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Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean

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Ten species of shark belonging to three families were recorded from Aldabra Atoll. *Carcharhinus melanopterus* and *Negaprion acutidens* were the most abundant species in the lagoon, while *Carcharhinus albimarginatus* was the most common shark outside the reef. Twelve hundred sharks of six species were tagged and individual recapture rates varied from 15 to 34%. Some specimens of *C. melanopterus* were caught up to seven times. All five species for which recapture data were available are restricted in their movements at Aldabra. *C. melanopterus* in particular is very localized, normally remaining in an area of a few square kilometres. Length increment data obtained from tagging demonstrated a slow growth rate for *C. melanopterus*, averaging 3.5 cm a^{-1}, with no detectable difference between the growth rates of small and large individuals. Limited data for juvenile *Negaprion* and *C. albimarginatus* indicated average growth rates of 12.5 and 8.8 cm a^{-1} respectively. Population densities calculated for several areas in the lagoon varied from 19 to 198 *C. melanopterus* per square kilometre. It is suggested that *C. melanopterus* may be food-limited at Aldabra owing to the intensity of intra- and inter-species competition. *C. melanopterus* and *Negaprion* have restricted and almost identical reproductive cycles at Aldabra. *C. melanopterus* females mature at 110 cm total length and breed every second year giving birth to about four pups after a 10–11 month gestation period. Stomach contents of the more abundant species indicate that fish are the most important item in the diet, except for *Nebrius concolor* which feeds principally on octopus.

Introduction

The rich and undisturbed nature of the fish fauna of Aldabra was recognized by the 1968 Royal Society Expedition and its importance as a site suitable for ecological fish research was noted by Potts (1973). Published information on the shark fauna of Aldabra is very limited. Wheeler (1953) caught three sharks belonging to two species. Smith (1955) noted fourteen shark species in his check list of fish from Aldabra. Forster *et al.* (1970) reported nine species of predominantly deep water sharks at depths between 100 and 1000 m and provided information on catch rates, depth of capture, size distributions, and some other biological observations.

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Studies on sharks from other tropical areas of the south-west Indian Ocean are summarized by Bass *et al.* (1973, 1975*a*, 1975*b*, 1975*c*, 1975*d*, 1976) in their comprehensive study of the sharks of the east coast of southern Africa.

Aldabra provided an opportunity to examine the shark population from a virtually undisturbed atoll situated in a region where the shark fauna is not well known (Bass *et al.* 1973). This undisturbed state is important when studying large reef carnivores as they are usually the first to be exploited when an area is opened for tourism or fisheries (Potts 1981).

Description of the study area

Aldabra (09° 24′ S, 46° 20′ E) is an elevated coral limestone atoll (Stoddart 1967) 34 km long and 14 km wide enclosing a shallow lagoon of 208 km^2 (figure 1). The land rim is cut in a number of places by passes, the largest of which, Main Channel, is 700 m wide at its entrance. Main Channel extends its influence well inside the lagoon and this area is typified by large coral heads and shallow reefs. Away from Main Channel considerable areas of the lagoon are dry at low water. The bottom is mainly sand and light coral with a few areas of turtle grass (*Thalassia*) and weed. The perimeter of the lagoon, and of the larger enclosed islands, is mostly covered by dense mangroves. The reef flat is up to 500 m wide and dries to varying degrees at low water. At the reef edge is a rubble ridge and the bottom then drops rapidly away to around 1000 m in 1.5 km and 4000 m in 7 km. The tidal range at Aldabra is about 3 m with considerable tidal lags between different regions of the lagoon. The south-east trades usually blow at 11–21 knots† from April to October with the calmest weather occurring during the remainder of the year with the north-west monsoon. Sea surface temperatures off the reef edge vary between about 24 °C and 30 °C.

Sampling and methods

All sharks were caught on hook and line, the majority on handlines. Barbless hooks were used except where specimens were to be retained for subsequent examination. In most cases sharks were attracted to the fishing area by 'chumming' with slashed or chopped fish. Normally only one line was fished at a time. Shark fishing was usually carried out at the most effective times and places, generally around the mangroves at high water and in the drainage channels at low water, in all areas of the lagoon but was concentrated in the western half between Passe Gionnet in the north and Point Antendu in the south (figure 1). Outside the reef, work was limited by the weather, especially during the south-east trades, and was restricted to the western half of the atoll from Au Parc, Middle Island to Dune d'Messe, South Island. Abundance values obtained in this study are based on hook and line fishing (expressed as catch per hour). Some species may be more susceptible to the 'chumming' technique and to capture than others.

Fin tagging was carried out using Jumbo Rototags (Stevens 1976). Sharks were measured with a steel tape to the nearest millimetre, from the snout tip to the tip

† 1 knot ≈ 0.5 m s^{-1}.

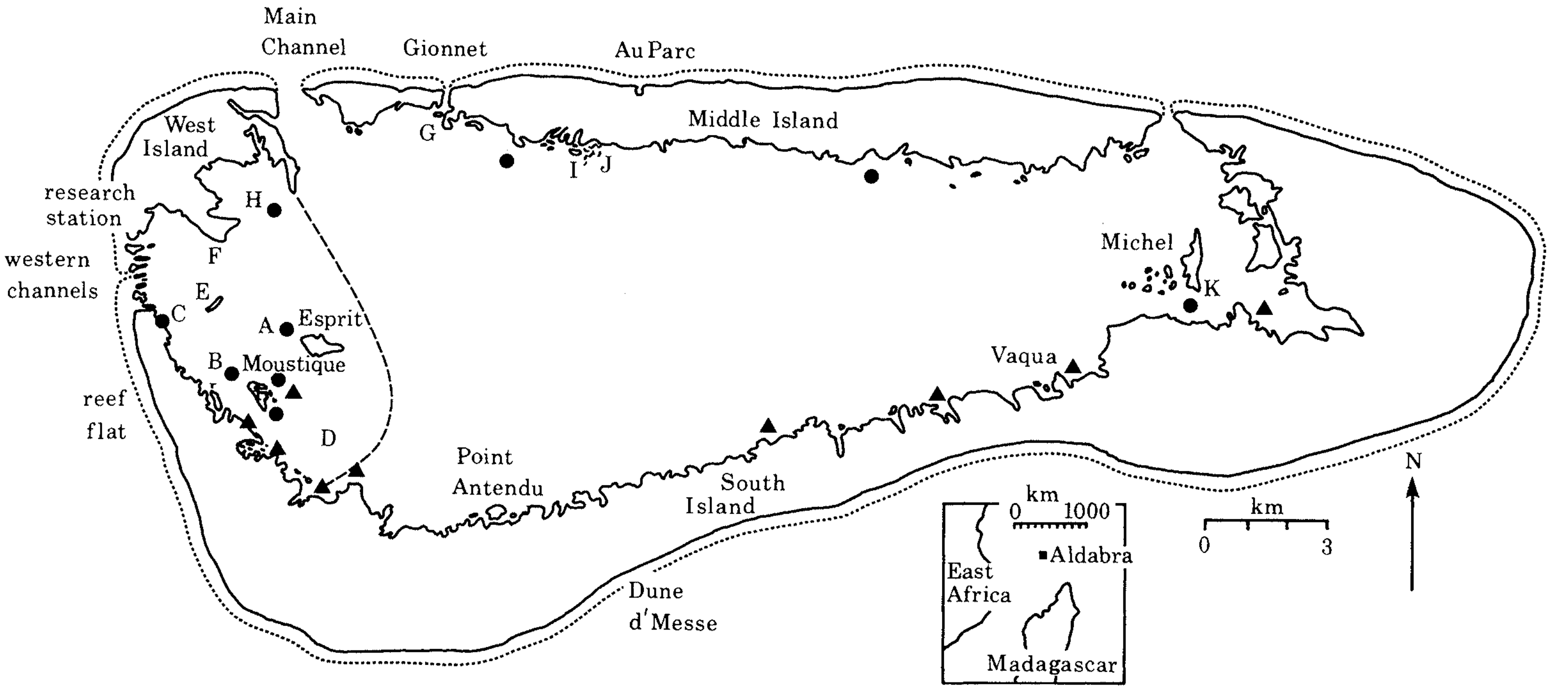

FIGURE 1. Aldabra Atoll. A to K and area 1 (bounded by dashed line) are tagging sites referred to in the text. Solid circles are positions where abundance of *Carcharhinus melanopterus* exceeds 4.5 sharks per hour, solid triangles where *Negaprion acutidens* abundance exceeds 1.0 sharks per hour.

of the upper caudal fin when fully extended posteriorly. If the shark tensed its muscles or moved during the procedure the measurement was repeated. To try to quantify the errors involved, each of two live *C. melanopterus* was subjected to ten replicate length measurements, the sharks being moved between each measurement. The total variation in length range recorded for each shark was 4 mm (s.d. 0.1 about the means). An independent check on measuring accuracy was possible from sharks that had been tagged and recaptured within a short period (less than 20 d). Data were available on eight fish which showed differences ranging from 1 to 8 mm (mean 2.9, s.d. 2.6) between their length on tagging and recapture. These methods indicate that it is possible to measure the majority of sharks to an accuracy of within 2–5 mm. Large sharks (more than 2.2 m) were tagged in the water alongside the boat and their lengths measured approximately. Visual tracking of *C. melanopterus* was carried out using small polystyrene floats attached by a length of monofilament to the first dorsal fin.

