Distribution, Size and Sex Composition, Reproductive Biology and Diet of Sharks from Northern Australia

J. D. Stevens and K. J. McLoughlin[A]

Division of Fisheries, CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tas. 7001, Australia.
[A] Present address: Bureau of Rural Resources, DPIE, GPO Box 858, Canberra, ACT 2601, Australia.

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, whereas 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 6-month gestation. The average size at birth varied from 27 to 75 cm and the average litter size varied from 2 to 34. The size at birth was about 40% of the size at maturity, which in turn was 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, and 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 *Eusphyra blochii* (Cuvier), *Sphyrna mokarran* (Rüppell) 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 summarized for comparison.

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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.

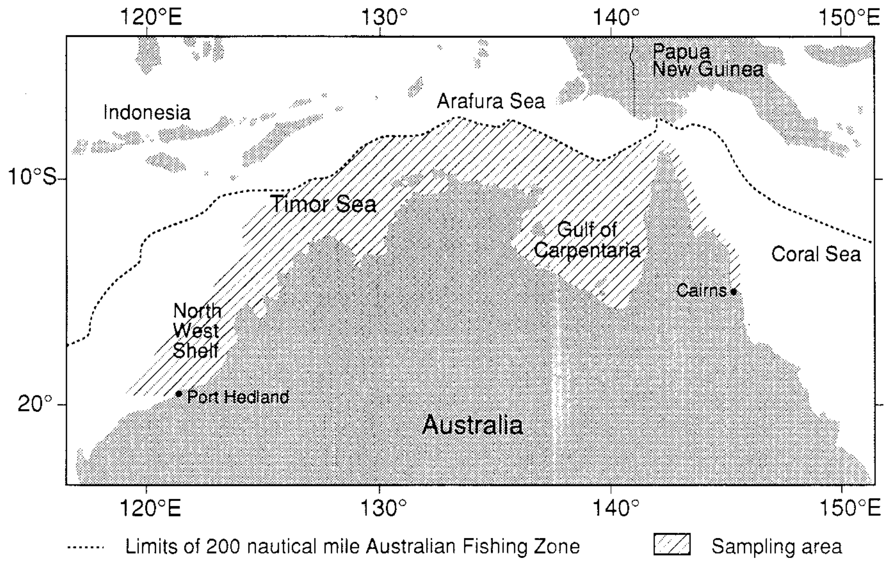

Fig. 1. Sampling area off northern Australia.

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	51–100	101–150	151–200	>200
North West Shelf	Hook and line	43	32	11	3	11
	Gill-net	11	0	0	0	0
	Trawl	634	596	223	45	189
Timor Sea	Hook and line	48	13	0	0	0
	Gill-net	144	116	2	0	0
	Trawl	30	74	29	4	7
Arafura Sea	Hook and line	119	59	0	0	0
	Gill-net	377	116	0	0	0
	Trawl	51	65	8	3	0
Gulf of Carpentaria	Hook and line	62	1	0	0	0
	Gill-net	156	0	0	0	0
	Trawl	62	31	0	0	0
NE Queensland	Hook and line	30	1	0	0	0
	Gill-net	44	3	0	0	0
	Trawl	0	0	0	0	0
All Areas	Hook and line	302	106	11	3	11
	Gill-net	732	235	2	0	0
	Trawl	777	766	260	52	196

Sharks were captured will 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 400–5000 m of mainline with 60–300 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).

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
Mustelus sp.	29	$FL = 0{\cdot}89TL + 0{\cdot}05$	0·967
	29	$TW = 1{\cdot}49 \times 10^{-3} TL^{3{\cdot}22}$	0·989
Hemigaleus microstoma	331	$FL = 0{\cdot}88TL - 1{\cdot}17$	0·999
	425	$TW = 3{\cdot}48 \times 10^{-3} TL^{3{\cdot}00}$	0·982
Hemipristis elongatus	58	$FL = 0{\cdot}79TL + 1{\cdot}43$	0·981
	30	$TW = 1{\cdot}62 \times 10^{-3} TL^{3{\cdot}21}$	0·970
Carcharhinus amblyrhynchoides	94	$FL = 0{\cdot}81TL - 1{\cdot}52$	0·997
	67	$TW = 2{\cdot}65 \times 10^{-3} TL^{3{\cdot}21}$	0·975
C. amblyrhynchos	28	$FL = 0{\cdot}88TL - 4{\cdot}46$	0·999
	24	$TW = 7{\cdot}46 \times 10^{-3} TL^{2{\cdot}98}$	0·971
C. amboinensis	198	$FL = 0{\cdot}79TL - 0{\cdot}68$	0·997
	104	$TW = 1{\cdot}94 \times 10^{-3} TL^{3{\cdot}27}$	0·986
C. brevipinna	40	$FL = 0{\cdot}85TL - 3{\cdot}21$	0·998
	35	$TW = 1{\cdot}13 \times 10^{-3} TL^{3{\cdot}33}$	0·988
C. dussumieri	175	$FL = 0{\cdot}830TL - 0{\cdot}24$	0·991
	453	$TW = 3{\cdot}03 \times 10^{-3} TL^{3{\cdot}12}$	0·935
C. falciformis	22	$FL = 0{\cdot}84TL - 4{\cdot}02$	0·996
	23	$TW = 4{\cdot}66 \times 10^{-3} TL^{3{\cdot}05}$	0·990
C. macloti	211	$FL = 0{\cdot}82TL - 1{\cdot}05$	0·997
	127	$TW = 3{\cdot}91 \times 10^{-4} TL^{3{\cdot}55}$	0·830
C. plumbeus	117	$FL = 0{\cdot}82TL - 1{\cdot}13$	0·995
	150	$TW = 1{\cdot}42 \times 10^{-3} TL^{3{\cdot}31}$	0·984
Galeocerdo cuvier	53	$FL = 0{\cdot}88TL - 15{\cdot}71$	0·996
	86	$TW = 2{\cdot}62 \times 10^{-4} TL^{3{\cdot}57}$	0·993
Loxodon macrorhinus	174	$FL = 0{\cdot}83TL - 1{\cdot}51$	0·993
	283	$TW = 4{\cdot}79 \times 10^{-4} TL^{3{\cdot}44}$	0·955
Rhizoprionodon acutus	483	$FL = 0{\cdot}820TL - 0{\cdot}70$	0·998
	413	$TW = 3{\cdot}74 \times 10^{-3} TL^{3{\cdot}01}$	0·945
R. taylori	223	$FL = 0{\cdot}85TL - 1{\cdot}18$	0·954
	148	$TW = 2{\cdot}17 \times 10^{-4} TL^{3{\cdot}75}$	0·836

Length and Weight Measurements

Sharks were measured to the nearest centimetre in terms of either total length (TL) or fork length (FL). For TL, the tail was allowed to take a natural position and the top caudal lobe was then placed parallel to the body axis. Where required, fork lengths were converted to total lengths 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 (<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 with 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 with 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. Gonadosomatic index (GSI) was calculated (for mature fish only) as the gonad weight/total body weight × 100. The number, lengths and sex of the 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.

Text Format

A separate account for each species comprises 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, standardized format in which nsd indicates 'not significantly different from', and *n* is the sample size.

Results and Discussion of Species

(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 of 122–303 m (see section on distribution). Subsequently, B. Seret (Museum National d'Histoire Naturelle, Paris, 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 I.S.R. Munro Fish Collection, CSIRO Marine Laboratories, Hobart.

Distribution

Present study: Captured by trawl on the North West Shelf and slope off Western

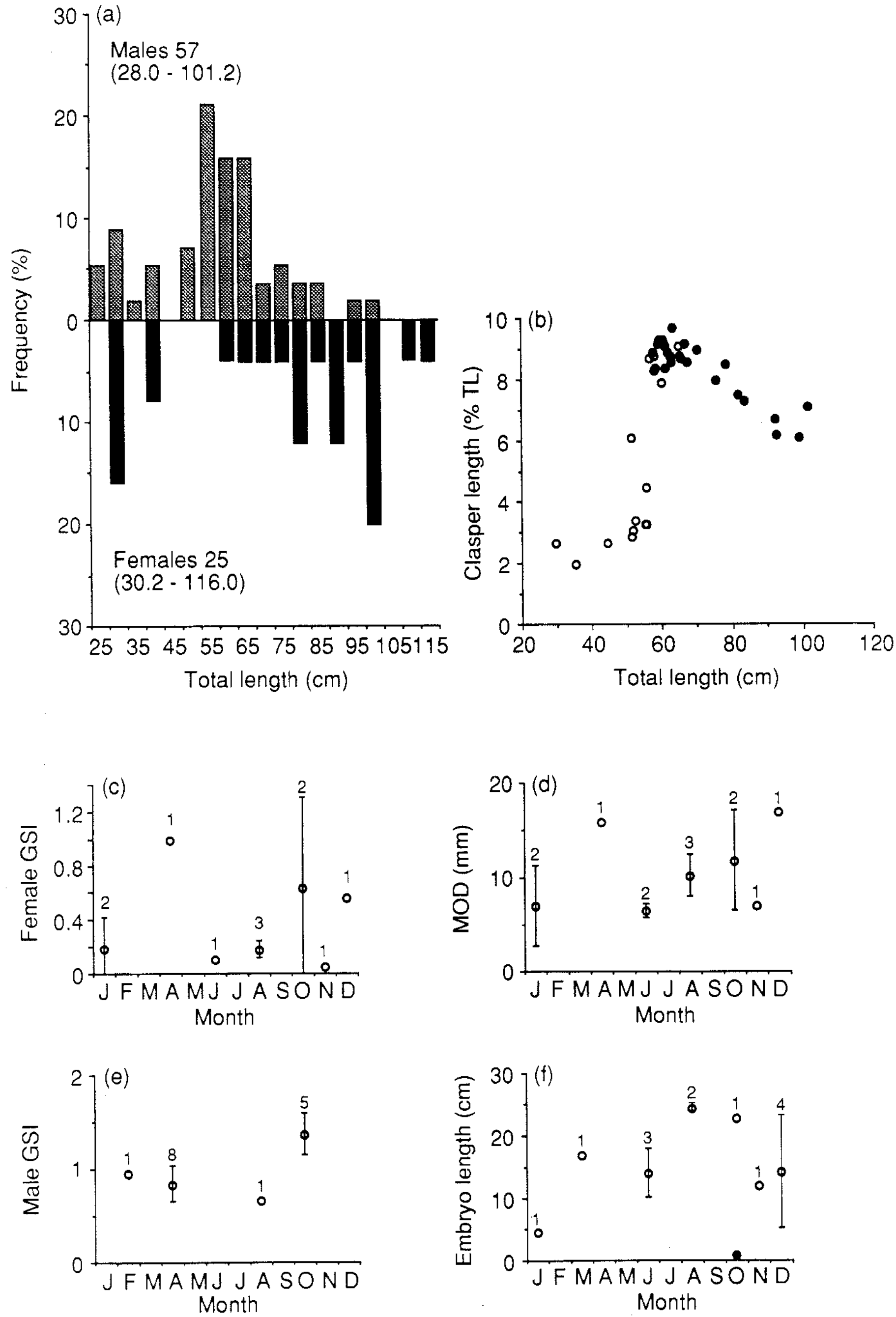

Fig 2. *Mustelus* sp. (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not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

Australia, off north-eastern Queensland and (1 record) in the Arafura Sea. Taken in depths of 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 through confusion with the similar *M. antarcticus*.

Size

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

Sex ratio

Embryos nsd 1:1, *post partum* 30·5% female, χ^2 test $P < 0 \cdot 001$ (present study, Table 3).

Table 3. Sex ratio of sharks from northern Australia
***P < 0·001; **P < 0·01; *P < 0·05; ns, not significant

Species	Embryos			*Post partum*		
	n	% Female	Significance	*n*	% Female	Significance
Mustelus sp.	92	54·3	ns	82	30·5	***
Hemigaleus microstoma	451	48·8	ns	464	38·8	***
Hemipristis elongatus	23	56·5	ns	478	46·4	ns
Carcharhinus amblyrhynchoides	22	36·4	ns	277	13·0	***
C. amblyrhynchos	20	35·0	ns	66	59·1	ns
C. amboinensis	6	33·3	ns	379	46·2	ns
C. brevipinna	–	–	–	2110	45·4	**
C. dussumieri	211	47·4	ns	569	46·2	ns
C. falciformis	–	–	–	34	32·4	*
C. macloti	125	44·0	ns	3142	58·0	***
C. plumbeus	109	45·0	ns	430	56·5	**
Galeocerdo cuvier	–	–	–	299	56·5	*
Loxodon macrorhinus	106	48·1	ns	279	37·3	***
Rhizoprionodon acutus	393	55·7	*	1622	32·2	***
R. taylori	198	55·1	ns	385	53·0	ns

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. 2*b*). 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. 2*c–f*) show no discernible 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 ($r^2 = 0 \cdot 33$, $P < 0 \cdot 05$), 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.

