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A COMPARATIVE STUDY OF THE LIFE HISTORY,  
DISTRIBUTION AND ECOLOGY OF THE SANDBAR  
SHARK AND THE GRAY REEF SHARK IN HAWAII.

University of Hawaii, Ph.D., 1971  
Zoology

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A COMPARATIVE STUDY OF THE LIFE HISTORY, DISTRIBUTION  
AND ECOLOGY OF THE SANDBAR SHARK AND THE  
GRAY REEF SHARK IN HAWAII

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION  
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Most of the field data upon which this study is based were collected by the Cooperative Shark Research and Control Program. Funds for this program were provided by the National Science Foundation (Grant No. GB-6139), the Oceanic Institute and a special state appropriation.

## ABSTRACT

The principle objective of this dissertation is to compare the ecology of 2 inshore Hawaiian sharks and to determine what factors are responsible for their local distribution. The sandbar shark, Carcharhinus milberti (Müller and Henle, 1841), is the most abundant shark around the high Hawaiian Islands but occurs nowhere else in the central Pacific. The gray reef shark, Carcharhinus menisorrhah (Müller and Henle, 1841), is abundant in inshore areas throughout the central Pacific. In Hawaii, however, it seldom occurs near the main islands but is common around the smaller islands and islets.

Around Oahu, adult sandbar sharks are significantly more abundant in the leeward areas between Diamond Head and Kaena Point (south and west coasts). Juveniles, on the other hand, were caught only in the windward areas. At Niihau, adults were caught in greatest numbers off the windward side (southeast coast) and no juveniles were caught. Gray reef sharks rarely occur around Oahu. At Niihau, catch rates for adults were greatest on the leeward side (north-west coast). Juveniles were caught only around the northern half of the island.

Mature males of both species tend to occur in deeper water than the rest of the population. Females and juveniles occur at the shoalest depths of the species range with sub-adults at intermediate depths. The sex-maturity groups of the sandbar shark all occur at greater depths than those of the gray reef shark.

The life histories of the 2 species are similar with respect to size at birth and maturity, fecundity and gestation period. Possible differences in growth rate and reproductive season are unlikely to influence local distribution. Distribution, however, was found to be correlated with physical factors of the environment. The sandbar shark occurs most commonly where currents are weak and where the bottom is level with a substratum of fine rubble, sand or mud. The gray reef shark is generally associated with clear water and hard bottom of rugged relief. These associations are more pronounced amongst juveniles than for adults and the above factors may be requisites for nursery areas.

The diets of the sandbar shark and the gray reef shark are broadly overlapping. Both prefer fish with cephalopods ranking second. The sandbar shark tends to eat more crustaceans than the gray reef shark which may be related to its heavier tooth structure.

The study species are preyed upon most heavily by the tiger shark and the galapagos shark. Predation does not appear to influence distribution though it probably plays a major role in limiting population size.

It is concluded that differences in the distribution of the sandbar shark and the gray reef shark in Hawaii are probably a function of associations, especially among juveniles, with particular bottom types, turbidities and current velocities.

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## CHAPTER I

### INTRODUCTION

#### A. Background

Most people regard sharks as creatures which endanger human life. The shark's reputation as a man-eater, however, is greatly exaggerated. Only a few species have been positively implicated in attacks on humans, and the number of injuries and fatalities due to shark attacks is extremely small when compared with the millions of people who swim in the oceans around the world. Sharks are of greater concern to commercial fisheries. In some countries they are fished for their meat, fins and hides. More important, however, their habits of eating hooked fish, tearing nets, etc. are economically damaging to other fisheries. Ecologically, sharks are important members of many marine communities in which they are often the top carnivores or principal scavengers.

Despite their importance, the larger sharks have received little attention from ecologists beyond notes on distribution and lists of stomach contents. This is a consequence of the extraordinary amount of effort and expense necessary for a successful field study on animals as large and active as sharks. Comprehensive studies of the ecology of larger sharks are few. Those most noteworthy are Olsen's (1954) investigation of the biology of Galeorhinus australis in Australia; Backus' et al. (1956) report on the natural history of Carcharhinus longimanus; Strasburg's

(1958) work on the pelagic sharks of the central Pacific; Springer's (1960) summary of the natural history of Carcharhinus milberti in the Western Atlantic; Jensen's (1966) review of the life history of Squalus acanthias; and Clarke's (1971) study of the ecology of Sphyrna lewini in Hawaii. (Common names for these species as well as those discussed below are listed in Appendix A). Of the above, the paper by Springer is the most extensive and will be used as a reference on numerous occasions in this dissertation as it deals with one of the species discussed herein.

Until recently, little was known about the ecology of inshore sharks in Hawaii and some common species had not even been identified. Excepting Clarke's (1971) work on Sphyrna lewini, the only studies in the literature dealing with Hawaiian sharks (Ikehara, 1961; Tester, 1969) have had a limited distribution and are concerned primarily with fishing methods and catch statistics rather than ecology. Extensive ecological data, however, were gathered under the auspices of the Cooperative Shark Research and Control Program (Tester, 1969). The present study is based upon these data.

## B. The Problem

My investigation involves an ecological comparison of 2 inshore species of carcharhinid sharks with emphasis on factors accounting for their local distribution in Hawaii. The sandbar shark, Carcharhinus milberti (Müller and Henle, 1841), is the most common shark in the Hawaiian Islands and is especially abundant around the large, high islands.

The gray reef shark, Carcharhinus menisorrah (Müller and Henle, 1841), is also a common shark in the inshore Hawaiian environment, but only in certain areas. This species is rarely found around the high islands where C. milberti is so common, but is abundant around the offshore islets of Kaula and Molokini. C. milberti and C. menisorrah are present together in substantial numbers only at Niihau and Kahoolawe, which are intermediate between the main islands and small islets in terms of size and elevation.

The principal objective of this study is to determine what factors are responsible for the distribution of these species in Hawaii. I shall consider physical factors, particularly those related to size and elevation of different islands, and biological factors including interactions between the study species, and competitive and predatory relationships with other sharks.

### C. Systematics

Most living sharks are included in Carcharhinidae (requiem sharks). Most of the carcharhinids fall within the genus Carcharhinus (gray sharks). This genus is distributed worldwide in tropical and subtropical seas and includes the most common moderate-to large-sized sharks in these regions. Generic characteristics are summarized by Bigelow and Schroeder (1948).

Presently, the systematics of the genus Carcharhinus are in a confused state. Sharks are virtually lacking in external meristic

characteristics so most species are distinguished on the basis of color and proportional measurements, both of which are often dependent upon size and age of the individual. The problem is further complicated by their generally large size which makes them difficult to collect in adequate numbers and to preserve for later reference. Garrick (1967) has found vertebral counts to be a useful tool in carcharhinid taxonomy and has reduced the 103 nominal species of Carcharhinus to 28. His final evaluation, however, is yet to be published, so the systematics of the genus remain chaotic.

Ten species of sharks commonly occur in inshore (depths less than 50 fathoms) Hawaiian waters. Two of these are hammerhead sharks (Sphyrna spp) and will not be dealt with further. The remaining 8 species are all carcharhinids and can be identified from the key in Appendix B.

Carcharhinus milberti is a heavy-bodied species (Fig. 1) and can be various shades of brown or gray dorsally and creamy-white ventrally. The tips and trailing edges of the fins of young individuals often have a fine band of white pigment. Most of this white is soon lost, however, and at maturity only the tips and trailing edges of the pectorals, anal and caudal of some individuals are white.

C. milberti has a prominent ridge between the 2 dorsals, but its most distinctive morphological characteristic is the large first dorsal situated far forward, originating over the axil of the pectoral. Also, its dermal denticles are widely spaced and non-overlapping. The

Figure 1. Female Carcharhinus milberti. Precaudal length is 132.1 cm.

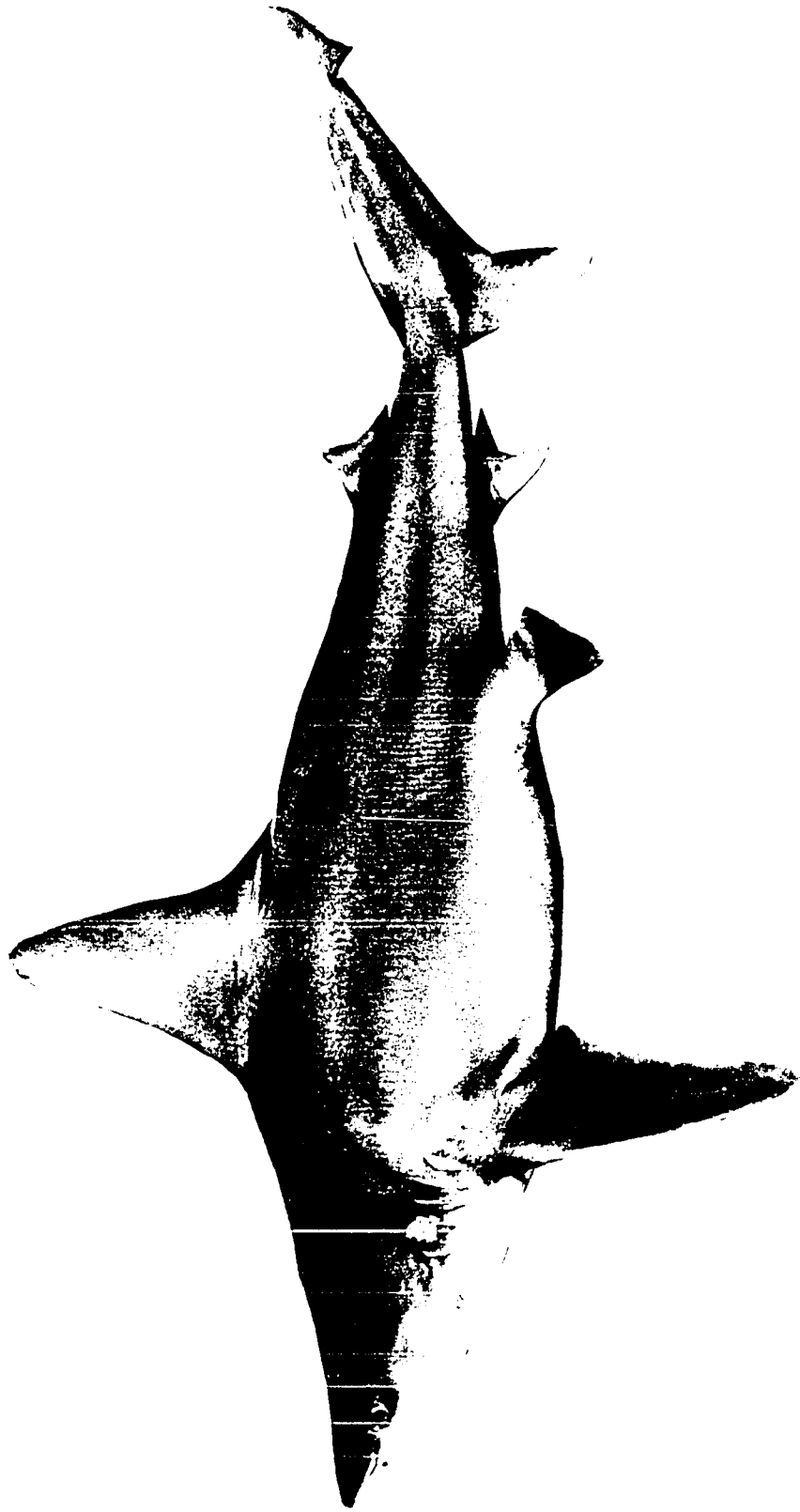




Figure 2. Anterior view of upper and lower teeth of Carcharhinus milberti (lower set) and Carcharhinus menisorrhah (upper set). Only teeth from left side of jaw are pictured, the symphyisial teeth are at the left and the lateral teeth at the right.

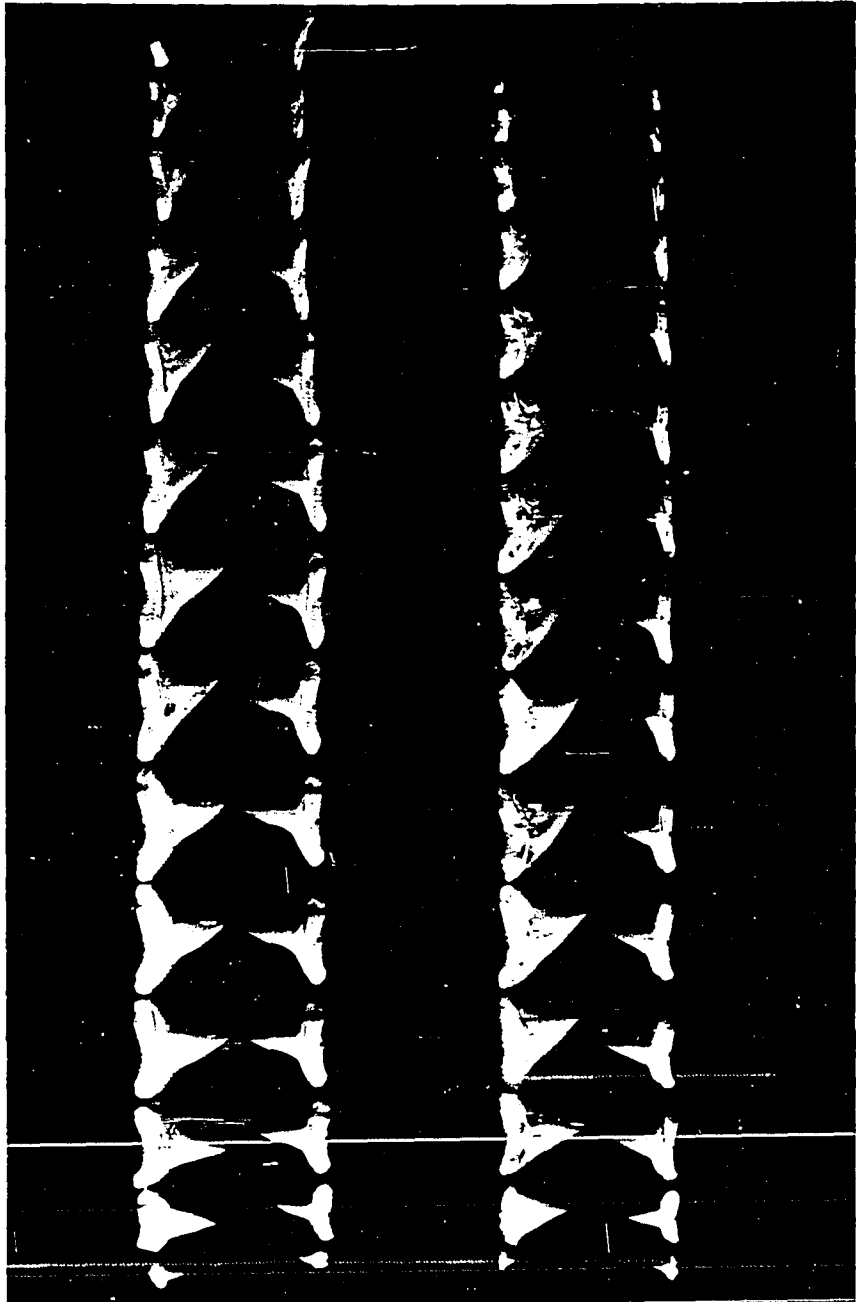


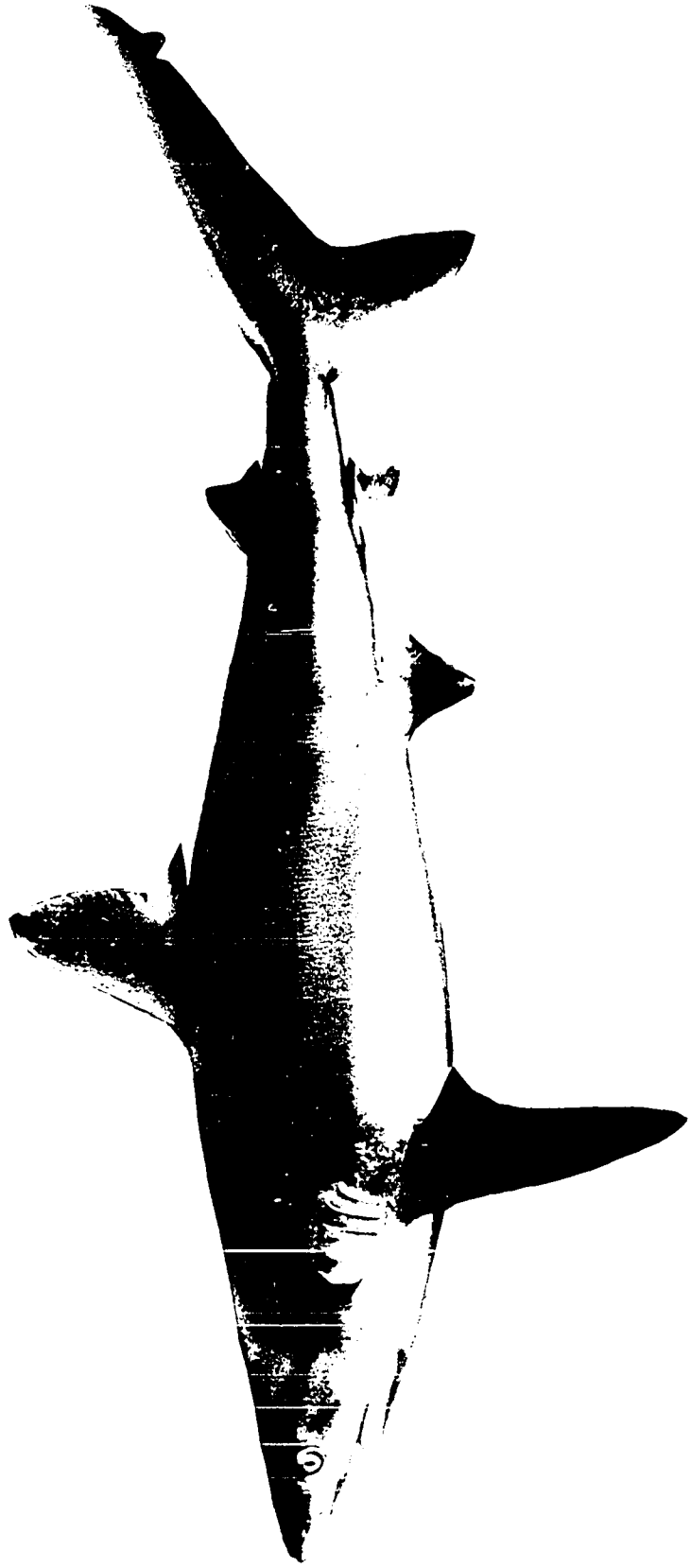
Figure 3. Upper and lower teeth (fourth series, left side) of Carcharhinus milberti (right) and Carcharhinus menisorrah (left).

