, travelling straight-line distances of up to 1148 km. A number of sharks have moved offshore from inshore areas closed to foreign (Taiwanese) fishing, onto the commercial grounds.

Tagging shows that there is some mixing of *Carcharhinus limbatus* and *C. sorrah* (commonly known as blacktip sharks) between different areas, but life-history information suggests that there are two stocks of *C. limbatus*.

Sharks, in particular *C. limbatus* and *C. sorrah*, comprise a greater proportion of the inshore catch, while longtail tuna (*Thunnus tonggol*) and spanish mackerel (*Scomberomorus* spp.) are more abundant in the offshore Taiwanese fishery.

Exploratory fishing in inshore regions has yielded large catches, with up to seven tonnes taken in 1000 metres of net for five minutes fishing time. Average catches by the Taiwanese are about one t from 8000 m of net fished for six hours.

The NPFSSRP is a co-operative study between CSIRO, the Department of Primary Industry, and the Northern Territory, Queensland and Western Australian fisheries authorities. The program is jointly funded

by J. D. Stevens and A. G. Church
Dr John Stevens and Mr Tony Church are biologists with CSIRO's Fisheries Research Division*.

by the Fishing Industry Research Trust Account, the Northern Territory Fishing Industry Research and Development Trust Account and the Queensland and Western Australian State Fisheries.

It is a biological investigation of northern Australian pelagic fish stocks which currently support a licensed Taiwanese fishery of about 9000 t a year and a small developing Australian fishery.

Sharks comprise 62 per cent by weight of the total Taiwanese catch; the two main species, *C. limbatus* and *C. sorrah*, contribute 37 per cent and 12 per cent by weight respectively. Bony fish account for 38 per cent of the catch with *T. tonggol* and *Scomberomorus* spp. the most abundant, providing 24

per cent and 8 per cent of the catch by weight respectively.

The main objectives of the program are to obtain information on the size, geographical distribution, mortality, recruitment and yield potential of northern pelagic stocks currently taken by the Taiwanese gillnet fishery off northern Australia. This, together with data previously collected by the CSIRO from the Observer Program (see *Australian Fisheries* February 1984) on the growth, reproduction, population structure (in terms of size composition and sex ratio), and dietary habits of sharks will be used by the Department of Primary Industry (DPI) for planning and implementation of improved management strategies for the fishery.

Vessel and gear

The 21-m commercial gillnet vessel *Rachel* has been chartered for



Figure 1. Tagging a blacktip shark (*Carcharhinus limbatus*).

*PO Box 21, Cronulla, NSW 2230.

the program. It has two net drums, one holding two 500-m panels of 15-cm mesh monofilament nylon gillnet, each 10 m deep, and the other containing a net incorporating panels of 10, 15, 20 and 25-cm mesh to test mesh selectivity.

Rachel's operations are less labour-intensive than the Taiwanese gillnet vessels: the gear can be set and hauled by as few as two people. The hydraulic net drums are used to haul the net over the bow and along the full length of the vessel. Other fishing gear includes a 60 hook/1000m longline, troll lines and handlines.

Methods and preliminary results

Several methods are being used to answer our questions: a large-scale tagging project, exploratory fishing, biological and electrophoretic sampling, and gear selection experiments. Sampling is being carried out between Broome and Cape York, both in inshore regions closed to Taiwanese fishing, and offshore on the main commercial grounds.

Shark tagging

Although all species are being tagged (17 species to date) effort is concentrated on the two common blacktip sharks, *C. limbatus* and *C. sorrah*. Sharks must be healthy to be suitable for tagging: two main methods are used for catching them. During the day sharks are berleyed to the boat using chopped fish, and then captured by handlines with barbless hooks. At night, short sets are made with the gillnet.

We found on the first cruise that one km of 15-cm mesh monofilament net, set and hauled immediately, often resulted in excessively large catches, and thus heavy mortality of sharks towards the end of the haul. Subsequently the net was divided in two so that it could be used as single 500-m lengths in areas where sharks were abundant.

The sharks are brought on board, measured, marked with a plastic tag clipped together through a pre-punched hole in the first dorsal fin, and then released. (See Figure 1.) Contrary to popular opinion, sharks are delicate and require

Table 1. Tag-recapture information for five species of shark from which returns have been made

Species	No. tagged*	No. recaptured	Max. time of liberty (days)	Max. distance travelled (km)
<i>Carcharhinus limbatus</i>	2539	41	570	1148
<i>C. sorrah</i>	1532	7	482	741
<i>C. maclovi</i>	800	2	30	217
<i>C. amboinensis</i>	81	2	43	13
<i>Galeocerdo cuvieri</i>	14	1	48	167

* 281 sharks of a further 12 species have been tagged from which no returns have been reported.

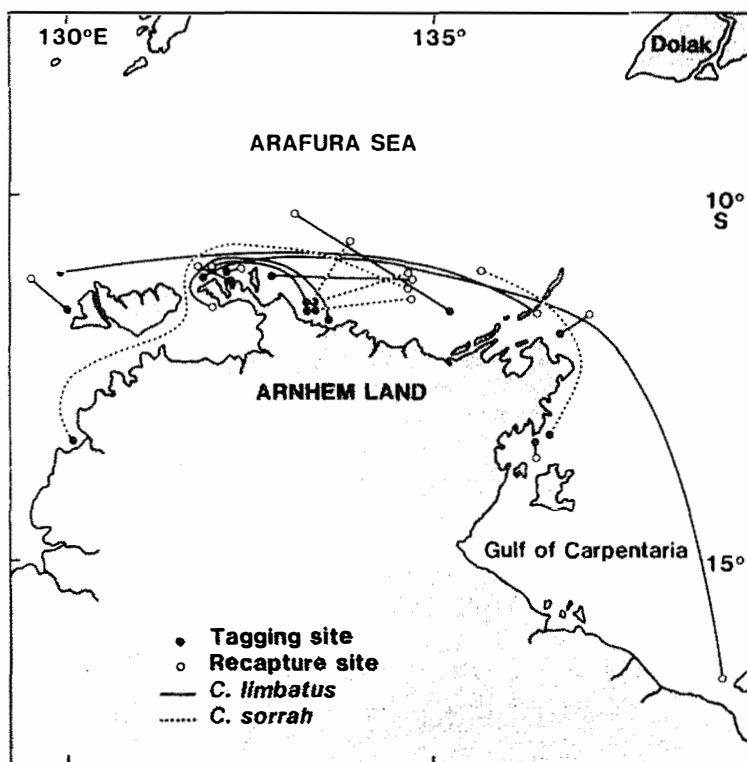


Figure 2. Significant movements shown by *Carcharhinus limbatus* and *C. sorrah*.

careful handling to ensure maximum survival. Experience during a pilot tagging study by the Northern Territory Fisheries Division and CSIRO has indicated that sharks caught by gillnet survive longer in the net during winter, when lower water temperatures result in a lowering of the shark's metabolic rate.

Of 5247 sharks tagged by the end of May (including 705 tagged in a pilot study between February and December 1983) 53 have been recaptured.

This return rate is much lower

than expected, probably because the Taiwanese reached their annual catch quota early. Consequently they have not been fishing for some three months, during which time over 3000 sharks have been tagged.

Recapture details for the five species from which returns have been made are shown in Table 1. A further 12 species have been tagged from which no recaptures have been reported yet.

Significant movements by *C. limbatus* and *C. sorrah* are shown in Figure 2. A *C. limbatus* tagged off Port Essington travelled a straight-

line distance of 1148 km to near Wellesley Island in the south-eastern Gulf of Carpentaria in 77 days. A *C. sorrah* tagged in Anson Bay moved 741 km in 329 days and was recaptured in the Taiwanese commercial grounds west of the Wessel Islands. Several other sharks have moved from inshore closed areas into the commercial area.

This kind of information on shark movements will aid in defining the geographical limits of the stock(s). Tagging will also provide information on growth rates and will help in estimating recruitment, mortality and stock size.

Mackerel and tuna tagging

Fish are caught by trolling using lures with barbless hooks. A nylon dart-tag is implanted below the second dorsal fin while the fish is restrained and measured in a tagging cradle.

Twenty-six narrow-barred spanish mackerel (*S. commerson*) have been tagged, together with two *S. munroi* and one *S. semifasciatus*. No recaptures have been reported to date. No longtail tuna, *T. tonggol*, have been trolled by *Rachel* and very few have been caught in the gillnet. However, a few have been tagged further offshore by the DPI Observer vessel.

Electrophoresis

Tissue samples from *C. limbatus*, *C. sorrah* and *S. commerson* are being collected for electrophoretic analysis by Dr J. Shaklee at the CSIRO Marine Laboratory at Cleveland. Electrophoresis, a procedure in which the types of proteins in muscles are analysed, should provide an independent method of examining whether the population of a particular species is made up of a single stock or several stocks.

While these three species range throughout northern Australia it is important in developing management strategies to know whether each exists as a single stock or several stocks. For example, is the Taiwanese fishery in the Arafura Sea also affecting populations in the Gulf of Carpentaria, Timor Sea and North West Shelf, or do these regions contain separate stocks

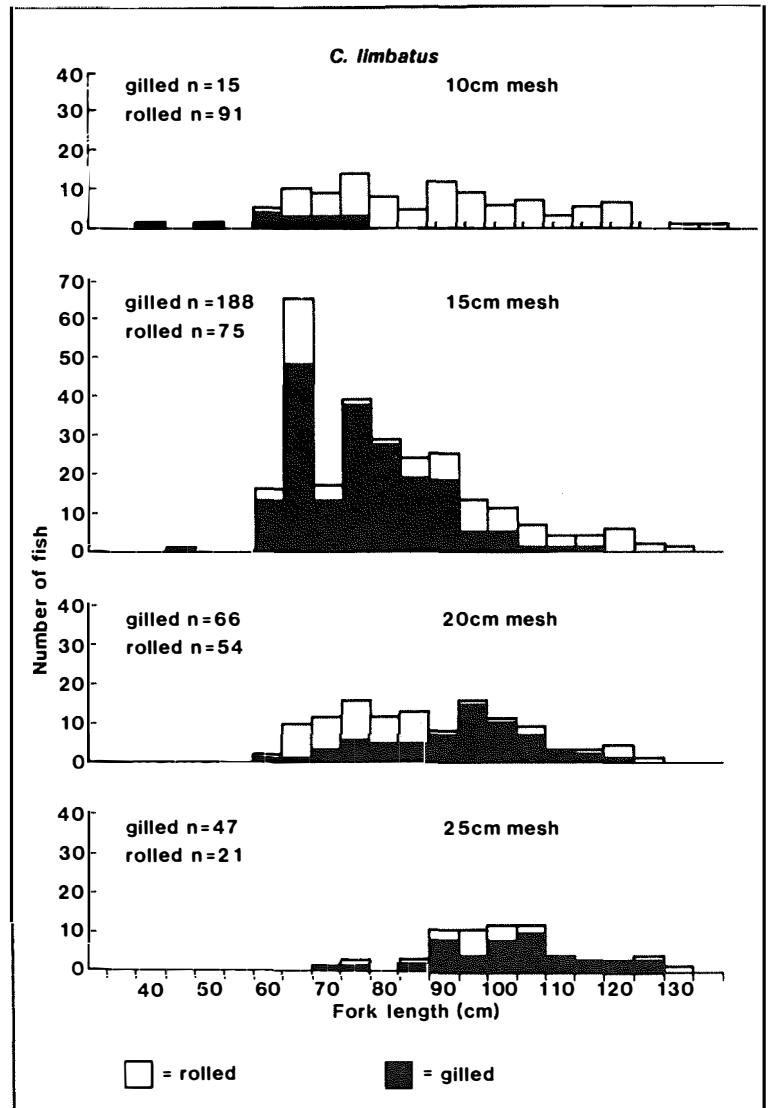


Figure 3. The size composition of the *Carcharhinus limbatus* catch in the mesh selectivity net.

which can be exploited independently? Inshore areas closed to Taiwanese fishing may be acting as reserves for the offshore grounds. If so, and these areas become heavily exploited, the accumulated fishing pressure may have disastrous consequences for the stock.

While results from electrophoretic studies are not yet available, tag returns from sharks certainly show some mixing between different regions.

Gear selectivity

Gillnets may not catch fish of different sizes equally well, so the

fish in the sample caught may not be representative of the actual population. The parameters derived for use in stock assessment models obtained from the sample population may therefore be biased, so it is necessary to test the selectivity of the gear used for sampling.

Gear selectivity is being investigated using a gillnet consisting of four separate panels of 10, 15, 20 and 25-cm mesh monofilament nylon. Each panel is 200 m long, 10 m deep, has a hanging coefficient of 0.63 and is separated from adjoining panels by about 100 m of headrope.

The net design resulted from

previous trials (by Dr J. Lyle of the NT Fisheries Division) which used a three-panelled net (10, 15 and 20 cm) to demonstrate the influence of mesh size on species and size composition of catches.

Selectivity effects are complicated by the fact that many sharks are captured by rolling rather than being gilled in the net, particularly large sharks in small mesh sizes. The separation of gilled and rolled individuals (see Figures 3 and 4), and the use of analytical techniques developed for the southern gummy shark fishery by Dr G. Kirkwood (CSIRO) and Dr T. Walker (Victorian Fisheries and Wildlife) should provide information allowing correction of any bias in the size composition of catches.

From results collected to date, the average fork lengths (snout to the fork of the tail) for gilled *C. limbatus* captured in the 10, 15, 20 and 25-cm mesh sizes are estimated to be 64, 76, 92 and 102 cm respectively. For *C. sorrah* these lengths are 71, 74 and 87 cm in the 10, 15 and 20-cm meshes respectively. Only one *C. sorrah*, 70-cm fork length, has been captured in the 25-cm mesh net, and this was by rolling.

Selectivity effects are also being examined by comparing the size composition of catches of the gillnets with catches of longlines set adjacent to the nets.

Exploratory fishing

Exploratory fishing is being conducted in areas closed to foreign vessels using either 500 or 1000 m of 15-cm mesh monofilament gillnet. Information on species composition, catch and effort are being collected in view of the developing Australian fishery. This work complements previous studies carried out by Dr J. Lyle and Mr G. Timms of the Northern Territory Fisheries Division. (See adjacent article.)

Table 2 shows that *C. limbatus* and *C. sorrah* together comprise 71.4 per cent by number of the total catch made by *Rachel* in inshore waters, while the only commercially important teleost (bony fish) contributing more than 1 per cent of the total catch is *Scomberomorus* spp (1.3 per cent). By comparison, in the offshore Taiwanese catch, *T. tong-*

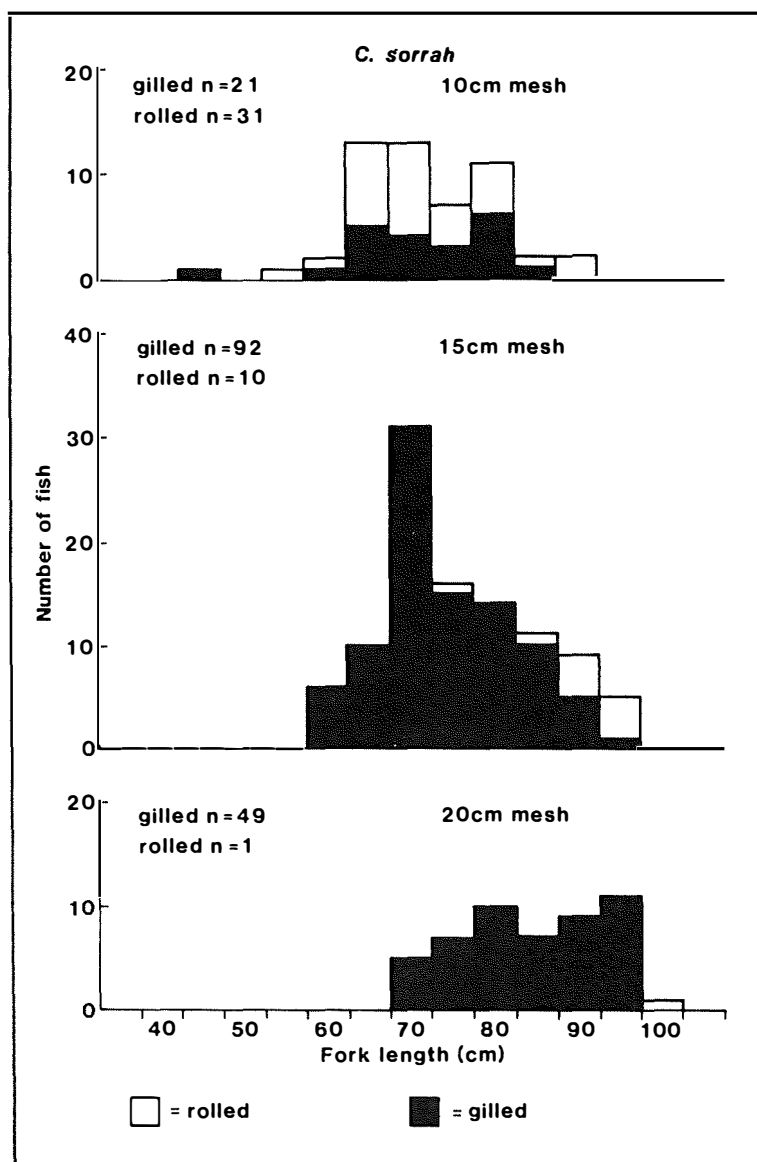


Figure 4. The size composition of the *Carcharhinus sorrah* catch in the mesh selectivity net.

gol is the most abundant species, accounting for 40.2 per cent by number, with *C. limbatus*, *C. sorrah* and *Scomberomorus* spp comprising 23.3, 11.5 and 5.8 per cent of the catch respectively.

In inshore areas very large catches were sometimes obtained, with up to seven t resulting from five minutes' fishing time (time between completion of set and start of haul) with 1000 m of monofilament net. However other regions produced poor results, indicating considerable patchiness in shark distribution.

On average the Taiwanese fish some 8000 m of multifilament net for six hours for a catch of about one t on the offshore grounds. By using either 500 or 1000 m of net on *Rachel*, depending on the concentration of sharks in a given area, the majority of sharks can be brought on board alive, thus maximising product quality.

Handlining in productive areas also guarantees a good quality product. On *Rachel* up to 80 sharks have been handlined in a seven-hour period.

Offshore fishing is also being carried out on the commercial Taiwanese grounds to compare catch rates with those from inshore areas. Earlier work by Dr Lyle suggested that the abundance of some species was related to certain environmental parameters, in particular water turbidity. More extensive measurements of these parameters are being recorded by *Rachel* at each fishing location to examine this question more thoroughly.

Biological information on shark, tuna and spanish mackerel is being collected from exploratory fishing sites for comparison with data obtained previously from the Taiwanese commercial area, through the DPI Observer program.

Variations in life-history data between different regions can provide further information about stocks. For example while tag returns already show some mixing of *C. limbatus* across northern Australia, there are variations in the size at sexual maturity and maxi-

Table 2. Species accounting for one percent or more of the total gill-net catch by number from 'Rachel'


<i>Species</i>	<i>Number caught</i>	<i>% of total catch</i>
<i>Carcharhinus limbatus</i>	4709	47.3
<i>C. sorrah</i>	2375	23.9
<i>C. macroti</i>	1645	16.5
<i>C. amblyrhynchoides</i>	141	1.4
<i>C. amboinensis</i>	97	1.0
<i>Rastrelliger kanagurta</i>	134	1.3
<i>Scomberomorus</i> spp.	132	1.3

mum size of this species, which suggest the presence of two stocks.

Observer program

The collection of tag-return information needs to continue for a period of at least three years after completion of field studies. The Commonwealth-funded observer program is an important part of the study: it checks the proportion of tags reported by the Taiwanese gill-netters. It will also continue to be an

important source of information on species composition, length-frequency and catch-effort data from the Taiwanese fishery.

The combination of length-frequency distributions and length-at-age information allows a relative length-at-age frequency distribution to be determined for the exploited population. Together with tag-recapture and catch-effort data this will provide information on recruitment, mortality and ultimately yield estimates for the fishery. 

Shark biology

The biology of two commercially important carcharhinid sharks from northern Australia. J. D. Stevens and P. D. Wiley. *Australian Journal of Marine and Freshwater Research*, 1986, **37**, 671-88

Observations on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzroyensis* (Whitley) from northern Australia. J. M. Lyle. *Australian Journal of Marine and Freshwater Research*, 1987, **38**, 701-10.

The biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from northern Australia. J. D. Stevens and J. M. Lyle. *Australian Journal of Marine and Freshwater Research*, 1989, **40**, 129-46.

Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. J. D. Stevens and K. J. McLoughlin. (In preparation).

Age and growth of two commercially important carcharhinid sharks from northern Australia. S. R. Davenport and J. D. Stevens. *Australian Journal of Marine and Freshwater Research*, 1988, **39**, 417-33.

Mortality rates in *C. tilstoni* and *C. sorrah*. (J. D. Stevens, working paper)

NORTHERN PELAGIC FISH STOCK RESEARCH

**Final Report to the Fishing Industry Research
and Development Council
Projects 83/49 and 86/87**

Part 2

Biology of Two Commercially Important Carcharhinid Sharks from Northern Australia

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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.

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.

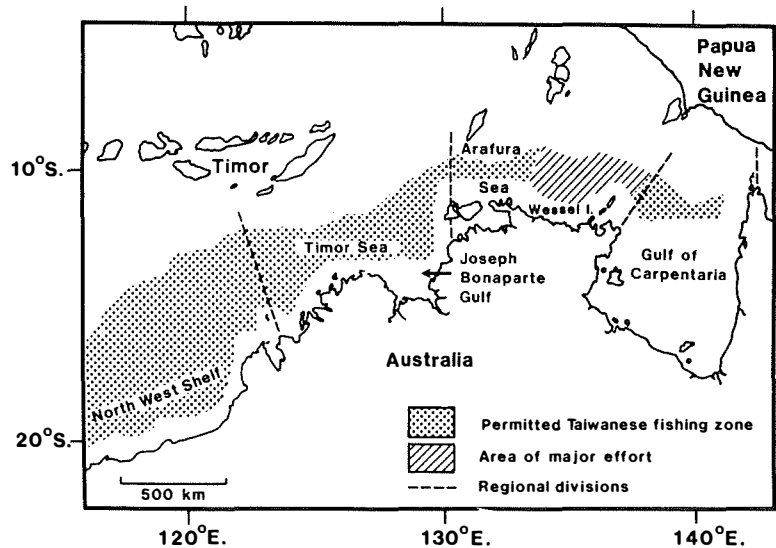


Fig. 1. Permitted Taiwanese gill-netting area off northern Australia in 1983.[†]

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 <i>C. tilstoni</i>		Number of <i>C. sorrah</i>	
		Measured	Dissected	Measured	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
<i>C. tilstoni</i>	Male and female	311	62.0–206.5	TW = $4.75 \times 10^{-3} TL^{3.06}$ TL = $6.65 TW^{0.311}$	0.91	< 0.001
<i>C. tilstoni</i>	Male and female	724	57.7–197.7	TL = $1.235 FL + 0.913$ FL = $0.803 TL - 0.075$	0.99	< 0.0001
<i>C. sorrah</i>	Male	53	54.3–107.3	TW = $7.09 \times 10^{-4} TL^{3.46}$ TL = $9.90 TW^{0.266}$	0.92	< 0.001
<i>C. sorrah</i>	Female	164	71.6–135.6	TW = $5.45 \times 10^{-4} TL^{3.51}$ TL = $11.10 TW^{0.255}$	0.90	< 0.001
<i>C. sorrah</i>	Male and female	626	53.0–151.8	TL = $1.196 FL + 4.72$ FL = $0.828 TL - 3.28$	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:

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

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: $P > 0.05$). For *C. sorrah* there is a significant difference between the weight-length relationships for males and for females (analysis of covariance: slopes and intercepts $P < 0.05$), 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 $P > 0.05$, intercepts $P < 0.05$), 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
<i>C. limbatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	0	1	2	0	2	0	4	0	1	1	
<i>C. tilstoni</i>	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. 2a. 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. 2b. 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).

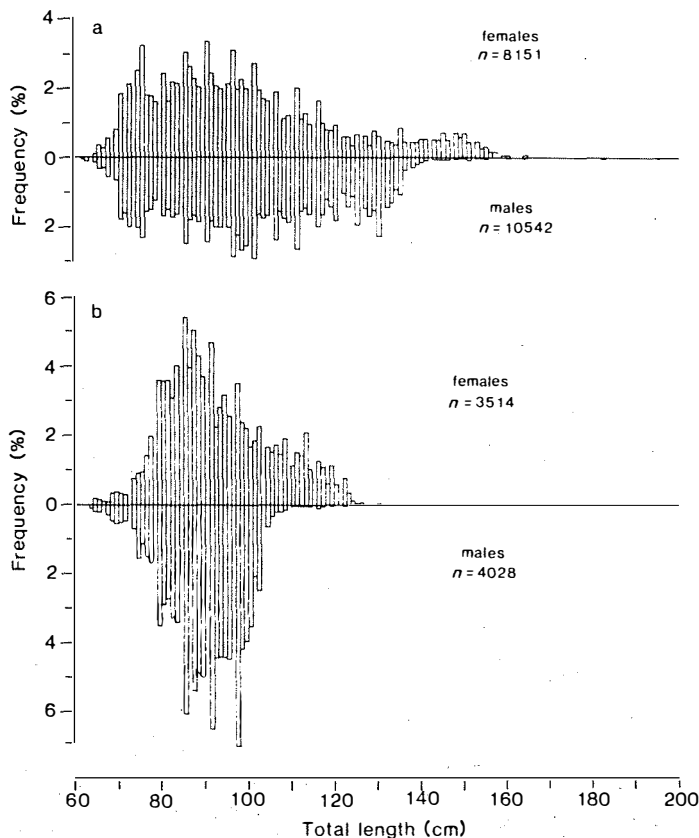


Fig. 2. Length-frequency distributions for *C. tilstoni* (a) and for *C. sorrah* (b) taken by the Taiwanese gill-net fishery in the Arafura and Timor Seas (1981–1983).

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 3a and 3c). 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. 3a). 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 $P < 0.05$; post-partum $P < 0.001$). 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.

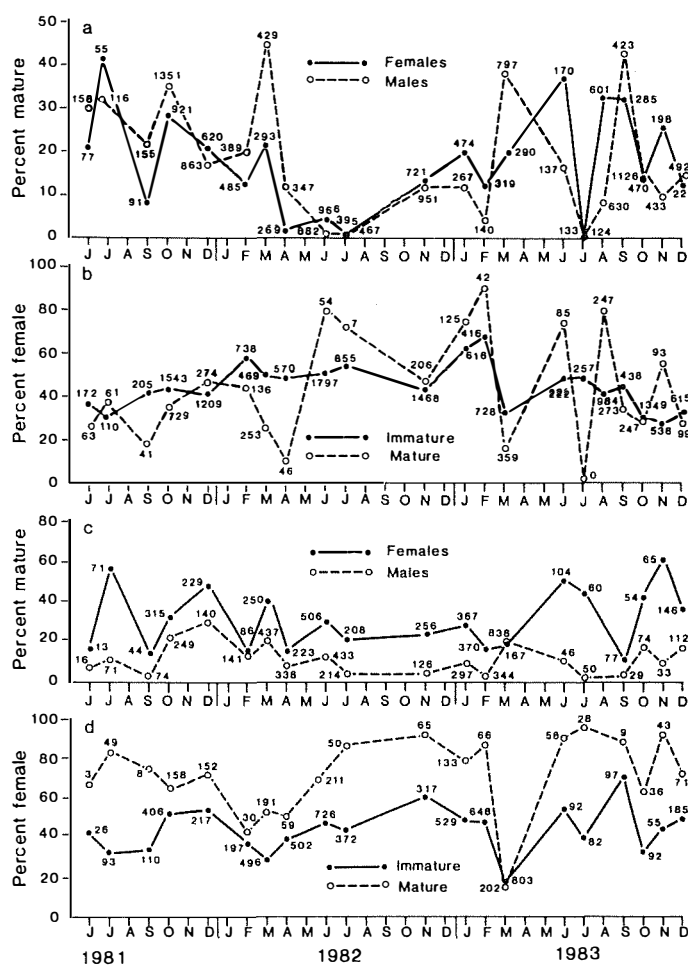


Fig. 3. Monthly proportions of mature *C. tilstoni* (a) and of the sexes for *C. tilstoni* (b) and of mature *C. sorrah* (c) and of the sexes for *C. sorrah* (d) from Taiwanese gill-net catches in the Arafura and Timor Seas. Numbers are sample size.

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, $P < 0.001$). 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, $P < 0.001$). 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

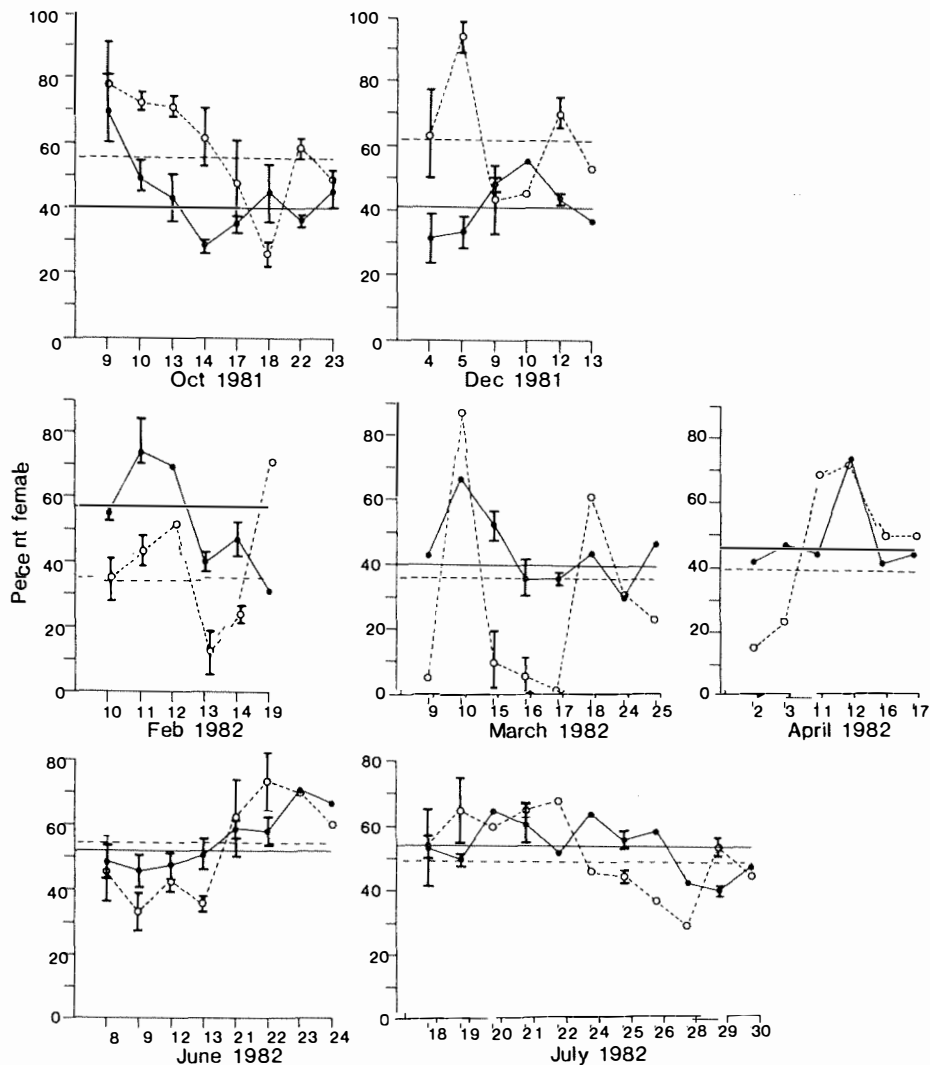


Fig. 4. Daily proportions of the sexes for *C. tilstoni* and *C. sorrah* from 7 months of Taiwanese gill-net catches in the Arafura and Timor Seas. Catches of from one to three vessels were used on any one day. x-Axis is day of the month; straight line is mean monthly value; bars are range of daily values.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

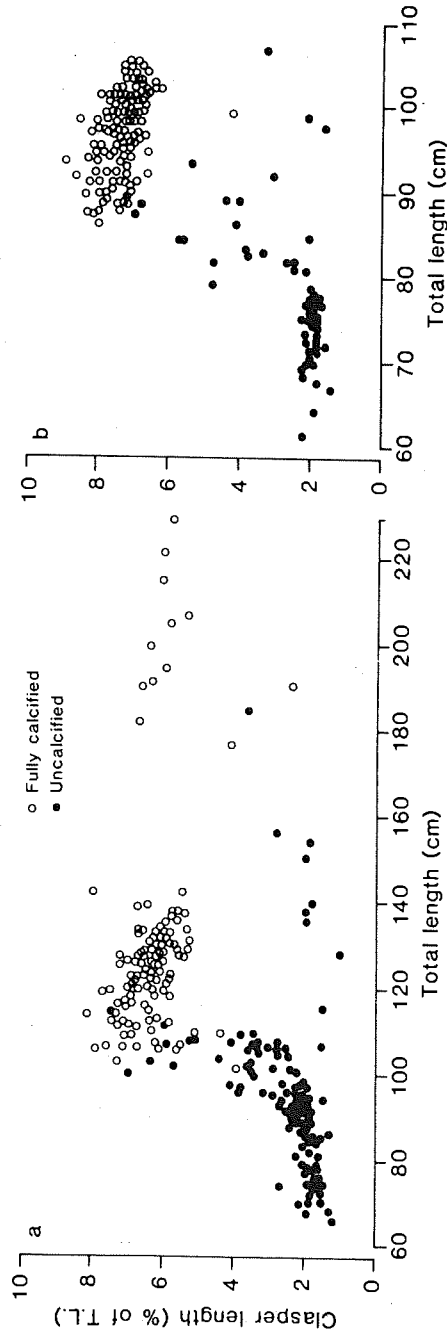


Fig. 5. Relationship between clasper length (expressed as a percentage of total body length) and total body length for *C. tilstoni* and *C. limbatus* (a) and for *C. sorrah* (b).

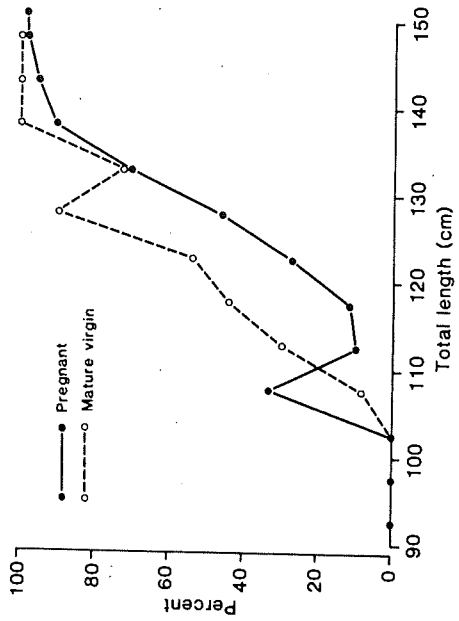


Fig. 6. Percentage of virgin *C. tilstoni* that were mature, and the percentage of *C. tilstoni* that were pregnant, by 5-cm length groups.

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 3a and 3c), 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 3a, 3b, 3c and 3d).

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. 5a. 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. 5a 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. 5b). 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 [$<0.30\%$ of body weight (BW)], during December it increased rapidly, reaching a peak in February (0.96% BW), after which it declined rapidly until May (Fig. 7a). 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. 7b). 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

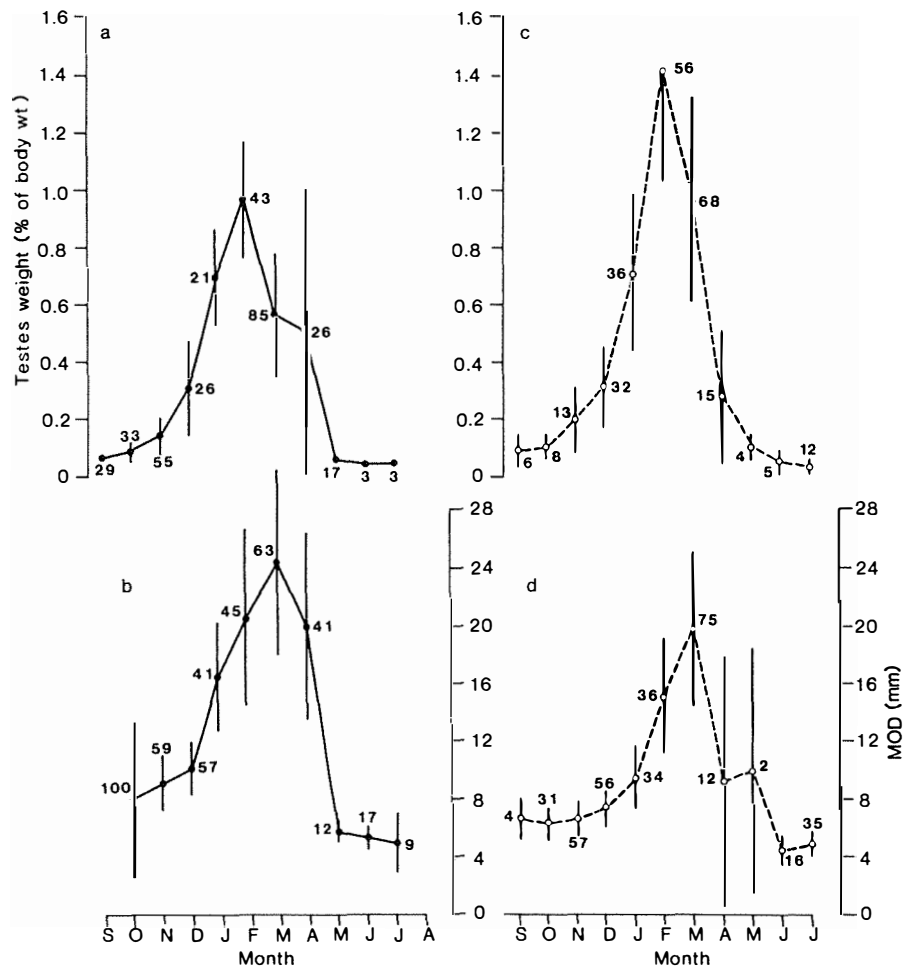


Fig. 7. Seasonal cycle of testes weight (expressed as a percentage of total body weight) for *C. tilstoni* (a) and for *C. sorrah* (c) and maximum ova diameter for *C. tilstoni* (b) and for *C. sorrah* (d) from the Arafura Sea, 1981–1983 data combined. Bars are standard deviation; numbers are sample 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. 7c). Maximum ovary weight (0.28% BW) and maximum ova diameter (20 mm) occurred in March (Fig. 7d). 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.

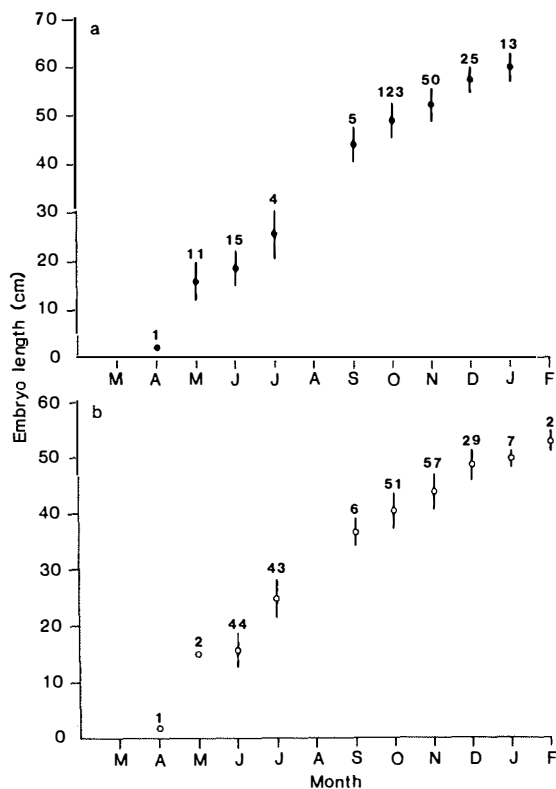


Fig. 8. Relationship between embryo length (TL) and time of year for *C. tilstoni* (a) and for *C. sorrah* (b) from the Arafura Sea. 1981–1983 data combined. Bars are standard deviation; sample sizes are numbers of litters.

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. 8a). 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. 8b). 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.

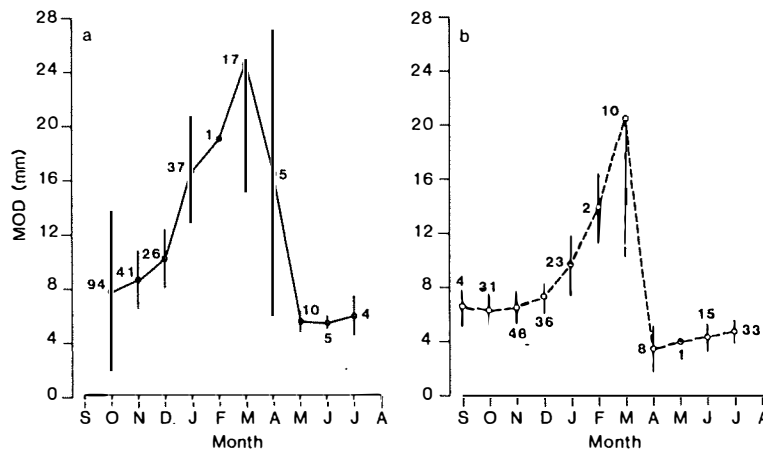


Fig. 9. Seasonal cycle of maximum ova diameter in pregnant and spent *C. tilstoni* (a) and *C. sorrah* (b) from the Arafura Sea. 1981-1983 data combined. Bars are standard deviation; numbers are sample size.

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*, $r^2 = 0.09$, $P < 0.001$; *C. sorrah*, $r^2 = 0.32$, $P < 0.001$), 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 9a and 9b 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	<i>n</i>	<i>C. tilstoni</i>			<i>n</i>	<i>C. sorrah</i>		
		% occurrence of:				% occurrence of:		
		fish	cephalopods	crustaceans		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					
		<i>C. tilstoni</i>			<i>C. sorrah</i>		
		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
<i>Thunnus tonggol</i>	P	—	1	1	—	—	—
<i>Auxis thazard</i>	P	—	1	1	—	2	2
<i>Euthunnus affinis</i>	P	—	—	—	—	1	1
<i>Rastrelliger kanagurta</i>	P	—	4	4	—	2	2
<i>Sarda orientalis</i>	P	—	1	1	—	—	—
<i>Scomberomorus</i> spp.	P	—	4	4	—	3	3
<i>Scomberomorus munroi</i>	P	—	1	1	—	—	—
<i>Coryphaena hippurus</i>	P	—	1	1	—	—	—
Hemiramphidae	P	—	5	5	—	—	—
Exocoetidae	P	—	1	1	—	2	2
<i>Chirocentris dorab</i>	P	—	—	—	—	1	1
Trichiuridae	P	1	13	14	—	7	7
<i>Megalaspis cordyla</i>	P	—	14	14	—	—	—
<i>Carcharhinus sorrah</i>	PP	—	1	1	—	—	—
<i>Hemipristis elongatus</i>	PP	—	1	1	—	—	—
<i>Carangoides gymnostethus</i>	PP	—	—	1	—	—	—
<i>Carangoides</i> spp.	PP	3	8	11	—	3	3
Carangidae	PP	9	85	94	5	13	18
Clupeidae	PP	10	46	56	1	15	16
<i>Apolectus niger</i>	PP	5	14	19	1	9	10
Sphyracidae	PP	1	—	1	—	—	—
<i>Dactyloptena</i> spp.	PP	—	2	2	1	—	1
Paralepididae	PP	—	1	1	—	—	—
<i>Rhizoprionodon acutus</i>	PD	—	1	1	—	—	—
Leiognathidae	PD	—	13	13	3	4	7
Lutjanidae	PD	—	2	2	—	—	—
<i>Arius</i> sp.	PD	—	4	4	—	1	1
<i>Mene maculata</i>	PD	—	—	—	—	2	2
Myctophidae	PD	—	1	1	—	—	—
<i>Paramonacanthus filicauda</i>	PD	—	2	2	1	—	1
Monacanthidae	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
<i>Saurida undosquamis</i>	D	1	1	2	—	—	—
Eel	D	—	2	2	1	2	3
<i>Muraenasox</i> 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					
		<i>C. tilstoni</i>			<i>C. sorrah</i>		
		S	L	T	S	L	T
Lethrinidae	D	—	1	1	—	1	1
<i>Centriscus</i> sp.	D	—	—	—	—	1	1
<i>Psettodes erumei</i>	D	—	1	1	—	—	—
Bothidae	D	—	1	1	—	1	1
Platycephalidae	D	—	1	1	—	—	—
Sciaenidae	D	1	—	1	—	—	—
Triacanthidae	D	—	1	1	—	—	—
<i>Trixiphichthys weberi</i>	D	—	1	1	—	—	—
Mullidae	D	—	4	4	—	2	2
<i>Fistularia</i> sp.	D	—	—	—	—	1	1
Scaridae	D	—	1	1	1	1	2
Priacanthidae	D	—	1	1	—	1	1
<i>Priacanthus tayenus</i>	D	2	1	3	—	—	—
Haemulidae	D	—	1	1	—	—	—
Uranoscopidae	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
<i>Loligo chinensis</i>	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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**Observations on the Biology of
Carcharhinus cautus (Whitley),
C. melanopterus (Quoy & Gaimard)
and *C. fitzroyensis* (Whitley) from Northern Australia**

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Abstract

The reproductive biology and diets of *C. cautus*, *C. melanopterus* and *C. fitzroyensis* from northern Australia are described. Males and females are usually mature at 84 and 91 cm, respectively, in *C. cautus*, 95 and 97 cm in *C. melanopterus*, and 88 and 100 cm in *C. fitzroyensis*. The species exhibit placental viviparity, have restricted breeding seasons, and individual females appear to breed annually. Breeding seasons for *C. cautus* and *C. melanopterus* are very similar: mating occurs between January and March, ovulation in February-March, and parturition in October-November. Individuals of *C. fitzroyensis* mate between May and July, ovulate between July and September, and give birth the following February-April. Gestation periods for the three species range from 7 to 9 months. Approximate sizes at birth are 40 cm for *C. cautus*, 48 cm for *C. melanopterus* and 50 cm for *C. fitzroyensis*. Mean litter sizes are 2.9 (range 1-5) for *C. cautus*, 3.8 (range 3-4) for *C. melanopterus* and 3.7 (range 1-7) for *C. fitzroyensis*. Teleost fish are an important component of the diets, with crustaceans and molluscs (mainly cephalopods) of lesser importance. Snakes are eaten by *C. melanopterus* and *C. cautus*.

Introduction

Previous studies of Australia's tropical sharks have been mainly taxonomic (e.g. Whitley 1940, 1945, 1967) and basic life-history data are limited for most species. With the implementation of the Australian Fishing Zone (AFZ) in 1979, Australia assumed responsibility for the management of the Taiwanese gill-net fishery for shark and other pelagic species off northern Australia (Millington and Walter 1981). Research programs were initiated to study the life histories of the commercially important shark species, and detailed accounts of the biology of the principal commercial species, *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes in Muller & Henle), are now available (Stevens and Wiley 1986).

Although of little commercial significance, *C. cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzroyensis* (Whitley) are relatively common in the estuarine and inshore waters of northern Australia. They also occur in the tropical and subtropical waters of Queensland and Western Australia (Garrick 1982; Compagno 1984). Elsewhere, *C. cautus* has been reported from Ugi and Solomon Islands, while *C. melanopterus* is more widely distributed, occurring from the central Pacific Ocean westward through the Indian Ocean to the Red Sea and east African coast (Garrick 1982; Compagno 1984). Virtually nothing is known about the biology of these species in Australian waters and what limited information is available has been summarised by Garrick (1982) and Compagno (1984). In this study, aspects of the reproductive biology and diets of these species from northern Australia are reported.

Materials and Methods

Sharks were collected between August 1982 and December 1986 from Darwin Harbour (12°30'S, 130°50'E.) and in waters about 4-40 km off the Northern Territory coast, primarily between longitudes 129°E. and 134°E. Gill nets were set over intertidal mudflats and immediately adjacent to the shore in Darwin Har-

bour. In the offshore region, gill nets were set to within 3 m of the surface and allowed to drift (Lyle and Timms 1984). Gill nets were made of monofilament nylon with mesh sizes of 10, 15, 17.5 or 20 cm. Most sharks were caught in either the 15- or 17.5-cm mesh gill nets. A small number of additional specimens were caught by longline.

In all, 277 specimens of *C. cautus*, 121 of *C. melanopterus* and 18 of *C. fitzroyensis* were caught in Darwin Harbour. A further 13 specimens of *C. melanopterus* and 237 of *C. fitzroyensis* were taken offshore. Ten specimens of *C. fitzroyensis* were also collected from Taiwanese commercial gill-net catches taken within the AFZ to the north of Australia.

The total length (TL) and/or fork length (FL) of the sharks were measured to the nearest centimetre. The former was determined with the upper caudal fin lobe extended parallel to the body axis. Fork lengths were converted into total lengths using relationships presented in Table 1. Subsamples of each species were weighed to the nearest 0.1 kg for total body weight (BW), and length-weight relationships were calculated (Table 1).

Table 1. Total length-body weight and total length-fork length relationships for *Carcharhinus cautus*, *C. melanopterus* and *C. fitzroyensis* from northern Australia

All relationships are highly significant ($P < 0.001$). TL, total length (cm); FL, fork length (cm); BW, body weight (kg)

Species	Sex	Sample No.	Size range (TL cm)	Relationship	r^2
<i>C. cautus</i>	♂, ♀	223	56.0-119.0	BW = $(1.42 \times 10^{-6})TL^{3.334}$	0.95 ^A
		102	55.3-112.0	TL = $1.16FL + 3.86$	0.98
				FL = $0.85TL - 2.16$	
<i>C. melanopterus</i>	♂, ♀	94	80.7-125.1	BW = $(3.25 \times 10^{-7})TL^{3.649}$	0.96 ^A
		68	48.3-125.1	TL = $1.16FL + 4.16$	0.99
				FL = $0.85TL - 2.90$	
<i>C. fitzroyensis</i>	♂, ♀	109	74.6-134.6	BW = $(1.42 \times 10^{-6})TL^{3.292}$	0.96 ^A
		176	69.0-134.6	TL = $1.19FL + 4.35$	0.99
				FL = $0.84TL - 3.27$	

^ACoefficient of determination (r^2) based on linear regression of $\ln(BW)$ against $\ln(TL)$.

Assessment of reproductive state followed Bass *et al.* (1973). Males were considered to be mature when claspers were elongated and clasper cartilages were rigid from calcification. Females were considered to be mature when distinct ova were present in the ovary, oviductal glands were fully differentiated from the oviducts, and uteri were expanded and no longer thin and strap-like. Females with vaginal hymen intact were judged to be virgin. Gonads from mature individuals of both sexes were removed, cleaned of attached epigonal tissue, and weighed to the nearest 0.1 g. Diameters of the largest ova in the ovaries were measured to the nearest millimetre to determine maximum ova diameter (MOD). Sex and length of embryos were noted.

Stomach contents were examined in subsamples of each species and occurrence of prey recorded. Recognisable food items were generally identified to family level and where possible to genus or species. The number of stomachs in which a particular prey type occurred was expressed as a percentage of the total number of stomachs that contained food.

Results

Size and Sex Ratio

Size distributions by sex are shown in Figs 1a, 2a and 3a. On average, females were larger than males and in each case the largest individuals sampled were female. The largest male and female specimens, respectively, were 101.0 and 119.0 cm TL for *C. cautus*, 112.0 and 125.1 cm TL for *C. melanopterus*, and 126.0 and 134.6 cm TL for *C. fitzroyensis*. With the exception of *C. melanopterus*, newly born individuals were not caught (refer to section on reproduction). Although there were slightly more females amongst the *C. cautus* and *C. melanopterus* samples, 52.7% and 56.6% females, respectively (Figs 1a and 2a), the sex ratios did not differ significantly from 1:1 (χ^2 test, $P > 0.05$). In contrast, there were significantly more males in the *C. fitzroyensis* sample (χ^2 test, $P < 0.001$): females accounted for only 38.1% of the total (Fig. 3a).