Total lengths (t.l.) of all sharks retained were measured with a sliding rule reading to the nearest millimetre (Stevens 1975). Body masses were taken either on a steel yard or on calibrated spring balances reading to the nearest 100 g except for embryos which were weighed to the nearest gram. Determination of reproductive state follows the methodology of Bass *et al.* (1973).

Species composition

Between November 1977 and November 1978, 1317 sharks were captured at Aldabra. Nine species were caught comprising six carcharhinids, two sphyrnids and one orectolobid (table 1). In addition one specimen of the blunthead shark, *Triaenodon obesus* Müller and Henle (family Carcharhinidae), was photographed during diving operations off the reef edge. Some data on tooth counts, vertebral counts and proportional body dimensions of these sharks have been deposited in the archives of the Royal Society.†

Species accounts

Carcharhinus melanopterus Quoy and Gaimard (blackfin reef shark)

C. melanopterus is the most abundant species at Aldabra. This shark is most numerous in the lagoon during the day (table 2) where it is widely distributed, although it favours shallow water and occurs in water as shallow as 20 cm. In these areas it is always the most abundant species, except in certain locations along the south coast mangroves. *C. melanopterus* is also found in the passes, mostly in transit, on the reef flat, particularly where there is ready access to the lagoon, and occasionally along the reef edge where it was never caught in water deeper than 10 m. Areas of greatest abundance were around the islands of Esprit and Moustique at the western end of the lagoon. The highest catch rate recorded was 28 individuals in 2.6 h (10.8 sharks per hour) off Moustique while the highest catch rate in one fishing session was 73 sharks in 8.5 h (8.6 sharks per hour), also near Moustique. Areas where the abundance exceeded 4.5 sharks per hour are shown in figure 1.

† Copies of the material deposited may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, West Yorkshire LS23 7BQ, U.K. (reference SUP 10044).

TABLE 1. SPECIES COMPOSITION, SIZE RANGE AND NUMBERS OF SHARKS CAUGHT AT ALDABRA

species†	number tagged	total catch	t.l. range/cm male	female
Carcharhinus melanopterus	1003	1046	49.0–128.0	56.0–140.0
C. albimarginatus	44	52	75.0–222.1	89.0–204.7
C. wheeleri	33	41	70.0–158.0	67.0–182.1
C. falciformis	2	9	208.4–245.8	216.1–220.7
Negaprion acutidens	131	155	65.0–242.1	71.0–239.9
Galeocerdo cuvieri	0	1	229.2	—
Sphyrna lewini	0	1	250.3	—
S. zygaena	0	1	—	208.2
Nebrius concolor	5	11	172.0–237.8	120.1–231.4

† One specimen of *Triaenodon obesus* was photographed but not captured.

TABLE 2. CATCH PER HOUR OF *C. MELANOPTERUS* AND *N. ACUTIDENS* BY AREA AT ALDABRA

	day (423.8 h)			night (159.1 h)		
area	*C. melanopterus*	*N. acutidens*	total time/h	*C. melanopterus*	*N. acutidens*	total time/h
lagoon	3.5	0.4	314.6	0.7	0.6	35.5
passes	1.6	0.02	88.1	0.7	0.3	107.7
reef flat	1.7	0	9.8	0	0	4.9
reef edge	0.2	0	11.3	0	0.1	11.0

Night-time abundance was lower in all areas (table 2). On a monthly basis the daytime abundance of *C. melanopterus* in the lagoon varied from 6.1 in December (38.4 h) to 1.4 (14.5 h) in June.

At Aldabra *C. melanopterus* are born at about 50 cm t.l. and females attain a maximum size of about 140 cm t.l. This is considerably smaller than maximum lengths reported elsewhere in the Indian Ocean where this shark is known to reach at least 160 cm t.l. (Bass *et al.* 1973). Male *C. melanopterus* reach a maximum size of about 130 cm t.l. at Aldabra (table 1). The size–frequency distributions are shown in figure 2 and are typical of an unfished population with a high proportion of large individuals, particularly in the males. The length distributions are representative of the population as all size ranges from newly born fish to those around the maximum size appeared to be equally susceptible to hook and line fishing. Monthly length–frequency distributions showed no evidence of containing recognizable age classes, despite the restricted breeding season at Aldabra. The October–January samples contained more small fish in the 45–55 cm t.l. range, presumably from the influx of newly born pups following the October parturition period. Sample sizes were too small to compare length distributions at different fishing sites. However, there was no evidence of any discrete nursery areas for *C. melanopterus* at Aldabra.

The overall proportion of the sexes for *C. melanopterus* at Aldabra was 58.9 % female, which is significantly different from an expected value of 50 %, $p < 0.001$.

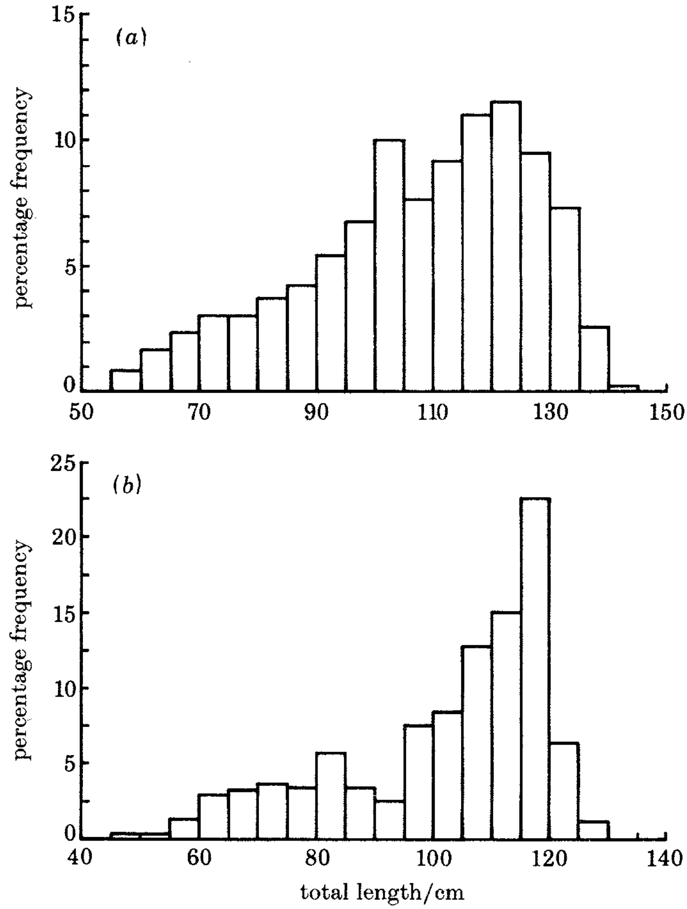

FIGURE 2. Length–frequency distribution for *Carcharhinus melanopterus* at Aldabra. (*a*) Females, (*b*) males.

Monthly variations are shown in table 3. All months except February showed a preponderance of females. The proportion of the sexes for *C. melanopterus* from different fishing sites was also examined; sites with less than 20 samples being excluded. Distinct differences from the total yearly average were found at three sites. However, all 20 fish from site K (85 % female) were taken in one fishing session, as were 24 of 26 fish from site H (92.3 % female) (figure 1). Forty out of 54 fish from site I (31.5 % female) were taken in two sessions. It was apparent that aggregations of sharks taken on any one fishing day might contain a high proportion of one sex, but this normally evened out over a number of diffferent days. Sites A and C (figure 1) showed a noticeably different proportion of the sexes over a number of sampling periods (67 % female) but this value was within the total monthly variation (table 3).

Overall, 1003 *C. melanopterus* were tagged at 86 sites around Aldabra. Of 233 individuals recaptured (23.2 %) 77 were recaught more than once and some individuals were captured seven times. When data from all sites were combined,

TABLE 3. MONTHLY PROPORTIONS OF THE SEXES (PERCENTAGE FEMALE) FOR SIX SPECIES OF SHARK AT ALDABRA

	C. melanopterus		*Negaprion acutidens*		*C. albimarginatus*		*C. wheeleri*		*Nebrius concolor*		*C. falciformis*	
	percentage	*n*	percentage	*n*	percentage	*n*	percentage	*n*	percentage	*n*	percentage	*n*
November	62.6	78	62.5	8	—	0	38.1	21	100.0	1	—	0
December	58.8	216	77.8	27	61.5	13	50.0	4	—	0	50.0	4
January	64.6	198	73.7	19	53.1	32	28.6	7	100.0	1	—	0
February	49.5	184	64.7	17	50.0	2	33.3	3	50.0	2	0	1
March	53.7	67	50.0	16	40.0	5	100.0	1	0	2	—	0
April	61.7	47	—	0	—	0	—	0	—	0	0	1
May	64.1	100	68.8	16	0	1	0	1	—	0	—	0
June	53.3	30	22.2	9	75.0	4	50.0	4	0	1	50.0	2
July	55.1	78	50.0	4	—	0	—	0	100.0	1	—	0
August	67.2	64	38.9	18	—	0	100.0	2	0	1	—	0
September	54.5	101	69.2	13	—	0	100.0	1	0	1	—	0
October	63.1	149	50.0	22	16.7	6	100.0	1	0	1	—	0
total	58.9	1312	59.8	169	50.8	63	44.4	45	36.4	11	37.5	8

n, Sample size (includes multiple recaptures from tagging).