A. anterior view

B. posterior view



Figure 4. Female Carcharhinus menisorrah. Precaudal length is 78.8 cm.



underparts. A distinctive feature of the coloration is the broad band of black pigment on the trailing edge of the caudal, especially on the lower lobe. The second dorsal, the anal, the pelvics, and the tips of the undersides of the pectorals are also darkly pigmented. The first dorsal, however, is never tipped with black. Some individuals may have a slight medial ridge between the first and second dorsals, but it is never distinct. Schultz et al. (1953) may be consulted for the morphometrics. Numbers of teeth expressed in a tooth formula for C. menisorrah were

13 or 14--1 or 2--13 or 14	14--1--14

the 11 sharks examined.

The teeth of C. menisorrah are figured above (Figs. 2 and 3). Those of the upper jaw are narrowly triangular with entirely serrate margins, the serrations being larger on the base and decreasing in size toward the tip. The first 2 teeth are erect and nearly symmetrical. The more lateral teeth have an increasingly distinct notch on the lateral side and begin decreasing in size and height relative to breadth at about the eighth or ninth tooth. The teeth are bladelike and arranged in a band with a single cutting edge. Thus, only a single tooth of each series is generally functional at one time. The teeth in the lower jaw are more or less symmetrical and narrowly triangular with a broad base. The more medial teeth have smooth shoulders and bases and are minutely serrated only near the tip of the cusp. Tiny serrations on the more

lateral teeth may extend all the way to the base which may also have a serrated or at least an irregular margin. As in C. milberti, the lower teeth are recurved and the outer 2 teeth of each series are usually functional.

#### D. Distribution

C. milberti occurs in tropical and subtropical portions of all major oceans. Bigelow and Schroeder (1948) report it from the Mediterranean, along the southern coast of Spain, in the Canaries, Cape Verdes, and off southern Brazil. In the western North Atlantic, Springer (1960) reports it from Cape Cod to the Gulf Coast of Florida, western Gulf of Mexico south to Costa Rica and occasionally off Cuba and the Bahama Banks. J.A.F. Garrick (pers. comm.) states that its Pacific and Indian Ocean range includes the Red Sea, Gulf of Oman (Muscat), Indonesia (Aru Island), China (Fukien and Ningpo), Japan (Nagasaki), and the Revillagigedo Islands. Garrick also verified literature accounts of C. milberti occurring in Western Australia (Whitley, 1944, as Galeolamna dorsalis), Swain Reefs off Queensland (Whitley, 1964, as Galeolamna stevensi), Madagascar (Fourmanoir, 1961, as Carcharhinus platyodon), and Mauritius and Seychelles (Wheeler, 1962). J. Bass (pers. comm.) reports that C. milberti ranges along the east coast of South Africa as far south as the Natal/Cape Province border.

In the central Pacific C. milberti occurs only in Hawaii. It has

not been reported from the Leeward Hawaiian Islands, but this may be a result of the difficulty in distinguishing it from Carcharhinus galapagensis, which has been reported as abundant in the area, or simply because it occurs uncommonly or deeper and has yet to be observed. I would expect it to be present, at least in the lower portion of the chain, because it is commonly caught at Niihau and Kaula about 240 km southeast of Nihoa.

These records show C. milberti occurring most often in tropical areas, though it does penetrate cooler waters. Its latitudinal extremes are 31°S in South Africa and 41°N at Cape Cod, Massachusetts. It is found most commonly along continental coasts and shelves.

C. menisorrah has been recorded from areas scattered throughout the warmer regions of the Pacific and Indian Oceans. A sampling of areas includes New Guinea (Fowler, 1941); Tuamotu Archipelago (Harry, 1953); Philippine Islands (Herre, 1953); Marshall Islands (Schultz et al., 1953); Gilbert Islands (Randall, 1955); and Guam (Kami, Ikehara, and DeLeon, 1968). J.A.F. Garrick (pers. comm.) has seen specimens from the Cook Islands, Phoenix Islands, Great Barrier Reef, Solomon Islands, Java Sea, Gulf of Thailand, India, and the western Indian Ocean. Randall (pers. comm.) has taken this species at Marcus, Mangareva, Society Islands and Henderson. Finally, Randall and Allen (MS) report C. menisorrah from Easter Island.

In tropical regions of the central Pacific, C. menisorrah is the

most abundant shark in the deeper inshore areas around most of the oceanic islands and in the lagoons of coral atolls. I have seen the species in the Line Islands (1,640 km south of Hawaii) and at Johnston Island (970 km southwest of Hawaii). E. Kridler and D. Olsen (pers. comm.) state it is probably the most abundant shark in the Leeward Hawaiian Islands and report it from Nihoa, Necker, French Frigate Shoal, Laysan, and Pearl and Hermes Reef. I have seen photographs of C. menisorrah from Midway.

Thus C. menisorrah occurs in tropical and subtropical waters from the western Indian Ocean eastward to the Hawaiian chain and Easter Island. It is reported from as far south as Easter Island (28°S) to a northern extreme in Midway (28°N). It has a narrower latitudinal as well as longitudinal range than C. milberti. The distribution of C. menisorrah is usually restricted to smaller islands as pointed out by Garrick (pers. comm.).

## CHAPTER II.

### MATERIALS AND METHODS

#### A. Cooperative Shark Research and Control Program

Most of my field data on Hawaiian sharks result from the Cooperative Shark Research and Control Program which operated from July 1967 through June 1969 and was directed by Dr. Albert L. Tester (1969). Objectives of the program were to survey the species of sharks present in inshore Hawaiian waters and to study their ecology, to determine if shark abundance could be significantly reduced by fishing effort, and to recommend future measures for controlling abundance.

Sharks were fished from the 58-foot sampan Alika by longline, light longline and handline. The basic unit of longline gear was the "basket" consisting of 10 coils of 3/8-inch polypropylene line 20 fathoms long. A floater on a 10-fathom floatline was attached to the middle of each basket and a 3-fathom dropper bearing a hook was suspended between each of the five 20-fathom lengths on either side resulting in 8 hooks per basket. The droppers consisted of 2 fathoms of 3/8-inch polypropylene line with weight attached, a swivel, 1 fathom of 3/32-inch woven galvanized wire leader and a No. 14/0 hook. Flags on 10-fathom floatlines were attached to the ends of each basket. Because hooks were large, the longline gear was selective for sharks which

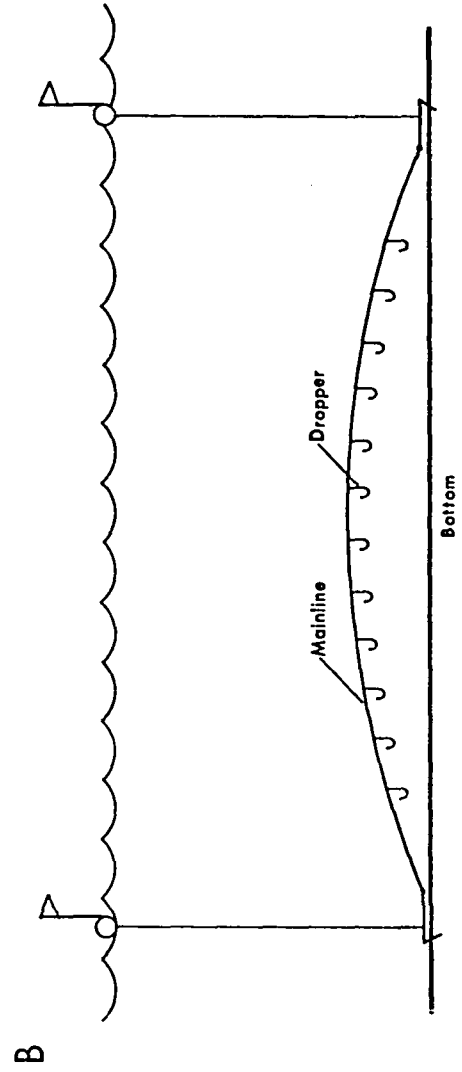
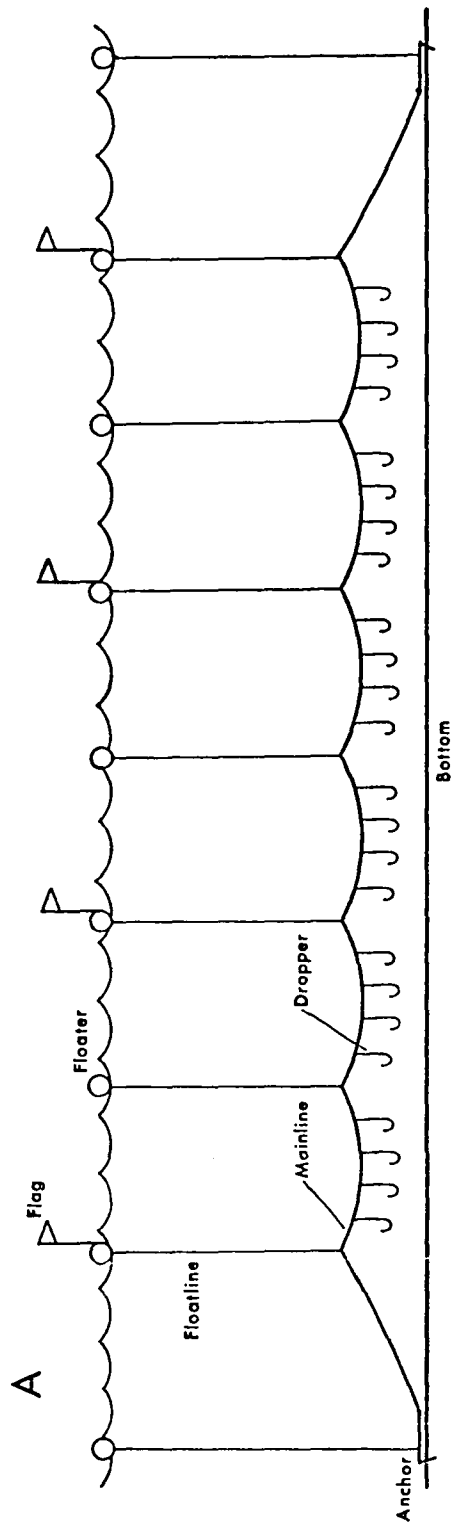
generally had precaudal lengths larger than 80 cm.

Fishing methods were standardized for areas fished on a regular basis each quarter. In "standard fishing" 3 baskets of fishing gear were connected and anchored at both ends to form a "section" which is illustrated in Fig. 5. An entire "standard set" consisted of 3 sections (72 hooks) spaced at intervals within a designated area. The gear was set parallel to shore at a depth of 15 to 30 fathoms (usually 20 to 25 fathoms). In all but a portion of one circuit the bait was 1/2 or 1/3 of a skipjack tuna, Katsuwonus pelamis, weighing 1 to 4 kilograms. The line was set at dusk and hauled soon after daybreak.

The standard longline was designed to suspend the baits just above the bottom when set in water 20 fathoms deep. A SCUBA dive following one set confirmed the success of the design. The hooks adjacent to floatlines were dangling about 3 fathoms above the bottom while the 2 hooks in between were within 1 fathom of the bottom. This was under ideal conditions where the bottom was level and there was no current.

When the standard fishing for each quarter was completed, the remaining time was allotted to "experimental fishing" in which the routine was varied in several ways. As in standard fishing, a set usually consisted of 9 baskets of gear, but they were often tied together to form a single unit rather than 3 separate sections. In several areas the mainline was set perpendicular to shore at depths

Figure 5. A. One section of standard longline gear (not drawn to scale).  
B. Light longline gear (not drawn to scale).



between 5 and 100 fathoms or set parallel to shore at depths of 50 to 200 fathoms to gain data on depth distribution. When fishing in deeper water, the hooks were usually lying on the bottom instead of suspended above it.

Various baits including porpoise, fresh fish, squid, and cat were used. The "alternate-bait technique" was employed to examine food preferences. In this procedure 2 types of bait (e. g., porpoise and skipjack) were placed on alternate hooks giving the shark a choice of baits. To determine which species feed high in the water column, the gear was anchored in deep water (100 to 200 fathoms) while retaining the floaters and flags utilized in standard fishing to suspend the hooks near the surface.

Light longline gear was often set in the evenings in the same area as the longline. It was designed to catch sharks too small (generally less than 80 cm precaudal length) to be hooked on the heavier gear. It consisted of 2 flags attached to anchors at either end of a 130-fathom length of 3/8-inch polypropylene mainline (Fig. 5). Twelve droppers were attached to this line at 10-fathom intervals. A dropper consisted of 1 fathom of 1/8-inch polypropylene line (with or without attached weight), a swivel, 1/2 fathom of stranded 3/32-inch stainless steel leader and the hook (No. 7/0). Small chunks of skipjack were the usual baits. The mainline was not suspended from floaters on the surface, but polypropylene line is bouyant and, because little weight was used,

the hooks were probably off the bottom. The light longline was easily modified to fish at any depth merely by making the appropriate adjustments on the length of line between the anchors and flags. Depths between 10 and 65 fathoms were fished regularly with this gear and it was set once at 100 fathoms and again at 200 fathoms.

Handlines were also used to catch small sharks. Handlining was usually done at night at depths of 10 to 60 fathoms. Live-caught sharks were either tagged and released immediately or retained in a live well aboard the Alika and transported to a shore facility for further study.

Small sharks to be tagged and released were brought on board, identified, sexed and measured as quickly as possible. Sharks larger than about 120 cm total length had to be tagged without lifting the animal from the water so accurate length measurements were unobtainable. Large sharks were restrained off the stern of the Alika by the hookline in their mouth and a rope around their tail. Special pliers were used to tag sharks on the lower trailing edge of the first dorsal with a monel metal strap tag (Fig. 6). The small tags measured 2.8 X 0.8 cm (clamped) and the large ones measured 4.0 X 1.0 cm (clamped). Tags and pliers were supplied by the American Institute of Biological Sciences' Shark Research Panel.

Most of the fishing effort was concentrated around the island of Oahu. Its perimeter was divided into 16 contiguous areas (Fig. 7) which were fished at least once during each quarter for the 2-year

1.

