

Distribution, reproduction and diet of the gray reef shark *Carcharhinus amblyrhynchos* in Hawaii

Bradley M. Wetherbee^{1,*}, Gerald L. Crow², Christopher G. Lowe¹

¹Zoology Department, 2538 The Mall, University of Hawaii, Honolulu, Hawaii 96822, USA

²Waikiki Aquarium, 2777 Kalakaua Ave., Honolulu, Hawaii 96815, USA

ABSTRACT: Distribution, reproduction, and diet of the gray reef shark *Carcharhinus amblyrhynchos* were investigated using data collected during shark control programs in the main Hawaiian Islands (MHI) and during research fishing in the Northwestern Hawaiian Islands (NWHI). A total of 472 sharks were caught between 1967 and 1980. These sharks have a restricted distribution in the MHI; they were collected only in the vicinity of Niihau and Molokini islands, but were one of the most abundant sharks throughout the NWHI. Catch rate was higher for males than for females in standard longline fishing at all locations and during all seasons. Most sharks were caught at depths between 20 and 60 m, and depth distribution of the sexes was similar, although females were more common at shallower depths. Males ranged in size from 79 to 185 cm total length (TL), and matured at between 120 and 140 cm TL. Females ranged in size between 63 and 190 cm TL and matured at about 125 cm TL. Litter size ranged from 3 to 6, with an average of 4.1 pups. Size at birth was estimated to be just over 60 cm TL. Most sharks (85%) consumed teleosts, but some fed on cephalopods (29.5%), and crustaceans (4.9%). For sharks in the largest size classes, the frequency of occurrence of teleosts declined, whereas that of cephalopods increased.

KEY WORDS: Gray reef shark · Hawaii · Distribution · Reproduction · Diet

INTRODUCTION

The gray reef shark *Carcharhinus amblyrhynchos* is widely distributed in the Indian, and western and central Pacific Oceans, ranging from the eastern coast of southern Africa, to the Hawaiian and Tuamotu archipelagos (Garrick 1982, Compagno 1984). This shark is common on outer reef slopes of islands and continents, as well as in lagoons and passes to the open ocean (Hobson 1963, McKibben & Nelson 1986). It is distinguished from other carcharhinids by the absence of an interdorsal ridge, and the presence of a conspicuous black margin on the trailing edge of the caudal fin (Johnson 1978, Garrick 1982). However, Compagno (1984) suggested that the very similar appearing black tail reef shark *Carcharhinus wheeleri* may be a synonym of *C. amblyrhynchos*.

The gray reef shark has attained a reputation for aggressiveness and has been responsible for a number of attacks on humans (Hobson et al. 1961, Fellows & Murchison 1967, Read 1971). Not surprisingly, most studies have concentrated on behavioral aspects, such as feeding (Hobson 1963), activity patterns (McKibben & Nelson 1986), and agonistic display (Johnson & Nelson 1973, Barlow 1974, Nelson 1982, Nelson et al. 1986). Age and growth of this shark have also been investigated (DeCrosta et al. 1984, Radtke & Cailliet 1984). This species forms part of the shark fishery in Thailand, and is caught for flesh and fins in other locations (Compagno 1984, Last & Stevens 1994). Despite its wide distribution, use in scientific studies, and occurrence in fisheries, very little is known about the life history of *C. amblyrhynchos*.

The gray reef shark is one of the most abundant sharks in the low, remote, largely uninhabited, Northwestern Hawaiian Islands (NWHI), and also occurs in the main Hawaiian Islands (MHI) (Wass 1971,

*E-mail: bwetherb@zoogate.zoo.hawaii.edu

DeCrosta et al. 1984). The purpose of this study is to provide information on the distribution, reproduction, and diet of the gray reef shark based on data collected from sharks captured during fishing programs in Hawaii.

METHODS

Most of the data used in this study came from original data sheets of the Hawaii Cooperative Shark Research and Control Program, which ran from 1 June 1967 through 30 June 1969 (Tester 1969). In this program, sharks were captured using standard longlines, light-tackle longlines (12 hooks), and handlines. Standard longlines consisted of three 800 m sections, 24 hooks per section. Lines with hooks baited primarily with skipjack tuna *Katsuwonus pelamis* were set late in the afternoon, parallel to shore, in depths averaging 45 m, and were retrieved the following morning. Fishing was conducted from a tuna fishing boat in designated areas around the 8 MHI (Wetherbee et al. 1994).

Sharks were also captured during control programs that operated in the MHI in 1971 and 1976 (see Wetherbee et al. 1994). Data collected for sharks captured with longlines, handlines, and by spearfishing in the NWHI between 1978 and 1980 (DeCrosta et al. 1984) were also examined. Additional data came from sharks captured at Enewetak Atoll and Johnston Atoll (see Wass 1971). The data from both atolls was combined since the exact site of capture was not differentiated.

Depth of capture, precaudal length (PCL), total length (TL), sex, and weight (occasionally) were recorded for each shark. All lengths in this study refer to TL. For males, the length and degree of calcification of claspers were noted, and for females, the diameter of the 6 largest ova and uterus width were measured. The number, sex, and TL of embryos in pregnant females were also recorded. We classified males with elongate (>120 mm) and calcified claspers as mature, and those with small uncalcified claspers as immature. Females with large developing ova and large uteri were classified as mature, whereas those with small ova (<5 mm) and thin uteri (<5 mm) were classified as immature. Some small sharks were measured, tagged and released in the MHI.