55 % of recaptures came from the tagging site, with 81 % captured within 1 km and 93 % within 2 km of the tagging site. When fish which did not move are excluded, the average distance moved was 1.2 km and the maximum distance travelled, measured as a straight line between tagging and recapture position was 5.1 km. Data from tagging sites where 25 or more fish were tagged are presented in table 4 and, for the major tagging site, in figure 3. Tag returns from the lagoon show

TABLE 4. RECAPTURE DATA FOR *C. MELANOPTERUS* FROM INDIVIDUAL TAGGING SITES AT ALDABRA

tagging site	number tagged	recapture rate (%)	percentage recaptured: at tagging site	within 1 km	within 2 km	maximum distance travelled km
A	116	50.9	53.6	66.7	84.1	2.8
B	89	47.2	57.4	96.3	100.0	1.7
C	48	42.0	71.4	81.0	95.2	2.8
D	41	22.0	77.8	77.8	88.9	3.4
G	30	26.7	100.0	100.0	100.0	—
J	29	13.8	100.0	100.0	100.0	—
F	28	25.0	28.6	71.4	85.7	2.7
H	26	11.5	33.3	66.7	100.0	1.3
E	26	26.9	85.7	85.7	85.7	2.1
I	26	19.2	80.0	100.0	100.0	0.4

that *C. melanopterus* tend to congregate in drainage channels during low water and then move over the flats to the mangroves on the incoming tide. Tag returns showed movement of some *C. melanopterus* between the lagoon and reef flat. Results strongly suggest that this type of movement was restricted to individuals occupying areas close to the passes and that the majority of fish remained in the lagoon throughout the tidal cycle. Regular fishing and tagging operations adjacent to a pass on the reef flat near the research station show that in this region there is a difference in movements between day and night. During the day *C. melanopterus* were only present on the reef flat at the pass entrance for a short period on the flood tide before entering the lagoon, while at night they stayed in this area throughout the high tide period. The proportions of the sexes of tagged fish were 56.3 % female, that of single recaptures 59.3 % female (sample number 150. difference from expected value of 56.3 % not significant, $p > 0.050$) but that of multiple recaptures 74 % female (sample number 77; difference from expected value of 56.3 % significant, $p < 0.005$). It might be thought that multiple recaptures comprised a high proportion of recaptures from the tagging site and that this was indicative of males having a less restricted range than females. In fact only about half (55.3 %) of multiple recaptures were made at the tagging site and while there was some evidence that larger males had a less restricted range (table 5), data were too limited to draw definite conclusions.

Fifteen *C. melanopterus* were tracked visually, by means of small polystyrene floats attached to the shark, for up to 7 h and over straight line distances of up to 2.5 km. In the lagoon the general pattern of movement was typical of the fin

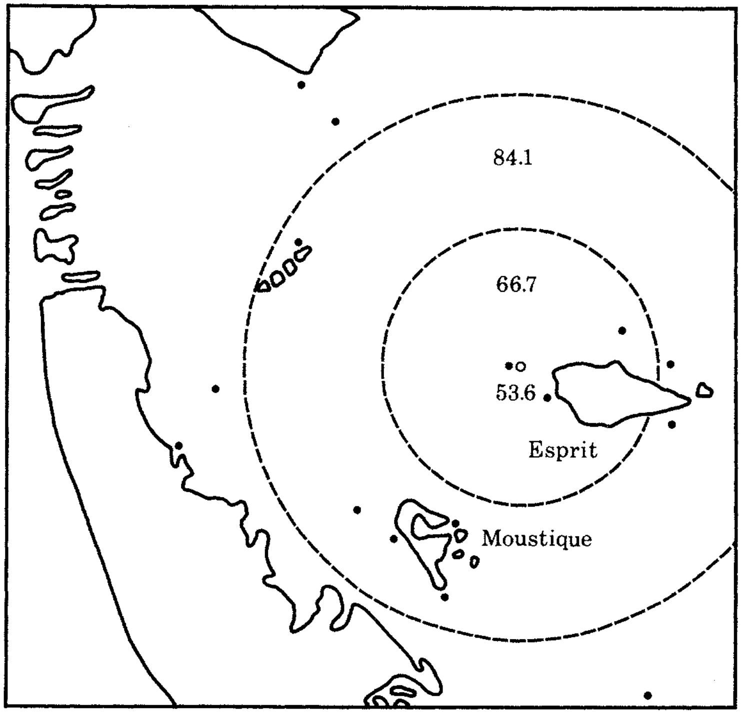

FIGURE 3. Percentage of *Carcharhinus melanopterus* recaptured by distance from site A off Esprit Island in the lagoon at Aldabra. Open symbol tagging site, solid symbols recapture positions. Inner circle of radius 1 km, outer circle radius 2 km. (Number of sharks tagged 116, recapture rate 50.9 %).

TABLE 5. ANALYSIS OF *C. MELANOPTERUS* MOVEMENT DATA AT ALDABRA BY SEX AND SIZE (t.l.) OF SHARK

	females		males	
	< 100 cm	⩾ 100 cm	< 100 cm	⩾ 100 cm
average distance moved/km	1.2	1.3	1.6	2.1
recaptured at tagging site (%)	52.4	56.3	56.0	50.0
recaptured within 1 km (%)	82.9	81.3	76.0	57.1
recaptured within 2 km (%)	93.9	93.8	92.0	85.7
sample number	11	45	11	10

tag returns with the fish retreating and advancing with the tide. Fish rarely moved in a straight line for more than a few minutes. They appeared to be continually searching, crossing and recrossing their path, often remaining in a small area for an hour or two before moving off and repeating this pattern in another area. On the reef flat, tracked *C. melanopterus* usually kept close to the shore, sometimes swimming into the surf zone along beaches. The movements of a 120 cm t.l. *C. melanopterus* tracked for a 7 h period in the lagoon are shown in figure 4. Tracked sharks exhibited apparently normal behaviour mixing freely with other non-tagged individuals.

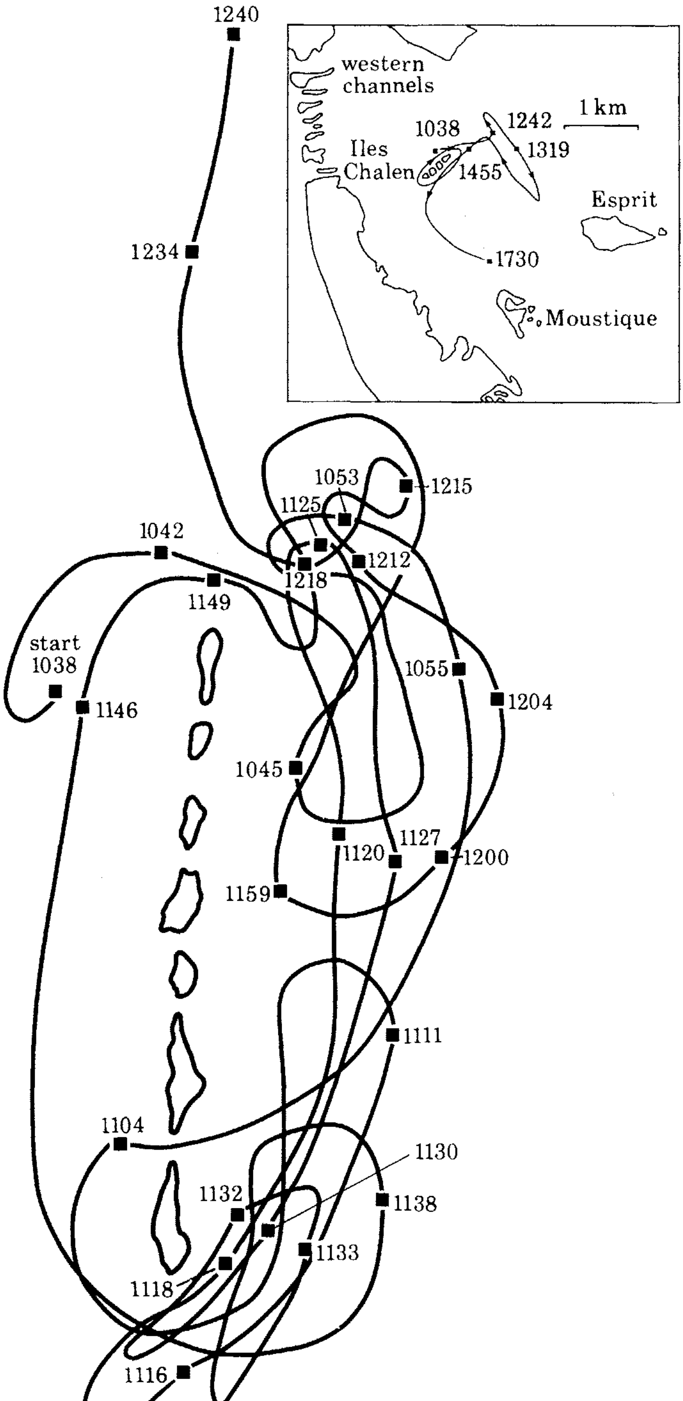

FIGURE 4. Detailed movements of a 120 cm t.l. *Carcharhinus melanopterus* tracked for 2 h around Iles Chalen (site E) in the lagoon at Aldabra with, inset, the general pattern of movement of this shark over 7 h.