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

Species	Occurrence in stomachs with food (%)								No. stomachs examined	No. stomachs with food
	Crust.	Ceph.	Mollsc	Fish	Rept.	Bird	Mamm.	Other		
Mustelus sp.	94·2	17·4	1·5	27·5	—	—	—	2·9	70	69
H. microstoma	3·0	98·5	0·3	1·2	—	—	—	0·9	446	331
H. elongatus	—	67·5	—	50·6	—	—	—	—	111	83
C. amblyrhynchoides	6·3	3·9	—	91·3	—	—	—	—	186	127
C. amboinensis	22·2	11·1	—	83·3	—	—	—	—	31	18
C. brevipinna	2·0	7·8	—	86·3	—	—	—	3·9	111	51
C. dussumieri	26·2	20·7	—	76·2	—	—	—	—	526	324
C. macloti	1·1	4·4	—	94·5	—	—	—	—	216	91
C. plumbeus	7·8	21·7	0·9	87·8	—	—	—	1·7	181	115
G. cuvier	15·6	15·6	2·6	62·3	58·4	2·6	2·6	7·8	98	77
L. macrorhinus	60·4	18·8	1·0	76·3	—	—	—	1·9	258	207
R. acutus	10·4	18·9	1·2	93·3	—	—	—	2·4	315	164
R. taylori	34·2	2·6	—	79·0	—	—	—	—	68	38

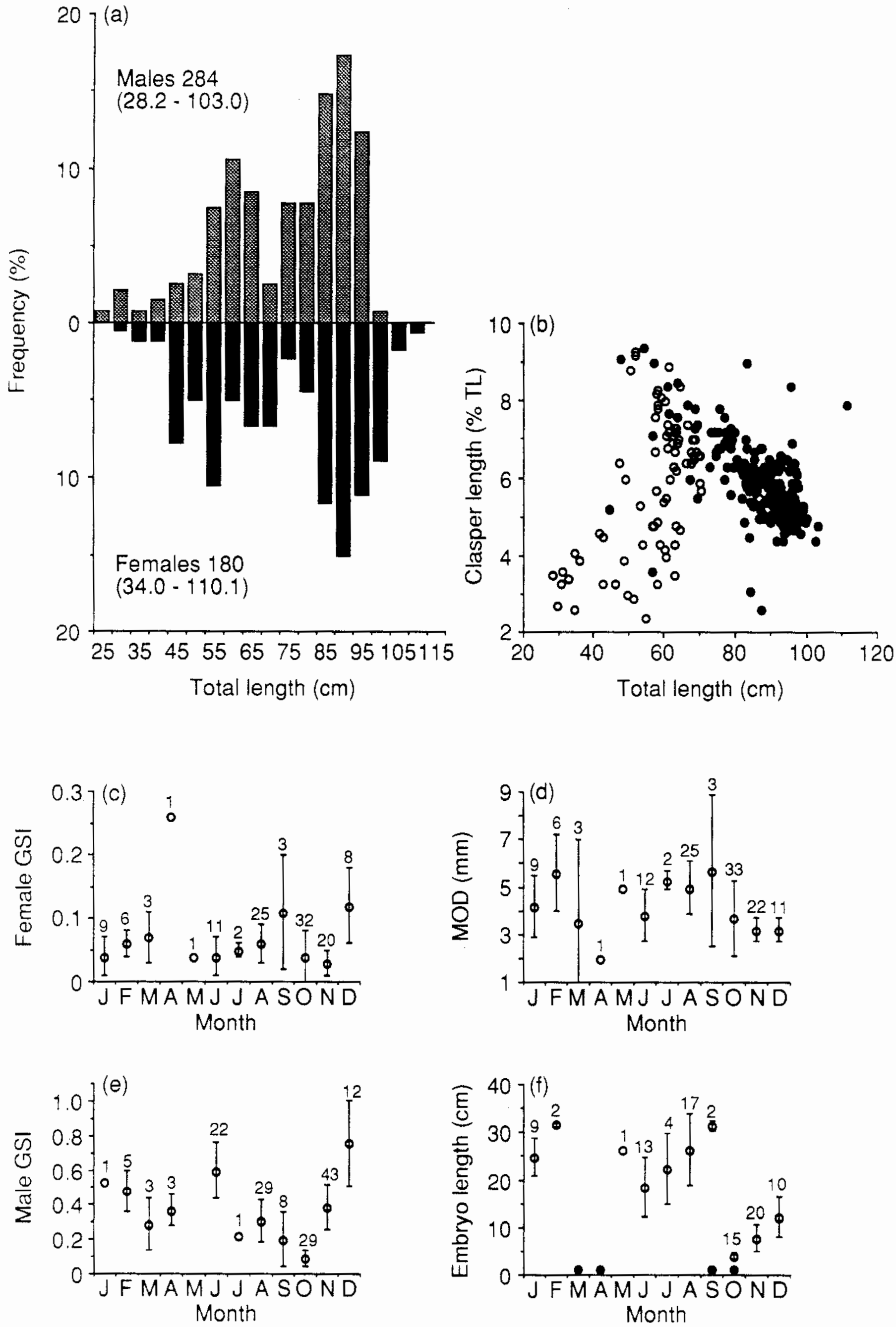

Fig. 3. *Hemigaleus microstoma.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers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

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, and all of the identifiable fish were strictly demersal species (Appendix 1).

(2) *Hemigaleus microstoma* Bleeker; 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) (QM I14517, I13590; WAM 6852.001, 6853.001). Taken in depths of 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. 3*a*).

Sex ratio

Embryos nsd 1:1; *post partum* 38·8% females, χ^2 test $P < 0 \cdot 001$ (present study, Table 3).

Reproduction

Additional data support the observations of Stevens and Cuthbert (1983) that males mature at about 60 cm (Fig. 3*b*) 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. 3*c*, *e*). However, seasonal differences in pup length suggest that two litters may be produced each year (Fig. 3*f*). 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. 3*f*). Embryos from the March–April batch of ova increased from 19 cm in June to 31 cm in September, while those from the September–October batch increased 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 6 months. There is some indication from Figs 3*c* and 3*d* that female GSI and MOD peak between February and April and again in September, which suggests that 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. 3*e*), some 2–3 months before the proposed ovulation periods. However, the increased ovary weight in December (Fig. 3*c*) 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 to 19 with a mean of 8, and there was a significant relationship between increasing litter size and maternal length ($r^2 = 0 \cdot 35$, $P < 0 \cdot 001$).

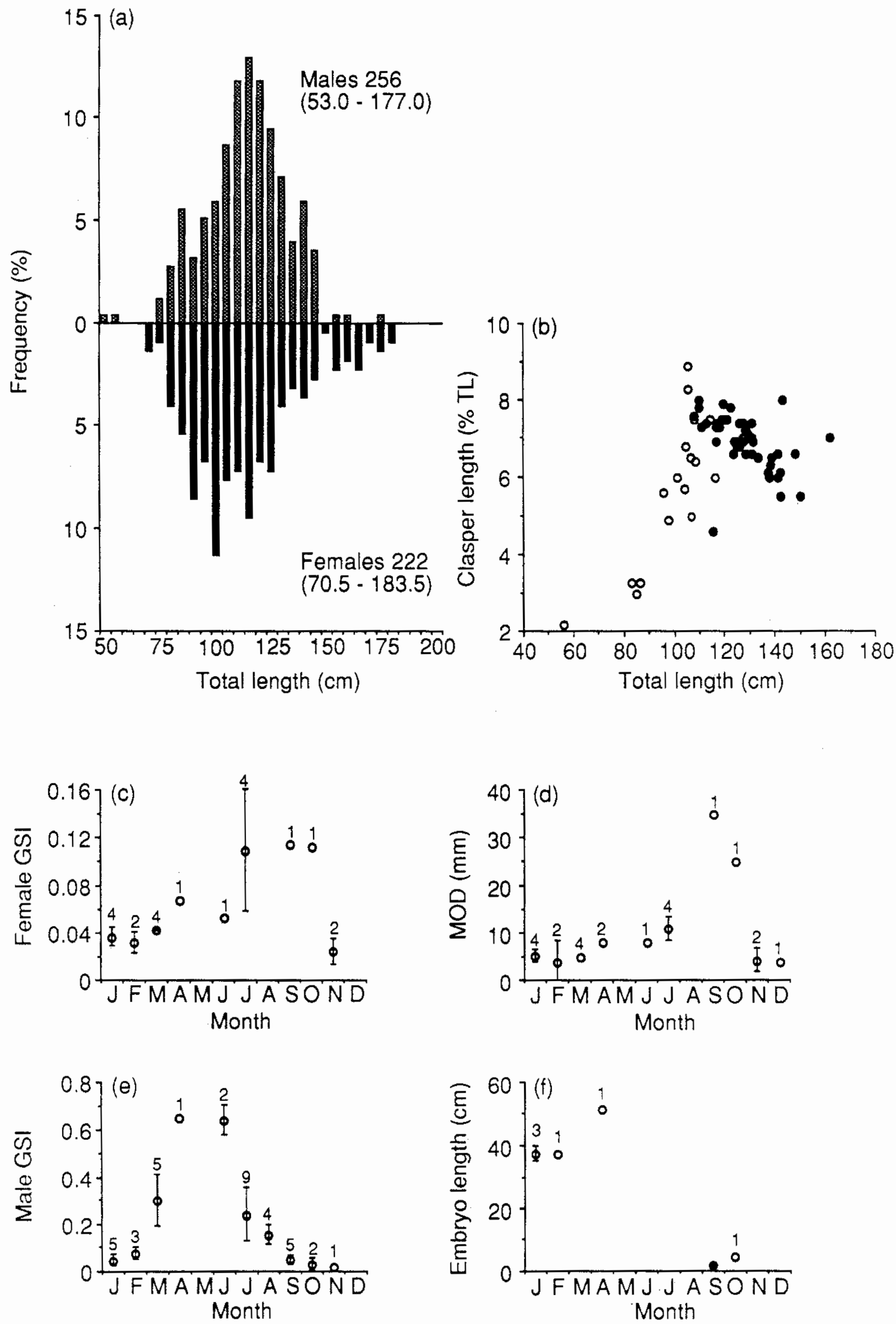

Fig. 4. *Hemipristis elongatus*. (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not calcified; ●, claspers calcified. (*c*) Female gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*d*) Maximum ova diameter (MOD) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*e*) Male gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*f*) Embryo length by month (solid 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); 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 of 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. 4*a*).

Sex ratio

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

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

Reproduction

All that is known of reproduction in this species is summarized 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 (1949*c*) described the reproductive system of one pregnant female containing six embryos.

In Australian waters, males mature at about 110 cm (Fig. 4*b*); 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. 4*e*), with female GSI and MOD reaching a maximum around September when the ova are about 3·5 cm in diameter (Fig. 4*c*, *d*). The only female with ova *in utero* was caught in September. The limited data in Fig. 4*f* show an increase in pup length from about 5 cm in October to 52 cm TL in April. These data suggest that 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 (during the period when pregnant fish occurred) among mature fish is 30%, which suggests that individual females breed, at the most, every other year, but the sample of 27 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 ($r^2 = 0{\cdot}87$, $P < 0{\cdot}01$).

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 1949*b*).

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 (of those identifiable all were demersal species), including a number of elasmobranchs (Table 4 and Appendix 1). No other prey categories were recorded.

(4) *Carcharhinus altimus* (Springer); bignose shark

Distribution

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

Present study: Northern Australian waters 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 I23718-002). 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 and the 204-cm one was mature. The smallest of two pregnant and one spent fish was 240 cm TL.

C. altimus pups are born in September–October off Madagascar (Fourmanoir 1961). Bass *et al.* (1973) noted 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 to 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 stomachs 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.