Stomach contents were identified to the lowest possible taxa and were quantified on the basis of percentage of occurrence: (number of stomachs that contained a prey item/number of stomachs that contained food) × 100. Dietary overlap was calculated for small (50–100 cm), medium (100–150 cm) and large (150–200 cm) size classes using the Simplified Morisita Index (C_{HI}) (Krebs 1989). Degree of overlap was consid-

ered low (0–0.29), medium (0.3–0.59), or high (>0.6), following Langton (1982). Prey diversity of each of the 3 size classes was calculated using the Shannon-Weiner Diversity Index (H') (Krebs 1989).

RESULTS

Distribution

A total of 367 gray reef sharks were caught in Hawaii, 277 from the MHI and 90 from the NWHI (Table 1). All but 3 of these sharks from the MHI were captured during the 1967 to 1969 Hawaii Cooperative Shark Research and Control Program. The other 3 MHI sharks were captured in the smaller-scale shark control programs conducted in 1971 and 1976. Only limited data were available for 105 sharks captured at Johnston and Enewetak atolls. Almost all sharks from the MHI were captured at either Niihau or Molokini. By far the largest number of sharks (189) was captured at Niihau, a low island located at the northern end of the MHI, which is inhabited by only a few hundred native Hawaiians (Fig. 1). Thirty-six sharks were caught at Ka'ula Rock, a small island located 40 km SW of Niihau, and 45 sharks were caught at Molokini, the remnant of a small crater near the island of Maui.

In longline fishing in the MHI, the highest catch rates were at Molokini, Ka'ula Rock, and Niihau (Table 1). The overall longline catch rate was 0.32 sharks/100 hooks, and for only those areas where gray reef sharks were captured, the rate was 1.52 sharks/100 hooks (on 4673 hooks). Although the majority of fishing in the MHI was conducted in waters surrounding the island of Oahu, not a single gray reef shark was caught on 11905 longline hooks set near this island (see Wetherbee et al. 1994). However, Wass (1971) reported that several gray reef sharks were captured off Oahu in other fishing.

The composition of catches in the MHI varied with gear used. Of 71 sharks captured on longlines, 40 were mature (31 males 9 females), and 26 were immature (15 males 11 females). In handline fishing, all but 4 of 179 sharks caught were immature. Niihau was the only location where a large number of mature sharks was captured with either gear (37 sharks). In areas where sharks were abundant, immature sharks were caught more frequently than mature sharks (Table 1).

In the NWHI, sharks were caught virtually everywhere that fishing was conducted (Table 1). In longline fishing, the highest catch rates were at Necker Island (although only 16 hooks were set) and French Frigate Shoals. The overall catch rate of 8.78 sharks per 100 hooks for the NWHI was substantially higher than for the MHI. Again, longline fishing resulted in the cap-

Table 1. *Carcharhinus amblyrhynchos*. Numbers of hooks set, sharks caught, and catch per unit effort, CPUE (sharks per 100 hooks) at locations where gray reef sharks were captured in the main Hawaiian Islands (MHI), Northwestern Hawaiian Islands (NWHI), and Johnston and Enewetak atolls on longlines (LL) and handlines (HL). F: females, M: males, FFS: French Frigate Shoals

Location	No. of LL hooks	Mature		Immature		Unknown	Total	CPUE	
		F	M	F	M				
MHI									
Niihau	LL	2020	6	27	6	10	2	51	2.52
	HL		1	3	56	60	18	138	
Ka'ula Rock	LL	168	0	3	0	3	1	7	4.17
	HL		0	0	16	9	4	29	
Kauai	LL	709	2	0	0	0	1	3	0.42
Maui	LL	72	0	0	1	0	0	1	1.39
Molokini	LL	63	0	0	4	2	0	6	9.52
	HL		0	0	20	14	5	39	
Kaho'olawe	LL	152	1	1	0	0	0	2	1.31
Hawaii	LL	1489	0	0	0	0	1	1	0.07
Total		4673	10	34	103	98	32	277	1.52
NWHI									
Midway	LL	79	0	0	3	1	0	4	5.06
	HL		0	0	7	6	0	13	
FFS	LL	383	8	32	0	0	0	40	10.44
	HL		4	3	1	0	3	11	
Maro Reef	LL	80	2	1	0	0	0	3	3.75
	HL		0	0	4	2	1	7	
Necker	LL	16	0	2	0	0	0	2	12.5
	HL		2	0	0	0	1	3	
Laysan	HL		2	0	0	0	0	2	
Pearl & Hermes	HL		0	0	0	0	1	1	
Nihoa	HL		0	0	2	2	0	4	
Total		558	18	38	17	11	6	90	8.78
Johnston & Enewetak atolls			51	33	10	7	4	105	