Figure 6. A. Tagging a shark.  
B. Tag in position on first dorsal and pliers  
used for attachment.

A



B

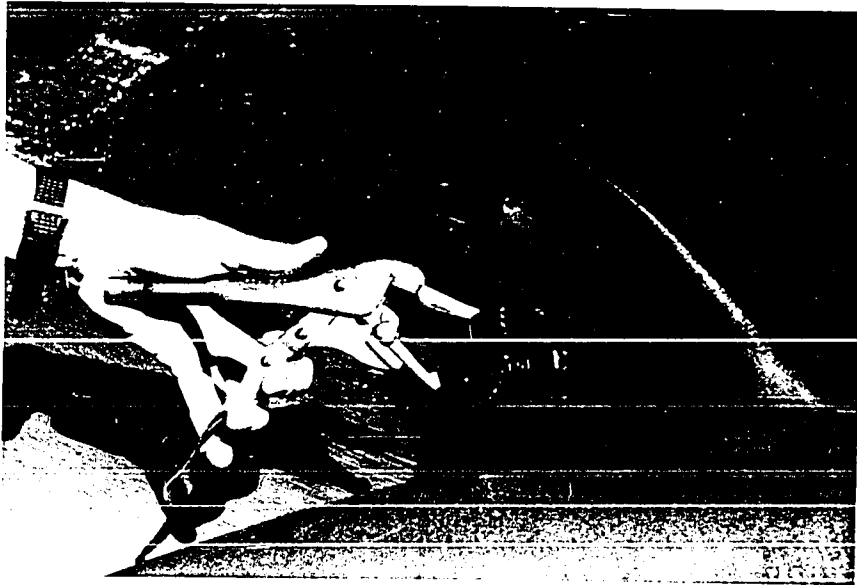
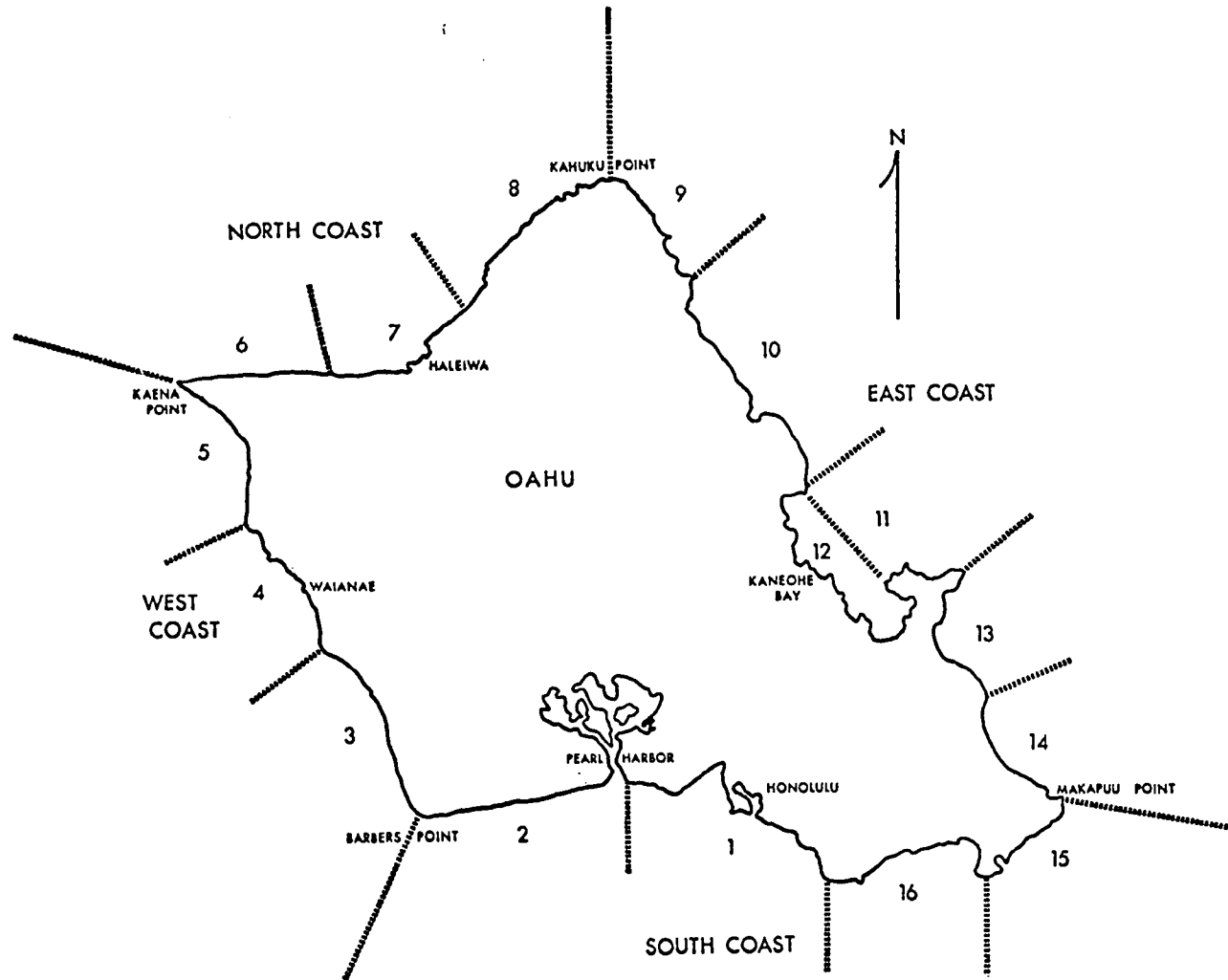


Figure 7. Fishing areas around Oahu.



period of the fishing program. The island of Niihau and a section of the west coast of Hawaii (Kawaihae) were also fished quarterly. Other islands were fished sporadically depending upon scientific interest, weather, and available time.

Niihau was fished heavily because C. menisorrah is abundant there. The island is also a good area for releasing tagged sharks because of its isolation and sparse human population (in more populated areas, some people object to releasing tagged sharks). Kawaihae was fished regularly by agreement with the Oceanic Institute which had expended considerable fishing effort in that area for 5 previous quarters.

Research assistants were aboard the fishing vessel whenever the gear was set and hauled. They collected and recorded pertinent data for each set (time of start and finish of setting and hauling, exact location of gear by triangulation, depth by fathometer tracing, kind and condition of bait) as well as general observations of weather, sea state, etc.

Surface temperatures were measured to the nearest  $0.1^{\circ}\text{C}$  with a standard bucket thermometer as the gear was set in the late afternoon. At the fishing depth, temperatures were measured to the nearest  $0.1^{\circ}\text{C}$  with a reversing thermometer attached to a Nansen Bottle. Water samples were collected by the Nansen Bottle and from the sea surface for salinity measurements. Salinities were determined electrometrically to the nearest  $0.01^{\circ}/_{\text{OO}}$  by the Hawaii Branch of the Marine Fisheries Services, National Oceanographic and Atmospheric Agency. Turbidity

was determined after hauling the gear by measuring the extinction depth, to the nearest foot, of a Secchi Disc.

As the gear was hauled, the scientist recorded for each hook the presence or absence of bait, or the species of shark caught. For each shark recovered and killed, he recorded the length, weight (when possible), sex, and size and condition of uterus or claspers. Stomach contents were examined and noted. Eggs and embryos were counted and measured.

#### B. Shark Fishing in Other Pacific Areas

Nine days were spent during April 1969 fishing for sharks at Johnston Island. Light longline gear (set and hauled from a small boat) and handlines were used exclusively. An attempt was made to fish in as wide a variety of ecological conditions (depth, bottom type, turbidity, etc.) as was possible during the short time available.

During July 1969, sharks were fished at Eniwetok Atoll, Marshall Islands. Because many of the small hooks on the light longline were broken off by large sharks at Johnston, a longline designed to catch large as well as small sharks, and which could be conveniently handled from a small boat, was utilized at Eniwetok. It consisted of a single basket of the longline gear used during the Cooperative Shark Research and Control Program. It was anchored at both ends and hauled by lines attaching the anchors to marker bouys. In addition to the usual 8

droppers with No. 14/0 hooks, 7 light longline droppers with smaller hooks were tied to the mainline midway between the larger hooks. The resulting unit of gear included 8 large and 7 small hooks and is termed the "mixed longline." As at Johnston, the line was set over a variety of bottom types and depths during the day as well as at night and both parallel and perpendicular to the shoreline. Extra floaters were sometimes tied directly to the mainline in an attempt to keep the line from fouling on the bottom in shallow water.

The mixed longline was also used while shark fishing at Fanning Atoll during January 1970. Again, the gear was fished from a small boat in overnight sets. Sharks were also handlined from a boat and from shore during this period.

#### C. Other Sources of Data

During the fishing operations there were numerous opportunities for skin and SCUBA diving throughout the Hawaiian Islands. Sharks were often observed and, whenever possible, they were identified, their total length was estimated, and the location, bottom type, and other environmental factors were noted. The only available data for C. menisorrah at Molokai and Hawaii were obtained in this manner as this species was not captured there.

Several individuals acknowledged previously have presented me with data from the Hawaiian Islands, Leeward Hawaiian Islands, Line

Islands, Johnston Island, Eniwetok Island, Marcus Island, and South Africa. When these data are combined with mine, 795 C. milberti and 453 C. menisorrah are represented. Location and method of capture for all individuals are listed in Table 1.

#### D. Kewalo Basin Research Facility

Live sharks were maintained at the Kewalo Basin Branch of the Hawaii Institute of Marine Biology in a tank 15.3 m in diameter and 1.5 m deep or in smaller tanks with a diameter of 3.1 m and a depth of 0.9 m. A sun-shade of Propalite (92% shade) was erected (early summer, 1969) over the main tank to retard the growth of algae. Fresh sea-water was delivered at the rate of 570 l/min. At weekly intervals, the water level was lowered to a depth of about 1/2 m to facilitate sweeping and vacuuming the tank to prevent build-up of algae and detritus.

Both C. milberti and C. menisorrah (63 to 180 cm long) were maintained for periods up to 30 months. The smaller sharks were caught on handlines and were transported to Kewalo Basin in the live-well of the Alika. The adults were caught near the facility. They were towed into the harbor while still on the hookline, then swathed in heavy canvas and carried to the edge of the tank. After measurements were taken, the hook was removed and the animal was lowered into the tank.

When necessary, sharks were anesthetized with M.S. 222

TABLE 1. -- Number and source of Carcharhinus milberti and Carcharhinus menisorrah on which the present study is based.

Location	Fishing Method	<u>C. milberti</u>	<u>C. menisorrah</u>
Hawaii	Longline	652	68
Hawaii	Light longline	78	16
Hawaii	Handline	59	190
Hawaii	Trammel net <sup>a</sup>	-	3
Hawaii	Hook and line <sup>b</sup>	6	1
Eniwetok	Mixed longline	-	45
Eniwetok	Mixed longline <sup>c</sup>	-	46
Eniwetok	Spear and hook <sup>d</sup>	-	5
Fanning	Mixed longline	-	5
Fanning	Handline <sup>d</sup>	-	27
Palmyra	Handline <sup>d</sup>	-	19
Johnston	Light longline	-	16
Johnston	Handline <sup>d</sup>	-	6
Marcus	Spear and hook <sup>d</sup>	-	6
Total		795	453

- <sup>a</sup> Data from Maciolek  
<sup>b</sup> Data from Faughnan  
<sup>c</sup> Data from Milisen and Brock  
<sup>d</sup> Data from Randall

(tricaine methanesulfonate) using a variation of the method described by Gilbert and Wood (1957). A 1:1,000 solution of the powdered anesthetic and sea-water was prepared and placed in a 20-liter rectangular wooden tank. Sharks up to 120 cm long were netted out of the main tank and immersed in the solution for 15 to 60 seconds (depending on how soon they ceased struggling). On a few occasions, smaller sharks (less than 70 cm total length) were held by the tail and dipped headfirst into a plastic bucket containing the anesthetic for approximately 5 seconds, then held out for 20 to 30 seconds before repeating the procedure. Sharks dunked 3 or 4 times succumbed to the anesthetic.

Sharks larger than 120 cm were anesthetized in the large tank. The water level was lowered to a depth of 1/2 m and the shark was wrestled or lured over a net measuring 2.4 X 3.0 m hanging along the wall of the tank and extending out on the floor. When the shark was in position, the net was pulled up, leaving the animal suspended against the wall just above the water line. M.S. 222 was then poured or squirted on the gills of the shark for 2 to 5 minutes until it ceased struggling.

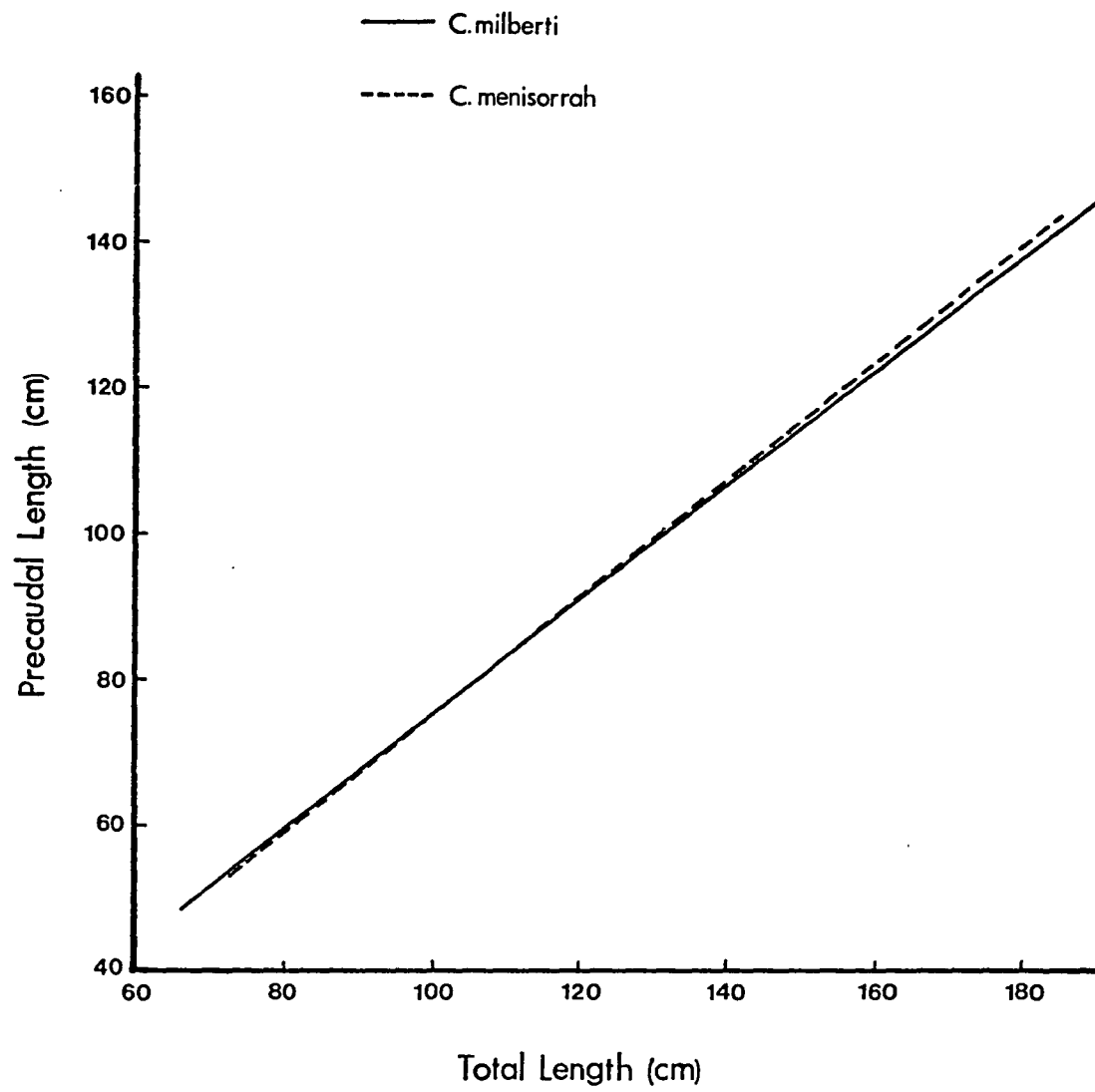
Once anesthetized, the sharks could be laid out for length measurements, photographs, tooth examination, etc. for periods up to 5 minutes. When the animal was returned to the water, its gills were rinsed with running sea-water. It was then "walked" around the tank for a few minutes and released.