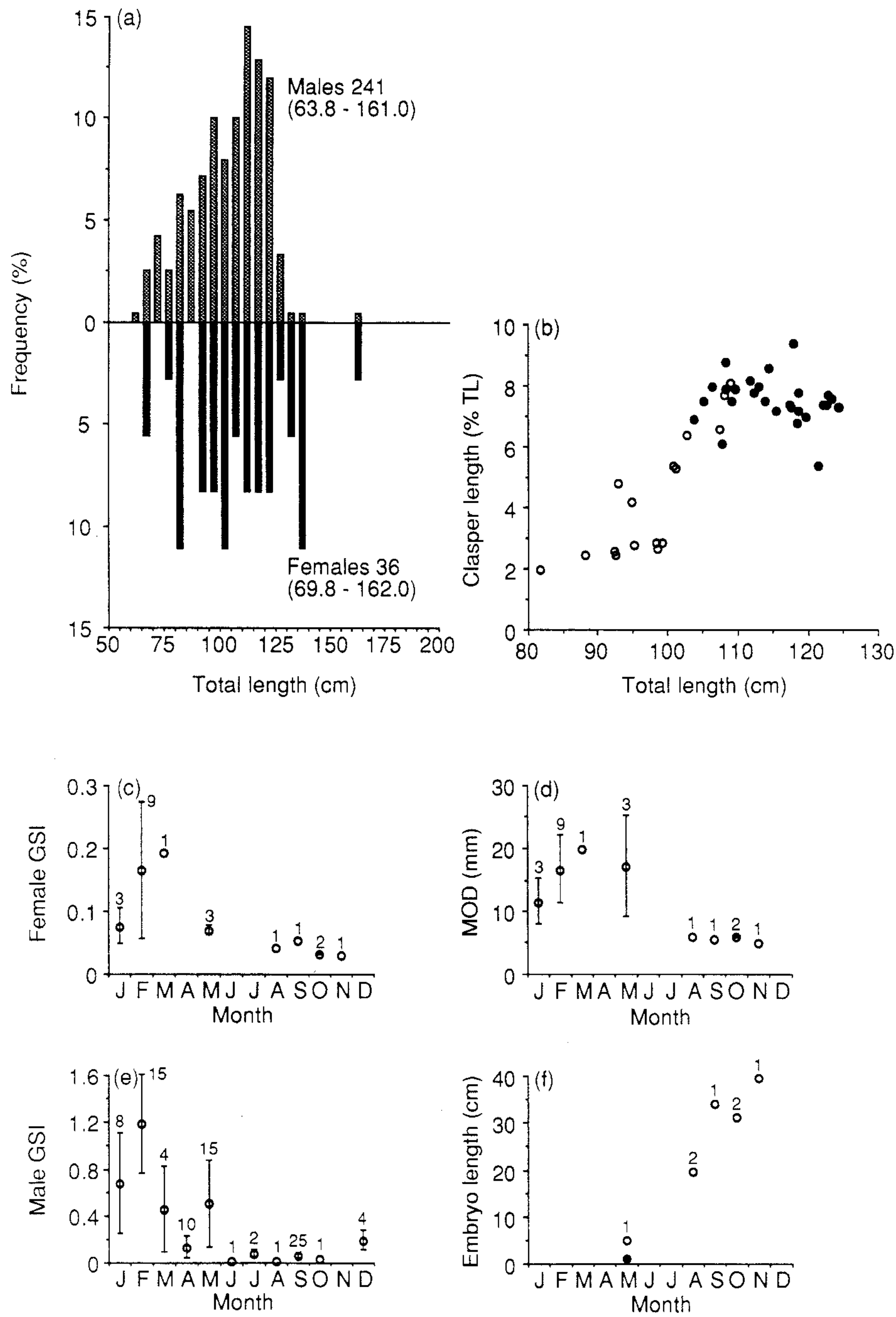

Fig. 5. *Carcharhinus amblyrhynchoides.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length;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

(5) *Carcharhinus amblyrhynchoides* (Whitley); 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. 5*a*).

Sex ratio

Embryos nsd 1:1; *post partum* 13% female, χ^2 test $P < 0 \cdot 001$ (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. 5*b*); 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, and 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. 5*e*). Data on females are more limited but GSI and MOD are highest around March (Fig. 5*c*, *d*). This suggests that 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. 5*f*). Spent fish were recorded mainly in February (with one in March) which suggests parturition in January–February and a gestation period of 9–10 months. Since embryos are 40 cm long after 7 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 of 1–9 (nine litters sampled); there were insufficient data to determine whether litter size increased with maternal length. Of the 20 mature females examined, 80% were pregnant, indicating that individual females breed each year. Although there is considerable variation in male GSI during the breeding season (Fig. 5*e*) the high mean value in February of $1 \cdot 2$ with a standard deviation of $0 \cdot 43$ suggests 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) were the major prey item, occurring in 91% of stomachs containing food, with crustaceans present in 6% and cephalopods in 4% (Table 4).

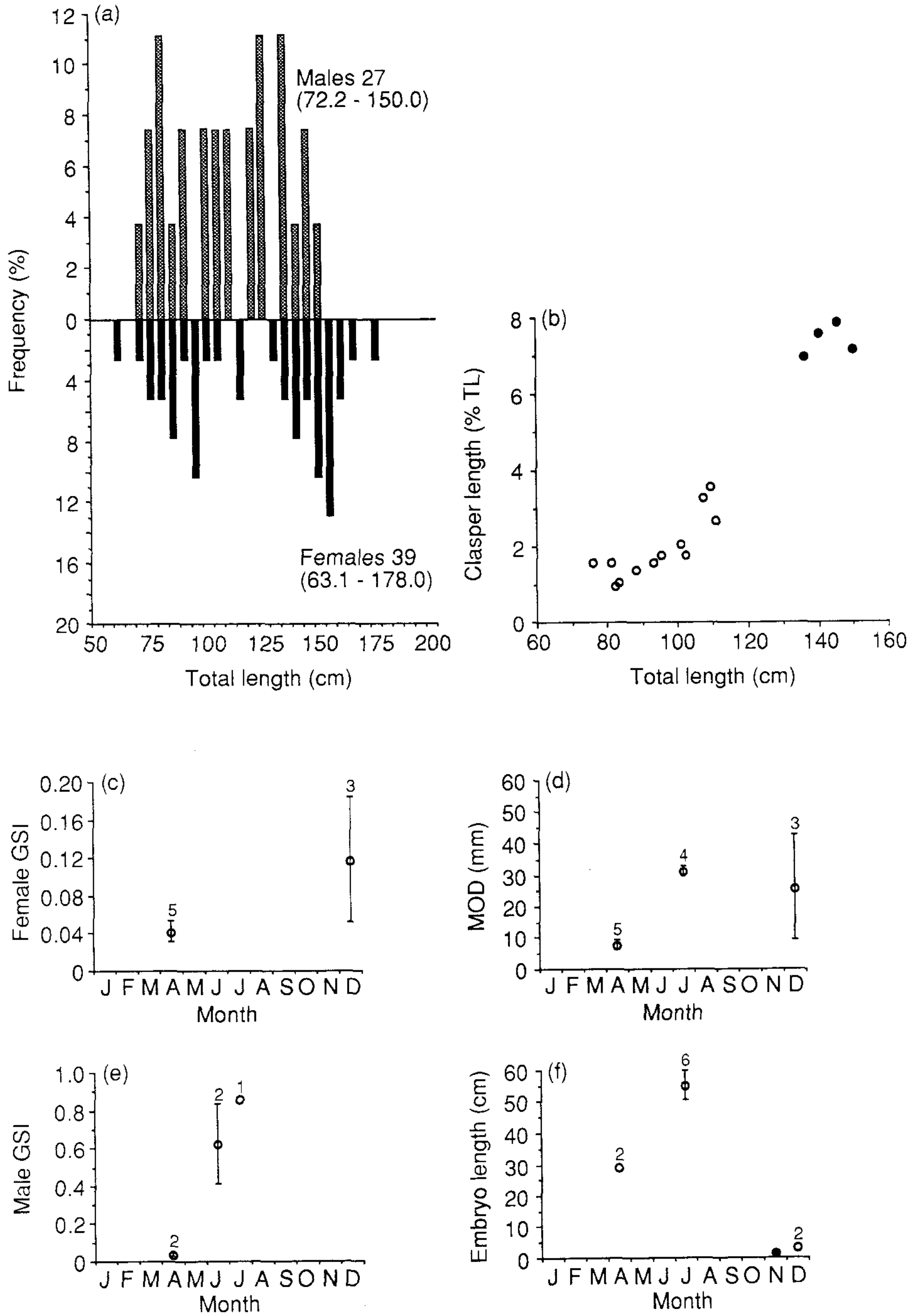

Fig. 6. *Carcharhinus amblyrhynchos.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length;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

(6) *Carcharhinus amblyrhynchos* (Bleeker); 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-eastern 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 14 m to near the surface 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. 6*a*).

Sex ratio

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

Reproduction

Males 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. 6*b*). 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), whereas 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.

The few data from northern Australia on monthly variation in GSI, MOD and embryo length, suggest that the reproductive cycle is seasonal (Fig. 6*c*–*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 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. 6*f*), the gestation would be about 9 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 3, 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) noted 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* (Müller & Henle); pigeye shark

Distribution

Literature: Tropical in the eastern North Atlantic (Nigeria) and Indo-West Pacific

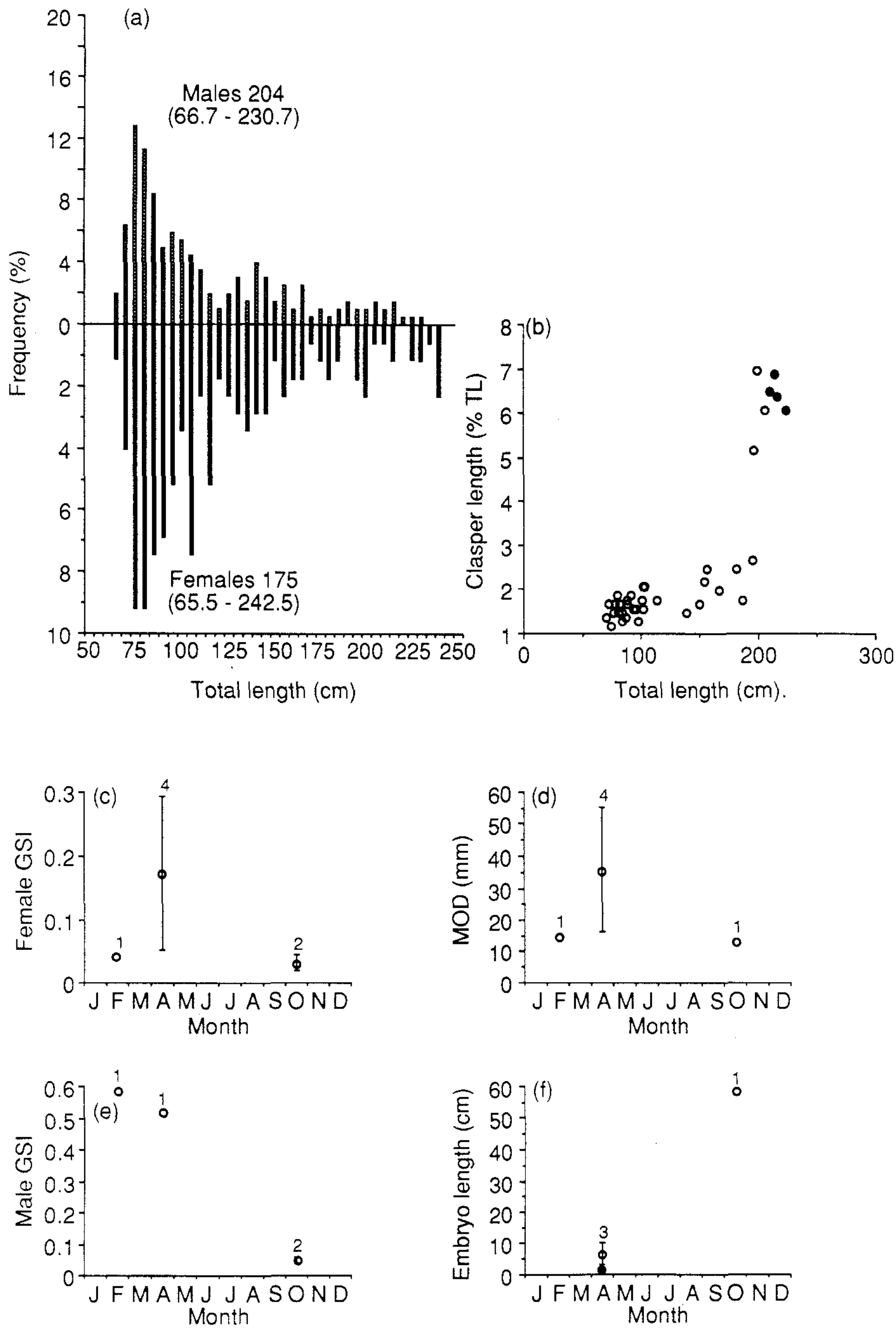

Fig. 7. *Carcharhinus amboinensis.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○,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

(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. 7*a*).