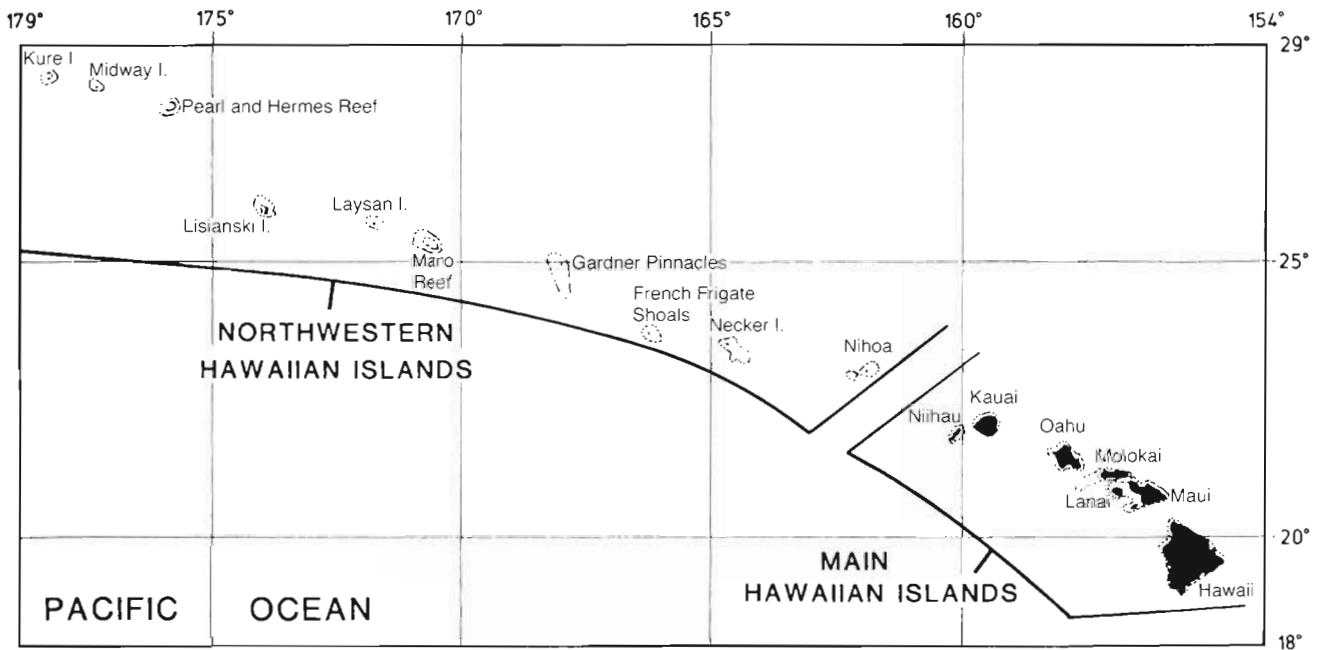


Fig. 1. Map of the Hawaiian Archipelago

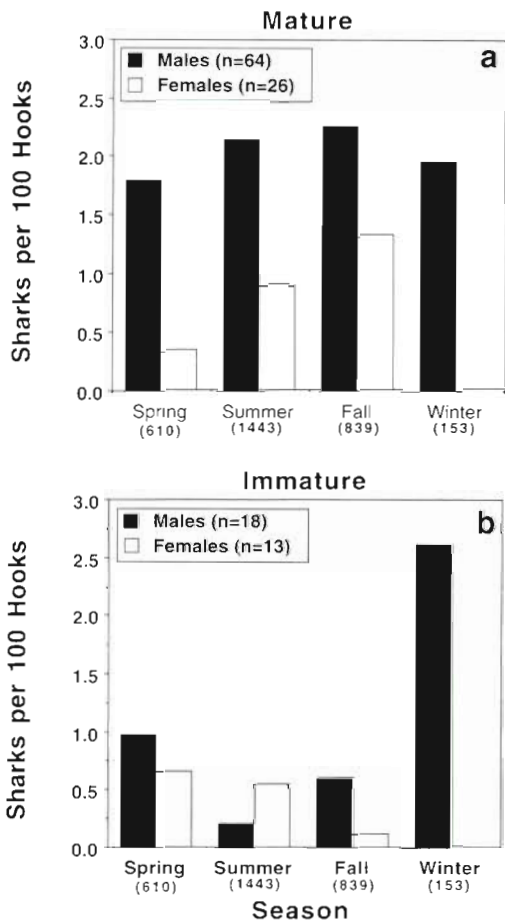


Fig. 2. *Carcharhinus amblyrhynchos*. Catch rate (sharks per 100 hooks) during different seasons for gray reef sharks captured in longline fishing in the main Hawaiian Islands. (a) Mature sharks; (b) immature sharks. Numbers in parentheses are hooks set during each season

ture of primarily mature sharks (45 of 49 sharks were mature), with a predominance of males (35 males : 10 females). For sharks captured by handline or spear, 11 were mature and 24 were immature. In contrast to Hawaii, fewer mature males than females were caught at Enewetak and Johnston atolls (Table 1).