When first returned to the water, the sharks swam awkwardly and in a disoriented fashion, but they recovered in 10 to 30 minutes and would feed soon after. Only once did a shark show any ill effects from the above procedures. This was a mature female C. milberti which never recovered from what was probably an overdose of the anesthetic. She swam around the wall of the tank in a labored manner for several hours and finally died. No other problems were encountered during hundreds of anesthetizations.

#### E. Length Measurements

Length measurements are the easiest to take in the field and are probably the best means of measuring size for most purposes. Total length (horizontal distance between the tip of the snout and the tip of the caudal in the normal swimming position) is dependent upon the angle at which the caudal is positioned and must be estimated if a portion of the caudal is missing. For carcharhinids, which have a distinct precaudal pit on the dorsal surface of the caudal peduncle, precaudal length (horizontal distance between the tip of the snout and the deepest part of the precaudal pit) is a more consistent and accurate measure of size and will generally be used in this report. Fig. 8 can be used to convert from one measurement to the other.

Figure 8. Regression of precaudal length (Y) on total length (X) for 542 Hawaiian Carcharhinus milberti ( $\hat{Y} = 0.784 X - 3.022$ ) and 54 Carcharhinus menisorrah ( $\hat{Y} = .801 X - 4.610$ ).



CHAPTER III.  
LIFE HISTORY

A. Size

1. Size at Maturity and Maximum Size

Shortly before sexual maturity is attained in male elasmobranchs, their claspers begin to lengthen rapidly. Enlargement of the testes to functional size is immediately followed by calcification of the clasper cartilages (Springer, 1960). Minimum size at maturity for male sharks can easily be estimated from plots of clasper length (distance between the joint at the proximal end and the clasper tip) and calcification status against precaudal length for a representative sample of individuals.

The breadth of the flattened uterus at the widest point is used (Springer, 1960) to determine sexual maturity among female sharks. A mature female is defined as an individual whose uterus breadth is at least as great as the breadth of a fully contracted uterus following parturition. Minimum size at maturity was estimated from plots of uterus breadth against precaudal length.

C. milberti

C. milberti males in Hawaii appear to mature at an average precaudal length of about 110 cm with a minimum clasper length of 130 mm (Fig. 9). Precaudal lengths of mature males averaged 119.4 cm

Figure 9. Relationship between clasper length and precaudal length for Hawaiian Carcharhinus milberti.



and ranged from 109 to 132 cm. Calcified clasper lengths averaged 157 mm; and the largest measured 180 mm.

The precaudal length at which female Hawaiian C. milberti mature is estimated from Fig. 10. The breadth of a fully contracted uterus following parturition is larger than 20 mm so it appears that females reach maturity at a precaudal length of about 115 cm. Average size at maturity was 130.7 cm and the largest measured 146 cm.

Mature Hawaiian C. milberti are smaller than their conspecifics in other areas. Springer (1960) found that minimum lengths at maturity in the Western North Atlantic correspond to precaudal lengths of 138 cm for males and 140 cm for females and that the average length for mature males is 154 cm and for mature females is 162 cm. J. Bass (pers. comm.) reports that male C. milberti from South Africa mature at a precaudal length of 115 cm and attain a maximum precaudal length of 140 to 145 cm.

#### C. menisorrah

C. menisorrah males from Hawaii mature at a precaudal length of approximately 100 cm with a minimum clasper length of 140 mm (Fig. 11). Precaudal lengths of 22 mature males ranged from 102 to 137 cm with an average of 121.3 cm. Clasper lengths ranged from 140 to 162 mm with an average of 152 mm.

Data are available for only 6 mature female C. menisorrah

Figure 10. Relationship between uterus breadth and precaudal length for Hawaiian Carcharhinus milberti.

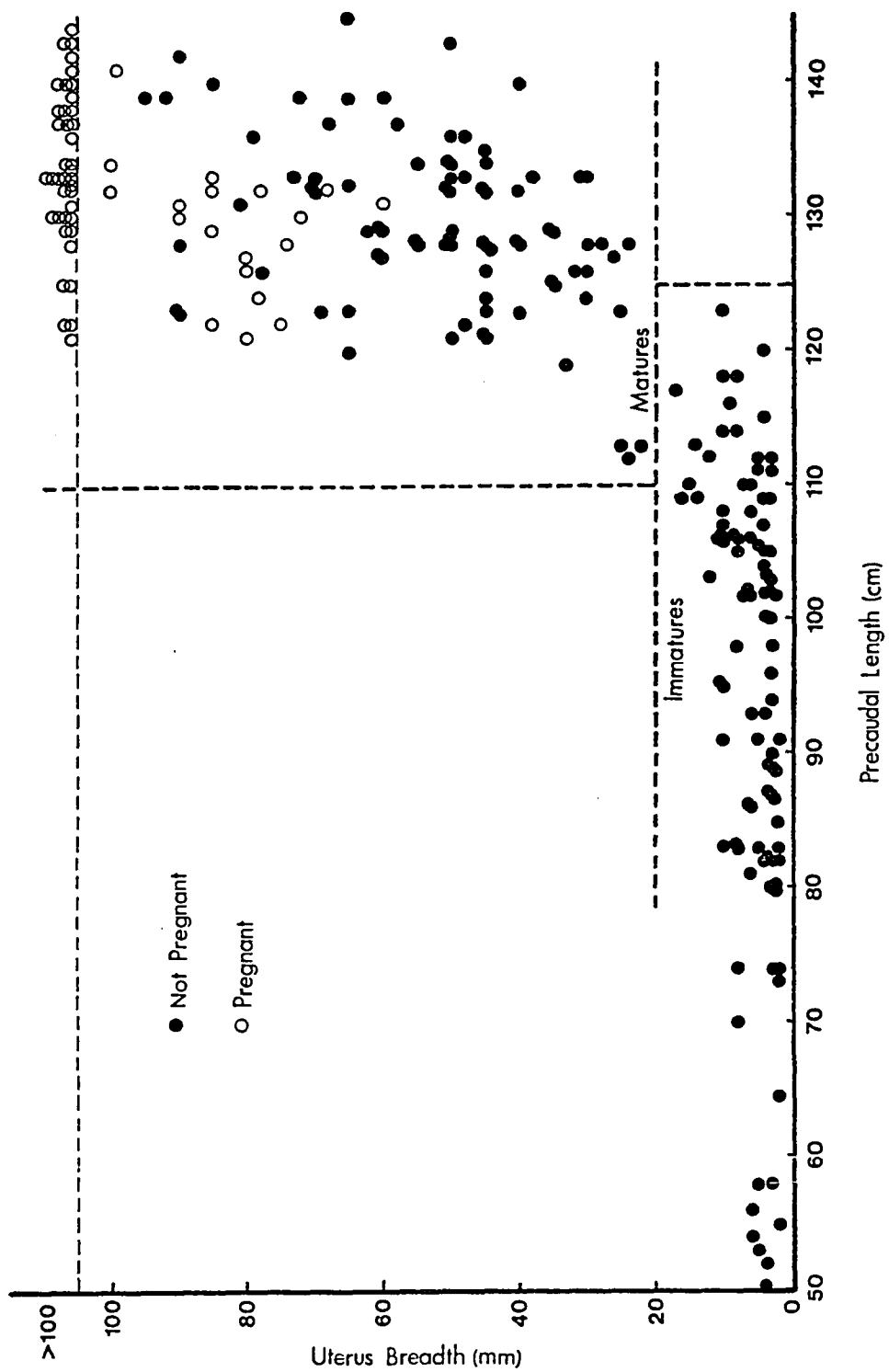
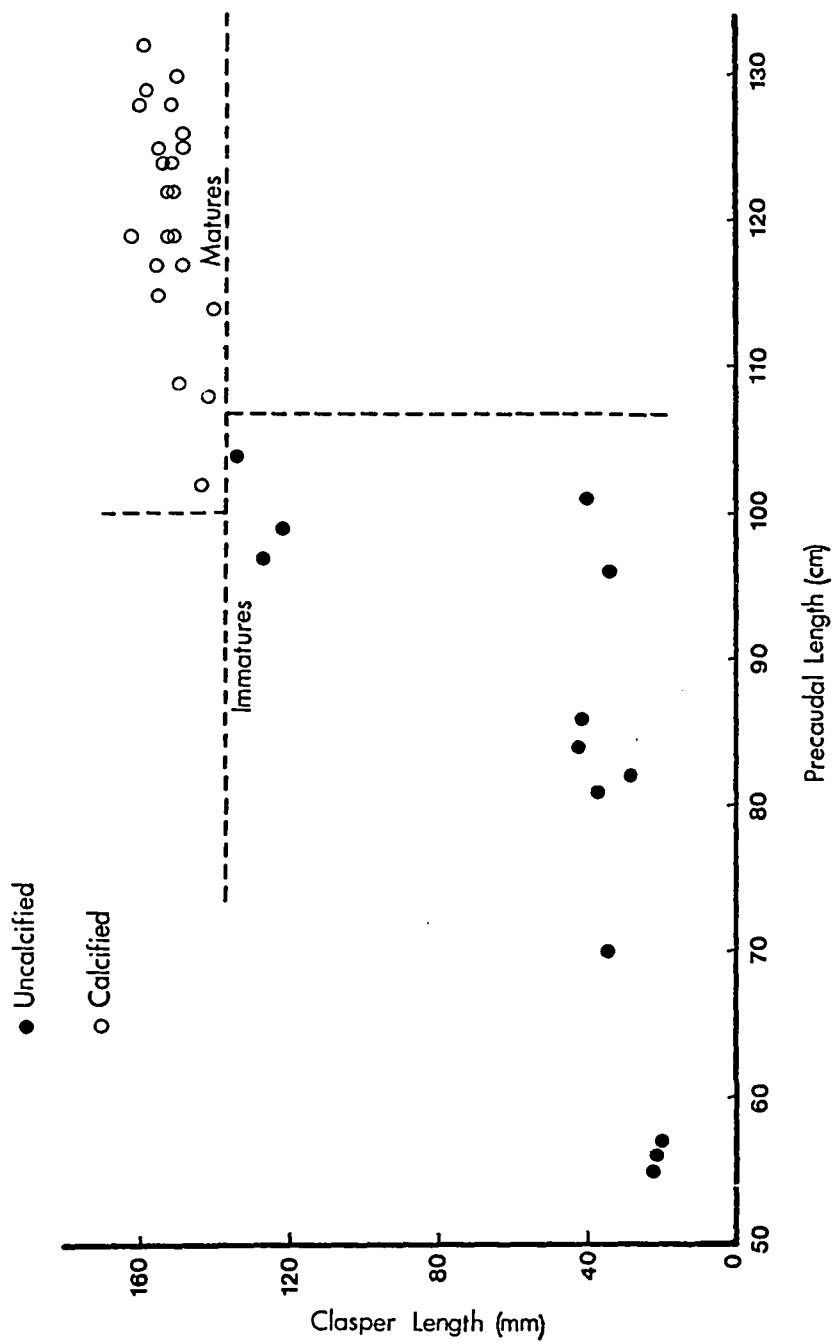


Figure 11. Relationship between clasper length and calcification status and precaudal length for Hawaiian Carcharhinus menisorrah.



captured in Hawaii. They are termed mature because 4 were pregnant and the other 2 had enlarged uteri. Precaudal lengths ranged from 129 to 136 cm with an average of 133.0 cm. Because the largest immature female measured only 95 cm, the data do not permit estimation of the size at which maturity is attained and are not graphed. Quite likely female C. menisorrah mature, like the males, at a slightly smaller size than C. milberti (ca. 105 cm).

Contrary to the situation for C. milberti, Hawaiian C. menisorrah are larger than their conspecifics in other areas. Mature Hawaiian males and females averaged 121.3 and 133.0 cm respectively; those from Eniwetok averaged only 103.0 and 109.0 cm. Also, the sizes at maturity are larger for Hawaiian sharks than for Eniwetok sharks. Sample sizes are small from other island areas and adequate maturity data are not available. However, a comparison of maximum sizes suggests that Hawaiian sharks attain a larger size.

Size data for both species are summarized in Table 2. Mature males are generally smaller than mature females. This is true for all species of Hawaiian carcharhinids and is confirmed by Springer (1960) for western North Atlantic carcharhinids. It is also evident from the table that Hawaiian C. milberti and C. menisorrah are roughly the same size at all stages of maturity.

## 2. Size at Birth

TABLE 2. -- Summary of size data (precaudal lengths in cm) for Carcharhinus milberti and Carcharhinus menisorrah at birth and maturity for both sexes in various localities.

Species	Sex	Area	Length at Birth	N	Min. Length at Maturity	Ave. Length of Matures	Max. Length
						+ S. D.	
<u>C. milberti</u>	Male	Hawaii	45-51	104	110	119.4 + 6.1	132
"	Female	"	45-51	185	115	130.7 + 7.0	146
"	Male	West. N. Atl.	45	-	138	152	174
"	Female	"	45	-	140	162	180
"	Male	S. Africa	-	-	115	-	140-145
<u>C. menisorrah</u>	Male	Hawaii	45-50	22	100	121.3 + 9.3	137
"	Female	"	45-50	6	c. a. 105	133.0 + 2.6	136
"	Male	Eniwetok	-	35	85-90	103.0 + 7.0	115
"	Female	"	-	41	96-97	109.0 + 7.0	122
"	Male	Johnston	-	8	-	-	115
"	Female	"	-	17	-	-	118
"	Male	Line Is.	-	43	-	-	122
"	Female	"	-	36	-	-	121

Of 90 juvenile C. milberti caught in Hawaii, the smallest had precaudal lengths of 45, 48, 49 and 49 cm. Four pups born in the tank at Kewalo measured 47.8, 51.0, 51.0 and 51.2 cm at birth. The largest embryos found within uteri measured 50, 50, 49.5 and 49.5 cm. Precaudal length at birth for Hawaiian C. milberti, therefore, is generally between 45 and 51 cm. Springer (1960) found the length at birth for western North Atlantic C. milberti to be slightly smaller. He reports total lengths corresponding to precaudal lengths from 31 to 47 cm with an average of 45 cm.

Of 200 juvenile C. menisorrah captured in Hawaiian waters the smallest measured 47, 48, 49 and 50 cm. No females were captured with embryos approaching full term. Length at birth is, apparently, from 45 to 50 cm.

## B. Growth

### 1. Growth in Captivity

Thirty-five C. milberti and C. menisorrah were maintained for varying lengths of time in the large tank at Kewalo Basin. Thirteen C. milberti and 4 C. menisorrah lived for at least 4 months. The growth data discussed below were generated by these 17 individuals. Ten of the above died during the study, but all deaths were from unnatural causes (overdose of anesthetic, copper sulfate poisoning, jumping out of the tank, etc.) and the sharks appeared to be in good health at the time of

their death. In fact, most lived longer than the record periods of captivity listed by Clark (1963).

The shark feeding program was determined arbitrarily since food requirements in the natural environment were unknown. Instead of feeding a set amount each period, morsels of food were simply thrown into the tank at 2- to 3-day intervals until the rate of feeding decreased markedly. Cut pieces of frozen skipjack or akule, Trachurops crumenophthalmus, were the usual food. Fresh or frozen red snapper, jack, eel, small reef fish, smelt, octopus and squid were also fed frequently. The sharks seemed to prefer frozen smelt, which do not occur in Hawaii, above all else.

At 1- to 8-week intervals the sharks were anesthetized and their precaudal lengths measured. The growth data obtained are listed in Appendix C and are plotted for 9 of the 13 C. milberti in Fig. 12 and all 4 C. menisorrah in Fig. 13. The 4 C. milberti which do not appear in Fig. 12 have growth curves similar to those plotted but are not shown because of space limitations.

In an attempt to determine age at maturity, the data were fitted to a von Bertalanffy growth curve. This is an exponential curve in which the rate of growth is proportional to the difference between the actual size of an animal and its asymptotic size. It has wide application as a model for animal growth (von Bertalanffy, 1960) and has the general formula  $x = a(1 - be^{-kt})$  where "x" is size at age t, "t" is the time

Figure 12. Growth of captive Carcharhinus milberti at the Kewalo Basin facility.  
A, male; C, female; D, female; E, male; F, female; G, female;  
H, female; J, male; K, female.