Size at Maturity

The claspers of immature males are short, flexible and grow slowly in relation to the length of the shark. During the adolescent phase, claspers elongate rapidly, becoming rigid from calcification when fully mature. This pattern of development typically produces an S-shaped curve

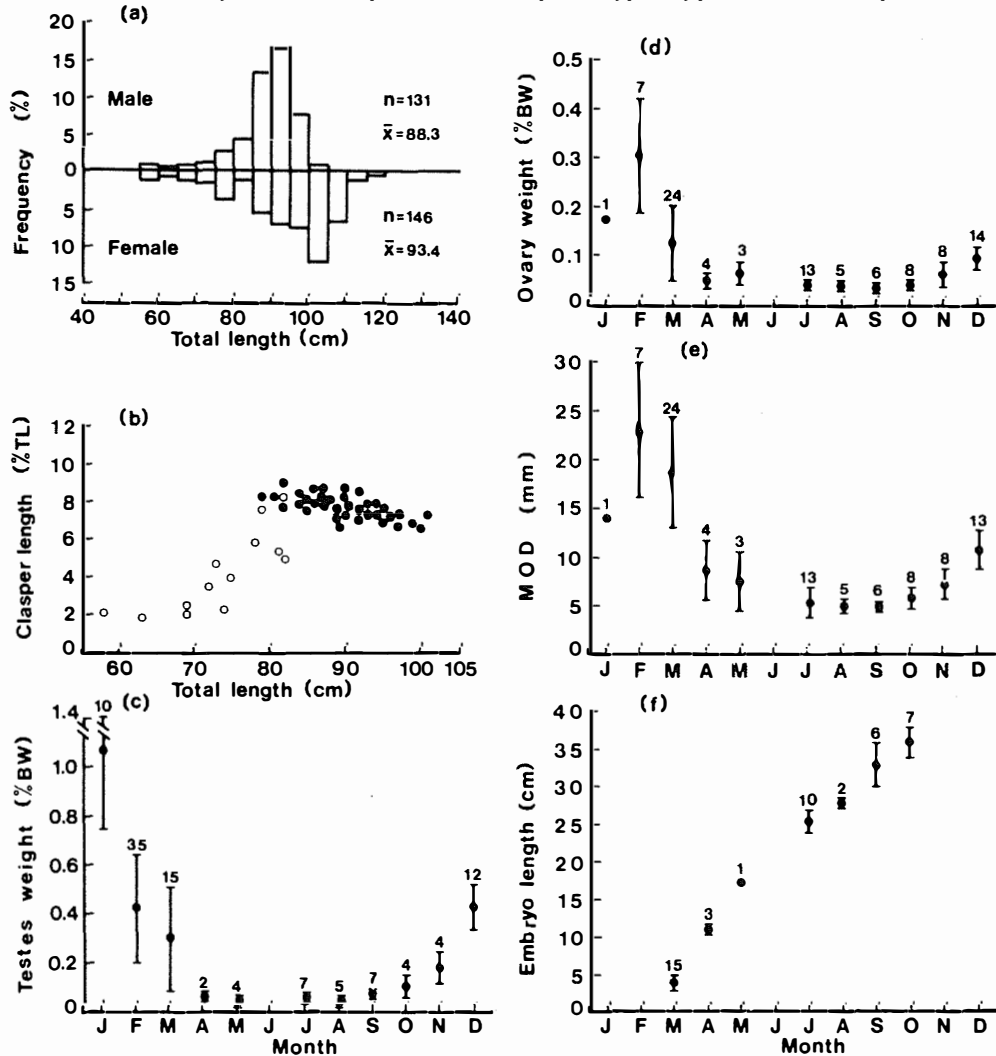


Fig. 1. *Carcharhinus cautus*. (a) Length-frequency distribution. n , Sample size; \bar{x} , mean length. (b) Relationship between clasper length (expressed as percentage of total length) and total length. \circ Claspers not calcified. \bullet Claspers calcified. (Some data points have been omitted to enhance clarity.) (c) Relationship between testes weight [expressed as percentage of total body weight (BW)] and time of year. (d) Relationship between ovary weight (% BW) and time of year. (e) Relationship between maximum ova diameter (MOD) and time of year. (f) Relationship between total length of embryos and time of year. Bars are standard deviation; in (c)–(e), numbers are sample sizes, in (f), numbers represent number of litters.

of the type shown for *C. cautus* in Fig. 1b. The smallest mature male *C. cautus* was 79 cm TL and all individuals over 84 cm TL were mature. Size at maturity in females, determined from ovary and genital tract condition, was about 91 cm TL. The smallest mature virgin recorded was 85 cm TL and the smallest pregnant individual was 88 cm TL. Calcification of claspers in *C. melanopterus* first occurred at about 93 cm TL and all males were mature by 95 cm TL (Fig. 2b). Females were mature by 97 cm TL. The smallest mature virgin was 91 cm TL and the smallest pregnant individual was 95 cm TL. Male *C. fitzroyensis* were usually mature

by 88 cm TL; the smallest mature individual examined was 81 cm TL (Fig. 3b). All females over 100 cm TL were mature. The smallest mature virgin was 89 cm TL and the smallest pregnant female was 99 cm TL.

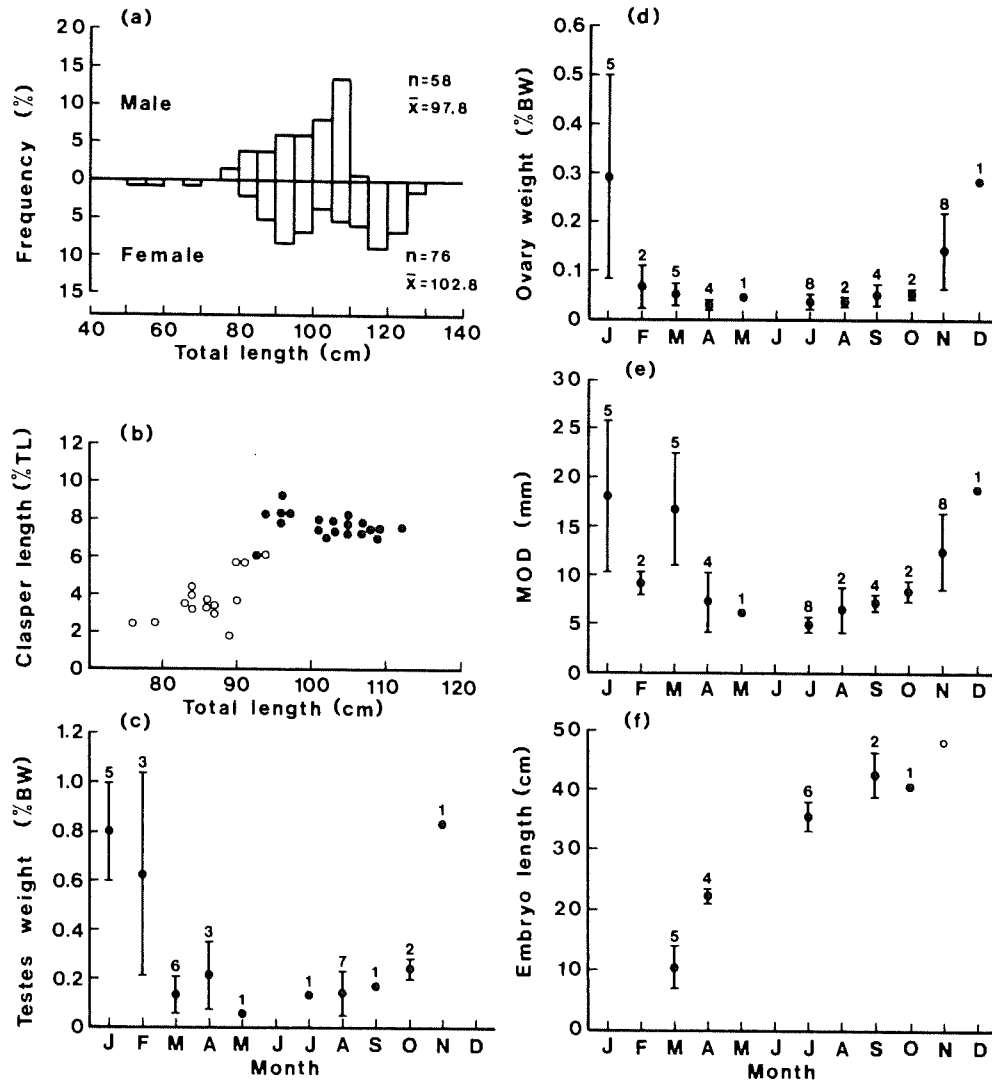


Fig. 2. *Carcharhinus melanopterus*. (a) Length-frequency distribution. n , Sample size; \bar{x} , mean length. (b) Relationship between clasper length (expressed as percentage of total length) and total length. \circ Claspers not calcified. \bullet Claspers calcified. (Some data points have been omitted to enhance clarity.) (c) Relationship between testes weight [expressed as percentage of total body weight (BW)] and time of year. (d) Relationship between ovary weight (% BW) and time of year. (e) Relationship between maximum ova diameter (MOD) and time of year. (f) Relationship between total length of embryos and time of year. Bars are standard deviation; in (c)-(e), numbers are sample sizes, in (f), numbers represent number of litters.

Reproduction

The species are viviparous with well-developed yolk-sac placentae. Data on gonad condition, analysed on a monthly basis, indicate distinct seasonal reproductive cycles for each species.

Testes weight in *C. cautus* was low between April and September (about 0.07% BW) and increased to a peak (over 1.0% BW) in January, after which it fell sharply (Fig. 1c). Most mature males had sperm present in their seminal vesicles in February and March (37 of 39 mature specimens). During the remainder of the year, only one individual was observed to

have sperm present (October). Monthly variation in ovary weight, which reflects ova development, follows a similar cycle to that for testes weight though is out of phase by 1 month. Between April and October, ovary weight was reduced (less than 0.06% BW) (Fig. 1d) and MOD ranged between 5 and 10 mm (Fig. 1e). By February ovary weight had increased to about

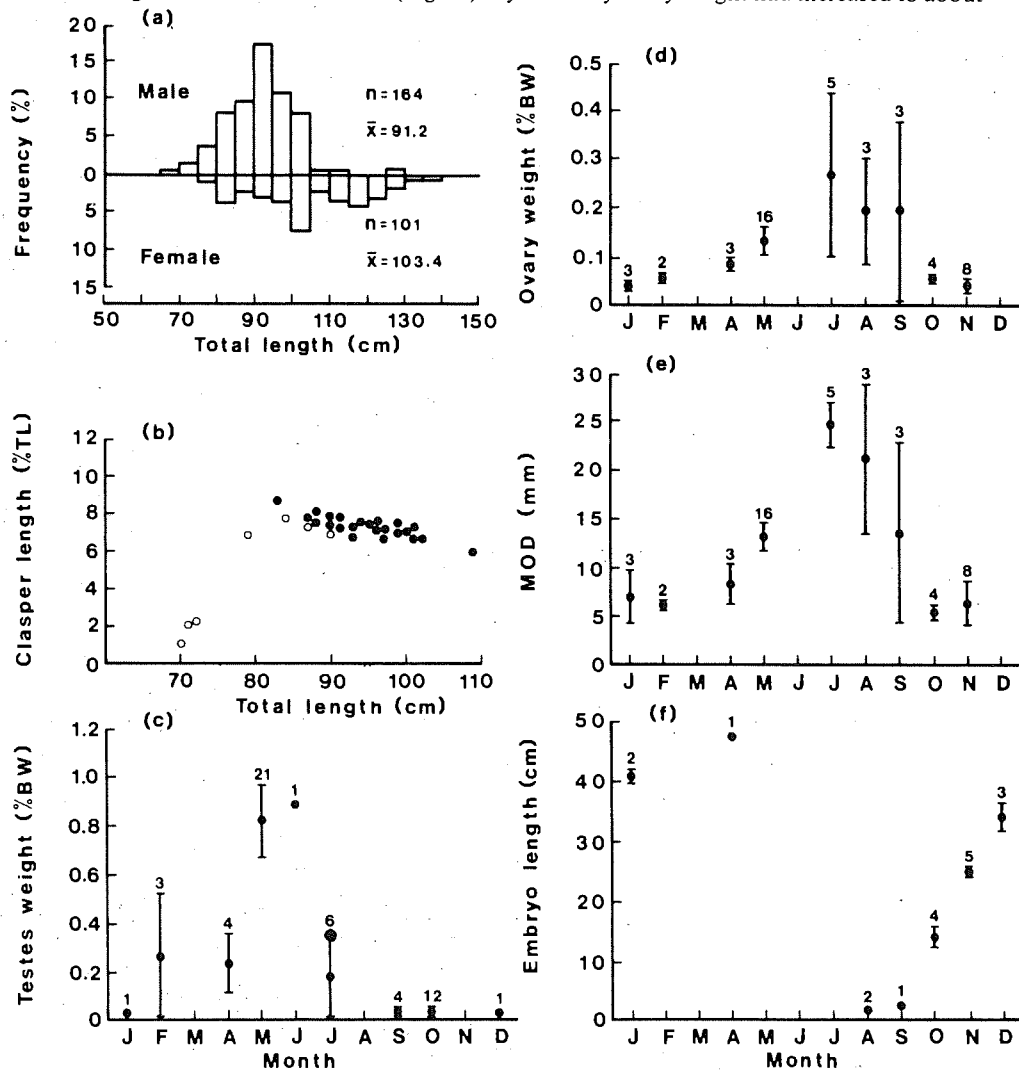


Fig. 3. *Carcharhinus fitzroyensis*. (a) Length-frequency distribution. n , Sample size; \bar{x} , mean length. (b) Relationship between clasper length (expressed as percentage of total length) and total length. \circ Claspers not calcified. \bullet Claspers calcified. (Some data points have been omitted to enhance clarity.) (c) Relationship between testes weight [expressed as percentage of total body weight(BW)] and time of year. (d) Relationship between ovary weight (% BW) and time of year. (e) Relationship between maximum ova diameter (MOD) and time of year. (f) Relationship between total length of embryos and time of year. Bars are standard deviation; in (c)-(e), numbers are samples sizes, in (f), numbers represent number of litters.

0.3% BW, and ripe ova, exceeding about 20 mm and up to 31 mm, were present in February and March. Changes in gonad condition, the occurrence of four females with mating scars in early March and the appearance of eggs *in utero* in some individuals in February and March indicate that mating probably occurs between January and March, followed by ovulation in February-March. Embryos were first visible in March and gravid individuals were recorded until October. Embryos increased in size from about 5 cm TL in March to about 36 cm TL

in October (Fig. 1f). The largest embryo examined was 39.0 cm TL. Spent females occurred in October and November, indicating that young are born at this time. The gestation period, defined as the time between the appearance of fertilised ova in the uteri and parturition, is thus 8–9 months, and probable size at birth is 40 cm TL.

The reproductive cycle for *C. melanopterus* is similar to that for *C. cautus*. Testes weight rose from a low level (less than 0.2% BW) in September to a peak (about 0.8% BW) in November and January (Fig. 2c). Most mature males examined between January and April (14 of 16 specimens) had sperm in their seminal vesicles. With the exception of two individuals (one in July and the other in September), sperm was not present in seminal vesicles of fish examined at other times of the year. Ovary weight was high between December and January (nearly 0.3% BW) (Fig. 2d) and MOD was about 20 mm (Fig. 2e). Ripe ova of up to 25 mm were also recorded in March. The comparatively low ovary weights and MOD in February are attributable to two individuals with gonads in an apparent resting state: uteri were expanded but ova were small and without yellow yolk typical of the pre-ovulatory condition. The paucity of material in November–December and the absence of females with mating scars make it difficult to establish the precise timing of the mating season. Available data suggest, however, that *C. melanopterus* probably mate in January and February. Since embryos up to 17 cm TL were present in March (Fig. 2f), it is probable that ovulation occurs at least as early as February. A female with uterine eggs was recorded in March, indicating that ovulation extends into that month as well. Embryos grew rapidly to over 40 cm TL by September and October (Fig. 2f). The largest embryo examined was 46.8 cm TL (September) and the smallest free-living specimen, with an obvious umbilical scar, was 48.3 cm TL (November). Based on the occurrence of spent individuals, parturition occurs in November, which gives a gestation period of 8–9 months and birth size of about 48 cm TL.

The timing of the reproductive cycle in *C. fitzroyensis* is out of phase with the other two species. Testes weight peaked at around 0.8% BW in May and June (Fig. 3c) and sperm was present in the seminal vesicles of most mature males examined between May and July (29 of 35 specimens). Individuals examined in February, April and September also had small quantities of sperm present (4 of 12 specimens). This evidence suggests that mating may take place between May and July. Ovary weights were greatest in July (nearly 0.3% BW) (Fig. 3d) and MOD averaged over 20 mm in July and August with ripe ova also present in September (Fig. 3c). Females with uterine eggs were first observed in late July but based on MOD it seems likely that the period of ovulation may extend through August and into early September. Embryos were first visible in late August and by the following April embryos had grown to over 47 cm TL (Fig. 3f). The largest embryo examined was 48.7 cm TL. Spent females were recorded from February through to May, which suggests a gestation period of between 7 and 9 months. Size at birth for *C. fitzroyensis* is probably 50 cm TL.

During the periods in which gravid fish were present, 84% of mature non-virgin females of *C. cautus*, 80% of those of *C. melanopterus* and 82% of those of *C. fitzroyensis* were either pregnant or recently spent. This evidence suggests that individual females breed every year.

Litter sizes averaged 2.9 for *C. cautus* (range 1–5, mode 4; based on 53 litters), 3.8 for *C. melanopterus* (range 3–4, mode 4; based on 19 litters) and 3.7 for *C. fitzroyensis* (range 1–7, no distinct mode; based on 23 litters). Females accounted for 44.6% of 92 embryos of *C. cautus*, 38.2% of 68 embryos of *C. melanopterus* and 46.8% of 47 embryos of *C. fitzroyensis*. In each case, embryo sex ratios did not differ significantly from 1:1 (χ^2 test, $P > 0.05$). There were significant positive relationships between number of young and length of the mother in *C. cautus* ($r^2 = 0.22$, $P < 0.001$) and *C. fitzroyensis* ($r^2 = 0.73$, $P < 0.001$). Although a significant relationship was determined for *C. melanopterus* ($r^2 = 0.64$, $P < 0.001$), it is not considered meaningful because of the restricted range in litter sizes (three to four embryos).

Diet

The stomachs of 40–64% of all specimens examined for stomach contents were empty (Table 2). Fish (primarily teleosts) were the most frequently occurring prey, present in nearly

70% of *C. cautus* and *C. melanopterus* and 84% of *C. fitzroyensis* stomachs that contained food (Table 2). Most of the fish was at advanced stages of digestion, which made identifications difficult. A considerable diversity of typically pelagic and demersal fish was identified, however (Appendix 1). Predation on elasmobranchs was rare. Crustaceans were recorded in about 23% of *C. cautus* stomachs, with prawns, crabs (in particular, portunids) and manta shrimps (Squillidae) the most frequently identified groups. Crustaceans, mainly prawns and manta shrimps, were also frequently taken by *C. fitzroyensis* (19% of stomachs) but were only occasionally eaten by *C. melanopterus* (5% of stomachs). Cephalopods, mainly squid and octopus, were of some significance to the diets of *C. cautus* (13% of stomachs) and *C. melanopterus* (23% of stomachs). Snakes occurred in about 6% of *C. cautus* and 23% of *C. melanopterus* stomachs. Details of taxa identified from the stomachs are provided in Appendix 1.

Table 2. Percentage occurrence of major prey groups in the stomachs of *C. cautus*, *C. melanopterus* and *C. fitzroyensis* from northern Australia

Species	Occurrence (%) in stomachs					No. of stomachs with food	No. of stomachs examined	% of stomachs empty
	Pisces	Crustacea	Mollusca	Reptilia	Aves			
<i>C. cautus</i>	68.9	23.2	13.3	6.0	0.7	151	268	43.7
<i>C. melanopterus</i>	67.6	5.4	23.0	23.0	0	74	123	39.8
<i>C. fitzroyensis</i>	83.7	18.6	2.3	0	0	43	118	63.6

Discussion

Compagno (1984) notes that *C. cautus* apparently inhabits shallow shelf waters but may range into deeper waters. The absence of the species amongst the offshore samples in this study suggests a marked preference for shallow coastal waters. Both *C. melanopterus* and *C. fitzroyensis* were found from the intertidal offshore to depths of at least 40 m. Throughout its range, *C. melanopterus* is known to be particularly abundant on or around reef areas (Compagno 1984).

According to Garrick (1982), *C. cautus* and *C. fitzroyensis* may grow to about 150 cm TL, and *C. melanopterus* has been reported up to 180 cm TL, though specimens rarely exceed 160 cm TL. The maximum sizes recorded in this study are considerably smaller — 120 cm TL for *C. cautus*, 135 cm TL for *C. fitzroyensis* and 125 cm TL for *C. melanopterus* — and may indicate that the species do not grow as large in northern Australian waters. However, gill nets are size-selective; any larger individuals in the population may have avoided capture.

Published information on size at maturity for the species in Australian waters is very limited. Whitley (1943) described a female specimen of *C. fitzroyensis* of 117.4 cm TL from the Fitzroy River (Queensland) and noted that it contained developing ova of 8 mm diameter. From the Shark Bay region (Western Australia), Whitley (1945) reported on an immature female of *C. cautus* of 91.8 cm TL and a mature male and an immature female of *C. melanopterus* (reported as *spallanzani*) of 126.5 and 109.0 cm TL, respectively. Further, in a brief reference, Whitley (1967) suggested that *C. cautus* and *C. fitzroyensis* first breed at about 4 ft (c. 120 cm TL) and *C. melanopterus* at about 4 ft 3 ins (c. 130 cm TL). The present findings indicate that off northern Australia, the three species mature and breed at sizes smaller than those suggested by Whitley (1967). Outside Australian waters, *C. melanopterus* matures at lengths generally in excess of 110 cm TL (Gohar and Mazhar 1964; Bass *et al.* 1973; Randall and Helfman 1973; Stevens 1984).

The reproductive cycle of *C. melanopterus* in northern Australia differs from its cycle in other parts of the world. At Aldabra, individual females breed every second year and have a slightly longer gestation period of 10–11 months (Stevens 1984). The breeding cycle in the Red Sea is not clear; Melouk (1957) postulated a gestation period of 16 months and Gohar

and Mazhar (1964) reported two periods of parturition, one in January and another in June. Biannual birth seasons may also apply for *C. melanopterus* from Madagascar (Fourmanoir 1961) and French Polynesia (Johnson 1978). No accounts of the reproductive cycles are available for *C. cautus* or *C. fitzroyensis*.

Gestation periods for most *Carcharhinus* species are in the range 9–12 months, though some species may take up to 16 months (Compagno 1984). By comparison, the sharks studied here have relatively short gestation periods.

Based on limited data, Compagno (1984) reported that size at birth for *C. cautus* is probably 35–39 cm TL, which is close to the size determined in this study. Size at birth for *C. melanopterus* is given as between 46 and 52 cm TL from Madagascar (Fourmanoir 1961) and 50 cm TL from Aldabra (Stevens 1984), which compare with about 48 cm TL for northern Australia. In the Marshall Islands, free-living individuals of only 33 and 36 cm TL have been reported, indicating a much smaller size at birth in that area (Bonham 1960). Although there is no published information on size at birth for *C. fitzroyensis*, free-living individuals of 51 cm TL, which is close to the suggested birth size, have been caught off Townsville, north Queensland (*C. Simpfendorfer*, personal communication).

The species studied here have low fecundity as do most other sharks of the genus *Carcharhinus* (Compagno 1984). Although there are no other reports of litter sizes for *C. cautus* and *C. fitzroyensis*, litter sizes of two to five (commonly four) have been reported for *C. melanopterus* from outside Australia (Melouk 1957; Fourmanoir 1961, 1976; Randall and Helfman 1973; Johnson 1978; Stevens 1984).

Several authors have reported relationships between number of embryos and mother size that suggest that bigger individuals produce larger litters (Olsen 1954; Bass *et al.* 1973; Gubanov 1978; Parsons 1983; Stevens and Wiley 1986). Similar relationships exist for *C. cautus* and *C. fitzroyensis*, though the biological significance of the relationship for *C. cautus* is unclear since only 22% of the variation in litter size could be attributed to differences in the length of the mother.

Sharks generally produce equal numbers of male and female embryos (Springer 1960; Bass *et al.* 1973; Gubanov 1978; Parsons 1983). There are exceptions: Stevens and Wiley (1986), for instance, found that *C. tilstoni* from certain areas off northern Australia produce significantly more male embryos. The sharks studied here had equal sex ratios before and, with the exception of *C. fitzroyensis*, after birth. Males predominated amongst the post-partum sample of *C. fitzroyensis*, probably reflecting spatial segregation of the sexes, a phenomenon that is well known amongst some shark species (Springer 1940; Olsen 1954; Parsons 1983; Stevens 1984).

Whitley (1945) reported that *C. cautus* consume small fish (e.g. *Saurida*, *Sillago* and *Dasson*) and crabs and that *C. melanopterus* eat cephalopods and fish. The only reference to diet for *C. fitzroyensis* is given by Whitley (1943) and is based on a single specimen, which contained prawn and fish remains. The diet of *C. melanopterus* from the other parts of the world has been described as chiefly comprising fish, with lesser quantities of crustaceans and molluscs also eaten (Fourmanoir 1961; Bass *et al.* 1973; Randall and Helfman 1973; Stevens 1984). In this study, fish were an important component of the diets of the three species, occurring in over two-thirds of all stomachs examined. Crustaceans and cephalopods occurred much less frequently. The occurrence of snakes in the diets of *C. cautus* and *C. melanopterus* is noteworthy and has been discussed elsewhere (Lyle and Timms 1987).

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Appendix 1. List of organisms found in the stomachs of *C. cautus*, *C. melanopterus* and *C. fitzroyensis*

C. cautus

TELEOST: Ariidae, Plotosidae, Belonidae, Clupeidae, Engraulidae, *Apolectus niger*, Mugilidae, Muraenidae, *Toxotes chatareus*, Labridae, Sparidae, Teraponidae, Tetraodontidae, Attenuariidae, Ephippidae, *Scomberoides* sp., *Sillago* sp., *Lates calcarifer*, Gobiidae, unidentified fish.
 ELASMOBRANCH: *Carcharhinus dussumieri*, unidentified shark.
 CRUSTACEA: *Metapenaeus dalli*, unidentified prawns, Portunidae, *Portunus pelagicus*, *Scylla* sp., unidentified crabs, *Thalassina squamifera*, Squillidae, Isopoda.
 MOLLUSC: Cephalopoda (squid, cuttlefish, octopus), *Melo* sp.
 REPTILE: *Fordonia leucobalia*, *Cerberus rynchops*, unidentified snakes.
 AVES: Unidentified bird (fledgling).

C. melanopterus

TELEOST: Labridae, Sparidae, Ephippidae, *Zabidius novemaculatus*, Lutjanidae, Apogonidae, *Chanos chanos*, Platycephalidae, Monacanthidae, unidentified fish.
 ELASMOBRANCH: Unidentified ray.
 CRUSTACEA: Unidentified prawns, Maiidae.
 MOLLUSC: Cephalopoda (squid, octopus).
 REPTILE: *Acrochordus granulatus*, *Hydrelaps darwiniensis*, *Lapemis hardwickii*, *Hydrophis* sp., unidentified snakes.

C. fitzroyensis

TELEOST: Ariidae, Tetraodontidae, *Scomberoides* sp., Gobiidae, Platycephalidae, Nemipteridae, Cynoglossidae, *Saurida* sp., Diodontidae, Sciaenidae, unidentified fish.
 ELASMOBRANCH: Unidentified ray.
 CRUSTACEA: *Penaeus* sp., *Parapenaeopsis cornuta*, unidentified prawns, unidentified crabs, Squillidae.
 MOLLUSC: Cephalopoda (squid).

Biology of Three Hammerhead Sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from Northern Australia

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Abstract

The hammerhead sharks *Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini* form part of the incidental catch of a commercial gill-net fishery off northern Australia. Of the specimens sampled between June 1980 and December 1986, 46% of *S. mokarran*, 41% of *E. blochii* and 31% of *S. lewini* were females. Few adult female *S. lewini* were caught and it is suggested that these occur offshore of the study area. In northern Australia, the usual size at maturity of male *E. blochii*, *S. lewini* and *S. mokarran* is 108, 150 and 225 cm total length (TL), and of females is 120, 200 and 210 cm TL, respectively. *S. mokarran* and *E. blochii* gave birth in January and February/March, respectively, after a gestation period of 10-11 months. *S. lewini* appears to have a more extended seasonal cycle: the young are born between October and January after 9-10 months gestation. Size at birth is about 45-50 cm TL in *E. blochii* and *S. lewini*, and 65 cm TL in *S. mokarran*. Mean litter size is 12 in *E. blochii*, 15 in *S. mokarran* and 17 in *S. lewini*. Individual *E. blochii* females breed every year, whereas *S. mokarran* females probably breed every other year. Fish are an important component of the diet of all three species as, to a lesser extent, are cephalopods for *S. lewini* and crustaceans for *S. mokarran* and *E. blochii*.

Introduction

Hammerhead sharks (family Sphyrnidae) are distributed throughout the tropical and warm-temperate waters of the world. The family has two genera: *Eusphyra*, comprised of a single species; and *Sphyrna*, in which seven species have been recognised (Compagno 1984). Three hammerhead species—*Eusphyra blochii* (Cuvier), *Sphyrna mokarran* (Ruppell) and *Sphyrna lewini* (Griffith and Smith)—are known from northern Australia and are regularly caught by commercial gill-net fishermen.

E. blochii has a tropical Indo-West Pacific distribution from the Arabian Gulf through India and Indonesia to northern Australia, occurring in shallow continental-shelf waters (Gilbert 1967; Compagno 1984). *S. mokarran* is circum-tropical in the Atlantic, Pacific and Indian Oceans. It occurs both close inshore and well offshore and has been recorded from the surface over deep water, to depths of about 80 m, as well as from shallow areas only about 1 m deep (Gilbert 1967; Compagno 1984). Some populations, such as those off Florida and in the South China Sea, migrate to higher latitudes in the warmer months (Taniuchi 1974; Compagno 1984). *S. lewini* has a cosmopolitan distribution in tropical and warm temperate seas. It occurs both close inshore and well offshore and has been found from the intertidal zone, where the young are often taken in bays and estuaries, down to at least 275 m depth (Gilbert 1967; Compagno 1984). This species sometimes forms large schools that, in some areas, migrate to higher latitudes in summer, whereas in other regions it apparently does not migrate (Taniuchi 1974; Bass *et al.* 1975; Compagno 1984).

Compagno (1984) summarizes what is known of the biology of these three hammerhead sharks. No specific studies have dealt with their biology in Australian waters: what little information exists is often anecdotal and cannot be related to a particular species with any reliability.

Considerable research effort has been focused on the northern Australian shark fishery, with initial studies concentrated on documenting the life histories of the principal commercial species, *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes in Muller and Henle) (Stevens and Wiley 1986; Davenport and Stevens 1988). Hammerhead sharks represent a minor component of the gill-net catch by number (up to 10%) but, because of the large size attained by some specimens, are more significant in terms of weight.

This paper reports on the biology of the three hammerhead sharks from northern Australia.

Materials and Methods

Sampling Methods

Sharks were collected from northern Australian waters from June 1980 to December 1986. The majority were obtained from Taiwanese commercial gill-net catches and from research cruises. Some specimens were obtained from a study of sharks in Darwin Harbour and from monitoring Australian commercial gill-net catches. Additional length data were also obtained from the Taiwanese fishery; these sharks were measured by personnel placed on board the vessels. The area sampled is shown in Fig. 1.

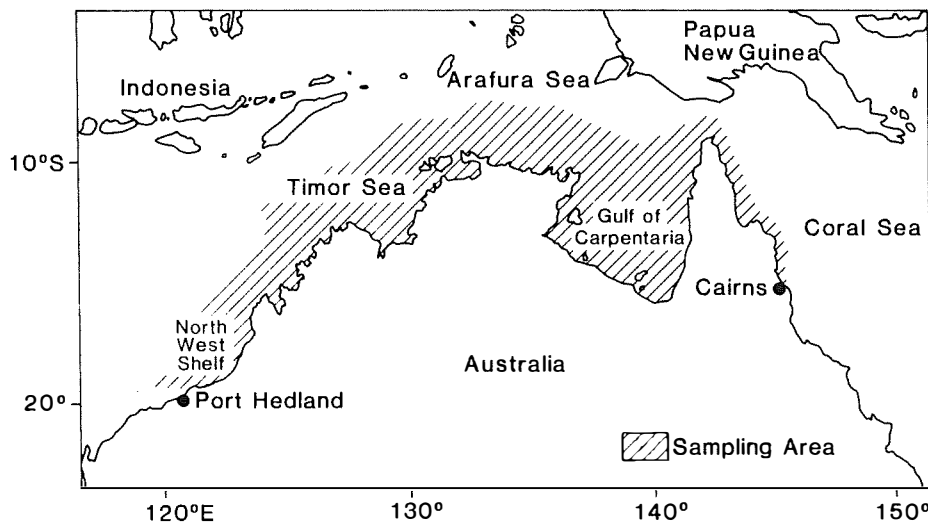


Fig. 1. Sampling area off northern Australia.

Sharks were captured with gill-nets, longlines, demersal trawls and handlines. Gill-nets used in the Taiwanese fishery were constructed of multifilament nylon with a diagonal stretched mesh averaging 17 cm (14.5 to 19.0 cm) and were about 15 m deep from the headrope to the footrope. From 8 to 16 km of net were set close to the surface. More detailed descriptions of sampling from this fishery are given by Stevens and Wiley (1986). Most gill-nets used on research cruises were of 15 cm stretched mesh monofilament, 500 to 1200 m long and approximately 11 m deep. Gill-nets were set within 3 m of the surface. Some sharks were caught in gill-nets designed to study gear selectivity; panels of 10, 15 and 25 cm mesh monofilament were used. Each panel was 200 m long and 10 m deep, and was separated from adjoining panels by 100 m of headrope. Longlines consisted of 400 to 5000 m of mainline with 60 to 300 hooks that were fished both on the surface and the bottom. Further details of gear used on research cruises are given by Lyle and Timms (1984), Stevens and Church (1984) and Stevens and Wiley (1986).

Length and Weight Measurement

Sharks were measured to the nearest centimetre either as total lengths (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 lengths (FL). Fork lengths were converted to total lengths using equations derived in this study (Table 1). Sharks were weighed on calibrated spring balances reading to the nearest 500 g, except for the smaller specimens (<25 kg), which were weighed to the nearest 100 g. Lengths were converted to weights using the TL and total weight relationships shown in Table 1. 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).

Table 1. Total length–total weight and total length–fork length relationships for hammerhead sharks from northern Australian waters
T, total length (cm); *F*, fork length (cm); *W*, total weight (g)

Species	Sample size	Equation	r^2
<i>E. blochii</i>	263	$T = 1.31F + 3.10$	0.996
	178	$W = 2.71 \times 10^{-4} T^{3.56}$	0.975 ^A
<i>S. mokarran</i>	261	$T = 1.29F + 3.58$	0.994
	117	$W = 1.23 \times 10^{-3} T^{3.24}$	0.991 ^A
<i>S. lewini</i>	454	$T = 1.30F + 1.28$	0.994
	252	$W = 3.99 \times 10^{-3} T^{3.03}$	0.985 ^A

^A Coefficient of determination (r^2) based on linear regression of $\ln(W)$ against $\ln(T)$.

Reproductive State

The reproductive state was determined by the method of Bass *et al.* (1973). Males were considered to be mature when the claspers were elongated and the clasper cartilages were rigid from calcification. The claspers of immature males are short and flexible, and grow slowly in relation to the length of the shark. During adolescence the claspers elongate rapidly, becoming rigid from calcification when fully mature. This pattern of development typically produces an S-shaped curve when relative clasper length is plotted against body length. Females were considered to be mature when distinct ova were present in the ovary, oviducal glands were fully differentiated from the oviducts, and the posterior sections of the oviducts (functional uteri) were expanded. Females with the vaginal hymen intact were judged to be virgin. The largest egg(s) in the ovary were measured with calipers to the nearest millimetre to determine maximum ova diameter (MOD). Gonads were excised from the surrounding epigonal organ and weighed to 0.1 g. The gonadosomatic index (GSI) was calculated as the gonad weight/total body weight $\times 100$. The number, lengths and sex of embryos were recorded.

Stomach Contents

Recognizable prey items from stomach contents were generally identified to family and, where practicable, to genus or species. Identifications 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.

Results and Discussion*Distribution*

In Australian waters, *E. blochii* has been recorded from Queensland (south to 18°S) (Ogilby 1908), the Northern Territory (Compagno 1984) and the Timor Sea off Western Australia (Sainsbury *et al.* 1984). In this study *E. blochii* was caught throughout the sampling area north of 15°S, but was not taken on the North West Shelf.

S. mokarran and *S. lewini* have been recorded from Western Australia, the Northern Territory, Queensland and New South Wales (Whitley 1948; Gilbert 1967; Stevens *et al.*

1982; Compagno 1984; Sainsbury *et al.* 1984; Stevens 1984). Although *S. mokarran* was not recorded during a 4-year study of sharks caught by sport fishermen off New South Wales (Stevens 1984), two specimens were caught subsequently in February and March 1983 off Port Stephens on the New South Wales coast (32°40'S). The southern limit of the range of this species off Western Australia is uncertain. *S. lewini* has been found south to Geopraphe Bay (33°50'S) off Western Australia (Hutchins and Thompson 1983) and Sydney (34°S) on the east coast (Stevens 1984). *S. mokarran* and *S. lewini* were caught throughout the region sampled in this study.

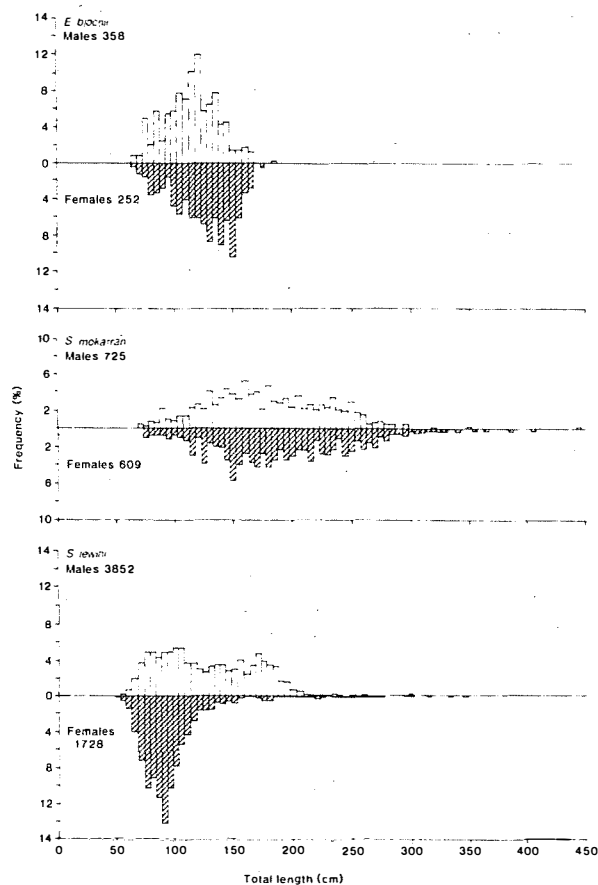


Fig. 2. Length-frequency distributions from northern Australia for *E. blochii*, *S. mokarran* and *S. lewini*.

Size and Sex Ratio

E. blochii

The maximum size reported for this species is about 152 cm TL (Setna and Sarangdhar 1949a). The largest male and female *E. blochii* examined during this study were 169 cm TL. Somewhat larger individuals—a 186 cm male and a 176 cm TL female—were recorded in the samples of length data from the fishery, but were not seen by the authors (Fig. 2). No newly born *E. blochii* were caught, the smallest specimen being 65 cm TL (refer to section on reproduction).

E. blochii litters from Indian waters have been reported to be predominantly female (Setna and Sarangdhar 1949a), but no data were given to support this conclusion. There is

little published information on the sex ratios of post-partum populations. In northern Australian waters the embryonic sex ratio for *E. blochii* did not differ significantly from 1 : 1, with females accounting for 45.6% of 215 individuals. However, the sampled post-partum population showed a significant excess of males: 41.3% of 610 *E. blochii* were female (χ^2 test, $P < 0.001$). The sampled population of *E. blochii* in inshore waters (< 50 km) was 35.3% female, whereas 63.4% of the offshore (> 50 km) population was female.

S. mokarran

S. mokarran of around 600 cm have been reported (Gilbert 1967; Compagno 1984), but individuals over 400 cm TL would appear to be rare. The largest male *S. mokarran* examined in this study was 332 cm and the largest female 390 cm, although a male of 445 cm and a female of 409 cm TL were recorded in the length data from the fishery (Fig. 2). The smallest *S. mokarran* we examined was 65.9 cm TL, close to this species' size at birth.

The sex ratio of embryos in *S. mokarran* is usually close to 1 : 1 (Fourmanoir 1961; Cadenat and Blache 1981; Compagno 1984), but there is little information on the sex ratios of post-partum populations. The sex ratio among *S. mokarran* embryos sampled from northern Australia did not differ significantly from 1 : 1, females accounting for 50.1% of 385 individuals. The sex ratio of the sampled post-partum population showed a significant excess of males: 45.7% of 1334 *S. mokarran* were female (χ^2 test, $P < 0.01$).

S. lewini

Compagno (1984) gives the maximum size of *S. lewini* as about 370–420 cm TL; however, the largest reliably measured specimens appear to be a 295 cm male (Bass *et al.* 1975) and a 309 cm female (Clarke 1971). Klimley and Nelson (1981) estimated the largest specimens observed during free diving as 340 cm TL. A 281 cm TL male was recorded from New South Wales (Stevens 1984). The largest male *S. lewini* we examined was 239 cm and our largest female 316 cm, while the largest in the fishery's length data were a 301 cm male and a 346 cm TL female (Fig. 2). The smallest *S. lewini* we examined was 46.8 cm TL, close to the species' size at birth.

Records of gravid *S. lewini* are rare and the only information on the sex ratio at birth is that a single litter of 30 pups contained 14 females and 16 males (Bass *et al.* 1975). The proportion of the sexes among newly born *S. lewini* in a pupping area in Hawaii was 1 : 1 (Clarke 1971), whereas in schools of mainly juvenile and adolescent individuals in the Gulf of California females predominated (Klimley and Nelson 1981). Bass *et al.* (1975) noted that males comprised 63.4% of the juvenile and adolescent segment of the population off Natal. Adult *S. lewini* females are rarely caught (Clarke 1971; Bass *et al.* 1975). In northern Australian waters the sex ratio of *S. lewini* embryos was not significantly different from 1 : 1 with females accounting for 53.0% of 66 individuals. The sex ratio of the sampled post-partum population showed a significant excess of males: 31.0% of 5580 *S. lewini* were female (χ^2 test, $P < 0.001$). The sex ratio was 1 : 1 in fish up to 100 cm; above 150 cm TL, females were rare (Fig. 2). Sexual segregation has been reported in numerous shark species (Springer 1940; Parsons 1983). The scarcity of adult females of *S. lewini* in any of the areas sampled in this study suggests that the segregated females may be occupying a different habitat, possibly in deeper water beyond the continental shelf.

Reproduction

E. blochii

Compagno (1984) states that *E. blochii* probably matures at a metre or less in total length. The smallest adult male and female recorded by Setna and Sarangdhar (1949a) were 109 and 104 cm TL, respectively. In northern Australia, males mature at about 108 cm TL (Fig. 3a); the smallest mature specimen we recorded was 102 cm and the largest specimen

with incompletely calcified claspers was 113 cm TL. Females mature at about 120 cm TL, based on the condition of the ovary and genital tracts, and on the size of the smallest pregnant fish.

Setna and Sarangdhar (1949a) and Appukuttan (1978), working with a small data base from Indian waters, reported that mating in *E. blochii* took place during July–August, early pregnancy in September–October and parturition from March to May. From these observations, Appukuttan (1978) suggested that the gestation period was about one year.

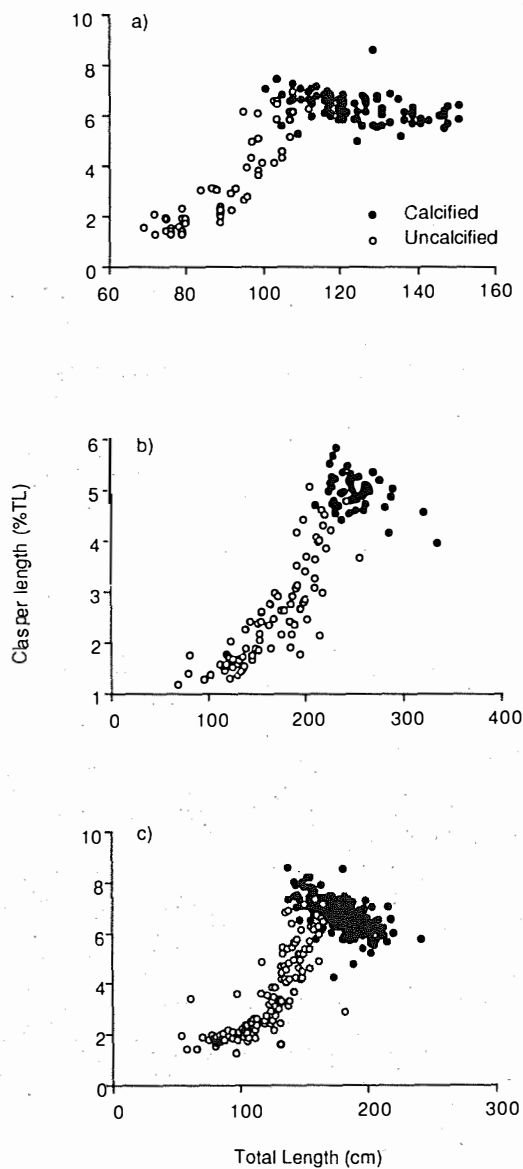


Fig. 3. Relationship between clasper length (expressed as a percentage of total body length) and total body length for (a) *E. blochii*, (b) *S. mokarran* and (c) *S. lewini*.

However, as Compagno (1984) noted, these data suggest a gestation period of nearer 8–9 months. Litter sizes from Indian waters ranged from 3–11 and averaged 6.7. The size at birth was given as about 46 cm; free-swimming young with fresh umbilical scars were between 43 and 50 cm TL (Setna and Sarangdhar 1949a, 1949b; Appukuttan 1978).

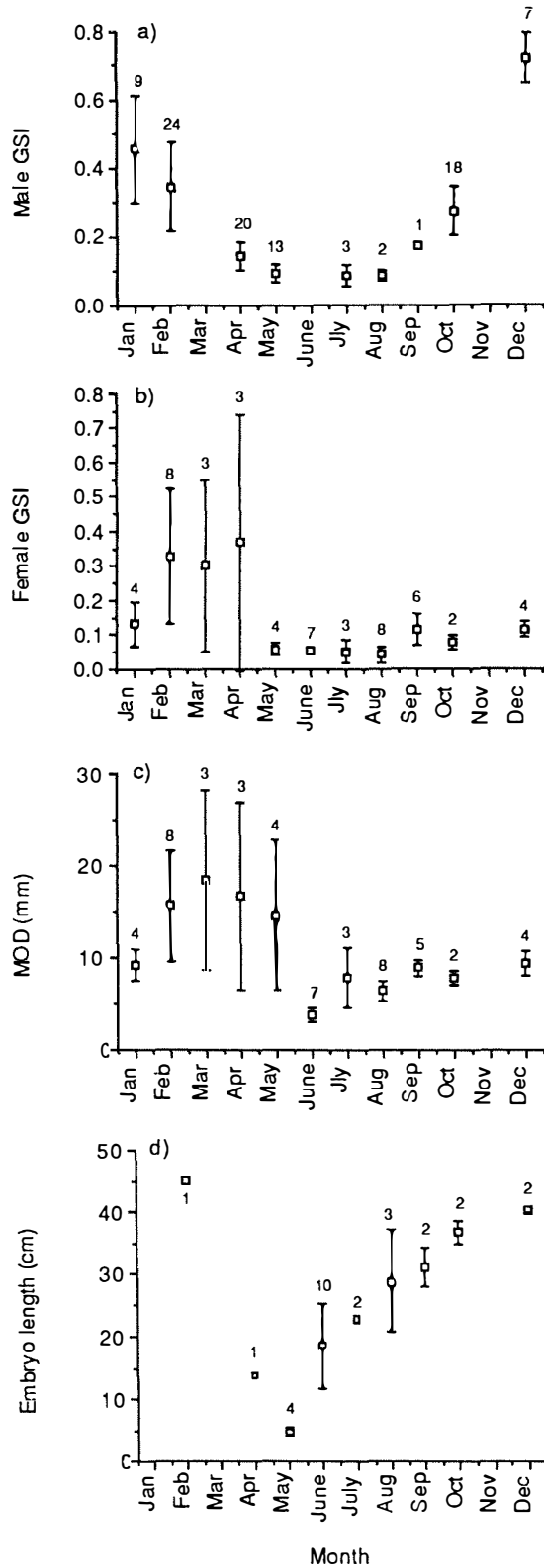


Fig. 4. *E. blochii*. Seasonal cycle of (a) male gonadosomatic index (GSI), (b) female GSI (c) maximum ova diameter and (d) pup length. Plots are mean values; bars are one standard deviation; numbers are sample size [sample size in (d) is number of litters].

Monthly changes in gonad condition show that *E. blochii* has a distinct seasonal reproductive cycle in northern Australian waters. The male gonadosomatic index (GSI) is reduced between May and August (0.08) after which it increases to a peak around December (0.7) before declining (Fig. 4a). The female GSI is also low between May and August (about 0.05) and highest from February to April (0.30 to 0.37) (Fig. 4b). Maximum ova diameter (MOD), which is reflected in ovary weight, peaks in March with some ova up to 27.5 mm in diameter (Fig. 4c). These data suggest that mating occurs between December and February and that females ovulate in March–April when the ova are about 20 mm in diameter. Embryos were first visible in April–May and increased in size through the year, reaching about 45 cm TL by the following February (Fig. 4d). The largest embryo examined was 47.4 TL.

Spent fish were observed in February and March, suggesting that the pups are born at this time. Size at birth is thus about 45–47 cm TL and the gestation period is 10–11 months. Variation in embryo length (Fig. 4d) between April (14 cm) and May (4.4 cm) suggests that either the period of ovulation may be extended in some individuals, or that there may be some variation in the ovulation period from year to year (data are summed over several years).

Of all mature non-virgin females examined during the pregnancy period, 72% were pregnant or spent, and of those above 140 cm TL, 85% were pregnant. These observations suggest that *E. blochii* females breed each year. The high GSI of males during the breeding season (Fig. 4a) provides evidence of annual breeding in males.

Litter size in *E. blochii* ranged from 6–25 with a mean of 11.8 (32 litters sampled). Although there is a significant relationship between increasing litter size and maternal length ($r^2 = 0.21$, $P < 0.01$), the biological significance of this relationship is unclear, as nearly 80% of the variation in litter size was attributable to factors other than maternal length. In northern Australia *E. blochii* appears to have larger litters and a longer gestation period than in Indian waters.

S. mokarran

The size at maturity of *S. mokarran* was reported to be 234–269 cm for males and 250–300 cm TL for females (Fourmanoir 1961; Compagno 1984). In Australian waters, maturity is attained at slightly smaller sizes: about 225 cm for males (Fig. 3b) and 210 cm TL in females. The smallest mature male examined in this study was 210 cm and the largest immature male was 258 cm TL. A female specimen of 168 cm and another of 200 cm were recorded as mature non-virgins; however, this seems unlikely, as the smallest preovulatory, pregnant and spent females were 229, 228 and 219 cm TL, respectively. Several mature non-virgins were recorded in the 210–220 cm length range. The largest immature female was 239 cm TL.

The reproductive cycle of *S. mokarran* has been most fully described by Cadenat and Blache (1981). These authors noted an annual breeding cycle in West African waters, where mating occurred from the end of July to September. Early embryos of 3–9 cm were present in September, and pups about 67 cm TL were born some 11 months later in August. Clark and von Schmidt (1965) combined their data with those of Springer (1940) and estimated that the time of birth in Florida waters was late spring to early summer. Fourmanoir (1961) recorded embryos of about 25 cm and 35 cm in June and July, respectively, off Madagascar which, if the gestation period was similar to that of West Africa, would mean birth in the Southern Hemisphere summer. The size at birth in *S. mokarran* was reported to be from 50–70 cm TL and litter sizes varied from 13–42 (Bigelow and Schroeder 1948; Fourmanoir 1961; Cadenat and Blache 1981).

In our study in northern Australian waters, seasonal examination of male GSI in *S. mokarran* suggests that they mate in October–November (Fig. 5a), although one of two females with mating scars was caught in January, the other in May. In contrast, female

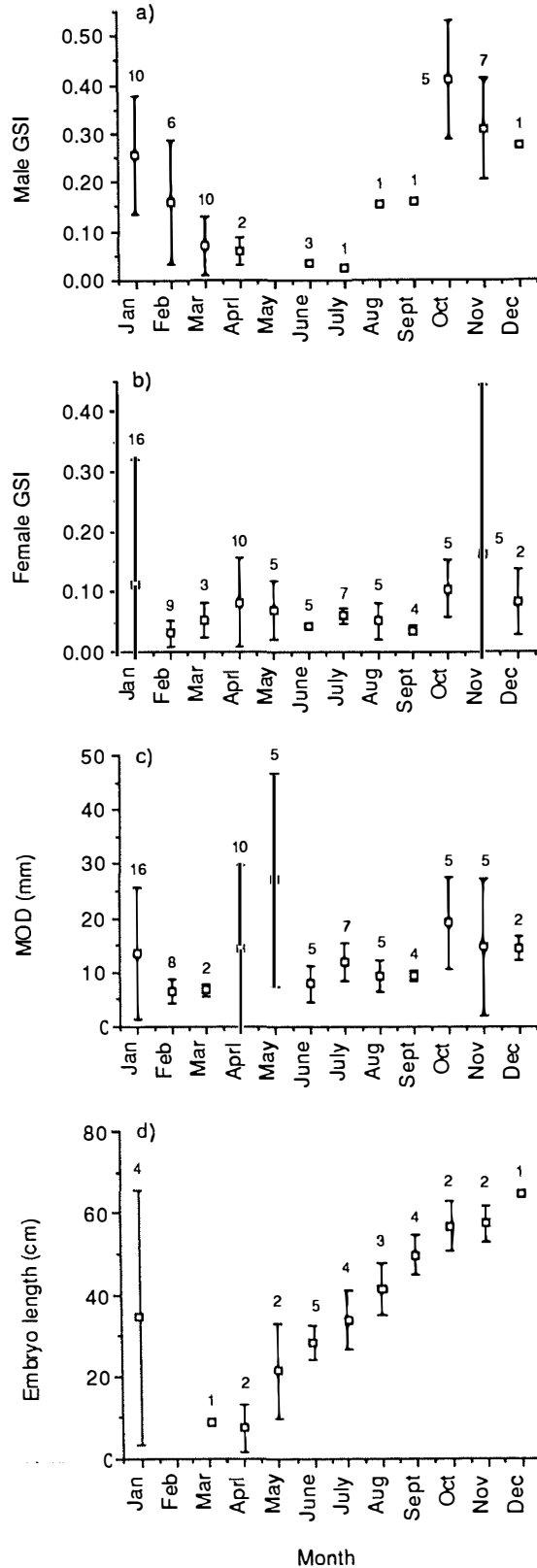


Fig. 5. *S. mokarran*. Seasonal cycle of (a) male gonadosomatic index (GSI), (b) female GSI, (c) maximum ova diameter (MOD) and (d) pup length. Plots are mean values; bars are one standard deviation; numbers are sample size [sample size in (d) is number of litters].