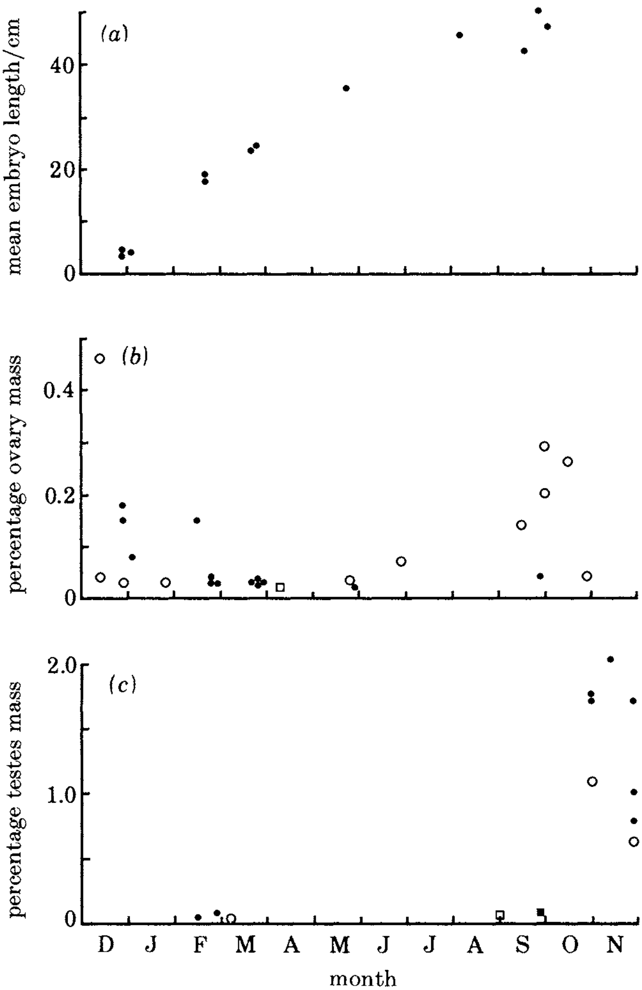

FIGURE 5. (*a*) The relation between mean embryo total length and time of year for *Carcharhinus melanopterus* from Aldabra. (*b*) The relation between relative ovary size (ovary mass/total body mass × 100) and time of year for *Carcharhinus melanopterus* from Aldabra. Solid circles; pregnant, open circles; not pregnant, and open square; immature. (*c*) The relation between relative testes size (testes mass/total body mass × 100) and time of year for *Carcharhinus melanopterus* and *Negaprion* from Aldabra. Solid symbols; *Carcharhinus melanopterus*, open symbols; *Negaprion*. Circles; mature, squares; immature.

Growth data from tagging were available from 243 *C. melanopterus* from the lagoon and covered the total size range of the species at Aldabra. Individuals were at liberty for up to 324 d and on recapture 75 % showed an increase in length. Of fish that had apparently decreased in size, 80 % had been at liberty for less than six months. To construct an age–length curve it is necessary to relate the growth increment to fish size. However, a plot of growth increment per unit time against the average length during the growing period (Jones 1976) for *C. melanopterus* showed no significant difference between the growth of small and large individuals

($r = 0.018, p > 0.05$). It is therefore not possible to construct a growth curve which conforms to the asymptotic relation typical of fish growth. The average growth rate for *C. melanopterus* was 2.9 millimetres per month (s.d. 1.9), with no detectable difference between the sexes. Growth *in utero* is much faster and even in near-term embryos of 45–50 cm t.l. is more than 20 millimetres per month (figure 5*a*). Owing

TABLE 6. *C. MELANOPTERUS* POPULATION SIZE AND DENSITY AT MAJOR TAGGING SITES IN THE LAGOON AT ALDABRA

site	mean population size	confidence limits	individuals per square kilometre	biomass / $g\ m^{-2}$
A	307	265–355	80	0.6
B	154	129–185	129	0.9
C	123	99–154	47	0.3
D	85	43–199	60	0.4
E	69	47–107	198	1.4
F	53	18–263	19	0.1
area 1	2055	1762–2348	62	0.4

95% Confidence limits for area 1 from standard deviation, for sites A–F from Poisson distribution (Ricker 1943). Biomass calculated from length–mass relations.

to the possibility of initial measuring inaccuracies the quality of growth data obtained from tagging would be expected to improve with time, especially if growth rates were very slow. However, in this study the results were not improved when only recaptures after nine months were considered.

Some three years after this study was carried out, data on four tags were received from the warden of Aldabra, two of which were from *C. melanopterus*. A 129 cm t.l. female was recovered after *ca.* 2.5 years from its tagging site. No size on recapture was given. A female of 116 cm t.l. on tagging was at liberty for 1426 d during which time it grew 6 cm (1.5 cm a^{-1}). This shark had been recaptured three times previously, no growth data were available on first recapture but on second recapture it had grown 2.5 cm in 72 d (12.5 cm a^{-1}) and on third recapture 4.7 cm in 324 d (2.8 cm a^{-1}). This specimen was presumably mature when originally tagged and the recapture information suggests increasing refinement of growth data with time. All recaptures came from the same area.

Population estimates for *C. melanopterus* were determined for a number of tagging sites where the majority of growth data was obtained (sites A to F in figure 1 and table 6). A modification of Schnabel's method (Ricker 1943; Jones 1976) for multiple marking experiments was used. Population densities for each site were computed within a circle of radius equal to the average distance moved by individuals from that site. Movement of tagged fish between adjacent sites gave evidence of the degree of immigration and emigration. Density figures were then adjusted for emigration knowing the percentage of sharks moving outside the calculated area (table 6). As a comparison an overall figure was calculated for an area of 33 km^2 (area 1 in figure 1 and table 6) containing all the movements of sharks

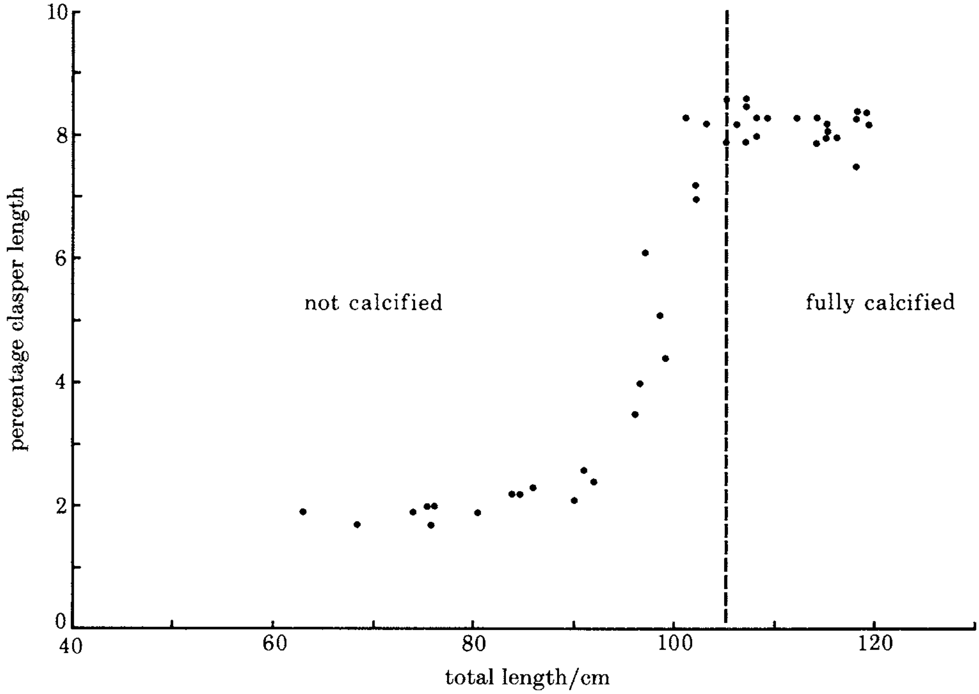

FIGURE 6. The relation between relative clasper size (100 × clasper length/total body length) and total body length (cm) for *Carcharhinus melanopterus* from Aldabra.

from these sites. Although *C. melanopterus* was tagged all around the lagoon (total area 208 km^2) no movement was observed in or out of this region.

Sexual maturity in male *C. melanopterus* is attained at about 105 cm t.l. (figure 6) using the criteria of clasper size and calcification (Bass *et al.* 1973).

The largest virgin (specimens were judged to be virgin if a hymen still sealed the vaginal opening) *C. melanopterus* from 30 specimens examined was 101.8 cm t.l., while the smallest mature (based on the condition of the ovary and genital tracts) non-virgin was 118.6, and the smallest pregnant individual 124.7 cm t.l. No fish between 101.8 and 118.6 cm t.l. were dissected. However, of 39 tagged specimens with mating scars, the smallest was 112 cm t.l. These data show that sexual maturity in female *C. melanopterus* is reached at about 110 cm t.l.

C. melanopterus has a restricted breeding season at Aldabra with parturition occurring in October (figure 5*a*). About half of the mature females are pregnant during the year and individuals breed every other year. Examination of the changes in relative ovary mass in figure 5*b* demonstrates the reproductive cycle in the two groups of mature female fish present during the year. Sharks at the onset of pregnancy in December still have a relatively high ovary mass owing to the presence of remaining ripe ova or large corpora lutea. During pregnancy these are reabsorbed and as the next batch of ova are still small the ovary mass is low and remains so until parturition in October. The ovary mass and ova diameter are still small at parturition in October showing that these fish will not become pregnant that year. The other group of fish start the year in a resting condition in December with a low ovary mass. Ova size starts increasing in June resulting in an increasing ovary mass which presumably reaches a maximum in October–November, suggesting that ovulation occurs at this time. The largest ova measured in this study were about 3.5 cm in diameter which is the size given at ovulation by Melouk (1957), although Gohar & Mazhar (1964) recorded ova as large as 5 cm.