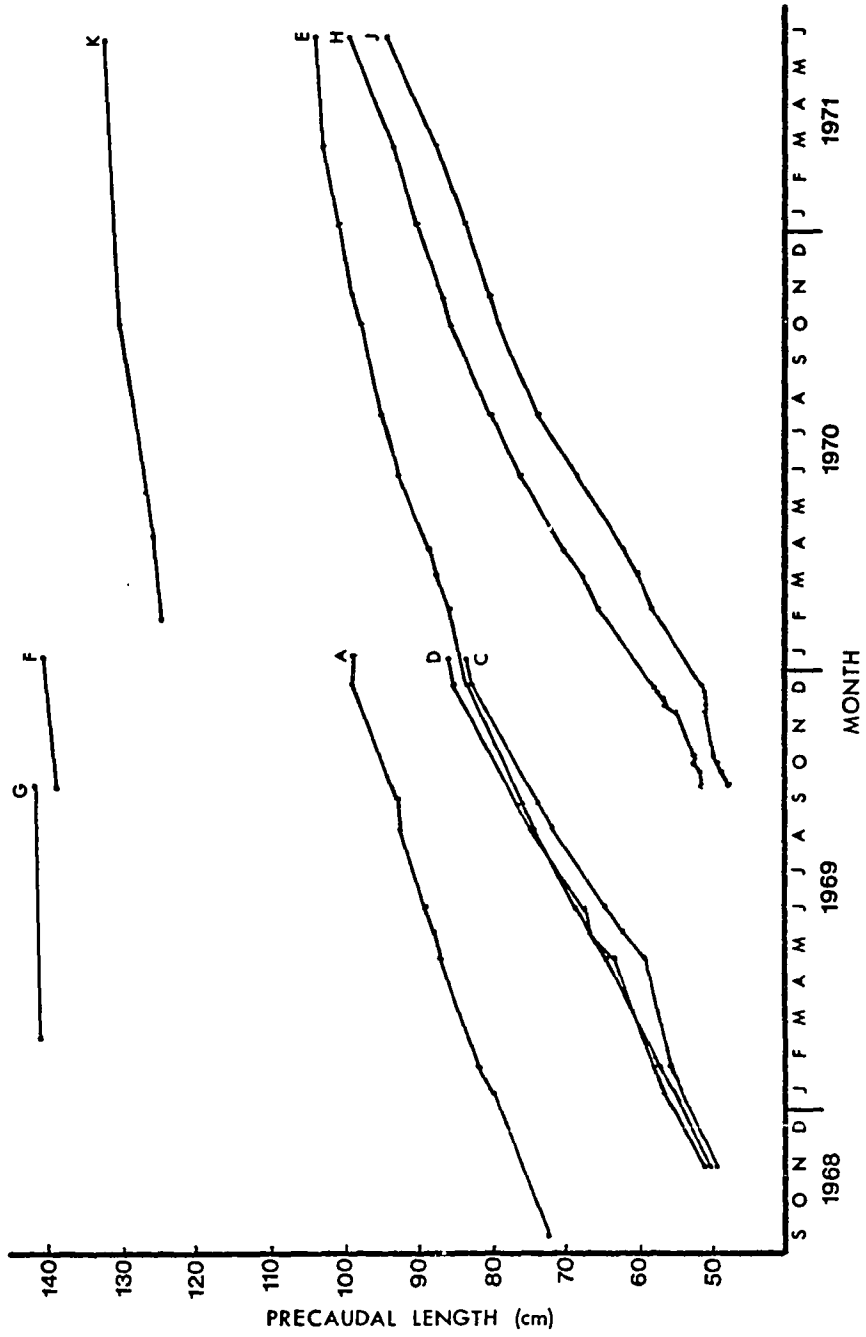
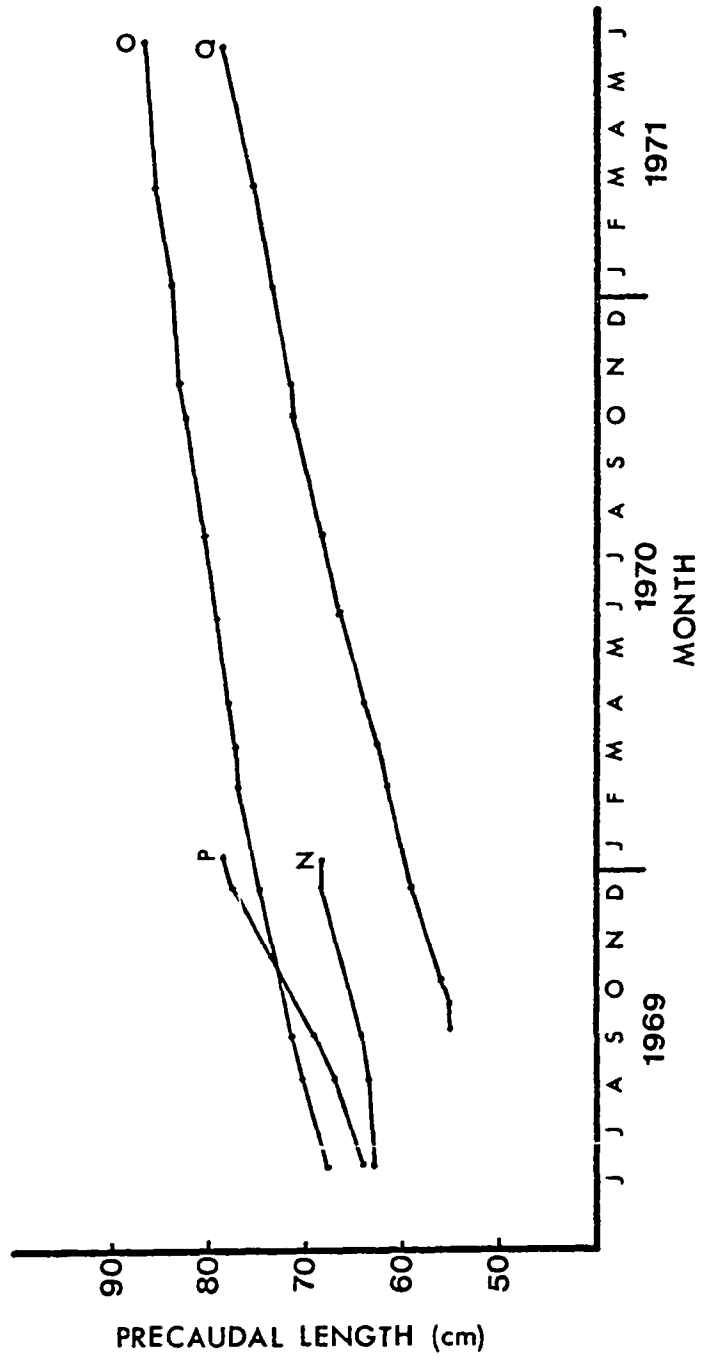


Figure 13. Growth of captive Carcharhinus menisorrah at the Kewalo Basin facility. N, male; O, male; P, female; Q, female.



interval since birth, "a" is asymptotic size, "b" is related to the size (c) of the animal at birth ( $c = a(1-b)$ ), and "k" is "an indication of the rate of proportional growth of the animal" (Fabens, 1965) or a constant "determining the rate of change in length increment" (Ricker, 1958). It is assumed that "k" is constant from birth to the asymptotic limit of growth, i. e. if there is a point of inflexion in the growth curve, it occurs prior to birth. This assumption may or may not be valid for the above data. There is an indication of a point of inflexion at about 58 to 64 cm for curves C and D (pups born in open water and transferred to the tank) of Fig. 12 and at about 51 to 56 cm for curves J and H (pups born in the tank). The possibility of an inflexion is ignored, however, on the assumption that, if true, it would not greatly affect the estimate of age at maturity.

The von Bertalanffy curve was fitted to the data using Fabens' (1965) computer program given the average length at birth ( $c = 47$  cm) and triplets of data (x, y and d): "x" and "y" being 2 precaudal lengths (cm) of a particular shark and "d", the time interval (days) between the 2 measurements.

Von Bertalanffy growth equations were calculated separately for both sexes of C. milberti. The equation for males, based on 49 triplets of data, is:  $x = 139.4 (1 - 0.6629e^{-0.001100t})$  where "x" is precaudal length (cm) and "t" is time since birth (days). The calculated value for asymptotic size is 139.4 cm which is a little larger than the length of

the largest male captured in the field (132 cm). The von Bertalanffy curve for male C. milberti is plotted in Fig. 14. Comparison of the theoretical average length at the end of 1 year (77 cm) with the interpolated lengths for actual data at the end of 1 year (assuming each individual was born at a length of 47 cm) for curves E (78 cm) and J (77 cm) in Fig. 12 indicates a remarkably close fit. It, therefore, appears that the von Bertalanffy equation adequately describes the growth of captive male C. milberti at the Kewalo Basin facility.

Growth data for captive female C. milberti also fit the model well. The equation, based on 57 triplets of data, is:

$$x = 149.0(1 - 0.6845e^{-0.001026t}).$$

The curve is plotted in Fig. 15.

Again, the theoretical asymptotic size (149.0 cm) is slightly larger than the largest individual captured in the field (146 cm). Theoretical length after 1 year of growth is 78 cm which closely approximates the interpolated lengths for actual data after 1 year's growth for curves C (77 cm), D (79 cm) and H (80 cm) in Fig. 12.

Field data indicate that mature females are larger than mature males, likewise, the theoretical asymptotic size derived from the von Bertalanffy equation is larger for females than for males. Fig. 14 indicates that males reach their minimum mature size (110 cm) at 1,050 days. Fig. 15 indicates that females attain mature size (115 cm) in a similar length of time (1,070 days). Thus, females are larger because they grow faster and not because they live longer or require

Figure 14. Von Bertalanffy growth curve for male Carcharhinus milberti at the Kewalo Basin facility.  $X = 139.4(1 - 0.6629e^{-0.001100t})$  where x is precaudal length (cm) and t is age (days).

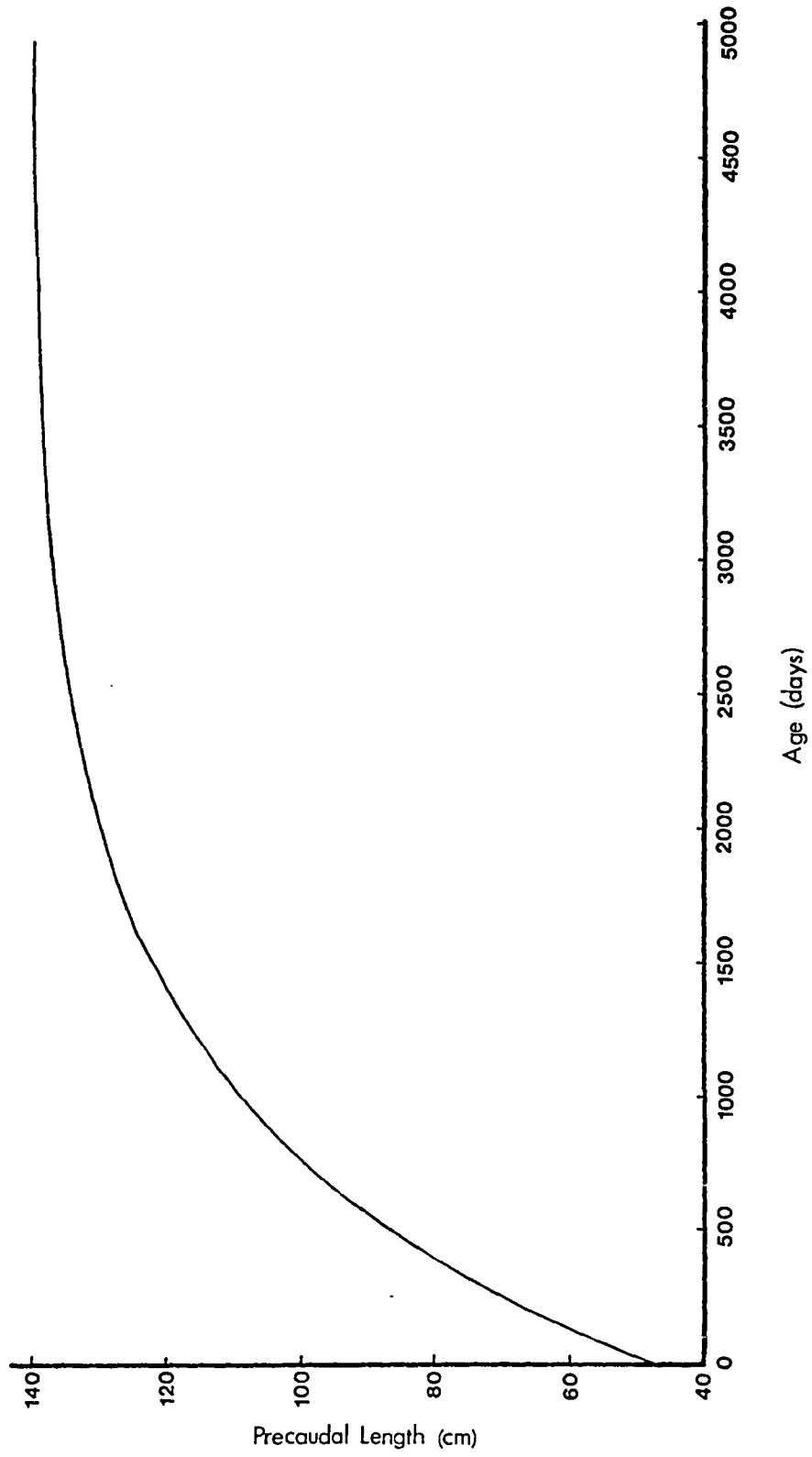
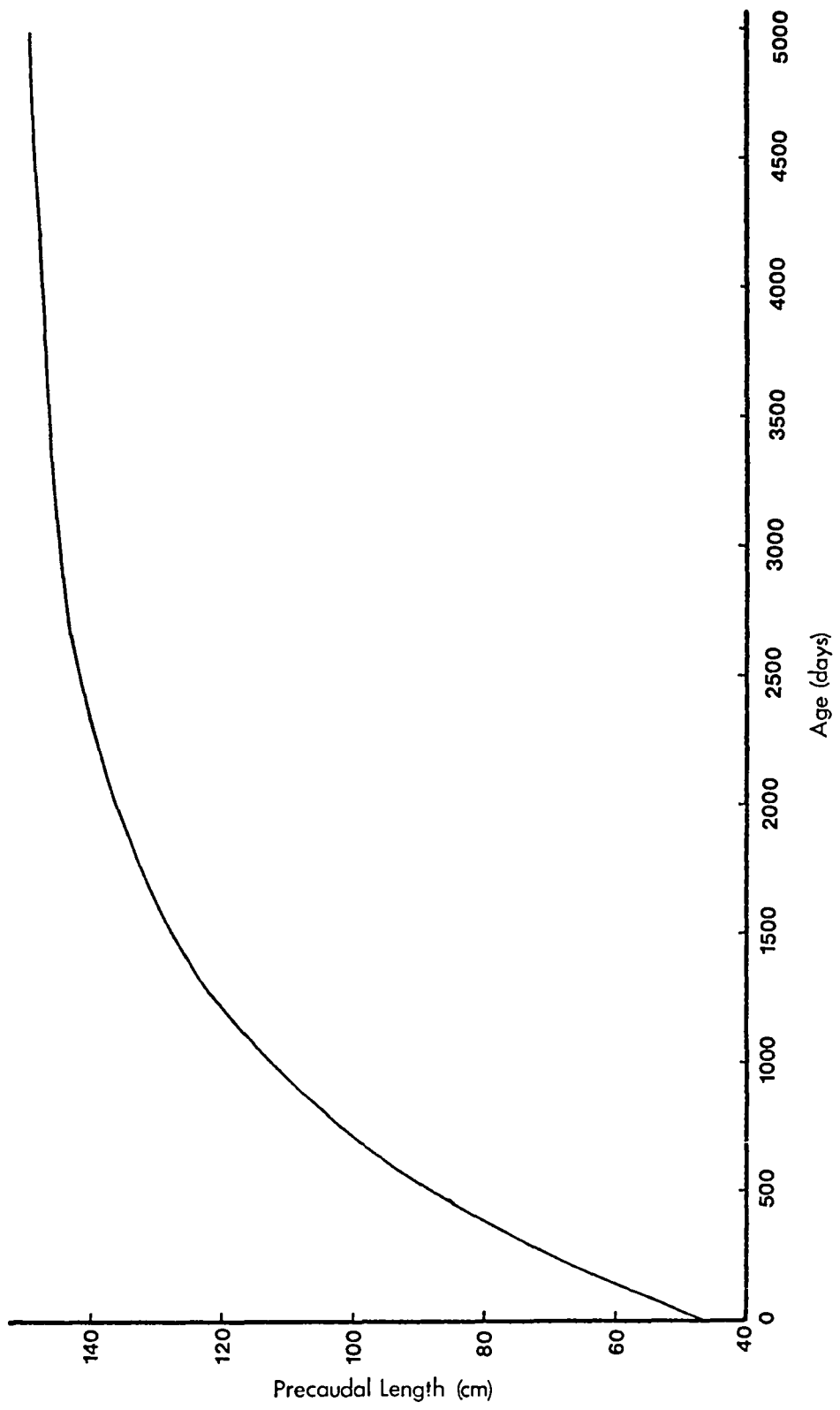


Figure 15. Von Bertalanffy growth curve for female Carcharhinus milberti at the Kewalo Basin facility.  $X = 149.0(1 - 0.6845e^{-0.001026t})$  where x is precaudal length (cm) and t is age (days).



more time to reach maturity.