GSI and MODs show no clear trend during the year (Fig. 5*b, c*). When MOD is examined separately for pregnant and non-pregnant fish, the pattern is somewhat clearer and suggests that ova size increases up to February–March. However, females with ova in their uteri were found in February, April and July, so ovulation may take place over an extended period.

Figure 5*d* shows a clear relationship between embryo size and time of year. Embryo size increased from about 8 cm in March to 64 cm in December, with birth occurring in December–January, giving a gestation period of about 11 months. Seven spent fish were recorded, all in January and February. The size at birth is about 65 cm; the largest embryo observed was 64 cm and the smallest free-swimming specimen was 66 cm TL.

Since only 59% of *S. mokarran* above 220 cm TL were pregnant, and as fish with near-term embryos did not contain a new batch of ripening ova in their ovaries, females probably breed every other year. Males, however, appear to breed annually, based on the high GSI of specimens examined during the breeding season (Fig. 5*a*).

The mean litter size from 30 litters was 15.4 with a range of 6–33, and there is a significant relationship between increasing maternal length and litter size ($r^2 = 0.56$, $P < 0.01$).

S. lewini

The size at maturity of male *S. lewini* in the south-western Indian Ocean was reported as 140–165 cm (Bass *et al.* 1975) and in the Atlantic as 180–185 cm (Bigelow and Schroeder 1948; Cadenat and Blache 1981; Branstetter 1987). Information on maturity in females is very limited: Bass *et al.* (1975) recorded a 212 cm specimen that was ‘adolescent, possibly mature, but still virgin’; Clarke (1971) noted a 214 cm specimen that was immature. Branstetter (1981) recorded a 204 cm mature virgin and, subsequently (Branstetter 1987), a non-virgin 236 cm female and a 248 cm virgin which were both immature, and a 249 cm mature non-virgin. Only three pregnant individuals seem to have been taken: a 307-cm specimen from Durban (Bass *et al.* 1975) and two from Hawaii of 304 and 309 cm TL (Clarke 1971).

In Australian waters, maturity in male *S. lewini* is attained over an extended length range: 140–160 cm TL, as indicated in Fig. 3*c*. The smallest mature specimen was 135 cm and the largest immature male was 161 cm TL. Data on female *S. lewini* are few: of the 137 fish examined, 91% were both less than 150 cm TL and immature. Only two females between 150 and 220 cm were examined: the 166 cm one was an immature virgin but the 152 cm one was judged to be a mature non-virgin. The next smallest mature non-virgin, smallest pre-ovulatory, pregnant and spent fish were 228, 229, 238 and 256 cm TL, respectively. If maturity depends on age rather than length, a wide range of lengths at first maturity may result. However, it seems more likely that the stage of maturity of the 152 cm fish was incorrectly determined. In the absence of more data on adult specimens, females would appear to mature at around 200 cm TL.

Little is known of the reproductive cycle of *S. lewini*. Clarke (1971) found that females in Hawaii gave birth throughout the year but the birth rate was highest between April and October. Litter sizes varied from 15–31 (based on three litters) and the size at birth was about 40–50 cm TL (Clarke 1971; Bass *et al.* 1975).

In northern Australian waters the GSI of males peaked from September to December, suggesting that mating occurs at this time (Fig. 6*a*). One of two fish with mating scars was recorded in January, the other in March. Data on seasonal variation in female GSI and MOD and in pup size are few and show no clear trend (Fig. 6*b–d*). Three fish in a pre-ovulatory condition were caught between January and March; this suggests that ovulation may occur at this time. The occurrence of four near-term pregnant fish (all with mean pup lengths of 48 cm) captured between October and January, together with a spent fish in February, suggests that the birth period may be protracted. If ovulation occurs from January to March and birth from October to January, then the gestation period for

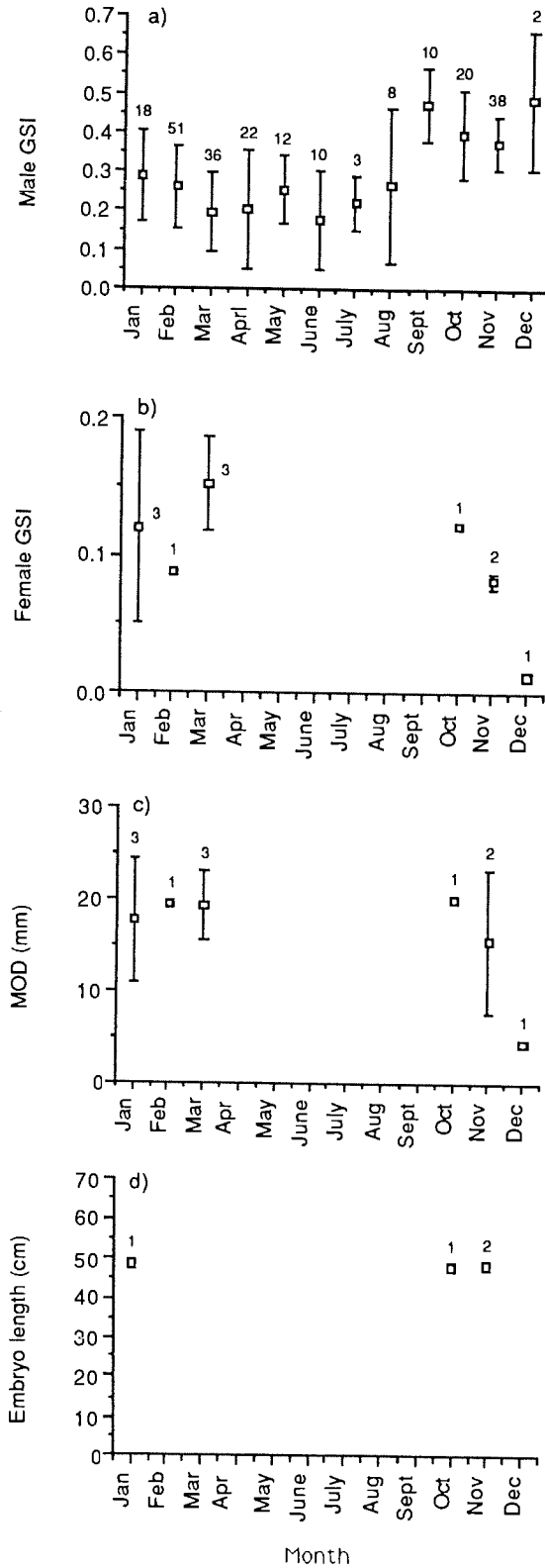


Fig. 6. *S. lewini*. Seasonal cycle of (a) male gonadosomatic index (GSI), (b) female GSI, (c) maximum ova diameter (MOD) and (d) pup length. Plots are mean values; bars are one standard deviation; numbers are sample size [sample size in (d) is number of litters].

S. lewini in northern Australian waters would be some 9–10 months. As the largest embryos recorded were 49.5 cm and the smallest free-swimming specimen was 46.8 cm, the size at birth is probably 45–50 cm TL. Mean litter size from four litters was 16.5, with a range from 13–23.

Data are not sufficient to determine the breeding frequency of females. It is not clear whether all males breed each year, as GSIs for some fish during the suggested mating period (September to December) are similar to values for some individuals outside this period (Fig. 6a).

Diet

E. blochii

The diet of *E. blochii* has not previously been studied, but Compagno (1984) suggested that it consisted of small fishes, cephalopods and crustaceans. The stomach contents of 336 *E. blochii* from northern Australia were examined; 14.6% were empty. Of the 287 specimens whose stomachs contained food, 92.7% had preyed on fish, 14.3% on crustaceans and 4.5% on cephalopods (Table 2). Most of the identifiable fish and crustaceans were clupeids and penaeids (Appendix 1).

Table 2. Distribution of prey, by major prey category, in the stomachs of *E. blochii*, *S. mokarran* and *S. lewini* which contained food

Species	Stomachs examined		Percentage of stomachs with prey category		
	Total	With food	Fish	Cephalopod	Crustacea
<i>E. blochii</i>	336	287	92.7	4.5	14.3
<i>S. mokarran</i>	347	304	87.5	4.6	17.1
<i>S. lewini</i>	660	518	87.3	31.1	5.2

S. mokarran

S. mokarran has been reported to take a variety of prey, including teleost and elasmobranch fish (mainly demersal species), crabs and squid. It seems especially to favour stingrays and other batoids, groupers and sea catfishes (Compagno 1984). Elasmobranch fish were the commonest items in the stomachs of eight *S. mokarran* examined by Bass *et al.* (1975), occurring in five specimens. Teleost fish were found twice, cephalopod, crustacean and seaweed once, and one shark stomach was empty.

Of 347 stomachs examined from northern Australian *S. mokarran*, 12.4% were empty. Of the remainder, 87.5% contained fish, 17.1% crustaceans and 4.6% cephalopods (Table 2). The fish, which included numerous sharks and rays, were mainly demersal species (Appendix 1).

S. lewini

S. lewini has been reported to take a wide variety of fish prey, including some elasmobranchs, together with cephalopods and crustaceans (Compagno 1984). Clarke (1971) found that newly born *S. lewini* from a nursery area in Hawaii fed mainly on reef fish and crustaceans, while adult stomachs contained a high proportion of squid. In the south-western Indian Ocean, 53% of 186 *S. lewini* had food in their stomachs, and, of these, 80% contained teleost fish (mainly pelagic species), 24% molluscs (principally squid), 9% crustaceans and 1% elasmobranch fish. Five stomachs from *S. lewini* off New South Wales contained fish (including elasmobranchs in two specimens) and three also contained cephalopods (Stevens 1984).

Of 660 *S. lewini* examined from northern Australia, 21.5% had empty stomachs. Fish were found in 87.3% of stomachs containing food, cephalopods in 31.1% and

crustaceans in 5.2% (Table 2). In contrast to *S. mokarran*, cephalopods (mainly squid and cuttlefish) occurred more frequently than crustaceans in the stomachs.

Ecology

Three species of hammerhead—*E. blochii*, *S. mokarran* and *S. lewini*— are sympatric off northern Australia. *E. blochii* is found only in tropical areas, whereas *S. mokarran* and *S. lewini* make seasonal incursions into cooler water. A fourth species, *S. zygaena*, also occurs in Australia but appears to remain in the relatively cool waters of the southern half of the continent (Stevens 1984).

Data collected in this study with regard to stomach contents indicate differences in diet that may reflect niche separation among these hammerheads. *E. blochii* and *S. mokarran* appear to feed to a great extent on or near the bottom, as indicated by the higher occurrence of crustaceans and demersal fish species in their stomachs. In the case of *S. mokarran* the diet also included numerous elasmobranchs. *S. lewini* stomachs contained a smaller percentage of crustaceans and a greater percentage of cephalopods, which suggests that this species leads a more pelagic way of life. Cephalopods were the commonest prey found in *S. zygaena* stomachs from New South Wales (Stevens 1984) which indicates a similar pelagic existence for this shark.

From the sex ratios of the embryos of all three species examined in this study, it appears that about equal numbers of males and females are born. However, among the post-partum populations, males predominate. Sexual segregation is least marked in *S. mokarran* and all size groups, including neo-natals, were present in the study area. There were relatively more female *E. blochii* in offshore than in inshore regions. *E. blochii* neo-natals were not caught, which suggests they were in separate nursery areas outside the present study region (possibly close inshore). Adolescent and mature female *S. lewini* were also rarely caught in the sampling area, but new-born pups, juveniles of both sexes and adult males were present. The limited data from New South Wales suggest that there are also few, or no, females further south (Stevens 1984). Mature female *S. lewini*, particularly gravid individuals, have seldom been recorded anywhere (Clarke 1971; Bass *et al.* 1975; Branstetter 1987). In other areas, this species forms large migrating schools and is sexually segregated (Klimley and Nelson 1981; Compagno 1984; Klimley 1987). In Hawaii, Clarke (1971) found that Kaneohe Bay was a pupping and nursery area for *S. lewini*. He suggested that the adults spent most of their time offshore, possibly living in mid-water, and only moved inshore for pupping and breeding. In Australia the larger females may also normally occur over deeper water, possibly at the edge of the continental shelf, and only move into the sampling area for a short period to mate and give birth. In catches of *S. zygaena* from New South Wales, Stevens (1984) found that there were no mature males; adolescent fish of both sexes and mature females were taken from September to May. Specimens less than about 120 cm TL were not caught, but this was almost certainly due to gear selectivity.

S. mokarran and *E. blochii* have similar seasonal reproductive cycles, giving birth in December–January and February–March, respectively, after a gestation period of 10–11 months. *S. zygaena*, which gives birth between January and March off New South Wales, probably has a similar cycle and gestation time (Stevens 1984). *S. lewini* has a more extended cycle, with births occurring from October to January (and possibly throughout the year) after a 9–10 month gestation period. The pups of all four species are thus liberated in the Austral spring-to-autumn period when conditions are presumably more favourable for their development. Individual *E. blochii* females breed each year and *S. mokarran* females every second year, data are not sufficient to show female breeding periodicity in *S. lewini* or *S. zygaena* (Stevens 1984). In Australian waters, litter sizes are essentially similar in *E. blochii*, *S. mokarran* and *S. lewini*, but larger in *S. zygaena* (Stevens 1984). There does not seem to be a clear inter-species relationship between litter size and size-at-birth or maximum size. It might be expected that *E. blochii*, which breeds every year, would have

considerably smaller litters than *S. mokarran*, which breeds every second year, but this is not the case. In *S. zygaena* maturity is reached at about 85% of maximum length (Stevens 1984), whereas in the other species it is reached between 50–70% of maximum length. Possibly *S. zygaena* has larger litters to compensate for attaining maturity at a later stage.

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Appendix 1. Distribution of prey in the stomachs of 287 specimens of *E. blochii*, 304 of *S. mokarran* and 518 of *S. lewini*

Prey item	Number of stomachs		
	<i>E. blochii</i>	<i>S. mokarran</i>	<i>S. lewini</i>
Unidentified elasmobranch	—	3	—
Unidentified shark	1	30	1
<i>Squalus</i> sp.	—	—	1
Scyliorhinid	—	1	—
<i>Carcharhinus amboinensis</i>	—	1	—
<i>C. sorrah</i>	—	5	—
<i>C. tilstoni</i>	—	2	—
Sphyrnidae	—	2	—
Unidentified ray	—	22	1
<i>Rhina ancylostoma</i>	—	—	—
Rhinobatidae	—	9	—
Dasyatididae	—	14	1
<i>Himantura uarnak</i>	—	3	—
Urolophidae	—	1	—
Unidentified teleost	153	137	330
Eel	—	6	4
Muraenesocidae	—	2	—
Congridae	—	1	1
Clupeidae	78	4	41
<i>Megulops cyprinoides</i>	1	—	—
<i>Herklotsichthys</i> sp.	1	—	—
<i>Sardinella</i> sp.	3	—	—
<i>Sardinella isabella</i>	1	—	—
Engraulididae	1	—	—
<i>Setipinna tenuifilis</i>	4	—	—
<i>Stolephorus</i> sp.	4	—	—
<i>Chirocentrus dorab</i>	5	—	—
<i>Chanos chanos</i>	—	1	—
Garfish	—	—	1
Belonidae	2	1	1
<i>Rhynchorhamphus georgei</i>	1	—	—
Exocoetidae	—	—	2
Synodontidae	2	2	36
<i>Saurida</i> spp.	1	1	4
<i>Saurida undosquamis</i>	—	1	3
Ariidae	—	10	—
<i>Arius thalassinus</i>	—	1	—
Ariidae eggs	2	—	—
Plotosidae	—	1	—
Platycephalidae	1	6	2
Dactylopteridae	—	—	1
Priacanthidae	—	—	1
Apogonidae	—	—	1
<i>Sillago</i> sp.	1	—	1
<i>Rachycentron canadus</i>	—	6	—
Carangidae	4	4	14
<i>Caranx</i> sp.	—	—	1
<i>Megalaspis cordyla</i>	—	—	2
<i>Apolectus niger</i>	4	4	3
<i>Mene maculata</i>	—	—	1
Leiognathidae	14	—	10
<i>Secutor</i> sp.	1	—	—

Appendix 1 (contd)

Prey item	Number of stomachs		
	<i>E. blochii</i>	<i>S. mokarran</i>	<i>S. lewini</i>
Lutjanidae	—	—	1
<i>Lutjanus malabaricus</i>	—	1	—
<i>Lutjanus sebae</i>	—	1	—
Nemipteridae	3	10	23
<i>Nemipterus mesoprion</i>	—	—	1
<i>Pentapodus</i> sp.	—	1	—
Gerridae	1	—	—
<i>Plectorhinchus</i> sp.	—	1	—
Lethrinus sp.	—	—	1
Sciaenidae	1	1	—
<i>Scolopsis</i> sp.	1	—	—
Mullidae	—	—	1
<i>Upeneus moluccensis</i>	—	—	1
Sphyraenidae	1	1	—
Polynemidae	2	—	1
Labridae	—	1	—
Scaridae	—	—	1
Mugilidae	2	—	—
<i>Champsodon guentheri</i>	—	—	1
Callionymidae	—	—	3
Trichiuridae	5	2	12
Scombridae	—	7	8
<i>Euthynnus affinis</i>	—	2	1
<i>Rastrelliger</i> sp.	1	—	—
<i>Rastrelliger kanagurta</i>	5	—	—
<i>Scomberomorus</i> sp.	2	2	2
<i>Istiophorus platypterus</i>	—	1	—
<i>Psettodes erumei</i>	—	1	—
Flatfish	—	—	1
Bothidae	—	—	1
Cynoglossidae	—	6	—
Triacanthidae	—	—	1
Balistidae	—	2	2
Monacanthidae	—	—	1
Ostraciidae	—	1	2
Tetraodontidae	—	—	3
<i>Lagocephalus sceleratus</i>	—	1	—
Diodontidae	—	8	3
<i>Lates calcarifer</i>	—	1	—
Total fish	266 (92.7%)	266 (87.5%)	452 (87.3%)
Unidentified cephalopod	10	2	43
Squid	3	8	81
Cuttlefish	—	5	48
<i>Sepia eliptica</i>	—	—	1
Octopus	—	—	1
Total cephalopod	13 (4.5%)	14 (4.6%)	161 (31.1%)
Unidentified crustaceans	—	3	1
Decapod	—	1	1
Stomatopod	—	10	1
Squillidae	3	6	3
<i>Squilla</i> sp.	—	—	1

Appendix 1 (contd)

Prey item	Number of stomachs		
	<i>E. blochii</i>	<i>S. mokarran</i>	<i>S. lewini</i>
Natantid	—	—	2
Unidentified prawns	29	18	10
Penaeidae	—	—	1
<i>Penaeus</i> spp.	2	7	6
<i>Penaeus merguensis</i>	1	1	—
<i>Penaeus monodon</i>	—	1	—
<i>Trachypenaeus</i> sp.	3	—	—
<i>Atypopenaeus formosus</i>	1	—	—
<i>Metapenaeopsis</i> sp.	1	—	—
<i>Metapenaeus</i> sp.	—	—	1
Scyllaridae	—	10	—
<i>Panulirus</i> sp.	—	1	—
Unidentified crab	—	3	—
Portunidae	—	2	—
<i>Portunus sanguinolentus</i>	1	—	—
Total crustaceans	41 (14.3%)	52 (17.1%)	27 (5.2%)
Gastropod	—	1	—
Bivalve	—	—	1
Holothurian	—	1	—
Turtle	—	1	—
Mammal bones	—	1	—
Bone	—	—	1
Unidentified material	—	1	2

Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia

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Abstract

The distribution, size composition, sex ratio, reproductive biology and diet of 17 species of shark from the families Triakidae, Hemigaleidae and Carcharhinidae from northern Australia were examined. In most of these species the sex ratio of the embryos is 1:1, while in the post-partum populations there were significantly more males than females. The results indicate four broad reproductive strategies among these sharks. In most species reproduction was distinctly seasonal with individual females giving birth each Austral summer (annual cycle) after a gestation period of 9-12 months. A second group had a very similar cycle except that individual females gave birth every second year (biennial cycle). A third group had an annual cycle but breeding was continuous throughout the year; these were mostly small bottom-associated sharks. One species had a seasonal cycle but gave birth twice each year (biannual cycle) after a six months gestation period.

The average size at birth varied from 27-75 cm and the average litter size varied from 2-34. The size at birth is about 40% of the size at maturity, which in turn is about 70% of the maximum size. Diets ranged from omnivorous to highly selective. Fish was an important component of the diet in all but one species. There was evidence of partitioning of food resources among sympatric, morphologically similar, sharks.

Introduction

Between 1974 and 1986 a Taiwanese surface gill-net fishery operated in offshore waters of the Timor and Arafura Sea off northern Australia. Shark was the major component of the catch, although longtail tuna, *Thunnus tonggol*, and spanish mackerel, *Scomberomorus* spp. were also target species. Australia assumed management responsibilities for the fishery after the Australian Fishing Zone was introduced in 1979. In the early 1980s a small Australian fishery, based on the same species, began operations in the same region, but close inshore. These fisheries stimulated considerable research interest into the biology of northern Australian sharks. Initial studies concentrated on documenting the life-histories of the principal commercial species, *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes). The population structure, reproductive biology, diet, age and growth of these sharks were reported on by Stevens and Wiley (1986) and Davenport and Stevens (1988). However,

biological data on other species were also collected. Stevens and Lyle (1989) described the population structure, reproductive biology and diet of the hammerhead sharks *Eusphyrna blochii* (Cuvier), *Sphyrna mokarran* (Rupell) and *Sphyrna lewini* (Griffith and Smith). Similar information for *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy and Gaimard) and *C. fitzroyensis* (Whitley) was provided by Lyle (1987). The remaining data for other species are reported in this paper. As relevant data on many of these sharks are available from other areas, this information is reviewed and summarised for comparison.

Materials and Methods

Sampling Methods

Sharks were collected from northern Australian waters from June 1980 to October 1987, mostly from Taiwanese commercial gill-net catches and research cruises. Some specimens were obtained from a study of sharks in Darwin Harbour (Lyle 1987) and from monitoring Australian commercial gill-net catches. Length data were also obtained from the Taiwanese fishery by commonwealth observers on board the vessels. The area sampled is shown in Fig. 1.

Sharks were captured with gill-nets, longlines, demersal trawls and handlines. The gill-nets used in the Taiwanese fishery were constructed of multifilament nylon with a diagonal stretched mesh averaging 17 cm (14.5 to 19.0 cm); they were about 15 m deep from the headrope to the footrope. Net length varied between vessels and averaged about 8 km in 1980 and about 16 km in 1986. The nets were allowed to drift and were set close to the surface. A more detailed description of sampling this fishery is given in Stevens and Wiley (1986). Most gill-nets used on research cruises were of 15 cm stretched mesh monofilament, 500 to 1200 m long and approximately 11 m deep; they were set within 3 m of the surface. Some sharks were caught in gill-nets designed to study gear selectivity; panels of 10, 15, 20 and 25 cm mesh monofilament were used. Each panel was 200 m long and 10 m deep, and was separated from adjoining panels by 100 m of headrope (Stevens and Church 1984). Longlines, which were fished both on the surface and the bottom, consisted of 400 to 5000 m of mainline with 60 to 300 hooks. Demersal tows were made with a New Zealand Frank & Bryce trawl with a 32 m footrope (3 m opening height at 3 knots) and a German Engel high-opening trawl with a 49 m footrope (6 m opening height at 3 knots).

Further details of the gear used on research cruises are given by Lyle and Timms (1984), Stevens and Church (1984) and Stevens and Wiley (1986). The number of stations occupied in each area off northern Australia, by fishing method and depth zone, is shown in Table 1.

Some additional information on shark distribution was obtained from examining material in the Australian Museum (AM), Western Australian Museum (WAM) and the Queensland Museum (QM).

Length and weight measurements

Sharks were measured to the nearest centimetre either as total lengths (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 lengths (FL). Fork lengths were converted to total lengths using equations derived in this study (Table 2).

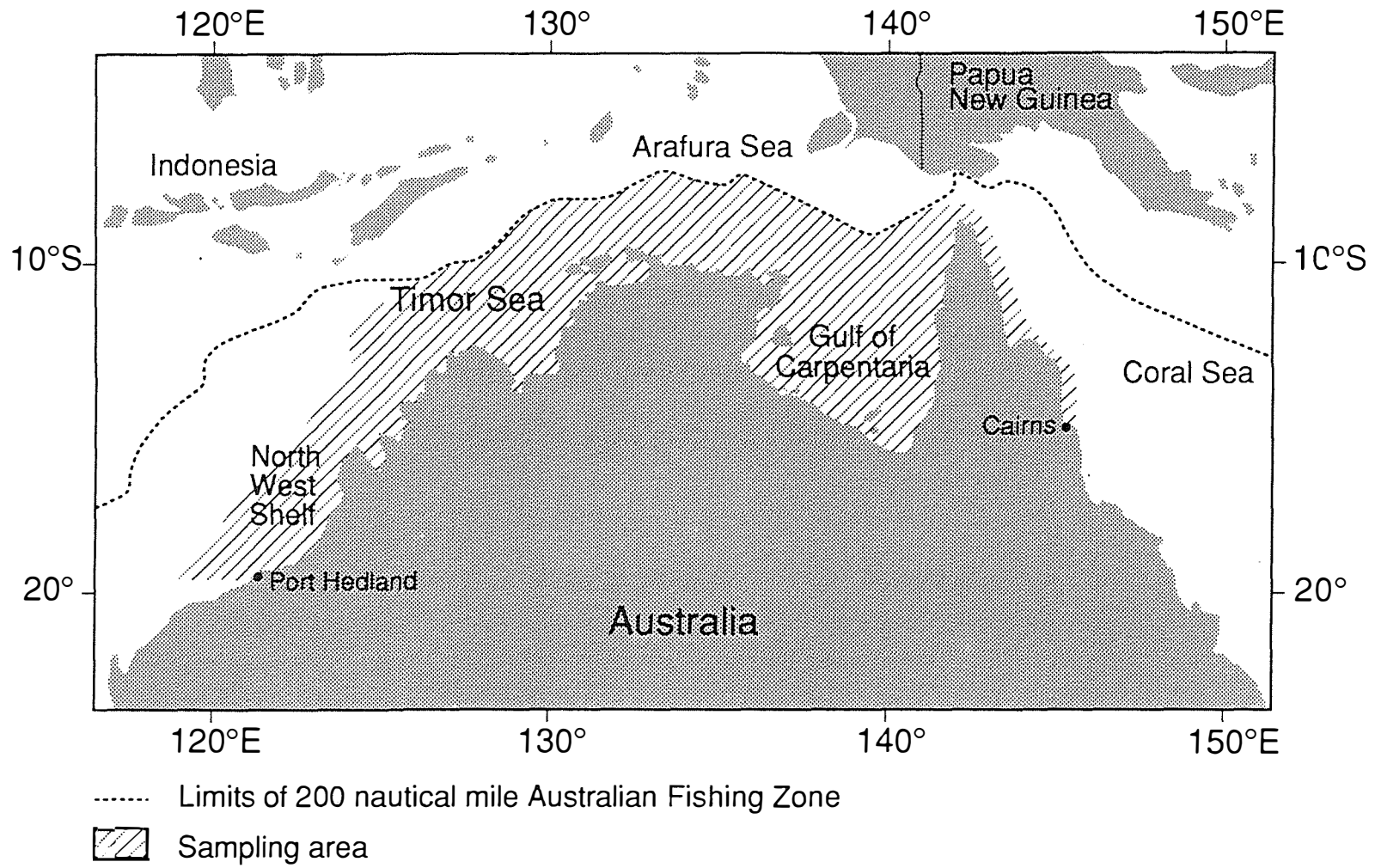


Fig.1. Sampling area off northern Australia.

Table 1. Number of stations occupied in each area off northern Australia, by fishing method and depth zone.

Area	Fishing method	Depth zone (m)				
		0-50	50-100	100-150	150-200	>200
North West Shelf	Hook & line	43	32	11	3	11
	Gill-net	11	0	0	0	0
	Trawl	634	596	223	45	189
Timor Sea	Hook & line	48	13	0	0	0
	Gill-net	144	116	2	0	0
	Trawl	30	74	29	4	7
Arafura Sea	Hook & line	119	59	0	0	0
	Gill-net	377	116	0	0	0
	Trawl	51	65	8	3	0
Gulf of Carpentaria	Hook & line	62	1	0	0	0
	Gill-net	156	0	0	0	0
	Trawl	62	31	0	0	0
NE Queensland	Hook & line	30	1	0	0	0
	Gill-net	44	3	0	0	0
	Trawl	0	0	0	0	0
All Areas	Hook & line	302	106	11	3	11
	Gill-net	732	235	2	0	0
	Trawl	777	766	260	52	196

Sharks were weighed on calibrated spring balances reading to the nearest 500 g, except for the smaller specimens (< 25 kg), which were weighed to the nearest 100 g. Lengths were converted to weights using the TL and total weight 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). Males were considered to be mature when the claspers were elongated and the clasper cartilages were rigid from calcification. The claspers of immature males are short, flexible and grow slowly in relation to the length of the shark. During adolescence the claspers elongate rapidly, becoming rigid from calcification when fully mature. This pattern of development typically produces an S-shaped curve when relative clasper length is plotted against body length. Females were considered to be mature when distinct ova were present in the ovary, oviducal

Table 2. Total weight-total length and fork length-total length relationships (sexes combined) for sharks from northern Australian waters.

TL, total length (cm); FL, fork length (cm); TW, total weight (g); n, number in sample. Coefficient of determination (r^2) based on linear regression of $\ln(TW)$ against $\ln(TL)$.

Species	n	Equation	r^2
<i>Mustelus</i> sp.	29	FL = 0.89TL + 0.05	0.967
	29	TW = $1.49 \times 10^{-3}TL^{3.22}$	0.989
<i>H. microstoma</i>	331	FL = 0.88TL - 1.17	0.999
	425	TW = $3.48 \times 10^{-3}TL^{3.00}$	0.982
<i>H. elongatus</i>	58	FL = 0.79TL + 1.43	0.981
	30	TW = $1.62 \times 10^{-3}TL^{3.21}$	0.970
<i>C. amblyrhynchoides</i>	94	FL = 0.81TL - 1.52	0.997
	67	TW = $2.65 \times 10^{-3}TL^{3.21}$	0.975
<i>C. amblyrhynchos</i>	28	FL = 0.88TL - 4.46	0.999
	24	TW = $7.46 \times 10^{-3}TL^{2.98}$	0.971
<i>C. amboinensis</i>	198	FL = 0.79TL - 0.68	0.997
	104	TW = $1.94 \times 10^{-3}TL^{3.27}$	0.986
<i>C. brevipinna</i>	40	FL = 0.85TL - 3.21	0.998
	35	TW = $1.13 \times 10^{-3}TL^{3.33}$	0.988
<i>C. dussumieri</i>	175	FL = 0.830TL - 0.24	0.991
		TW = $3.03 \times 10^{-3}TL^{3.12}$	0.935
<i>C. falciformis</i>	22	FL = 0.84TL - 4.02	0.996
	23	TW = $4.66 \times 10^{-3}TL^{3.05}$	0.990
<i>C. macloii</i>	211	FL = 0.82TL - 1.05	0.997
	127	TW = $3.91 \times 10^{-4}TL^{3.55}$	0.830
<i>C. plumbeus</i>	117	FL = 0.82TL - 1.13	0.995
	150	TW = $1.42 \times 10^{-3}TL^{3.31}$	0.984
<i>G. cuvier</i>	53	FL = 0.88TL - 15.71	0.996
	86	TW = $2.62 \times 10^{-4}TL^{3.57}$	0.993
<i>L. macrorhinus</i>	174	FL = 0.83TL - 1.51	0.993
	283	TW = $4.79 \times 10^{-4}TL^{3.44}$	0.955
<i>R. acutus</i>	483	FL = 0.820TL - 0.70	0.998
	413	TW = $3.74 \times 10^{-3}TL^{3.01}$	0.945
<i>R. taylori</i>	223	FL = 0.85TL - 1.18	0.954
	148	TW = $2.17 \times 10^{-4}TL^{3.75}$	0.836

glands were fully differentiated from the oviducts, and the posterior sections of the oviducts (functional uteri) were expanded. Females with the vaginal hymen intact were judged to be virgin. The largest egg(s) in the ovary were measured with calipers to the nearest millimetre to determine maximum ova diameter (MOD). Gonads were excised from the surrounding epigonal organ and weighed to 0.1 g. Gonosomatic indices (GSI) were calculated (for mature fish only) as the gonad weight/total body weight x 100. The number, lengths and sex of the embryos were recorded.

Stomach contents

Recognisable prey items from stomach contents were generally identified to family and, where practicable, to genus or species. Identifications 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.

Text format

The approach taken in this paper has been to provide separate accounts for each species, each comprising a literature review (where available), results and specific discussion. The species accounts are followed by a general discussion of sex ratios, reproductive biology and diet of Australian, principally carcharhinid, sharks. Because information on distribution and population structure is subsidiary to the main data on reproductive biology and diet, the sections on distribution, size and sex ratio are dealt with in an abbreviated, standardised format. Because of the volume of information to be presented and the problems of repetition when dealing with successive species, it was felt that this format provided a more concise presentation for these subsidiary data. In each section the literature information is presented first and our data second. In the abbreviated format sections, nsd and n indicate 'not significantly different from' and the sample size, respectively.

Results and Discussion of Species

Species Accounts

(1) *Mustelus* sp.

This shark is very similar to, and was originally identified as, *Mustelus manazo* Bleeker (starspotted smooth-hound) but unlikely depth distributions made the identification suspect. Compagno (1984) stated that *M. manazo* occurs in the intertidal and subtidal regions, often close inshore; in contrast *Mustelus* sp. was captured at depths between 122-303 m (see section on distribution). Subsequently, Dr Bernard Seret (Museum National d'Histoire Naturelle, Paris 75231, personal communication) recorded this shark from off New Caledonia and confirmed that it was currently undescribed. *Mustelus* sp. will be described by Dr Seret. A voucher specimen (H 2255-01) from northern Australia has been deposited in the ISRMUNRO Fish Collection, CSIRO Marine Laboratories, Hobart, Tasmania 7001.

Distribution

Present study: Captured by trawl on the North West Shelf and slope off Western Australia, off north-east Queensland and (1 record) in the Arafura Sea. Taken in depths between 122-303 m; occurred in 5% of trawls in more than 100 m on the North West Shelf.

In Australia, this species apparently does not occur outside the tropics, although its presence in temperate areas may have been overlooked due to confusion with the similar *M. antarcticus*.

Size

Males 28-101 cm; females 30-116 cm TL (present study, Fig.2a)

Sex ratio

Embryos nsd 1:1, post-partum 30.5 % female, χ^2 test $P < 0.001$ (present study, Table 3).

Table 3. Sex ratio of sharks from northern Australia

Species	Embryos			Post-partum		
	n	% Female	Sign.	n	%Female	Sign.
<i>Mustelus</i> sp.	92	54.3	ns	82	30.5	***
<i>H. microstoma</i>	451	48.8	ns	464	38.8	***
<i>H. elongatus</i>	23	56.5	ns	478	46.4	ns
<i>C. amblyrhynchoides</i>	22	36.4	ns	277	13.0	***
<i>C. amblyrhynchos</i>	20	35.0	ns	66	59.1	ns
<i>C. amboinensis</i>	6	33.3	ns	379	46.2	ns
<i>C. brevipinna</i>	-	-	-	2110	45.4	**
<i>C. dussumieri</i>	211	47.4	ns	569	46.2	ns
<i>C. falciformis</i>	-	-	-	34	32.4	*
<i>C. macloti</i>	125	44.0	ns	3142	58.0	***
<i>C. plumbeus</i>	109	45.0	ns	430	56.5	**
<i>G. cuvier</i>	-	-	-	299	56.5	*
<i>L. macrorhinus</i>	106	48.1	ns	279	37.3	***
<i>R. acutus</i>	393	55.7	*	1622	32.2	***
<i>R. taylori</i>	198	55.1	ns	385	53.0	ns

*** $P < 0.001$

** $P < 0.01$

* $P < 0.05$

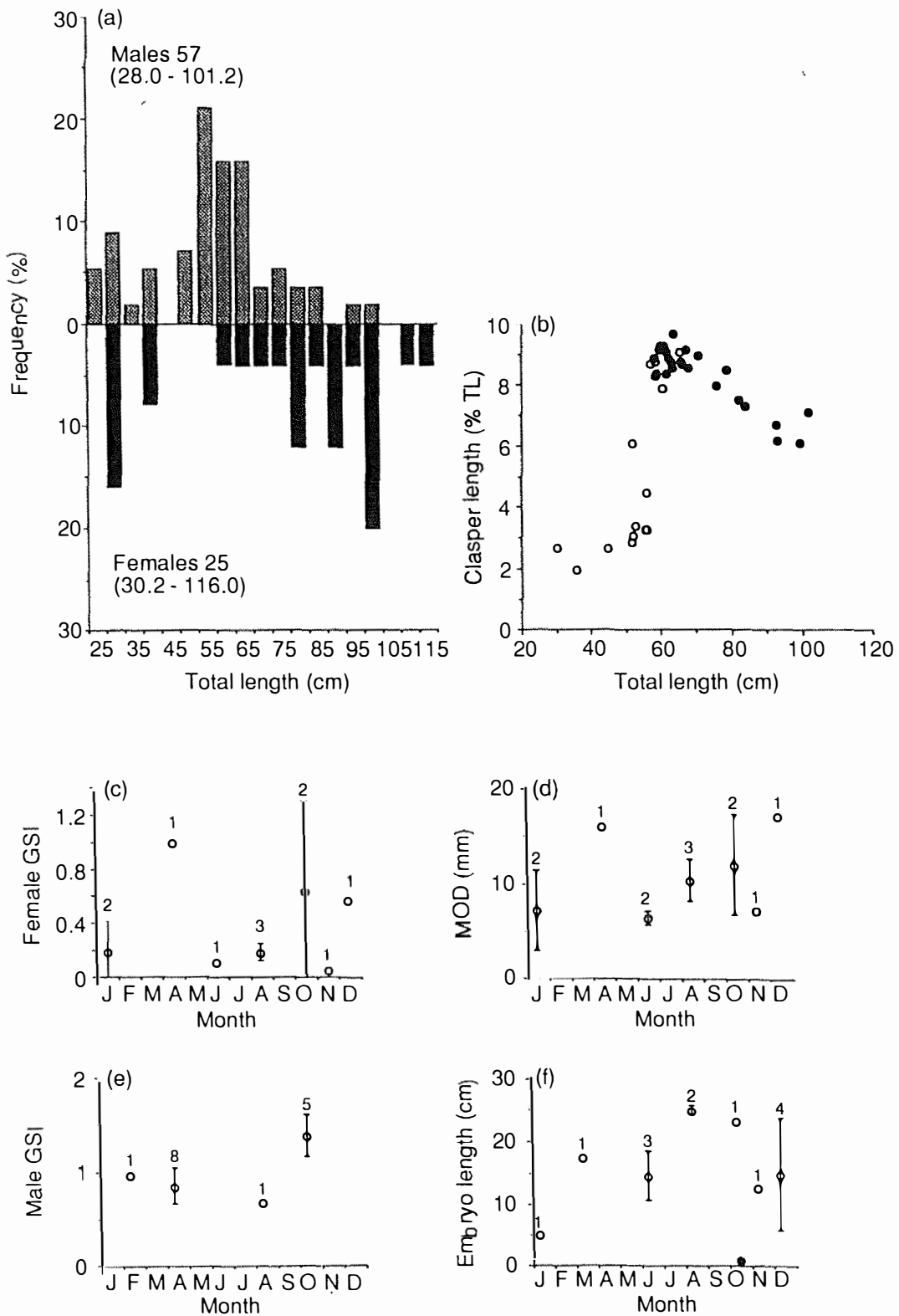


Fig. 2. *Mustelus* sp. (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

Reproduction

In northern Australia, males mature at about 60 cm; the smallest mature fish was 58 cm and the largest immature specimen was 61 cm TL (Fig. 2b). Females also mature at about 60 cm; the smallest preovulatory and pregnant fish were 62 cm and 65 cm TL, respectively.

The rather limited data on GSI, MOD and embryo length (Fig. 2c-f) show no discernable seasonal trends and hence no evidence of a seasonal reproductive cycle in northern Australian waters, or possibility of determining the gestation period. Litter size ranged from 4-17, with a mean of 9 (13 litters sampled). Although there was a significant relationship between larger litters and maternal length ($r^2 = 0.33$, $P < 0.05$), nearly 70% of the variation in litter size was attributable to factors other than maternal length. The size at birth is about 27 cm; the largest embryo was 27 cm and the smallest free-swimming specimen was 28 cm TL. Of 14 mature females, 13 were pregnant, which suggests that individual females breed each year. Further evidence of a continuous cycle comes from examining the MOD of pregnant fish, which in *Mustelus* sp., increases with embryo size through gestation. The diameter of the ova increases slowly through early pregnancy and then increases rapidly as parturition approaches. Following birth the female has a new batch of ripe ova in the ovary.

Diet

Of 69 *Mustelus* sp. stomachs which contained food, 94% contained crustaceans, 28% fish and 17% cephalopods (Table 4). Most of the crustaceans were crabs, while the of the identifiable fish were strictly demersal species (Appendix 1).

Table 4. Percentage occurrence of major prey groups in the stomachs of sharks from northern Australia.

Species	% Occurrence in stomachs with food								Stomachs	Stomachs
	Crust	Ceph	Mollusc	Fish	Rept	Bird	Mamm	Other	examined	with food
									n	n
<i>Mustelus</i> sp.	94.2	17.4	1.5	27.5	-	-	-	2.9	70	69
<i>H. microstoma</i>	3.0	98.5	0.3	1.2	-	-	-	0.9	446	331
<i>H. elongatus</i>	-	67.5	-	50.6	-	-	-	-	111	83
<i>C. amblyrhynchoides</i>	6.3	3.9	-	91.3	-	-	-	-	186	127
<i>C. amboinensis</i>	22.2	11.1	-	83.3	-	-	-	-	31	18
<i>C. brevipinna</i>	2.0	7.8	-	86.3	-	-	-	3.9	111	51
<i>C. dussumieri</i>	26.2	20.7	-	76.2	-	-	-	-	526	324
<i>C. macloii</i>	1.1	4.4	-	94.5	-	-	-	-	216	91
<i>C. plumbeus</i>	7.8	21.7	0.9	87.8	-	-	-	1.7	181	115
<i>G. cuvier</i>	15.6	15.6	2.6	62.3	58.4	2.6	2.6	7.8	98	77
<i>L. macrorhinus</i>	60.4	18.8	1.0	76.3	-	-	-	1.9	258	207
<i>R. acutus</i>	10.4	18.9	1.2	93.3	-	-	-	2.4	315	164
<i>R. taylori</i>	34.2	2.6	-	79.0	-	-	-	-	68	38

(2) *Hemigaleus microstoma* Bleeker, 1852 (sicklefin weasel shark)

Observations on the identification and biology of this species, based on 71 specimens from Australian waters, were reported in a previous paper (Stevens and Cuthbert 1983). Subsequently, a further 426 specimens have been collected from northern Australia, contributing further to our knowledge of this shark.

Distribution

Literature : Tropical waters of the Indo-West Pacific (Compagno 1984).

Present study: Northern Australian waters extending south to Moreton Bay, Queensland (27° 20'S, 153° 15'E) and Shark Bay, Western Australia (26° 10'S, 113° 11'E) (QMI 14517, I 13590; WAM 6852.001, 6853.001). Taken in depths between 17-167 m; occurred at 12% of trawl stations in less than 150 m; rarely taken by gill-net or hook and line. This was the shark taken most frequently by trawl on the North West Shelf.

Size

Maximum TL 97 cm female from northern Australia (Stevens and Cuthbert 1983).

Males 28-103 cm; females 34-110 cm TL (present study, Fig.3a).

Sex ratio

Embryos nsd 1:1; post-partum 38.8% females, χ^2 test $P < 0.001$ (present study, Table 3).

Reproduction

Additional data support the observations of Stevens and Cuthbert (1983) that males mature at about 60 cm (Fig. 3b) and that females are adolescent at 50 cm but do not reach full maturity until about 65 cm TL. Examination of GSI by month does not show a clear pattern (Fig. 3c & e). However, seasonal differences in pup length suggest that two litters may be produced each year (Fig. 3f). With the exception of one litter averaging 26 cm TL in May, the data can be interpreted as forming two series. Females with eggs in utero were recorded in March and April, and again in September and October (Fig. 3f). Embryos from the March/April batch of ova increase from 19 cm in June to 31 cm in September, while those from the September/October batch increase from 4 cm in October to 31 cm in February. Since birth occurs at about 30 cm (the largest embryo recorded was 34 cm and the smallest free-swimming individual was 27 cm) the gestation period for each litter would be about six months. There is some indication from Figs. 3c & d that female GSI and MOD peak between February and April and again in September, which suggests ovulation is around these times; this agrees with the finding of ova in utero in March/April and September/October. Male GSI peaks in June and December (Fig. 3e), some 2-3 months before the proposed ovulation periods. However, the increased ovary weight in December (Fig. 3c) does not fit in with this reproductive pattern.

The pregnancy rate among mature females was 93%, which suggests that females breed each year; this is supported by the MOD of pregnant fish, which increases with embryo size during gestation, so that near-term pregnant fish generally have large ova approaching their size at ovulation. Litter sizes ranged from 1-19 with a mean of 8, and there was a significant relationship between increasing litter size and maternal length ($r^2 = 0.35$, $P < 0.001$).

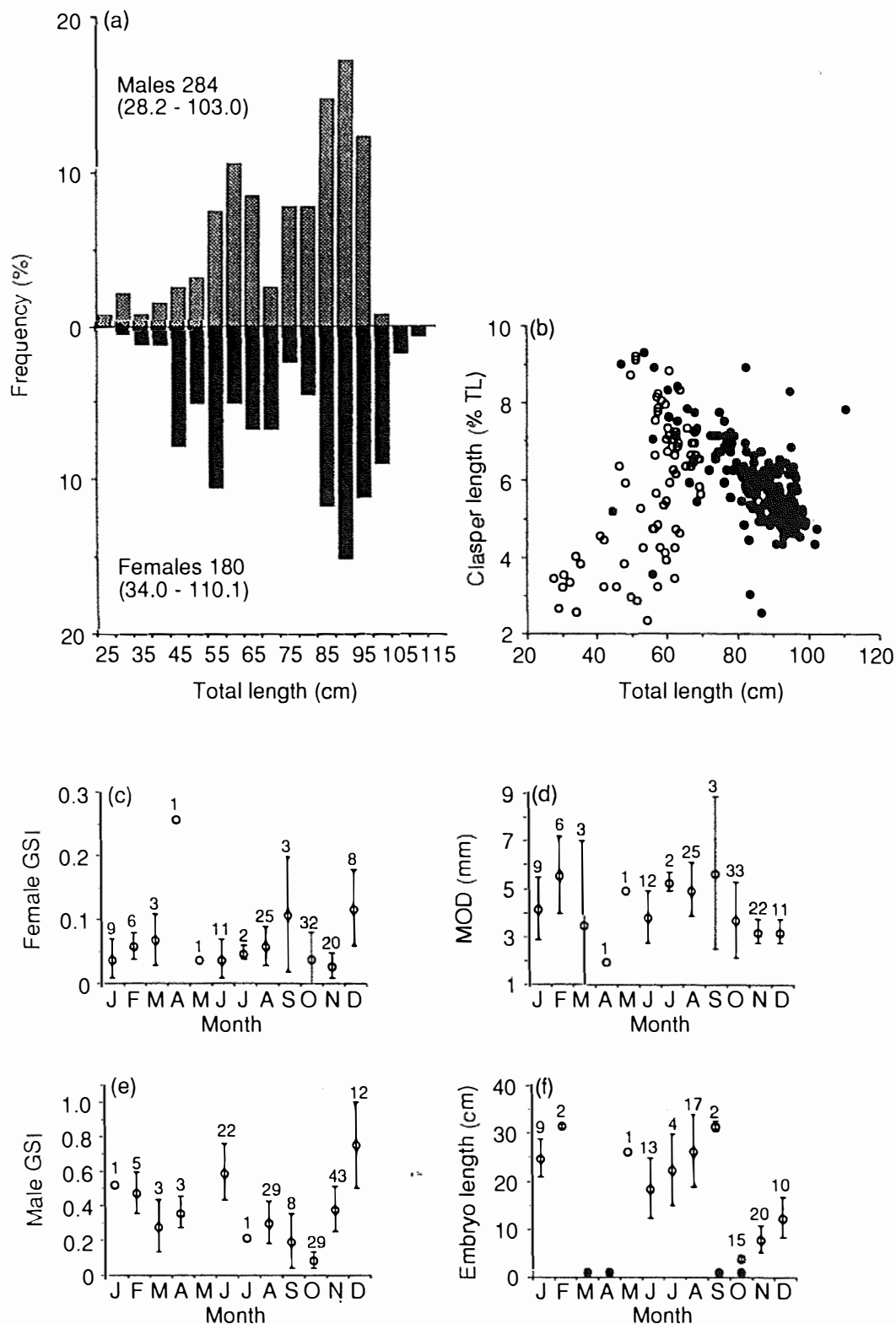


Fig. 3. *Hemigaleus microstoma* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

Diet

Additional data support the observations of Stevens and Cuthbert (1983) that *H. microstoma* is a highly selective feeder preying mainly on cephalopods, particularly octopus. Of 446 specimens examined, 74% had food in their stomachs. Cephalopods were found in 99% of these stomachs, crustaceans in 3%, fish in 1% and miscellaneous items in 1% (Table 4). The majority of identifiable cephalopods were octopus (Appendix 1).

(3) *Hemipristis elongatus* (Klunzinger, 1871) snaggletooth shark

Distribution

Literature: Tropical Indo-West Pacific; continental and insular shelves at depths of 1-30 m (Compagno 1984). Throughout northern Australia from Lizard Island, NE Queensland (14° 40'S, 145° 27'E) to Exmouth Gulf, Western Australia (22° 10'S, 114° 20'E) (Bass 1979; Sainsbury *et al.* 1985).

Present study: Captured in depths between 13 -132 m; occurred at 11% of gill-net and 1% of trawl stations in less than 100 m; rarely taken by hook and line.

Size

Maximum TL 230-240 cm (Compagno 1984).

Males 53-177 cm; females 71-184 cm TL (present study, Fig.4a).

Sex ratio

Embryos, four males in a litter of six (Setna and Sarangdhar 1949b).

Embryos and post-partum nsd 1:1 (present study, Table 3).

Reproduction

All that is known of reproduction in this species is summarised in Compagno (1984). He noted that the size at birth is about 45 cm, males are adolescent at 73-106 cm and adult at 120-145 cm, females are adult at 170-218 cm TL, and have 6-8 young per litter. Setna and Sarangdhar (1949b) described the reproductive system of one pregnant female containing six embryos.

In Australian waters, males mature at about 110 cm (Fig. 4b); the smallest mature male was 108 cm and all males above 116 cm TL (with the exception of one fish of 127 cm) were mature. Females mature at 110-120 cm.

H. elongatus appears to have a distinct seasonal reproductive cycle in northern Australia. Male GSI reaches a peak of 0.6-0.7 between April and June (Fig. 4e), with female GSI and MOD reaching a maximum around September when the ova are about 3.5 cm in diameter (Fig. 4c & d). The only female with ova in utero was caught in September. The limited data in Fig. 4f show an increase in pup length from about 5 cm in October to 52 cm TL in April. These data suggest mating takes place around June, ovulation in September and parturition in about April, giving a gestation period of some 7-8 months. The pregnancy rate among mature fish is 25%, which suggests that individual females breed, at the most, every other year, but the sample of 32 specimens is small. The largest embryos averaged 52 cm and the smallest free-swimming specimen was 53 cm; size at birth is probably about 52 cm TL. Mean litter size was 6 (range 2 to 11 and there was a significant relationship between increasing maternal length and larger litters ($r^2 = 0.87$, $P < 0.01$).

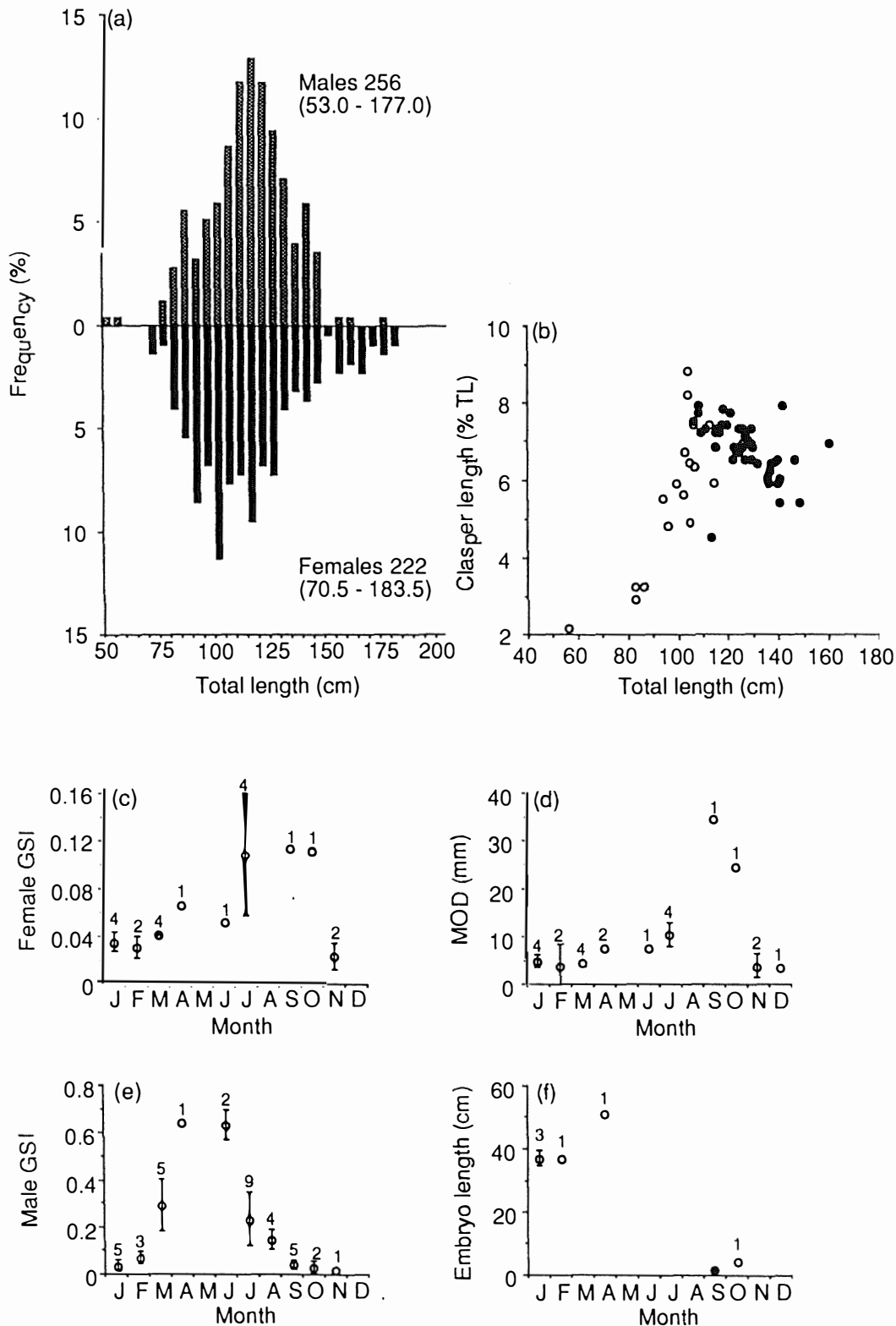


Fig. 4. *Hemipristis elongatus* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

Diet

H. elongatus in Bombay waters, take a variety of fish prey (including smaller sharks and rays), as well as prawns and shrimps (Setna and Sarangdhar 1949c).

