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Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawai'i

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Synopsis

Catch records from the Hawai'i Cooperative Shark Research and Control Program, which operated in Hawai'i from 1967–1969, were examined and data on the Galapagos shark, *Carcharhinus galapagensis* were analyzed. A total of 304 Galapagos sharks was caught, predominantly with longlines. More female sharks were caught than males, and the catch was skewed geographically. On the island of O'ahu the highest catch rates occurred along the north and south coasts. High catch rates also occurred near points of land, where longshore currents converge. Average depth of capture was greater for juveniles (45.1 m) and mature males (60.2 m), than for subadults (38.8 m) and mature female sharks (34.2 m). Males appear to reach maturity between 205 and 239 cm total length, and females between 215 and 245 cm. Litter size ranged from 4 to 16 pups, with an average of 8.7. In Hawaiian waters Galapagos sharks are born at just over 80 cm total length. Mating and parturition apparently occur early in the year, and gestation is estimated to be about 12 months. Stomach contents consisted mainly of teleosts and benthic prey, and ontogenetic changes in diet occurred as sharks increased in size. Sharks consumed a smaller proportion of teleosts and more elasmobranchs with increasing size. Dietary diversity also increased with increasing size of shark.

Introduction

The Galapagos shark, *Carcharhinus galapagensis*, has a circumglobal distribution in warm and temperate waters (Garrick,[1] Compagno 1984). This species is essentially limited to oceanic islands, although large individuals have been reported on the high seas and close to continental shelves (Kato et al.,[2] Pinchuk 1981, Taniuchi et al. 1985). They are often the most common inshore species at oceanic islands off Central and South America (Beebe & Tee-Van 1941, Limbaugh 1963, Edwards & Lubbock 1982). The Galapagos shark is also abundant in both the main Hawaiian Islands (MHI) and the Northwestern Hawaiian Islands (NWHI) (Tester,[3] Taylor & Naftel,[4] De Crosta et al. 1984). Because these sharks are common and aggressive, they are

[1] Garrick, J.A.F. 1982. Sharks of the genus *Carcharhinus*. NOAA Tech. Rep. NMFS Circ. 445. 194 pp.

[2] Kato, S., S. Springer & M.H. Wagner. 1967. Field guide to eastern Pacific and Hawaiian sharks. U.S. Fish Wildlife Ser. Circ. 271. 47 pp.

[3] Tester, A.L. 1969. Cooperative Shark Research and Control Program final report 1967–69. University of Hawai'i, Honolulu. 80 pp.

[4] Taylor, L.R. Jr. & G. Naftel. 1978. Preliminary investigations of shark predation on the Hawaiian monk seal at Pearl and Hermes Reef and French Frigate Shoals. U.S. Marine Mammal Commission Report No. MMC 77/07. 34 pp.

considered a danger to humans, as well as a nuisance to commercial fishermen (Garrick & Schultz 1963, Randall 1963, Kato[5]).

Despite their abundance and occasional interaction with humans, the biology of this species is poorly understood. Studies have concentrated mainly on systematics and the differentiation of the Galapagos shark from closely allied species such as the dusky shark, *Carcharhinus obscurus* (Rosenblatt & Baldwin 1958, Garrick 1967, Bass et al. 1973). The main source of knowledge about reproduction of the Galapagos shark is from Tester (1969), who listed litter sizes of 10 pregnant females. Information on size at maturity, gestation, size at birth, and seasonality of mating and pupping remains fragmentary because the majority of Galapagos sharks examined have been juveniles. Information on the diet of Galapagos sharks outside of Hawai'i is also limited to a few references (Bass et al. 1973, Edwards & Lubbock 1982, Castro 1983). Galapagos sharks have been tagged in several locations (Davies & Joubert 1967, Bass et al. 1973, Bass 1977), and one individual crossed open water to move between small oceanic islands in the eastern tropical Pacific (Kato & Carvallo 1967). Limbaugh (1963) provided anecdotal observations on preferred substrate and depth of occurrence for this species. De Crosta et al. (1984) examined age, growth, and energetics of Galapagos sharks in the NWHI.

To provide more detailed information on the biology of the Galapagos shark, we analyzed raw data collected during the Hawai'i Cooperative Shark Research and Control Program (Tester 1969), and other shark fishing programs in the Hawaiian Islands (Naftel,[6] De Crosta et al. 1984). Although most of these data were collected over 25 years ago, they represent a substantial contribution to the understanding of the biology of the Galapagos shark.

[5] Kato, S. 1964. Sharks of the genus *Carcharhinus* associated with the tuna fishery in the eastern tropical Pacific Ocean. U.S. Fish Wildlife Ser. Circ. 172. 22 pp.

[6] Naftel, G. 1976. Report of the Shark Utilization/Student Training Program conducted by the R/V Easy Rider under grants from State of Hawai'i, Department of Planning and Economic Development, State of Hawai'i Marine Affairs Coordinator's Office, August-September 1976 in the waters of Maui and Kaua'i. 32 pp.