In the MHI, the catch rate of mature males on longlines was relatively constant throughout the year, but was more variable for mature females, and no mature females were captured in winter (Fig. 2a). Sample size for immature sharks was small, but catch rates for males were also higher than for females (Fig 2b)

Although the depth ranges of capture for mature males and females largely overlapped, there is some indication that males occurred at greater depths (Fig. 3a). Sixteen of 19 mature sharks captured at depths of less than 10 m were females, whereas 14 of the 17 mature sharks captured deeper than 50 m were males. The majority of immature sharks of both sexes

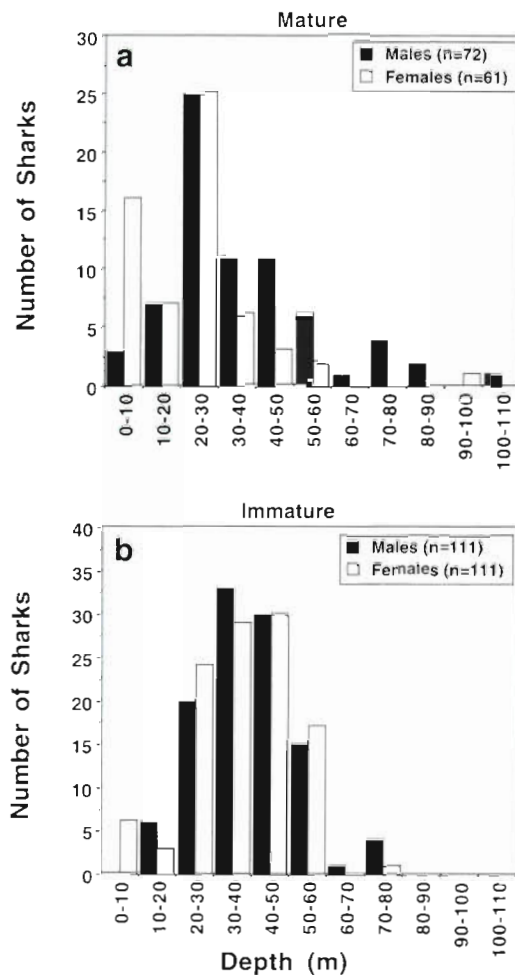


Fig. 3. *Carcharhinus amblyrhynchos*. Numbers of gray reef sharks captured at 10 m depth intervals in longline fishing in Hawaii. (a) Mature sharks; (b) immature sharks

were captured at depths between 20 and 60 m (Fig 3b). The average depth (± 1 SD) of capture for mature females was 22.2 m \pm 15.8 (range = 1 to 91 m, n = 61); for mature males, 36.2 m \pm 20.0 (range = 5.5 to 106.1 m, n = 72); for immature females, 37.1 \pm 13.4 (range = 5.5 to 73.2 m, n = 111); and for immature males, 39.3 \pm 12.8 (range = 11.0 to 80.5 m, n = 111).

Reproduction

Since total length measurements tend to be more variable when different observers take measurements, a linear regression was used to convert PCL to TL (in cm):

$$TL = 4.146 + 1.262 PCL \quad (r^2 = 0.995, n = 409)$$

A length-frequency histogram for all sharks examined showed that more sharks in the larger size classes

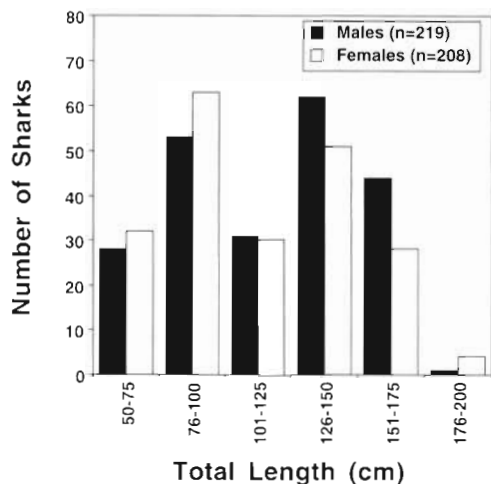


Fig. 4. *Carcharhinus amblyrhynchos*. Length frequency histogram for male and female gray reef sharks from Hawaii, and Johnston and Enewetak atolls

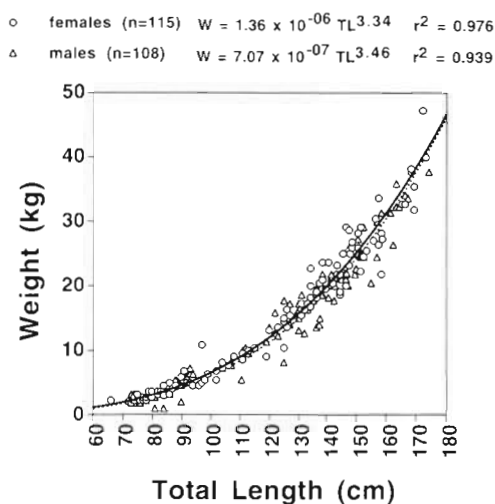


Fig. 5. *Carcharhinus amblyrhynchos*. Length-weight relationship for male and female gray reef sharks captured in Hawaii. Solid line: females, dashed line: males

were males, whereas there were more females in the smaller size classes (Fig. 4). A peak in numbers in the 76–100 cm size class was apparently due to the large number of small sharks captured with handlines. The largest female captured was 190 cm, and the largest male was 185 cm (and only 1 other male was greater than 170 cm). The sex ratio of males to females differed significantly from unity ($\chi^2 = 264.1$, $p = 0.001$, $n = 326$). The length-weight relationships were similar for the 2 sexes (Fig. 5).

As males reached 120 cm, there was a rapid increase in the length and degree of calcification of the claspers (Fig. 6). The smallest male with calcified claspers was

119 cm, and short, uncalcified claspers were recorded for males up to 140 cm.