TABLE 7. MEAN WET MASS OF THE EMBRYO, YOLK SAC AND FOETAL PLACENTA BY MONTH IN *C. MELANOPTERUS*, *N. ACUTIDENS* AND *C. WHEELERI* AT ALDABRA

	species	mass of embryo g	mass of yolk sac g	mass of placenta g
December	*C. melanopterus*	0.4 (10)	8.8 (9)	0
January	*N. acutidens*	0.9 (7)	21.6 (6)	0
February	*C. melanopterus*	33.8 (4)	74.4 (2)	7.6 (2)
March	*N. acutidens*	—	72.5 (2)	—
May	*C. melanopterus*	216.8 (5)	9.7 (2)	6.5 (2)
June	*C. wheeleri*	1920.8 (4)	6.6 (2)	22.9 (2)
August	*C. wheeleri*	1493.1 (3)	9.5 (1)	17.1 (1)
September	*C. melanopterus*	510.3 (8)	5.5 (2)	6.7 (2)

Sample size in parentheses.

Testes weight (figure 5*c*) follows a similar cycle peaking in October–November, at which time the seminal vesicles are turgid with sperm, indicating the onset of the mating season. The percentage of females bearing mating scars is highest in November providing further confirmation of the mating period. The gestation period is thus 10–11 months with ovulation and mating occurring in October–November, early pregnancy in December and parturition the following October.

C. melanopterus is viviparous with a well developed yolk sac placenta (Gilbert 1981). The embryos are encased by an egg membrane and enclosed in separate uterine compartments. At Aldabra the size of the eggcase following ovulation measures 3.9 cm by 2.6 cm. In December the embryos average 4 cm t.l., have well developed external gills, and are attached to the as yet unmodified yolk sac by a short umbilical cord. By February the placenta has formed and is weakly attached to the uterine wall. The umbilical cords are without appendiculae, the embryos still have external gills, and fin markings are becoming apparent. The placentae are well established by March (mean embryo size 24 cm t.l.) although the yolk sac still contains diffuse, pale yellow yolk. External gills have been reabsorbed and all the fins have clear black markings. By May the yolk sac is greatly reduced and contains only clear fluid. Data on changes in mass of the yolk sac and placenta through pregnancy are presented in table 7. Liver size appears to decline during pregnancy, presumably as food reserves become depleted following establishment of the placenta in February–March ($W = 8.531-0.0108\,T$, where W is liver mass expressed as a percentage of body mass and T is time in days). However, the relation was not significant, $p > 0.10$, probably owing to the small sample size (16).

TABLE 8. STOMACH CONTENTS OF SHARKS AT ALDABRA

species	number of specimens	number empty	number everted	number containing: fish	cephalopod	other mollusc	crustacean	miscellaneous
C. melanopterus	42	21	0	15	1	2	4	10
N. acutidens	24	8	2	10	1	2	1	6
C. albimarginatus	8	3	0	5	1	0	0	0
C. wheeleri	8	4	2	1	1	0	0	0
C. falciformis	7	4	1	2	0	0	0	2
Nebrius concolor	6	0	0	3	6	1	0	3

TABLE 9. PREY ITEMS FROM 21 *C. MELANOPTERUS* STOMACHS AT ALDABRA

category	prey item	number of stomachs in which item occurred
fish	unidentified	10
	Balistid	2
	Labrid	2
	Scarid	1
	Ctenochaetus strigosus	1
	Scarus ghobban	1
	Lethrinella xanthocheilus	1
	Upeneus arge	1
crustacean	unidentified	1
	Decapod	1
	Brachyuran	2
	Portunid	1
	Stomatopod	2
mollusc	Cephalopod	1
	bivalve	1
	Gastropod	1
	Aplysia spp.	1
miscellaneous	*Thalassia* spp.	7
	algae	3
	Hydrozoan	2
	Bryozoan	1
	coral	2
	stones	1
	eye lens	1
	unidentified	2

The two smallest free-swimming *C. melanopterus* captured at Aldabra were 49 and 52 cm t.l. males taken in December. The smaller shark had a clear umbilical scar (no note was made of the 52 cm specimen). The largest pups examined were 49.6 and 51.4 cm t.l., indicating the size at birth to be about 50 cm t.l. The average litter size from 15 specimens was 3.7 with a range of 2–5. There was no relation between length of the mother and litter size over the range examined (122.8–134.2 cm t.l.). The proportion of the sexes among embryos was 44.1 % female (34 embryos from nine specimens).

Data on stomach contents of *C. melanopterus* separated into broad prey categories are given in table 8 and show that fish is the main item in the diet.

Miscellaneous items include turtle grass, coral, Hydrozoa, Bryozoa and stones. A more detailed breakdown of prey items taken by *C. melanopterus* is presented in table 9. No difference was noted in the number of stomachs containing food between *C. melanopterus* captured at night (11 specimens) or in the day (30 specimens) from the lagoon. The size of fish prey taken by nine *C. melanopterus* of 84.0–129.9 cm (mean 109.1 cm) t.l. ranged from 5 to 45 cm (mean 16.8 cm) t.l.

The length (L) mass (W) relation for 42 *C. melanopterus* 68.5–136.1 cm t.l. is described by the equation:

$$W = 1.004 \times 10^{-6}\, L^{3.39}\ (r = 0.988).$$

The data on 12 males and 30 females were pooled owing to the small sample size. The length–mass equation for 44 uterine embryos ranging from about one month old (3.0 cm t.l.) to near term pups (51.4 cm t.l.) is also given below:

$$W = 5.991 \times 10^{-6}\, L^{2.97}\ (r = 0.998).$$

The equations were obtained by fitting a power curve of the form $y = ax^b$ by the method of least squares. The difference between the two regressions is highly significant ($p < 0.001$).

Negaprion acutidens Rüppell (*lemon shark*)

Negaprion is the second most abundant species in the lagoon with small individuals up to about 180 cm t.l., occupying similar shallow-water habitats to *C. melanopterus*. Larger individuals were sometimes seen in shallow water in the lagoon during the day but were very wary of the boat and almost all were caught at night near deeper water associated with Main Channel. *Negaprion* occurs on the reef flat and close to the reef edge under similar conditions to *C. melanopterus* (table 2). It is most numerous along the perimeter of the southern half of the lagoon where turbid, silty conditions seem to favour it, rather than *C. melanopterus*. The highest catch rate recorded was 3.1 sharks per hour (0.8 h) just east of Vaqua (figure 1). Areas where the abundance exceeded 1.0 sharks per hour are shown in figure 1.

The size distribution of *Negaprion* at Aldabra is shown in table 1 and figure 7*a*, where the sexes were combined owing to the small sample numbers. The length at birth is about 60 cm t.l. and all sizes are represented in the catch. The maximum length at Aldabra of about 240 cm is smaller than in other Indian Ocean areas where this shark attains at least 300 cm t.l. (Bass *et al.* 1975*b*). Small *Negaprion* up to about 180 cm were caught during the day, accounting for the drop in the size–frequency distribution at about 160 cm t.l., while the larger fish were almost all taken at night. The single, large mode at 230–240 cm t.l. is probably an artefact. Several fish in this size range were tagged and only approximate lengths were recorded owing to the difficulty in measuring these large sharks at night.

The overall proportion of the sexes for *Negaprion* was 59.8 % female (169 fish). Monthly variations are shown in table 3. Only June and August showed a predominance of males.

Overall, 131 *Negaprion* were tagged at 43 sites around Aldabra. Nineteen individuals were recaptured (14.5 %) of which five were recaught more than once

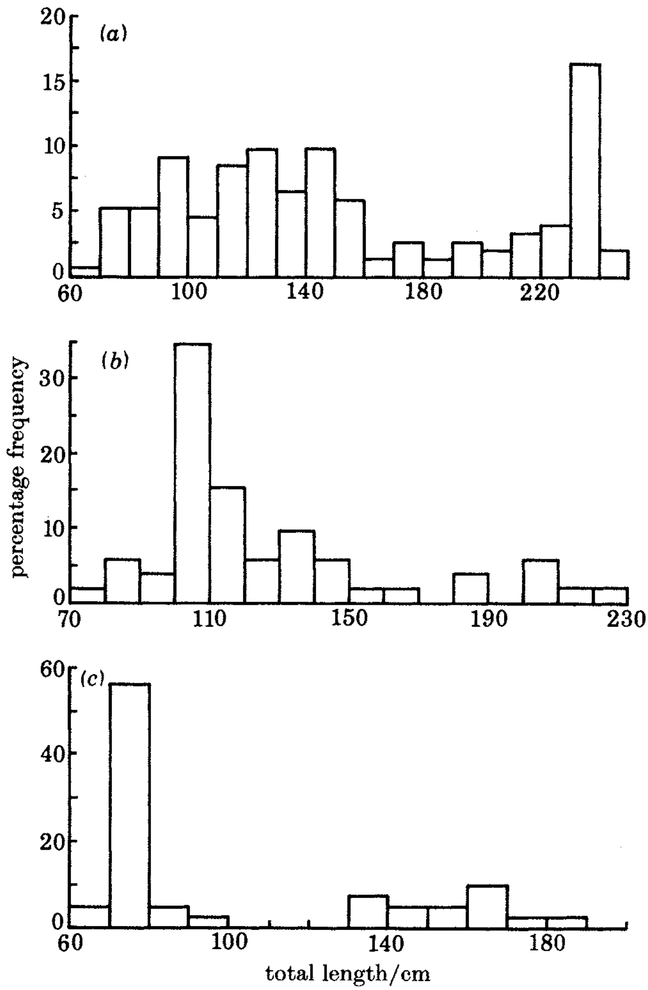

FIGURE 7. Length–frequency distribution for (*a*) *Negaprion acutidens*, (*b*) *Carcharhinus albimarginatus*, (*c*) *Carcharhinus wheeleri* at Aldabra.