Methods

The majority of the data analyzed in this study were taken directly from the original data sheets of the Hawai'i Cooperative Shark Research and Control Program, which ran from 1 June 1967 to 30 June 1969 (Tester 1969). Fishing gear consisted of longlines set from a tuna fishing boat in designated areas around the eight main Hawaiian Islands. Fishing was concentrated in eight successive circuits around the island of O'ahu, with one circuit during each spring, summer, fall and winter for the two years that the program operated (see Wetherbee et al. 1994). Standard longlines consisted of three 800 m sections, 24 hooks per section. Lines were set in the afternoon, parallel to shore, in depths of about 45 m and retrieved at dawn the following morning. Skipjack tuna, *Katsuwonus pelamis*, was the primary bait used. In addition to standard longline fishing, sharks were collected on a light longline (12 hooks) and handlines. Sharks were also caught in experimental fishing trials, consisting of deep-water longline sets, bait preference tests and sets perpendicular to shore. Experimental fishing was conducted primarily off the south shore of O'ahu.

Additional data were obtained from unpublished records of the Shark Utilization/Student Training Program (Naftel 1976) for sharks caught off Kaua'i and Maui, and for sharks from the NWHI from unpublished data of De Crosta et al. (1984). Sharks were collected in these studies by longlining methods similar to those used in the Hawai'i Shark Research and Control Program.

In each program, depth of capture, precaudal length (PCL), total length (TL), sex, and weight (occasionally) were recorded for each shark. All lengths reported in this study are total lengths (TL). A linear regression is provided for conversion of TL to precaudal length (PCL): $PCL = -1.17034 + 0.75865\ TL$ ($r^2 = 0.992$, $n = 235$), since total length measurements may have been variable when different observers took measurements.

Reproductive condition of sharks was examined

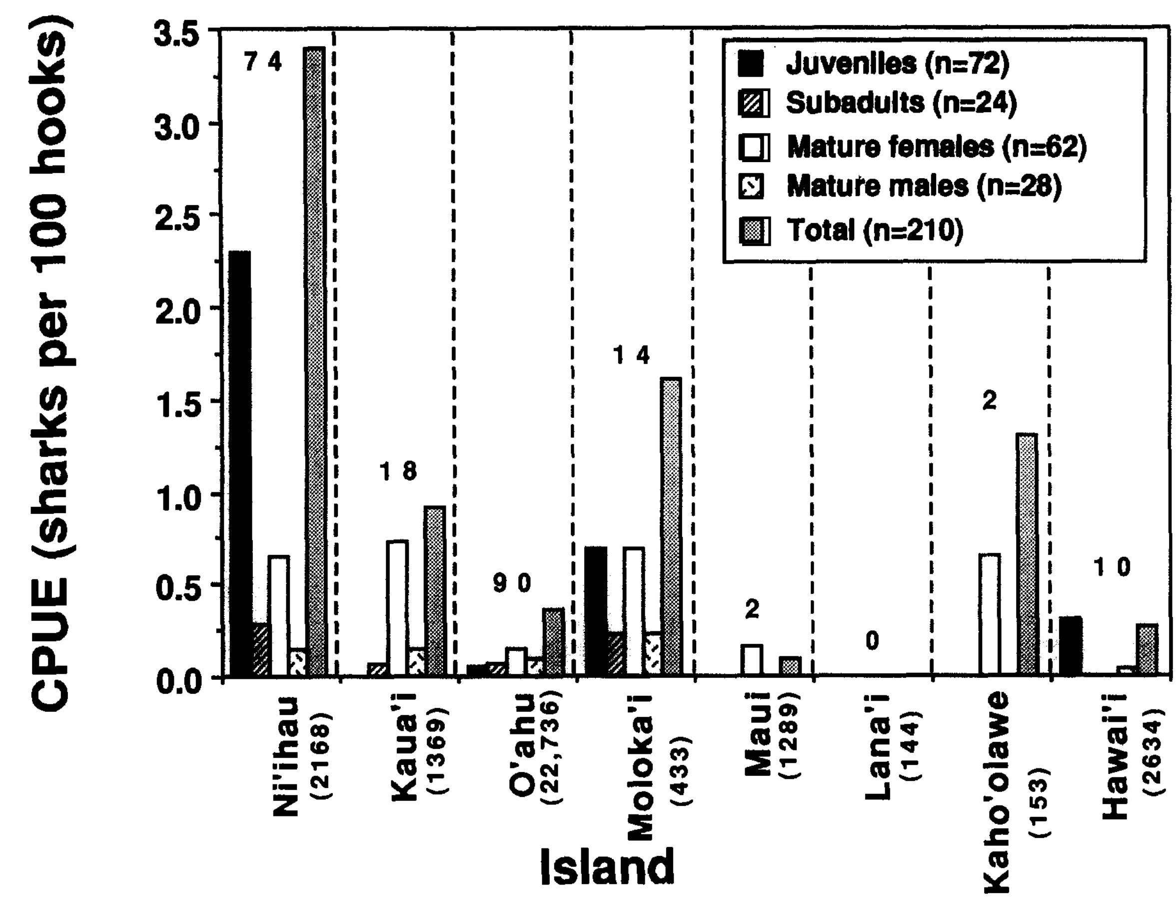

Fig. 1. Catch per unit effort (CPUE) for Galapagos sharks of various levels of maturity caught in longline fishing in waters surrounding the main Hawaiian Islands during the Hawai'i Cooperative Shark Research and Control Program, 1967 to 1969, and the Shark Utilization/ Student Training Program, 1976. Numbers above columns represent number of sharks caught at each island, and numbers in parentheses are total hooks fished at each island.