Of 111 northern Australian specimens examined, 75% had food items in their stomachs. Of these, 68% contained cephalopods (mainly squid and cuttlefish) and 51% contained fish (all demersal species), including a number of elasmobranchs (Table 4 and Appendix 1). No other prey categories were recorded.

(4) *Carcharhinus altimus* (Springer, 1950) bignose shark

Distribution

Literature: Tropical and warm-temperate in the Pacific, Indian and Atlantic Oceans, and the Mediterranean and Red Sea (Compagno 1984). Western Australia (North West Shelf) (Sainsbury *et al.* 1985). Depths from 100 m down to 430 m, occasionally shallower (Compagno 1984).

Present study: Northern Australian waters south to Rottnest Island, 32° 00'S, 115° 30'E, on the west coast (WAM 15072 to 15077. 001) and northern New South Wales on the east coast (AM I 23718-002). Five specimens captured by longline on the North West Shelf, near the surface in 400-810 m; one caught by trawl in the same area at 82 m.

Size

Maximum TL 286 cm male (Paraiso 1957).

Males 151-204 cm (n = 2); females 60-250 cm TL (n = 4) (present study).

Sex ratio

Eleven adult males and 15 adult females from the western Atlantic (Springer 1960); 11 males and 20 females from Natal coast (Bass *et al.* 1973).

Two males and four females (present study).

Reproduction

In the western Atlantic, the smallest mature specimens recorded by Springer (1960) were a 216 cm male and a 226 cm female. The smallest of four mature females from Madagascar measured 234 cm TL (Fourmanoir 1961).

Of the two males caught in the present study, the 151 cm specimen was immature while the 204 cm one was mature. The smallest of two pregnant and one spent fish was 240 cm TL.

C. altimus are born in September/October off Madagascar (Fourmanoir 1961). Bass *et al.* (1973) note that the embryos recorded by Springer (1950) in the western Atlantic would probably have been dropped in the northern summer. In the Mediterranean this shark gives birth in August and September (Morenos and Hoyos 1983). Litter sizes range from 3-15, the gestation period is unknown, and the size at birth is reported to be between 70 and 90 cm TL (Bass *et al.* 1973; Compagno 1984).

In the present study, two pregnant and one spent female were captured in April. The litter sizes were six and eight, and the pups from both litters averaged 42 cm TL. A 60 cm TL female with an open umbilical scar was caught in February.

Diet

C. altimus is reported to eat a variety of fish, including elasmobranchs, and cephalopods; a high proportion of the prey items are demersal species (Bass *et al.* 1973).

The stomach contents of five specimens were examined in this study, three were empty. Fish (a scombrid and a *Raja* sp. egg case) were found in two stomachs, cephalopods in one stomach and a crustacean (*Metanephrops* sp.) in one stomach.

(5) *Carcharhinus amblyrhynchoides* (Whitley, 1934) graceful shark*Distribution*

Literature: Tropical Indo-West Pacific; continental and insular shelves (Compagno 1984). Cape Bowling Green, Queensland (19° 20'S, 147° 25'E), the Northern Territory (Lyle and Timms 1984) and the "northwestern coast" (Garrick 1982; Compagno 1984).

Present study: Inshore waters from the north-eastern Gulf of Carpentaria to Cape Londonderry, Western Australia (14°S, 127°E). Near the surface in 12 to 48 m. Taken at 7% of gill-net stations and 4% of hook and line stations in the 0-50 m depth zone.

Size

Maximum TL 167 cm female from the Gulf of Thailand (Garrick 1982).

Males 64-161 cm; females 70-162 cm TL (present study, Fig.5a).

Sex ratio

Embryos nsd 1:1; post-partum 13% female, χ^2 test $P < 0.001$ (present study, Table 3).

Reproduction

Neither the size at maturity nor the reproductive biology of *C. amblyrhynchoides* has been reported in the literature. Males mature at about 108 cm in northern Australia (Fig.5b); the smallest mature specimen was 104 cm and the largest immature one was 110 cm TL. Females mature at about 115 cm; the smallest mature fish was a 110 cm virgin, while the smallest pregnant specimen was 120 cm TL.

The male GSI of *C. amblyrhynchoides* varies seasonally, being low from June to October and highest in February (Fig. 5e). Data on females are more limited but GSI and MOD are highest around March (Fig. 5c & d). This suggests they mate about February and ovulate in March or April. Limited information on pregnant females shows that in May early embryos of around 5 cm are present, and by November these have increased in length to about 40 cm TL (Fig. 5f). Spent fish were recorded mainly in February (with one in March) which suggests parturition in January/February and a gestation period of 9 to 10 months. Since embryos are 40 cm long after seven months, their size at birth is probably between 50 and 60 cm TL, for the smallest free-swimming specimen recorded was 65 cm and the size of the closely related *C. tilstoni* at birth is 60 cm TL (Stevens and Wiley 1986). Compagno (1984) estimated the size at birth of *C. amblyrhynchoides* as about 52-55 cm TL, presumably based on the largest embryo (55 cm) and smallest free-swimming specimen (52 cm) observed by Garrick (1982).

The average litter size for *C. amblyrhynchoides* in this study was three, with a range from 1-9 (nine litters sampled); there was insufficient data to determine whether litter size increased with maternal length. Of the mature females examined, 100% were pregnant, indicating that individual females breed each year. Although there is considerable variation in

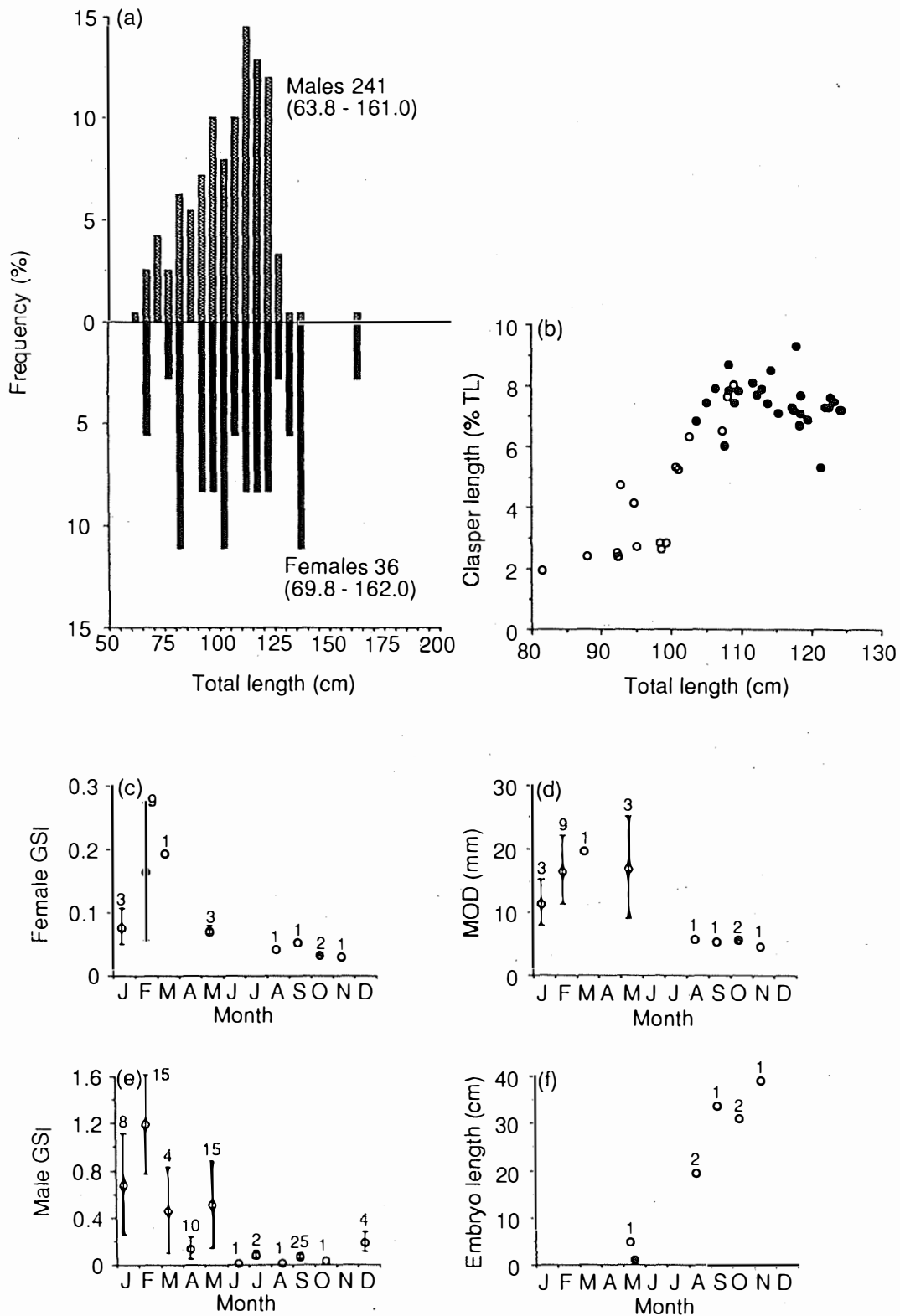


Fig. 5. *Carcharhinus amblyrhynchooides*. (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

male GSI during the breeding season (Fig. 5e) the high mean value in February of 1.2 with a standard deviation of 0.43 suggest that males breed annually.

Diet

The diet of *C. amblyrhynchoides* has not been described, however, Compagno (1984) states that it probably eats mostly fish.

Of 186 *C. amblyrhynchoides* stomachs examined from northern Australia, 32% were empty. Fish (both pelagic and demersal species) was the major prey item, occurring in 91% of stomachs containing food, with crustaceans present in 6% and cephalopods in 4% (Table 4).

(6) *Carcharhinus amblyrhynchos* (Bleeker, 1856) grey reef shark

Distribution

Literature: Tropical Indian Ocean and western central Pacific. Western Australia (Exmouth Gulf, 22° 36'S, 113° 38'E), the Northern Territory (Lyle and Timms 1984) and north-east Queensland (Swain Reef, 22° 00'S, 152° 30'E) (Garrick 1982; Compagno 1984). Intertidal zone down to 170 m depth (Fourmanoir 1976).

Present study: Caught throughout the study area, by gill-net and longline, from near the surface to 14 m down in 120 m depth of water.

Size

Maximum TL about 190 cm (Bass *et al.* 1973), although females of 233 cm and 255 cm TL have apparently been recorded (Garrick 1982; Compagno 1984).

Males 72-150 cm; females 63-178 cm TL (present study, Fig. 6a).

Sex ratio

Embryos and post-partum nsd 1:1 (present study, Table 3).

Reproduction

Male *C. amblyrhynchos* mature at about 130-135 cm (Wass in Bass *et al.* 1973), females at 130-140 cm TL (Bass *et al.* 1973; Fourmanoir 1976).

The size at which males mature could not be determined with any precision in the present study, as no specimens between 111 cm (the length of the largest immature male) and 135 cm TL (the smallest mature male) were caught (Fig. 6b). Females mature at about 135 cm, although data were few. The smallest mature non-pregnant specimen was 137 cm and the smallest pregnant individual was 140 cm TL.

The only observation on seasonality of reproduction comes from Fourmanoir (1976), who reported parturition at the beginning of winter in New Caledonian waters. Litter sizes in Hawaii averaged 5, with a range of 3-6 (Tester 1969), while litters in the Marshall Islands ranged from 1-3 (Schultz *et al.* 1953; Bonham 1960). The size at birth is between 45 and 67 cm TL (Bass *et al.* 1973; Fourmanoir 1976; Compagno 1984). Compagno (1984) notes that the gestation period is about 12 months, but does not give the source of this figure.

From the few data from northern Australia on monthly variation in GSI, MOD and embryo length, it appears the reproductive cycle is seasonal (Fig. 6c-f). Mean embryo length increases from 3.5 cm in December to 55 cm TL in July. The size at birth is about 63 cm as

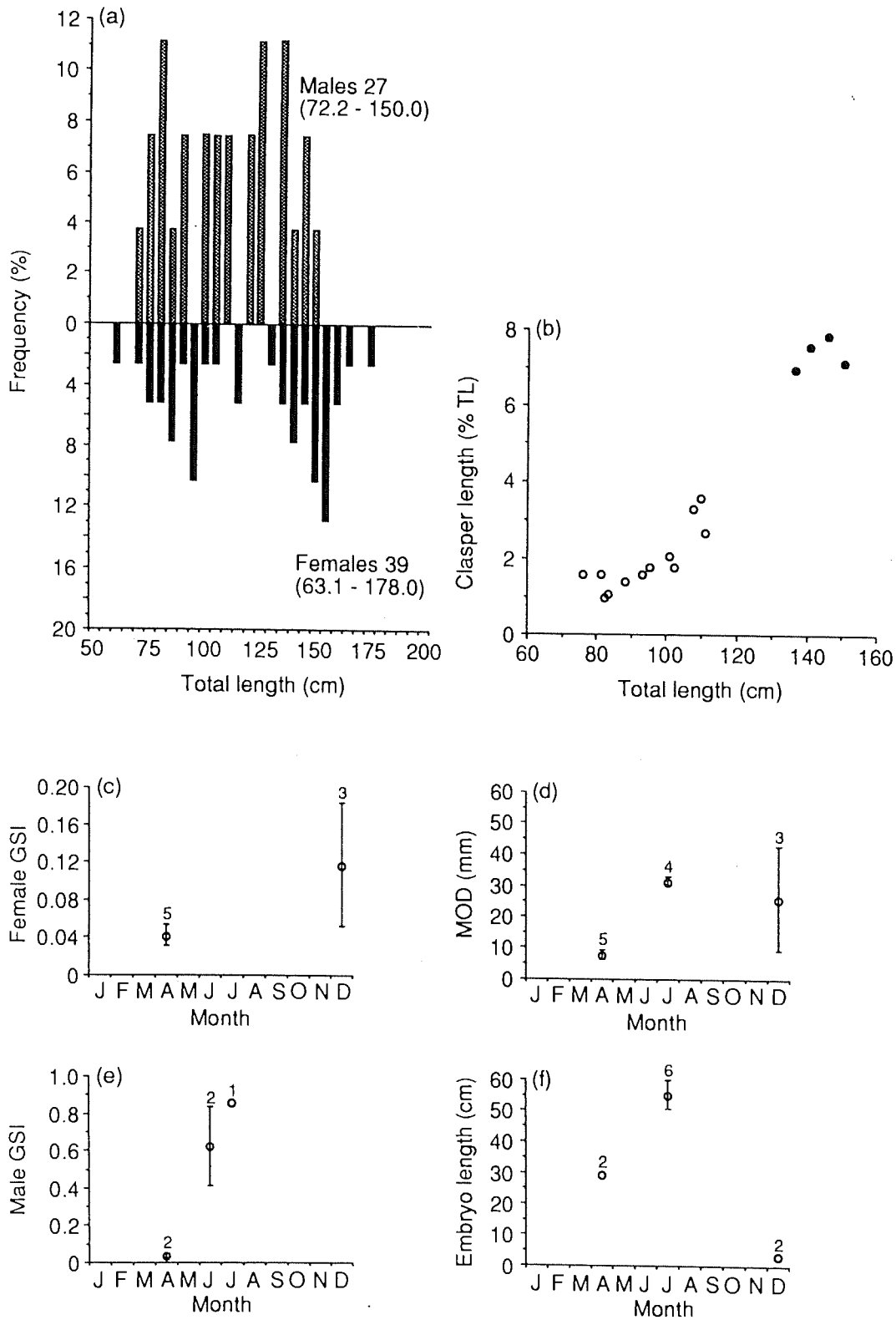


Fig. 6. *Carcharhinus amblyrhynchos* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

the largest embryos were 64 cm and the smallest free-swimming individual was 63 cm TL. If parturition occurs in August and ova are present in utero in November (from Fig. 6f), then gestation would be about nine months. The exact period of mating and ovulation cannot be determined from the data on male GSI and female GSI and MOD, but the trend agrees with this proposed cycle. Litter sizes averaged three, with a range of 2-3.

Diet

C. amblyrhynchos is normally found near coral reefs, where it tends to feed near the bottom rather than in midwater. Bass *et al.* (1973) and Compagno (1984) note that it feeds on small fishes, cephalopods and crustaceans.

Of the 17 specimens examined for stomach contents in this study, 15 were empty. One shark had eaten a scombrid and another contained algae.

(7) *Carcharhinus amboinensis* (Muller & Henle, 1839) pigeye shark

Distribution

Literature: Tropical in the eastern North Atlantic (Nigeria) and Indo-West Pacific (Compagno 1984). Queensland (Fitzroy River area, 23° 30'S, 150° 45'E) (Whitley 1943), the Northern Territory (Stevens *et al.* 1982) and Western Australia (Timor Sea and North West Shelf) (Sainsbury *et al.* 1985). Inshore in depths from the intertidal to 60 m.

Present study: Caught throughout the sampling area in depths from 11 m, to near the surface in 100 m; occurred at 10% of gill-net and hook and line stations in the 0-50 m depth zone, rarely caught by trawl.

Size

Maximum TL 196 cm for males and 223 cm for females off South Africa (Bass *et al.* 1973), although the species possibly attains 280 cm TL (Fourmanoir 1961).

Males 67-231 cm; females 66-243 cm TL (present study, Fig 7a).

Sex ratio

About equal numbers of the sexes are present in catches off the Natal coast (Bass *et al.* 1973).

Embryos and post-partum nsd 1:1 (present study, Table 3).

Reproduction

Bass *et al.* (1973) provide the only information on size at maturity, noting that males mature at about 195 cm and females at about 200 cm TL in South African waters.

Most of the *C. amboinensis* captured in this study were juvenile or adolescent and only a few mature specimens were examined. Fig. 7b indicates that maturity in males is attained at about 208 cm TL. Females mature at about 215 cm; the smallest pre-ovulatory fish was 219 cm, while the smallest of five pregnant or spent females was 226 cm TL.

Compagno (1984), referring to *C. amboinensis*, states that "little is known of its reproductive biology". Kreft (1968) recorded a 72 cm embryo from the eastern Atlantic, and Bass *et al.* (1973) estimated from a free-swimming individual they examined that birth probably occurs at 75 cm TL. They noted that nothing is known about litter size or gestation period.

Information on seasonal variation in GSI is not sufficient to discern a reproductive cycle in Australian waters. The few data show a relatively high male GSI and MOD from February to April (Fig. 7d & e) which, together with observed ova in utero in April, suggests this

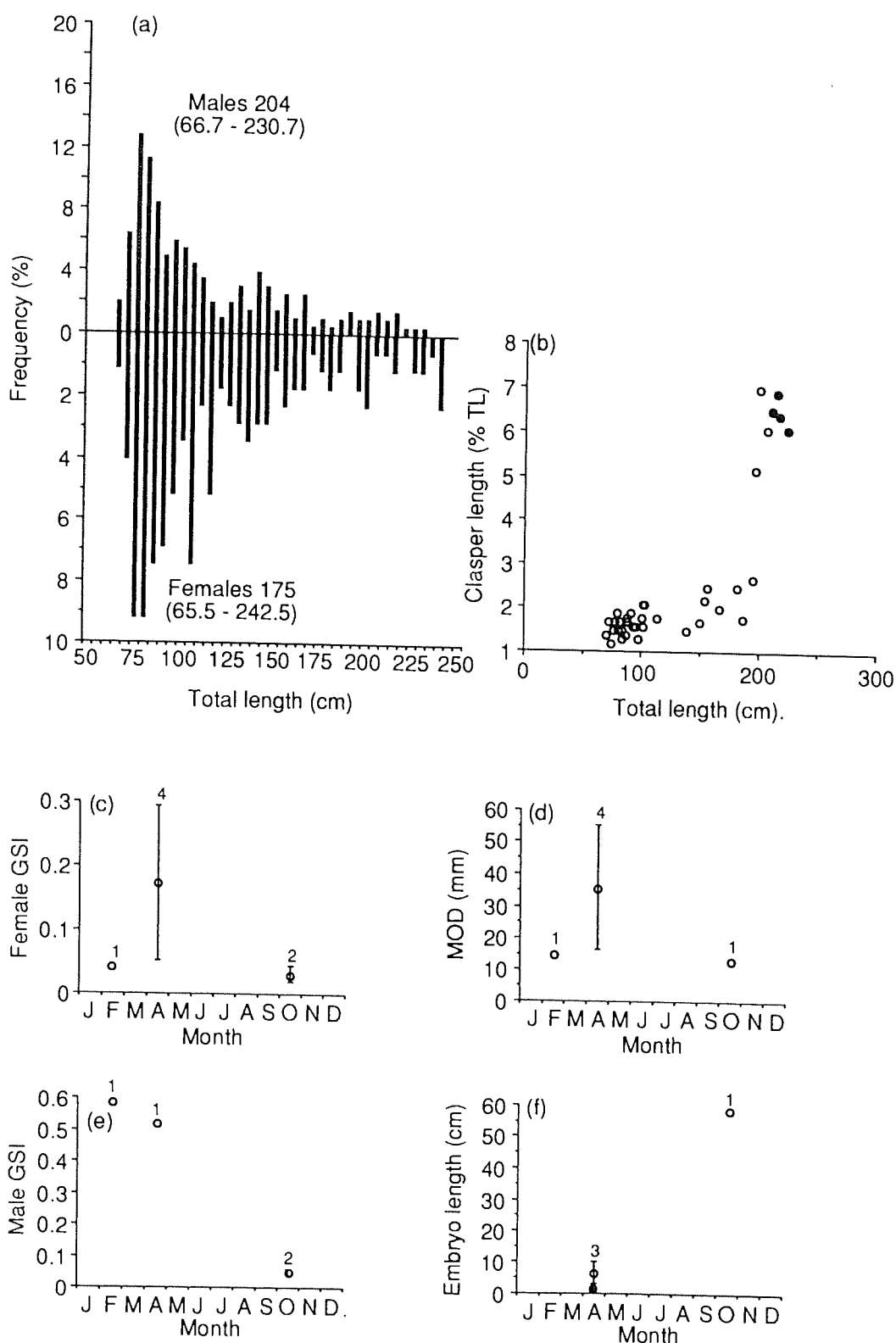


Fig. 7. *Carcharhinus amboinensis* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

may be the main ovulation period. Embryos from three litters in April and one in October averaged 7 and 59 cm TL, respectively (Fig. 7f). The largest embryos were 59 cm and the smallest free-swimming individual was 66 cm, which suggests the birth size is 60-65 cm TL. Litter sizes averaged 9, with a range from 6-13.

Diet

C. amboinensis is reported to feed predominantly on bottom-living fishes, including elasmobranchs, together with cephalopods, other molluscs and crustaceans (Bass *et al.* 1973).

Of 35 specimens from northern Australia, 51% had food items in their stomachs. Fish occurred in 83%, crustaceans in 22% and cephalopods in 11% of these stomachs (Table 4 and Appendix 1).

(8) *Carcharhinus brevipinna* (Muller & Henle, 1839) spinner shark

Distribution

Literature: Tropical and warm temperate Atlantic and Indo-West Pacific; continental and insular shelves (Compagno 1984). Northern Australian waters south to Sydney (34°10'S, 151°10'E) and Geographe Bay (39°30'S, 115°00'E) (Sainsbury *et al.* 1985; Stevens 1984; Hutchins and Swainston 1986).

Present study: Captured in depths between 13-150 m; occurred at 19% of gill-net and 5% of hook and line stations in less than 100 m depth. Rarely caught by trawl.

Size

Maximum TL 263 cm male in the Atlantic (Cadenat and Blache 1981) and 278 cm female in the Indo-Pacific (Wheeler 1953). Natal waters are a nursery area for neo-natals (Bass *et al.* 1973)

Males 66-260 cm; females 71-276 cm (present study, Fig.8a).

Sex ratio

Adult females caught throughout the year in Natal, adult males caught between November and March (Bass *et al.* 1973). Females dominated a sample of 34 specimens from the Gulf of Mexico (Branstetter 1981). About equal numbers of each sex caught in New South Wales waters (no small fish in this sample) (Stevens 1984).

Post-partum 45.4% female, χ^2 test $P < 0.01$ (present study, Table 3).

Reproduction

Considerable information on the reproductive biology of *C. brevipinna* has been published. Size at maturity varies in populations from different areas. Males are mature at 160 cm off Brazil and females at 170 cm (Sadowsky 1967), while they are not mature until 180-200 cm and 200-210 cm, respectively, off South Africa (Bass *et al.* 1973).

There were no reproductive data off northern Australia for males between 165 cm (at and below which size all specimens were immature) and 195 cm (the smallest mature shark) (Fig. 8b). Stevens (1984) suggested *C. brevipinna* from New South Wales attained maturity at about 215 cm. However, considering both sets of Australian data it seems more likely that males normally mature around 195 cm TL. It was not possible to determine maturity in

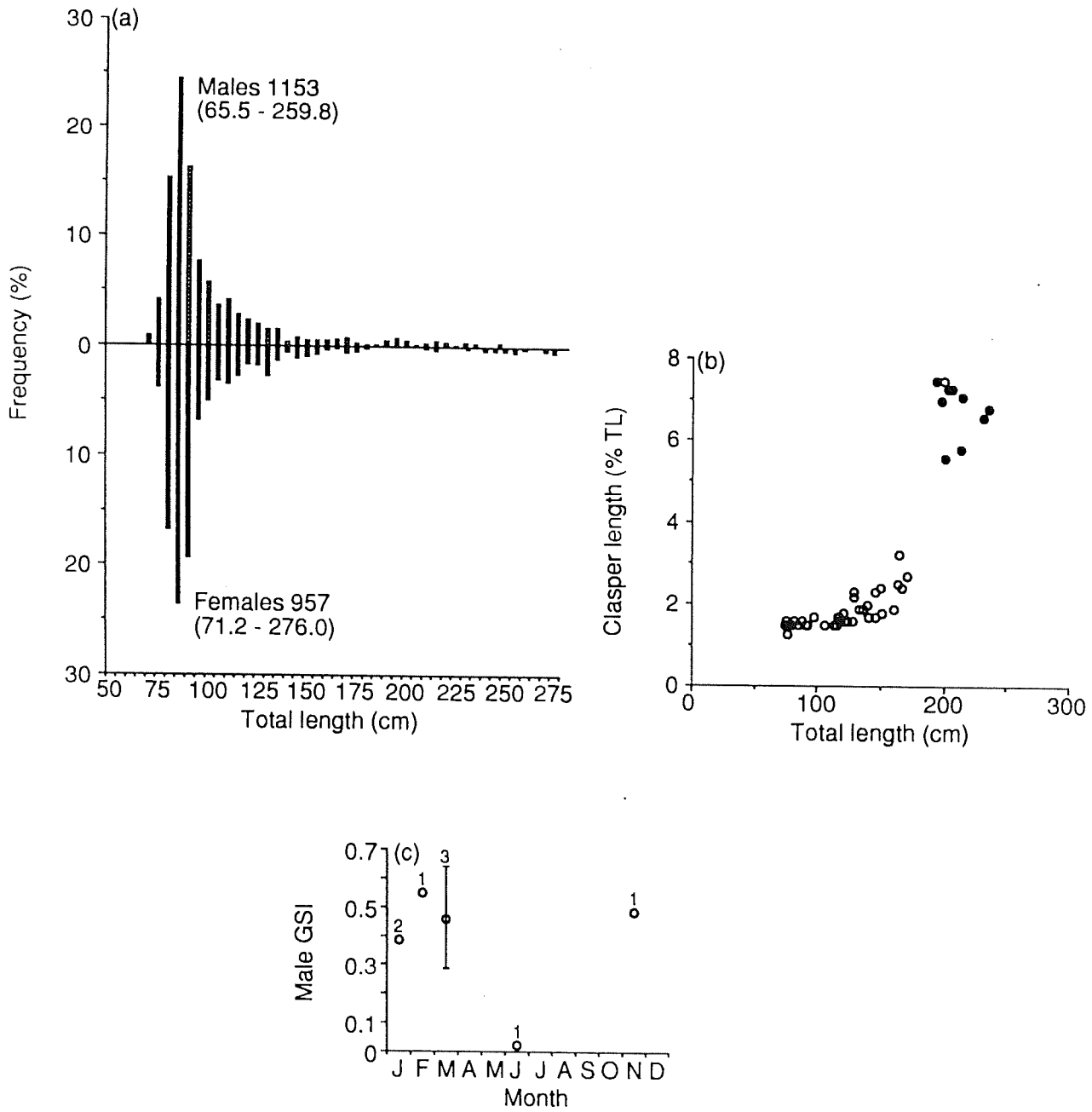


Fig. 8. *Carcharhinus brevipinna* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (circles are mean values; bars are one standard deviation; numbers are sample size).

females, as adults are rare in northern waters and only three mature specimens were examined for reproductive state. New South Wales specimens appear to reach maturity at about 210 cm; the largest mature virgin examined was 208 cm, while the smallest of six pregnant or spent fish was 251 cm TL (Stevens 1984).

Studies on *C. brevipinna* from various geographical regions indicate that it has a seasonal reproductive cycle. Birth normally occurs from April to May off South Africa (Bass *et al.* 1973), May to June in the Gulf of Mexico (Branstetter 1981) and June to July off north-west Africa (Cadenat and Blache 1981); mating is reported in June and July in the Gulf of Mexico (Branstetter 1981) and mainly in November off Brazil (Sadowsky 1967). The size at birth is usually from 60-80 cm TL and litter sizes vary from 3-15, with larger females carrying more young (Springer 1960; Bass *et al.* 1973; Cadenat and Blache 1981; Branstetter 1981; Compagno 1984). Branstetter (1981) suggested that individual females breed every other year in the Gulf of Mexico. Litter sizes in New South Wales waters ranged from 8 -13, the size at birth was 70-80 cm TL and the parturition period was around March-April (Stevens 1984).

Data on mature *C. brevipinna* from northern Australian waters are insufficient to deduce seasonal patterns of gonad activity. Male GSI was low in June and high from November to March (Fig. 8c). The GSI of three females - one each in April, October and November - was 0.03, 0.06 and 0.05, respectively. The MOD of these three fish was 7 mm, 12 mm and 13 mm, respectively. The female caught in November (276 cm TL) was pregnant with 12 embryos averaging 48.6 cm TL.

Diet

The literature indicates that *C. brevipinna* feeds primarily on small teleost fish, particularly pelagic species, together with some cephalopods (Bass *et al.* 1973; Cadenat and Blache 1981; Compagno 1984; Stevens 1984).

Of 111 northern Australian specimens, 46% had food items in their stomachs. Fish (mainly pelagic species) were found in 86% of these, with cephalopods occurring in 8%, crustaceans in 2% and miscellaneous items in 4% (Table 4 and Appendix 1).

(9) *Carcharhinus dussumieri* (Valenciennes, 1839) whitecheek shark

Distribution

The distribution of this species is uncertain, due to confusion with the very similar *C. sealei* (Pietschmann). Garrick (1982) gives several characters for separating *C. dussumieri* and *C. sealei* but states that vertebral numbers, particularly precaudal counts, provide the best means of distinguishing between them. He also notes that precaudal counts for his material form a continuum with 54-74 for *C. dussumieri* and 74-85 for *C. sealei*, but states that "such a presentation masks the trenchant differences between the species in localities where they are sympatric". Garrick (1982) examined Whitley's (1939) specimen of *Platypodon coatesi* from Queensland and assigned it to *C. sealei* on the basis of its first dorsal fin shape, precaudal (77) and monospondylous vertebral numbers, and "most other characters". However, he found it differed from *C. sealei* and resembled *C. dussumieri* in a number of other characters, including a caudal vertebral count of 71. Garrick (1982) stated that "in the absence of other Australian material it is not possible to

assess the significance of these differences". Based on these observations the distribution of *C. dussumieri* was recorded as extending in coastal tropical waters from the Persian Gulf eastwards to Japan and south through Malaya to Borneo and Java, but not Australia, while *C. sealei* was recorded from Australia (Garrick 1982; Compagno 1984). Examination of material collected during the present study resulted in ambiguous identifications using Garrick's (1982) combination of characters (first dorsal fin shape, tooth shape and number, pectoral fin and mouth proportions). However, precaudal vertebral counts of 51 specimens (mean 70.7, range 63-75, SD 2.9) suggest that the Australian species is *C. dussumieri* and not *C. sealei*. The species distribution extends throughout northern Australia (Sainsbury *et al.* 1985).

C. dussumieri was caught throughout the present study area in depths between 12-168 m, but rarely deeper than 150 m. This shark occurred at 13% of gill-net, 9% of hook and line and 8% of trawl stations in less than 100 m depth. It was the shark taken most frequently by trawl in the Arafura Sea and Gulf of Carpentaria (36% of stations in less than 100 m depth), but was taken less often in the Timor Sea and North West Shelf.

Size

Maximum TL about 100 cm (Compagno 1984), although the largest specimens actually measured appear to be a male of 82 cm and a female of 83 cm TL (Garrick 1982).

Males 42-87 cm; females 38-88 cm (present study, Fig 9a).

Sex ratio

Embryos and post-partum nsd 1:1 (present study, Table 3).

Reproduction

Garrick (1982) stated that males reached maturity at 65-70 cm and, although he had no direct evidence, thought that maturity in females would be expected in the size range of 70-75 cm TL.

In northern Australia, males mature at about 70 cm (Fig. 9b); the smallest mature specimen was 64 cm and the largest immature specimen was 74 cm TL. Maturity in females is also attained at about 70 cm; the smallest mature non-pregnant fish was 71 cm and the smallest pregnant fish was 67 cm TL.

Garrick (1982) and Compagno (1984) have summarised what is known of the reproductive cycle of *C. dussumieri*. The usual litter size is two, rarely four, and reproduction does not appear to be seasonal, although Teshima and Mizue (1972) found that pupping off Borneo was more frequent in July and August. The size at birth is 31-39 cm TL (Garrick 1982). Off Borneo, individual females appear to breed each year (Teshima and Mizue 1972).

Examination of GSI, MOD and embryo length through the year off northern Australia showed no evidence of a clear seasonal reproductive cycle (Fig. 9c,d & e). In most months, females in all stages of pregnancy were taken from those with eggs in utero to those with near-term pups

(Fig. 9f). Because females breed throughout the year it was not possible to obtain the gestation period. The mean litter size was 2 with a range from 1-3. The largest embryos found were 40 cm and the smallest free-swimming individual caught was 38 cm, indicating a size at birth of 38-40 cm TL. Of the mature females, 98% were pregnant or spent, which indicates that *C. dussumieri* breeds each year. MOD in pregnant fish increases with embryo size, providing further evidence of a continuous cycle in females. The ova size increases

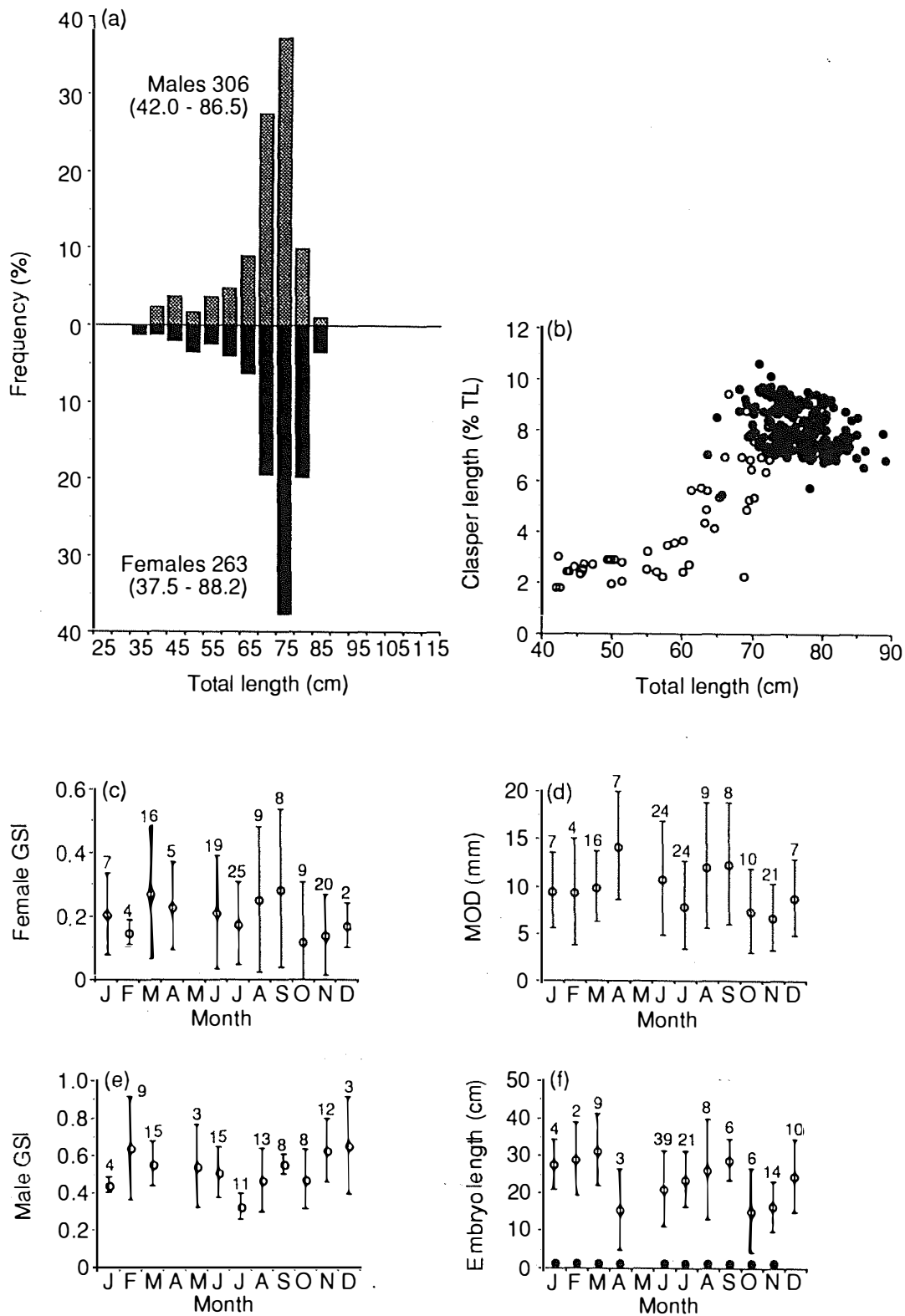


Fig. 9. *Carcharhinus dussumieri* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

slowly through early pregnancy and then rapidly as parturition approaches.

Diet

The literature contains no information on the diet of this shark, although Compagno (1984) notes that it probably feeds on small fishes, cephalopods and crustaceans.

Of 526 *C. dussumieri* from northern Australia, 62% had food in their stomachs. Fish occurred in 76%, crustaceans in 26% and cephalopods in 21% of these (Table 4). Most prey items were demersal (Appendix 1).

(10) *Carcharhinus falciformis* (Bibron, 1839) silky shark

Distribution

Literature: Circum-tropical in coastal and oceanic waters (Compagno 1984). Sydney area off New South Wales (Stevens 1984) and the North West Shelf off Western Australia (Sainsbury *et al.* 1985). Open ocean from the surface to at least 500 m depth; occasionally recorded in inshore areas as shallow as 18 m (Compagno 1984).

Present study: North West Shelf, near the surface in depths of 42 to 920 m, mostly in more than 150 m. Arafura Sea, near the surface in 67 m (1 record). All specimens captured by hook and line.

Size

Maximum TL about 330 cm (Garrick *et al.* 1964). Size segregation occurs with adults found seaward of the young (Compagno 1984). Aggregations of juveniles of both sexes reported in relatively shallow water in the Gulf of Mexico (Branstetter 1981).

Males 86-235 cm; females 83-243 cm (present study, Fig. 10a).

Sex ratio

Compagno (1984) notes that the few data "shows no strong tendency for sexual segregation, but this may very well occur".

Post-partum 32.4% female, χ^2 test $P < 0.05$ (present study, Table 3).

Reproduction

Male *C. falciformis* from the western north Atlantic mature at 218 cm, and females at 234 cm TL (Springer 1960). A pregnant female of 213 cm TL was recorded from the central Pacific (Strasburg 1958). Male *C. falciformis* from the east coast of Australia mature at 210-215 cm, and females at about 200 cm TL (Stevens 1984).

In the present study, it was found that males from the north-west coast of Australia mature at about 210 cm (Fig. 10b). Females up to 150 cm were immature virgins, while a 215 cm TL specimen was pregnant.

Embryo size and time of year in the Gulf of Mexico show some correlation (Branstetter 1986). However, *C. falciformis* from other areas, including the east coast of Australia, show no reproductive seasonality (Strasburg 1958; Fourmanoir 1961; Cadenat and Blache 1981; Stevens 1984). Litter sizes range from 2-15, the gestation period is unknown, and the size at birth is about 70-85 cm TL (Poll 1951; Springer 1960; Fourmanoir 1961; Cadenat and Blache 1981; Garrick 1982; Compagno 1984). Off the east coast of Australia, litter sizes ranged from 5-8 with a mean of 7 (Stevens 1984).

Few data on reproduction were collected in the present study. Male GSI was highest in

January (Fig. 10c). A pregnant female taken in April was carrying eight pups averaging 3.2 cm; this shark had a GSI of 0.03 and a MOD of 5 mm. A 247 cm TL specimen caught in January was in a pre-ovulatory condition and had a GSI of 0.39 and a MOD of 38 mm. The smallest free-living specimen caught was 83 cm, supporting observations that the size at birth is 70-85 cm TL (Compagno 1984).

Diet

C. falciformis feeds primarily on fish, taking pelagic and inshore teleosts, together with smaller numbers of cephalopods and crustaceans. It is often found in association with schools of tuna (Compagno 1984).

The stomachs of 26 *C. falciformis* from north-west Australia were examined; 2 were everted, 19 were empty and 5 contained food. Fish (including a monacanthid and a balistid) were found in four stomachs, cephalopods (including *Sepia* sp. and a *Argonauta* sp.) in four, and crustacean (portunid crab) in one.

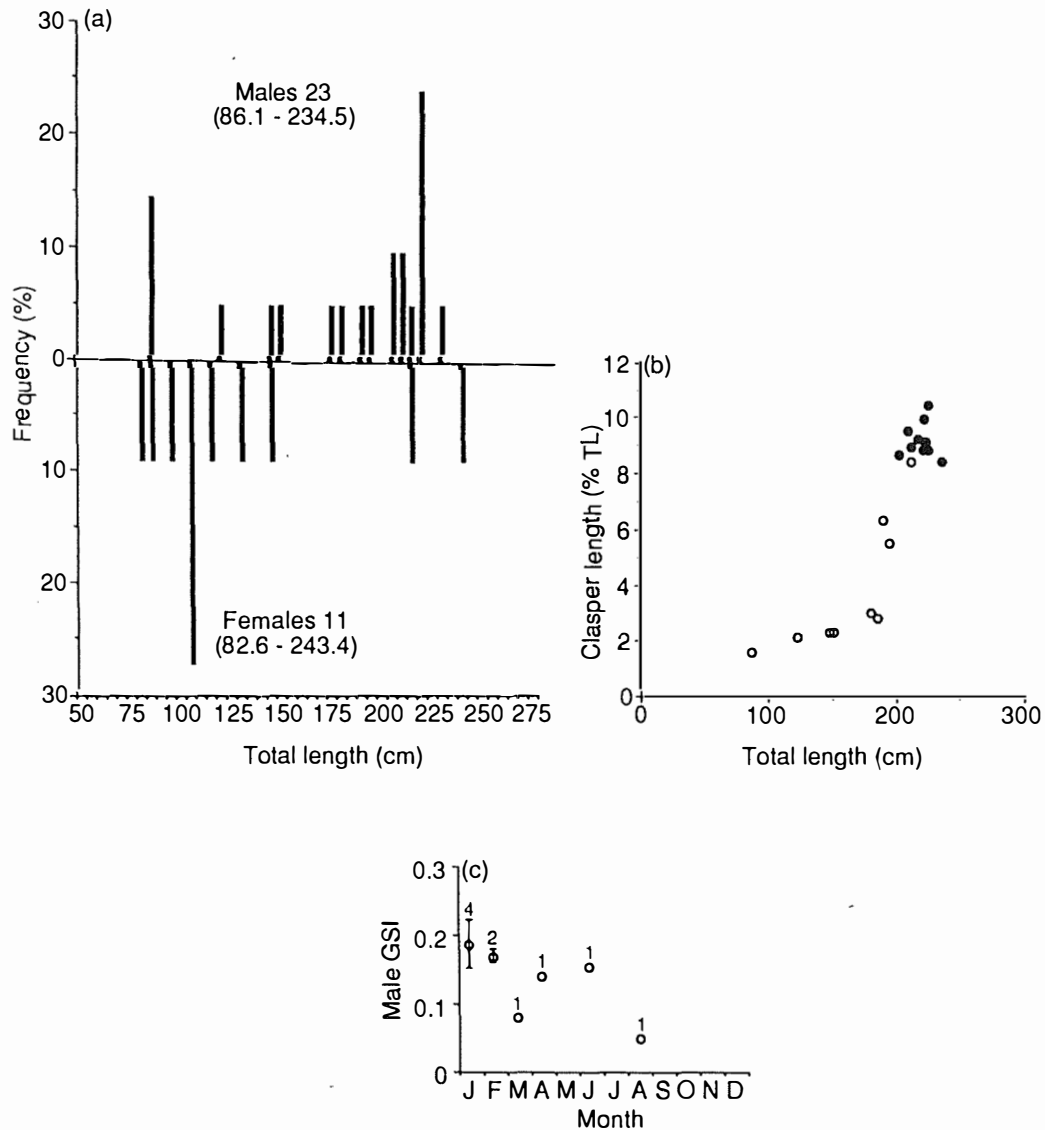


Fig. 10. *Carcharhinus falciformis* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (circles are mean values; bars are one standard deviation; numbers are sample size).

(11) *Carcharhinus macloiti* (Muller and Henle, 1839) hardnose shark*Distribution*

Literature: Tropical inshore Indo-Pacific (Compagno 1984). North West Shelf, Arafura Sea and Gulf of Carpentaria (Sainsbury *et al.* 1985).

Present study: Captured throughout the sampling area; may occur further south but distribution limits unknown. Taken in depths between 7-165 m, most frequently in the Timor Sea where it was caught at 58% of gill-net and 46% of hook and line stations in less than 100 m. Rarely caught by trawl.

Size

Maximum TL 89 cm female (Setna and Sarangdhar 1949a).

Males 43-96 cm; females 60-108 cm (present study, Fig. 11a).

Sex ratio

In Bombay waters 95% of the landings are reported to be male (Setna and Sarangdhar 1949a).

Embryos nsd 1:1; post-partum 58% female, χ^2 test $P < 0.001$ (present study, Table 3).

When the post-partum sample was split by fishing method, the 15 cm mesh gill-net catch was 56.8% female and the hook and line catch 65.3% female. These proportions are significantly different from each other (X^2 test $P < 0.005$). As the size composition of the catches from the two fishing gears was the same (suggesting there was no difference in selectivity), and as the majority of the catches from both fishing methods were generally taken from the same region and on the same cruises, it is most likely these differences reflect small-scale seasonal or area variations in sex ratio.

Reproduction

Setna and Sarangdhar (1949a) report the size at maturity of males as 69 cm TL. Females were rare in their samples but the smallest pregnant female they reported was 76 cm TL.

In northern Australia, males mature at about 74 cm (Fig. 11b), although some may mature when slightly smaller; all males captured over 75 cm TL were mature. Females attain maturity at about 70-75 cm; the smallest mature non-pregnant *C. macloiti* was 70 cm and the smallest pre-ovulatory and pregnant individuals were both 78 cm TL.

From Setna and Sarangdhar's (1949a) few data it appears reproduction is seasonal in Bombay waters, with parturition occurring around March/April when the pups are 45-50 cm TL. The data are too few to determine the gestation period.

The apparent increase in the male GSI in August/September in the present study may indicate seasonality, but there are no data for June or July (Fig. 11e). Female GSI and MOD show considerable variation and no clear seasonal trend is apparent (Fig. 11c & d). However, there is a reasonable relationship between embryo length and time of year (Fig. 11f), with embryos increasing from about 8 cm in August to 44 cm in July. The degree of variation observed in pup length, particularly in May and November, together with the fact that fish with ova in utero were found in April, August and November, suggests that the periods of mating, ovulation and parturition may be extended. It appears that July is the main parturition period and that gestation lasts about 12 months (Fig. 11f). Of the mature females, 82% were pregnant, which indicates that individual females breed each year, but this is not

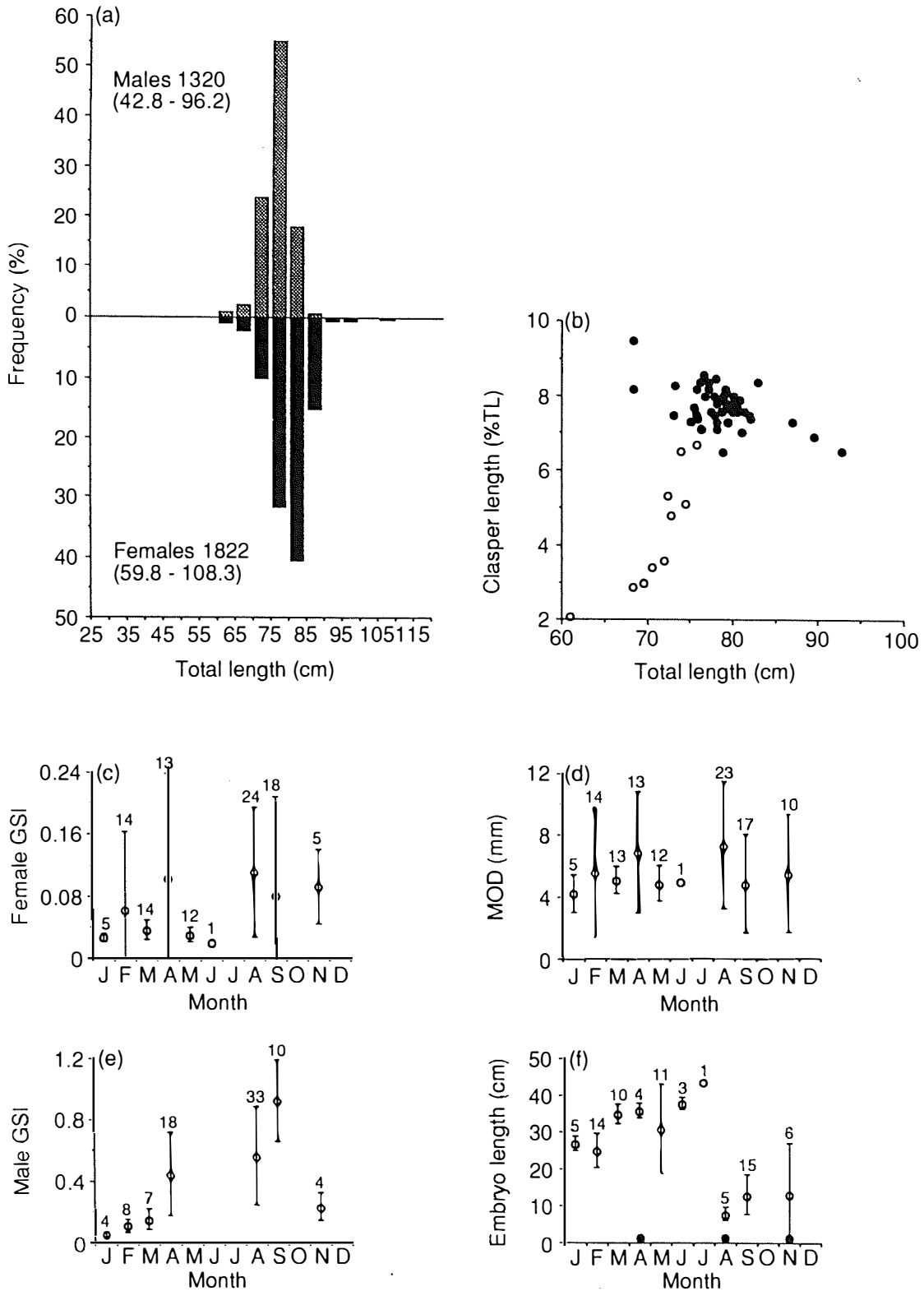


Fig. 11. *Carcharhinus macloiti* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

supported by the MOD's observed in pregnant fish, which never exceeded 9 mm. The size of the ova at ovulation is about 2 cm as observed in this study and in Setna and Sarangdhar's (1949a). It seems more likely that *C. macloiti* females breed every other year and that our sampling reflects a higher proportion of pregnant fish than are actually present in the population. The largest pups recorded were 44 cm and the smallest free swimming individual was 43 cm, suggesting the birth size in Australian waters is about 40-45 cm TL. Mean litter size was two with a range from 1-2, which is in agreement with the findings of Setna and Sarangdhar (1949a).