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. Maturity in males is attained at about 208 cm TL (Fig. 7*b*). Females mature at about 215 cm; the smallest pre-ovulatory fish was 219 cm, and the smallest of five pregnant or spent females was 226 cm TL.

Compagno (1984) stated that 'little is known of its reproductive biology'. Krefft (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. 7*d*, *e*) which, together with observed ova *in utero* in April, suggests that this may be the main ovulation period. Embryos from three litters in April and one in October averaged 7 and 59 cm TL, respectively (Fig. 7*f*). The largest embryos were 59 cm and the smallest free-swimming individual was 66 cm, which suggests that the birth size is 60–65 cm TL. Litter sizes averaged 9, with a range of 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* (Müller & Henle); 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 (33°30′S,115°00′E) (Sainsbury *et al.* 1985; Stevens 1984; Hutchins and Swainston 1986).

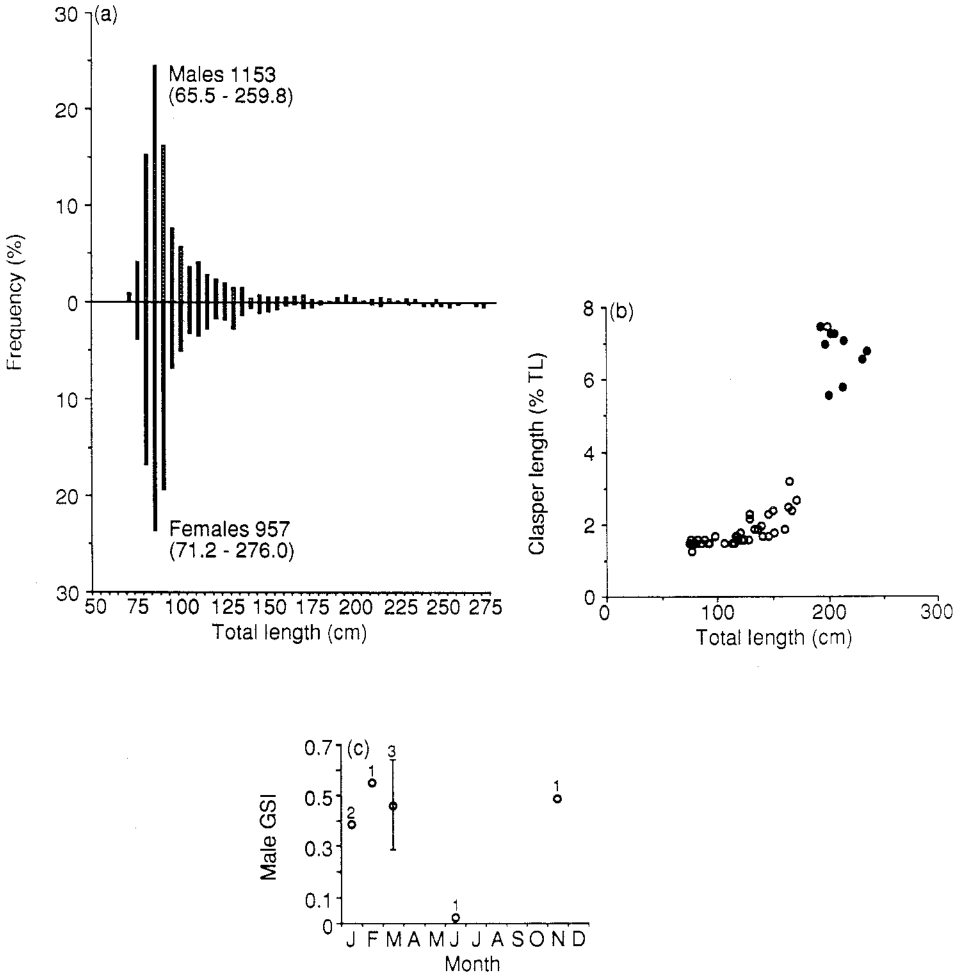

Fig. 8. *Carcharhinus brevipinna.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○,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

Present study: Captured in depths of 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). Waters off Natal are a nursery area for neo-natals (Bass *et al.* 1973).

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

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 45·5% female, χ^2 test $P < 0{\cdot}01$ (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), whereas they are not mature until 180–200 cm and 200–210 cm, respectively, off South Africa (Bass *et al.* 1973).

There were no data on reproduction for males off northern Australia between 165 cm (at and below which size all specimens are immature) and 195 cm (the smallest mature shark) (Fig. 8*b*). Stevens (1984) suggested that *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 at about 195 cm TL. It was not possible to determine maturity in 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, and 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-western 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 60–80 cm TL and litter sizes vary from 3 to 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. 8*c*). 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); whitecheek shark

Distribution

The distribution of this species is uncertain, because of 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'.

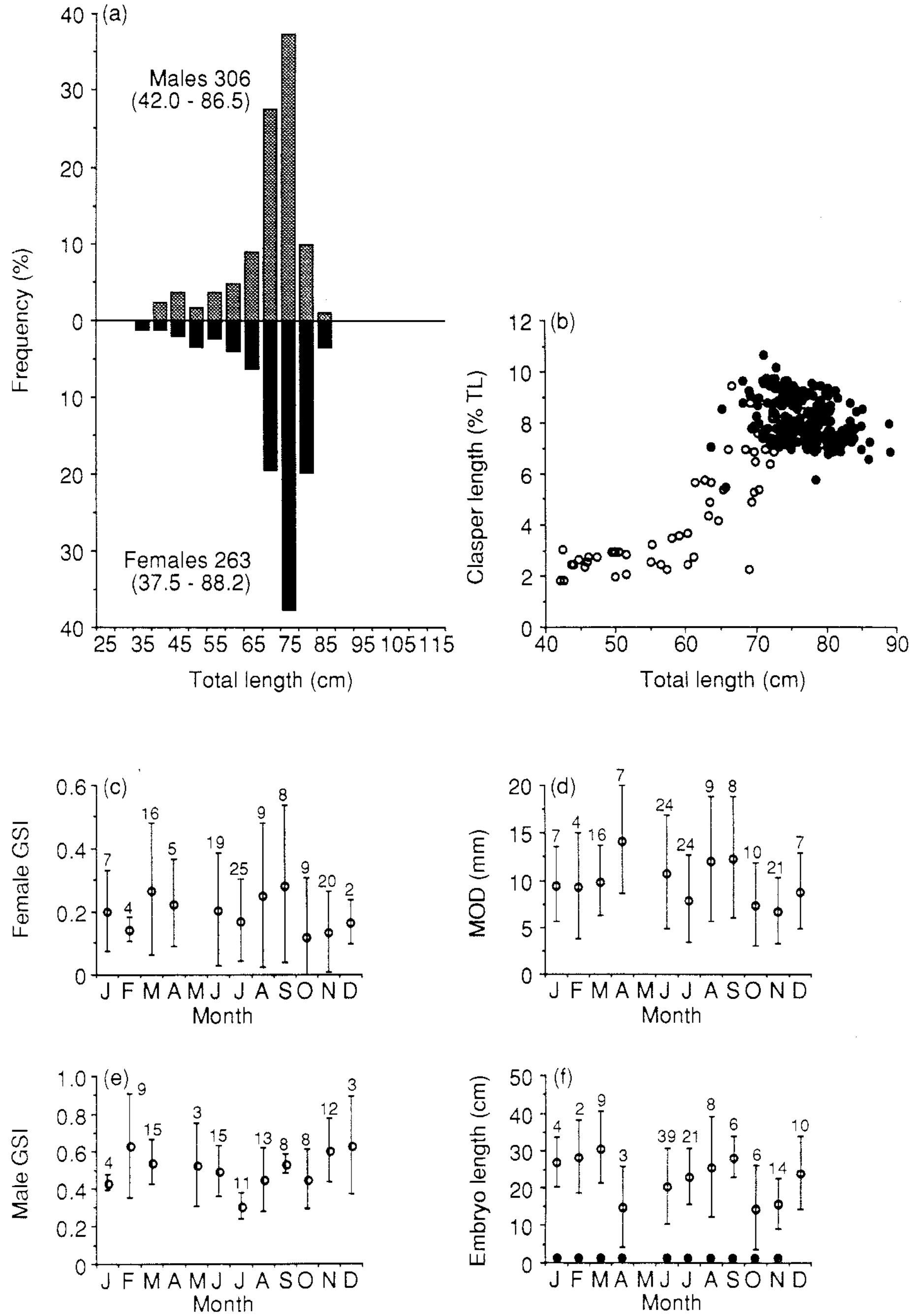

Fig. 9. *Carcharhinus dussumieri.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○,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

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, whereas *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, s.d. 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 and 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. 9*a*).

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. 9*b*); 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 summarized 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. 9*c*–*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. 9*f*). Because females breed throughout the year it was not possible to estimate the gestation period. The mean litter size was 2 with a range of 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 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) noted 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); 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. 10*a*).

Sex ratio

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

Post partum 32·4% female, χ^2 test $P < 0 \cdot 05$ (present study, Table 3).

Reproduction

Males 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). Males 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. 10*b*). 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, shows no reproductive seasonality (Strasburg 1958; Fourmanoir 1961; Cadenat and Blache 1981; Stevens 1984). Litter sizes range from 2 to 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 to 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. 10*c*). 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).

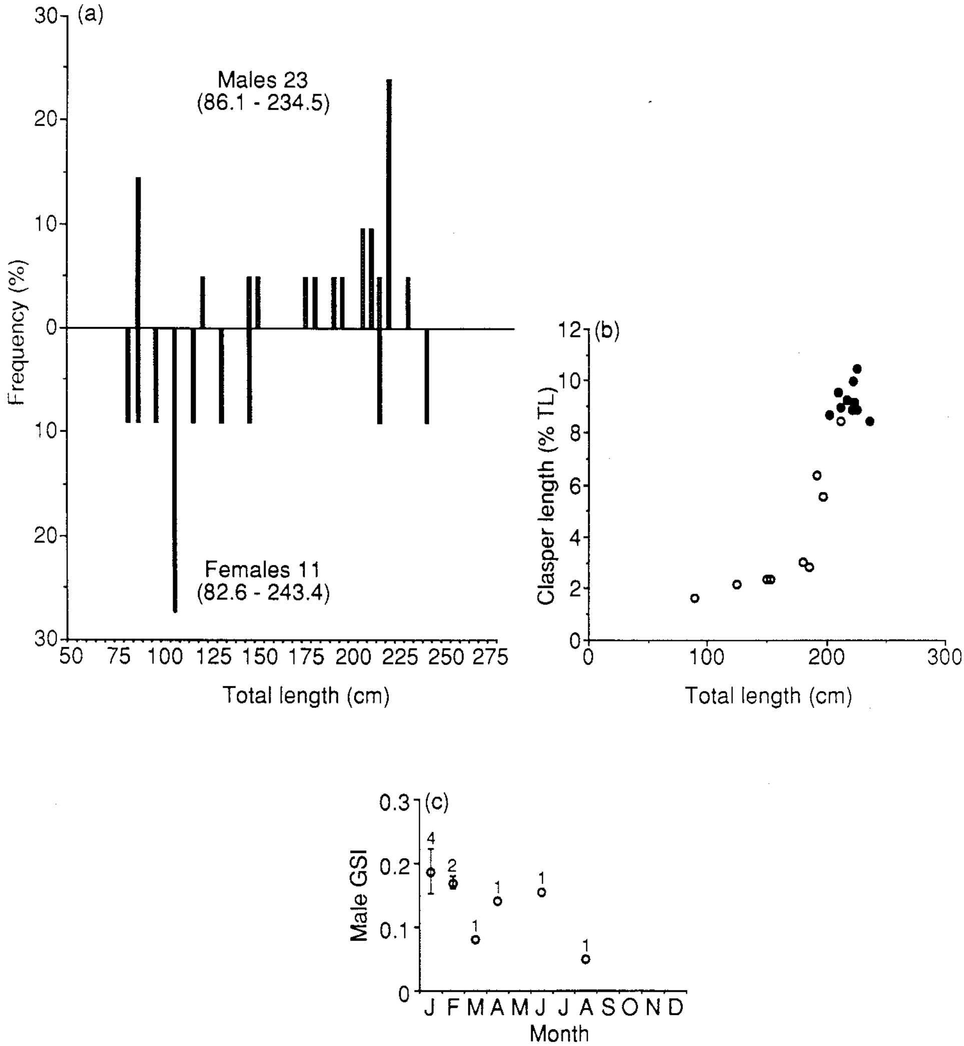

Fig. 10. *Carcharhinus falciformis.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○,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

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

(11) *Carcharhinus macloti* (Müller and Henle); 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 and 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.