and some were caught four times. All but one of the *Negaprion* recaptured were less than 130 cm t.l. and these individuals showed very similar movements to *C. melanopterus*. When the data from all sites were combined, 52 % of recoveries were made at the tagging site, 83 % within 1 km and 91 % within 2 km. When the data for those sharks which did not move are excluded the average distance moved was 1.3 km and the maximum distance travelled by an individual was 5 km. One *Negaprion* tagged on the reef flat was subsequently recaught in the lagoon adjacent to Main Channel. This shark could have travelled along the reef flat and entered the lagoon through Main Channel or moved directly across the lagoon via the Western Channels. The proportion of the sexes of tagged *Negaprion* was 55.2 % female, that of individuals recaught only once was 57.1 % female while of the five multiple recaptures all were female.

Growth data were available for 16 *Negaprion* (four males) from 74.5 to 121.2 cm t.l. on release of which all but one had increased in length on recapture after 41–294 d. No relation was apparent on plotting the increment per unit time against the average length during the growing period. However, all these fish were immature and represented only 26 % of their total size range at Aldabra. The average growth rate, both sexes combined, was 10.4 millimetres per month. Growth *in utero* was much faster, being of the same order as in *C. melanopterus*.

Two long-term recoveries of tagged *Negaprion* were made. Both were females at liberty for 1426 d, one specimen was 127 cm t.l. on tagging and grew 60 cm (15.4 cm a^{-1}). The other was 136 cm and grew 61 cm (15.6 cm a^{-1}). This growth rate for immature specimens is slightly higher than the 12.5 cm a^{-1} determined during the year spent on Aldabra. Both these *Negaprion* were recaught in the same area where they were tagged.

Negaprion has a reproductive cycle almost identical to that of *C. melanopterus* at Aldabra. The gestation period is 10–11 months with about half the mature females breeding each year. Parturition occurs in October, ovulation and mating during October–November and early pregnancy in December. Determination of the size at sexual maturity was affected by the shortage of specimens, particularly in those dissected, between 190 and 220 cm t.l. However, both sexes appear to reach sexual maturity at about 220 cm t.l. at Aldabra. The smallest free-swimming *Negaprion* captured was a 65 cm male taken in January, while the largest embryo examined was 54.5 cm t.l. The size at birth is therefore presumed to be 55–60 cm t.l. The egg case, following ovulation, measures some 9 cm by 3.6 cm. Placental formation is apparent by March at which time the embryos still have the remnants of their external gills. The umbilici are without appendiculae. The average litter size in *Negaprion* at Aldabra was 9.3 (range 6–12) in the four litters examined. The proportion of the sexes among embryos from the only litter where the sex was recorded was 66.7 % male.

Data on stomach contents of *Negaprion* are given in table 8. Fish recorded in the diet consisted of unidentified species from seven stomachs, balistids from three and scarids from one stomach. The cephalopod recorded was an octopod and the stomach containing crustacea had an isopod and an unidentified crab.

The length–mass relation for 24 *Negaprion* (75.0–242.1 cm t.l.) is described by the equation:

$$W = 1.208 \times 10^{-6}\, L^{3.29} \; (r = 0.998).$$

Data were not separated by sex because the sample was too small.

Carcharhinus albimarginatus Rüppell (silvertip shark)

All specimens of *C. albimarginatus* were caught within 1 km seaward of the reef edge with the exception of one individual taken just inside Main Channel, close to deep water, at night. They were caught both at the surface and at depths down to 75 m, and possibly 159 m, on droplines. Approximately equal numbers of each sex were captured (table 3) and the size distributions show that most were immature fish of 100–120 cm t.l. (figure 7*b*). While no pregnant individuals were captured at Aldabra, the size at birth in other Indian Ocean areas is between 70 and 80 cm t.l. (Bass *et al.* 1973). *C. albimarginatus* taken at Aldabra thus range from recently born individuals of about 70 cm to mature fish of 220 cm t.l. Insufficient numbers were caught to determine the maximum size, but elsewhere in the Indian Ocean it is around 280 cm t.l. (Bass *et al.* 1973).

Most of the 44 *C. albimarginatus* tagged were immature fish up to 150 cm t.l. This species was tagged only off the reef and in the western half of the atoll between Main Channel in the north and Dune d'Messe in the south. The return rate of this species (34%) was the highest of any of the sharks marked at Aldabra. Three individuals were recaptured more than once. This species was less restricted in its movements than *C. melanopterus* or *Negaprion* with 6.7% recaptured at the tagging site, 33% within 1 km and 67% within 2 km. Distances moved were larger and averaged 4 km, one individual having moved 7 km.

The average growth rate of five *C. albimarginatus* (three males) for which data were available was 7.3 millimetres per month. These sharks ranged from 87.5 to 134.0 cm t.l. on release and were at liberty between 73 and 266 d. As they were all small immature fish they were presumably at the faster stages of their growth.

Only three female *C. albimarginatus* were dissected. An individual of 110 cm was immature, a specimen of 188.1 cm was a mature virgin while another of 204.7 cm was fully mature and no longer virgin. The claspers of seven tagged *C. albimarginatus* were measured and a further four specimens were dissected. Males were fully mature by 202.4 cm t.l. and a plot of relative clasper size against body length suggested maturity at around 170–180 cm t.l. Of three mature males, testes mass was at a resting level (0.04% of body mass) in June, while in mid-December and late October testes masses were 0.21 and 0.36% of body mass, respectively. While no firm conclusions can be drawn from three individuals these values suggest a cycle similar to *C. melanopterus* and *Negaprion* (figure 5*c*).

Carcharhinus wheeleri Garrick (short-nosed blacktail shark)

C. wheeleri occurs along the reef edge, on the reef flat and in, or near the edge of, the deep water passes. Recently born pups were taken in the lagoon from the western Esprit Drainage channel (site A in figure 1) between November and March. The size at birth of *C. wheeleri* at Aldabra is 65–70 cm t.l. and the large mode in the length–frequency distribution (figure 7*c*) at about 75 cm t.l. represents these newly born individuals captured in the lagoon. The largest specimen (182 cm t.l.) is slightly bigger than the largest (172 cm t.l.) recorded by Wheeler (1962) from the Mauritius–Seychelles region.

Thirty-three *C. wheeleri* were tagged, of which 18% were recaptured. However, these were all newly born specimens tagged and recaptured at site A.

C. wheeleri males mature at about 110–120 cm t.l., but there were insufficient data to determine length at maturity in females. The smallest pregnant specimen captured was 145.7 cm t.l. Based on four litters, the smallest embryos occurred in January (34.4 cm t.l.) and the largest in June (68.7 cm t.l.) while two other pregnant *C. wheeleri* captured in August and October had embryos of 63.3 and 52.0 cm t.l. respectively. The largest embryo observed was 69.5 cm and the smallest free-swimming specimen 67 cm, suggesting the size at birth to be around 70 cm t.l. Between November and March, 27 recently born *C. wheeleri* were captured at site A near Esprit Island, suggesting that this region functions as a nursery area for at least part of this species population at Aldabra. No individuals of this size were caught during the rest of the year, or at any time elsewhere at Aldabra. Of the nursery population 77.8 % were caught in November, and 7.4 %, 11.1 %, 0 % and 3.7 % in December, January, February and March respectively. The mean size of the November fish was 75.1 cm (range 67–82 cm) t.l. This suggests that the peak of the parturition period is around October but that the season is more extensive than in *Negaprion* or *C. melanopterus* with some fish giving birth as early as July and others as late as February. *C. wheeleri* with near-term embryos had small ova (0.9–1.0 cm) and low ovary masses (0.03–0.06 % of body mass) suggesting they would not breed again that year. One individual captured in late February had a ripening ovary with maximum ova diameter of 1.6 cm and an ovary of 0.11 % of body mass. Of three mature males captured, one specimen collected in early January had small testes (0.09 % of body mass) and little sperm in the seminal vesicles or epididymus while two specimens captured in mid-February had ripening testes (0.26 and 0.35 % of body mass). Both of these sharks had little sperm in their seminal vesicles but the epididymus of the individual with the larger gonads was turgid with sperm.

C. wheeleri exhibits placental viviparity and the umbilici are without appendiculae. Litter sizes varied from two to four with a mean of 3.3 in the four specimens examined. The proportion of the sexes of 13 embryos from four litters was 53.8 % male.