Diet

Compagno (1984) notes that *C. macloiti* probably feeds on small fishes, cephalopods and crustaceans, but that its diet has apparently not been reported.

Of 216 specimens examined from northern Australia, 42% had food items in their stomachs. Of these, 95% contained fish (both pelagic and demersal species), 4% cephalopods and 1% crustaceans (Table 4 and Appendix 1).

(12) *Carcharhinus plumbeus* (Nardo, 1827) sandbar shark

Distribution

Literature: Tropical and warm temperate in the Pacific, Indian and Atlantic Oceans (including Mediterranean Sea); continental and insular shelves and oceanic banks (Compagno 1984). Western Australia (south to Esperance, 33°52'S, 121°54'E), the Northern Territory, Queensland and northern New South Wales (Garrick 1982; Stevens *et al.* 1982; Sainsbury *et al.* 1985; Hutchins and Swainston 1986). Most abundant in depths less than 30 m off Natal (Bass *et al.* 1973). Three individuals recorded near the surface in water of 1200 to 2000 m deep (Springer 1960). Intertidal to 280 m, favouring the bottom (Compagno 1984).

Present study: Not caught in the Gulf of Carpentaria or Queensland; most frequently captured on the North West Shelf, where it was the second most common species caught by longline (45% of stations over less than 200 m of water). Taken in depths between 18 and 206 m; trawl-caught individuals most frequently captured between 150 and 200 m.

Size

Maximum TL varies with location. Hawaii - males 172 cm, females 190 cm (Wass 1973); Atlantic - unrecorded sex 239 cm (Bigelow and Schroeder 1948), males 226 cm, females 234 cm (Springer 1960, Clark and von Schmidt 1965, Branstetter 1981, Cadenat and Blache 1981); south-west Indian Ocean - males 213 cm, females 218 cm (Fourmanoir 1961, Wheeler 1962, Bass *et al.* 1973).

Males 66-204 cm; females 69-208 cm TL (present study, Fig. 12a).

Sex ratio

Embryos about 1:1 in all areas from which information is available (Springer 1960; Taniuchi 1971; Wass 1973; Bass *et al.* 1973; Baranes and Wendling 1981). Post-partum about 1:1 in Hawaii (Wass 1973); females outnumber males by about 5 or 6:1 in south-eastern U.S.A. (Compagno 1984).

Embryos nsd 1:1; post-partum 56.5% female, χ^2 test $P < 0.05$ (present study, Table 3).

When the post-partum sample was separated by fishing method, the sex ratio was about 1:1 for trawl and 15 cm mesh gill-net catches (sample sizes 53 and 49, respectively) but there

were significantly more females in the longline sample (328 fish, 58.5% female; χ^2 test, $P < 0.01$). The proportion of females in the longline catch was 50.5% among fish less than 160 cm TL and 69.9% female among fish greater than 160 cm TL. The trawl and longline sample both came from the North West Shelf and were collected over the same time period; the difference in sex ratio is presumably explained by differences in selectivity of the fishing gear, the trawl catch containing few fish over 160 cm TL. The gill-net catch came from the Arafura Sea and was comprised mainly of fish over 160 cm; the difference in sex ratio from the longline catch may reflect other factors such as area or season.

Reproduction

C. plumbeus shows considerable variation in size at maturity between different regions. In Hawaii, males are mature at 131 cm and females at 144 cm TL (Wass *in* Bass *et al.* 1973), while in the north-west Atlantic males are not mature until 180 cm and females until 183 cm TL (Springer 1960). In the south-west Indian Ocean, Bass *et al.* (1973) state that males mature at 160 to 170 cm and females in the region of 170 cm TL.

Male *C. plumbeus* in the present study were mature at about 156 cm TL (Fig. 12b) The largest male with incompletely calcified claspers was 161 cm and the smallest mature male was 150 cm TL. Females mature at about 155 cm TL. The smallest mature female was 149 cm, the smallest pregnant female was 158 cm, and the largest immature specimen was 161 cm TL.

C. plumbeus has relatively distinct seasonal reproduction in other areas, with the young born during spring or summer in both hemispheres after a gestation period of 8-12 months (Springer 1960; Taniuchi 1971; Wass 1973; Bass *et al.* 1973; Cadenat and Blache 1981). Litter sizes vary from a mean of 6 and a range of 1-8 in Hawaii (Wass 1973) to a mean of 9 and a range of 1-14 in the north-west Atlantic (Springer 1960). Springer's (1960) data do not show litter size increasing with maternal size. However, Compagno (1984), in summarising the data for *C. plumbeus*, states that litter size varies directly with size of the mother. He presumably bases this statement on the observation that in areas where the adults reach a smaller maximum size the litter sizes tend to be smaller (Wass 1973; Bass *et al.* 1973). *C. plumbeus* is normally between 60 and 75 cm TL at birth (Taniuchi 1971; Bass *et al.* 1973), although Springer (1960) noted that some individuals may be born prematurely at lengths of less than 51 cm TL. Mature females breed every other year, or less frequently (Compagno 1984).

Examination of the GSI's and MOD suggests *C. plumbeus* has a seasonal reproductive cycle in northern Australia, with mating and ovulation occurring between November and April (Fig. 12c,d & e). Embryo length increased from 7.1 cm in April to 52.5 cm in February (Fig. 12f), so birth presumably occurs in February or March, giving a gestation period of about one year. The largest embryo observed was 53 cm and the smallest free-swimming individual was 66, which suggests the birth size is about 60 cm TL. The mean litter size in 18 specimens was 6, with a range of 3-8. There was a significant relationship between increasing litter size and increasing maternal length ($r^2 = 0.32$, $P < 0.05$); however, about 70% of the variation in litter size is attributable to factors other than maternal length. The pregnancy rate among mature females is 57%, which suggests they breed every other year. Further evidence of breeding periodicity was obtained by examining the gonads of pregnant females. Since the gestation period is about 12 months, pregnant females would be

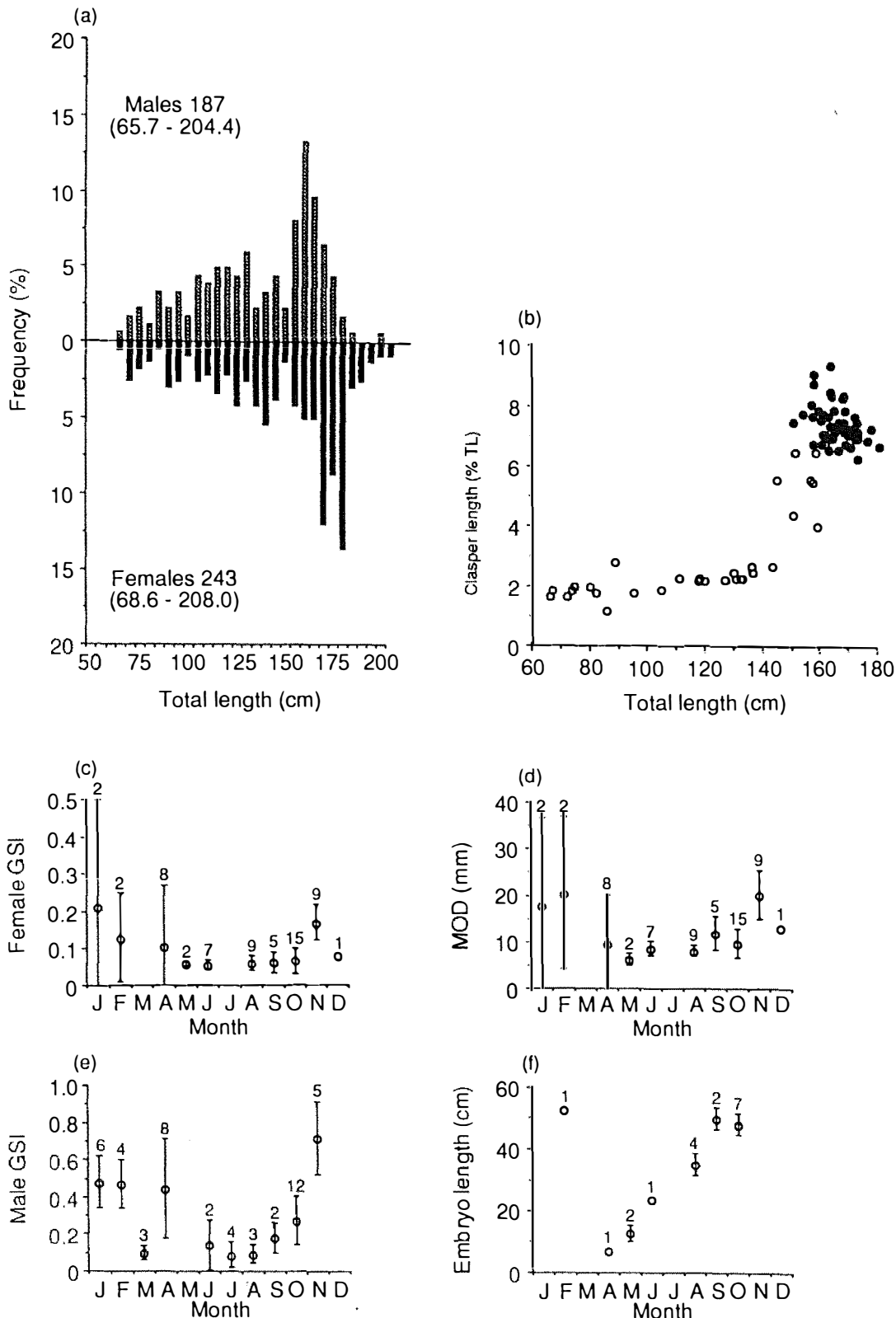


Fig. 12. *Carcharhinus plumbeus* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

expected to have a new batch of ripening ova if they are to breed again the next year. However, this is not the case as all near term females examined had small ova of between 6 and 13 mm diameter.

Diet

C. plumbeus feeds primarily on small bottom fishes, along with smaller numbers of molluscs and crustaceans. Bass *et al.* (1973) examined 29 specimens with food in their stomachs; 80% contained fish, 32% molluscs, 16% crustaceans, 8% elasmobranchs and 4% other material. Medved and Marshall (1981), in a feeding study of young *C. plumbeus* from a shallow nursery ground in the north-west Atlantic, found that blue crabs (*Callinectes sapidus*) occurred in 52% of stomachs containing food. As these crabs were abundant in the area, the sharks may have been opportunistic. Springer (1960) regards *C. plumbeus* as a very discriminating feeder and thinks that it is more successful than some of its larger carcharhinid relatives, citing as evidence the more regular liver weight in this species. Compagno (1984) repeats Springer's observation on feeding success, stating that more *C. plumbeus* are found with nearly full stomachs than are larger carcharhinids such as *C. leucas*, *C. obscurus* and *Galeocerdo*. However, this is not supported by the data of Bass *et al.* (1973) and Wass (1973), who found that 45 to 46% of *C. plumbeus* stomachs contained food compared to 51% of *C. obscurus* and 65% of *C. leucas*.

Of 181 *C. plumbeus* from northern Australia, 64% had food items in their stomachs. The most frequently occurring item in the diet was fish (mainly demersal species) which was found in 88% of stomachs, followed by cephalopods (22%) and crustaceans (8%). Molluscs, other than cephalopods, were found in 1%, and miscellaneous items in 2% of stomachs containing food (Table 4 & Appendix 1).

(13) *Galeocerdo cuvier* (Peron & LeSueur, 1822) tiger shark

Distribution

Literature: Circumglobal in tropical and warm temperate seas (Compagno 1984). Northern Territory, Queensland, New South Wales, South Australia and Western Australia (Paxton *et al.* 1989).

Present study: Captured throughout the study area in depths between 7 and 180 m. One of the most common sharks caught by longlining, occurring at 21% of stations in less than 200 m; less often caught by gill-net and only rarely by trawl. Is a regular seasonal visitor south to about Cape Naturaliste (33°30'S, 115°00'E) and the southern New South Wales coast. Records from South Australia may be erroneous.

Size

Maximum TL possibly up to 7.4 m, although few individuals exceed 5.5 m (Compagno 1984). Size segregation in South Africa has been reported; the main adult population and the nursery areas appear to be restricted to the more tropical regions, with mainly immature and adolescent specimens captured off Natal (Bass *et al.* 1975).

Males 85-357 cm; females 79-418 cm (present study, Fig. 13a).

Most *G. cuvier* in the catches from northern Australia were immature or adolescent. Large mature individuals were rarely caught, probably due to the selectivity of the fishing gear (Fig. 13a).

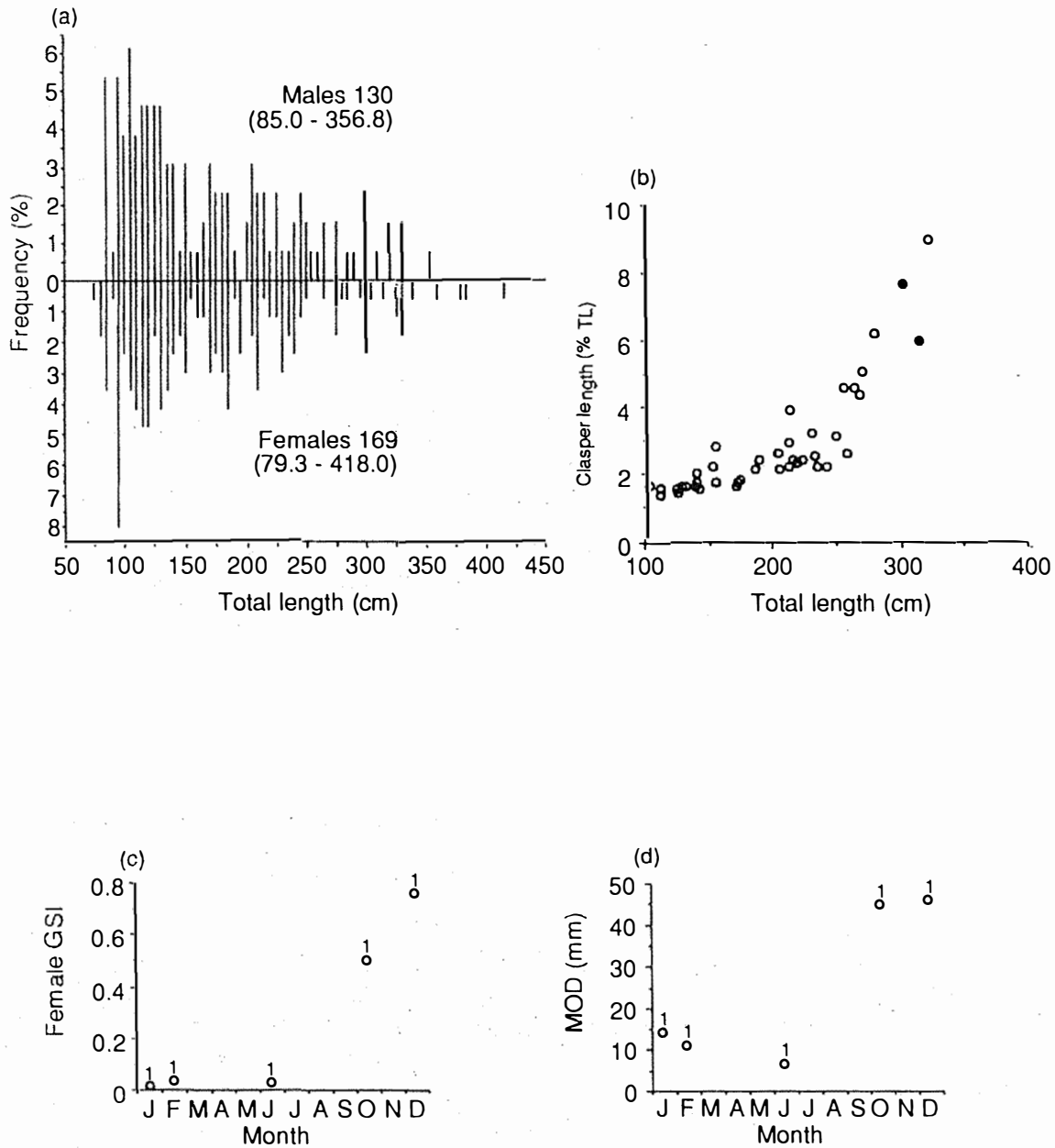


Fig. 13. *Galeocerdo cuvier* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c and d circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month.

Sex ratio

Females outnumbered males by 2.5:1 off Florida (Clark and von Schmidt 1965).

Post-partum 56.5% female, χ^2 test $P < 0.05$ (present study, Table 3).

The sex ratio was not significantly different from 1:1 in the 15 cm mesh gill-net catch (146 fish, 53.4% female) taken in the Arafura Sea, but there were significantly more females in the longline catch (59.9% female, χ^2 test, $P < 0.05$). The longline catch was made up of 83 fish from the North West Shelf (50.6% female) and 61 fish, mainly from the Arafura Sea (70.5% female). The difference in sex ratio between the two Arafura Sea samples can be explained by gear selectivity. The preponderance of females in the longline was a relection of the fish over 200 cm TL, most of which were female; in fish smaller than 200 cm the sex ratio was about 50:50. The gill-net sample from the Arafura Sea had a 1:1 sex ratio because relatively few fish above 200 cm TL were caught. *G. cuvier* has a broad, blunt snout that would prevent large specimens from passing through the 15 cm mesh and because of their strength they would be unlikely to break only a few meshes (thus effectively increasing the mesh size) but would probably break right through the net. The higher proportion of large females taken in the Arafura Sea was not evident in the North West Shelf longline sample where about equal numbers of males and females above 200 cm TL were caught.

By comparison, more males than females were taken by sport fishermen off New South Wales and fish less than 180 cm TL were not caught. Males between 188 and 225 cm were not uncommon in the New South Wales sample, while only one female of less than 225 cm TL was captured (Stevens 1984).

Reproduction

Male *G. cuvier* are reported to attain maturity between 226 and 290 cm and females between 250 and 350 cm TL, depending on location (Compagno 1984).

The northern Australian data, though few, support Stevens's (1984) observations that males reach maturity at about 305 cm in males (Fig 13b) and females at 330 cm TL. The largest immature female recorded in the present study was 307 cm and the smallest mature non-pregnant, pre-ovulatory and spent fish were 365 cm, 380 cm and 326 cm TL, respectively.

Compagno (1984) summarises what is known of the reproductive cycle of *G. cuvier*: this species pups in spring and summer in both hemispheres and mates in spring in the northern hemisphere. The gestation period is about a year, litter sizes range from 10-82 and the size at birth is 50-75 cm TL.

Very few mature specimens were examined in this study. The GSI and MOD of five females shown in Fig. 13c & d suggest that ovulation takes place around December. No pregnant females were captured. One spent fish taken in February, together with two from New South Wales (Stevens 1984), suggests they pup in summer. The smallest free-swimming individual caught was 79.3 cm TL.

Diet

The indiscriminate feeding habits of *G. cuvier* are legendary: the diet includes a wide variety of bony fish and elasmobranchs, together with marine reptiles, marine mammals, sea birds, invertebrates and carrion (Compagno 1984). Stevens (1984) described similar stomach contents in *G. cuvier* from off New South Wales.

Of 98 northern Australian specimens, 79% had food items in their stomachs. Of these,

62% contained fish, 58% reptiles, 16% crustaceans and 16% cephalopods. Ostraciids and tetraodontids were found in 33% of the stomachs that contained fish. Molluscs (other than cephalopods), birds, mammals and miscellaneous items were found in a few stomachs (Table 4). The reptile prey consisted of sea snakes and turtles, sea snakes occurring in 43% of stomachs (Appendix 1). Lyle and Timms (1987) also recorded aquatic snakes in the stomachs of *Galeocerdo cuvier*, *Carcharhinus melanopterus* and *C. cautus* from northern Australia.

(14) *Prionace glauca* (Linnaeus, 1758) blue shark

Distribution

Literature: Cosmopolitan in tropical and temperate waters (Compagno 1984). All Australian States except the Northern Territory (Whitley 1940; Scott *et al.* 1974; Hutchins and Thompson 1983; Stevens 1984); not reported from the shallow waters of the Arafura Sea and Gulf of Carpentaria. Oceanic, only occasionally coming close inshore. Found from the surface down to at least 220 m, often showing tropical submergence (Compagno 1984).

Present study: Nine specimens taken by longline on the north-western continental slope of Western Australia, from near the surface in waters of 212-920 m depth.

Size

Maximum TL 383 cm TL (Bigelow and Schroeder 1948). This species shows distinct size segregation associated with seasonal migrations and reproduction (Strasburg 1958; Gubanov and Grigor'yev 1975; Stevens 1976; Pratt 1979; Stevens 1984).

Females 232-300 cm (n = 9) (Present study)

Sex ratio

Embryos about 1:1 in the Pacific and Indian Ocean (Suda 1953; Gubanov and Grigor'yev 1975) but Stevens (1984) found significantly more male embryos off New South Wales (60% male, χ^2 test, $P < 0.001$). Distinct sex segregation has been reported in post-partum populations (Strasburg 1958; Gubanov and Grigor'yev 1975; Stevens 1976; Pratt 1979; Stevens 1984).

Reproduction

Sexual maturity in male *P. glauca* is attained over a wide size range. The smallest mature male found by Pratt (1979) in the north-west Atlantic was 182 cm; 50% of his sample were mature at 218 cm and 100% were mature at 280 cm TL. Off New South Wales, Stevens (1984) found 36% of males were mature at 222-250 cm and 100% were mature at 280 cm TL. Pratt (1979) reported immature female *P. glauca* up to 160 cm, subadults (which were sexually active, but not pregnant) from 170-220 and fully mature females longer than 220 cm TL. Stevens (1984) recorded mature, non-pregnant fish from New South Wales in the size range 218-249 cm (mean 231 cm), while pregnant females were between 241 and 316 cm (mean 267 cm TL). In the eastern Pacific, Williams (in Pratt 1979) caught pregnant females as small as 183 cm TL. In the north-west Atlantic, *P. glauca* has a complex reproductive cycle; subadult females copulate in spring and store sperm for a year before fertilization occurs. Gestation takes 9-12 months and the young are born in spring and summer (Pratt 1979). Off the east coast of Australia, parturition is from October to November (Stevens 1984). Reproduction may not be seasonal in tropical areas (Gubanov and Grigor'yev 1975).

Litter sizes vary considerably with an overall range of 4-135 being reported (Compagno 1984); off New South Wales they ranged from 4-57 with a mean of 32 (Stevens 1984). The size at birth is 35-50 cm TL (Bass *et al.* 1973; Pratt 1979; Compagno 1984).

Of nine adult females caught in the present study, eight (ranging from 232-300 cm TL) were pregnant. Seven of these, caught in April 1982, contained pups between 2.7 and 13.2 cm TL (average 7.9 cm), while one had 59 eggs in utero. A female taken in June 1983 was pregnant with pups of 13 cm TL. The litter sizes of these fish averaged 34, with a range from 11-49. These data suggest a seasonal reproductive cycle off Western Australia, with ovulation occurring about March. If gestation lasts 9-12 months (Suda 1953; Pratt 1979) parturition would occur between December and March.

Diet

The numerous studies of this shark's stomach contents and diet are summarised in Compagno (1984). *P. glauca* feeds primarily on small teleost fish and cephalopods; however, invertebrates, small sharks, mammalian carion and seabirds are taken occasionally. Although most of the prey are pelagic, these sharks also take bottom fishes and invertebrates in coastal waters.

Of the nine stomachs examined in the present study, five were empty, three were everted and one contained an unidentified fish.

(15) *Loxodon macrorhinus* Muller and Henle, 1839 (sliteye shark)

Distribution

Literature: Tropical Indo-West Pacific (Compagno 1984). North West Shelf and Timor Sea off Western Australia (Sainsbury *et al.* 1985), the Northern Territory (Lyle and Timms 1984) and Queensland, south to the Brisbane area (27° 25'S, 153° 15'E) (Springer 1964). Inshore on continental and insular shelves in depths between 7-80 m, both at the surface and near the bottom (Compagno 1984).

Present study: Captured throughout the study area except off north-east Queensland (although known to occur there) in depths between 19-100 m. Most frequently taken on the North West Shelf, where it was one of the more common sharks caught in trawls. Occurred at 7% of trawl stations and 4% of hook and line stations on the North West Shelf in less than 100 m depth. Rarely caught by gill-net.

Size

Maximum TL 91 cm (Wheeler 1959).

Males 42-80 cm; females 40-88 cm (present study, Fig 14a).

Sex ratio

Embryos nsd 1:1, post-partum 37.3% female, χ^2 test $P < 0.001$ (present study, Table 3).

Reproduction

Compagno (1984) states that male *L. macrorhinus* mature at between 62-66 cm, and females at 79 cm TL, but the source of these data is not clear. Springer (1964) and Bass *et al.* (1975) report that males are immature at 66 cm and mature at about 73-75 cm TL. A 77 cm specimen recorded by Nair *et al.* (1974) was pregnant.

Male *L. macrorhinus* from Australian waters mature at about 64 cm (Fig. 14b), the

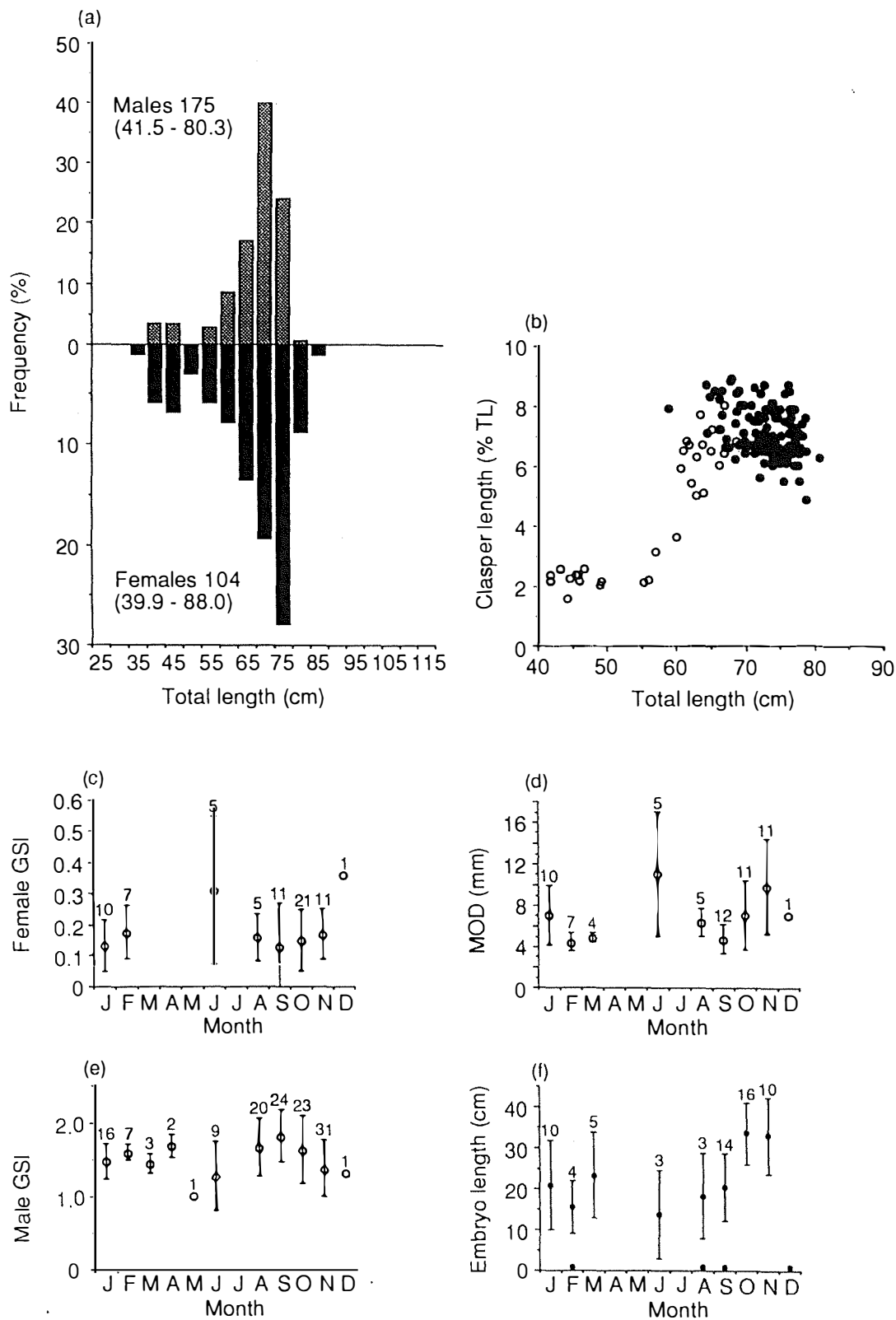


Fig. 14. *Loxodon macrorhinus* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For Figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

smallest mature specimen was 59 cm and the largest immature specimen was 68 cm TL. Females may mature as small as 56 cm TL; the smallest mature non-pregnant female was 58 cm and the smallest pregnant female was 57 cm, although 92% of pregnant females were more than 65 cm TL.

Nothing is known about the seasonality of reproduction in other areas. Litter sizes vary from 2-4 and the size at birth is 40-43 cm TL (Springer 1964; Bass *et al.* 1975).

The GSI's and MOD show no clear seasonal trend in Australian waters (Fig. 14c,d & e). In most months the range in size of embryos carried by pregnant females is considerable (Fig. 14f), although these data indicate that the largest pups occur in the October/November period. *L. macrorhinus* appears to breed throughout the year but there may be a peak in parturition around October and November. Females probably breed every year, for 96% of mature specimens over 65 cm TL were pregnant, and the MOD of pregnant fish increases with embryo size. Ova diameter increasing slowly in early pregnancy and then increasing rapidly as parturition approaches. The largest embryo observed was 46 cm and the smallest free-swimming specimen 40 cm, which suggests the size at birth is 40-46 cm TL. The mean litter size from 58 litters was 2 with a range of 1-2.

Diet

L. macrorhinus is reported to feed on small fishes, crustaceans and cephalopods (Compagno 1984).

In the present study, 80% of 258 stomachs examined contained food. The most frequently occurring items were fish (almost entirely demersal species) and crustaceans which were in 76% and 60%, respectively, of the stomachs containing food. Cephalopods were found in 19% of the stomachs, while other molluscs and miscellaneous items were found in a few stomachs (Table 4 and Appendix 1).

(16) *Rhizoprionodon acutus* (Rupell,1837) milk shark

Distribution

Literature: Tropical eastern Atlantic and Indo-West Pacific (Compagno 1984). Throughout northern Australia from the Brisbane area of the east Queensland coast (27° 25'S, 153° 15'E) to the North West Shelf of Western Australia (Springer 1964; Sainsbury *et al.* 1985). Occurs in depths of less than 1 m to about 200 m, either in midwater or near the bottom (Compagno 1984).

Present study: Captured throughout the study area in depths between 9 and 126 m, mostly between 50 and 100 m. Occurred at 24% of gill-net, 14% of hook and line and 5% of trawl stations in less than 100 m depth. This was one of the most common sharks caught by trawl in the Gulf of Carpentaria. Extends south to the Shark Bay area, 26° 10'S, 113° 11'E, on the west coast (WAM 26673.001).

Size

Maximum TL usually about 100 cm (Springer 1964; Nair *et al.* 1974; Bass *et al.* 1975), but recorded up to 178 cm in the eastern Atlantic off the African coast (Cadenat and Blache 1981). Springer (1964) notes that populations from different areas may vary in maximum size.

Males 35-89 cm; females 35-98 cm (present study, Fig. 15a).

Sex ratio

Embryos 55.7% female, χ^2 test $P < 0.05$; post-partum 32.2% female, χ^2 test $P < 0.001$ (present study, Table 3).

When the post-partum sample was separated by fishing method there were significantly more males in the 15 cm mesh gill-net and longline catch (66.0% and 71.1% male, respectively), while the trawl catch was not significantly different from 1:1 (55.1% male). These differences may be partially explained by gear selectivity; longlines caught a narrow size range (67-86 cm), gill-nets (15 cm mesh) caught fish from 51-98 cm and trawls caught a wider size range (33-95 cm TL). When the small sharks that were not caught by gill-net or longline were excluded from the trawl sample, the proportion of males rose to 58.2% (χ^2 test, $P < 0.05$). Area, depth or season might also account for the differences in sex ratio: the demersal trawl sample came mainly from the Gulf of Carpentaria and North West Shelf, while the pelagic longline and gill-net catch came mainly from the Arafura Sea.

Reproduction

The size at which *R. acutus* mature is reported to be between 68 and 72 cm for males, and between 70 and 80 cm TL for females (Bass *et al.* 1975; Cadenat and Blache 1981), although Springer (1964) noted mature males as small as 62 cm in the Red Sea.

In Australian waters, male *R. acutus* mature at about 75 cm TL (Fig. 15b); the smallest mature male recorded was 73 cm and the largest immature male was 80 cm TL. Females mature at about 75 cm TL; the smallest mature female was 73 cm and the largest immature female was 75 cm TL.

In the south-west Indian Ocean and the eastern Atlantic, *R. acutus* has a relatively restricted seasonal reproductive cycle: mating occurs in summer with parturition some 12 months later. Compagno (1984) states that off Bombay, India, birth occurs in winter. However, from the references Compagno cited, he probably based this observation on the data of Setna and Sarangdhar (1949b), who recorded a single pregnant female with embryos of about 16 cm TL in November. According to the data of Bass *et al.* (1975) and Cadenat and Blache (1981) embryos of this size would be born the following summer. Litter sizes in the south-west Indian Ocean ranged from 2-8 with a mean of 5, and in the eastern Atlantic from 1-6 with a mean of 3 (Bass *et al.* 1975; Cadenat and Blache 1981). The size at birth ranges from as small as 25 cm in the Philippines to 40 cm TL off Senegal (Springer 1964; Bass *et al.* 1975; Cadenat and Blache 1981).

In northern Australian waters, *R. acutus* breeds throughout the year. Pregnant females in various stages of development from eggs in utero to near full-term pups were caught in most months (Fig. 15f). Seasonal data on GSI and MOD show no clear trend through the year (Fig. 15c, d & e). Of 197 mature females above 75 cm TL, 97% were pregnant which suggests that females breed each year. Annual breeding is supported by the condition of the ovaries of pregnant fish: the size of their ova increases with pup length, so that following parturition a new batch of ripe ova is ready for ovulation. The mean litter size was 3, with a range of 1-6. There was a significant relationship between increasing litter size and increasing maternal length ($r^2 = 0.12$, $P < 0.001$) although about 90% of the variation in litter size was attributable to factors other than maternal length. As the largest embryos examined were 36.8 cm and the smallest free-swimming specimen was 34.6 cm, the size at birth is probably between 34 and 38 cm TL.

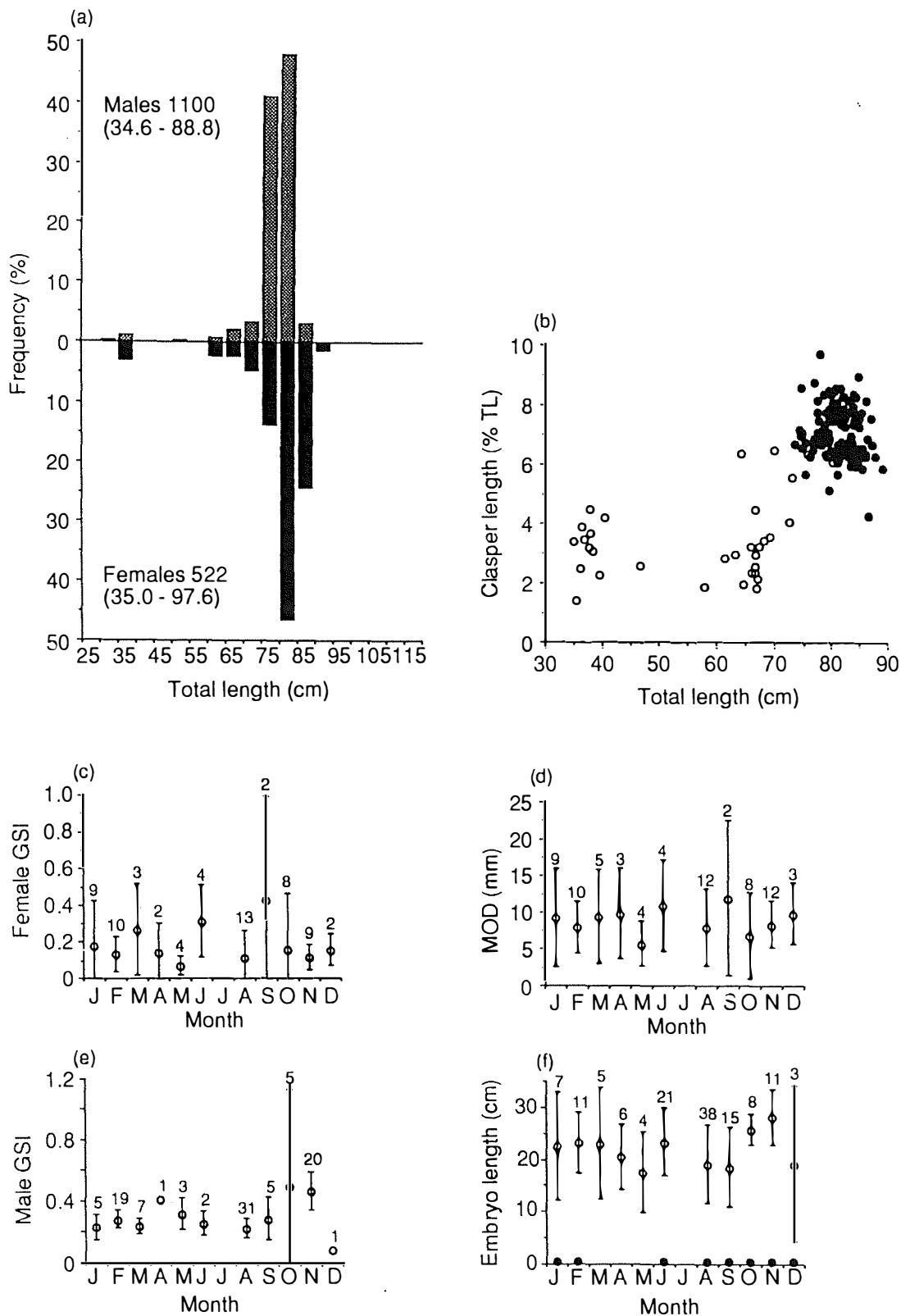


Fig. 15. *Rhizoprionodon acutus* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

Diet

R. acutus feeds primarily on small teleost fish but also takes cephalopods, crustaceans and gastropods (Cadenat and Blache 1981; Compagno 1984; Randall 1986).

Of 315 *R. acutus* stomachs examined in the present study, 52% contained food. Fish (predominantly demersal species) occurred in 93%, cephalopods in 19% and crustaceans in 10% of these stomachs. A few stomachs contained molluscs (other than cephalopods) and miscellaneous items (Table 4 and Appendix 1).

(17) *Rhizoprionodon taylori* (Ogilby, 1915) Australian sharpnose shark

Distribution

Literature: Northern Australia from the North West Shelf to south Queensland (Deception Bay, 27° 10'S, 153° 05'E) (Springer 1964; Sainsbury *et al.* 1985).

Present study: Captured in depths between 9 and 111 m. Occurred at 12% of gill-net, 5% of hook and line and 1% of trawl stations in less than 100 m depth. Taken infrequently in trawls on the North West Shelf and appears to be uncommon in this area. Extends south on the east coast to the Brisbane area, 27° 25'S, 153° 15'E (QMI 14909) and on the west coast to Broome, 18° 00'S, 122° 24'E (WAM 29178.001).

Size

Maximum TL 67 cm TL (Springer 1964)

Males 40-55 cm; females 38-66 cm (present study, Fig 16a).

Sex ratio

Embryos and post-partum nsd 1:1.

Reproduction

The two males of 31 and 41 cm TL Springer (1964) examined were immature. No information is available on maturity in females.

The relationship between relative clasper length and body length does not show the S-shaped plot typical of most species (Fig. 16b) because immature fish were absent from the sample, presumably as a result of gear selectivity. Males apparently mature at about 43 cm: the smallest mature specimen was 42 cm and the largest immature specimen was 47 cm TL. Females mature at about 45 cm: the smallest mature non-pregnant, pre-ovulatory and pregnant specimens were 44, 47 and 46 cm, respectively, and the largest immature female was 51 cm TL.

Nothing is known of the reproduction of *R. taylori*, other than that it is viviparous with a yolk-sac placenta and that the number of young per litter is two (Compagno 1984).

Examination of GSI and MOD in this study reveal no clear seasonal pattern, although there is an indication that female GSI and MOD are highest around February (Fig. 16c & d). However, the plot of pup length suggests there is a seasonal birth period (Fig. 16f). Females with ova in utero were found from February to September, but small embryos were only found from July to September and large embryos from October to December. Mr Colin Simpfendorfer (James Cook University, Townsville 4811, personal communication) noted a

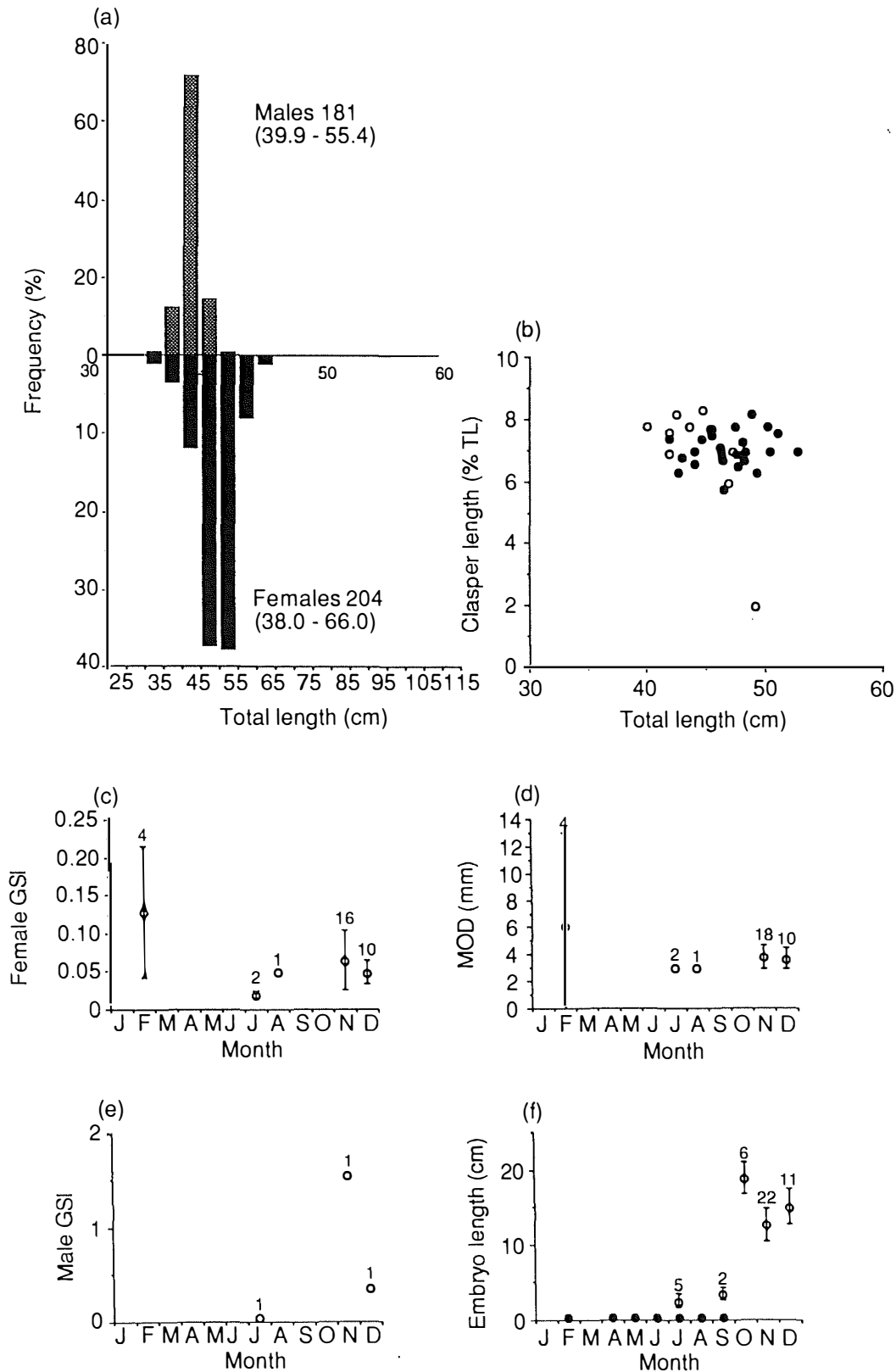


Fig. 16. *Rhizoprionodon taylori* (a) Length-frequency distributions from northern Australia. (Numbers after the sex are sample size; numbers in parenthesis are size-range in cm TL). (b) Relationship between clasper length (percentage of total body length) and total body length. (Open circles, claspers not calcified; solid circles, claspers calcified). (c) Female gonadosomatic index (GSI) by month. (For figs. c-e circles are mean values; bars are one standard deviation; numbers are sample size). (d) Maximum ova diameter by month. (e) Male gonadosomatic index (GSI) by month. (f) Embryo length by month (Open circles are eggs in utero). Plots are mean values; bars are one standard deviation; numbers are number of litters.

similar pattern with *R. taylori* in the Townsville area (19°13'S, 146°48'E) and suggested that females suppress the development of ova until July or August. Suppression of egg development has also been recorded in *Rhinobatus horkelii* (Lessa 1982). The smallest free-swimming specimen taken was 38 cm, while the largest embryos recorded were 22 cm; since Springer (1964) examined a 31 cm specimen that he stated was not an embryo, the size at birth would appear to be about 25-30 cm TL. The mean litter size was 5, with a range of 1-8, and there was a significant relationship between increasing litter size and increasing maternal length ($r^2 = 0.39$, $P < 0.001$). Individual females appear from the 99% pregnancy rate and the MOD of pregnant fish, to breed each year. The ova size increases with pup length through gestation, slowly at first and then rapidly as parturition approaches, so that a new batch of ripe ova is ready for ovulation shortly after birth.

Diet

Nothing has previously been recorded about the diet of this shark.

Of 68 northern Australian specimens, 56% had food items in their stomachs. Fish occurred in 79%, crustaceans in 34% and cephalopods in 3% of these stomachs (Table 4 and Appendix 1).

General Discussion

Sex ratio

The sex ratios of the embryos and post-partum specimens of 15 species of shark were examined in the present study; similar data on 8 other species of northern shark had previously been collected by Stevens and Wiley (1986), Lyle (1987) and Stevens and Lyle (1989). The sex ratio of the embryos in 19 out of the 20 species examined (data were not available for three species) was not significantly different from 1:1. In one species, *Carcharhinus tilstoni*, significantly more males were born in the Arafura Sea (53.8% male, χ^2 test $P < 0.05$), although on the North West Shelf the ratio for this species was about 1:1 (Stevens and Wiley 1986). A 1:1 sex ratio among shark embryos has also been reported by Springer (1940), Suda (1953), Gubanov (1978), Francis (1980) and Parsons (1983). However, Stevens (1984) found significantly more male embryos among *P. glauca* litters from New South Wales (60% male, χ^2 test, $P < 0.001$).

Among the post-partum population the sex ratio was about equal in 7 species; however, in 13 of the remaining 16 species the sampled populations comprised significantly more males. Females predominated in the adult population of *C. plumbeus* off southern Florida: Springer (1960) suggested that this was a result of higher male mortality. Convincing evidence of an overall population bias in sex ratio depends on thorough seasonal and geographical sampling of the total population, which is not claimed for the present study. The noted differences in the sex ratios are more likely a consequence of sexual segregation, a phenomenon that is widespread among elasmobranchs (Springer 1940). Various forms of sexual segregation and their functions have been suggested by Backus *et al.* (1956), Strasburg (1958) and Springer (1967). The underlying causative factors are generally thought to be associated with either reduction of intra- and interspecies competition or reproduction or migration. Data collected during this study, where some species were sampled by several different fishing methods, show that apparent biases in sex ratios can be attributable to the selective properties of the fishing gear.

Reproduction

It is possible to make some generalisations from the data on reproduction in northern Australian hemigaleid, carcharhinid and sphymid sharks (Table 5). Most of the species are placentally viviparous and produce litters of 2-4 pups, which are about 60 cm TL at birth, after a gestation period of about 10 months. The size at birth is about 40% of the size at maturity, which in turn is about 70% of the maximum size. Most species have a seasonal cycle, with individual females giving birth each year in the Austral summer. Of 23 species examined, 19 had seasonal reproductive cycles; only four breed throughout the year. Three of the non-seasonal breeding species (*C. dussumieri*, *L. macrorhinus* and *R. acutus*) were small (maximum TL about 100 cm), bottom-associated sharks with relatively broad diets (based on the number of major prey categories occurring in more than 10% of stomachs [Table 4]). The two other small, bottom-associated species (*H. microstoma* and *R. taylori*), which are seasonal breeders, had more specific diets (Table 4). Perhaps seasonal availability of suitable prey for neo-natal sharks is less critical for bottom-associated species with more general diets. However, this does not explain why *C. falciformis*, a pelagic species feeding primarily on fish (Compagno 1984), appears to breed throughout the year. Parturition in the seasonal breeding sharks is most common between October and April, with a peak in January/February (Table 5). In a study of the distribution of the larvae of 104 families of fish in the waters over the North West Shelf, Young *et al.* (1985) showed that maximum larval densities occurred between October and December. If this is the pattern throughout northern Australia, then many of these teleost species would be in the prey size range suitable for neo-natal sharks by the peak parturition period of January/February.

The reproductive parameters between species vary considerably (Table 5) and it is interesting to examine the relationships between parameters and to speculate on the possible selective advantages of one reproductive strategy over another. From the data in Table 5, larger litters are correlated with a smaller birth size relative to the size at female maturity for that species ($r^2 = 0.54$, $P < 0.001$, $n = 23$). There is also a positive correlation between the size at which females mature and the total size of the litter (expressed as mean number in the litter times the average size at birth) ($r^2 = 0.64$, $P < 0.001$, $n = 23$). This may be related to the increased carrying capacity of larger sharks and to the age at sexual maturity. Large size in sharks presumably confers advantages in terms of reducing the likelihood of being preyed on. To reach a large size, more energy must be put into growth, which in turn means that reproduction will be delayed until relatively late in life. If sexual maturity is generally attained at older ages in larger species of sharks compared to smaller species, then larger litters will represent a mechanism to compensate for the delay in reproduction. While there is some evidence for smaller shark species maturing earlier (Davenport and Stevens 1988), age and growth information for most species reported on in this study is currently unavailable.

Diet

Dietary information for about 20 species of northern Australian sharks is available as a result of this study and the work of Stevens and Wiley (1986), Lyle (1987) and Stevens and

Table 5. Summary of reproductive parameters for female northern Australian hemigaleid, carcharhinid and sphyrid sharks. (Dash indicates no data. Column legend from left to right: Species, female maximum TL (cm), female TL at maturity (cm), TL at birth (cm), mean litter size, gestation period (months), female breeding frequency, number of pups produced per year, birth period, size at birth as a % of female size at maturity, and female size at maturity as a % of maximum size).

Species	Max TL	Maturity TL	Birth TL	Litter number	Gestation period	Breeding frequency	Pups /year	Birth period	%	%
<i>H.microstoma</i>	110	65	30	8	6	Biannual	16	Feb&Sept	46	59
<i>H.elongatus</i>	184	115	52	6	7-8	Biennial	3	April	45	63
<i>C.altimus</i>	280?	225?	60	7	-	-	-	-	27	80
<i>C.amblyrhynchoides</i>	162	115	55	3	9-10	Annual	3	Jan/Feb	48	71
<i>C.amblyrhynchos</i>	178	135	63	3	9	-	-	Aug	47	76
<i>C.amboinensis</i>	243	215	63	9	9	-	-	Nov/Dec	29	88
<i>C.brevipinna</i>	276	210	75	11	12	-	-	Mar/Apr	36	76
<i>C.dussumieri</i>	88	70	38	2	-	Annual	2	All year	54	80
<i>C.falciformis</i>	243	210	75?	7	-	-	-	All year	36	86
<i>C.macloiti</i>	108	73	43	2	12	Biennial	1	July	59	68
<i>C.plumbeus</i>	208	155	60	6	12	Biennial	3	Feb/Mar	39	75
<i>G.cuvier</i>	450?	330	65?	-	12	-	-	Jan/Feb	20	73
<i>P.glauca</i>	323?	220	43	34	9-12	-	-	Dec/Mar	20	68
<i>L.macrorhinus</i>	88	57	43	2	-	Annual	2	All year	75	65
<i>R.acutus</i>	98	75	38	3	-	Annual	3	All year	51	77
<i>R.taylori</i>	66	45	28	5	10-11	Annual	5	Dec/Jan	62	68
<i>E.blochii*</i>	176	120	46	12	10-11	Annual	12	Feb/Mar	38	68
<i>S.lewini*</i>	346	200	48	17	9-10	-	-	Oct-Jan	24	58
<i>S.mokarran*</i>	409	210	65	15	11	Biennial	7.5	Dec/Jan	31	51
<i>C.cautus+</i>	119	91	40	3	8-9	Annual	3	Oct/Nov	44	76
<i>C.melanopterus+</i>	125	95	48	4	8-9	Annual	4	Nov	51	76
<i>C.fitzroyensis+</i>	135	95	50	4	7-9	Annual	4	Feb/Apr	53	70
<i>C.tilstoni#</i>	180	115	60	3	10	Annual	3	Jan	52	64
<i>C.sorrah#</i>	152	95	50	3	10	Annual	3	Jan	53	63

* data from Stevens and Lyle (1989)

+ data from Lyle (1987)

data from Stevens and Wiley (1986)

Lyle (1989). Some general statements on the feeding strategies of sharks in this region can be made, with the proviso that these data are based on frequency of 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 numbers and weight or volume of prey items.