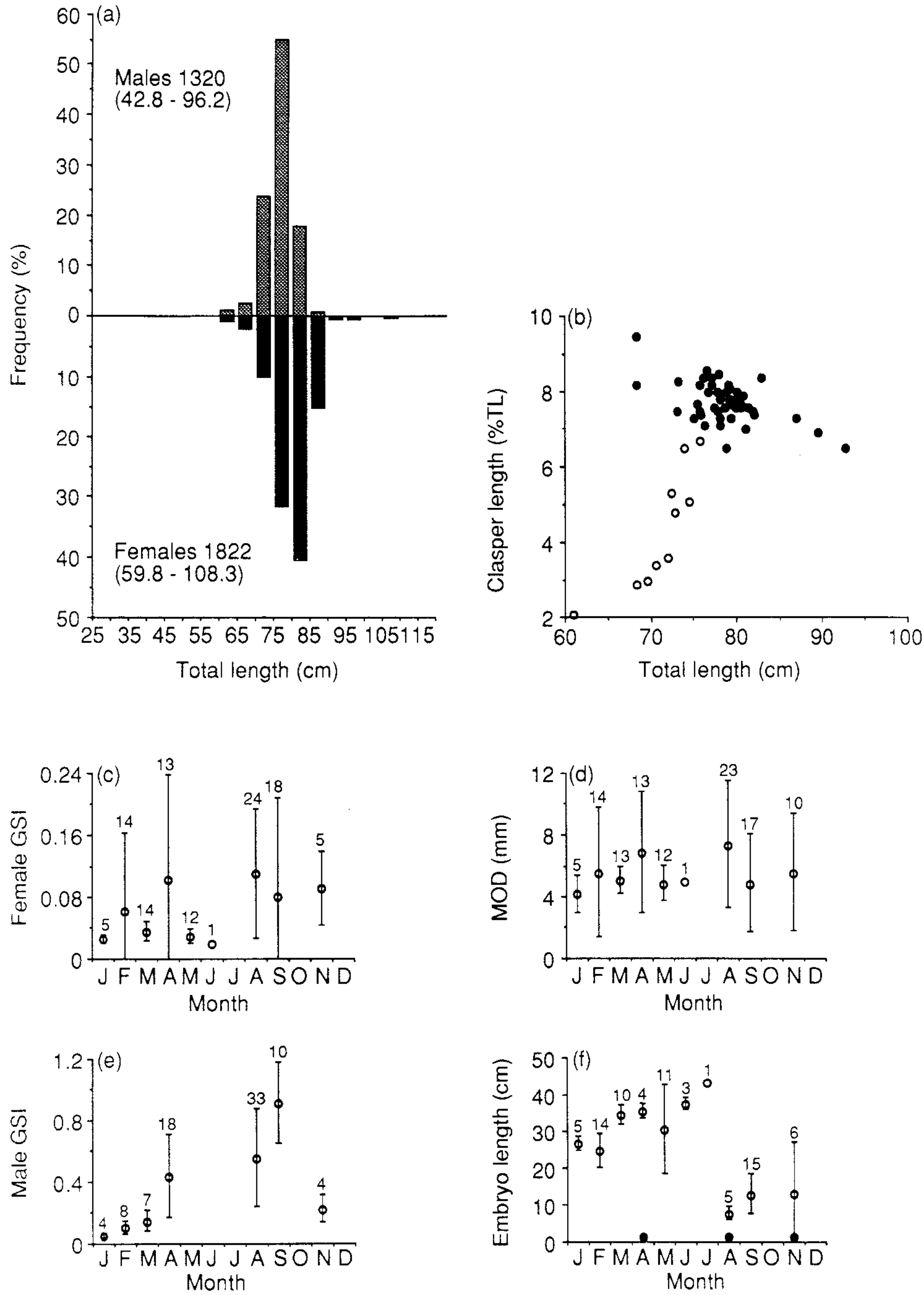

Fig. 11. *Carcharhinus macloti.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers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

Size

Maximum TL 89 cm female (Setna and Sarangdhar 1949*a*).
Males 43–96 cm; females 60–108 cm (present study, Fig. 11*a*).

Sex ratio

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

Embryos nsd 1:1, *post partum* 58% female, χ^2 test $P < 0{\cdot}001$ (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 (χ^2 test $P < 0{\cdot}005$). As the size composition of the catches from the two fishing gears was the same (suggesting that 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 that these differences reflect small-scale seasonal or area variations in sex ratio.

Reproduction

Setna and Sarangdhar (1949*a*) reported 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. 11*b*), 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. macloti* was 70 cm and the smallest pre-ovulatory and pregnant individuals were both 78 cm TL.

From Setna and Sarangdhar's (1949*a*) few data it appears that 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. 11*e*). Female GSI and MOD show considerable variation and no clear seasonal trend is apparent (Fig. 11*c*, *d*). However, there is a reasonable relationship between embryo length and time of year (Fig. 11*f*), 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. 11*f*). Of the mature females, 82% were pregnant, which indicates that individual females breed each year, but this is not supported by the MODs 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 (1949*a*). It seems more likely that *C. macloti* 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 that the birth size in Australian waters is about 40–45 cm TL. Mean litter size was two with a range of 1–2, which is in agreement with the findings of Setna and Sarangdhar (1949*a*).

Diet

Compagno (1984) notes that *C. macloti* 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); 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. 12*a*).

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 5:1 or 6:1 in south-eastern USA (Compagno 1984).

Embryos nsd 1:1; *post partum* 56·5% female, χ^2 test $P < 0{\cdot}05$ (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 $P < 0{\cdot}01$). 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 comprised mainly 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), wheres 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, males mature at 160–170 cm and females in the region of 170 cm TL (Bass *et al.* 1973).

Males in the present study were mature at about 156 cm TL (Fig. 12*b*). 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

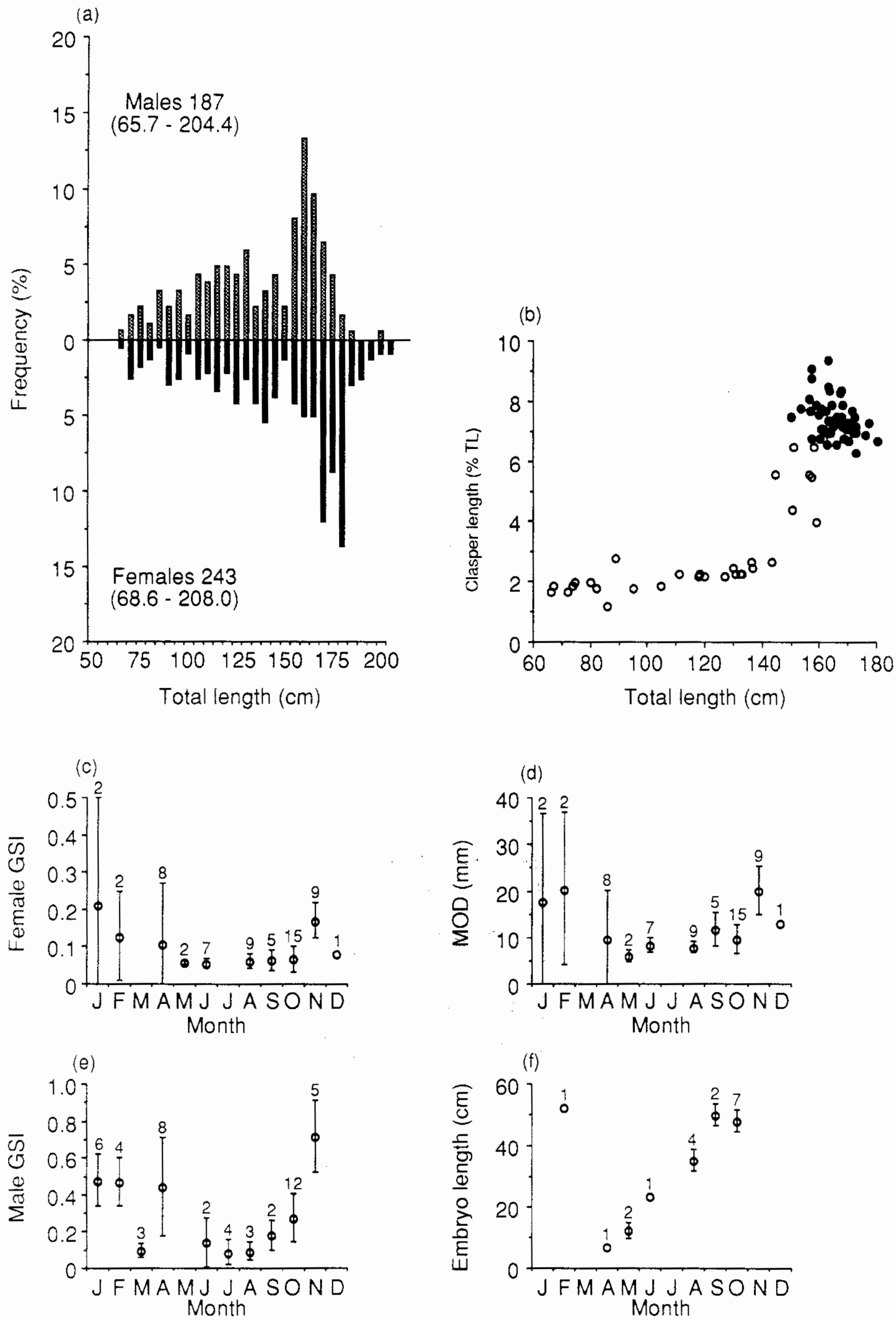

Fig. 12. *Carcharhinus plumbeus*. (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not calcified; ●, claspers calcified. (*c*) Female gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*d*) Maximum ova diameter (MOD) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*e*) Male gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*f*) Embryo length by month (solid circles are eggs *in utero*); plots are mean values; bars are one standard deviation; numbers are number of litters.

(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 summarizing 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 (Bass *et al.* 1973; Wass 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 GSIs and MOD suggests that *C. plumbeus* has a seasonal reproductive cycle in northern Australia, with mating and ovulation occurring between November and April (Fig. 12*c*–*e*). Embryo length increased from 7·1 cm in April to 52·5 cm in February (Fig. 12*f*), so birth presumably occurs in February or March, giving a gestation period of about 1 year. The largest embryo observed was 53 cm and the smallest free-swimming individual was 66 cm, which suggests that 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 ($r^2 = 0 \cdot 32$, $P < 0 \cdot 05$); 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 that 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 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* individuals are found with nearly full stomachs than are larger carcharhinids such as *C. leucas*, *C. obscurus* and *Galeocerdo cuvier*. However, this is not supported by the data of Bass *et al.* (1973) and Wass (1973), who found that 45–46% of *C. plumbeus* stomachs contained food compared with 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 and Appendix 1).

(13) *Galeocerdo cuvier* (Peron & LeSueur); 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. 13*a*).

Most *G. cuvier* individuals 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. 13*a*).

Sex ratio

Females outnumbered males by 2·5:1 off Florida (Clark and von Schmidt 1965).

Post partum 56·5% female, χ^2 test $P < 0 \cdot 05$ (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, $P < 0 \cdot 05$). 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 sample was a reflection of the fish over 200 cm TL, most of which were female; in fish smaller than 200 cm the sex ratio was about 1:1. 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 samples, whereas only one female of less than 225 cm TL was captured (Stevens 1984).