and length and degree of calcification of claspers was noted for males, and diameter of the 6 largest ova and the width of the uterus were measured in females. Number of pups, total length, and sex of each was also recorded. During the Shark Utilization/Student Training Program and the NWHI fishing, reproductive tracts of many sharks were not examined. Based on the level of development of reproductive structures we grouped sharks into three stages of maturity: mature, subadults (same size class as mature sharks, but sexually immature), and juveniles (smaller size class than mature and subadults) (following Yano & Tanaka 1984). Size ranges according to this classification were: juvenile, 88 to 201 cm; subadult, 202 to 247 cm; and mature, 205 to 300 cm.

Stomach contents of sharks from the Hawai'i Cooperative Shark Research and Control Program were identified to the lowest possible taxa and quantified in terms of percent of stomachs containing food that contained a prey item (%O). Dietary overlap was calculated for four, 50 cm size classes using the Simplified Morisita Index (C_H) (Krebs 1989). The degree of overlap was compared against Langton's (1982) scale: low (0–0.29), medium (0.30–0.59), and high overlap (> 0.60). Prey diversities of each size class were calculated using the Shannon-Weiner Diversity Index (H') (Krebs 1989).

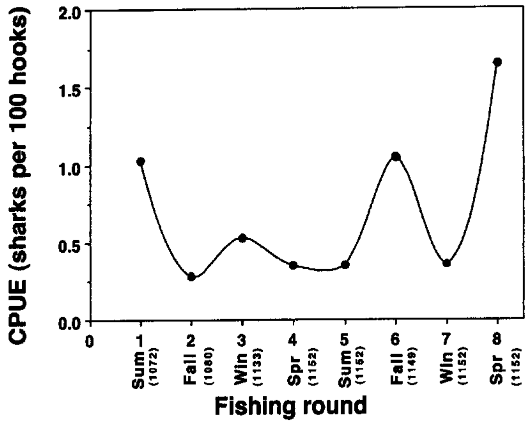

Fig. 2. Catch per unit effort (CPUE) of Galapagos sharks caught in longline fishing in successive fishing circuits around the island of O'ahu during the Hawai'i Cooperative Shark Research and Control Program, 1967 to 1969. The season during which the majority of fishing was conducted is shown below the CPUE for each round. Numbers in parentheses are total hooks fished in each circuit.

Results

Distribution

A total of 304 Galapagos sharks was caught in the three programs, 209 during the Hawai'i Cooperative Shark Research and Control Program, 12 during the Shark Utilization/Student Training Program, and 83 by De Crosta and others in the NWHI. Most of the Galapagos sharks captured in the MHI were caught off O'ahu (90) and Ni'ihau (74), with the highest catch per unit effort (nearly 3.5 sharks per 100 hooks) recorded at Ni'ihau (Fig. 1). Only 18 Galapagos sharks were captured at the cluster of islands that includes Moloka'i, Maui, Lana'i and Kaho'olawe. A high proportion of juveniles was caught at Ni'ihau both in standard longline fishing and with handlines.

Catch per unit effort of Galapagos sharks in successive fishing circuits around the island of O'ahu fluctuated during the two years of the Hawai'i Cooperative Shark Research and Control Program. There was no measurable long-term declining trend over time, and the highest catch rate was observed during the final circuit around O'ahu (Fig. 2). There was no apparent seasonal trend in overall catch per unit effort of Galapagos sharks, with the three highest catch rates occurring in three different seasons. However, there was seasonal variation in catch rate of different age classes. Highest catch rate for all levels of maturity occurred in the summer months and lowest catch rate occurred in spring for mature females, in the fall for juveniles, and in winter for mature males and subadults (Fig. 3).

Highest catch per unit effort around the island of O'ahu was reported from the north and south coasts, whereas fewer sharks were captured along the east coast and only two sharks were caught off the entire west coast (Fig. 4). Catch per unit effort was high for mature females on all but the western shoreline, and for mature males was high on the north and south shores, but low on the east and west shores of O'ahu. Catch rates of subadult sharks were similar to mature males, except that no subadults were caught along the west coast. Juvenile sharks were caught at a high rate along the north coast, but few were caught off the south and east coasts, and none off the west coast.