Templemen (1944) found no differences in the growth rates of the sexes for Squalus acanthias, a species in which mature females are larger than the males. Holland (1957) and Holden and Meadows (1962), however, concluded that females of this species do grow at a more accelerated rate than the males. Olsen (1954) reported no differences between the growth rates of the sexes for Galeorhinus australis.

For both sexes of C. milberti age at maturity, based on the von Bertalanffy curves, is about 3 years. Springer (1960), on the basis of little real evidence, suggests that growth from birth to maturity for C. milberti in the western North Atlantic probably takes about 2 years, but the interval may be as short as 1 year or as long as 3 years. Springer's estimate, thus, is close to that for captive Hawaiian C. milberti. Hawaiian C. milberti in the field, however, probably grow at a slower rate and require more than 3 years to attain maturity (see below).

Due to insufficient data, both sexes were combined when the von Bertalanffy equation was calculated for C. menisorrah. The equation, based on 34 triplets of data, is:  $x = 101.1 (1 - 0.5352e^{-0.001302t})$ . The calculated asymptotic size (101.1 cm) is unrealistic. Individuals as large as 137 cm were captured. Perhaps the data were still too few. Otherwise, one must conclude that the natural growth curve of C. menisorrah does not fit the model or that some factor associated with

captivity hindered growth.

It is unfortunate the C. menisorrah data do not show a valid fit to the von Bertalanffy model because it would enable an objective comparison of growth rate with C. milberti. A comparison can still be made, however, from an analysis of the growth data in Appendix C. Growth rates as the animals pass precaudal lengths of 60, 70 and 80 cm are easily calculated from the measured lengths nearest either side of these increments and the time interval between measurements. Average rates of 0.040, 0.057 and 0.024 cm/day were calculated for C. menisorrah with lengths of 60, 70 and 80 cm, respectively. For C. milberti of the same sizes, rates of 0.099, 0.097 and 0.077 cm/day were calculated. The growth rate of captive C. milberti is more than twice that of captive C. menisorrah at the Kewalo Basin facility. This however, may not be true in the natural environment. C. milberti may be better able to adjust to captivity.

## 2. Growth of Tagged Sharks

Growth rates of sharks in the field were estimated from tag-and-recapture data. In the present study, 86 C. milberti and 113 C. menisorrah were tagged and released. Most of the C. milberti were released around Oahu and Niihau. All C. menisorrah were released at Niihau, Molokini and Kaula. The bulk of the tagged sharks were juveniles though about 35 were mature or nearly so.

Twelve tagged sharks were recaptured and are listed in Table 3. Only one was a C. milberti. It was mature when tagged initially and showed no growth or movement during its 595-day period of liberty. The apparent shrinkage of 2 cm is probably due to errors of measurement.

Eleven C. menisorrah tags were recovered. The recovery percentage for this species was higher because the fishing was repeatedly done in the same, localized areas. Of 27 individuals tagged at Molokini, 6 were recovered. This area was fished in exactly the same place each time. The other 5 recaptures were made around Niihau where 64 C. menisorrah were tagged. None was caught more than 1/2 mile from its point of release.

Tagged C. menisorrah, even those at liberty for many months, showed little growth. In fact 2 showed apparent shrinkages of 1 cm which again are likely due to errors of measurement. The greatest length increase was 7 cm during a 252-day period. This is equivalent to a growth rate of 0.028 cm/day. For contrast, the captive C. menisorrah at Kewalo of the same size grew 7 cm during a 126-day period (0.056 cm/day).

Despite inadequacies of the data, it is worthwhile to make comparisons with the estimates of other investigators. The combined average growth of all 11 C. menisorrah was 0.0059 cm/day or about 22 mm/year. Kato and Carvalho (1967), in an eastern Pacific tagging study, calculated an average growth rate of 44 mm/year for

TABLE 3. -- Growth of tagged sharks.

Species	Date at Tagging	Precaudal Length at Tagging (cm)	Days at Liberty	Growth (cm)	Length Increase (cm/day)
<u>C. milberti</u>	8/08/67	122	595	-2	0
<u>C. menisorrhah</u>	9/26/67	49	19	0	0
"	11/16/67	71	566	3	0.0054
"	11/17/67	68	509	1	0.0020
"	6/06/68	101	3	0	0
"	6/10/68	58	252	7	0.0278
"	7/03/68	53	6	0	0
"	7/03/68	59	79	1	0.0127
"	8/17/68	77	235	-1	0
"	9/20/68	57	177	1	0.0056
"	9/20/68	53	177	2	0.0113
"	9/20/68	54	177	-1	0
				Average	0.0059

Carcharhinus albimarginatus and 40 mm/year for Carcharhinus galapagensis. The lengths of their tagged animals were similar to those of C. menisorrah in the present study. Other tagging studies on large sharks also indicate slow rates of growth. Hansen (1963) found 3 large Somniosus microcephalus grew 10 mm in 2 years, 150 mm in 14 years and 80 mm in 16 years. Olsen (1954) calculated average annual length increments for different age groups of Galeorhinus australis that ranged from 130 mm for 1-year-old sharks to 30 mm for 12-year-old sharks.

Tag-and-recapture data for C. menisorrah indicate a slower growth rate in the field than in the tank at Kewalo. It is unfortunate that no juvenile C. milberti were recaptured as it would be of great interest to see if they also grow slower in their natural environment.

### 3. Determination of Growth Rate from Tooth Replacement Data

Moss (1967) used a third, rather indirect, method to determine growth rates for sharks. Rate of tooth replacement and size difference between functional and replacement teeth are the basic data required. Age at maturity can be calculated knowing the length at birth and maturity, the number of tooth generations between birth and maturity and the mean length of time each generation is functional.

Breder (1942), James (1953) and Strasburg (1963) agree that elasmobranch teeth are continuously replaced. Older teeth in a

functional position along the outer border of the jaw are constantly lost and replaced by younger teeth through a process not entirely understood but summarized by Moss (1967). Rate of replacement appears to be relatively constant on a short-term basis and is independent of wear or injury to individual teeth.

Ifft and Zinn (1948) marked teeth with silver nitrate and found that the teeth of Mustelis canis are replaced at the rate of 1 row every 10 to 12 days. Märkel and Laubier (1968), using a tetracycline dye to mark the teeth of Scyliorhinus canicula, determined that a tooth generation is replaced every 5 weeks. The most comprehensive study of tooth replacement is that of Moss (1967) on young Negaprion brevirostris. For a group of healthy animals that were regularly fed, he calculated a mean functional tooth life of 7.8 days for teeth in the upper jaw and 8.2 days for teeth in the lower jaw.

The present investigation was patterned after Moss's (1967) study. Captive sharks were anesthetized and the cusps of alternate functional teeth of the first 8 series on either side of the symphysis of the upper jaw were clipped with wire cutters. Care was taken not to damage nerves and blood vessels in the pulp cavity or the surrounding gum tissue. The result was 8 recognizable teeth without serious impairment of the shark's ability to use its teeth for grasping and slicing food. At subsequent 4- to 10-day intervals, marked teeth still

in position were counted.

The imbricated and overlapping pattern of tooth position in the jaws of C. milberti and C. menisorrah requires the teeth to be lost individually. Consequently, the measure of replacement rate used in the present study is termed mean functional tooth life and is defined as the mean number of days a tooth remains in the functional position. Among the carcharhinids, only a single tooth of each series in the upper jaw is functional at any one time.

The mean functional tooth life for each shark was determined from regression of the number of marked teeth remaining in position against the number of days since the teeth were marked. The calculated regression line was forced through the point on the ordinate corresponding to the number of teeth originally marked. The "X" intercept (number of days when zero marks are present) is the estimate of mean functional tooth life. An example of the results and computations is in Appendix D.

The relationships between mean functional tooth life (upper jaw) and precaudal length are plotted for C. milberti in Fig. 16 and C. menisorrah in Fig. 17. Though the data are highly variable, it is plain that mean functional tooth life increases with size. Previous investigations have not shown this because they involved only juveniles or individuals of the same size. The regression lines plotted in Figs. 16 and 17 also indicate that mean functional tooth life is less for C.

Figure 16. Regression of mean functional tooth life on precaudal length for captive Carcharhinus milberti at the Kewalo facility.  $\hat{Y} = 0.215 X + 7.63$ .

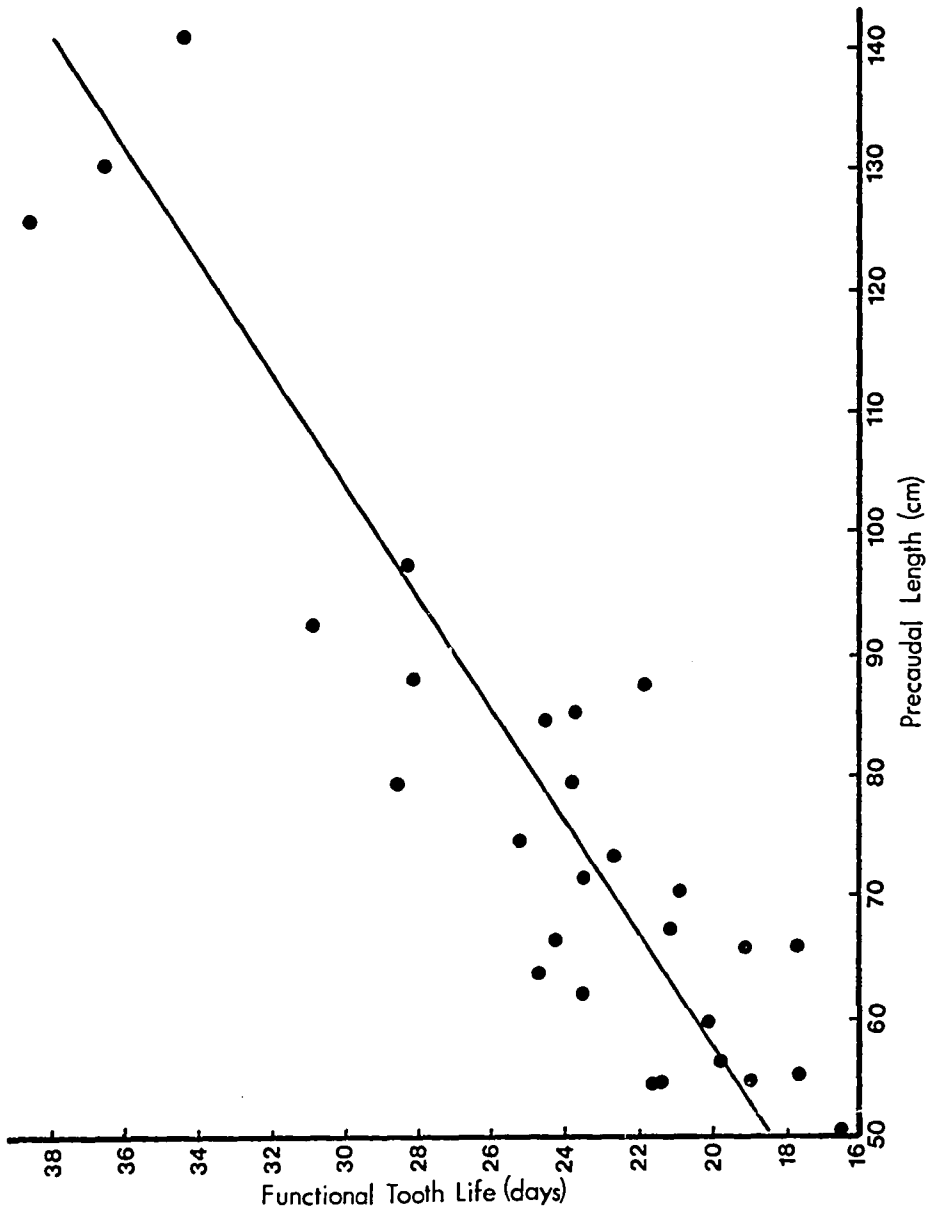
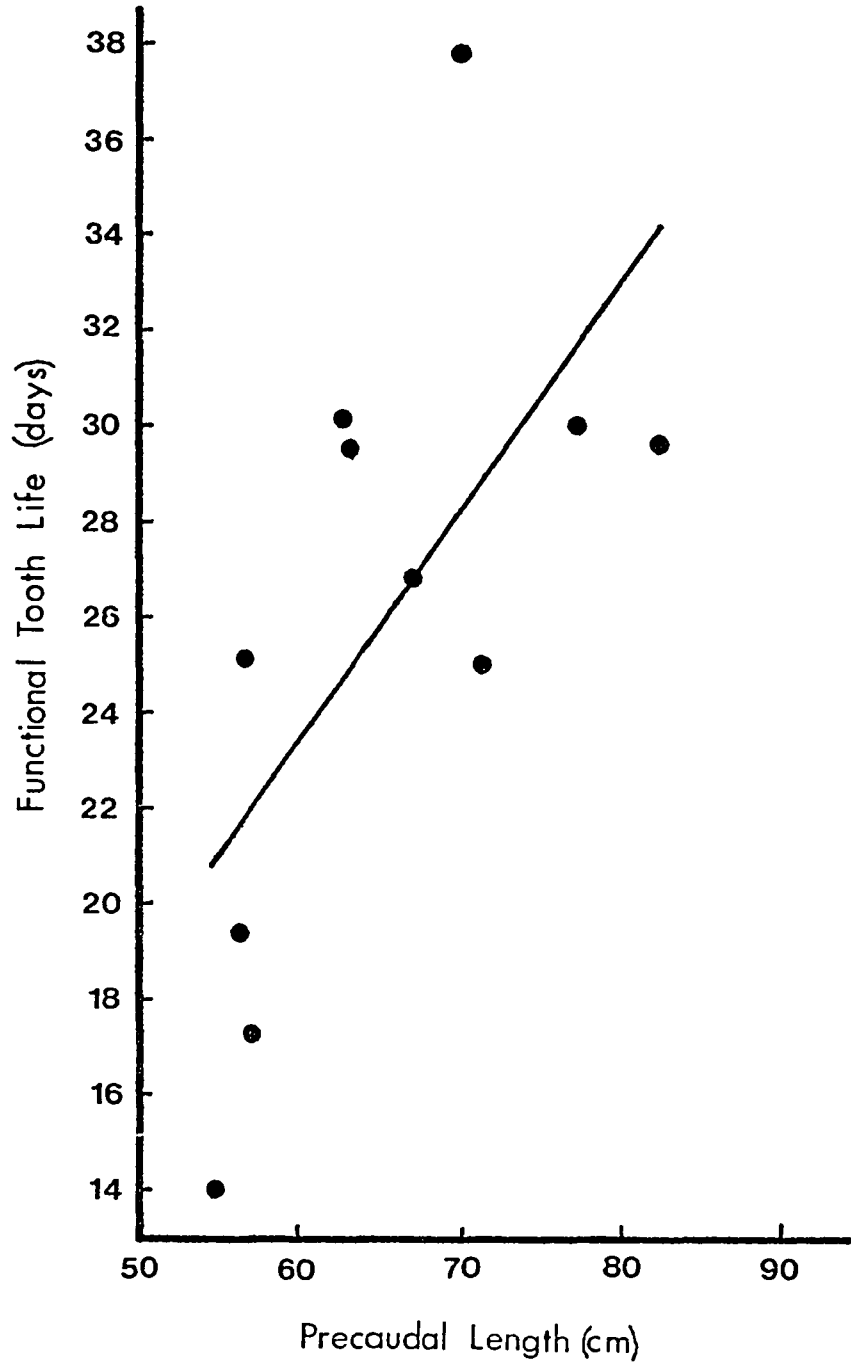


Figure 17. Regression of mean function tooth life on precaudal length for captive Carcharhinus menisorrhah at the Kewalo facility.  
 $\hat{Y} = 0.487 X - 5.98$



milberti than for C. menisorrah regardless of shark size. This would be expected because C. milberti has a higher growth rate, at least in the tank at Kewalo where the data on replacement rate were collected.