Reproduction

Males 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 Steven's (1984) observations that males reach maturity at about 305 cm (Fig. 13*b*) 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) summarizes 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 to 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 Figs 13*c* and 13*d* suggest that ovulation takes place around December.

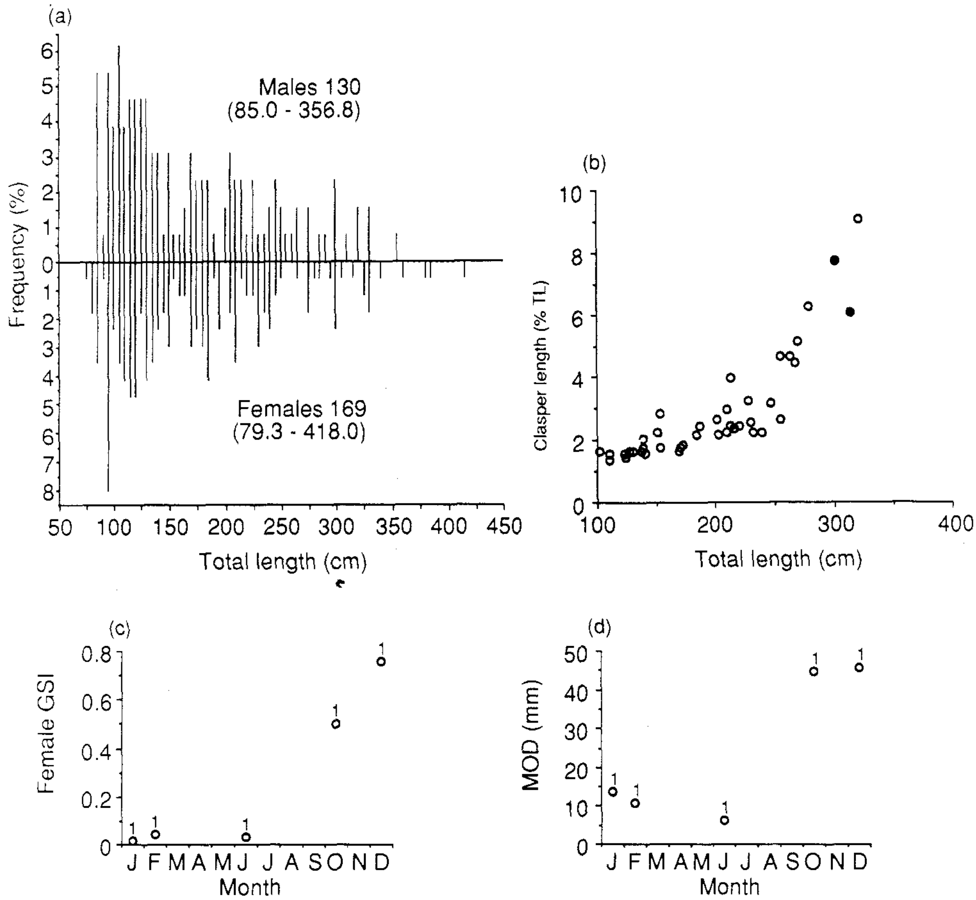

Fig. 13. *Galeocerdo cuvier*. (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not calcified; ●, claspers calcified. (*c*) Female gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*d*) Maximum ova diameter (MOD) by month; plots are mean values; bars are one standard deviation; numbers are sample size.

No pregnant females were captured. That one spent fish taken in February, together with two from New South Wales (Stevens 1984), suggests that 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); 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 (Bigelow and Schroeder 1948). Distinct size segregation associated with seasonal migrations and reproduction (Strasburg 1958; Gubanov and Girgor'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 $P < 0{\cdot}001$). 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 that 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 (1974) recorded mature, non-pregnant fish from New South Wales in the size range 218–249 cm (mean 231 cm), and 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 182 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 Girgor'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 summarized 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* Müller and Henle; 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 and 80 m, both at the surface and near the bottom (Compagno 1984).

Present study: Captured throughout the study area except off north-eastern Queensland (although known to occur there; Springer 1964) 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. 14*a*).

Sex ratio

Embryos nsd 1 : 1, *post partum* 37·3% female, χ^2 test $P < 0{\cdot}001$ (present study, Table 3).

Reproduction

Compagno (1984) states that males mature at 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.

Males from Australian waters mature at about 64 cm (Fig. 14*b*); the 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 to 4 and the size at birth is 40–43 cm TL (Springer 1964; Bass *et al.* 1975).

The GSIs and MOD show no clear seasonal trend in Australian waters (Fig. 14*c*–*e*). In most months the range in size of embryos carried by pregnant females is considerable (Fig. 14*f*), 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

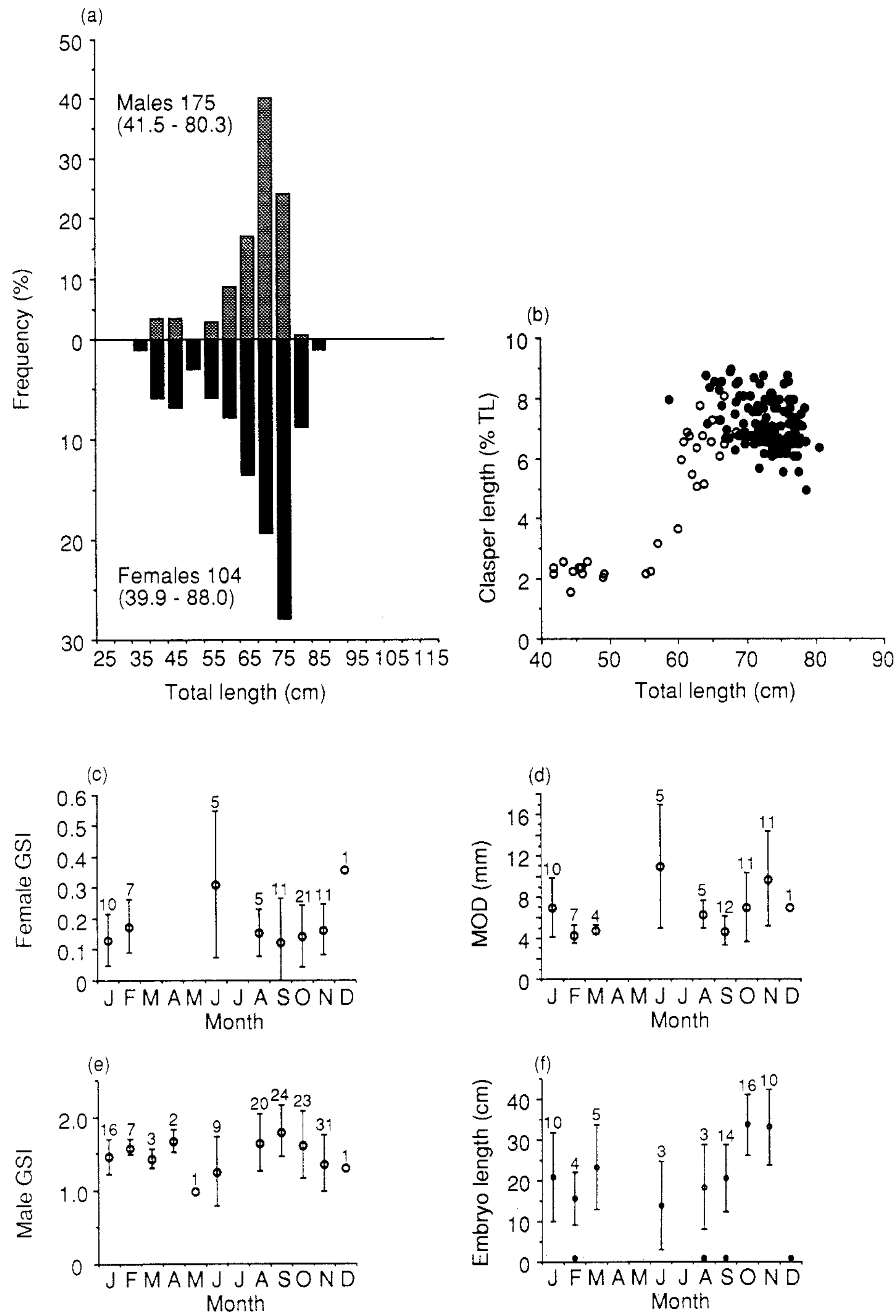

Fig. 14. *Loxodon macrorhinus.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not calcified; ●, claspers calcified. (*c*) Female gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*d*) Maximum ova diameter (MOD) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*e*) Male gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*f*) Embryo length by month (solid circles are eggs *in utero*); plots are mean values; bars are one standard deviation; numbers are number of litters.

rapidly as parturition approaches. The largest embryo observed was 46 cm and the smallest free-swimming specimen 40 cm, which suggests that 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 feeds 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, and other molluscs and miscellaneous items were found in a few stomachs (Table 4 and Appendix 1).

(16) *Rhizoprionodon acutus* (Rüppell); 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. 15*a*).

Sex ratio

Embryos 55·7% female, χ^2 test $P < 0 \cdot 05$; *post partum* 32·2% female, χ^2 test $P < 0 \cdot 001$ (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 $P < 0 \cdot 05$). 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, whereas the pelagic longline and gill-net catch came mainly from the Arafura Sea.

Reproduction

The size at which *R. acutus* matures 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.

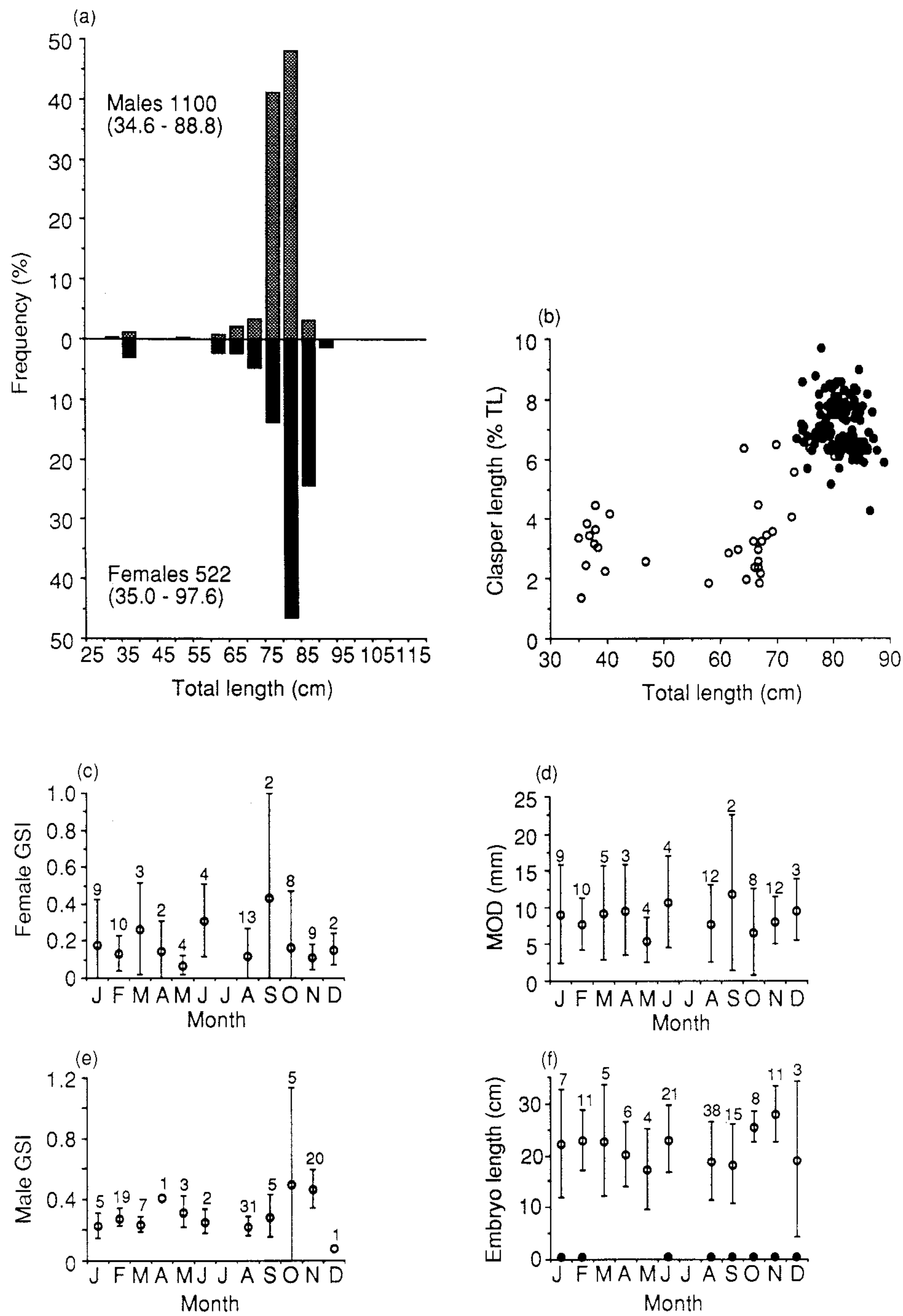

Fig. 15. *Rhizoprionodon acutus*. (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not calcified; ●, claspers calcified. (*c*) Female gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*d*) Maximum ova diameter (MOD) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*e*) Male gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*f*) Embryo length by month (solid circles are eggs *in utero*); plots are mean values; bars are one standard deviation; numbers are number of litters.