G. cuvier is the only species that can be described as truly omnivorous, taking a broad spectrum of prey types (Table 4 & Appendix 1). This is well documented from other areas and can be summarised by Compagno's (1984) statement: "the tiger shark is perhaps the least specialised of sharks as far as feeding is concerned.....it is a sea-hyena, a potent predator-scavenger that opportunistically exploits its environment". In contrast, *H. microstoma* has a highly specialised diet consisting almost entirely of cephalopods, most of which are small octopods. These octopods are not abundant in benthic samples (Dr Sebastian Rainer, CSIRO Marine Laboratories, Perth 6020, personal communication). *H. microstoma* is obviously very efficient at locating and capturing them but has no obvious morphological features that would give it a selective advantage in catching this prey. *C. maclovi* appears to be a specialist fish feeder; only a few stomachs examined contained prey other than fish. While *H. elongatus* stomachs did not contain very high percentages of any one prey category, the diet consisted entirely of fish and cephalopods, which occurred in approximately equal percentages in the stomachs.

Of the prey categories found in stomachs that contained any food, fish was found in more than 25% of the stomachs of all species examined, except for *H. microstoma* (1%). Crustaceans occurred in more than 25% of *C. dussumieri*, *L. macrorhinus*, *R. taylori* and *Mustelus* sp. stomachs, and cephalopods in more than 25% of the stomachs of *H. microstoma* and *H. elongatus*. Reptile prey were eaten by only two species, to any extent: snakes by *G. cuvier* and *C. melanopterus* (Lyle and Timms 1987) and turtles by *G. cuvier*. Similarly, only *G. cuvier* and *S. mokarran* stomachs contained relatively high percentages of elasmobranchs (Stevens and Lyle 1989).

Partitioning of available food resources among sympatric, morphologically similar sharks that occupy the same habitat is evident in some cases. *C. dussumieri*, *H. microstoma*, *L. macrorhinus* and *R. acutus* all reach a maximum length of about 1 m and are common in demersal trawls from the same depth range on the North West Shelf. *H. microstoma* is a specialist cephalopod feeder. The other three species contained roughly equal proportions of cephalopods in their stomachs. *R. acutus* took a higher percentage of fish than either *C. dussumieri* or *L. macrorhinus*, but the most notable difference was in the proportions of crustaceans in the stomachs: 10% for *R. acutus*, 26% for *C. dussumieri* and 60% for *L. macrorhinus*. Similarly, Lyle (1987) found that two morphologically similar carcharhinids, *C. melanopterus* and *C. cautus*, from shallow, inshore, mangrove areas in Darwin harbour included similar proportions of fish and cephalopods in their diet, but *C. cautus* took more crustaceans and *C. melanopterus* more aquatic snakes. In contrast, there is no obvious partitioning of prey among *C. tilstoni*, *C. sorrah*, *C. amblyrhynchoides* and *C. brevipinna*, which are sympatric in the Arafura Sea and are essentially pelagic. All four species feed primarily on fish, which occur in 82-92% of their stomachs, with cephalopods and crustaceans comprising the remainder of their diet. The occurrence of cephalopods and crustaceans was somewhat higher in *C. sorrah* than in the other species, but otherwise there was no major difference in the occurrence of these prey items between species.

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Appendix 1. Frequency of occurrence of prey in the stomachs of 13 species of shark from northern Australia. (M, *Mustelus* sp.; Hm, *H. microstoma*; He, *H. elongatus*; Ca, *C. amblyrhynchoides*; Cam, *C. amboinensis*; Cb, *C. brevipinna*; Cd, *C. dussumieri*; Cm, *C. macloiti*; Cp, *C. plumbeus*; Gc, *G. cuvier*; Lm, *L. macrorhinus*; Ra, *R. acutus*; Rt, *R. taylori*.)

Prey item	Number of stomachs												
	M	Hm	He	Ca	Cam	Cb	Cd	Cm	Cp	Gc	Lm	Ra	Rt
Unidentified fish	13	2	22	30	8	28	163	62	69	30	104	106	24
Unidentified elasmobranch	-	-	2	-	1	-	-	-	1	1	-	1	-
Elasmobranch liver	-	-	-	1	-	-	-	-	-	-	-	-	-
Elasmobranch egg case	-	-	-	-	-	-	-	-	-	1	-	-	-
Unidentified shark	-	-	1	4	-	-	-	-	2	1	-	-	-
Scyliorhinid	-	-	-	-	-	-	-	-	1	-	-	-	-
Unidentified ray	-	1	4	-	-	-	-	-	-	-	-	-	-
<i>Rhina ancylostoma</i>	-	-	-	-	-	-	-	-	-	1	-	-	-
Dasyatidae	-	-	8	-	-	-	-	-	1	-	-	-	-
<i>Amphotistius</i> sp.	-	-	1	-	-	-	-	-	-	-	-	-	-
Unidentified teleost	-	-	1	45	-	-	-	-	-	-	-	-	-
Eel	1	-	-	-	-	-	8	-	1	1	8	5	-
Muraenidae	-	-	1	-	-	-	3	-	-	-	-	-	-
<i>Gymnothorax</i> sp.	-	-	-	-	-	-	-	-	-	-	-	2	-
Muraenesocidae	-	-	-	-	-	-	1	-	-	-	-	-	-
Ophichthidae	-	-	-	1	-	-	-	-	-	-	-	-	-
Congridae	-	-	1	-	-	-	-	-	2	-	1	1	-
<i>Gnathophis</i> sp.	-	-	-	-	-	-	1	-	-	-	-	1	-
Clupeidae	-	-	-	8	3	11	3	14	-	-	-	7	2
<i>Pellona</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Pellona ditchella</i>	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Sardinella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	3	-
<i>Sardinella isabella</i>	-	-	-	-	-	-	-	1	-	-	-	-	-
Engraulidae	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Stolephorus</i> sp.	-	-	-	-	-	-	3	-	-	-	-	-	-
<i>Chirocentrus dorab</i>	-	-	-	-	-	-	-	1	-	-	-	-	-
Synodontidae	-	-	-	-	-	-	1	-	-	-	-	2	-
<i>Saurida</i> spp.	-	1	-	-	-	-	7	4	2	-	-	1	-
<i>Saurida undosquamis</i>	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Trachinocephalus myops</i>	-	-	-	-	-	-	-	-	1	-	-	-	-

Brush-toothed lizard	-	-	-	-	-	1	-	-	-	-	-	-
Myctophidae	-	-	-	-	-	1	-	-	-	-	-	-
Ariidae	-	-	-	6	1	-	-	-	-	-	1	-
Ariidae eggs	-	-	-	1	-	-	-	-	-	-	-	-
Plotosidae	-	-	-	1	-	-	-	-	-	-	-	-
Batrachoididae	-	-	-	-	-	-	-	-	-	-	1	-
<i>Halieutaea</i> sp.	-	-	-	-	-	1	-	-	-	-	-	-
Bregmacerotidae	2	-	-	-	-	20	-	-	36	3	-	-
Monocentridae	-	-	-	-	-	-	-	1	-	-	1	-
<i>Antigonia rhomboidea</i>	-	-	-	-	-	-	-	1	-	-	-	-
Fistulariidae	-	-	-	-	-	1	-	-	-	-	-	-
<i>Centriscus</i> sp.	-	-	-	-	-	1	-	-	-	-	-	-
Syngnathidae	-	-	-	-	-	-	-	-	-	-	1	-
<i>Hippocampus</i> sp.	-	-	-	-	-	-	-	-	-	1	-	-
Scorpaenidae	-	-	-	-	-	4	-	-	4	1	-	-
Triglidae	-	-	-	-	-	-	-	-	2	-	-	-
Platycephalidae	-	-	-	1	-	2	-	-	6	-	-	-
<i>Elates ransonneti</i>	-	-	-	-	-	3	2	-	-	2	-	-
<i>Onigocia</i> sp.	-	-	-	-	-	-	-	-	-	-	1	-
Hoplichthyidae	-	-	-	-	-	-	-	1	-	-	-	-
Dactylopteridae	-	-	-	-	-	-	-	-	-	-	1	-
<i>Pegasus draconis</i>	-	-	-	-	-	-	-	-	-	1	-	-
Teraponidae	-	-	-	1	-	-	-	-	-	-	-	-
Priacanthidae	-	-	-	-	-	1	-	1	-	-	-	-
Apogonidae	-	-	-	-	-	1	-	-	2	-	-	-
<i>Sillago</i> sp.	-	-	-	1	-	-	-	-	-	-	1	-
Carangidae	-	-	-	2	5	-	1	2	-	1	1	-
<i>Decapterus</i> sp.	-	-	-	-	-	-	-	3	-	-	-	-
<i>Megalaspis cordyla</i>	-	-	-	-	-	-	-	1	-	-	-	-
<i>Selaroides leptolepis</i>	-	-	-	-	-	-	-	-	-	-	1	-
Leiognathidae	-	-	-	8	-	1	3	7	1	2	11	2
<i>Dipterygonotus balteatusi</i>	-	-	-	-	-	-	-	-	-	1	-	-
Lutjanidae	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lutjanus vittus</i>	-	-	-	1	-	-	-	-	-	-	-	-
Nemipteridae	-	-	-	-	-	1	17	2	3	-	2	-
<i>Nemipterus peronii</i>	-	-	-	-	-	-	-	1	-	-	-	-
<i>Pentapodus porosus</i>	-	-	-	-	-	-	-	-	-	-	1	-
Gerridae	-	-	-	-	-	1	-	-	-	-	-	-
<i>Lethrinus choerorynchus</i>	-	-	-	-	-	-	-	1	-	-	-	-
Mullidae	-	-	-	-	-	1	3	-	2	-	1	1
<i>Upeneus sulphureus</i>	-	-	-	-	-	1	-	-	-	-	-	-
Pomacanthidae	-	-	-	-	-	-	-	1	1	-	-	-
Mugilidae	-	-	-	-	-	1	-	-	-	-	-	-

Polynemidae	-	-	-	-	1	-	-	-	-	-	-	-	-
Labridae	-	-	-	1	-	-	2	-	3	-	-	-	-
<i>Choerodon monostigma</i>	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Xyrichtys jacksonensis</i>	-	-	-	-	-	-	-	-	-	-	1	-	-
Scaridae	-	-	-	-	-	-	-	-	-	-	1	-	-
Mugilidae	-	-	-	-	-	-	-	-	-	-	-	-	-
Mugiloididae	-	-	-	-	-	-	-	-	1	-	-	-	-
<i>Parapercis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	1	-
Uranoscopidae	1	-	-	-	-	-	1	-	-	-	1	-	-
Champsodontidae	-	-	-	-	-	-	-	-	1	-	3	-	-
<i>Champsodon</i> sp.	-	-	-	-	-	-	-	-	-	-	1	-	-
Sandeel	-	-	-	-	-	-	1	-	1	-	5	-	-Gobiidae
	-	-	-	-	-	-	1	-	-	-	1	-	-
Callionymidae	-	-	-	-	-	-	2	-	-	-	1	-	-
Trichiuridae	-	-	-	-	-	-	-	-	3	-	-	-	-
Scombridae	-	-	-	-	-	1	-	-	1	1	-	1	-
<i>Euthynnus affinis</i>	-	-	-	1	-	-	-	-	-	-	-	-	-
<i>Rastrelliger</i> sp.	-	-	-	-	-	-	1	-	2	-	-	2	-
<i>Rastrelliger kanagurta</i>	-	-	-	4	-	-	-	-	-	-	-	-	-
<i>Scomberomorus</i> sp.	-	-	-	2	-	-	-	1	-	-	-	-	-
Istiophoridae	-	-	-	-	1	-	-	-	-	1	-	-	-
<i>Istiophorus platypterus</i>	-	-	-	-	-	-	-	-	-	1	-	-	-
Flatfish	-	-	-	-	-	-	8	-	-	-	2	2	1
Bothidae	1	-	-	-	-	-	5	-	1	-	2	-	-
Cynoglossidae	-	-	-	-	-	-	2	-	-	-	-	-	-
Balistidae	-	-	-	-	-	-	1	-	1	-	-	-	-
<i>Abalistes stellaris</i>	-	-	-	-	-	-	-	-	-	3	-	-	-
Monacanthidae	-	-	-	-	-	2	4	-	-	-	-	7	1
<i>Paramonacanthus filicauda</i>	-	-	-	-	-	-	5	-	-	-	-	1	-
Ostraciidae	-	-	-	-	-	-	-	-	-	1	-	-	-
Tetraodontidae	1	-	-	-	-	-	1	-	1	12	1	-	-
<i>Lagocephalus sceleratus</i>	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Lagocephalus inermis</i>	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>Lagocephalus</i> sp.	-	-	-	-	-	-	1	-	-	2	-	-	-
Diodontidae	-	-	5	-	-	-	-	-	-	-	-	-	-
Unidentified cephalopod	3	181	13	5	-	-	20	-	7	6	16	13	1
Squid	4	13	23	-	1	4	21	4	6	-	3	8	-
Loliginidae	-	1	-	-	-	-	4	-	-	-	-	1	-
<i>Loligo chinensis</i>	-	-	-	-	1	-	-	-	1	-	-	-	-
Cuttlefish	-	4	22	-	-	-	5	-	3	6	-	1	-
Sepiolidae	1	2	-	-	-	-	-	-	-	-	5	-	-

Octopus	4	161	4	-	-	-	14	-	8	1	12	8	-
Unidentified crustacea	10	1	-	-	-	-	6	-	-	-	7	4	3
Ostracod	-	1	-	-	-	-	-	-	-	-	-	-	-
Eumalocostracan	-	-	-	-	-	-	-	-	-	-	1	-	-
Stomapopod	13	1	-	-	2	-	27	-	3	3	17	2	3
Isopod	3	-	-	-	1	-	1	-	2	-	1	-	-
Euphausiid	2	-	-	-	-	-	-	-	-	-	1	-	-
Decapod	5	-	-	-	-	-	1	-	-	-	-	-	-
Squillidae	-	-	-	3	-	-	-	-	-	-	-	-	-
<i>Squilla</i> sp.	2	-	-	3	-	-	1	-	-	1	8	-	-
Natantid	10	-	-	-	-	-	2	-	-	-	14	-	-
Unidentified prawns	3	-	-	-	-	-	56	1	2	-	40	8	3
Penaeidae	3	1	-	-	-	-	3	-	1	-	29	2	1
<i>Penaeus</i> spp.	-	-	-	2	-	-	-	-	-	-	-	-	-
<i>Penaeus esculentus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Trachypenaeus fulvus</i>	-	-	-	-	-	-	1	-	-	-	-	-	-
Caridae	1	-	-	-	-	-	-	-	-	-	3	-	-
Alpheid shrimp	1	-	-	-	-	-	-	-	-	-	1	-	-
Scyllaridae	1	-	-	-	-	-	-	-	-	2	-	-	-
Nephropsidea	2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Linneaparis trygonis</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Callianassa</i> sp.	-	1	-	-	-	-	1	-	-	-	2	-	-
<i>Upogebia</i> sp.	-	-	-	-	-	-	-	-	-	-	3	-	-
Galatheididae	1	-	-	-	-	-	-	-	-	-	-	-	-
Paguridae	1	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified crab	27	5	-	1	-	1	10	-	1	4	23	1	2
<i>Ranina ranina</i>	-	-	-	-	-	-	1	-	-	-	-	-	-
Portunidae	2	-	-	-	1	-	1	-	-	3	-	-	-
Seaweed	-	-	-	-	-	2	-	-	1	-	-	-	-
Bryozoan	-	1	-	-	-	-	-	-	-	-	-	-	-
Black coral	-	-	-	-	-	-	-	-	-	1	-	-	-
Annelid	-	-	-	-	-	-	-	-	-	-	1	-	-
Polychaete	-	1	-	-	-	-	-	-	-	-	-	-	-
Gastropod	-	-	-	-	-	-	-	-	-	1	1	2	-
Bivalve	1	-	-	-	-	-	-	-	1	-	1	-	-
<i>Anadara</i> sp.	-	1	-	-	-	-	-	-	-	-	-	-	-
Crinoid	-	1	-	-	-	-	-	-	-	-	-	-	-
Ophiuroid	-	-	-	-	-	-	-	-	-	-	1	-	-
Holothurian	-	-	-	-	-	-	-	-	-	-	1	-	-
Salp	-	-	-	-	-	-	-	-	-	-	-	1	-
Turtle	-	-	-	-	-	-	-	-	-	12	-	-	-

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

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Abstract

The age and growth of *Carcharhinus tilstoni* and *C. sorrah*, the two most abundant shark species in commercial gill-net catches off northern Australia, were investigated by the examination of vertebral rings. Corroborating evidence for age and growth estimates was obtained from length-frequency distributions and tag-recapture data. To aid validation of these estimates, tetracycline was injected into sharks at the time of tagging. Growth is relatively rapid in the first year of life: vertebral ageing indicated 17 cm growth in total length (TL) for *C. tilstoni* and about 20 cm for *C. sorrah* during the first year after birth. By the time the sharks are 5 years old, growth has declined to 8-10 cm per year in *C. tilstoni* and 5 cm per year or less in *C. sorrah*. The von Bertalanffy growth parameters for *C. tilstoni* are $L_{\infty} = 194.2$, $K = 0.14$, $t_0 = -2.8$ for females, and $L_{\infty} = 165.4$, $K = 0.19$, $t_0 = -2.6$ for males; for *C. sorrah* the parameters are $L_{\infty} = 123.9$, $K = 0.34$, $t_0 = -1.9$ for females, and $L_{\infty} = 98.4$, $K = 1.17$, $t_0 = -0.6$ for males. The greatest recorded ages for *C. tilstoni* were 12 years for females and 8 years for males, and for *C. sorrah*, 7 years for females and 5 years for males. Sexual maturity is reached early: at 3 to 4 years in *C. tilstoni* and 2 to 3 years in female *C. sorrah*.

Introduction

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

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

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

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

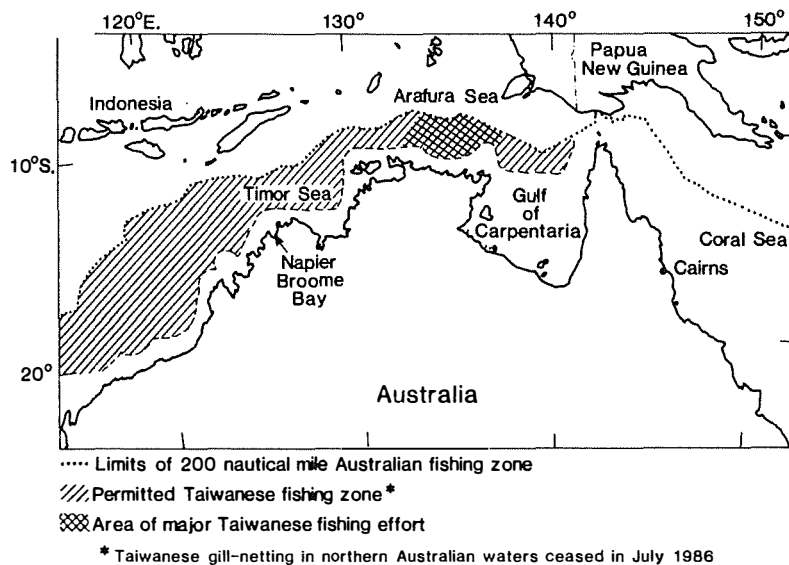


Fig. 1. Study area in northern Australian waters.

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

Materials and Methods

Sharks were sampled, from 1980 to 1984, by observers on Taiwanese commercial gill-netting vessels operating inside the AFZ off northern Australia. These vessels worked multi-filament nylon gill-nets (stretched-mesh 14.5 to 19.0 cm; average 17.0 cm) that consisted of panels at least 15 m deep from headrope to footrope and 15 m long, connected to form a gill-net of 8 to 14 km in length. The nets were set close to the surface just before dusk. Hauling, which began around midnight, took up to 10 hours.

The selectivity of the gill-nets probably affects the size distribution of sharks caught by the commercial fishery, and may select against the capture of *C. tilstoni* and *C. sorrah* at the extremes of their size range. However, as Stevens and Wiley (1986) noted, gill-nets captured individuals close to the

size at birth. They also noted that the largest specimens caught by longline, which presumably has no maximum size selection for these species, were a similar size to those caught by gill-net.

Observers sampled about 1.5% of the sets made by Taiwanese gill-netters in the AFZ between April 1981 and October 1983 (Stevens and Wiley 1986). Length-frequency data on 18 201 *C. tilstoni* and 7748 *C. sorrah* were collected between June 1981 and December 1983, with all months of the year, except May, represented. The sharks were measured to the nearest centimetre either as total lengths (TL), for which the tail was allowed to take a natural position and the top caudal lobe was then placed parallel to the body axis, or as fork lengths (FL). Fork lengths were converted to total lengths using the relationships derived by Stevens and Wiley (1986): for *C. tilstoni*, $TL = 0.913 + 1.235 FL$; for *C. sorrah*, $TL = 4.715 + 1.196 FL$.

Vertebral Ageing

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

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

Of all these methods, ninhydrin staining of whole vertebrae was chosen for its ease of use, good and consistent results on the species in this study, and relatively low cost. Before staining, the vertebrae were separated and trimmed of excess tissue. The remaining connective tissue was removed from the cone surface by soaking the vertebrae in a 5.25% sodium hypochlorite solution (Schwartz 1983) for up to an hour, depending on the size of the vertebrae. Care was taken to avoid 'over-bleaching', which interferes with subsequent absorption of the stain. The vertebrae were then washed thoroughly in tap water and stained in a 1% ninhydrin-in-ethanol (98%) solution. Immersion for at least 6 h was usually required for effective staining.

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

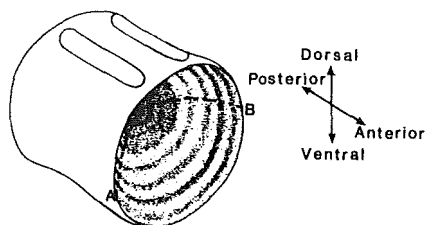


Fig. 2. Representation of shark vertebra. Measurements of vertebral radius and radii of unstained bands were taken along the line A-B.

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

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

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

Length-frequency Data

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

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

Tag-recapture

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

Scientists participating in the programme measured the length of the sharks at both the time of tagging and recapture. The fishermen usually froze the sharks for subsequent examination by fisheries officers. There was no apparent relationship between the amount of shrinkage due to freezing and either the length of the shark (*C. tilstoni*; $n = 62$, $r = 0.047$, $P > 0.05$, *C. sorrah*; $n = 57$, $r = 0.252$, $P > 0.05$) or the period of freezing. The lengths of these sharks were, therefore, adjusted for freezer shrinkage by adding a mean correction factor, of 1.4 cm FL for *C. tilstoni* and 1.1 cm FL for *C. sorrah*. Growth data on sharks that had been at liberty for less than 1 month were not included, because measurement errors are magnified when growth increments from short-term recaptures are converted to growth per year (Casey *et al.* 1985). Growth data were grouped in 10 cm length intervals and examined for differences in growth rates. Growth increment and period-at-liberty data for all recaptured sharks that had been at liberty for a month or longer were analysed by a von Bertalanffy computer program (Kirkwood 1983) to obtain the parameters L_{∞} and K .

Tetracycline

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

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

Results

Vertebral Ageing

A regression of total length on vertebral radius showed a linear relationship for both male and female *C. tilstoni*. As there was a significant difference between the sexes (F -test: $0.01 < P < 0.05$), the data were treated separately. Similarly, in *C. sorrah* there was a linear relationship between total length and vertebral radius. Data for males and females were combined, as there was no significant difference between the sexes (F -test: $P > 0.05$). The regression estimates are shown in Table 1.

Table 1. Relationship between total length (cm) and vertebral radius (mm) in *Carcharhinus tilstoni* and *C. sorrah*
a, *b*, Constants in Fraser's (1916) formula $L = a + bR$, where *L* is total length and *R* is the vertebral radius

Species	<i>a</i> (s.e.)	<i>b</i> (s.e.)	<i>n</i>	<i>R</i> ²
<i>C. tilstoni</i> females	17.39 (1.30)	15.98 (0.19)	258	0.966
<i>C. tilstoni</i> males	12.93 (2.55)	16.97 (0.46)	132	0.912
<i>C. sorrah</i> sexes combined	19.90 (1.70)	15.99 (0.37)	214	0.899

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

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

	Von Bertalanffy growth parameters	From vertebral ring counts		From modal analysis		From tag-recapture	
		Females	Males	Females	Males	Females	Males
<i>C. tilstoni</i>		(<i>n</i> = 257)	(<i>n</i> = 132)	(<i>n</i> = 28) ^A	(<i>n</i> = 32) ^A	(<i>n</i> = 86)	(<i>n</i> = 91)
	<i>L</i> _∞ (cm TL)	194.2 (7.9)	165.4 (11.9)	181.4 (38.9)	156.8 (15.2)	218.2 (28.8)	139.5 (4.6)
	<i>K</i> (yearly)	0.14 (0.02)	0.19 (0.03)	0.19 (0.08)	0.25 (0.06)	0.08 (0.02)	0.20 (0.02)
	<i>t</i> ₀ (years)	-2.8 (0.3)	-2.6 (0.4)	-2.1 (0.5)	-1.9 (0.3)	—	—
<i>C. sorrah</i>		(<i>n</i> = 133)	(<i>n</i> = 80)			(<i>n</i> = 20) ^A	(<i>n</i> = 27) ^A
	<i>L</i> _∞ (cm TL)	123.9 (3.4)	98.4 (1.8)			122.4 (11.9)	97.3 (4.0)
	<i>K</i> (yearly)	0.34 (0.05)	1.17 (0.18)			0.12 (0.06)	0.44 (0.22)
	<i>t</i> ₀ (years)	-1.9 (0.2)	-0.6 (0.1)			—	—

^A*n* = number of mean modal lengths derived from length frequency data using Macdonald-Pitcher method.

The ninhydrin-treated vertebrae of near-term embryos showed a stained area around the primordial notochord. In some new-born and young sharks, there were stained bands on the portion of the cone surface formed prior to birth. These bands are presumably formed *in utero*, perhaps in response to changes in nutrient sources during embryonic development (cf. Casey *et al.* 1985). The average vertebral radius for the new-born sharks was 3.0 mm

for *C. tilstoni* ($n = 3$) and 2.3 mm for *C. sorrah* ($n = 3$). Outside the stained area on the vertebrae of some new-born and young sharks is a broad unstained area. In larger sharks, the position of this unstained area coincides with a marked change in the topography across the cone surface. Since this first, unstained band on the vertebra appears at or just after the time of birth, it is referred to as the 'birth ring'. Subsequent bands appear as alternating violet, ninhydrin-stained and white, unstained bands.

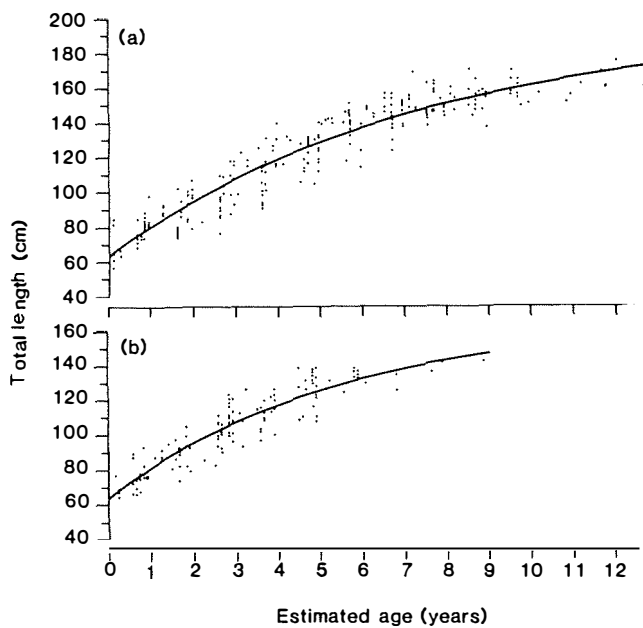


Fig. 3. Von Bertalanffy growth curves for *C. tilstoni* derived from vertebral ageing: (a) females, (b) males.

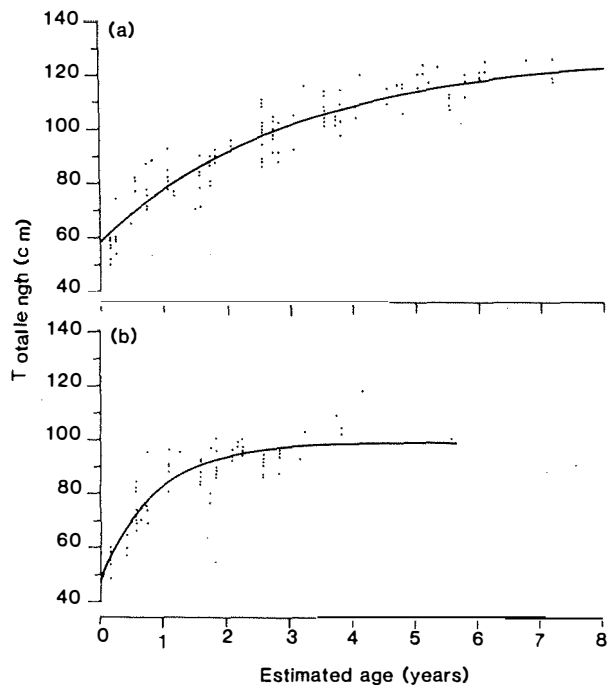


Fig. 4. Von Bertalanffy growth curves for *C. sorrah* derived from vertebral ageing: (a) females, (b) males.

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

While the size at birth and growth in the first 4 years are similar in *C. tilstoni* of both sexes, there is a significant difference (F -test: $0.01 < P < 0.05$) between the growth curves for males and females (Fig. 3), with females growing faster and larger than males after the fourth year. The L_{∞} values of 194.2 cm for females and 165.4 cm for males (Table 2) are, respectively, similar to and lower than the largest sizes recorded during this sampling programme (a female of 196.0 cm and a male of 183.7 cm TL). The estimates of 63 cm (female) and 65 cm (male) for the length at birth (Table 3) approximate to the size at birth recorded by Stevens and Wiley (1986). The K values, 0.14 year^{-1} for females and 0.19 year^{-1} for males (Table 2), imply that the growth curve for males approaches its asymptote more quickly than does the curve for females.

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

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

Based on Stevens and Wiley's (1986) observed size at maturity, vertebral ageing indicates an age-at-maturity in *C. tilstoni* of 3–4 years for both sexes (at which time females have reached 59% and males 67% of their asymptotic length). The oldest *C. tilstoni* of each sex aged in this study were a female of 12 years at 168.9 cm (87.0% of asymptotic length) and a male of 8 years at 142.0 cm TL (85.9% of asymptotic length).

There was a significant difference between the growth curves for male and female *C. sorrah* (F -test: $P < 0.01$) (Fig. 4), the male curve showing very rapid growth in the first year and reaching an early asymptote as indicated by the extremely high K value of 1.17 (Table 2). The L_{∞} values of 123.9 cm for females and 98.4 cm for males (Table 2) are considerably lower than the largest sizes recorded during this programme (a female of 151.8 cm and a male of 131 cm TL). Estimates for the length at birth of 58 cm for females and 47 cm TL for males (Table 4) are, respectively, somewhat higher and lower than the 52 cm TL length at birth observed by Stevens and Wiley (1986).

In *C. sorrah* females, the age at maturity is 2–3 years; in males 1–2 years (at which time females have reached 76.7% and males 91.5% of their asymptotic length). The oldest *C. sorrah* individuals aged in this study were females of 7 years which were between 115.0 and 123.4 cm (92.8–99.6% of asymptotic length), while the oldest male was 5 years and 100 cm TL, slightly longer than the asymptotic length for males.

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

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

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

Modal Analysis

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

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

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

Tag Recapture

By January 1986, 4.4% of all tagged *C. tilstoni* (214 of 4839) and 1.9% (56 of 2926) of tagged *C. sorrah* individuals had been returned. After the freezer correction factor was applied, 'negative growth' was recorded in 12 *C. tilstoni* specimens from a total of 181 tag returns (6.6%) and 5 *C. sorrah* specimens from 45 tag returns (11%) for which growth information was available. The number of returned sharks showing 'negative growth' decreased as the period of liberty after tagging increased. Of the sharks that had been at liberty for less than a month, 16.6% of the *C. tilstoni* and 50% of the *C. sorrah* specimens

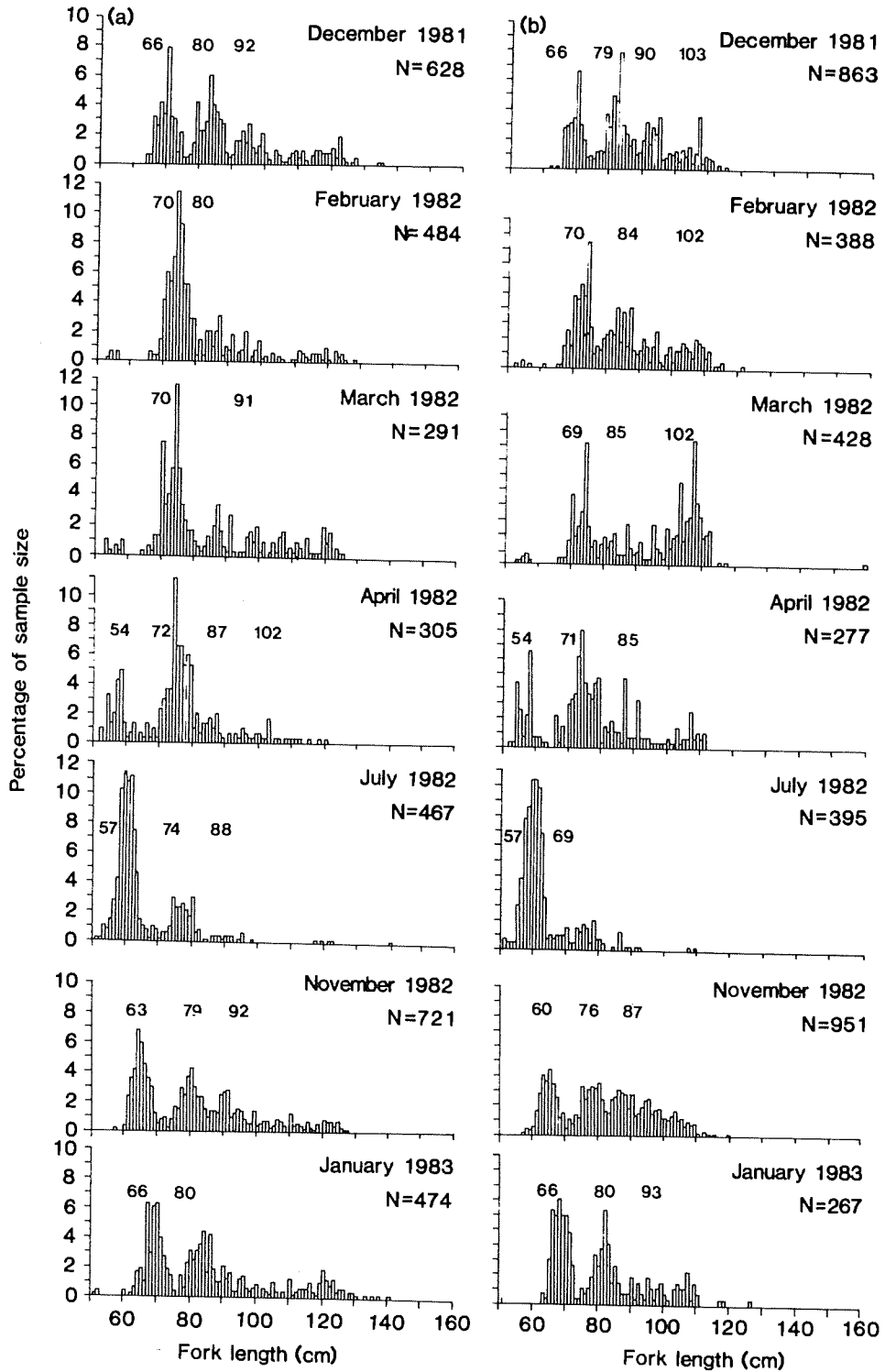


Fig. 5. Length-frequency data for *C. tilstoni*, December 1981–January 1983. Values above the histograms are means derived by the Macdonald–Pitcher method: (a) females, (b) males.

showed 'negative growth'. For sharks at liberty between 1 month and 1 year, 5.8% of the *C. tilstoni* and 8.6% of the *C. sorrah* specimens showed 'negative growth'; for sharks at liberty for more than 1 year, these values were 2.9% for *C. tilstoni* and 6.3% for *C. sorrah*.

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

Total length (cm)	Growth per year (cm)			
	Females	<i>n</i>	Males	<i>n</i>
≤80	11.1	26	10.9	18
81-90	12.3	23	10.3	24
91-100	10.2	15	8.8	14
101-110	5.4	10	6.9	10
111-120	7.2	2	4.5	11
>120	7.3	10	2.2	14

When the tag return data were analysed for the 177 *C. tilstoni* individuals at liberty for a month or longer, a significant difference was apparent in the growth rate between the sexes (*F*-test: $P < 0.001$). This difference in growth rate between the sexes is greatest in sharks over 110 cm TL (Table 5). The largest recaptured sharks of each sex were a female of 151 cm and a male of 126 cm TL.

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

Total length (cm)	Growth per year (cm)	<i>n</i>
≤80	9.8	5
81-90	2.4	16
91-100	2.2	15
101-110	2.0	9
111-120	2.6	2

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

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

Tetracycline

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

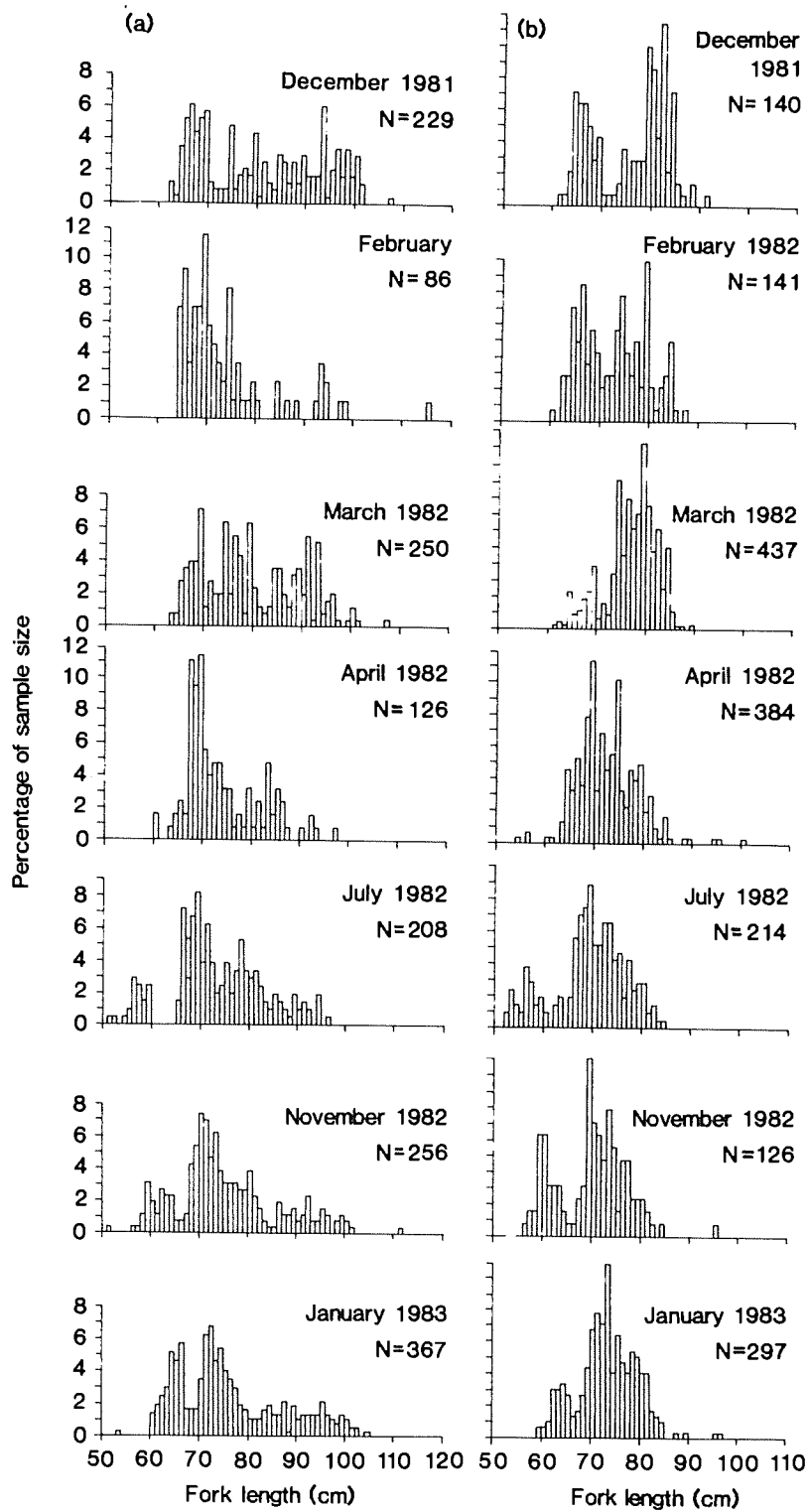


Fig. 6. Length-frequency data for *C. sorrah*, December 1981–January 1983: (a) females, (b) males.

Each vertebra bore a stained band distal to the fluorescent tetracycline ring, and, except for the shark recaptured after 83 days, part of a further unstained band was also present. On the vertebrae of two sharks at liberty for 379 and 381 days, this unstained band was complete, and distal to it was the beginning of the next stained band (Fig. 7). The single injected *C. sorrah* specimen that was returned had been at liberty for 199 days and showed a 'negative growth' of 2.5 cm. Under ultraviolet radiation, OTC fluorescence could be seen at the extreme periphery of the cone surface and in patches on the sides of the vertebra.

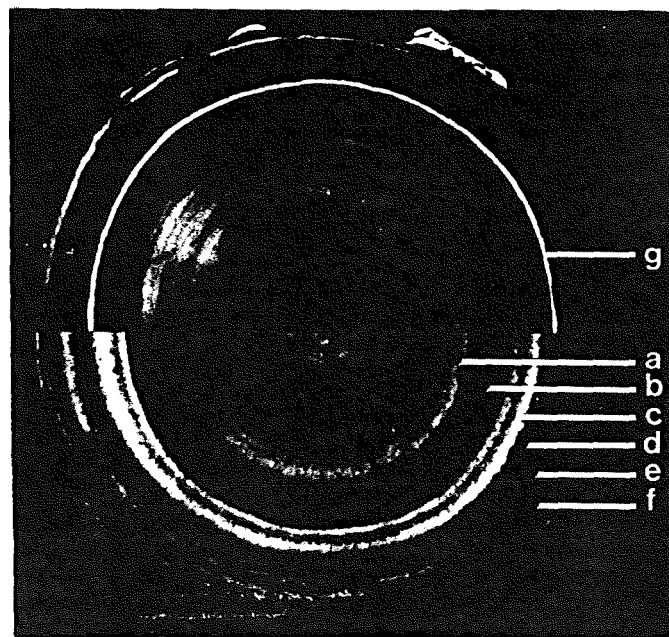


Fig. 7. Vertebra of a *C. tilstoni* specimen (total length 95.8 cm), tagged and injected with tetracycline on 16 March 1985 at the end of the Austral summer, recaptured on 1 April 1986 after 379 days of liberty. The lower half of the illustration was photographed under daylight to show the pattern of ninhydrin staining; the upper half under u.v. radiation. The tetracycline appears under u.v. illumination as a bright, narrow ring. Its position corresponds to the start of the 1985 dark-stained 'winter' band on the daylight photograph. *a*, Birth ring formed early in 1984; *b*, 1984 'winter' band; *c*, 1984/85 'summer' band, Age I; *d*, 1985 'winter' band; *e*, 1985/86 'summer' band, Age II; *f*, start of 1986 'winter' band; *g*, tetracycline ring.

Discussion

Annual Nature of the Growth Bands

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

Evidence that bands in young *C. tilstoni* are annual was provided by the examination of tetracycline-labelled vertebrae from ten recaptured sharks. These *C. tilstoni* specimens were from 84 to 96 cm TL, at which size vertebral ageing puts them at between 1 and 2 years of age. Eight of these sharks were injected at the end of the 1984/85 Austral summer and, except for one, were caught early the following summer in November and December. All vertebrae bore a stained band distal to the fluorescent unstained band, and except for

one shark caught in June, part of the next unstained band was visible. These observations suggest that the tetracycline-labelled unstained band was formed during the 1984/85 Austral summer and that the subsequent stained band was laid down during the following winter. The presence of part of the next unstained band on the vertebrae of the seven sharks captured in November and December provides reasonable evidence that its formation is well under way by November. The other two sharks were injected in March 1985 and recaptured in April 1986. The vertebrae of these sharks (Fig. 7) display a tetracycline ring at the start of the 1985 stained (winter) band. Distal to this stained band is an unstained band, presumably formed during the 1985/86 Austral summer, and the start of the next stained band (1986 winter), suggesting that the winter bands begin to appear on the vertebrae around March. To date, the results do not indicate how long it takes for the tetracycline to be deposited in the vertebral tissues, but do indicate that the dosage and administration of tetracycline were sufficient for its inclusion into the vertebral tissues of both species. The incorporation of the tetracycline ring within an unstained (summer) band on the vertebral centrum of summer-injected sharks verifies the ninhydrin-staining technique, in which the organically rich, rather than the heavily calcified, bands are stained.

Growth and Length-at-age

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

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

When the von Bertalanffy growth curve is fitted to the vertebral ageing data for *C. sorrah* females (Fig. 4), the curve provides a reasonable fit to the data, except for sharks less than 1 year old. The von Bertalanffy growth curve is not a good fit to the vertebral ageing data for males, particularly for sharks less than a year old and more than 3 years old. The relatively low L_{∞} value of 98.4 cm TL, derived from the vertebral ageing of males, is probably influenced by the concentration of vertebral samples over the first three year-classes. Only a few samples of older fish could be obtained, so the growth curve derived by vertebral ageing is tentative.

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

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

Analysis of tag-recapture data (sexes combined) (Table 6) suggests an annual growth of about 10 cm for sharks up to 80 cm TL whereas vertebral ageing indicates a growth increment of 19 cm for *C. sorrah* females of a similar size. For sharks between 110 and 120 cm TL, the annual growth rate estimated from tag data is 2.0–2.6 cm while that from vertebral ageing is 2–5 cm per year.

Differences in growth rates and length-at-age values derived by modal analysis and

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

Tag returns for both species indicate a slower growth rate than is suggested by the other methods. Negative and zero growth in tagged sharks have been reported previously (Ketchen 1975; Casey *et al.* 1985). Gruber (1981) noted a slower rate of growth in tagged than in untagged lemon sharks, *Negaprion brevirostris*, held under semi-natural conditions. Possibly the stress of capture is reflected in a disrupted growth pattern. The vertebrae of the one tetracycline-injected *C. sorrah* specimen recaptured after 199 days at liberty fluoresced only at the periphery of the cone surface and in patches along the sides of the vertebra. This indicated that there had probably been no deposition of skeletal tissue since injection. The shark 'grew' a negative 2.5 cm during this period.

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

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

$$\begin{aligned} C. \textit{tilstoni}; \text{ females } K &= 0.45; \text{ males } K = 0.54. \\ C. \textit{sorrah}; \text{ females } K &= 0.50; \text{ males } K = 0.61. \end{aligned}$$

These are well outside the range of K values (0.1–0.2) derived by Holden for other elasmobranchs, and the range of most of the K values obtained in this study (Table 2). In these two species, at least, the *in utero* growth rates are far higher than the *post-partum* growth rates: 60 cm (*C. tilstoni*) and 52 cm (*C. sorrah*) in just 10 months (Stevens and Wiley 1986).

Information in the literature indicates that there is considerable variation in growth between shark species. Beamish and McFarlane (1985) aged spiny dogfish, *Squalus acanthias*, to 70 years. This species matures at, on average, 23 years in females and 14 years in males, and grows between 1.5 and 3.3 cm per year (Ketchen 1975). The Australian school shark, *Galeorhinus galeus*, lives to at least 40 years; the females mature at 10 years (Grant *et al.* 1979). In contrast to the slow growth in spiny dogfish, length-frequency information analysed by Pratt and Casey (1983) for the mako, *Isurus oxyrinchus*, indicated growth rates of 55 cm per year for ages 0–1 and 36 cm per year for ages 1–2. The oldest shark in their samples was an 11.5-year female of 354 cm TL. The blue shark, *Prionace glauca*, is another fast-growing species. Using vertebral ring counts, Stevens (1975) reported that blue sharks grew from 45 cm at birth to a length of 300 cm in just 10 years. They reach maturity at about 220 cm TL (Pratt 1979) which is, using Stevens' vertebral ageing results, between 6 and 7 years of age. *Rhizoprionodon terraenovae* is a small shark that grows rapidly in the first two years (30 cm in year 1 and 15 cm in year 2) and matures early: males mature at 2.0–2.4 years (80–85 cm TL) and females at 2.4–2.8 years (85–90 cm TL) (Parsons 1985).

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

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

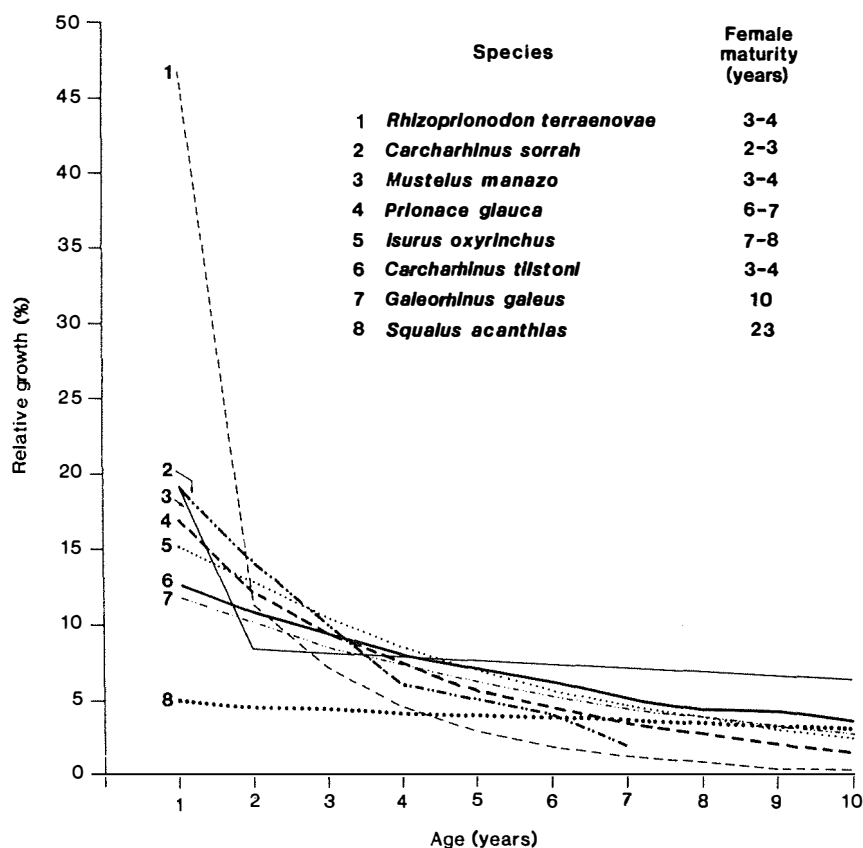


Fig. 8. Relative growth [yearly growth increment/(maximum size minus length at birth)] over the first 10 years of life in eight shark species: 1. *Rhizoprionodon terraenovae* (Parsons 1985). 2. *Carcharhinus sorrah* (this study). 3. *Mustelus manazo* (Taniuchi *et al.* 1983). 4. *Prionace glauca* (Cailliet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

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Mortality rates in *C. tilstoni* and *C. sorrah*

Methods

Total mortality from catch curves

To estimate total mortality Z , age-length keys (Ricker 1975) were constructed for the two species by 5 cm length class using 372 *C. tilstoni* and 190 *C. sorrah* sampled between 1981 and 1983. Data for the sexes were combined so that comparison could be made with estimates of Z obtained from tagging. The age-length keys were used in conjunction with length-frequency data for some 18,000 *C. tilstoni* and 7,500 *C. sorrah* obtained from the Taiwanese fishery over the same period, to estimate the age structure of the catch. The length-frequency sample is assumed to be representative of the stock. Because the length data were collected from 15 cm stretched-mesh gill-nets they were adjusted using the selectivities derived in this study from mesh selectivity experiments. A catch curve was constructed by plotting the natural log of the age-frequency composition against age class (Gulland 1969). Total instantaneous mortality, Z , is estimated from the slope of the least-squares linear regression fitted to the descending right hand limb of the plot.

Total mortality from tag-recapture

Total instantaneous mortality, Z , was estimated from the decline in tag-recaptures with time. For the purposes of the analysis, recaptures were restricted to Australian gill-netters that operated in inshore waters where most of the tags were released. Data for the sexes were combined because of the relatively low sample sizes. An estimate of Z is obtained from the slope of the least-squares regression fitted to a plot of the natural log of tag-return numbers against years at liberty.

Natural and fishing mortality

Natural mortality (M) and fishing mortality (F) were estimated from the equation:

$$F/Z = n/N \quad (\text{Since } F + M = Z)$$

where n = number of tag returns and N = number tagged.