The highest catch per unit effort for O'ahu was recorded in areas adjacent to points of land. Ninety-one percent of juveniles, 88% of subadults, 80% of adults, and 83% of all sharks combined were caught

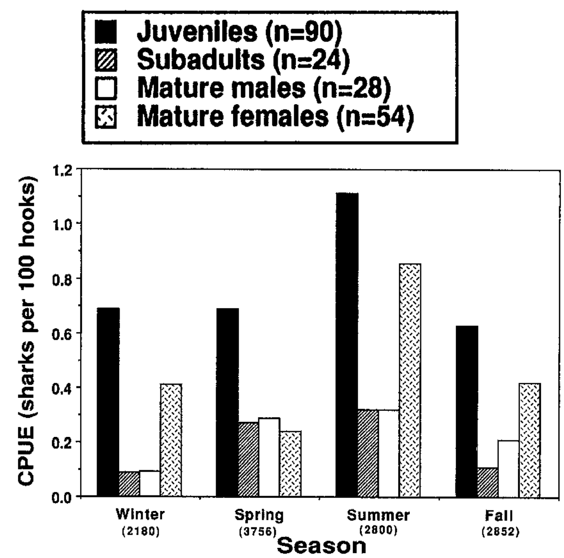

Fig. 3. Seasonal catch per unit effort (CPUE) for Galapagos sharks of various levels of maturity caught in longline fishing in waters surrounding the main Hawaiian Islands during the Hawai'i Cooperative Shark Research and Control Program, 1967 to 1969. Numbers in parentheses are total hooks fished in each season.

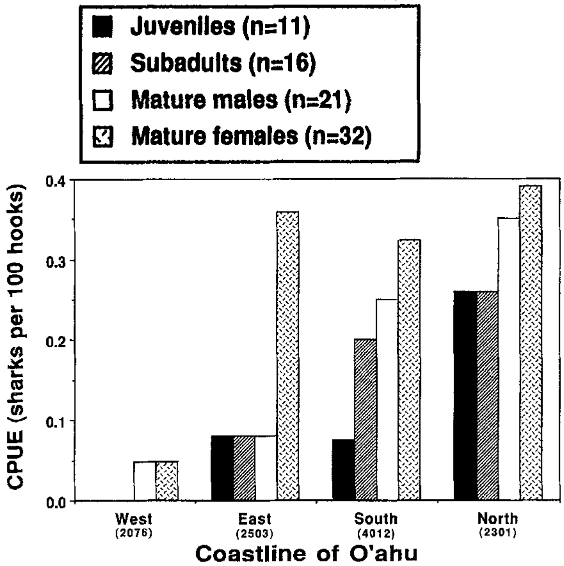

Fig. 4. Catch per unit effort (CPUE) for Galapagos sharks of various levels of maturity caught in longline fishing along various portions of the coast of O'ahu during the Hawai'i Cooperative Shark Research and Control Program, 1967 to 1969. Numbers in parentheses are total hooks fished in each area.

in fishing areas near Barber's Point, Ka'ena Point, Kahuku Point, Makapu'u Point and Kawaihoa Point, although only 50% of fishing effort was conducted in these areas. There was some evidence that sharks occurred in groups, as 30% of sharks caught off O'ahu were caught in groups of two or more on the same 24-hook section of longline.

For sharks captured during the Hawai'i Cooperative Shark Research and Control Program, the average depth of capture for mature females was 34.2 m (range = 0–78 m, SD = 12.5 m, n = 51), for subadults, 28.8 m (13–85 m, SD = 18.3 m, n = 31), for juveniles, 45.1 m (0–138 m, SD = 23.3 m, n = 90), and for mature males, 60.2 m (20–286 m, SD = 59.8 m, n = 31). The majority of Galapagos sharks were caught at depths of less than 80 m, but sharks captured deeper tended to be juveniles (50%) and mature males (43%). Of the seven sharks caught at depths greater than 100 m, five were mature males, and the maximum depth of capture recorded (286 m) was for a mature male.

Biology

A length-frequency histogram revealed that mature females were caught in the greatest abundance, with another slight peak of smaller sharks, 125 to 150 cm (Fig. 5). The sex ratio of females to males (1.5:1) differed significantly from unity (chi-squared = 7.45, $p < 0.05$, n = 260). The largest female caught was 300 cm, and the largest male was

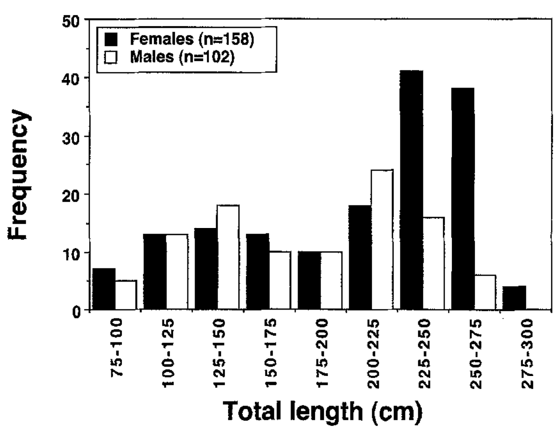

Fig. 5. Length-frequency histogram for Galapagos sharks. Data are pooled from the Hawai'i Cooperative Shark Research and Control Program, 1967–1969, the Shark Utilization/Student Training Program, 1976, and the Northwestern Hawaiian Islands, 1978–1980.