For females there was a rapid increase in the development of the uterus for sharks just over 125 cm TL (Fig 7). All females shorter than 125 cm TL had uteri less than 5 mm in diameter, and all females longer than 127 cm TL had uteri larger than 15 mm in diameter. Maximum ova diameter was measured for only 8 females, and did not reveal time of ovulation. The data gathered allowed only limited inference of seasonality of reproduction. Mating scars were noted on only 1 individual, which was captured in March. Very small embryos (average 2.5 cm) were observed in uteri of a pregnant female also caught in March. However, eggs were observed in uteri of a female captured in July in the NWHI.

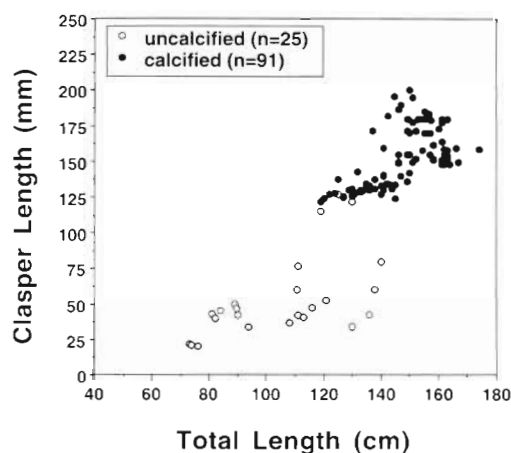


Fig. 6. *Carcharhinus amblyrhynchos*. Clasper length versus total length of male gray reef sharks captured in fishing in Hawaii

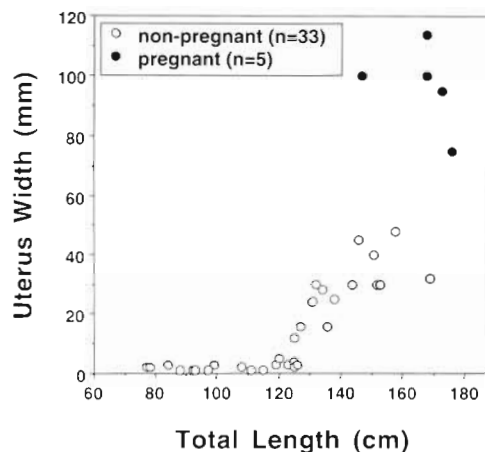


Fig. 7. *Carcharhinus amblyrhynchos*. Uterus width versus total length of female gray reef sharks captured in fishing in Hawaii

Fourteen of 29 (48.3%) mature females captured in Hawaii and examined internally were pregnant. These pregnant females ranged in size from 141 to 183 cm ($n = 14$), whereas those from Johnston and Enewetak were between 133 and 157 cm ($n = 19$). Between 3 and 6 embryos were found in pregnant females from Hawaii (average 4.1, SD = 1.44, $n = 13$), whereas females from Johnston and Enewetak contained between 1 and 4 embryos (average 2.5, SD = 0.96, $n = 19$). A regression analysis showed little association between TL of pregnant females and the number of pups in uteri ($r^2 = 0.22$). Embryos from Hawaii ranged in size from 2.5 cm (March) to 39.2 cm (November), and the largest from Johnston/Enewetak averaged 49.6 cm (date unknown). A 63 cm shark captured in July had a visible umbilical scar and was the smallest free-swimming shark caught in Hawaii. The next smallest individuals were 4 sharks (65 to 67 cm) captured between July and November.

Of 113 sharks tagged, 11 (9.7%) were recaptured, all in close proximity to the tagging sites. Time at liberty ranged from 3 to 566 d (average = 200 d). Total length of tagged sharks averaged 85 cm, and ranged from 65 cm to 138 cm. Only 6 of the 11 sharks recaptured showed positive growth, which averaged 3.9 cm yr⁻¹, based on increase in PCL.

Diet

Of 153 stomachs examined, 61 (39.9%) contained food. The diet of sharks of all size classes was dominated by teleost fishes (85.2%), but stomachs also con-

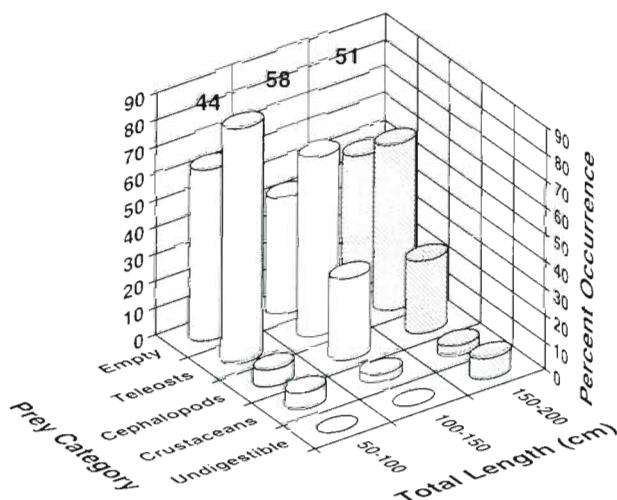


Fig. 8. *Carcharhinus amblyrhynchus*. Percentage of occurrence of prey items in stomachs of 3 size classes of gray reef sharks caught in Hawaii. Numbers above columns are sample sizes for each size class