Results

Catch curves

The age structure (sexes combined) of the Taiwanese catch of *C. tilstoni* and *C. sorrah* sampled between 1981 and 1983 is shown in Tables 1 & 2. For *C. tilstoni*, all age classes including the 0⁺ fish are fully recruited. However, there is a significant bow in the catch curve with ages 4-9 having a much steeper slope than ages 0-4 so that the data are better represented by fitting two separate regression lines (Fig. 1a). This gives the following estimates of Z:

Age	Z	95% confidence interval
0-4	0.13	0.07-0.19
5-9	0.47	0.24-0.71
0-9	0.34	0.26-0.42

For *C. sorrah* the 0⁺ fish are not fully recruited; using ages 1-7 gives an estimate of Z = 0.60 (95% confidence interval 0.49-0.71) (Fig.1b).

Tag-recapture

The number of tags returned from the Australian gill-net fishery for *C. tilstoni* and *C. sorrah* are shown below:

Years at liberty	Number of recaptures	
	<i>C. tilstoni</i>	<i>C. sorrah</i>
1	73	18
2	28	7
3	34	7
4	23	4
5	10	0
6	6	1
Total	174	37

The estimates of Z using all the data are 0.46 for *C. tilstoni* (95% confidence interval 0.26-0.65) and 0.54 for *C. sorrah* (95% confidence interval 0.32-0.76) (Figs.2a & b).

Table 1. Age structure of the Taiwanese catch for *C. tilstoni* (sexes combined)

TL	n	Selectivity	Adjusted n	0	+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+
60-64.9	20	.38	53	53												
65	245	.50	490	490												
70	1157	.63	1837	1684	153											
75	1540	.75	2053	1208	725	120										
80	1637	.85	1926	1177	642	107										
85	1636	.93	1759	400	880	479										
90	1687	.98	1721	91	996	362	272									
95	1808	1.0	1808	100	502	1004	201									
100	1617	.99	1633		408	612	510	102								
105	1244	.96	1296		65	713	259	259								
110	1256	.91	1380			244	649	487								
115	1044	.84	1243			335	526	287	86							
120	846	.76	1113			209	348	348	139	69						
125	830	.68	1221				287	646	215	72						
130	884	.59	1498				150	824	375	150						
135	465	.51	912					159	357	317	40	40				
140	229	.43	533					25	25	203	102	127	51			
145	224	.36	622							100	249	224	50			
150	197	.30	657							33	329	66	164	33	33	
155	83	.25	332								39	39	156	98		
160	24	.20	120									52	17	17		17
165	16	.16	100										20	60		20
170	5	.13	38										19	19		
				5203	4371	4185	3227	3137	1508	1327	548	517	227	33	37	

Table 2. Age structure of the Taiwanese catch for *C. sorrah* (sexes combined)

TL	n	Selectivity	Adjusted n	0 ⁺	1 ⁺	2 ⁺	3 ⁺	4 ⁺	5 ⁺	6 ⁺	7 ⁺

50-54.9											
55											
60	7	.29	24		24						
65	77	.44	175	175							
70	150	.60	250	159	68	23					
75	424	.75	565	226	339						
80	1270	.88	1443	541	902						
85	1487	.97	1533	153	920	358	102				
90	1291	1.0	1291		413	775	103				
95	1220	.98	1245	83	249	747	83	83			
100	766	.92	833		40	198	476	79	40		
105	280	.83	337			61	123	61	92		
110	296	.71	417			26	104	156	104	26	
115	148	.60	247				16	32	80	80	32
120	104	.48	217						87	87	43

				1337	2955	2188	1007	411	403	193	75

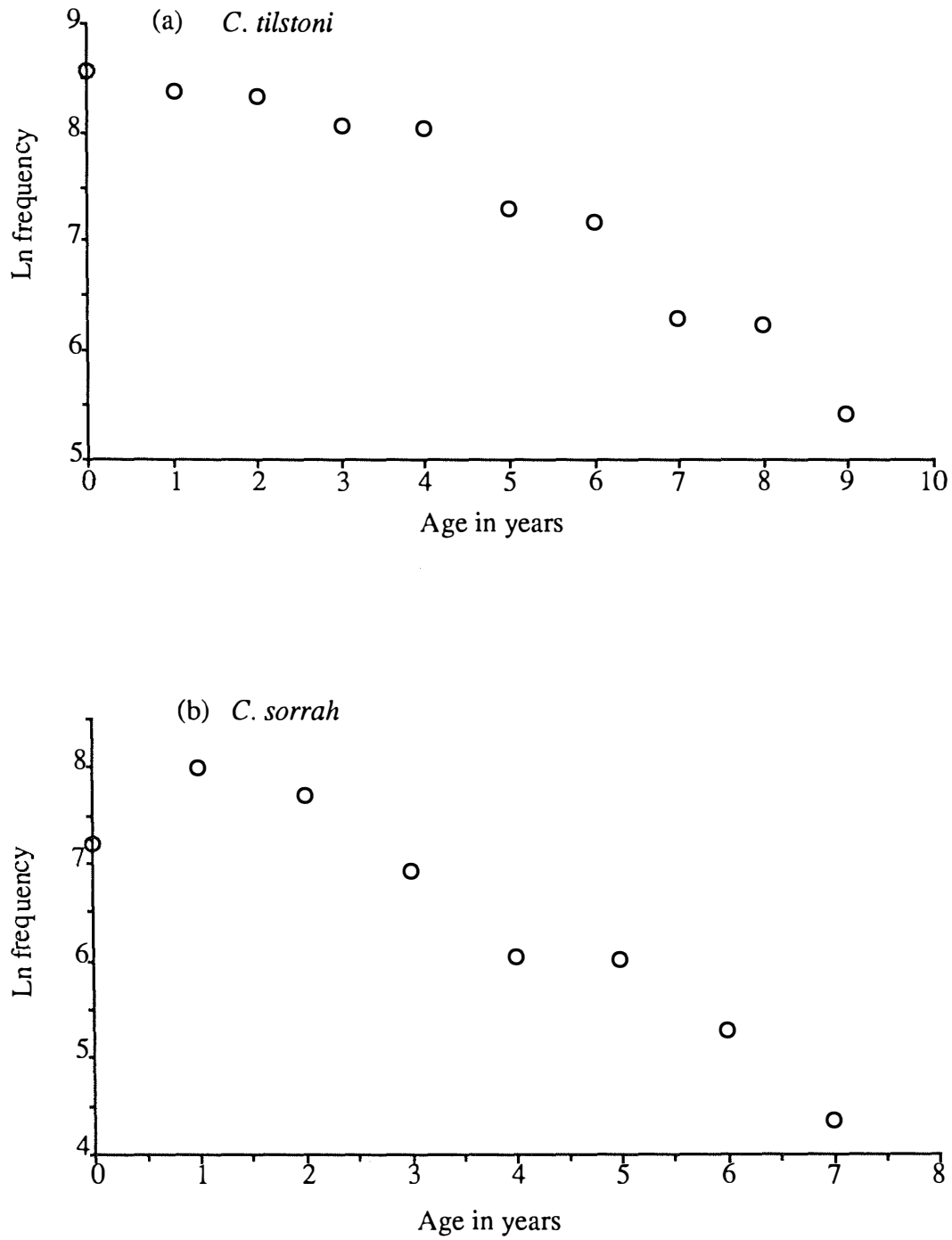


Fig. 1. Catch curves for *Carcharhinus tilstoni* and *C. sorrah* (sexes combined)

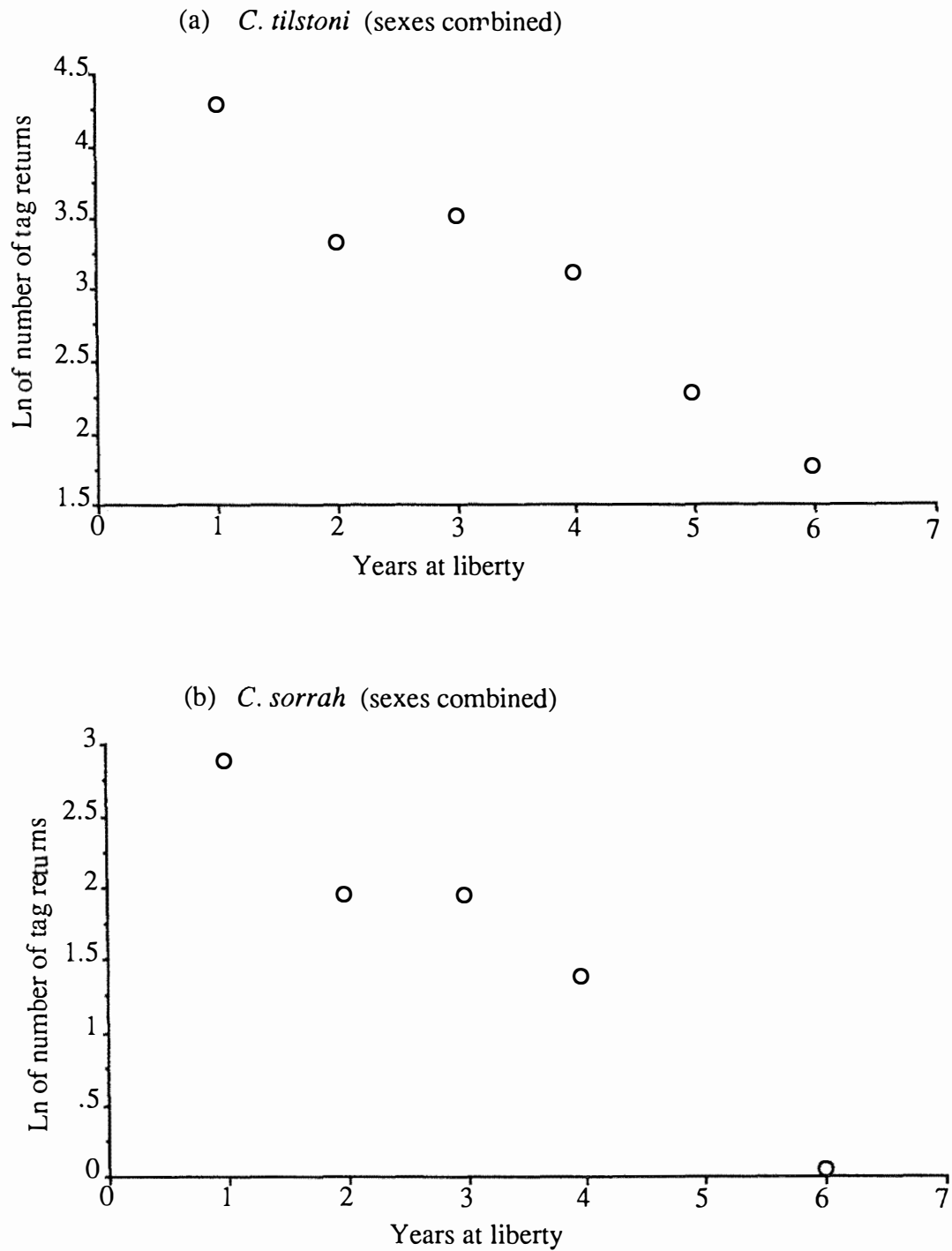


Fig. 2. Decline in the number of tagged *Carcharhinus tilstoni* and *C. sorrah* returned by the Australian gill-net fishery.

Discussion

The catch curve for *C. tilstoni* has a bowed appearance suggesting different mortality fields before and after age 4. Possible explanations for this apparent increased mortality after age 4 are emigration of larger fish out of the area, different catchability or a higher natural or fishing mortality on these age classes. Emigration of large fish seems unlikely in view of fishing being carried out over most of the stock's geographical range and the fact that the tag-return data shows relatively restricted movements, particularly among mature fish. Higher natural mortality would normally be expected in the young age classes as a result of predation; the data suggest the opposite. Higher fishing mortality on sharks more than 4 years old (during 1981-1983 when these data were collected) might be a result of higher Taiwanese exploitation prior to declaration of the AFZ in 1979. Sharks of 4-9 years would have recruited to the fishery between 1973 and 1978. However, Taiwanese fishing effort off Australia was not high until 1975, and landing data suggest that catches taken from an equivalent area before and after the AFZ were not very different.

In the absence of a satisfactory explanation for the variation in apparent Z of from 0.13-0.47 from the catch curve, depending on the age classes chosen, we use the value of 0.34 obtained when the regression is fitted to all the data (ages 0-9). The estimate of Z obtained from the catch curve for *C. tilstoni* is based on data from the offshore Taiwanese fishery. When the tag-return data were used and total mortality separated into fishing and natural mortality —

for the Taiwanese fishery: $F/0.34 = 5/86$, thus $F = 0.02$; $M = 0.32$

The estimate of Z of 0.46 from tag-returns for *C. tilstoni* is based on the inshore Australian fishery. When Z is separated into fishing and natural mortality —

for the Australian fishery: $F/0.46 = 174/4384$, thus $F = 0.02$; $M = 0.44$

An M of 0.44 appears unrealistically high for a shark with a life span of about 12 years (see section on population modelling).

For *C. sorrah* it is not possible to split the estimate of Z of 0.60 from the Taiwanese fishery (obtained from the catch curve) into fishing and natural mortality as there were no recaptures of the 61 sharks tagged offshore. Partitioning our estimate of Z of 0.54 from the inshore fishery —

for the Australian fishery: $F/0.54 = 37/2637$, thus $F = 0.01$; $M = 0.53$

C. sorrah has been aged to at least 7 years and so mortality figures of 0.5-0.6 seems much too high (see section on population modelling).

References

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Shark gill-net selectivities

Gill-net mesh selectivities for two species of commercial carcharhinid sharks taken in northern Australia. K. J. McLoughlin and J. D. Stevens.
(In preparation).

Gill-net mesh selectivities for two species of commercial carcharhinid shark taken in northern Australia

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Abstract

Experiments designed to estimate gill-net mesh selectivities for two species of commercially important sharks in northern Australia were carried out between 1983 and 1984. The gamma distribution model of Kirkwood and Walker (1986) was used to obtain length-specific selectivities for *C. tilstoni* and *C. sorrah* caught in nets with stretched-mesh sizes of 10, 15, 20 and 25 cm. Captured sharks were categorized as gilled or rolled (tangled) in the nets. The data for *C. sorrah* fitted the model better than the data for *C. tilstoni*.

Introduction

Pelagic fish stocks off northern Australia were harvested by Taiwanese gill-net fishermen from the early 1970s until 1986. Before management measures were introduced annual catches from waters between northern Australia, Papua New Guinea and Indonesia averaged about 25000 tonnes live weight. Following declaration of the Australian Fishing Zone in 1979, restrictions were placed on fishing area and vessel numbers and a catch quota of 7000 tonnes processed weight (about 10000 tonnes live weight) was imposed. Shark comprised about 80% of the catch by weight. Two species, *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes in Muller & Henle), accounted for about 60% of the total catch by weight.

In the early 1980s a small Australian gill-net fishery for shark developed off the Northern Territory, and subsequently extended to northern Western Australia and northern Queensland. Annual landings have fluctuated from about 100 to 400 tonnes. The species composition of the catch taken in inshore waters (< 12 nm) by the Australians is similar to that taken offshore by the Taiwanese.

These fisheries resulted in considerable research effort being directed at development and management of the pelagic stocks. A number of studies have reported on gear, marketing, species composition, stock structure and the biology of the exploited species in these fisheries (Millington and Walter 1981; Lyle 1984; Lyle and Timms 1984; Lyle *et al.* 1984; Stevens and Wiley 1984; Welsford *et al.* 1984; Davenport and Stevens 1988; Lavery and

Shaklee 1989). A major objective of this research was to examine the population dynamics and yield potential of the shark stocks.

Gill-nets are highly selective in terms of the size of fish that they catch. A prerequisite to any shark stock assessment work using data collected by gill-net is an understanding of the selective properties of this fishing gear. This paper reports on experiments to estimate length-specific selectivities for *C. tilstoni* and *C. sorrah* caught by gill-net.

Materials and Methods

Two experiments to investigate gear selectivity in the northern pelagic gill-net fishery were carried out, the first of these by the Northern Territory Fisheries Division (NTFD) between February and December 1983 (Lyle and Timms 1984). A total of 31 mesh selectivity sets were made in waters of the Northern Territory between Joseph Bonaparte Gulf and the Goulburn Islands. The net used incorporated three panels of different mesh size, 10, 15 and 20 cm (4, 6 and 8") stretched monofilament nylon mesh. Each panel was 189 m long and was separated from adjoining panels by 100 m of rope. The net specifications are given in Table 1. The number of meshes for each panel was varied in an attempt to produce nets of approximately equal depth. The 21 m gill-netter 'Rachel' was used for the work. The gill-net was fished from a net reel at the stern of the vessel and was set near the surface. When setting, the vessel headed down wind; the floats were clipped on as the net was fed over the stern. At the completion of the set a rope attached to the end of the net was led forward through the bow roller and back to the net reel where it was made fast. The vessel then hung off the net by the bow. In strong wind conditions the net was cast off and allowed to drift free of the vessel. The net was hauled over the bow roller, along the length of the vessel where the catch was removed, and back onto the net drum.

Table 1. Gill-net specifications

	Stretched mesh size (cm)		
	10	15	20
Mesh drop	135	101	67
Hanging coefficient	0.63	0.63	0.63
Hung length (m)	189	189	189
Hung depth (m)	10.5	11.7	10.5
Monofilament gauge	18	30	70
Head rope diameter (mm)	16	16	16
Lead rope diameter (mm)	8	8	8
Float line length (m)	3	3	3
Space between floats (m)	20	20	20

A second mesh selectivity experiment was carried out during the Northern Pelagic Programme (NPP) from January to October 1984. A total of 65 sets were made in inshore waters off northern Australia between Broome and Karumba. The net used consisted of four separate panels of 10, 15, 20 and 25 cm (4, 6, 8, and 10") stretched mesh monofilament nylon. Each panel was 200 m long, 10 m deep, had a hanging coefficient of 0.63 and was separated from adjoining panels by 100 m of headrope (Fig1). Other net specifications were the same as shown in Table 1. These experiments were also conducted from the F.V. 'Rachel' and the setting and hauling procedures were as described above.

The majority of sets were made at night and all panels were set together at any one fishing site. In the NTFD experiment set duration was generally in excess of two hours, in the subsequent experiment the average set duration was about 2.5 hours. Fishing times for each panel were kept relatively constant by alternating which end of the net was set first. Actual fishing times for each panel were not recorded, only the setting time (start of set to end of set), fishing time (end of set to start of haul) and hauling time (start of haul to end of haul) for the complete net.

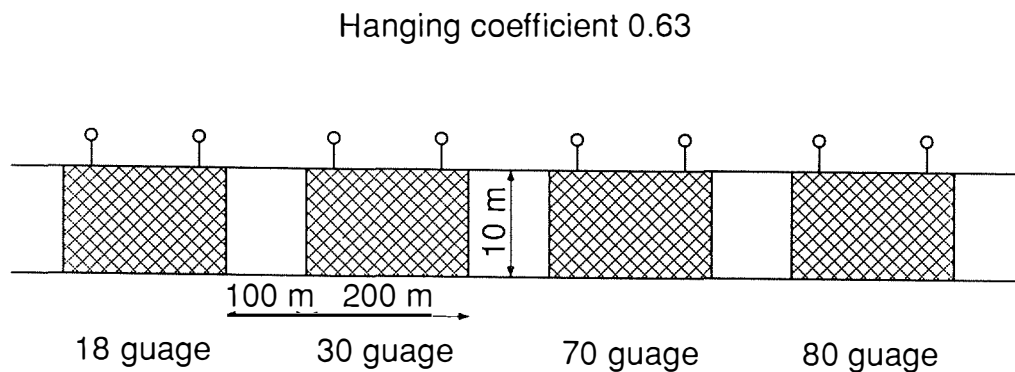


Figure 1. The mesh selectivity net used in the Northern Pelagic Programme.

After each haul the species, sex and length of sharks captured in each of the panels was recorded. Since gill-nets can capture fish by entanglement as well as by holding them in the meshes, it was noted whether captured sharks were gilled or rolled (tangled). Sharks were categorized as rolled if they were not held by a mesh around the gill region (unless they bore an obvious mesh mark suggesting they had fallen out during the hauling process) or if they had broken several meshes before becoming meshed.

Mesh selectivities were examined using the methods of Kirkwood and Walker (1986) in which an assumed selectivity function is fitted directly to the catch data from the different mesh sizes, with the parameters of the selectivity function being estimated simultaneously across mesh sizes and length-classes. Kirkwood and Walker (1986) assumed that the

selectivity function follows a gamma distribution, and used maximum likelihood estimates to fit the data to this distribution.

Calculations were performed using the Nelder-Mead simplex algorithm (Nelder and Mead 1965). The functional form used to model the selectivities as a function of length, l , is:

$$\left(\frac{l}{\alpha\beta}\right)^\alpha e^{-\left(\frac{l}{\beta}\right)}$$

where α and β are specified in terms of the mesh size and length-class. To do this, we further assume that:

(1) the length at maximum selectivity for net i is proportional to the mesh size, so that:

$$\alpha\beta = \varnothing_1 m_i$$

and

(2) the variance is a constant \varnothing_2 over different nets.

Assumptions (1) and (2) lead to a quadratic equation for positive β and imply that:

$$\beta = -0.5 \left[\varnothing_1 m_i - \left(\varnothing_1^2 m_i^2 + 4 \varnothing_2 \right)^{0.5} \right]$$

Results

The catch data for *C. tilstoni* and *C. sorrah* were pooled by species for each mesh size for the 65 stations conducted during the NPP. The frequency with which each species was caught by 5 cm length class in each of the mesh sizes are shown in Fig . 2. The catches are shown separately for gilled and rolled fish. Calculated total fishing times for each panel are also given. Setting time averaged 15 minutes for the complete net and, since it probably took this long to settle in the water and take up correct fishing configuration, set time was ignored. Total fishing time was the known time between the end of the set and the start of the haul plus hauling time. Hauling time was calculated by adding the mean time taken to haul the panel without any catch (6 mins) to the mean time taken to clear one shark (0.6 mins) times the number of sharks in that panel.

Before applying the Kirkwood and Walker (1986) estimating procedure it is necessary to examine the form of the observed data and the assumptions to be used in the procedure. Holt (1963) showed that a plot of the natural logarithm of the ratios of the catches from a pair of nets of different mesh size against length gave a linear relationship. If the ratios of the catches of a given length from two mesh sizes is greater than one then the log ratio will be positive. Conversely, if the ratios of the catches of a given length from two mesh sizes is

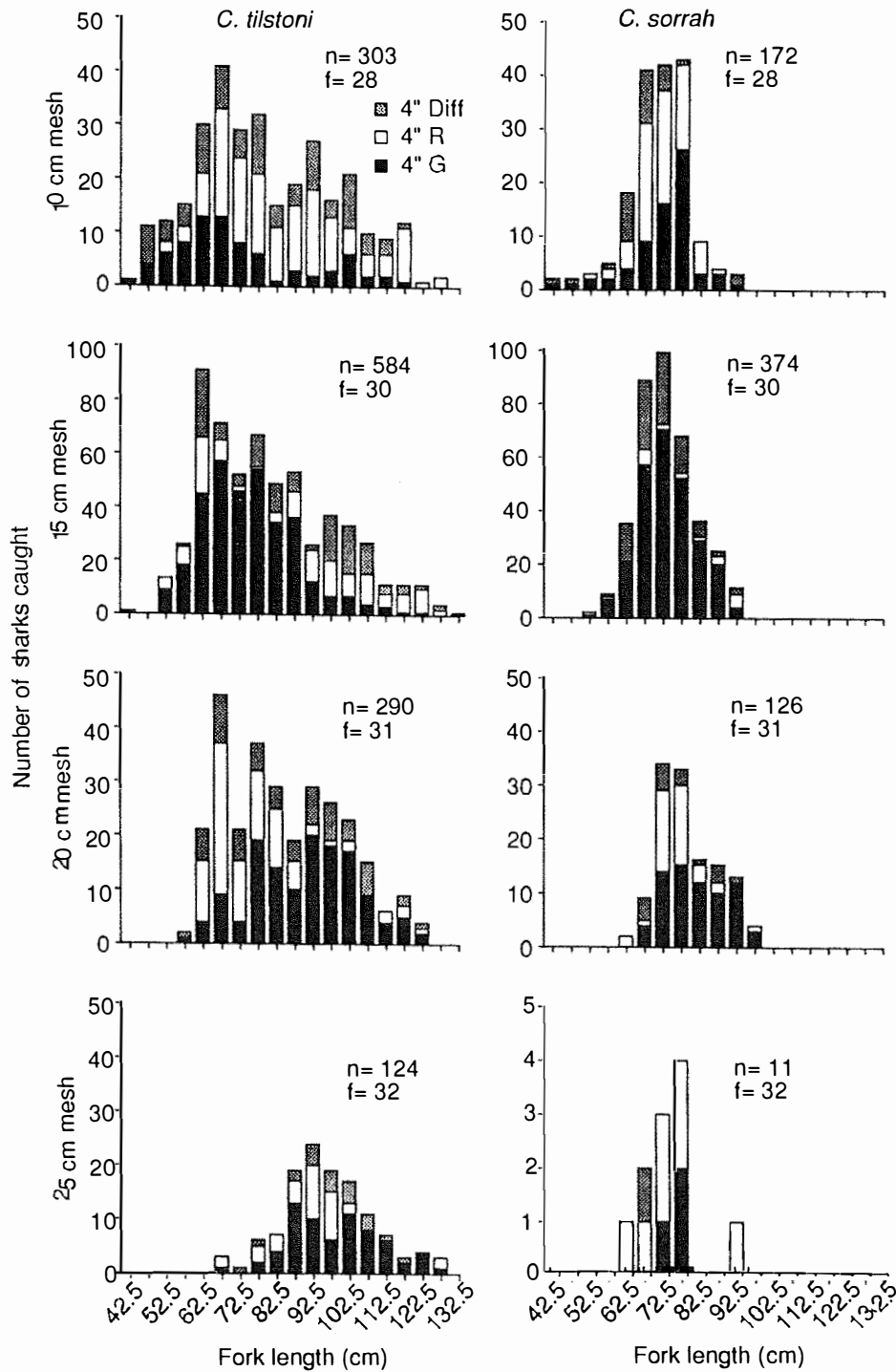


Figure 2. Catches of *C. tilstoni* and *C. sorrah* in the 10, 15, 20 and 25 cm stretched mesh panels of the Northern Pelagic Programme mesh selectivity net (N = Total catch sample size; F = Fishing time in km hrs; catches are shown separately for gilled (G) and rolled (R) fish. As not all sharks were recorded as gilled or rolled, Diff = the difference between total catch and the sum of gilled and rolled fish).

less than one then the log ratio will be negative. It would be expected that for a range of lengths the larger mesh would initially select fewer fish, resulting in a negative log ratio. As the length increases the larger mesh would become more selective, thus increasing the ratio of the catches from the two nets. When plotted this results in a line of positive slope crossing the axis at some point (Fig. 1 in Holt 1963). When we applied this technique to the NPP data for *C. tilstoni* and *C. sorrah* this pattern was not clearly observed, although the data for *C. sorrah* were marginally better than those for *C. tilstoni* (Figs. 3 & 4). In general, the 25/20 cm plots were unreliable as catches from the 25 cm mesh net were very low. The plots suggest that the 15 cm mesh net virtually always outcaught both the 10 cm and 20 cm mesh nets. There was some improvement for *C. tilstoni*, particularly for the 20/15 cm mesh plot, when the gilled only data were used (Fig. 3). When the data from the NTFD experiment were plotted the results for *C. tilstoni* were similar to the expected pattern, particularly for the gilled only data (Fig. 5). The *C. sorrah* data showed a positive slope, but the catches were again dominated by the 15 cm mesh net (Fig. 6). Other differences between the two data sets can be seen when Fig. 7 is compared to Fig. 2.

In addition to some differences in the overall slope of the histograms between the two data sets, there are marked differences in the patterns of those sharks which were gilled or rolled. In the NPP data there are large numbers of sharks recorded as rolled over most of the length range for each mesh size. In the NTFD data rolling has occurred much more frequently for the larger sharks in each mesh size. It might be expected that the NTFD data are more realistic with the incidence of sharks rolling in a mesh size which precluded gilling being greater for large rather than small sharks (Hamley 1975; Kirkwood and Walker 1986). In fact one of the assumptions of the Kirkwood and Walker (1986) model is that the selectivity curve follows a gamma distribution (right skew). However, taking for example the *C. tilstoni* data with length midpoints of 57.5 and 62.5 cm captured in the 20 cm mesh net, it can be seen that the NTFD data contains no sharks recorded as rolled whereas the NPP data contained a relatively high proportion of rolled sharks. Peak selectivity would be expected to occur where girth slightly exceeds the size of the perimeter of the mesh, i.e. at a size where the logarithm of the girth/mesh perimeter ratio is just larger than zero. For the 57.5 and 62.5 cm midpoints the values of log girth/mesh perimeter are less than one (Table 2), and thus less than ideal for capture by this net. In this case it might have been expected that the NTFD captures for these length classes and mesh size would have included some rolled sharks. The assumption that length at maximum selectivity is proportional to mesh size (Kirkwood and Walker 1986) seems reasonable as there is a good fit between length and girth for both *C. tilstoni* and *C. sorrah* (Tables 2 & 7). As noted by Kirkwood and Walker (1986) the assumptions of equal fishing power at maximum selectivity and constant variance of selectivities across nets are difficult to assess directly. There is some suggestion from the NPP data that the 25 cm mesh has a lower fishing power and the 15 cm mesh has a higher fishing power.

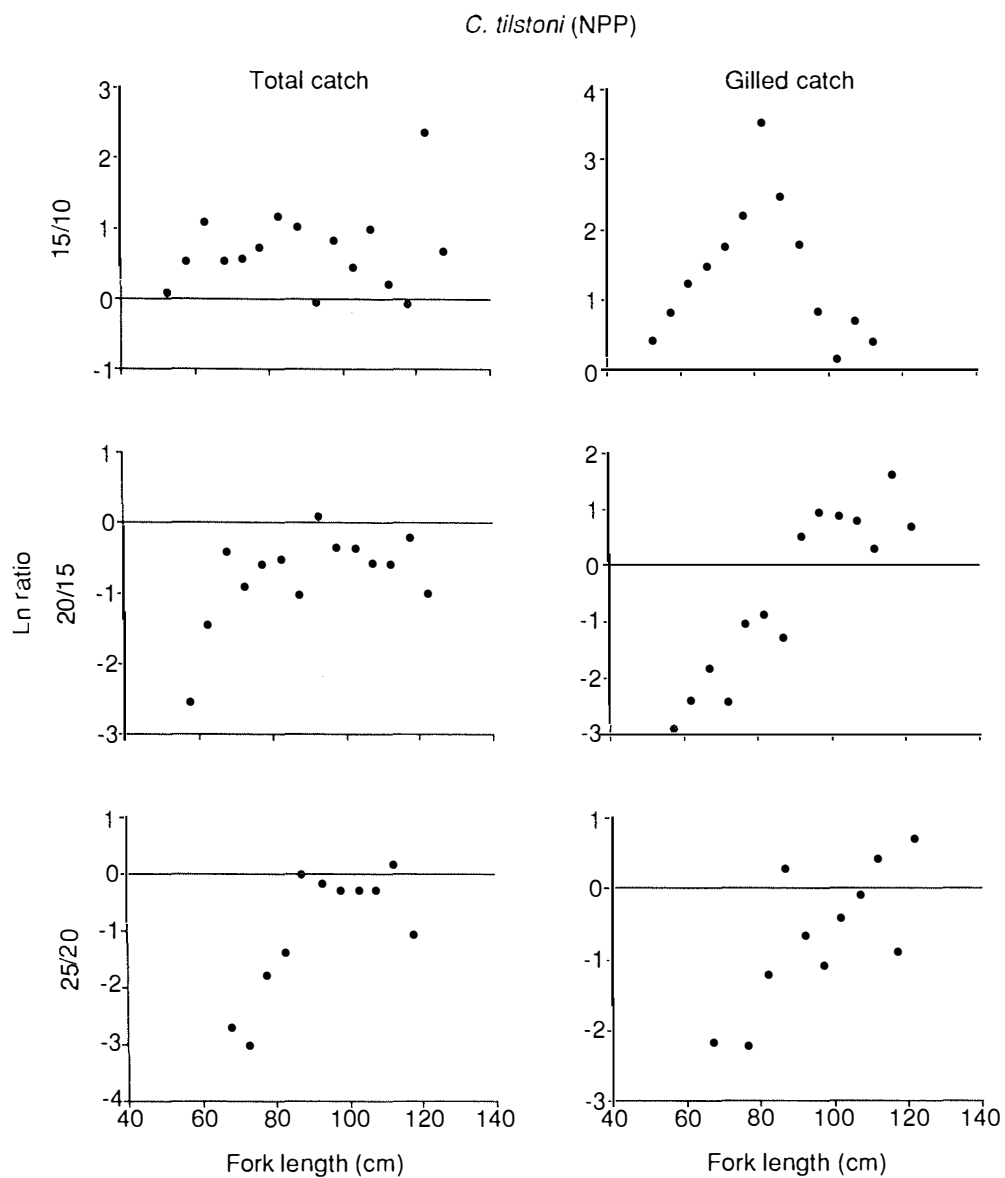


Figure 3. The relationship between the log of the ratios of the catches between paired panels of the mesh selectivity net, and the length of *C. tilstoni*, using the Northern Pelagic Programme data. (Total catch and gilled catch are shown separately).

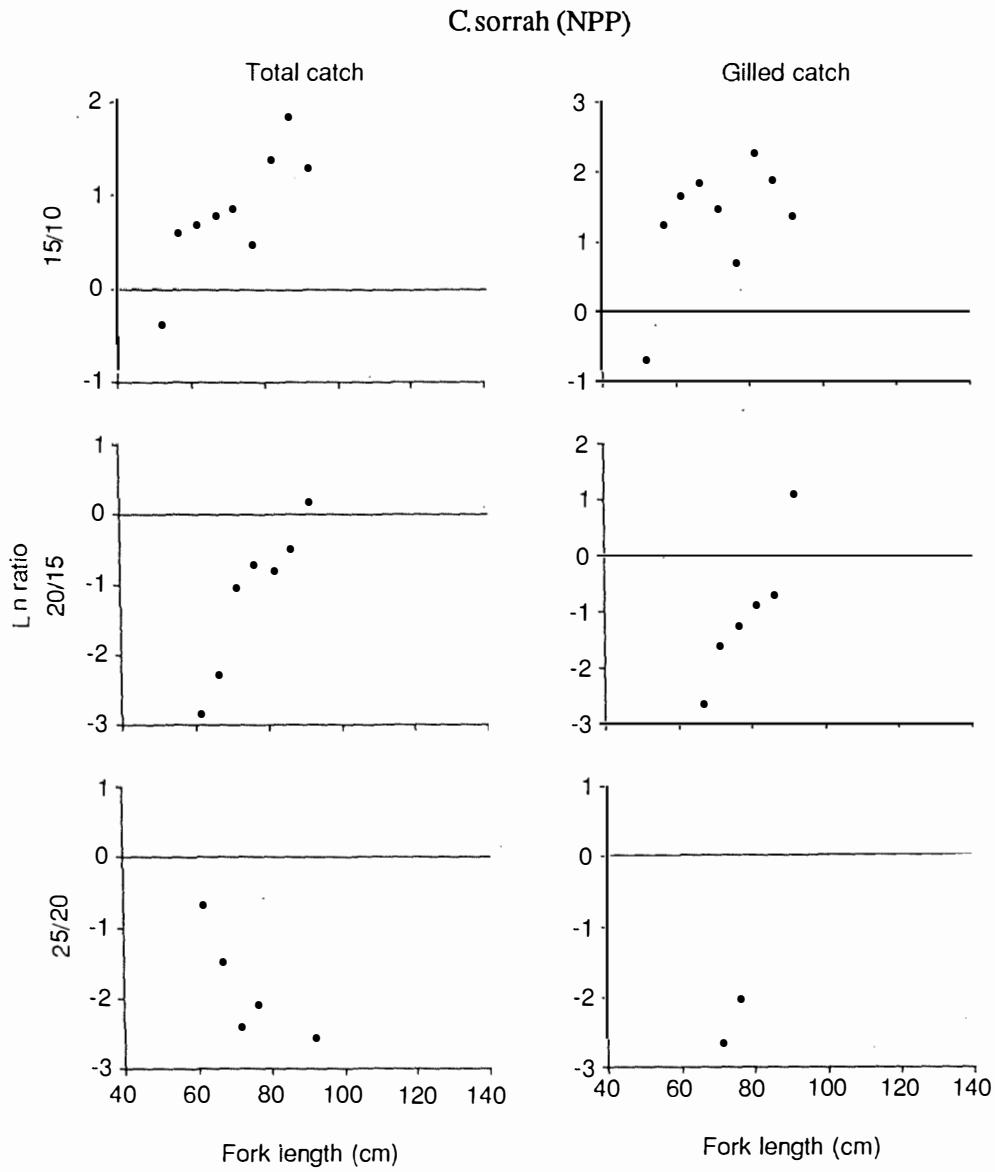


Figure 4. The relationship between the log of the ratios of the catches between paired panels of the mesh selectivity net, and the length of *C. sorrah*, using the Northern Pelagic Programme data. (Total catch and gilled catch are shown separately).

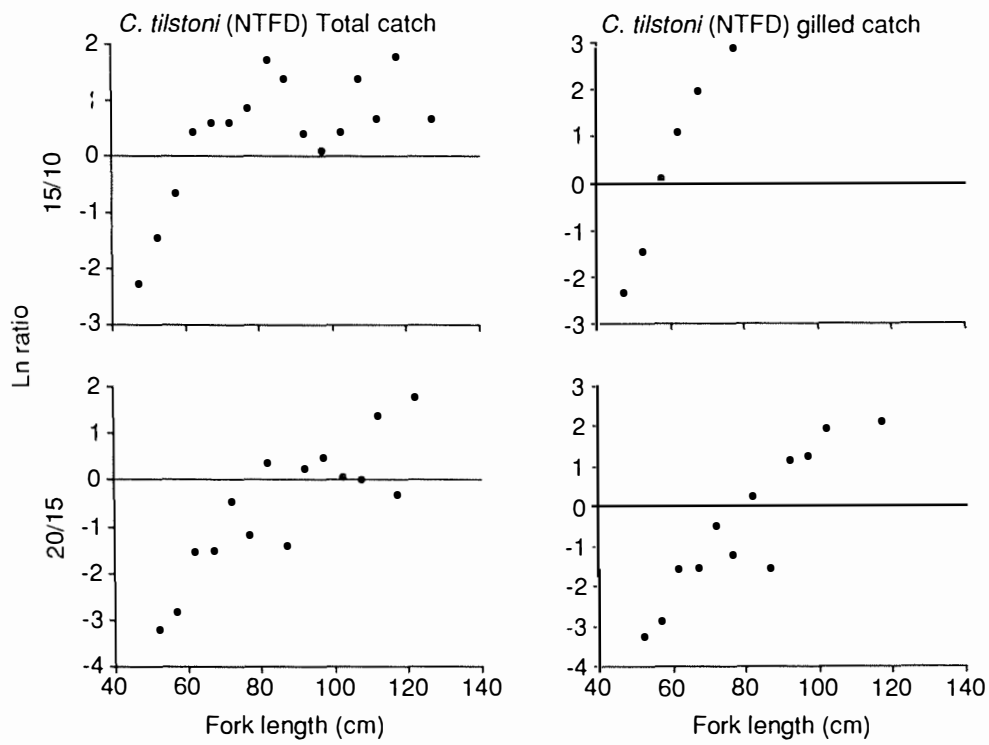


Figure 5. The relationship between the log of the ratios of the catches between paired panels of the mesh selectivity net, and the length of *C. tilstoni*, using the Northern Territory Fisheries Division data. (Total catch and gilled catch are shown separately).

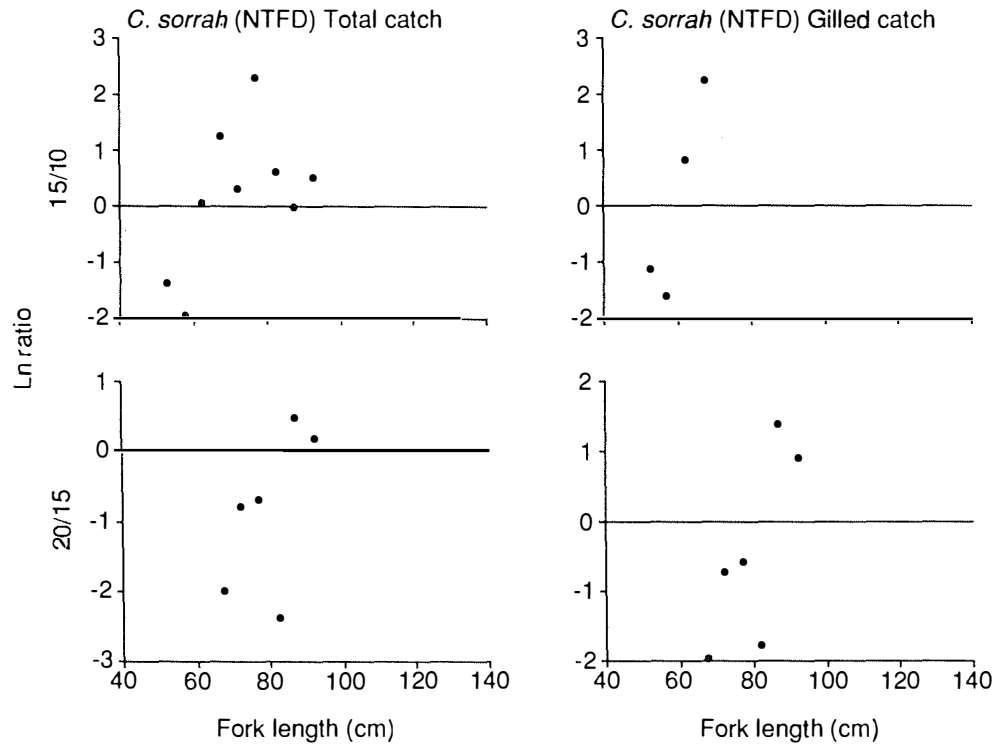


Figure 6. The relationship between the log of the ratios of the catches between paired panels of the mesh selectivity net, and the length of *C. sorrah*, using the Northern Territory Fisheries Division data. (Total catch and gilled catch are shown separately).

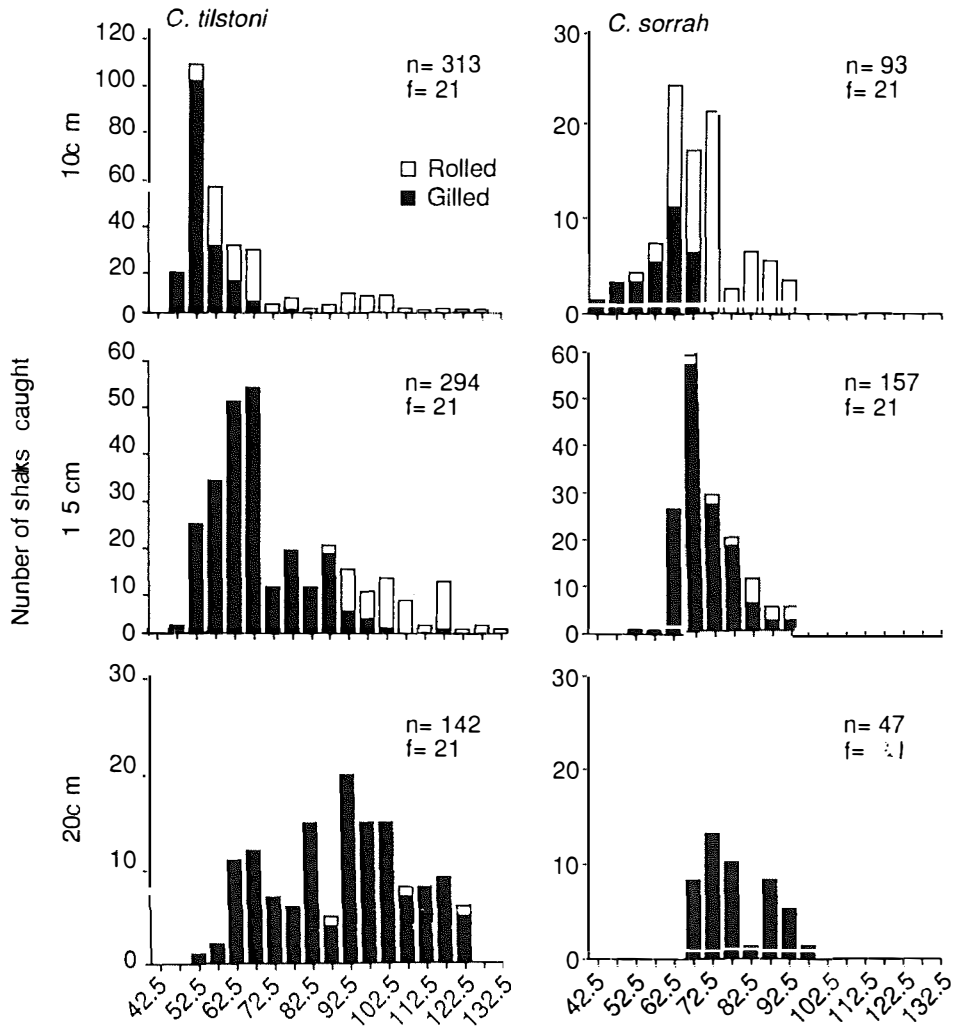


Figure 7. Catches of *C. tilstoni* and *C. sorrah* in the 10, 15 and 20 cm stretched mesh panels of the Northern Territory Fisheries Division mesh selectivity net (N = Total catch sample size; F = Fishing time in km hrs; catches are shown separately for gilled (G) and rolled (R) fish. As not all sharks were recorded as gilled or rolled, Diff = the difference between total catch and the sum of gilled and rolled fish).

Table 2. Relationship between fork length, girth and perimeter of the gill-net stretched-mesh size for *C. tilstoni* (Girth = 0.501 X length - 3.095, $r^2 = 0.925$)

Fork length (cm)	Girth (cm)	Log girth/mesh perimeter			
		10 cm	15 cm	20 cm	25 cm
42.5	18.2	-0.11	-0.52	-0.80	-1.03
47.5	20.7	0.02	-0.39	-0.67	-0.90
52.5	23.2	0.13	-0.27	-0.56	-0.78
57.5	25.7	0.23	-0.17	-0.46	-0.68
62.5	28.2	0.33	-0.08	-0.37	-0.59
67.5	30.7	0.41	0.01	-0.28	-0.50
72.5	33.2	0.49	0.09	-0.20	-0.42
77.5	35.7	0.56	0.16	-0.13	-0.35
82.5	38.2	0.63	0.23	-0.06	-0.28
87.5	40.7	0.70	0.29	0.00	-0.22
92.5	43.2	0.75	0.35	0.06	-0.16
97.5	45.7	0.81	0.41	0.12	-0.11
102.5	48.2	0.86	0.46	0.17	-0.05
107.5	50.7	0.92	0.51	0.22	0.00
112.5	53.2	0.96	0.56	0.27	0.05
117.5	55.8	1.01	0.60	0.32	0.09
122.5	58.3	1.05	0.65	0.36	0.14
127.5	60.8	1.10	0.69	0.40	0.18
132.5	63.3	1.14	0.73	0.44	0.22
137.5	65.8	1.17	0.77	0.48	0.26

Stretched mesh size (cm)	Mesh perimeter (cm)
10	20.32
15	30.48
20	40.64
25	50.80

The best fit for the *C. tilstoni* data using the Kirkwood and Walker (1986) model is provided by the NTFD results:

$$\hat{\phi}_1 = 131.6 \text{ (s.e. 2.3)} \text{ and } \hat{\phi}_2 = 63948 \text{ (s.e.6873)}.$$

Predicted catches for the fitted model are shown in Table 3, and the corresponding relative selectivities are shown for each net in Table 4. An indication of the fits obtained using the gamma distribution, and a normal distribution model, are shown in Fig 8.

When the two data sets are combined the resulting peak selectivities are similar but the spread is different:

$$\hat{\phi}_1 = 134.0 \text{ (s.e. 2.0)} \text{ and } \hat{\phi}_2 = 110631 \text{ (s.e.10533)}.$$

The standard errors for $\hat{\phi}_1$ indicate that the peak selectivities are relatively well estimated. This is supported by the data in Table 2. With $\hat{\phi}_1 = 131.6$, peak selectivity for the 15 cm mesh would be 79 cm. At a mid length of 77.5 cm the log of the ratio of girth to mesh perimeter (G:MP) is 0.16.

The *C. sorrah* data fits the model better than the *C. tilstoni* data. Combining the two data sets, and using the NTFD data on its own, both give adequate fits to the model.

Combined data (10,15 and 20 cm mesh only):

$$\hat{\phi}_1 = 123.1 \text{ (s.e. 1.1)} \text{ and } \hat{\phi}_2 = 33565 \text{ (s.e.2537)}.$$

NTFD data:

$$\hat{\phi}_1 = 123.2 \text{ (s.e. 2.8)} \text{ and } \hat{\phi}_2 = 33800 \text{ (s.e.6805)}.$$

Using the combined data set, predicted catches for the fitted model are shown in Table 5, and the corresponding relative selectivities are shown for each net in Table 6. An indication of the fits obtained using the gamma distribution, and a normal distribution model, are shown in Fig. 8. While these peak selectivity values agree reasonably well with the girth/mesh perimeter data in Table 7 they tend to be closer to where $\log G:MP = 0$. Thus in *C. sorrah* the girth is closer to the size of the mesh perimeter, rather than slightly larger than the mesh perimeter as in *C. tilstoni*. Since *C. sorrah* are more slender at a given length than *C. tilstoni* it might have been expected that the length at peak selection for *C. sorrah* would have been greater. However, this is not the case with peak selectivity in the 15 cm mesh net being 74 cm for *C. sorrah* and 79 cm for *C. tilstoni*.

Table 3. Catches of *C. tilstoni* by length class and stretched mesh size predicted by the Kirkwood and Walker (1986) model using the NTFD data.

Fork length class (cm)	Predicted catch in net of mesh size (cm):		
	10	15	20
45.0-49.9	17.3	5.5	0.2
50.0-54.9	94.4	43.3	2.7
55.0-59.9	62.0	39.0	4.0
60.0-64.9	51.5	42.6	6.8
65.0-69.9	43.1	45.2	10.7
70.0-74.9	9.2	11.9	4.0
75.0-79.9	10.6	16.4	7.5
80.0-84.9	7.7	14.0	8.6
85.0-89.9	6.6	13.8	10.9
90.0-94.9	8.2	19.5	19.3
95.0-99.9	5.4	14.1	17.2
100.0-104.9	4.9	14.2	20.9
105.0-109.9	2.0	6.2	10.9
110.0-114.9	1.1	3.5	7.2
115.0-119.9	2.0	6.9	16.2
120.0-124.9	0.6	2.3	6.0

Table 4. Relative selectivities for *C. tilstoni* by length class and stretched mesh size estimated by the Kirkwood and Walker (1986) model using the NTFD data.

Fork length class (cm)	Selectivity for net of mesh size (cm):		
	10	15	20
45.0-49.9	0.97	0.31	0.01
50.0-54.9	1.00	0.46	0.03
55.0-59.9	0.98	0.62	0.06
60.0-64.9	0.92	0.76	0.12
65.0-69.9	0.84	0.88	0.21
70.0-74.9	0.74	0.96	0.32
75.0-79.9	0.64	1.00	0.46
80.0-84.9	0.54	0.99	0.61
85.0-89.9	0.45	0.94	0.74
90.0-94.9	0.37	0.87	0.86
95.0-99.9	0.30	0.78	0.95
100.0-104.9	0.23	0.67	0.99
105.0-109.9	0.18	0.57	1.00
110.0-114.9	0.14	0.47	0.96
115.0-119.9	0.11	0.38	0.89
120.0-124.9	0.08	0.30	0.80

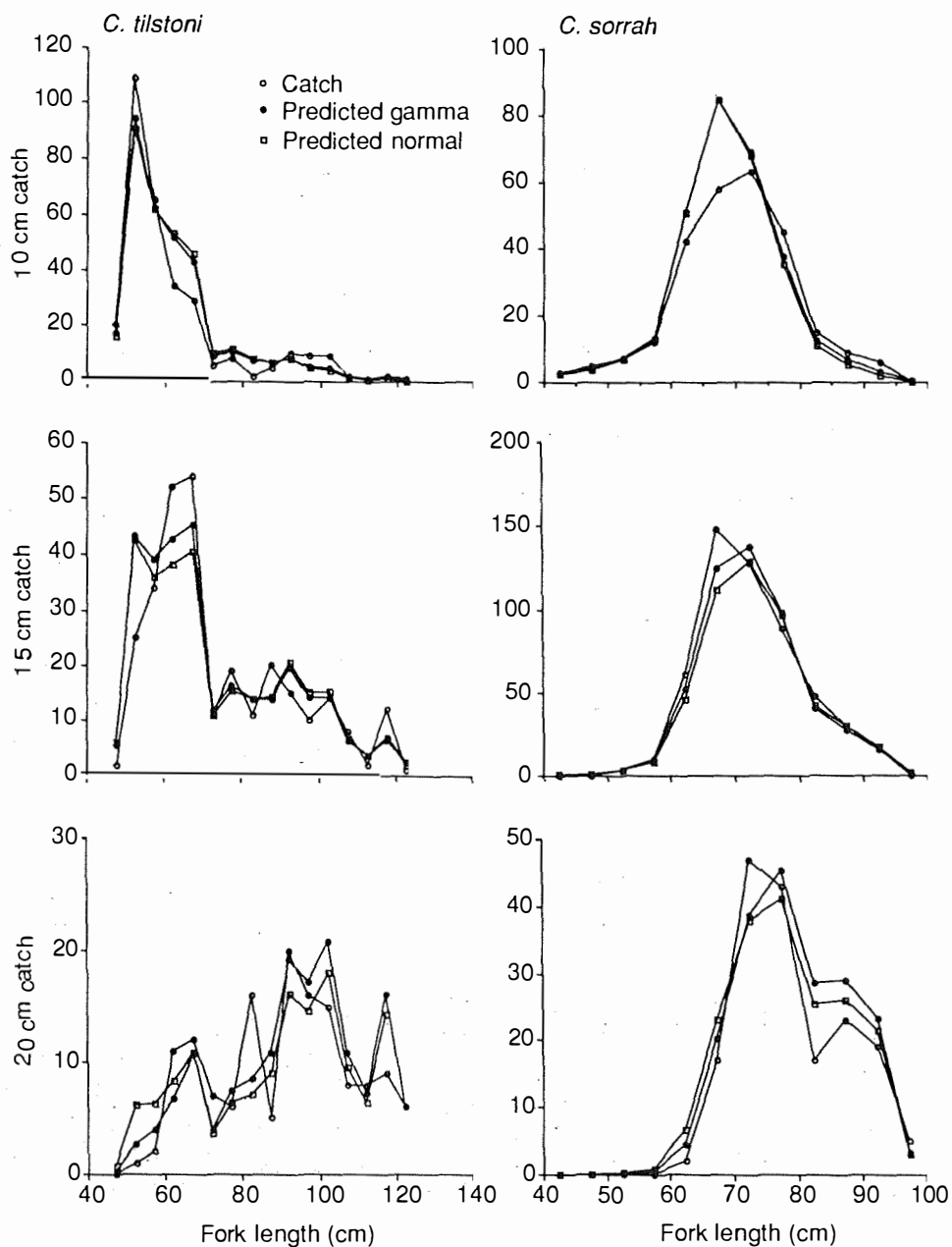


Figure 8. Observed catches of *C. tilstoni* and *C. sorrah* in the 10, 15 and 20 cm stretched mesh panels compared to the catches predicted using either a gamma or normal distribution model. (Catches of *C. tilstoni* from the Northern Territory Fisheries Division net; catches of *C. sorrah* using the combined data set).