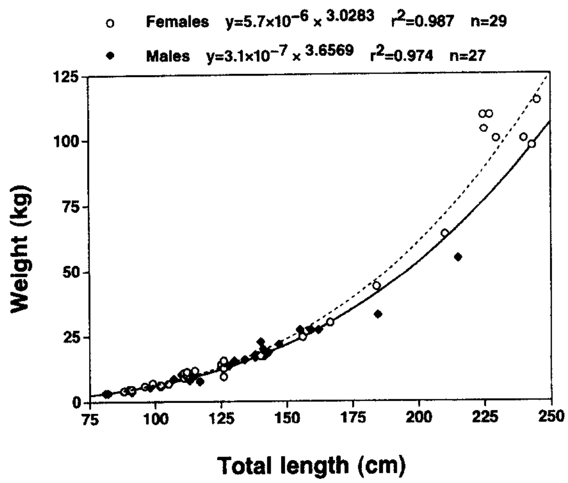

Fig. 6. Length-weight relationship for Galapagos sharks based on data pooled from the Hawai'i Cooperative Shark Research and Control Program, 1967–1969, the Shark Utilization/Student Training Program, 1976, and from the Northwestern Hawaiian Islands, 1978–1980. Solid line = males, dashed line = females.

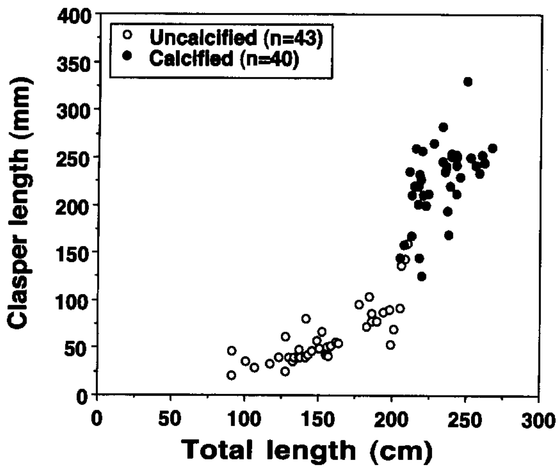

Fig. 7. Length of calcified and uncalcified claspers versus total length of male Galapagos sharks. Data are pooled from the Hawai'i Cooperative Shark Research and Control Program, 1967–1969, and the Northwestern Hawaiian Islands, 1978–1980.

267 cm. Figure 6 gives the total length-whole wet weight relationship for female and male Galapagos sharks. Females tended to be heavier than similar sized males, and obtained larger sizes than males.

There was a sharp increase in clasper length and a rapid increase in calcification of claspers in male sharks greater than 200 cm (Fig. 7). The smallest male with calcified claspers was 205 cm, whereas an individual 239 cm was recorded as having claspers that were not completely calcified (although the next largest male with uncalcified claspers was 210 cm).

There was a rapid increase in development of the uteri and ova in female sharks as they exceeded 200 cm (Fig. 8). The smallest female with well developed ova and uteri was 215 cm, whereas two, 245 cm individuals had small, undeveloped uteri and appeared to be immature. Sharks with ova and with uteri approaching 5 mm appeared to be mature.

The smallest pregnant female was 243 cm. Only 15 of 83 (18%) mature females examined were pregnant. The number of female and male embryos was approximately equal (40:41), as was the number of embryos in the left and right uteri (62:60). Litter size ranged from 4 to 16 with an average of 8.7 (n = 14), although there is some uncertainty whether two of the 14 pregnant females contained embryos or

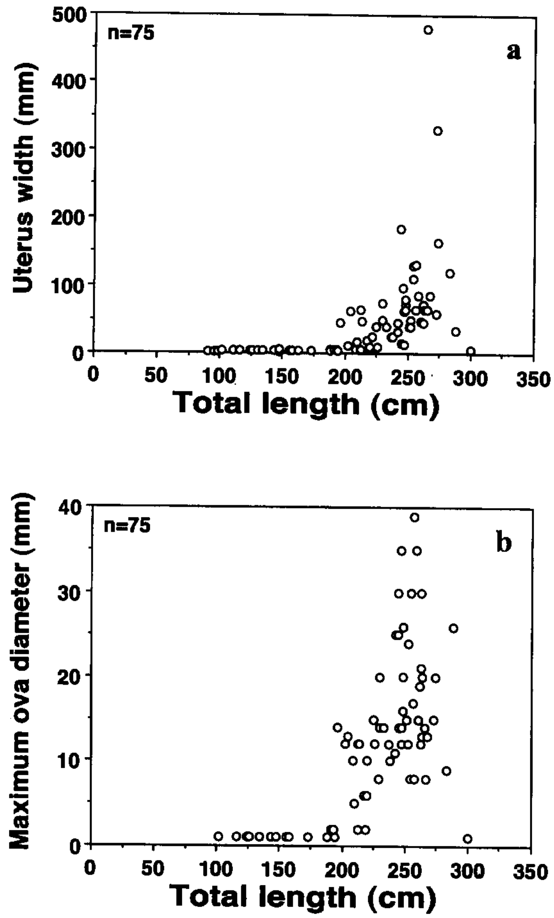

Fig. 8. a – Width of uterus and b – maximum ova diameter versus total length of female Galapagos sharks. Data are pooled from the Hawai'i Cooperative Shark Research and Control Program, 1967–1969, and the Northwestern Hawaiian Islands, 1978–1980.

uterine eggs. Maximum size of embryos was 81 cm in a female caught in mid-March. The smallest free-swimming shark was an 83 cm individual caught in August, and the four smallest free-swimming sharks (all captured in late August-early September) averaged 86 cm. Average size of 48 embryos from six pregnant females captured in August was 37 cm. Means and standard deviations for each month were calculated based on the largest ova measured in each mature female. This maximum ova diameter increased from a minimum in March (5.7 mm, ± 8.1) to a maximum in December (30.5 mm, ± 6.4) (Fig. 9). Mating scars were observed on five mature females, three in January, one in March, and one on a pregnant female in June.