Table 2. *Carcharhinus amblyrhynchus*. Stomach contents of 3 classes of gray reef sharks collected in the Hawaiian Islands, expressed as percentage of occurrence. Lengths are total lengths in cm. Of 153 stomachs examined, 61 contained food (39.9%)

	50-100 cm (n = 44)	100-150 cm (n = 58)	150-200 cm (n = 51)	Total
Teleostei	87.5	66.7	61.5	85.2
Muraenidae	0	9.1	0	4.9
Holocentridae	18.8	0	0	4.9
Scorpaenidae	0	3.0	0	1.6
Chaetodontidae	6.3	0	0	1.6
Pomacentridae	0	3.0	0	1.6
Scaridae	0	0	3.8	1.6
Zanclidae	0	3.0	0	1.6
Acanthuridae	0	0	7.7	3.3
Monacanthidae	0	0	7.7	3.3
Unidentified	56.2	48.5	42.3	59.0
Cephalopoda	6.2	30.3	26.9	29.5
Octopus	6.2	26.1	15.4	18.0
Squid	0	3.0	7.7	4.9
Unidentified	0	6.1	7.7	6.6
Crustacea	6.2	3.0	3.8	4.9
Lobster	0	3.0	0	1.6
Shrimp	0	0	3.8	1.6
Unidentified	6.2	0	0	1.6
Undigestible	0	0	7.7	3.3
Empty	63.6	43.1	49.0	60.1

tained cephalopods (29.5%) and crustaceans (4.9%) (Table 2). In terms of frequency of occurrence, there was an decrease for teleosts, and an increase for cephalopods for sharks in the largest 2 size classes (Fig. 8). Only stomachs of sharks in the largest size class contained undigestible items. The Simplified Morisita Index of dietary overlap (C_H) revealed a low degree of overlap between small and medium size sharks ($C_H = 0.25$), and between small and large sharks ($C_H = 0.20$). For the medium and large size classes, C_H was high (0.66). The Shannon-Weiner Index of dietary diversity (H') was similar for all size classes, but increased from 0.54 for the smallest size class, to 0.70 for the medium size sharks, and 0.71 for the largest sharks.

DISCUSSION

Distribution

The gray reef shark was the third most common shark captured in fishing programs in Hawaii, exceeded only by the sandbar *Carcharhinus plumbeus* and tiger *Galeocerdo cuvier* sharks (Wetherbee et al. 1994). However, the number of gray reef sharks caught on longlines was low in comparison to other species,

and large catches on handlines in a few fishing areas greatly increased the number captured.

Capture of sharks at only a few locations, despite longline sets of over 20000 hooks in the MHI, illustrates the rarity of this species, and suggests that other species of sharks are frequently misidentified as gray reef sharks by SCUBA divers and others in Hawaii. It is possible that catch rates were low because little fishing was conducted in habitats preferred by gray reef sharks (outer reef slopes and steep dropoffs), but this shark is rarely observed in these areas by knowledgeable divers (R. Pyle pers. comm., R. Kosaki pers. comm.).

The scarcity and patchy distribution of gray reef sharks in the high, populated, MHI in contrast to their cosmopolitan presence in the low, unpopulated NWHI, raises a number of questions about determinants of their geographical distribution. Similar differences in abundance of gray reef sharks at small, low, islands and atolls in contrast to larger, high islands has been suggested for other parts of the Pacific (Johnson 1978, McKibben & Nelson 1986).

Several factors might influence the distribution of this species on a local scale. Differences in underwater topography at different types of islands is one possibility, since this shark is thought to be bottom-oriented, and to prefer areas of rugged terrain, strong currents, and the leeward sides of islands (Hobson 1963, Wass 1971, Johnson 1978). Coral cover, and associated ecosystem structure, is another potential factor since coral reefs are generally less developed at younger, high islands in comparison to older, low islands and atolls. Water temperature and oceanographic effects of high islands on the surrounding waters may also influence distribution. Large human populations (which more commonly occur at high islands) may affect distribution through such factors as habitat degradation and fishing pressure. For example, Wass (1971) suggested that this shark prefers clear water, and that waters surrounding islands with large human populations tend to be more turbid. Competition between gray reef sharks and other species is another possibility. Wass (1971) theorized that Galapagos *Carcharhinus galapagensis* and sandbar sharks were spatially segregated within Hawaii, and Kato & Carvallo (1967) found that Galapagos sharks were segregated from silvertip sharks *C. albimarginatus* at Socorro Island. Comparison of resource overlap between the gray reef shark and sympatric carcharhinids may reveal evidence of competition.

The very localized abundance of gray reef sharks at Molokini (the only area in the lower MHI where they were common) is striking. They are now rarely observed at Molokini (J. Randall pers. comm., M. Severns pers. comm.). The patchy distribution and site

fidelity (as indicated by tag and recapture sites) of this shark has apparently contributed to its having been fished out at Molokini, and suggests that local populations may be quickly decimated by modest fishing pressure.