Other species

Based on the capture of nine silky sharks, *Carcharhinus falciformis* Müller and Henle, together with several others observed during fishing, this species occupies the zone from about 0.5 km off the reef edge seawards at Aldabra. One individual was caught over 4000 m of water, 8 km west of the research station, the maximum distance offshore that fishing operations were conducted from the atoll. *C. falciformis* was often associated with large schools of *Thunnus albacares*. The giant sleepy shark, *Nebrius concolor* Rüppell, was caught only in the lagoon with the largest specimens taken close to feeder branches of Main Channel. This species was also observed and photographed on the reef edge during diving operations. Sphyrnid sharks were observed on 12 occasions along the reef edge, usually close to the passes. However, only one scalloped hammerhead, *Sphyrna lewini* Griffith and Smith, and one smooth hammerhead, *Sphyrna zygaena* Linnaeus, were caught. Although large tiger sharks, *Galeocerdo cuvieri* Lesueur, have been caught occasionally in the past, only one was captured, 0.5 km beyond the reef opposite the research station during this study.

The nine *C. falciformis* captured ranged from 208.4 to 245.8 cm t.l. and represent only a small segment of the size range of this species. A similar situation existed for *Nebrius* where all individuals other than a 120.1 cm female were between 172 and 237.8 cm t.l. The bigger individuals were taken together with the larger *Negaprion* in, or close to, the deep water of Main Channel at night.

Although only two *C. falciformis* were tagged, one was subsequently recaught 140 d later and 11 km from where it was marked. This species, being semi-oceanic in habit, might be expected to be far more wide ranging.

Three male and four female *C. falciformis* were dissected. A 216.1 cm female was a mature virgin while individuals of 220.3 and 220.7 cm t.l. were fully mature and no longer virgin. A 208.4 cm male was immature while fish of 239 cm t.l. and above were fully mature. The gonads of all mature fish were in a resting condition. Of four male *Nebrius*, a 198.5 cm specimen was immature, one of 225.6 cm was just mature and another of 237.8 cm t.l. captured in October, was fully mature with ripening testes (0.77 % of body mass). A 120.1 cm female was immature while another of 231.4 cm t.l. was fully mature. A male *Galeocerdo* of 229.2 cm and a male *S. zygaena* of 208.2 cm were immature while a female *S. lewini* of 250.3 cm t.l. was mature.

The stomachs of all six *Nebrius* examined contained cephalopods (table 8) of which all those identified (three out of nine) were octopods. The stomach of the *S. lewini* contained cephalopod material (five beaks and seven eye lenses) as did that of *S. zygaena* (six beaks), together with unidentified fish and algal material. The *Galeocerdo* had five tetrodontids, a fragment of mollusc shell and turtle grass in its stomach.

Discussion

Species composition and distribution

During the year spent at Aldabra ten species of shark were recorded (nine captured and one positively identified and photographed). Smith (1955) recorded an additional seven species, *Hexanchus griseus*, *Scoliodon palasorrah* (this species was possibly a misidentification of *Rhizoprionodon acutus*), *Carcharhinus limbatus*, *Mustelus manazo*, *Carcharias taurus* (*Odontaspis taurus*), *Stegastoma fasciatum* (*S. varium*) and a *Squatina* sp. The fact that Smith (1955) managed to record 14 species in three days was almost certainly due to the number of different collecting methods employed. In the present study only hook and line fishing was carried out. Forster *et al.* (1970) fished between 100 and 1000 m at Aldabra and accounted for several species not recorded by Smith (1955) or the present study (*Heptranchias perlo*, *Pseudotriakis microdon*, *Centrophorus* spp., *Centrophorus squamosus*, *Centroscymnus owstoni*, and *Squalus* spp.). Forster (1982) also fished with droplines at Aldabra during the present study, but no deep water sharks were caught.

The three most common sharks on coral reefs of the tropical and subtropical Indo-Pacific region are considered to be *Carcharhinus melanopterus*, *Carcharhinus amblyrhynchos* and *Triaenodon obesus* (Randall 1977). Based on hook and line fishing, *C. melanopterus* is certainly the most abundant species in the lagoon at Aldabra, while *Negaprion acutidens* and *C. wheeleri* are the next most common species as determined by the present study. *C. wheeleri* and *C. amblyrhynchos* are very similar and may yet be shown to be synonymous with the collection of further material. At Aldabra *Negaprion* rather than *Triaenodon* is abundant in the lagoon, presumably because the extensive sand flats and mangrove areas suit this species better, particularly the juveniles which occupy similar areas to *C. melanopterus*. *T. obesus* was seen and photographed during the present study but was never caught on hook and line. While this species is noted to be clumsy and ineffective in taking a mid-water bait (Hobson 1963) it seems highly unlikely that it is common at Aldabra. Both *C. melanopterus* and *C. wheeleri* (assumed here to be equivalent to *C. amblyrhynchos*) at Aldabra occupy similar habitats to other coral reef atolls (Hobson 1963; Bass *et al.* 1973; Randall & Helfman 1973; Randall 1977). The abundance, in terms of catch rate, of *C. melanopterus* was lower at night in all areas at Aldabra than during the day (table 2). However, night fishing was usually aimed at catching the larger *Negaprion* which were more difficult to catch during the day. Fishing was carried out at sites favourable to these *Negaprion* and far fewer lagoon sites were fished than during the day. It is possible that *Negaprion* competed more successfully for baits than *C. melanopterus*.

C. albimarginatus at Aldabra were caught within 1 km to seaward of the reef edge, while *C. falciformis* were taken from about 0.5 km seaward of the reef edge. Elsewhere in the south-west Indian Ocean *C. albimarginatus* is usually found near the edges of offshore banks and islands (Bass *et al.* 1973). However, it is occasionally taken further offshore (Fourmanoir 1961; Kato *et al.* 1967). At Aldabra *C. albimarginatus* were caught down to 75 m, and possibly 159 m, on droplines, while Forster *et al.* (1970) recorded this species down to 400 m and possibly even 800 m, while droplining in the south-west Indian Ocean. *C. falciformis* is principally oceanic in habit (Bass *et al.* 1973) and, as observed at Aldabra, is often associated with schools of tuna (Kato 1964) particularly *Thunnus albacares* (Bane 1966).

The larger *Nebrius* (more than 2 m), together with *Negaprion* of a similar size, were caught only where there was ready access to deep channels in the lagoon at Aldabra. Fourmanoir (1961) also found that these two species occupied similar habitats off Madagascar. The apparent scarcity of *Galeocerdo* at Aldabra is surprising in view of the large breeding populations of both sea birds and turtles, both of which are known to occur in the diet of this species (Fourmanoir 1961; Clark & von Schmidt 1965). The occurrence *S. zygaena* at Aldabra is interesting as this species is generally regarded as having an antitropical distribution (Gilbert 1967).

Movements and growth

All species for which recapture data are available at Aldabra show restricted movements, with *C. melanopterus* being very localized and usually remaining in a few square kilometres. This indicates little interchange between specimens from opposite ends of the lagoon. The high recapture rate of *C. albimarginatus*, and the fact that small fish tagged together were often recaught together, suggests that groups of small individuals patrol some 5 km of reef edge. Little information is available in the literature on movements of any of the species studied at Aldabra. Kato & Carvallo (1967) tagged 138 *C. albimarginatus* and four *C. falciformis* at the Revillagigedo Islands off the Mexican coast, obtaining recapture rates of 14 and 25 % respectively. Of 19 *C. albimarginatus* recaptured 14 were recovered at less than 1.6 km, and five at between 1.6 and 8 km from the tagging site. These sharks ranged from 54 to 163 cm (mean 69 cm) t.l. indicating that juvenile *C. albimarginatus* were restricted to the shallow water surrounding the islands. One *C. falciformis* was recaptured between 9.6 and 16 km from where it was tagged. In the same study

119 *C. falciformis* were tagged in the offshore area between southern California and Peru. Of four recaptures one came from the tagging area after ten weeks, two individuals travelled distances of 104 and 152 km in four and five months respectively, and the fourth moved 80 km in 3–4 d.

Johnson (1978) stated that tagging of *C. melanopterus* at Rangiroa Atoll, French Polynesia, indicated that some individuals remained in the same general area during the two years of the study. Hobson (1963) noted that he was seeing the same individual *C. melanopterus* day after day while working in a particular area at Eniwetok, Marshall Islands.

Conventional tagging, together with telemetric studies, has shown that *C. amblyrhynchos* at Rangiroa Atoll is localized and routine in its daily activity. One individual remained within 0.5 km^2 during the day and passed the same locations at approximately the same times during the 3 d that the acoustic tag was operational.

Tagging studies at Aldabra show that *C. melanopterus* has a very slow growth rate. The only published information on growth of *C. melanopterus* relates to a newly born individual maintained in captivity for two years (Randall 1977). During this period the shark grew from 48 to 94 cm t.l., equivalent to 22.9 cm a^{-1}. While growth in captivity cannot be taken as indicative of the growth rate in the wild this shows that *C. melanopterus* has the capacity for fairly rapid growth, at least in the first year of life. Tagging experiments can provide accurate growth data only if the marking process does not interfere with growth. The high recapture rate of *C. melanopterus* (23%), which includes numerous multiple recaptures of individual fish (32% of recaptures), together with the fact that released sharks sometimes returned immediately to the bait, suggests little trauma due to capture. Weed growth on some tags was considerable and it might be thought this would interfere with movements. However, from visual observations, even fish with considerable clumps of weed on the tag apparently experienced no difficulty in competing with untagged individuals for baits.