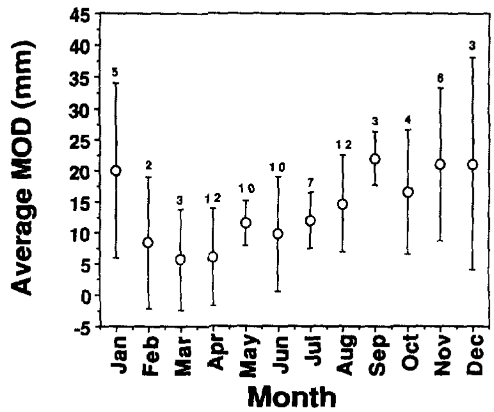

Fig. 9. Average maximum ova diameter (MOD) (± SD) versus month for female Galapagos sharks. Data are pooled from the Hawai'i Cooperative Shark Research and Control Program, 1967–1969, and from the Northwestern Hawaiian Islands, 1978–1980. Numbers above bars represent sample size for each month.

Diet

Of 178 stomachs examined, 96 (53.9%) contained food. Teleosts and cephalopods occurred most frequently in stomachs of sharks, with elasmobranchs and crustaceans becoming important as sharks increased in size (Table 1). Undigestible items and human refuse found in stomachs included leaves, rocks, coral, algae, paper, string, pork, salami, ham, and lettuce.

These data show ontogenetic dietary changes in the type of prey and diversity of food types. Stomachs of the smallest size class contained only teleosts and cephalopods (and one marine mammal that appeared to have been bait, scavenged from the fishing lines). In the two largest size classes, elasmobranchs and undigestible items occurred more frequently, and the largest size class consumed a much smaller proportion of teleosts (Fig. 10).

The Simplified Morisita Index of Overlap (C_H) indicated a low degree of overlap between sharks < 150 cm and those 251–300 cm, and between sharks 151–200 cm and those 251–300 cm. A high degree of overlap was observed between the 201–250 cm and 251–300 cm size groups. Comparisons between other size classes revealed medium dietary overlap (Table 2). Dietary diversity as measured by the Shannon-Weiner Diversity Index (H′) increased from 0.45 for sharks < 150 cm, to 0.51 for sharks between 151 and 200 cm, 0.62 for sharks 201–250 cm, and 0.89 for the largest size class (251–300 cm).

Discussion

Distribution

The Galapagos shark was one of the more common sharks in the MHI, but generally was not found in large aggregations, as described at other oceanic islands (Beebe & Tee-Van 1941, Limbaugh 1963, Edwards & Lubbock 1982). At Ni'ihau and in the NWHI, Galapagos sharks were more abundant, and, along with the grey reef shark, *Carcharhinus amblyrhynchos*, are the most common nearshore species (Taylor 1994). Differences in distribution of sharks between the high, MHI and the low islands of the NWHI are apparent in a number of species including Galapagos, grey reef and sandbar, *Carcharhinus plumbeus*, sharks (Wass 1971, De Crosta et al. 1984).

Fluctuation in catch rate of Galapagos sharks during successive fishing circuits around the island of O'ahu did not indicate that the level of fishing effort resulted in a measurable decrease in catch rate. Such fishing does not appear to be an effective means of controlling populations of this potentially dangerous species. Shark control programs in Hawai'i also had limited success in reducing populations of tiger, *Galeocerdo cuvier*, and sandbar sharks (Wetherbee et al. 1994). Peak catch rates of juvenile and mature female sharks in the summer might coincide with pupping, however, as discussed later, pupping appears to occur earlier in the year. High catch rates of mature male sharks in the spring and summer, and low catch rates in the winter may be evidence of onshore movement of males for mating, as has been observed for a number of other species of shark (Reid & Krogh 1992).

The predominance of Galapagos sharks caught on the north and south coasts of O'ahu indicates that this species has a restricted spatial distribution. Limbaugh's (1963) reported that Galapagos sharks were most often found over rugged terrain, and Wass (1971) suggested a preference for areas with strong currents. The observation that a majority of sharks were captured near points of land in the MHI suggests the sharks favor these areas. Most of these areas[7] are characterized by having currents that converge and move offshore at the point of land (Gerritsen[7]).

Interaction with other species of sharks may also be a factor in the distribution of Galapagos sharks. Wass (1971) theorized that Galapagos and sandbar sharks were spatially segregated within Hawai'i, and Kato & Carvallo (1967) found that Galapagos sharks were segregated from silvertip sharks, *Car-*

[7] Gerritsen, F. 1978. Beach and surf parameters in Hawai'i. Sea Grant Tech. Rep. University of Hawai'i Sea Grant, TR-78-02. 178 pp.

Table 1. Diet of Galapagos sharks, *Carcharhinus galapagensis* of four size classes from the Hawai'i Cooperative Shark Research and Control Program, 1967–1969. For each size class, n = number of stomachs containing the item and percent occurrence (%O) = number of stomachs containing the item in proportion to number of stomachs that contained food.