Segregation of sharks by sex or age group has been observed in many species, including several species in Hawaii (Wetherbee et al. 1994, Wetherbee et al. 1996). There is also evidence of sexual segregation in the gray reef shark. The capture of 3 times as many mature males (average depth of capture 36.2 m) as mature females (average depth of capture 22.2 m) supports the contention that males tend to occur at greater depths, since most longline fishing was conducted at about 45 m. The fluctuating catch rate of mature females may reflect seasonal movement of females out of fishing areas and into shallow-water, nursery areas. Large aggregations of mature females (some pregnant) have been observed in water only a few meters deep in the NWHI and at Johnston Atoll (Taylor 1994, A. Econimakis pers. comm.). There is also evidence of segregation of gray reef sharks by size class in Hawaii. Catches at Molokini and Ka'ula Rock were composed almost exclusively of juveniles, and these locations may serve (or have served) as nursery areas. In general, low catch rates for this species in the MHI limit our understanding of distributional patterns, although it is clear that these sharks have a restricted distribution in the MHI, and are uncommon near islands with large human populations.

Reproduction

Although Garrick (1982) described what was possibly a 254 cm male *Carcharhinus amblyrhynchos*, and Schultz et al. (1953) reported a 232 cm female, the largest sharks captured in Hawaii were considerably smaller. Wass (1971) suggested that this shark attains a larger size in Hawaii than elsewhere, but the largest (190 cm) of the nearly 400 specimens captured in Hawaii is similar to maximum sizes reported from other locations (Johnson 1978, Stevens & McLoughlin 1991, Last & Stevens 1994).

Examination of the development of reproductive structures of large numbers of sharks revealed that males mature at between 120 and 140 cm, and females at just over 125 cm in Hawaii. Other estimates of size at maturity have ranged between 130 and 150 cm for both sexes (Fourmanoir 1976, McKibben & Nelson 1986, Stevens & McLoughlin 1991). Based on growth rates of both captive and wild sharks, this corresponds to an age at maturity of 6 to 8 yr (Wass 1971, Radtke & Cailliet 1984), although Fourmanoir (1976) estimated that maturity was attained in as little as 3 yr.

Sizes of the smallest pregnant female in Hawaii (141 cm) and at Johnston and Enewetak (133 cm) were similar to those recorded from other locations (Bonham 1960, McKibben & Nelson 1986, Stevens & McLoughlin 1991). Based on the timing of mating scars and small embryos in uteri of females, and semen in seminal vesicles of males, mating and fertilization appear to occur between March and May in Hawaii, possibly continuing until July.

Based on the capture of females with 'near full-term pups', and small, free-swimming sharks (most with umbilical scars), pupping also appears to occur between March and July, with an apparent gestation period of 12 mo. However, small, free-swimming sharks were captured as late as November, and Nelson (pers. comm.) caught females with what he considered 'full term' embryos during the fall at Enewetak. The observation that approximately 50% of mature females captured were pregnant suggests that females reproduce every other year. There is little information in the literature on the reproductive cycle of this shark for comparison, other than speculation that in the southern hemisphere, parturition occurs in July and August, and gestation is between 9 and 12 mo (Fourmanoir 1976, Johnson 1978, Stevens & McLoughlin 1991).

The smallest free-swimming shark caught in Hawaii (63 cm) was similar in size to those recorded from other locations, and agrees with an estimated size at birth of 60 cm (Garrick 1982, McKibben & Nelson 1986). However, free-swimming sharks as small as 42 cm (Johnson 1978, Salini et al. 1992) and embryos as large as 64 cm (Stevens & McLoughlin 1991) have been examined. Litter size of sharks in Hawaii (average of 4.1) may be larger than in other locations, including the Johnston/Enewetak females (average of 2.5). Most studies have reported litter sizes between 1 and 4 (Schultz et al. 1953, Bonham 1960, Fourmanoir 1976, Stevens & McLoughlin 1991). The average growth rate of gray reef sharks tagged in Hawaii (3.9 cm yr^{-1} , based only on sharks that showed positive growth) was greater than previous estimates from this data (Tester 1969, Wass 1971). However, our estimate is still low in comparison to other studies, which have ranged from 9 to 25 cm yr^{-1} (Fourmanoir 1976, Johnson 1978, DeCrosta et al. 1984, Radtke & Cailliet 1984).

Diet

The finding that gray reef sharks in Hawaii feed primarily on teleosts, supplemented by invertebrates, is consistent with other reports. In previous studies, 65 to 88% of stomachs contained fish, and less than 25% of stomachs contained either cephalopods or crustaceans (Johnson 1978, Salini et al. 1990, Brewer et al. 1991). In

our study, the majority of prey items found in stomachs were reef-associated and benthic organisms, indicating that sharks primarily fed near the bottom. Ontogenetic changes in the type and diversity of prey consumed by the gray reef shark is consistent with reports for a number of other species of sharks (Wetherbee et al. 1990, 1996, Lowe et al. 1996).

CONCLUSIONS

Even though most of these data are nearly 30 yr old, they still represent an important contribution toward understanding the distribution, reproduction and diet of this species in Hawaii and throughout its range. An example of the usefulness of this information came in 1992, when a bill was introduced to the state legislature of Hawaii calling for eradication of sharks that pose a threat to humans. Among the species proposed to be targeted for such shark control efforts was the gray reef shark. Given that these sharks appear to be exceedingly rare in Hawaiian waters frequented by humans, directed fishing for this species for purposes of protection of humans was deemed to be unwarranted.