The procedure for determining the number of tooth generations between birth and maturity is described by Moss (1967) as follows:

"Strasburg (1963) demonstrated that tooth growth in elasmobranchs could be considered as occurring in increments of instantaneous growth, each increment occurring at the time of replacement. Thus, tooth width plotted against body length provides a stepped type of curve for any growing shark. By reason of the fact that the teeth in the first replacement row are larger than the older, functional ones, the effective growth increments of the teeth at the time of replacement can be measured. By plotting regressions of functional tooth width and replacement tooth width against body length, a set of nearly parallel lines is produced. These are then connected by horizontal and vertical tie lines."

The number of vertical tie lines between size at birth and size at maturity represents the number of tooth generations preceding maturity.

To calculate age at maturity for male C. milberti, the regression in Fig. 16 was solved for each precaudal length corresponding to a vertical tie line obtained from the foregoing method. This yielded a functional tooth life for each generation. The generation times were summed to get age at maturity. The results for Hawaiian C. milberti and C. menisorrah are tabulated below:

<u>C. milberti</u> , males	10.2 years
<u>C. milberti</u> , females	13.1 years

C. menisorrah, males            7.4 years

C. menisorrah, females        7.2 years

These estimates are only rough approximations because of data variability and questionable assumptions. One assumption, which is almost certainly violated, is that tooth replacement rate is the same for captive sharks at Kewalo as it is for animals in the field. Replacement rate is inversely correlated with growth rate and growth at Kewalo appears to be more rapid than in the field. It was assumed that there is no significant difference in rate of tooth replacement for males and females of equal size, but if their growth rates differ, replacement rate may also differ. A final assumption is that the relation between functional tooth life and body length is linear. In actuality, it may be curvilinear if there is a direct relation between growth rate and functional tooth life.

#### 4. Discussion of Growth-Rate Estimates

The feeding frequency of sharks in the natural environment can be roughly estimated from the percentage of stomachs containing food if the rate of digestion is known. To this end 3 captive C. milberti of approximately the same size (95 to 101 cm precaudal length) were starved for 4 days and then fed smelt or squirrelfish until satiated. The smelt were about 15 cm long and are narrow-bodied with thin skin and soft flesh. The squirrelfish were of similar length but are much deeper bodied. Their scales are large and heavy and their flesh is

firm. Both fish are pictured in Fig. 18 as are their partially digested remains. Two C. milberti which had been fed smelt were killed 24 and 48 hours after feeding and their stomach contents were examined and photographed. At 24 hours, small chunks of flesh and bones were recognizable amidst a gray mush of oil droplets and flocculated particles. At 48 hours, the mush was darker in color and more condensed. A few oil droplets were still visible but all flesh and bones had been broken down.

Because of the limited supply of similar-sized sharks of the same species, only one shark was fed squirreelfish. When its stomach contents were examined 48 hours later, flesh, bones and eye lenses were still present in the light-colored mush of oil droplets and flocculated material.

The death of several captive sharks as a result of copper sulfate poisoning yielded further data on the digestive rate for both C. milberti and C. menisorrah. The animals had been fed whole (25 cm long) and cut akule about 30 hours earlier. When their stomach contents were examined, some of the akule were still whole and most of the flesh remained on the bones implying that digestion had only just begun.

It appears that food is retained within the stomachs of C. milberti and C. menisorrah for about 2 days if the prey is small and soft. It takes 3 to 4 days for average-sized prey to pass through the stomach and probably longer for large and hard-to-digest items. Captive

Figure 18. Stomach contents from Carcharhinus milberti (precaudal lengths from 95 to 101 cm). A. Smelt: top, fresh; middle, after 24 hours digestion; bottom, after 48 hours digestion. B. Squirrelfish: top, fresh; bottom, after 48 hours digestion.

A



B



sharks at Kewalo probably always had food in their stomachs because they were fed at 2- to 3-day intervals.

Only 45% of the C. milberti and 29% of the C. menisorrah captured in the field had any food at all in their stomachs (see Chapter VII). If these are realistic values, it appears that sharks in the field feed only about 1/2 to 1/4 as often as the sharks at Kewalo. This is equivalent to about every 6 to 12 days. Also, the amount of food in the stomachs of captured sharks was often much less than stomach capacity which further accentuates differences in the amount eaten. Calculations using data from the captive sharks yielded higher growth rates and earlier ages at maturity than the other 2 methods. Other conditions being equal, it is likely that the captive sharks grew faster than normal because of the plentiful supply of food. Helfrich (1958) found that a damsel fish, Abudefduf abdominalis, grew faster in captivity than in the natural environment and attributed this to an abundance of food and a lack of competition for it.

The other 2 procedures used in the present investigation for obtaining growth rates are also unreliable due to data variability, questionable assumptions and lack of data. If there was a way to estimate the age of individual sharks in Hawaii (e. g., from annuli appearing on hard parts such as vertebrae), the problem would be solved. Since this does not seem possible, however, accurate

determination of growth rate and age at maturity for C. milberti and C. menisorrah must await either a more extensive tagging effort with numerous recoveries of both large and small individuals, or a growth study of captive sharks of both sexes at all stages of maturity maintained with a realistic feeding program.

### C. Reproduction

#### 1. Sex Ratio

At birth, the sex ratio for both species does not deviate significantly from 1:1. Embryos from 55 litters of Hawaiian C. milberti were sexed. Of the 308 embryos, 152 (49.4%) were males. Springer (1960) also found a 1:1 ratio (50.0% males) for 65 litters from the western Atlantic, as did Clark and von Schmidt (1965) for 21 litters (47% males). Because sample sizes for C. menisorrah are small, the data from Hawaii, Johnston and Eniwetok were combined. Examination of 22 litters revealed that 48.4% were males--again an apparent 1:1 ratio.

Concerning the sex ratio of adults, 50 female and 51 male C. milberti were captured on perpendicular sets of the longline which fished the entire depth range of the species. Apparently, the sex ratio for mature Hawaiian C. milberti is 1:1. Springer (1960), however, found a sex ratio of about 5 females to 1 male for C. milberti in the western North Atlantic. Likewise, Clark and von Schmidt (1965)

concluded that the sex ratio for C. milberti in the central gulf coast region of Florida is 6:1.

The sex ratio of mature C. menisorrah captured at Eniwetok is about 1:1 (41 females to 35 males). In the collection from Hawaii, however, there were only 8 mature females compared with 31 males. This ratio differs significantly from 1:1 (P less than .005). An effort was made to fish all areas and depths, especially those adjacent to concentrations of males, but females were never captured in substantial numbers. No explanation can be offered for the uneven sex ratio.

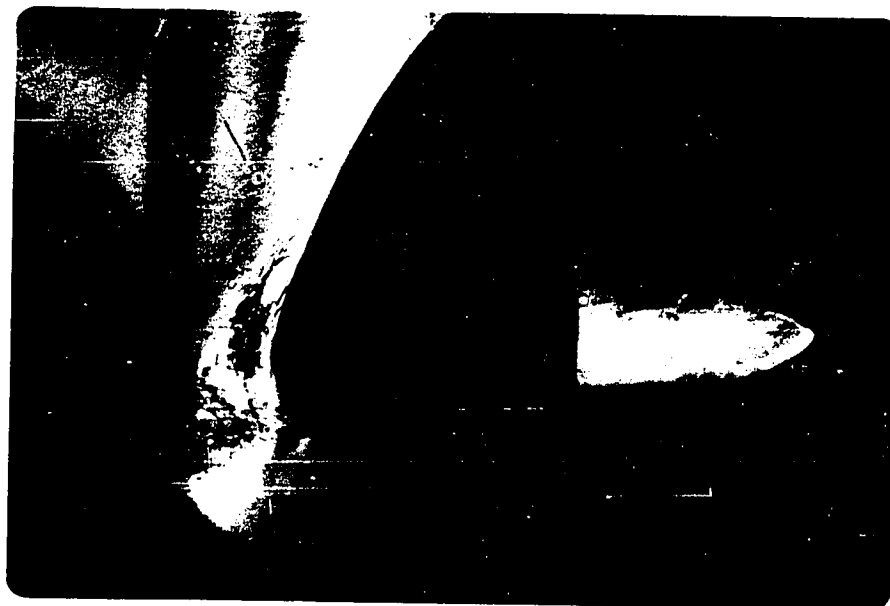
## 2. Courtship and Mating

Fertilization in all carcharhinids is internal. The paired intromittant organs of the males, termed claspers, are basally attached to the inner margins of the pelvics and border the cloaca. Normally, they extend posteriorly, but during fertilization, they are rotated forward and the cartilages in the tips expand like the ribs of a fan (Springer, 1960). Sperm is forced through the tubes formed by the rolled cartilages of the claspers and into the cloaca of the female.

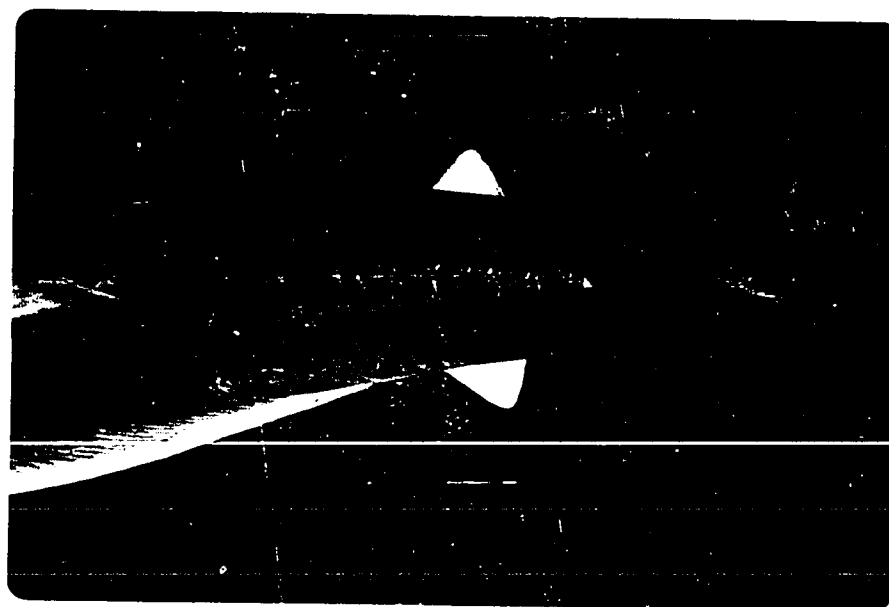
Little is known of the courtship behavior of carcharhinids. Probably the male persistently follows the female, occasionally bumping and nipping her, until she is induced to swim upside down, whereupon the claspers are inserted. Mating wounds (Fig. 19)

Figure 19. A. Fresh mating wounds on female Carcharhinus milberti.  
B. Mating scars on dorsal surface of female C. milberti.

A



B



sustained by the females during this period are of a minor nature as the males are inhibited from feeding (Springer, 1960). Females, however, are not so inhibited and males may sometimes be fatally injured by a hungry female during the mating process.

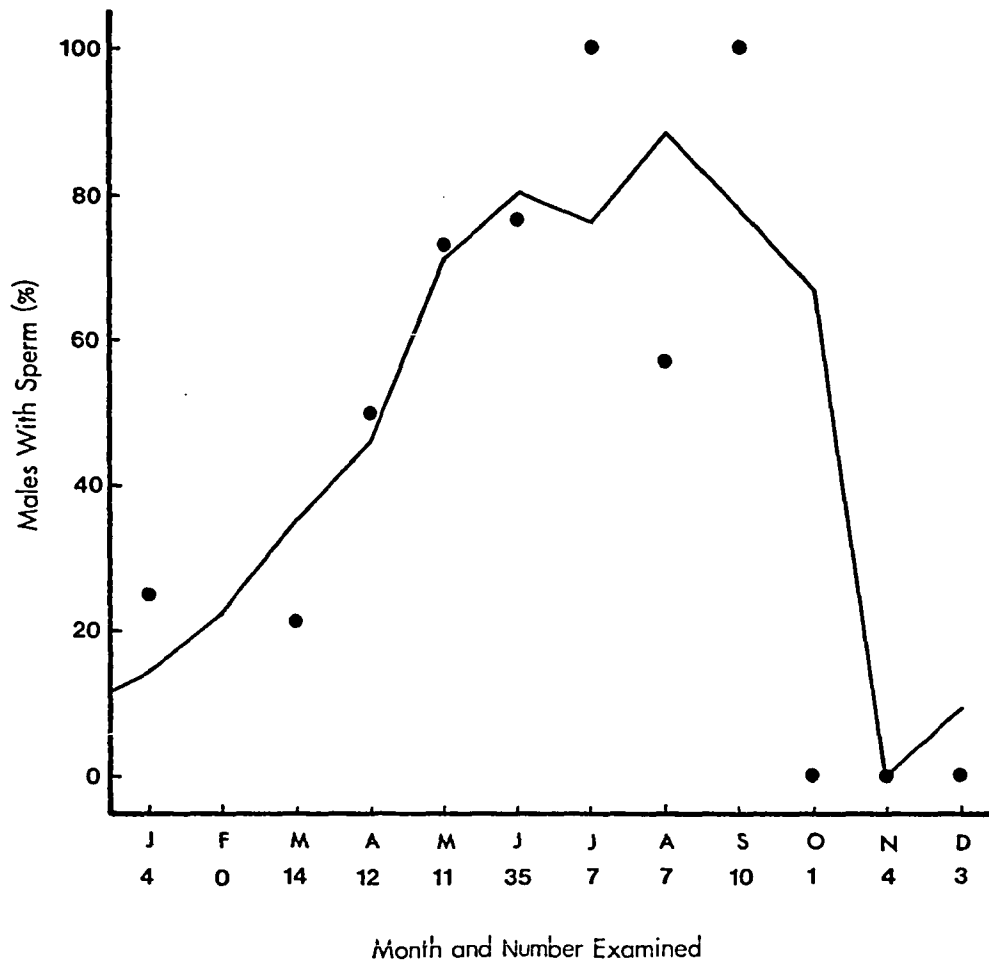
The courtship and mating behavior of C. milberti or C. menisorrhah was not observed. The reader is referred to Springer (1960) for a description of the mating pattern of large carcharhinids and for a complete discussion of their reproductive morphology.

### 3. Mating Season

The mating season for carcharhinids can be ascertained in several ways. Amongst the males, vascular congestion about the cloacal area at the base of the claspers and the presence of sperm in the seminal vesicles indicate the mating season has arrived. Mature ovarian eggs and fresh mating wounds are indicative of the mating season for females. Eggs in the uterus which have yet to begin development are further evidence.

When the percentage of mature male C. milberti with sperm in their seminal vesicles is plotted against the month of observation (Fig. 20), the data tend to peak during the summer. The highest percentages were found in July and September. Vascular congestion about the claspers was also noted during the summer months. Additional evidence for a summer mating season comes from an examination of

Figure 20. Monthly percentages of mature male Carcharhinus milberti from Hawaii with sperm in seminal vesicles. The line is a running average of the 3 nearest values.