Total number of stomachs examined	178	
Total number of stomachs with food	96	(53.9%)
Total number of empty stomachs	82	(46.1%)

Total length (cm)	< 150		151–200		201–250		251–300	
Stomachs examined	38		33		71		36	
Stomachs w/food	18		12		43		23	
Prey items	n	%O	n	%O	n	%O	n	%O
Teleostei	14	77.8	10	83.3	34	79.1	7	30.4
Muraenidae	2	11.1	–	–	1	2.3	–	–
Clupeidae	-	–	1	8.3	–	–	–	–
Synodontidae	1	5.6	–	–	–	–	–	–
Belonidae	–	–	–	–	1	2.3	–	–
Holocentridae	1	5.6	–	–	1	2.3	–	–
Priacanthidae	–	–	–	–	1	2.3	–	–
Carangidae	–	–	1	8.3	4	9.3	1	4.3
Lethrinidae	–	–	–	–	1	2.3	–	–
Pomacentridae	–	–	–	–	1	2.3	–	–
Scaridae	–	–	1	8.3	2	4.5	–	–
Acanthuridae	1	5.6	–	–	3	7.0	–	–
Scombridae	–	–	1	8.3	3	7.0	–	–
Balistidae	–	–	–	–	–	–	1	4.3
Monacanthidae	3	16.7	–	–	1	2.3	–	–
Serranidae	–	–	1	8.3	–	–	–	–
Diodontidae	1	5.6	–	–	4	9.3	2	8.7
unidentified	5	27.8	6	50.0	18	41.9	4	17.4
Elasmobranchii	–	–	–	–	6	13.9	7	30.4
shark	–	–	–	–	5	11.6	5	21.7
ray	–	–	–	–	1	2.3	2	8.7
Cephalopoda	6	33.3	4	33.3	11	25.6	8	34.8
squid	3	16.7	2	16.7	1	2.3	–	–
octopus	1	5.6	1	8.3	6	13.9	4	17.4
unidentified	2	11.1	1	8.3	4	9.3	4	17.4
Crustacea	–	–	2	16.7	3	7.0	2	8.7
Shrimp	–	–	1	8.3	1	2.3	–	–
Crab	–	–	–	–	2	4.6	–	–
Lobster	–	–	–	–	1	2.3	2	8.7
unidentified	–	–	1	8.3	–	–	–	–
Mammalia	1	5.6	–	–	–	–	1	4.3
Undigestible	1	5.6	–	–	7	16.3	5	21.7

Table 2. Simplified Morisita Index of Overlap comparing diets of Galapagos sharks, *Carcharhinus galapagensis*, belonging to four size classes.

Size class	< 150 cm	151–200 cm	201–250 cm	n
< 150 cm	–	–	–	18
151–200 cm	0.46	–	–	12
201–250 cm	0.34	0.48	–	43
251–300 cm	0.19	0.21	0.69	23

charhinus albimarginatus, at Socorro Island. Although Galapagos sharks in the MHI do not form large schools that swarm near boats or divers as has been observed at other oceanic islands, the high incidence of more than one shark caught on the same 24-hook section of line indicates that there may be some grouping behavior in sharks of all size classes.

Although the majority of sharks were captured at depths of 40 to 45 m, there is evidence that mature males and females are segregated by depth. Average depth of capture was 60.2 m for mature males, and 34.2 m for mature females, and only eight percent of mature females were captured at depths greater than 60 m, whereas 22% of mature males were caught at these depths. A deeper distribution for males may also explain why the sex ratio was skewed towards females, since few lines were set deeper than 60 m (Tester 1969). Segregation according to depth has been described in a number of species of sharks (Wass 1971, Simpfendorfer 1992).

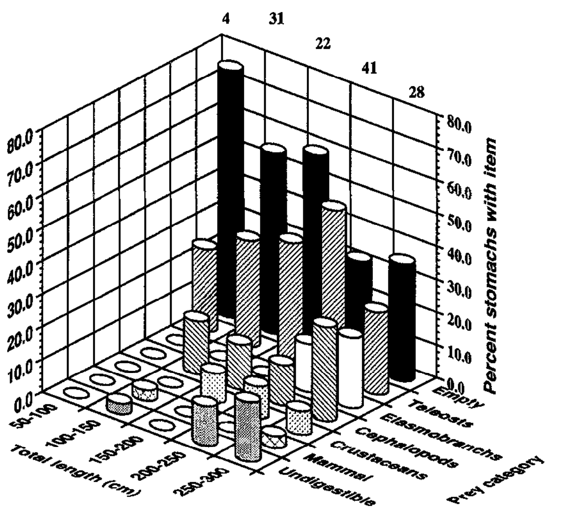

Fig. 10. Percent occurrence of prey items in stomachs for four size classes of Galapagos sharks caught in the main Hawaiian Islands during the Hawai'i Cooperative Shark Research and Control Program, 1967–1969.