Table 5. Catches of *C. sorrah* by length class and stretched mesh size predicted by the Kirkwood and Walker (1986) model using the combined NTFD and NPFSAP data.

Fork length class (cm)	Predicted catch in net of mesh size (cm):		
	10	15	20
40.0-44.9	2.7	0.3	0.0
45.0-49.9	4.1	1.0	0.0
50.0-54.9	7.2	3.0	0.1
55.0-59.9	13.3	8.9	0.4
60.0-64.9	51.0	52.2	4.5
65.0-69.9	84.8	124.2	20.2
70.0-74.9	68.9	137.4	38.7
75.0-79.9	37.8	98.2	45.3
80.0-84.9	12.3	40.2	28.8
85.0-89.9	6.9	27.5	29.2
90.0-94.9	3.3	15.4	23.3
95.0-99.9	0.3	1.6	3.2

Table 6. Relative selectivities for *C. sorrah* by length class and stretched mesh size estimated by the Kirkwood and Walker (1986) model using the combined NTFD and NPFSAP data.

Fork length class (cm)	Selectivity for net of mesh size (cm):		
	10	15	20
40.0-44.9	0.92	0.11	0.00
45.0-49.9	0.99	0.23	0.00
50.0-54.9	0.98	0.41	0.01
55.0-59.9	0.90	0.61	0.03
60.0-64.9	0.78	0.80	0.07
65.0-69.9	0.64	0.93	0.15
70.0-74.9	0.50	1.00	0.28
75.0-79.9	0.38	0.98	0.45
80.0-84.9	0.27	0.90	0.64
85.0-89.9	0.19	0.77	0.82
90.0-94.9	0.13	0.63	0.94
95.0-99.9	0.09	0.48	1.00

Table 7. Relationship between fork length, girth and perimeter of the gill-net stretched-mesh size for *C. sorrah* (Girth = 0.439 X length - 0.659, $r^2 = 0.879$)

Fork length (cm)	Girth (cm)	Log girth/mesh perimeter			
		10 cm	15 cm	20 cm	25 cm
42.5	18.0	-0.12	-0.53	-0.82	-1.04
47.5	20.2	-0.01	-0.41	-0.70	-0.92
52.5	22.4	0.10	-0.31	-0.60	-0.82
57.5	24.6	0.19	-0.22	-0.50	-0.73
62.5	26.7	0.27	-0.13	-0.42	-0.64
67.5	28.9	0.35	-0.05	-0.34	-0.56
72.5	31.1	0.43	0.02	-0.27	-0.49
77.5	33.3	0.49	0.09	-0.20	-0.42
82.5	35.5	0.56	0.15	-0.13	-0.36
87.5	37.7	0.62	0.21	-0.07	-0.30
92.5	39.9	0.67	0.27	-0.02	-0.24
97.5	42.1	0.73	0.32	0.04	-0.19
102.5	44.3	0.78	0.37	0.09	-0.14
107.5	46.5	0.83	0.42	0.13	-0.09
112.5	48.7	0.87	0.47	0.18	-0.04
117.5	50.9	0.92	0.51	0.22	0.00
122.5	53.1	0.96	0.55	0.27	0.04
127.5	55.2	1.00	0.59	0.31	0.08
132.5	57.4	1.04	0.63	0.35	0.12
137.5	59.6	1.08	0.67	0.38	0.16

Stretched mesh size (cm)	Mesh perimeter (cm)
10	20.32
15	30.48
20	40.64
25	50.80

Discussion

There are notable differences in the data between the two experiments reported here. One of the major reasons for the NTFD *C. tilstoni* data giving a better fit to the model is that more small specimens were caught with the 15 cm mesh net. *C. tilstoni* has a seasonal reproductive cycle giving birth in January and the growth rate is relatively fast (Stevens and Wiley 1984; Davenport and Stevens 1988). Although both experiments sampled around the birth period it appears that the Northern Territory experiment captured more of the neo-natal fish.

Comparison of Figs 2 & 7 suggest differences between the experiments in the pattern of gilled and rolled sharks; the NTFD data has rolling occurring more frequently for the larger sharks in a particular mesh size. Although we attempted to standardise methodology between the two experiments, there may still have been differences in the way the data were recorded.

The residuals in fitting the NPP data indicate that the 10 cm net is undercatching and the 15 cm net is overcatching. This pattern is much less evident in the NTFD experiment, but the 10 cm net still seems to be undercatching. This might suggest violation of the assumption of equal fishing power of the nets (Kirkwood and Walker 1986). However, a more likely reason may be the spread of nets chosen with respect to the size distributions of these two sharks. The modal catches for both shark species occur at lengths less than the length of maximum selectivity predicted by the Kirkwood and Walker model (1986). The lengths of shark which dominate the populations of both species may be too narrow for the range of mesh sizes used. In retrospect, it may have been better to have included 13 and 18 cm mesh nets in the experiments. Fitting the model with the fishing power varying gives a closer fit to the data but provides unrealistic values for the modal selectivities. The advantage of keeping fishing power equal is the reduction in the number of parameters to be estimated. Kirkwood and Walker (1986) do not believe that robust estimates of fishing power and selectivities can be obtained simultaneously.

Catches from the mesh selectivity nets were often low, particularly from some length classes. These low catches, together with tendency for both species to aggregate by size and sex, are probable reasons for not getting a better fit to the model. Fig. 8 shows, however, that the gamma distribution model does provide a better fit to the data than a normal distribution. Data from both species were pooled by sex, partly to increase the sample sizes, but also because there appeared to be no differences in the length-girth relationship between the sexes which would affect their selectivity curves. As noted by Kirkwood and Walker (1986) it would be necessary to separate the sexes for age-specific selectivities, since females grow longer than males (Stevens and Wiley 1984).

The mesh selectivity experiments reported on in this study were carried out in inshore waters off northern Australia. The Australian fishery operates in the same region and uses 15 cm monofilament mesh nets of very similar construction. The Taiwanese fishery operated further offshore, however, there are no apparent differences in the size composition of the sharks between these areas. A 15 cm mesh was also used by the Taiwanese, but the nets were of multifilament construction.

Acknowledgements

We acknowledge the assistance given by the Master and crew of FV *Rachel*. Many people helped in the collection of the data; in particular we thank Glen Cuthbert, Peter Wiley, Stephanie Davenport, Tony Church, Greg Timms and Dr Jeremy Lyle. This study was assisted by FIRTA grant 83/49.

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Shark population dynamics

Population estimates for *C. tilstoni* and *C. sorrah*.
(J. D. Stevens, working paper)

Population estimates for *C. tilstoni* and *C. sorrah*

Introduction

As noted by Walker (1988) the standard population models used in stock assessment of bony fish are not appropriate for shark gill-net fisheries. The Beverton and Holt yield per recruit, DeLury and Deriso models are inappropriate because of the close stock recruitment relationship in sharks and the selectivity of gill-nets which negate the assumption of constant catchability with age. The Schaefer surplus yield model should not be applied because the northern fishery is characterised as one of increasing fishing effort and declining catch per unit effort. It is now generally accepted that Schaefer analyses should only be applied where fishing effort has been varied considerably over the history of the fishery. Walker (1988) noted that a specific model was required for the southern shark fishery that took into account the effects of gear selectivity and the biological characteristics of sharks. The Southern Shark Assessment Group developed an age structured yield per recruit or dynamic pool model (T. I. Walker, Marine Science Laboratories, Queenscliff, Victoria 3225, personal communication) which we have adapted for the two principal shark species in the northern gill-net fishery.

To obtain approximate population estimates we used a modification of the Peterson method for tag-recapture data (Ricker 1975).

Methods

Dynamic pool model

The basis of the model is that for a given mesh size and selectivity one male and one female shark starting at age 0 are subjected to fishing and natural mortality over their life span. As a proportion of these two original fish the stock size, biomass, catch and number of pups born can be calculated for each age. The equilibrium state is determined by the fishing effort that results in the production of 2 pups over the animals' life span thus replacing the original two fish of age 0. The parameters required for the model are: gill-net selectivities, age and growth, natural mortality, catchability, weight-length and fecundity. The model assumes that:

- (1) The stock is in a state of equilibrium during year $T = 0$.
- (2) Biological parameters for growth and reproduction are constant and independent of stock size.
- (3) Fishing effort is applied uniformly over the stock (or portion of the stock).
- (4) Natural mortality and catchability do not vary with age.
- (5) Birth occurs at the beginning of each year.
- (6) Annual fish survival is given by e^{-M-F} where F is size selective fishing mortality and M is natural mortality.
- (7) Size selective fishing mortality is separable into a product of catchability, fishing effort, and a fishing gear selectivity factor (which is a function of fish length and net mesh size).

Derivation of the model is given in a manuscript currently being prepared for publication by T. I. Walker (Marine Science Laboratories, Queenscliff, Victoria 3225.)

Input parameter values to the model for *C. tilstoni* and *C. sorrah* are shown below:

Function/Parameter	Parameter values		Source
	<i>C. tilstoni</i>	<i>C. sorrah</i>	
Von Bertalanffy growth			Davenport & Stevens 1988
K	0.14	0.34	
L_∞	194.2	123.9	
t₀	-2.8	-1.9	
Allometric weight-length			Stevens & Wiley 1986
a	0.00475	0.0000545	
b	3.06	3.51	
Catchability			Leslie method (Ricker 1975)
q	0.0003	0.0003	
Selectivity			This study
o₁	164.2	155.2	
o₂	98141	51678	
Annual fecundity	3.0(age 4 & above)	3.1(age 4 & above)	Stevens & Wiley 1986
Natural mortality			This study
M	0.32	-	
Lifespan	12 yrs	8 yrs	Davenport & Stevens 1988

Peterson method

An estimate of population size vulnerable to the fishery at the time of marking was obtained using the Petersen estimate :

$$N = MC/R$$

where N is the population size at the time of marking, M is the number of marked fish, C is the catch taken and R is the number of recaptures. When the number of recaptures was small, a modified version of the equation was used : $N = (M+1)(C+1)/(R+1)$ (Ricker 1975). To

assess the affect of unequal vulnerability of fish of different sizes, the releases were grouped into a number of size classes, and the biomass of each size class estimated (Ricker 1975). The biomass of fish susceptible to gill-netting was estimated from:

$$B = \sum C_i M_i / R_i$$

where B is the biomass of fish susceptible to fishing, C_i is the catch of size class i, M_i is the number of fish released in size class i, and R_i is the number of recaptures of this size class.

Australian gill-net fishery

Choice of release area and time

The Australian fishery operates from 129° E to 138 ° E , and, because of the limited movement shown by most returns of *C. tilstoni* and *C. sorrah* (Stevens *et al.* In prep.), only releases in this area were included in the analysis. Tagging was carried out in this region from February 1983 to May 1985, with a total of 3,394 releases of *C. tilstoni* and 1,996 *C. sorrah*. However, most releases were made from January to June 1984 (2,438 and 1,383 releases respectively) and this was the release period chosen for the analysis.

Correction of numbers released due to tagging-induced mortality

Stevens *et al.* (In prep.) have shown that tagged sharks obtained by gill-net and longline suffered higher mortality than those released after being caught on handlines. This effectively reduces the number of sharks released in these categories. Handlined *C. tilstoni* were recaptured 2.09 and 6.37 times as often as gill-net and longline released sharks respectively, by the Australian gill-net fishery. The corresponding values for *C. sorrah* were 2.34 and 3.12. These values were used to calculate an 'effective number of releases', on the basis of a common (handline) release method as shown below:

	Release method			Total
	Handline	Gill-net	Longline	
<i>C. tilstoni</i>				
Initial number released	384	2029	25	2438
Correction factor	1	2.1	6.4	
Effective number of releases	384	966.2	3.9	1354.1
<i>C. sorrah</i>				
Initial number released	490	848	45	1383
Correction factor	1	2.3	3.1	
Effective number of releases	490	362.4	14.4	866.8

Choice of recapture period and elimination of prior returns

Recaptures from releases made in 1984 commenced in May, and the initial period for recaptures was set at July 1984 to December 1984. This was extended to June 1985, and then in one year intervals up to a maximum of three years, to assess the effect of prolonging the recapture period. There were 34 recaptures of *C. tilstoni* and 4 of *C. sorrah* prior to July 1984, and these were subtracted from the totals to give 1320.1 and 862.8 *C. tilstoni* and *C. sorrah* available at the start of the recapture period.

Catch data from the Australian fishery

Catch data were provided by the Northern Territory Department of Primary Industries and were in the form of total live weight of sharks caught. Since only *C. tilstoni* and *C. sorrah* are normally retained by the Australian fishery, total weight was converted to estimated species weight by multiplying by a factor of 0.74 for *C. tilstoni* and 0.26 for *C. sorrah*. The conversion factors were based on the proportions in which these species occurred in research catches.

Taiwanese gill-net fishery

The modified form of the Petersen equation was used because of the small number of recaptures from sharks released offshore.

Choice of release area and time

Although releases of tagged *C. tilstoni* did not cover the entire area fished by the Taiwanese in Australian waters, they were in the areas of heaviest fishing effort. Seventy-eight releases from August 1984 to March 1985 in the area 10-11 ° S; 132-140 ° E were used in this analysis.

Correction of numbers released due to tagging-induced mortality

Because of the small number of releases made offshore, correction factors for the extra mortality suffered by gill-net and longline released sharks were based on all the available data (all releases, and all recaptures, both inshore and offshore). The correction factors are given below:

	Release method			Total
	Handline	Gill-net	Longline	
Initial number released	0	18	60	78
Correction factor	1	1.65	2.67	
Effective number of releases	0	10.9	22.5	33.4

Choice of recapture period and elimination of prior returns

Only five recaptures were made from these offshore releases, one of them in August 1984, and the remainder from November 1985 to March 1986. The recapture period chosen for the population estimate was from July 1985 to June 1986, the latter date marking the closure of the Taiwanese fishery in Australian waters. The effective number of tagged *C. tilstoni* at the start of this period was thus 32.4.

Catch data from the Taiwanese fishery

Catches were obtained from the logbook data and were in the form of processed weight of all retained sharks. Based on data obtained in this study, shark processed weight represents 60% of total weight and *C. tilstoni* accounts for 60% of the shark catch.

Results

Dynamic pool model

Running the model with fishing effort set at 0 required a natural mortality of 0.38 for *C. tilstoni* and 0.36 for *C. sorrah* to achieve equilibrium. If the model is correct, this suggests that higher mortality estimates obtained from catch curves and tagging data are erroneous.

Taiwanese fishery

Applying the average Taiwanese effort of 755,000 km hrs expended between 1980-84, the effects on the simulated population of *C. tilstoni* and *C. sorrah* using a range of natural mortality values are shown below:

M	Number of pups produced*	
	<i>C. tilstoni</i>	<i>C. sorrah</i>
0.10	211	168
0.15	152	128
0.20	111	98
0.25	82	75
0.30	61	58
0.35	46	45

* 100 pups are required for the equilibrium state.

Using the M of 0.32 calculated for *C. tilstoni* from catch curves, the simulated population declines. Since CPUE in the fishery approximately halved between 1980-84 (and assuming changes in CPUE reflect changes in stock biomass) this suggests that an M of 0.32 is reasonable for *C. tilstoni*. The level of Taiwanese effort required to achieve equilibrium with

M set at 0.32 is 280,000 km hrs. Using the average CPUE value between 1980–84 this is equivalent to a catch of 1,893 tonnes live weight (1,136 tonnes processed weight) of *C. tilstoni* which should have been close to the maximum sustainable yield at this heavily exploited stage of the fishery.

Mortality estimates of 0.5-0.6 calculated for *C. sorrah* from catch curves and tagging data appear to be too high. Using the same M as for *C. tilstoni* (0.32) the amount of fishing effort required to achieve equilibrium is 190,000 km hrs, which would have been equivalent to a catch of 535 tonnes live weight (321 tonnes processed weight) at this stage in the fishery.

A plot of yield against fishing effort (with M set at 0.2) for stretched mesh sizes varying from 10-25 cm shows that the 15 cm mesh is the most efficient size for the Taiwanese fishery (Fig. 1).

Australian fishery

Between 1984-8 the average effort in the Australian fishery was about 12,000 km hrs. With this effort level as input to the model the effects on the simulated populations of *C. tilstoni* and *C. sorrah* using a range of M values are shown below:

M	Number of pups produced*	
	<i>C. tilstoni</i>	<i>C. sorrah</i>
0.10	616	423
0.15	430	317
0.20	305	239
0.25	220	181
0.30	160	138
0.35	118	105
0.40	88	81

* 100 pups are required for the equilibrium state.

With M set at 0.32 and fishing effort maintained at 12,000 km hrs the simulated populations of *C. tilstoni* and *C. sorrah* would be producing 141 and 124 pups respectively, suggesting they are underexploited. This is supported by CPUE data from the fishery which rose from 16 kg/km hr in 1984 to 45 kg/km hr in 1988.

Peterson method

Taiwanese fishery

The estimated population size for *C. tilstoni* vulnerable to the Taiwanese fishery in the area from 132° to 140° E is given below:

Recapture period	No. of recaptures	Catch of <i>C. tilstoni</i> (t)	Estimate of population size (t)	95% C.L. (t)
7/85-6/86 (1 yr)	4	2207.4	14750	6586-36880

t = tonnes live weight

The area to which this estimate applies accounts for approximately 147,000 km² of the total area of 425,000 km² fished by the Taiwanese fleet in Australian waters. However, using this result to calculate a total estimated population of *C. tilstoni* in the Taiwanese zone (42,000 tonnes) is almost certainly not valid, because their fishing effort was not uniform throughout the zone.

Australian fishery

The results for the different recapture periods, and for the length-stratified method applied to the one year recapture period, are shown below:

Recapture period (month/year)	No. of recaptures	Catch of <i>C. tilstoni</i> (t)	Estimate of population size (t)	95% C.L. (t)
7/84-12/84 (0.5 yr)	28	76.8	3620	2500-5450
7/84-6/85 (1 yr)	56	219.9	5180	3990-6740
7/84-6/85 **(1 yr)	"	"	6290	
7/84-6/86 (2 yr)	64	483.4	9970	7810-12740
7/84-6/87 (3 yr)	89	677.0	10042	8160-12360

** Estimate from length-stratified method

t = tonnes live weight

The number of recaptures was the same for the first and second 6-month periods, and the

increased population estimates reflect changes in the catch. The number of returns diminished after this period resulting in higher population estimates for the 2 and 3 year recapture periods. Recruitment would have commenced after December 1984, and would have progressively diluted the population of tagged individuals. The length-stratified method resulted in a higher estimate than the simple method, but did not have as pronounced an effect as the choice of recapture period.

Estimates of the population size of *C. sorrah* vulnerable to the Australian gill-net fishery are shown below:

Recapture period (month/year)	No. of recaptures	Catch of <i>C. sorrah</i> (t)	Estimate of population size (t)	95% C.L. (t)
7/84-12/84 (0.5 yr)	12	27.0	1860	1099-3357
7/84-6/85 (1 yr)	14	77.3	4500	2759-7700
7/84-6/86 (2 yr)	17	169.8	8200	5233-13538
7/84-6/87 (3 yr)	22	237.9	8970	6033-13942

t = tonnes live weight

The high proportion of recaptures in the first 6 months, and the low catch during this period resulted in a low population estimate. Subsequent estimates increased because of increasing catches and declining rates of tag returns.

Discussion

The dynamic pool model indicates that effort levels should not exceed about 280,000 km hrs for *C. tilstoni* and 190,000 km hrs for *C. sorrah* in the Taiwanese zone. During the period of heavy exploitation (1980-84) these effort levels would have translated into sustainable catches of about 1,900 tonnes for *C. tilstoni* and 540 tonnes live weight for *C. sorrah*. These estimates must be treated with caution because of uncertainty over parameter estimates, particularly mortalities for *C. sorrah*. The model is sensitive to estimates of mortality and catchability. For example, with M set at 0.20 for both species (instead of 0.32), the fishing effort to achieve equilibrium would rise to 820,000 and 750,000 km hrs for *C. tilstoni* and *C. sorrah* respectively. This is about equal to, or more than the average fishing effort expended by the Taiwanese during 1980-84. The model also assumes no density dependence of biological parameters.

Applying the Gulland (1971) or Pauly (1984) 'rule of thumb' equation ($MSY = 0.5$ or $0.2 MB_0$ where B_0 is the initial biomass and M is set at 0.32) to the 1980-84 sustainable catch estimates suggests that the population size in this period was about 19,000 tonnes and 5,400 tonnes live weight of *C. tilstoni* and *C. sorrah* respectively. These results are compared with estimates obtained using the Peterson method, and from some other less appropriate

techniques (see introduction) and are shown in Table 1.

Taking the estimate for the most recent period for the Taiwanese zone from the dynamic pool method gives a combined population of 24,280 tonnes. This compares to 19,010 tonnes calculated by the Peterson method for the most recent period for the Australian zone.

Dividing these estimates by the approximate area fished results in densities of 57 kg km² for the Taiwanese zone (425,384 km²) and 84 kg km² for the Australian zone (225,463 km²). The average annual CPUE for the period 1984-89 in the Australian fishery was 28 kg/km hr while for the Taiwanese fishery between 1984-86 it was 7 kg/km hr. If CPUE reflects stock abundance this suggests that either the population estimates for the Taiwanese area are too high or those for the Australian region are too low. The Peterson estimate for *C. tilstoni* (no estimate could be made for *C. sorrah*) in the Taiwanese zone represents a density of 100 kg km² which appears much too high.

Table 1. Approximate population estimates for *C. tilstoni* and *C. sorrah* (tonnes live weight).

Period	<i>C. tilstoni</i>	<i>C. sorrah</i>	Method
Taiwanese Fishery			
1977	45000	18750	Leslie ¹
1977	21000	8750	Catch ²
1979-86	37800	15750	Schaefer ³
1980-84	18930 ⁴	5350	Dynamic pool
1980-84	14750 ⁵	-	Peterson
Australian Fishery			
1984-85 ⁶	6290	4510	Peterson
1984-86 ⁶	9970	8200	Peterson
1984-87 ⁶	10040	8970	Peterson

1 Leslie method (Ricker 1975)

2 1977 catch (assumed to represent virgin state) with assumed exploitation rate of 0.3

3 See Fig. 2.

4 Refers to an area of 425,384 km²

5 Refers to an area of 147,000 km²

6 Estimates refer to the population present at the start of tagging (1984)

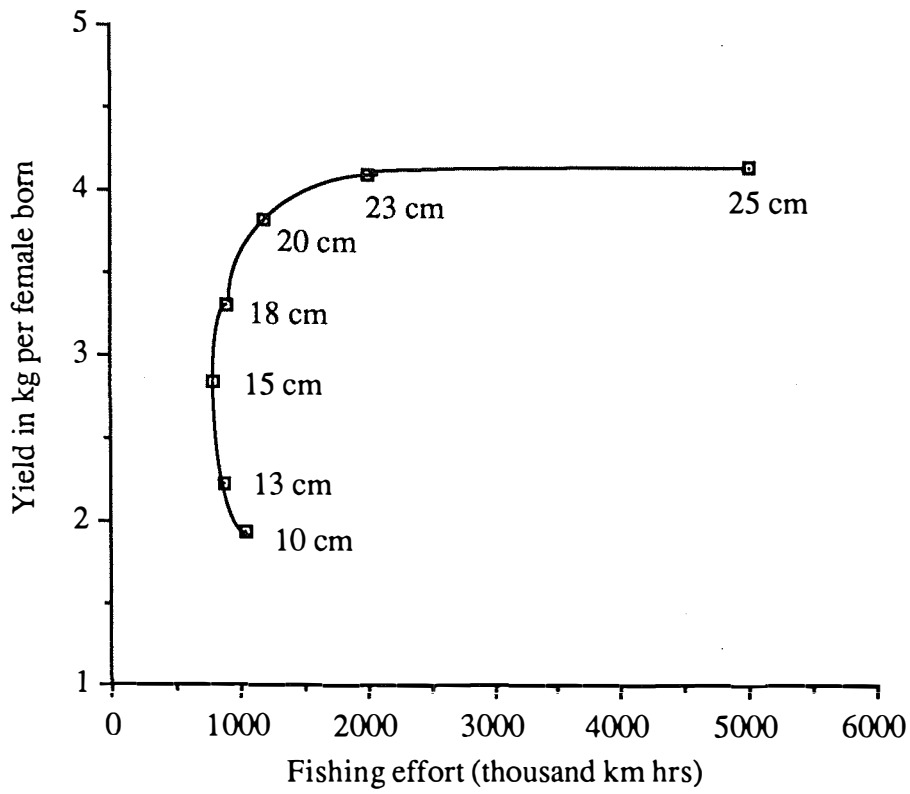


Fig. 1. Yield per recruit for mesh sizes varying from 10-25 cm.

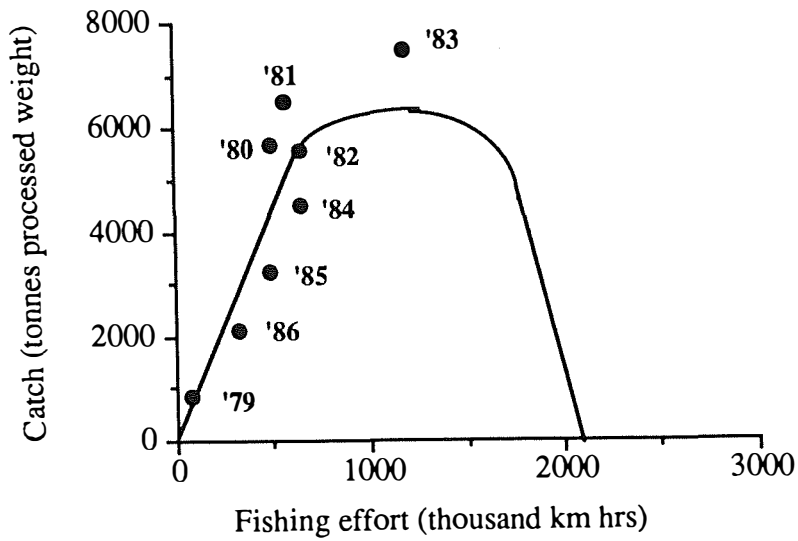


Fig. 2. Schaefer curve for Taiwanese total catch 1979-1986

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F. APPENDIX

1. Original grant applications

2. References

F. APPENDIX*** Details of original grant application**

F82/473

6600p

FISHING INDUSTRY RESEARCH TRUST ACCOUNT1) Title of Proposal

Northern Pelagic Fish Stock Research

2) Name of Applicant

CSIRO Division of Fisheries Research

3) Division Department or Section4) Proposal

An eight cruise biological investigation of northern Australian pelagic fish stocks which currently support a foreign fishery of 7000 tonnes annually. The principal components of the stocks are sharks (2 main species) comprising approximately 80% of the catch, tunas (at least 3 species) comprising approximately 15% of the catch, and mackerels (at least 2 species) comprising approximately 5% of the catch. Tunas and mackerels can, however, contribute up to 55% of the catch in some seasons. At present the only information that is available on these stocks derives from the commercial fishery and is limited by the constraints on that operation. Thus it has only been possible, for example, to gather some data on species composition, size and sex distributions, breeding and preliminary ageing by sampling from the commercial areas through the AFZ Observer Program. It has been impossible to make any assessment of other parameters, such as size and geographical discrimination of the stocks and estimates of mortality, recruitment and direct growth rates of species.

The proposal is aimed at gathering these latter data largely through a tagging program which cannot be conducted by sampling the commercial fishery.

(See also Section 8 for further description of the proposal).

5) Name of Person Responsible for Program

Dr S W Jeffrey

The overall program comprises financial contributions from Queensland, Western Australia and the Northern Territory. CSIRO agree to provide the majority of scientific manpower with lesser individual cruise manpower contributions by the States and NT. It is also proposed to appoint a program coordinator to be located at CSIRO for the duration of the program.

6) Qualifications of Staff to be employed on the Program

Scientific staff of the CSIRO and relevant State Fisheries Authorities. A scientific coordinator/administrator is to be appointed to ensure the smooth operation of the program.

7) Objectives

The major objective of the study is to obtain parameters on the size, geographical discrimination, mortality, recruitment and hence yield potential of the northern pelagic stocks. These data are necessary to enable a more scientifically defensible estimate of yield to be made. Such an estimate cannot at present be made because information on the stocks is available only from the commercial fleet which is confined to limited areas of the "known" distribution of some stocks. It is not known whether particular species are comprised of one, or several discrete stocks in northern waters. Resolution of this issue will assist in delimiting the level of potential yield available from the fishery and hence assist in guiding the development of the fishery.

8) Justification, Including Practical Application

The Australian Fishing Zone Committee (AFZC) at its sixth meeting (Hobart 14-15 August, 1980) agreed that "Research is urgently needed to establish the condition of the stocks (of northern pelagic fish)", and the following recommendation was made to the Australian Fisheries Council (AFC);

- "investigation of the state of the stocks of the gillnet fishery off the Northern Territory be endorsed in principle and that proposals should be developed in this regard for consideration by appropriate authorities".

The AFC at its 10th meeting in September 1980 endorsed the above recommendations as follows;

- "proposals for investigation of the state of the stocks in the gillnet fishery off the Northern Territory be developed for consideration by appropriate authorities".

In January 1981 a seminar (The Northern Pelagic Fish Seminar - AGPS publication, 177 pp, 1981) comprising the collective expertise in tropical pelagic fisheries from within Australia and including participation from Papua New Guinea and FAO was convened in Darwin to ascertain the state of knowledge of these stocks. It was concluded that such knowledge was limited and it was agreed that the need for data to assist in developing management strategies

on a scientific basis was of paramount importance. Three recommendations outlining the specific requirements for research were made, viz:

"A study of the taxonomy, population structure, biology and migrations of northern sharks should be undertaken. An assessment of the mercury content of the various species would also be highly desirable."

"A program of study on the biology, population structure, stock identity and migration of Spanish mackerels, especially *Scomberomorus commerson*, extending from the Great Barrier Reef area through Torres Strait, the Gulf of Carpentaria, the Arafura and Timor Seas to the NW Shelf area should be undertaken. (The Papua New Guinea delegation indicated their interest in the possibility of a joint study proposal in the Torres Strait area.) The Queensland delegate indicated that the Queensland Government was considering an extension of its Spanish mackerel work and would consider such a study of particular interest. Mackerel sometimes carry a ciguatera-type toxin which makes them unmarketable and studies on this problem would also be highly desirable."

"A similar program of study should be undertaken on the tuna species contributing or potentially likely to contribute to a northern fishery. In particular, attention should be directed towards longtail tuna (*Thunnus tonggol*) and mackerel tuna (*Euthynnus affinis*). The identity of tuna populations and early life history studies would be important aspects of such a program."

In July 1982 a group of scientists from the Northern Territory, Queensland, CSIRO and DPI met to develop a course of action to facilitate the implementation of appropriate research.

The need for this research has thus been recognised for some time as being necessary for sound scientific management of the northern pelagic stocks. At present the stocks are exploited by a foreign fleet of 30 vessels permitted to take a quota of 7000 tonnes annually (5,250 tonnes over 9 months in 1982/83 pending the outcome of joint venture proposals). The current state of knowledge does not even allow a strongly defensible/arguable position to be taken on the effect of the existing exploitation which is, however, assumed to be at a conservative level of yield potential.

However, sharks comprise 80% of the annual catch (two species *Carcharhinus limbatus* and *C. sorrah* comprise approximately 55% and 15% respectively) while tuna and mackerel can seasonally (winter) comprise as much as 55% of the catch. Shark fisheries are considered to be very sensitive to fishing pressure in view of their generally slow growth rates, late sexual maturity, long gestation period and low fecundity. Being high order predators, their abundance may also be affected by changes in their prey species caused by environmental factors or fishing pressure. Mackerels and tuna occur seasonally in the fishery but their pattern of movements is unknown. Consequently it is not clear whether fish from Queensland, Torres Strait, the Gulf of Carpentaria and Arafura and Timor Seas constitute separate stocks or whether they are all part of a single northern stock.

Although some useful research can (and has) been undertaken by sampling of the commercial fish catch, this is of limited use because the commercial catch is confined to particular geographical areas of fleet operation and is affected by particular fishing practices.

The proposed research, which is based predominantly on tagging fish, cannot be undertaken from commercial vessels whose net set duration results in most fish being brought on board dead and because retention of the catch for commercial profit is the objective. Tagging will, however, depend on the commercial fleet for the majority of recaptures and thus relies on co-operation with the Taiwanese. Monitoring of recaptures, as well as length-frequency data for mortalities, will continue beyond the one year duration proposed for this study through the Observer Program.

The proposed research will provide information on the parameters below (for sharks, mackerel and tuna) using the following techniques:

- assessment of stock size - tagging and catch effort data from exploratory fishing (areas closed to commercial operation)
- migration and stock discrimination - tagging, electrophoresis and comparison of biological data from Taiwanese and exploratory fishing data
- mortality rates - length-frequency distributions and tagging (requires mesh selectivity experiments)
- recruitment - as for mortalities
- age and growth - ageing from hard parts, tagging and length composition analysis.

The basic question is whether the three species groups form single stocks across northern Australia. At present there is no evidence to suggest that there are several discrete geographical stocks and hence the effect of fishing these species in any one location must, as a conservative view, be considered to affect the size and yield of the stocks over their entire geographical range.

However, large areas such as the Gulf of Carpentaria and other AFZ foreign fleet exclusion zones have been closed to fishing for these species, other than by one Australian operator. In the case of the Gulf of Carpentaria the closure will have been in force for five years (28 August 1978) by the time the proposed research commences. It is possible that if discrete stocks do exist, and are contained wholly or partly in the GOC for example, they will exhibit distinctly different population characteristics; eg, size composition, fecundity and even individual growth rate; to the stock(s) outside the GOC.

The research findings should indicate such differences if they exist, which together with the

above outlined information will enable a less equivocal assessment of stock size and yield capacities.

9) Location of Operation

Headquartered at CSIRO Cronulla with field operations centred on Darwin.

10) Proposal in Detail, Including Procedures

(a) Plan of Operation

(i) Method of Procedure-

- 12 month nominal operating period during 1983/84 financial year
- 8 x 24 day cruises
 - .. 7 day lay-over between cruises, therefore an 8 month use of vessel required
- aim to tag approximately 50 fish per night (based on Taiwanese catch figures), 1,000 per cruise, 8,000 for charter (expected return rate say maximum 10%, ie 800 tags)
- biological work, mesh selectivity, etc undertaken concurrently
 - .. use longline, gillnets and handlines
- Cruise 1 Pilot Study

	Darwin to Darwin
Manpower	NT 1
	CSIRO 2
- Cruise 2 Arnhem Land Inshore

	Darwin to Gove
Manpower	NT 1
	CSIRO 2
- Cruise 3 Gulf of Carpentaria

	Gove to Weipa
Manpower	NT 1
	CSIRO 2

- | | | |
|---|---|---|
| - | Cruise 4 "Mackerel" - Queensland
Manpower | Weipa to Weipa
QLD 1
CSIRO 1
DPI 1 |
| - | Cruise 5 Wessels
Manpower | Weipa to Gove
NT 1
CSIRO 1
DPI 1 |
| - | Cruise 6 Arnhem Land Inshore
Manpower | Gove to Darwin
NT 1
CSIRO 2 |
| - | Cruise 7 J B Gulf (Closed area)
Manpower | Darwin to Darwin
WA 1
NT 1
CSIRO 1 |
| - | Cruise 8 J B Gulf (Commercial area)
Manpower | Darwin to Darwin
CSIRO 1
NT 1
WA 1 |
- Cruise 1 may be directed elsewhere if the pilot studies can be carried out during the previous NT program (January - June 1983). (See Section 15)
 - Sequence of cruises may depend on initial starting date and timing of specific cruise objectives.
 - Manpower commitment represents levels of participation indicated by each organisation.

(ii) Facilities Available

staff and the facilities of the participating organisations.

(b) Supporting Data

(i) Previous Work in this or Related Fields -

-each participant organisation has individual researcher expertise which is outlined in the Northern Pelagic Fish Seminar Proceedings 1981.

11) Proposed Commencement Date and Anticipated Completion Date

Commencement - July 1983

Completion - June 1984 (including preliminary analysis)

12) Funds Requested

<u>Summary</u>	<u>Year 1</u>
(a) Total Salaries and Wages	\$ 30,000
(b) Total Operating Expenses	\$145,925
(c) Total Capital Items	Nil

Detail

(a) <u>Salaries and Wages</u>	
Scientific Coordinator/administrator (salary, payroll tax, holiday loading etc)	<u>\$ 30,000</u>
<u>Total Salaries and Wages</u>	<u>\$ 30,000</u>
(b) <u>Operating Expenses</u>	
Charter of vessel and fuel	\$112,500
purchase/hire/installation of gear	
- longline and hauler	\$ 1,875
- gillnet	\$ 6,750
- troll lines	\$ 375
- net drum	\$ 1,125
- tags (purchase)	\$ 3,600
- tags (reward and fish - reimbursement)	\$ 10,400
- planning and evaluation meetings (one before and after program in Sydney)	\$ 6,000
- Scientific Coordinator travel expenses	<u>\$ 3,300</u>
<u>Total Operating Expenses</u>	<u>\$ 145,925</u>
(c) <u>Capital Items</u>	<u>Nil</u>
<u>Total Capital Items</u>	<u>Nil</u>
Gross Total Cost	<u>\$175,925</u>

(d) Estimated Income Nil

Note:

- a) Gear estimates could be reduced depending on the gear possessed by the chartered vessel.
- b) Tag purchase is based on a cost of \$36 per 100 tags.
- c) Tag rewards are based on an estimated return of 800 (10% of release number) at \$5.00 per tag = \$4000.
- d) Tagged fish reimbursement is based on an estimated return of 800 fish of 10kg average weight at \$0.84 per kg = \$6,400.
- e) While all staff travel costs to conduct research on the vessel will be met by the participating organisations, it will be necessary to have a pre- and post-program meeting (planning and evaluation) of all involved scientists. This should take place at CSIRO in Sydney and is estimated to cost \$6000.
- f) Scientific Coordinator travel expenses are based on three return trips between Sydney, Queensland and Darwin and associated accommodation costs.

13) Funds to be provided by the Applicant or Sought from other Sources

As a joint research program between several organisations the total costs have been significantly reduced by substantial "promisory" contributions from each organisation. These contributions are based on the total funding of agreed segments of the program of eight cruises.

The basis of calculation of this contribution has been as follows:

Charter of vessel and fuel

(\$1,500 x 200 days)	\$300,000
Total on-vessel gear purchase/installation	<u>\$ 27,000</u>
<u>Total cost (8 cruises)</u>	<u>\$327,000</u>
<u>Individual cruise cost</u>	<u>\$ 40,875</u>

The WA Government has agreed to provide the cost of an individual cruise (nominally cruise 8) which relates to WA waters.

The NT Fisheries Authority Research and Development Committee has agreed to the provision of financial support for 3 cruises (nominally cruises 2,5 and 6) and are seeking their Minister's approval of this contribution.

The Qld Department of Primary Industries Division of Dairying and Fisheries have agreed in principle to support the program and will be recommending to the Queensland Fish Management Authority that support be provided for one cruise (nominally cruise 4). A decision will be made in early 1983.

This represents a total "promisory" contribution of \$204,375. Additional costs of participating organisation personnel travel (to and from the vessel) will also be met by the organisations.

A feature of the agreed provision (or proposals to be put forward by participating organisations for provision) of funds is that their commitment will, or is likely to be, dependent on a reciprocal commitment by FIRTA and each of the other (State/CSIRO) participating organisations.

Summary

Total program costs	\$380,300
Contributions from other sources	\$204,375
Funds sought from FIRTA	\$175,925

14) Co-operating Agencies and their Functions

The proposed program is a joint undertaking between CSIRO, Queensland, Western Australia, the Northern Territory and the Commonwealth Department of Primary Industry. (Papua New Guinea may be invited to participate in the 'mackerel cruise'.)

15) Is Similar Work Being Undertaken in Australia

Some work on mackerel has been undertaken by both Queensland and the Northern Territory Fisheries authorities and the NT has also initiated a limited exploratory, developmental and extension study to promote an Australian fishery utilising existing vessels and gear. This program will cover inshore areas initially confined to the eastern sector of Joseph Bonaparte Gulf and will involve 50-60 days of sea work using a chartered vessel similar to that required for the proposed program. Much of the preliminary operational and logistic characters of the NT study will be similar to those of the proposed study and will thus assist in facilitating a more rapid familiarisation and entry into the proposed programme. The NT study will incorporate a marketing and economic analysis of an Australian operation in conjunction with results of a recently completed mercury study on shark flesh.

Other than this work there is no similar work being undertaken and the existing and commercially collectable data are insufficient to provide answers to assist in development of a fishery and management of this resource (see Northern Pelagic Fish Seminar).

16) Plans for Reporting or Publishing Results

Agreement has been reached in principle on the break-down of specific organisational responsibility within the program and the allocation of publishing responsibility and benefit. It is proposed that results will be published in scientific and industry journals and a joint report will be prepared for FIRTA.

* **Details of original grant applications (cont.)**

FISHING INDUSTRY RESEARCH TRUST ACCOUNT

APPLICATION TO EXTEND AN EXISTING GRANT

Title

NORTHERN PELAGIC FISH STOCK RESEARCH

Background

- The present program is funded by FIRTA (\$175,925) together with contributions from the participating organisations. Total funds are \$380,300.
- Field work commenced in January 1984 and is presently scheduled to end on 5th October 1984. However, tag return information from commercial Taiwanese and Australian vessels is required for the next 2 to 3 years.
- Tagging and other research work has been limited in offshore areas due to bad weather and poor catch rates. Further work is required in offshore areas particularly in relation to the main commercial Taiwanese fishery.
- There has been more migration of sharks than expected. It is therefore proposed to extend the study area to include the geographic range of the resource so that the MSY estimate will be valid. Further funding is requested for a four cruise extension to the current program.
- A preliminary analysis of all data from the present program is scheduled for completion by 31 December 1984.

Objectives

- To obtain information on the biology and population dynamics of the pelagic resources of shark, mackerel and tuna in the northern AFZ.
- To use these data to calculate a Maximum Sustainable Yield (MSY) for these resources.
- To further examine the potential of the fishery for increased Australian participation.

Situation at 14th July 1984

The sixth cruise is now underway and the eighth cruise is due to finish on the 5th October.

Shark

Most objectives have been achieved, except for work on the offshore commercial grounds. This problem has been caused by bad weather and low catch rates.

More than 1000 sharks have been tagged each cruise; gear selection experiments, catch-effort data from exploratory fishing in inshore closed areas, and collection of electrophoretic and biological samples will be completed by the end of the eighth cruise.

Mackerel

Tagging, and collection of biological and electrophoretic samples will have been conducted in the area between Joseph Bonaparte Gulf and the eastern Gulf of Carpentaria by the end of the eighth cruise.

Tuna

Very few tuna have been caught in the areas covered so far. It appears that the majority of tuna occur in the offshore regions.

Justification for Proposed Extension

The majority of research effort has been directed at the shark stocks because of their importance in the fishery, size, and susceptibility to overfishing.

Shark

- It is very important that additional coverage of the offshore commercial grounds is undertaken for the following reasons.
 - a) Mortality studies require that sufficient tags are released within the main commercial grounds, from which the majority of recaptures are expected, as well as at varying distances from it.
 - b) Exploratory fishing in areas closed to the Taiwanese has demonstrated a substantial shark resource. Interpretation of these catches requires calibration of catch/effort data from the commercial Taiwanese grounds using the same vessel and

gear.

- Results from tagging show that movements are much greater than first thought (see attached figure) and indicate emigration from the study area. The accuracy of a final MSY estimate will be limited, and open to disagreement, if the study area is not expanded to include the geographic range of the resource. Of particular importance are the effects of the Torres Strait as a possible barrier to migrations, and the degree of mixing with populations off southern Papua New Guinea and on the North West Shelf region of Australia. The geographic range from which electrophoretic samples are collected needs to be expanded in association with this.
- Comparison of reproductive parameters from different regions indicate either:
 - a) the presence of two stocks of *C. limbatus* (the main shark species);
 - b) evidence of fishery induced changes on this species, whereby high fishing pressure has resulted in alterations to the time taken to reach sexual maturity and maximum size obtained.

Collection of biological data has shown that a proportion of the *C. limbatus* population mature at a much larger size, and reach a greater maximum size, than the majority of the population. More information on the relative numbers and distribution of these larger fish from a wider area is required to determine whether they constitute a separate stock, or whether they reflect the species' ability to vary reproductive rate in response to high fishing pressure.

- Ageing studies on *C. limbatus* and *C. sorrah* utilize two methods, interpretation of rings on the vertebrae and analysis of length-frequency distributions. Initial discrepancies in length-age data between these two methods have recently been resolved on the assumption that two rings are laid down each year. Reliable age information is required as input data for calculation of various population parameters. To confirm the hypothesis that two vertebral rings are laid down each year it is necessary to tag and inject new-born fish with a marker dye. Since the size at birth is known, the vertebrae of recaptured fish will reveal the number of rings laid down in the intervening period. This work has to be carried out around the January birth season.
- Growth rates obtained from tagging are much lower than expected from indirect ageing studies. This may reflect trauma due to capture, or the tag interfering with growth. Trauma due to capture is already being investigated, but separate tagging experiments, using a different tag, are required to study possible tag interference.
- Mortality estimates are affected by the degree of tag shedding. The fin tag used in this study was chosen partly because of its good retention qualities. However, rapid fin

thickening in *C. limbatus* and *C. sorrah* may be resulting in a higher shedding rate than anticipated. Double tagging experiments, using dart tags, are needed to check on tag shedding rates.

Mackerel

Results of electrophoretic analysis indicate different stocks on the east and west coasts of Australia, as well as in Papua New Guinea. The situation in the Timor and Arafura Sea, and Gulf of Carpentaria is still unclear. The proposed extension would allow collection of samples from northeast Queensland (between Cairns and Cape York), the Torres Strait and southern Papua New Guinea. Together with tagging in these areas, this would provide information on the number and relationships of the stocks over the entire region of northern Australia and southern Papua New Guinea. More work is required on the distribution, biology and population dynamics of mackerel throughout the area covered by the proposed extension.

Tuna

Present results indicate that tuna were only present in quantities offshore. Further work is needed to allow more intensive tagging and collection of biological data from this resource throughout the area covered by the proposed extension.

Proposed extension:

Because shark movements are much greater than expected the accuracy of an MSY estimate will be limited, and open to disagreement, if the study area is not expanded to include the geographic range of this resource. For this reason a four cruise extension to the current field work completion date of 5th October 1984 is requested; these cruises to be run in November 1984, January, February and March 1985; continuation of the Project Manager position until March 1985; six months nominal operating period during 1984/85; 4 x 24 day cruises.

Cruises 1-8	Present program	
Cruise 9	Broome to Darwin	Study area - North West Shelf
Cruise 10	Darwin to Gove	Study area - offshore Wessel Is.
Cruise 11	Gove to Thursday Is.	Study area - offshore Wessel Is.
Cruise 12	Thursday Is. to Cooktown	Study area - NE Queensland

The work needs to be carried out under the existing charter agreement while the present vessel, crew and gear are still available, allowing continuity of the program. A

substantial delay would result in the loss of the existing (and very satisfactory) vessel, necessitating the lengthy business of re-tendering. Few suitable vessels are available for this work.

Involvement of Western Australia, Northern Territory and Queensland

- Extension of this program has received the approval of the above State Fisheries Departments.
- In view of the timing of the survey relative to approved State and Commonwealth budgets for 1984/85, staff travel costs and allowances for Queensland and CSIRO will need to be met in part by FIRTA.
- Western Australian Department of Fisheries and Wildlife have agreed to provide two (2) research personnel together with travel funds and associated allowances.
- Northern Territory Fisheries Division have indicated an additional allocation of up to \$50,000 may be made available by the Northern Territory Fishing Industry Research and Development Trust Fund Advisory Committee. This will be supplemented by the provision of two (2) research personnel for field studies.

Funds Requested:Vessel:

	\$
- Charter (96 days @ \$1320 per day)	126,720
- Fuel (10 000 lt. @ 35c/lt. x 4 cruises)	14,000
- Outboard fuel	200
- Repositioning Fee (6 days @ \$1320/day)	7,920
- Food	2,900

Equipment:

- Tag purchase (5000 thereof)	1,300
- Tag return (10% @ \$10 each)	5,000
- Tetracycline	200
- Net repairs	800
- General equipment (inc. stationery, photography etc.)	2,000

Freight (Scientific equipment plus samples) (CSIRO) 2,000

Project Manager

- Wages (5 months)	12,000
- Travel (3 return visits - Darwin)	2,200

Manning Costs

(See addendum for breakdown of costs for participating organisations)

- Air fares	6,190
- Air freight	200
- Travel allowances	5,152
- Overtime and marine survey allowance	10,000

TOTAL \$198,782

LESS PROPOSED CONTRIBUTION BY NT-FIRTA \$42,000

TOTAL FUNDS REQUESTED **\$156,782**

ADDENDUM

BREAKDOWN OF MANNING COSTS BY PARTICIPATING ORGANISATIONS

Cruise	Personnel			
	W.A.	N.T.	Qld.	CSIRO
9	1 or 2			1 or 2
10		2		1
11			1 or 2	1 or 2
12			1 or 2	1 or 2

1 **CSIRO (costing based on a maximum of 7 person-cruises)**

	\$
- Air fares	5,000
- Travel allowances	4,000
- Overtime and marine survey allowance	<u>10,000</u>
TOTAL	<u>\$19,000</u>

2 **Queensland Department of Primary Industry**

	\$
- Air fares	1,190
- Air freight	200
- Travel allowances	<u>1,152</u>
TOTAL	<u>\$2,542</u>

APPENDIX 2

Publications (and manuscripts in preparation) resulting from the Northern Pelagic Fish Stock Research Program, and from associated work carried out by the Northern Territory Fisheries Division and the Fisheries Research Centre of the Queensland DPI on the northern stocks of shark, Spanish mackerel and longtail tuna are shown below.

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- Lavery, S., and Shacklee, J. B. (1989). Population genetics of two tropical sharks, *Carcharhinus tilstoni* and *C. sorrah*, in northern Australia. *Aust. J. Mar. Freshw. Res.* **40**, 541-57.
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- Lyle, J.M., and Timms, G.J. (1984). Survey shows potential for NT shark. *Aust. Fish.* **43** (9), 2-5.
- Lyle, J. M., and Timms, G. J. (1984). North Australia's multi-species shark fishery. Volume 4. Exploratory fishing survey of shark and other pelagic fish resources found in Northern Territory inshore waters. Department of Primary Production, Northern Territory, Fishery Report No.12, 75pp.
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- Lyle, J. M., and Read, A. D. (1985). Tuna in northern Australian waters: a preliminary appraisal. Department of Ports and Fisheries. Fisheries Report No. 14. 41pp.
- Lyle, J. M. (1987). Observations on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzroyensis* (Whitley) from northern Australia. *Aust. J. Mar. Freshw. Res.* **38**, 701-10.
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- Lyle, J. M., and Griffin, P. J. (1987). Evaluation of the suitability of longlining for shark in northern Australian waters. Department of Industries and Development Fishery Report No. 15, 34 pp.
- McLoughlin, K. J., and Stevens, J. D. Gill-net mesh selectivities for two species of commercial carcharhinid shark taken in northern Australia. In preparation.
- McPherson, G.R. Age and growth of *Scomberomorus commerson* (Lacepede, 1800) in north-east Queensland waters. In preparation.
- McPherson, G.R. Reproductive biology of narrow barred Spanish mackerel (*Scomberomorus commerson*) in Queensland waters. In preparation.
- Rohan, G., Church, A., and Clark, A. (1981). Northern Territory mackerel fishing program 1980/81. Department of Primary Production Fisheries Division Report No. 4, 55 pp.
- Stevens, J. D., and Davenport, S. Analysis of catch data from the Taiwanese gill-net fishery off northern Australia: 1979-1986. CSIRO Marine Laboratories Divisional Report. In preparation.
- Stevens, J. D., Davis, T. L. O., and Church, A. G. (1982). Results of shark gill-netting by the R.V. *Hai Kung* in the Arafura Sea. *Aust. Fish.* **41** (4), 39- 43.
- Stevens, J. D., and Church, A. G. (1984). Northern tagging project yields interesting results. *Aust. Fish.* **43** (9), 6-10.
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