In Australian waters, males mature at about 75 cm TL (Fig. 15*b*); 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-western 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 (1949*c*), 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-western Indian Ocean ranged from 2 to 8 with a mean of 5, and in the eastern Atlantic from 1 to 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. 15*f*). Seasonal data on GSI and MOD show no clear trend through the year (Fig. 15*c*–*e*). Of 197 mature females above 75 cm TL, 97% were pregnant; this suggests that females breed each year. Annual breeding is supported by the condition of the ovaries of pregnant fish; the size of their ova increase 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 ($r^2 = 0 \cdot 12$, $P < 0 \cdot 001$) 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.

Diet

R. acutus feeds primarily on small teleost fish but 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); 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 (QM I14909) and on the west coast to Broome, 18°00′S,122°24′E (WAM 29178.001).

Size

Maximum 67 cm TL (Springer 1964).

Males 40–55 cm; females 38–66 cm (present study, Fig. 16*a*).

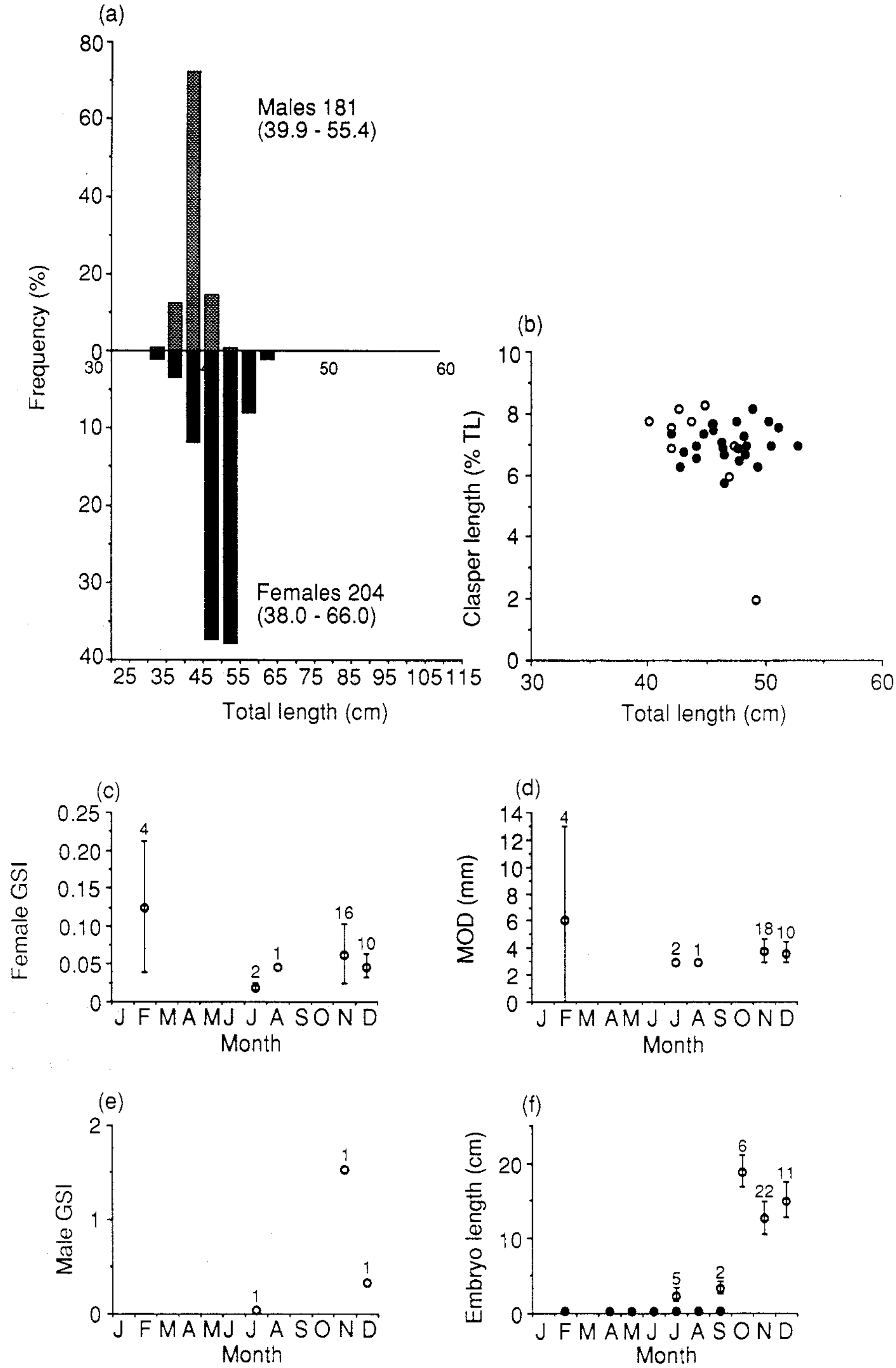

Fig. 16. *Rhizoprionodon taylori.* (*a*) Length-frequency distributions from northern Australia; numbers after the sex are sample size; numbers in parentheses are size range in cm TL. (*b*) Relationship between clasper length (expressed as a percentage of total body length) and total body length; ○, claspers not calcified; ●, claspers calcified. (*c*) Female gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*d*) Maximum ova diameter (MOD) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*e*) Male gonadosomatic index (GSI) by month; plots are mean values; bars are one standard deviation; numbers are sample size. (*f*) Embryo length by month (solid circles are eggs *in utero*); plots are mean values; bars are one standard deviation; numbers are number of litters.

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. 16*b*) because immature fish were largely absent from the sample, presumably as a result of gear slectivity. 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. 16*c*, *d*). However, the plot of pup length suggests that there is a seasonal birth period (Fig. 16*f*). Females with ova *in utero* were found from February to September, but small embryos were found only from July to September and large embryos from October to December. C. Simpfendorfer (James Cook University, personal communication) noted a 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 korkelii* (Lessa 1982). The smallest free-swimming specimen taken was 38 cm and 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 ($r^2 = 0{\cdot}39$, $P < 0{\cdot}001$). The 99% pregnancy rate and the MOD of pregnant fish suggest that individual females 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 beeen 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 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 $P < 0{\cdot}05$), 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).

Table 5. Summary of reproductive parameters for female northern Australian hemigaleid, carcharhinid and sphyrnid sharks
Dash indicates no data

Species	♀ Max. TL (cm)	♀ TL at maturity (cm)	TL at birth (cm)	Mean litter size	Gestation period (months)	♀ breeding frequency	Pups year^{-1}	Birth period	Size at birth (% of ♀ size at maturity)	♀ Size at maturity (% of max. size)
H. microstoma	110	65	30	8	6	Biannual	16	Feb. & Sept.	46	59
H. elongatus	184	115	52	6	7–8	Biennial	3	Apr.	45	63
C. altimus	280?	225?	60	7	–	–	–	–	27	80
C. amblyrhynchoides	162	115	55	3	9–10	Annual	3	Jan.–Feb.	48	71
C. amblyrhynchos	178	135	63	3	9	–	–	Aug.	47	76
C. amboinensis	243	215	63	9	9	–	–	Nov.–Dec.	29	88
C. brevipinna	276	210	75	11	12	–	–	Mar.–Apr.	36	76
C. dussumieri	88	70	38	2	–	Annual	2	All year	54	80
C. falciformis	243	210	75?	7	–	–	–	All year	36	86
C. macloti	108	73	43	2	12	Biennial	1	July	59	68
C. plumbeus	208	155	60	6	12	Biennial	3	Feb.–Mar.	39	75
G. cuvier	450?	330	65?	–	12	–	–	Jan.–Feb.	20	73
P. glauca	323?	220	43	34	9–12	–	–	Dec.–Mar.	20	68
L. macrorhinus	88	57	43	2	–	Annual	2	All year	75	65
R. acutus	98	75	38	3	–	Annual	3	All year	51	77
R. taylori	66	45	28	5	10–11	Annual	5	Dec.–Jan.	62	68
E. blochii[A]	176	120	46	12	10–11	Annual	12	Feb.–Mar.	38	68
S. lewini[A]	346	200	48	17	9–10	–	–	Oct.–Jan.	24	58
S. mokarran[A]	409	210	65	15	11	Biennial	7·5	Dec.–Jan.	31	51
C. cautus[B]	119	91	40	3	8–9	Annual	3	Oct.–Nov.	44	76
C. melanopterus[B]	125	95	48	4	8–9	Annual	4	Nov.	51	76
C. fitzroyensis[B]	135	95	50	4	7–9	Annual	4	Feb.–Apr.	53	70
C. tilsoni[C]	180	115	60	3	10	Annual	3	Jan.	52	64
C. sorrah[C]	152	95	50	3	10	Annual	3	Jan.	53	63

[A] Data from Stevens and Lyle (1989); [B] data from Lyle (1987); [C] data from Stevens and Wiley (1986).

However, Stevens (1984) found significantly more male embryos among *P. glauca* litters from New South Wales (60% male, χ^2 test $P < 0 \cdot 001$).

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 generalizations from the data on reproduction in northern Australian hemigaleid, carcharhinid and sphyrnid 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% 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.* (1986) 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 ($r^2 = 0 \cdot 54$, $P < 0 \cdot 001$, $n = 23$). 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) ($r^2 = 0 \cdot 64$, $P < 0 \cdot 001$, $n = 23$). 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 mature fish 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 than in smaller species, then larger litters will represent a mechanism to compensate for the delay in reproduction.

Although there is some evidence for smaller shark species maturing earlier (Davenport and Stevens 1988), age and growth information is currently unavailable for most of the species reported on in this study.

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 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 among stomachs. They do not show the overall contribution to the diet; this would require additional data on numbers and weight or volume of prey items.

C. cuvier is the only species that can be described as truly omnivorous, taking a broad spectrum of prey types (Table 4 and Appendix 1). This is well documented from other areas and can be summarized by Compagno's (1984) statement: 'the tiger shark is perhaps the least specialized 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 specialized diet consisting almost entirely of cephalopods, most of which are small octopods. These octopods are not abundant in benthic samples (S. F. Rainer, CSIRO Marine Laboratories, Perth, 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. macloti* 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 constituting 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.

Acknowledgments

We acknowledge the assistance given by the Australian Fisheries Service Observer Program and the Masters and crews of FRV *Soela*, FV *Rachel* and the Taiwanese fishing vessels. Many people helped in the collection and processing of samples; in particular we thank Glen Cuthbert, Peter Wiley, Stephanie Davenport, Tony Church, Greg Timms and the AFZ Commonwealth Observer teams. We are very grateful to Dr Jeremy Lyle for unpublished data on several species and to Sally Wayte for computing help. We thank John Gunn, Dr Jeremy Lyle, Dr Vivienne Mawson and Dr Roy Harden Jones for helpful comments on, and discussions about, the manuscript. This study was assisted by FIRTA grant 1983/49.