Acknowledgements. We thank M. DeCrosta, J. Parrish, L. Taylor Jr, A. Tester, R. Wass, and others for collecting the data. K. Holland, C. Mostello, D. Nelson, J. Parrish, and J. Randall offered helpful comments on the manuscript. This study is dedicated to the memory of D. Nelson.

LITERATURE CITED

- Barlow GW (1974) Derivation of threat display in the gray reef shark. *Mar Behav Physiol* 3:71–81
- Bonham K (1960) Note on sharks from Rongelap Atoll, Marshall Islands. *Copeia* 1960(3):257
- Brewer DT, Blaber SJM, Salini JP (1991) Predation on penaeid prawns by fishes in Albatross Bay, Gulf of Carpentaria. *Mar Biol* 109:231–240
- Compagno LJV (1984) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2, *Carcharhiniformes*. *FAO Fish Synop* (125)4:251–655
- DeCrosta MA, Taylor LR Jr, Parrish JD (1984) Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. In: Grigg RW, Tanoue KY (eds) *Proc 2nd Symp Res Invest NWHI, Vol 2. UNIH-SEA-GRANT-MR-84-01, University of Hawaii Sea Grant, Honolulu*, p 75–95
- Fellows DP, Murchison AE (1967) A noninjurious attack by a small shark. *Pacif Sci* 21:150–151
- Fourmanoir MP (1976) Requins de Nouvelle-Caledonie. *Nature Caledonienne* 12:23–29
- Garrick JAF (1982) Sharks of the genus *Carcharhinus*. NOAA Tech Rep NMFS Circ 445
- Hobson ES (1963) Feeding behavior in three species of sharks. *Pacif Sci* 17:171–194
- Hobson ES, Mautin F, Reese ES (1961) Two shark incidents at Enewetak Atoll, Marshall Islands. *Pacif Sci* 15:605–609

- Johnson RH (1978) Sharks of tropical and temperate seas. Les Editions du Pacifique, Singapore
- Johnson RH, Nelson DR (1973) Agonistic display in the gray reef shark, *Carcharhinus menisorrhah*, and its relationship to attacks on man. *Copeia* 1973(1):76–84
- Kato S, Carvalho AH (1967) Shark tagging in the eastern tropical Pacific Ocean, 1962–1965. In: Gilbert PW, Mathewson RF, Rall JP (eds) Sharks, skates and rays. Johns Hopkins Press, Baltimore, p 93–109
- Krebs CJ (1989) Ecological methods. Harper Collins Publishers, New York
- Langton RS (1982) Diet overlap between the Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis* and fifteen other northwest Atlantic finfish. *Fish Bull US* 80: 745–759
- Last PR, Stevens JD (1994) Sharks and rays of Australia. CSIRO, Australia
- Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environ Biol Fish* 47:203–211
- McKibben JN, Nelson DR (1986) Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bull Mar Sci* 38: 89–110
- Nelson DR (1982) Aggression in sharks: is the gray reef shark different? *Oceans* 24:45–55
- Nelson DR, Johnson RR, McKibben JN, Pittenger GG (1986) Agonistic attacks on divers and submersibles by gray reef sharks, *Carcharhinus amblyrhynchos*: antipredatory or competitive? *Bull Mar Sci* 38:68–88
- Radtke RL, Cailliet GM (1984) Age estimation and growth of the gray reef shark *Carcharhinus amblyrhynchos* from the Northwestern Hawaiian Islands. In: Grigg RW, Tanoue KY (eds) Proc 2nd Symp Res Invest NWHI, Vol 2. UNIH-SEA-GRANT-MR-84-01, University of Hawaii Sea Grant, Honolulu, p 121–127
- Read KRH (1971) Nonfatal shark attack, Palau Islands. *Micronesica* 7:233–234
- Salini JP, Blaber SJM, Brewer DT (1990) Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. *Mar Biol* 105:363–374
- Salini JP, Blaber SJM, Brewer DT (1992) Diets of sharks from estuaries and adjacent waters of the north-eastern Gulf of Carpentaria, Australia. *Aust J Mar Freshwat Res* 43:87–96
- Schultz LP, Herald ES, Lachner EA, Welander AD, Woods LP (1953) Fishes of the Marshall and Marianas Islands. *US Nat Mus Bull* 202:1–685
- Stevens JD, McLoughlin, KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. *Aust J Mar Freshwat Res* 42: 151–199
- Taylor LR Jr (1994) Sharks of Hawaii. University of Hawaii Press, Honolulu
- Tester AL (1969) Cooperative shark research and control program final report, 1967–1969. University of Hawaii, Honolulu
- Wass RC (1971) A comparative study of the life history, distribution, and ecology of the sandbar shark and gray reef shark in Hawaii. PhD dissertation, University of Hawaii, Honolulu
- Wetherbee BM, Crow GL, Lowe CG (1996) Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawaii. *Environ Biol Fish* 45:299–310
- Wetherbee BM, Gruber SH, Cortes E (1990) Diet, feeding habits, digestion, and consumption in sharks with special reference to the lemon shark, *Negaprion brevirostris*. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech Rep NMFS 90, p 29–47
- Wetherbee BM, Lowe CG, Crow GL (1994) A review of shark control in Hawaii with recommendations for future research. *Pacif Sci* 48:95–115

This article was submitted to the editor

Manuscript first received: November 8, 1996

Revised version accepted: March 3, 1997