Limbaugh (1963) estimated that Galapagos sharks lived in water 0–61 m deep, and Johnson (1978) listed a maximum depth of 180 m. The maximum depth of capture of a male shark (286 m) in Hawai'i indicates that these sharks may occasionally occur in relatively deep water. Average depth of capture for juvenile Galapagos sharks (45 m) in the MHI was greater than that of adult females (34 m) and subadults (38 m), and 19% of juveniles were captured at depths greater than 60 m. This clearly reflects a different depth distribution for juveniles than has been described at other oceanic islands. In locations outside the Hawaiian Islands, Galapagos sharks have been observed swimming in water so shallow that their backs were exposed to air (Limbaugh 1963, Castro personal communication). Kato & Carvallo (1967) also found that juveniles were restricted to very shallow water surrounding islands. Galapagos sharks have not been found to occupy these type of nursery-like areas in the Hawaiian Islands.

Biology

Based on over 300 Galapagos sharks captured in Hawai'i, maximum size attained is possibly smaller than in other parts of the world. The largest male from Hawai'i was 267 cm, whereas Randall (1963) described a 292 cm male from the Virgin Islands. The largest female captured in Hawai'i was 300 cm, but individuals approaching 350 cm have been mentioned elsewhere (Limbaugh 1963, Edwards & Lubbock 1982).

Determination of sexual maturity for males was based solely on length and calcification of claspers, and did not include examination of other commonly used indices of maturity such as condition of siphon sacs, testes, and seminiferous tubules. The rapid increase in clasper length and onset of calcification of claspers indicates that males approached maturity between 205 and 239 cm. For female sharks, determination of maturity was limited to measures of ova and uterus diameter, and did not include examination of the hymen, measure of gonadosomatic index, or inspection of the oviductal gland for the presence of sperm. Abrupt development of the ova and uterus indicates that females matured between 215 and 245 cm. Few captures of mature Galapagos sharks have been reported in the literature, but values for Hawaiian specimens are similar to estimates for size at maturity of 205 to 250 cm for both sexes (Bass et al. 1973, Garrick 1982).

Extrapolation of our estimated size at maturity to the von Bertalanffy growth curve generated by De Crosta et al. (1984), yields ages at maturity of 6–8 years for males and 6.5–9 years for females, although De Crosta et al. (1984) estimated that first reproduction for both sexes is reached in 10 years.

A description of litter size of Galapagos sharks in Hawai'i by Tester (1969) ranging from 6 to 16 (n = 10), with an average of 9.5 has often been cited (Bass et al. 1973, Compagno 1984, Last & Stevens 1994). Analysis of the catch data from Tester's specimens reveals a range of 4 to 16 embryos, with an average of 8.7, although it was not clear whether the maximum value in the data sheets referred to uterine eggs or embryos. Pups are born at just over 80 cm TL in Hawai'i, which may be larger than the size at birth in other locations. Although Bass et al. (1973) described size at birth as 70 to 80 cm, Limbaugh's (1963) estimate was 61 to 76 cm, and free-swimming Galapagos sharks as small as 57 cm were observed at islands in the eastern tropical Pacific (Beebe & Tee-Van 1941, Kato & Carvallo 1967).

The small proportion of pregnant sharks (18% of mature females) may indicate that they only breed every two or three years, or that pregnant females move out of areas commonly fished, possibly to the north, where juveniles are more abundant. This may explain why the lowest catch rates of mature females occurred in spring. Fresh mating scars on mature female sharks in January and March suggest that mating occurred in winter and spring. This coincides with a peak in maximum ova diameter, and presumably with ovulation and fertilization. A pregnant female with large embryos (81 cm) was caught in March, and the smallest free-swimming sharks were caught in August (average = 86 cm, n = 4) and November (average = 91 cm, n = 3). This suggests that pups are born in the spring. If fertilization occurs during the first few months of the year, and birth ensues the following spring, the gestation period would be about 12 months. Since pregnant females were only caught during three months of the year, and only one near-term female was examined, our estimate of embryonic growth is tentative. Further data are needed to fully understand the reproductive cycle of this species of shark.

Diet

In Hawai'i, small Galapagos sharks fed primarily on teleosts, whereas elasmobranchs were consumed more frequently in larger sharks. Cephalopods were important in the diet of sharks of all size classes. Galapagos sharks appear to feed primarily on demersal prey, as reported by other workers (Limbaugh 1963, Bass et al. 1973, De Crosta et al. 1984). However, the occurrence of scombrids, flying fish, and squid in stomachs illustrates that they were not limited to demersal prey (Edwards & Lubbock 1982). In addition, Wass (1971) reported that Galapagos sharks were occasionally found near the surface over deep water in Hawai'i, and were caught by fishermen trolling at the surface for game fish.

A low degree of dietary overlap between some size classes and an increase in dietary diversity with size demonstrated ontogenetic changes in the feeding habits of Galapagos sharks. Such ontogenetic dietary shifts appear to be common among sharks (Wetherbee et al. 1990, Lowe et al. 1996). Changes in feeding habits may be a reflection of differences in ability to capture prey, spatial distribution, or range of habitats encountered by sharks of different sizes (Cortes & Gruber 1990).

Data gathered during shark control programs in Hawai'i clearly represent a valuable source of information for poorly understood species such as the Galapagos shark. Despite the fact that over 25 years have passed since the majority of this information was collected, these data continue to contribute to a greater understanding of the biology of the Galapagos shark.

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