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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. macloti*; 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	–	–	–	–	–	–	–	–	–	–
Rhina ancylostoma	–	–	–	–	–	–	–	–	–	1	–	–	–
Dasyatididae	–	–	8	–	–	–	–	1	–	–	–	–	–
Amphotistius sp.	–	–	1	–	–	–	–	–	–	–	–	–	–
Unidentified teleost	–	–	1	45	–	–	–	–	–	–	–	–	–
Eel	1	–	–	–	–	–	8	–	1	1	8	5	–
Muraenidae	–	–	1	–	–	–	3	–	–	–	–	–	–
Gymnothorax sp.	–	–	–	–	–	–	–	–	–	–	–	2	–
Muraenesocidae	–	–	–	–	–	–	1	–	–	–	–	–	–
Ophichthidae	–	–	–	1	–	–	–	–	–	–	–	–	–
Congridae	–	–	1	–	–	–	–	–	2	–	1	1	–
Gnathophis sp.	–	–	–	–	–	–	1	–	–	–	–	1	–
Clupeidae	–	–	–	8	3	11	3	14	–	–	–	7	2
Pellona sp.	–	–	–	–	–	–	–	–	–	–	–	–	1
Pellona ditchella	–	–	–	–	–	–	–	–	–	–	–	1	–
Sardinella sp.	–	–	–	–	–	–	–	–	–	–	–	3	–
Sardinella isabella	–	–	–	–	–	–	–	1	–	–	–	–	–
Engraulididae	–	–	–	–	–	–	–	1	–	–	–	–	–
Stolephorus sp.	–	–	–	–	–	–	3	–	–	–	–	–	–
Chirocentrus dorab	–	–	–	–	–	–	–	1	–	–	–	–	–
Synodontidae	–	–	–	–	–	–	1	–	–	–	–	2	–
Saurida spp.	–	1	–	–	–	–	7	4	2	–	–	1	–
Saurida undosquamis	–	–	–	–	–	–	1	–	–	–	–	–	–
Trachinocephalus myops	–	–	–	–	–	–	–	–	1	–	–	–	–
Brush-toothed lizard fish	–	–	–	–	–	–	1	–	–	–	–	–	–
Myctophidae	–	–	–	–	–	–	1	–	–	–	–	–	–
Ariidae	–	–	–	6	1	–	–	–	–	–	–	1	–
Ariidae eggs	–	–	–	1	–	–	–	–	–	–	–	–	–
Plotosidae	–	–	–	1	–	–	–	–	–	–	–	–	–
Batrachoididae	–	–	–	–	–	–	–	–	–	–	–	1	–
Halieutaea sp.	–	–	–	–	–	–	1	–	–	–	–	–	–
Bregmacerotidae	2	–	–	–	–	–	20	–	–	–	36	3	–
Monocentridae	–	–	–	–	–	–	–	–	1	–	–	1	–
Antigonia rhomboidea	–	–	–	–	–	–	–	–	1	–	–	–	–
Fistulariidae	–	–	–	–	–	–	1	–	–	–	–	–	–
Centriscus sp.	–	–	–	–	–	–	1	–	–	–	–	–	–
Syngnathidae	–	–	–	–	–	–	–	–	–	–	–	1	–
Hippocampus sp.	–	–	–	–	–	–	–	–	–	–	1	–	–
Scorpaenidae	–	–	–	–	–	–	4	–	–	–	4	1	–
Triglidae	–	–	–	–	–	–	–	–	–	–	2	–	–
Platycephalidae	–	–	–	1	–	–	1	–	–	–	6	–	–
Elates ransonneti	–	–	–	–	–	–	3	2	–	–	–	2	–

Appendix 1 (*continued*)

Prey item	Number of stomachs												
	M	Hm	He	Ca	Cam	Cb	Cd	Cm	Cp	Gc	Lm	Ra	Rt
Onigocia sp.	–	–	–	–	–	–	–	–	–	–	–	1	–
Hoplichthyidae	–	–	–	–	–	–	–	1	–	–	–	–	–
Dactylopteridae	–	–	–	–	–	–	–	–	–	–	–	1	–
Pegasus draconis	–	–	–	–	–	–	–	–	–	–	1	–	–
Teraponidae	–	–	–	1	–	–	–	–	–	–	–	–	–
Priacanthidae	–	–	–	–	–	–	1	–	1	–	–	–	–
Apogonidae	–	–	–	–	–	–	1	–	–	–	2	–	–
Sillago sp.	–	–	–	1	–	–	–	–	–	–	–	1	–
Carangidae	–	–	–	2	–	5	–	1	2	–	1	1	–
Decapterus sp.	–	–	–	–	–	–	–	–	3	–	–	–	–
Megalaspis cordyla	–	–	–	–	–	–	–	–	1	–	–	–	–
Selaroides leptolepis	–	–	–	–	–	–	–	–	–	–	–	1	–
Leiognathidae	–	–	–	8	–	1	3	7	1	–	2	11	2
Dipterygonotus balteatusi	–	–	–	–	–	–	–	–	–	–	1	–	–
Lutjanidae	–	–	–	–	–	–	–	–	–	–	–	–	–
Lutjanus vittus	–	–	1	–	–	–	–	–	–	–	–	–	–
Nemipteridae	–	–	–	–	–	1	17	2	3	–	–	2	–
Nemipterus peronii	–	–	–	–	–	–	–	–	1	–	–	–	–
Pentapodus porosus	–	–	–	–	–	–	–	–	–	–	–	1	–
Gerridae	–	–	–	–	–	1	–	–	–	–	–	–	–
Lethrinus choerorynchus	–	–	–	–	–	–	–	–	1	–	–	–	–
Mullidae	–	–	–	–	–	1	3	–	2	–	1	1	–
Upeneus sulphureus	–	–	–	–	–	–	1	–	–	–	–	–	–
Pomacanthidae	–	–	–	–	–	–	–	–	1	1	–	–	–
Mugilidae	–	–	–	–	–	–	1	–	–	–	–	–	–
Polynemidae	–	–	–	–	1	–	–	–	–	–	–	–	–
Labridae	–	–	–	1	–	–	2	–	3	–	–	–	–
Choerodon monostigma	–	–	–	–	–	–	1	–	–	–	–	–	–
Xyrichtys jacksonensis	–	–	–	–	–	–	–	–	–	–	1	–	–
Scaridae	–	–	–	–	–	–	–	–	–	–	1	–	–
Mugilidae	–	–	–	–	–	–	–	–	–	–	–	–	–
Mugiloididae	–	–	–	–	–	–	–	–	1	–	–	–	–
Parapercis sp.	–	–	–	–	–	–	–	–	–	–	–	1	–
Uranoscopidae	1	–	–	–	–	–	1	–	–	–	1	–	–
Champsodontidae	–	–	–	–	–	–	–	–	1	–	3	–	–
Champsodon sp.	–	–	–	–	–	–	–	–	–	–	1	–	–
Sandeel	–	–	–	–	–	–	1	–	1	–	5	–	–
Gobiidae	–	–	–	–	–	–	1	–	–	–	1	–	–
Callionymidae	–	–	–	–	–	–	2	–	–	–	1	–	–
Trichiuridae	–	–	–	–	–	–	–	–	3	–	–	–	–
Scombridae	–	–	–	–	–	1	–	–	1	1	–	1	–
Euthynnus affinis	–	–	–	1	–	–	–	–	–	–	–	–	–
Rastrelliger sp.	–	–	–	–	–	–	1	–	2	–	–	–	2
Rastrelliger kanagurta	–	–	–	–	4	–	–	–	–	–	–	–	–
Scomberomorus sp.	–	–	–	2	–	–	–	1	–	–	–	–	–
Istiophoridae	–	–	–	–	1	–	–	–	–	1	–	–	–
Istiophorus platypterus	–	–	–	–	–	–	–	–	–	1	–	–	–
Flatfish	–	–	–	–	–	–	8	–	–	–	2	2	1
Bothidae	1	–	–	–	–	–	5	–	1	–	2	–	–
Cynoglossidae	–	–	–	–	–	–	2	–	–	–	–	–	–
Balistidae	–	–	–	–	–	–	1	–	1	–	–	–	–
Abalistes stellaris	–	–	–	–	–	–	–	–	–	3	–	–	–

Appendix 1 (*continued*)

Prey item	Number of stomachs M	Hm	He	Ca	Cam	Cb	Cd	Cm	Cp	Gc	Lm	Ra	Rt
Monocanthidae	–	–	–	–	–	2	4	–	–	–	–	7	1
Paramonocanthus filicauda	–	–	–	–	–	–	5	–	–	–	–	1	–
Ostraciidae	–	–	–	–	–	–	–	–	–	1	–	–	–
Tetraodontidae	1	–	–	–	–	–	1	–	1	12	1	–	–
Lagocephalus sceleratus	–	–	–	–	–	–	–	–	–	–	–	1	–
Lagocephalus inermis	–	–	–	–	–	–	–	–	–	1	–	–	–
Lagocephalus 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	–
Loligo chinensis	–	–	–	–	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	–	–
Stomatopod	13	1	–	–	2	–	27	–	3	3	17	2	3
Isopod	3	–	–	–	1	–	1	–	2	–	1	–	–
Euphausid	2	–	–	–	–	–	–	–	–	–	1	–	–
Decapod	5	–	–	–	–	–	1	–	–	–	–	–	–
Squillidae	–	–	–	3	–	–	–	–	–	–	–	–	–
Squilla 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
Penaeus spp.	–	–	–	2	–	–	–	–	–	–	–	–	–
Penaeus esculentus	–	–	–	–	–	–	–	–	–	–	–	–	1
Trachypenaeus fulvus	–	–	–	–	–	–	1	–	–	–	–	–	–
Caridae	1	–	–	–	–	–	–	–	–	–	3	–	–
Alpheid shrimp	1	–	–	–	–	–	–	–	–	–	1	–	–
Scyllaridae	1	–	–	–	–	–	–	–	–	2	–	–	–
Nephropsidea	2	–	–	–	–	–	–	–	–	–	–	–	–
Linneaparis trygonis	1	–	–	–	–	–	–	–	–	–	–	–	–
Callianassa sp.	–	1	–	–	–	–	1	–	–	–	2	–	–
Upogebia sp.	–	–	–	–	–	–	–	–	–	–	3	–	–
Galatheidae	1	–	–	–	–	–	–	–	–	–	–	–	–
Paguridae	1	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified crab	27	5	–	1	–	1	10	–	1	4	23	1	2
Ranina ranina	–	–	–	–	–	–	1	–	–	–	–	–	–
Portunidae	2	–	–	–	1	–	1	–	–	3	–	–	–
Seaweed	–	–	–	–	–	2	–	–	1	–	–	–	–
Bryozoan	–	1	–	–	–	–	–	–	–	–	–	–	–
Black coral	–	–	–	–	–	–	–	–	–	1	–	–	–
Annelid	–	–	–	–	–	–	–	–	–	–	1	–	–
Polychaete	–	1	–	–	–	–	–	–	–	–	–	–	–
Gastropod	–	–	–	–	–	–	–	–	–	1	1	2	–

Appendix 1 (*continued*)

Prey item	Number of stomachs												
	M	Hm	He	Ca	Cam	Cb	Cd	Cm	Cp	Gc	Lm	Ra	Rt
Bivalve	1	–	–	–	–	–	–	–	1	–	1	–	–
Anadara sp.	–	1	–	–	–	–	–	–	–	–	–	–	–
Crinoid	–	1	–	–	–	–	–	–	–	–	–	–	–
Ophiuroid	–	–	–	–	–	–	–	–	–	–	1	–	–
Holothurian	–	–	–	–	–	–	–	–	–	–	1	–	–
Salp	–	–	–	–	–	–	–	–	–	–	–	1	–
Turtle	–	–	–	–	–	–	–	–	–	12	–	–	–
Chelonia depressa	–	–	–	–	–	–	–	–	–	1	–	–	–
Sea snake	–	–	–	–	–	–	–	–	–	33	–	–	–
Albatross	–	–	–	–	–	–	–	–	–	1	–	–	–
Bird feathers	–	–	–	–	–	–	–	–	–	1	–	–	–
Unidentified mammal	–	–	–	–	–	–	–	–	–	1	–	–	–
Echidna	–	–	–	–	–	–	–	–	–	1	–	–	–
Delphinidae	–	–	–	–	–	–	–	–	–	1	–	–	–
Bone	–	–	–	–	–	–	–	–	–	1	–	–	–
Lamb chop	–	–	–	–	–	–	–	–	–	1	–	–	–
Unidentified material	2	–	–	–	–	–	–	–	–	1	1	3	–
Shell	–	–	–	–	–	–	–	–	1	1	–	–	–
Stones	–	–	–	–	–	–	–	–	1	–	–	–	–
Polythene bag	–	–	–	–	–	–	–	–	–	1	–	–	–

Manuscript received 7 September 1990; revised and accepted 17 December 1990