Fish standing crop estimates averaged from different coral reef regions vary from 35 to 193 g m^{-2} (Goldman & Talbot 1976) but any deductions based on biomass pyramids are complicated by the reversal of the 'traditional' pyramid in coral reef systems (Goldman & Talbot 1976). Although biomass estimates for *C. melanopterus* (table 6) do not appear high (unfortunately comparable data for other sharks are not available), it seems possible that *C. melanopterus* populations at Aldabra are limited by food resources. In many fish, intra-species competition may be reduced by the exploitation of different food resources by different size ranges. In the viviparous *C. melanopterus* newborn young have the same body form as adults and stomach content analysis at Aldabra shows that all sizes take very similar food items. *C. melanopterus* is a roving carnivore of the shallows and its diet overlaps that of other shark species in the lagoon, notably immature *Negaprion*. Although *Negaprion* is less abundant than *C. melanopterus*, biomass estimates were 0.1–0.5 g m^{-2}. There is also dietary overlap with predatory teleosts found in the same area such as sphyraenids, carangids, serranids, lutjanids and lethrinids. Aldabra has suffered minimal interference from man so the shark population is likely to be near the maximum that the environment can support. *C. melanopterus* has been shown to be very localized in its movements at Aldabra and it seems likely that the intensity of intra- and inter-species competition for food has resulted in a reduced growth rate.

The effect of population density on fish growth rates is well established although the exact relations between numbers, food supply and growth are still unclear (Le Cren 1958). In commercial culture fish may be held at a required size by varying the food supply and in certain stunted freshwater fish populations normal growth may be restored by increasing the food supply or reducing fish density (Alm 1946). However, there is little evidence of food-limited growth in marine fish outside captivity. Coral reefs are among the most productive ecosystems (Goldman & Talbot 1976) and theoretical ecologists suggest that food is rarely in short supply for coral reef fish and the resource more likely to be limiting is space (Smith & Tyler 1972; Sale 1977). While this may be true for the smaller residential species it seems unlikely for larger and more transient carnivores such as *C. melanopterus*.

Kato & Carvallo (1967) demonstrated a slower growth rate for juvenile *C. albimarginatus* from the eastern Pacific than was observed at Aldabra. Tag returns from six females 55.5–105 cm (mean 70.9 cm) t.l. at liberty between 5 and 9.5 months indicated an average growth rate of 3.1 cm a^{-1}. Eight males 60.5–113.5 cm (mean 73.1 cm) t.l. at liberty from 5 to 14 months showed more irregular growth with four fish having negative increments and the remainder averaging 5.4 cm a^{-1}. From observations on newborn *Negaprion brevirostris* (the Atlantic lemon shark) Springer (1950) estimated growth from birth to 175 cm t.l. in 650–700 d. Moss (1967) arrived at a similar estimate for this species based on tooth-replacement rates. However, these rapid growth rates are not confirmed by the studies of Gruber (1981) who suggests a much slower rate of growth in this species. Gruber (1981) used a computer simulation model to show that *N. brevirostris* attained a size of about 175 cm t.l. in 45 months. He demonstrated that captive individuals grew four times faster than free-living specimens and stated that these studies clearly showed that food is a limiting factor.

Reproduction

While several authors have provided observations on reproduction in *C. melanopterus*, no single study has elucidated the breeding cycle in this species. At Aldabra the size at birth was about 50 cm t.l. Fourmanoir (1961) stated that *C. melanopterus* was born at 46–52 cm off Madagascar. In the Red Sea Melouk (1957) recorded embryos of 40 and 50 cm and Gohar & Mazhar (1964) caught a free-swimming specimen of 61 cm t.l. The size at birth in the Pacific may be somewhat smaller as free-swimming individuals of 33, 36 and 37 cm have been recorded (Bonham 1960; Bass *et al.* 1973; Randall & Helfman 1973). Bass *et al.* (1973) provide evidence that sexual maturity in males is attained between 70 and 109 cm t.l. and between 92 and 112 cm t.l. in females. At Aldabra males mature at about 105 cm and females 110 cm t.l. Information in the literature on the breeding cycle of *C. melanopterus* is confused and fragmentary. Fourmanoir (1961), without presenting further evidence, says that there are two reproductive seasons off

Madagascar, June–July and December–January. Gohar & Mazhar (1964) also suggested two periods of parturition, January and June, in the Red Sea. However, Melouk (1957) suggested a different pattern from his work in the Red Sea. He postulated a 16-month gestation period based on the occurrence of two size groups of embryos during some three months of the year. At Aldabra *C. melanopterus* females breed every other year with ovulation and mating occurring in October–November, early pregnancy in December and parturition the following October. The gestation period is thus 10–11 months.

Negaprion has an almost identical cycle to that of *C. melanopterus* at Aldabra. Birth occurs at 55–60 cm t.l., maturity is attained about 220 cm t.l., females breed every other year and the gestation period is 10–11 months. The periods of ovulation, mating and parturition are the same as for *C. melanopterus*. Fourmanoir (1961) provides the only published data on reproduction of *N. acutidens* in the Indian Ocean. He recorded embryos of 62 cm t.l. in August and stated that the young measure 70–80 cm t.l. at birth. The length at maturity was given as about 240 cm, a female taken in January was reported to have enlarged ova, and the birth period was given as October–November. One litter containing 13 embryos was recorded. This information is in reasonable agreement with that obtained at Aldabra.

Summarizing the data of Fourmanoir (1961), Wheeler (1962) and Bass *et al.* (1973): *C. wheeleri* is born at between 65 and 75 cm t.l., both sexes mature around 120 cm t.l., and litter sizes range from one to four with a mean of 2.5. Mating occurs from July to September with parturition about a year later. At Aldabra the size at birth was about 70 cm, males matured at some 120 cm t.l. (insufficient data were available to determine size at maturity in females) and litter sizes varied from two to four with a mean of 3.3. The parturition period appeared to be extensive with births occurring from July through to February with a peak in October. Limited data suggested ovulation and mating around March. Reproductive information on *C. albimarginatus* at Aldabra was scant, males attained maturity at about 170–180 cm while females matured at about 200 cm t.l. These sizes are in agreement with those given by other workers in the Indian Ocean (Fourmanoir 1961; Wheeler 1962; Bass *et al.* 1973; Gubanov 1978). No pregnant *C. albimarginatus* were caught at Aldabra and the only information pertaining to the breeding cycle was restricted to males, suggesting mating in the November period. The data of Fourmanoir (1961), Wheeler (1962), and Bass *et al.* (1973) indicate parturition in December–January after a gestation period of about a year. However, Gubanov (1978) states that parturition may occur considerably later in the year (April–May) and that there may be little seasonality in the breeding cycle of this species.

Feeding

The diet and feeding behaviour of *C. melanopterus* in the Indo-Pacific has been reviewed by Bass *et al.* (1973) and Randall & Helfman (1973). Hiatt & Strasburg (1960) described this shark as a roving carnivore and scavenger of the shallow reef flats at Eniwetok Atoll, Marshall Islands. Dietary studies indicate a high proportion of empty stomachs with 58 % of 24 stomachs examined from Tahiti being empty

(Randall & Helfman 1973) and 62 % of 13 specimens from the south-west Indian Ocean containing no food (Bass *et al.* 1973). The most common items in the stomachs of *C. melanopterus* containing food were fish, molluscs and crustaceans (Randall & Helfman 1973). At Aldabra half of 42 *C. melanopterus* stomachs examined were empty. Fish were the commonest item in the diet and, as in other Indo-Pacific areas, tended to be species associated with shallow, sandy or coral areas. The number of miscellaneous items found in the stomachs, together with crustaceans and molluscs are evidence of this shark's catholic diet. Randall & Helfman (1973) and Johnson (1978) suggested that *C. melanopterus* may be more active and feed more at night. However, no difference was noted in the number of stomachs containing food between specimens captured at night or in the day in the lagoon at Aldabra, although the sample was limited. *Negaprion* had a similar diet to *C. melanopterus* at Aldabra, while limited data on *C. albimarginatus*, *C. wheeleri* and *C. falciformis* indicated that fish were the major component of their diet. *C. albimarginatus* is known to feed over an extensive depth range (Forster *et al.* 1970) including both benthic and pelagic fish in its diet (Bass *et al.* 1973). *C. wheeleri* and *C. falciformis* are also reported to take both surface- and bottom-dwelling fish, as well as cephalopods (Backus 1957; Strasburg 1958; Wheeler 1962; Bass *et al.* 1973). *C. falciformis* also eats tuna (*Thunnus albacares*) (Bane 1966). Octopus were the principal item in the diet of *Nebrius* at Aldabra. Fourmanoir (1961) noted that specimens from Madagascar fed chiefly on octopus and xanthid crabs, while Gohar & Mazhar (1964) recorded cephalopods (along with pieces of coral and fish) in the diet of this shark from the Red Sea. Tanaka (1973) demonstrated that the related nurse shark, *Ginglymostoma cirratum*, is capable of suction feeding, enabling this essentially nocturnal species to extract prey from holes and crevices in the coral. *Nebrius* may also be basically nocturnal and employ a similar feeding mechanism. This may explain how this sluggish shark is able to capture active prey such as a *Scomberoides* recorded from a *Nebrius* stomach in the present study.

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