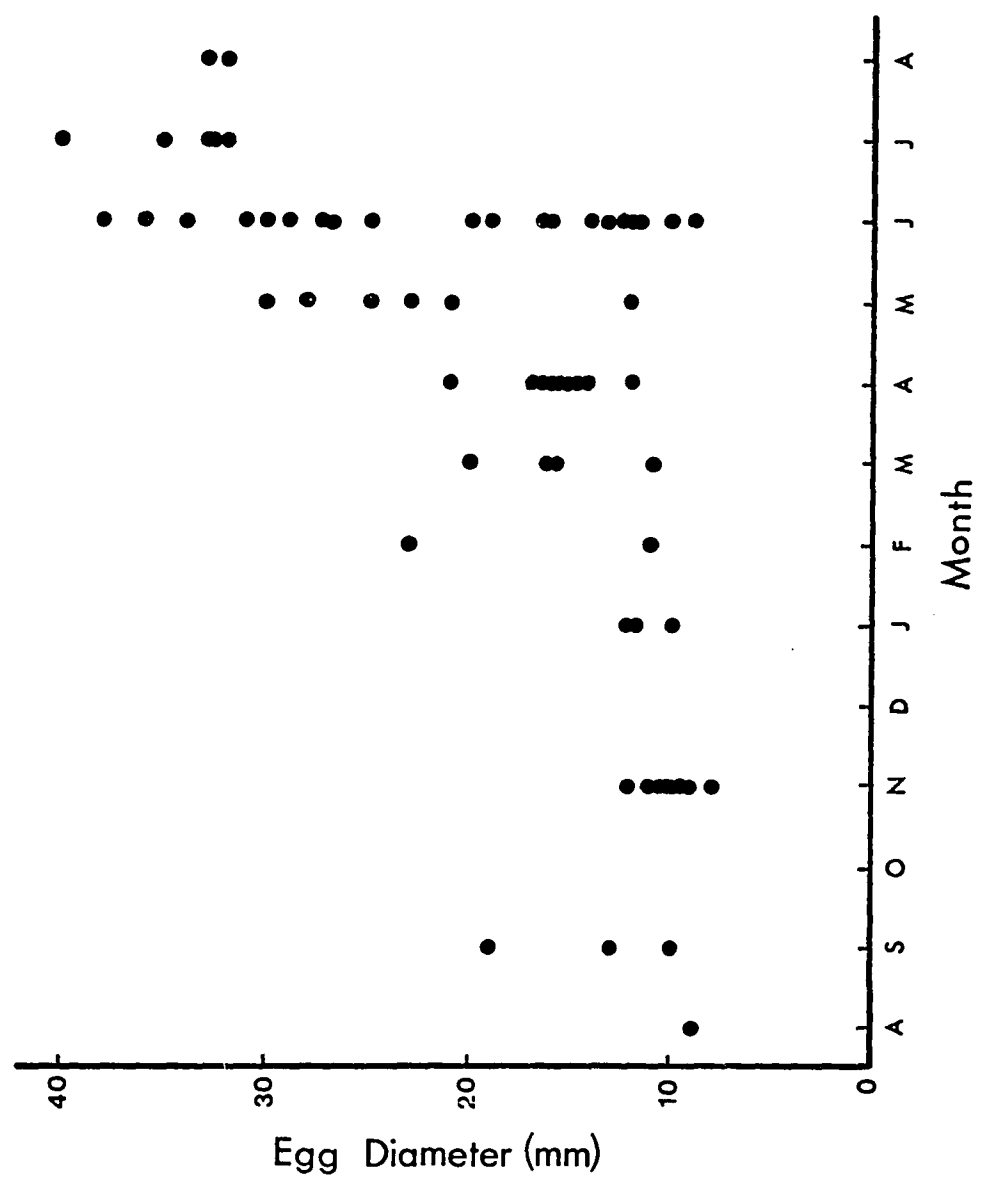
the vertical distribution of male C. milberti. In Chapter V it is concluded that mature males move inshore to the shallower depths occupied by the females during the spring and remain there throughout the summer.

Data from mature female C. milberti are in good agreement. The average diameter of the 4 largest ovarian eggs is plotted against the month of examination in Fig. 21. The eggs are generally small during the fall and winter months but begin increasing in size during the spring when they assume a redish-yellow coloration. Eggs reach the size at which ovulation occurs during June, July and August. Additionally, between the dates of July 23 and August 18, 11 females were captured with recently ovulated eggs in their uteri. Fresh mating wounds were also observed on several of these individuals.

Springer (1960) found an earlier mating season for C. milberti in the waters off southeastern Florida. He concludes that June is the period of maximum mating activity.

Determination of the mating season for Hawaiian C. menisorrah is difficult because of the lack of data. Most of the mature males examined in February, March and April had sperm in their seminal vesicles. None of the 8 males examined in June had sperm, but 4 out of 6 examined in August did. There are no data for the other 7 months. Mature females provide even fewer data. The only females captured with enlarged ovarian eggs were also pregnant. Speculation on the

Figure 21. Monthly average diameters of the 4 largest eggs in the ovaries of mature female Carcharhinus milberti from Hawaii. Values less than 8 mm not plotted.



mating season of C. menisorrah will be postponed to the section below on gestation periods.

#### 4. Development

Springer (1960) discusses the development of C. milberti and the reader is referred to TeWinkel (1950), Amoroso (1960) and Schlernitzauer and Gilbert (1966) for comprehensive discussions of the embryology of live-bearing sharks. The embryology of Hawaiian C. milberti is similar to that of other carcharhinids and will be briefly summarized.

Only the right ovary is functional. Approximately 8 months before ovulation, several ova begin enlarging and turn reddish-yellow as yolk is deposited. Upon reaching a diameter of 35 to 40 mm, about 5 or 6 ova are released from the ovary and proceed anteriorly through the body cavity and ostium to the right or left shell gland where fertilization probably takes place and where a thin, flexible membrane is laid down around each ovum. This transparent "shell" will stretch to enclose the embryo throughout its development. After passing through the shell gland, the eggs continue posteriorly through the oviducts and lodge in the thickened portion termed the uterus. Prior to maturity the uteri are less than 20 mm in breadth, but at maturity, they enlarge rapidly and reach breadths of about 60 mm at ovulation. They continue to expand and thicken as the embryos grow. Following parturition, they contract to a breadth of 20 to 40 mm. The ova remain in the uteri

for the remainder of the gestation period. Initially, the embryos derive their nourishment solely from the stored yolk. Later, there may also be absorption of nutrients from fluids in the oviducts. When the embryo reaches a length of about 30 cm (Springer, 1960), a pseudo-placenta is formed from the yolk sac which interdigitates with the wall of the uterus and allows the exchange of gases, nutrients and waste products between the embryo and the mother through an umbilical cord.

Both uteri are equally functional. Of 499 embryos collected from 90 pregnant C. milberti, 245 (49.1%) were in the right uterus.

## 5. Birth

A C. milberti captured on 12/27/68 and held at the Kewalo facility gave birth to 4 viable pups on 9/24/69. Because I observed the births and no account of the actual process is found in the literature, a description of the event follows.

At 1600 hours, I guided "Sandy" into a net hanging along the wall of the main tank. She struggled for 3 to 4 minutes before succumbing to the anesthetic and was then laid out on her side on a low table in the tank while length measurements (138.6 cm precaudal length) and tooth replacement data were taken. Sandy was rather heavy-bodied when captured off Kewalo Basin 9 months earlier and her girth had increased considerably since she was placed in the tank, so we suspected she was pregnant. On this day, however, we noticed vascular congestion and

edema about the cloacal region for the first time. When I stuck my finger through the cloacal aperture, I felt the tail of an embryo. In so doing, I must have ruptured the shell membrane because fluid spilled from the opening when I withdrew my finger. When the observations were completed, the anesthetic was flushed from Sandy's system by "walking" her around the tank for about 5 minutes until she began swimming on her own. About 10 minutes later, the tail of an embryo was protruding from her cloaca. I pulled the embryo out, and placed the pup in a smaller observation tank where it soon began swimming normally.

By 1800 Sandy had recovered from the anesthetic but was swimming more rapidly than was her usual habit. Also, the tails of 2 more embryos were protruding about 15 cm from her cloaca, swinging back and forth in unison with the caudal fin and peduncle area of the mother. At 1845 we saw a newborn pup swimming awkwardly about the tank and, because the posterior portion of a third embryo was visible, another birth appeared imminent. I re-entered the tank, in which the depth was now about 1 m, to observe the birth. Sandy was swimming at twice her normal rate and making frequent sharp turns. When more than half of the embryo was protruding from the cloaca, Sandy made a quick, 180° turn and left the pup at her pivot point. It sank slowly to the bottom making feeble, but uncoordinated, attempts to swim. It lay

on its side for 15 to 20 seconds, opening and closing its mouth and presumably pumping water over its gills. Then it wriggled rapidly, but awkwardly to the surface for 4 or 5 seconds before sinking slowly to the bottom again. Bursts of swimming toward the surface followed by decreasing periods of rest on the bottom were repeated several times. Gradually, the rate of swimming slowed and became more coordinated. Fifteen to 20 minutes after birth the pup was swimming continuously with a coordinated, but slightly more rapid motion than is normal for older individuals and in a more sinuous fashion--probably because the vertebral and caudal cartilages had not yet calcified.

A fourth embryo was born live and 4 others were stillborn. By 1945 Sandy had slowed to her normal swimming rate and had ceased her frequent turning maneuvers. The umbilical cords were still trailing from her cloaca. On the following day they were found on the floor of the tank along with remains of the pseudoplasentas and egg cases.

The pups were measured the day following their birth. The lengths of the live pups were: female, 67 cm total length, 51.2 cm precaudal length; female, 67 cm tl, 51.0 cm pcl; male, 67 cm tl, 51.0 cm pcl; and male, 63 cm tl, 47.8 cm pcl. The pups were all larger than 47 cm precaudal length which was the estimate of average length at birth derived from field data. This is probably because they were also born

later in the season than is usual for C. milberti (see following section). The conditions of confinement may have increased their period of pre-natal development.

Total lengths of the stillborns were: male, 33 cm; male, 33 cm; female, 32 cm; and female 32 cm. It is believed that stillborns are rare among Hawaiian C. milberti since dead embryos were seldom found in the uteri of captured specimens. Those occurring in the tank were probably the result of an injury sustained by the mother during capture or during her confinement in the tank.

Neither the pups nor their mother showed interest when food was offered about 4 hours after birth. On the following evening, however, Sandy fed well. Four days after they were born, at least one pup was observed feeding, and all took food on the fifth day.

At parturition a 1-centimeter remnant of the umbilicus protruded through a slit in the belly of each pup. This was absorbed after 2 weeks and the slit closed a week later leaving an obvious scar. During this 3-week period, the average increase in precaudal length of 3 pups (one was sacrificed at birth) was 1.2 cm. Umbilical scars had completely disappeared at 6 months of age, during which time the average precaudal length increase was 15.8 cm.

## 6. Gestation Period

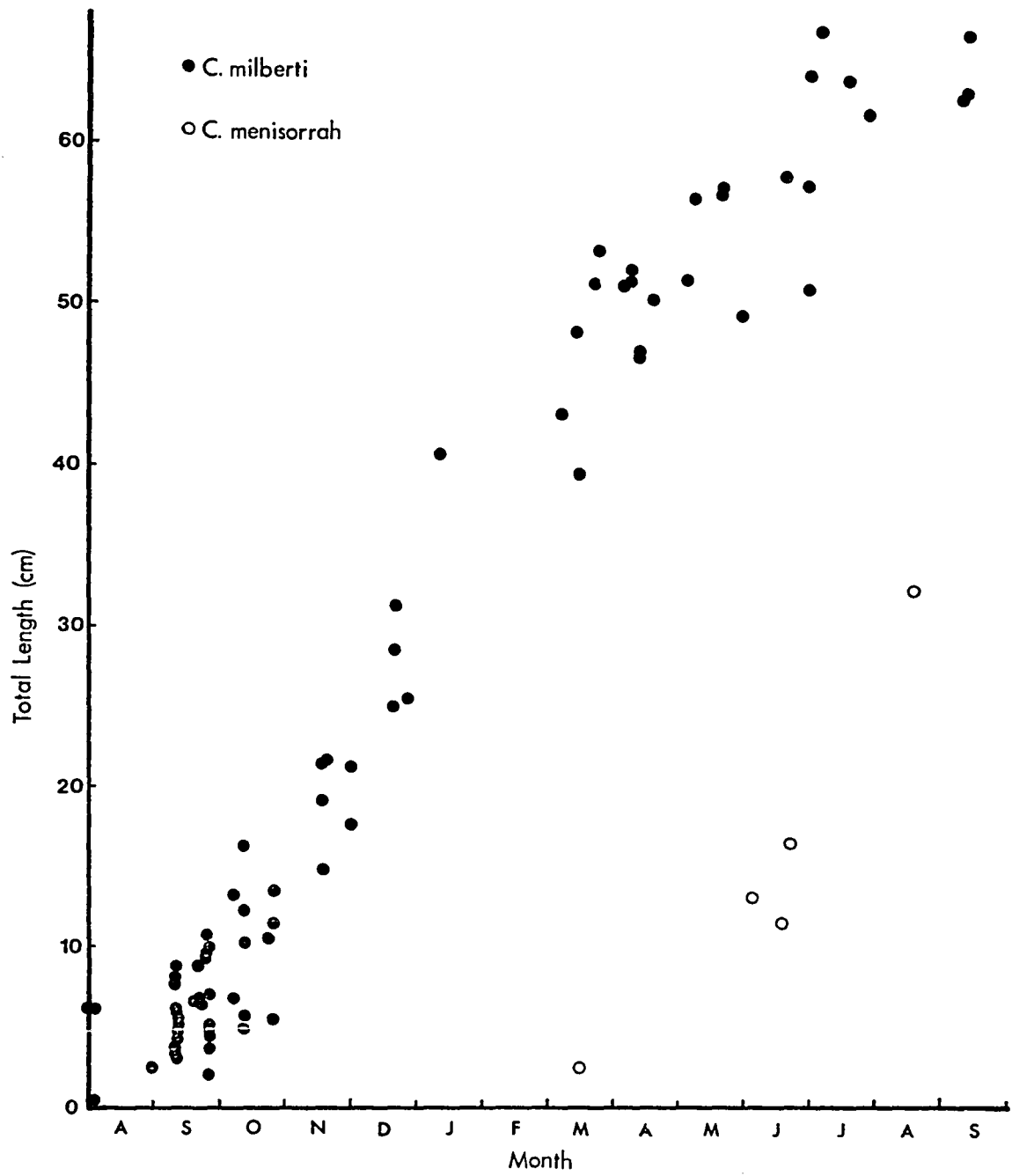
Average embryo size is plotted against date of measurement in

Fig. 22 for 80 C. milberti litters. The points intersect with the zero ordinate during the months of July, August and September, indicating that this is when development begins. These data agree with the time-of-mating estimates discussed above. Total lengths of C. milberti at birth average 64 cm (47 cm precaudal length). Embryos attain this size and are born during July, August and September, giving C. milberti a gestation period of about 12 months. The smallest free-swimming individuals of this species were caught during the late summer and early fall, lending further credence to a summer pupping season. Corroborative evidence is also furnished by 2 C. milberti which gave birth after being hauled aboard the deck of the Alika during the middle of September and by numerous spent females with enlarged, but flabby uteri captured during September and October.

Data on embryo size and month of examination are also plotted in Fig. 22 for 5 litters of Hawaiian C. menisorrah. Because the embryos were all small, the data give a fairly good indication of the time of year when development begins and, consequently, the mating season. The points intersect the zero ordinate during February, March, and April. The high percentage of ripe males captured during these months gives further indication that Hawaiian C. menisorrah mate during the late winter and early spring.

The length of the gestation period for C. menisorrah, as well as

Figure 22. Monthly average total lengths of embryos in litters of Hawaiian Carcharhinus milberti and Carcharhinus menisorrhah.



the pupping season, are not obvious from Fig. 22. However, the slope of the C. menisorrah data appears to parallel the C. milberti data indicating a similar rate of development for both species. Because size at birth is also the same, one might guess that the gestation period for C. menisorrah is also about 12 months long and, consequently, that the pups are born during February, March and April. This conclusion, however, is not supported by data from young C. menisorrah caught while handlining. The smallest individuals were captured during September, October and November and were small enough to have been recently born. One individual caught September 20th had a fresh umbilical scar, indicating it had been born within the past month. Possibly there are 2 mating and pupping seasons or maybe no well-developed season. Perhaps the gestation period is longer than 12 months. The final answers must await more data.

## 7. Fecundity

Forty-two percent of the mature female C. milberti captured in Hawaii were pregnant. This is considerably higher than the values of 17%, 18% and "substantially less than 1/3" calculated by Springer (1960) for C. milberti off the east coast of Florida and the value of 27% determined by Clark and von Schmidt (1965) for the central gulf coast of Florida. C. milberti in Florida, on the other hand, have larger litters than those in Hawaii. Ninety-one Hawaiian litters averaged 5.51

embryos (range: 1 to 8) compared to an average of 9 embryos per litter in Florida (Springer, 1960; Clark and von Schmidt, 1956).

Again, data for Hawaiian C. menisorrah are scanty. Five of the 8 mature females captured (63%) were pregnant, with an average of 5.0 embryos per litter (range: 3 to 6). At Eniwetok 37% (15 out of 41) of the mature females were pregnant while the average number of embryos per litter was only 2.32 (range: 1 to 4). The average size of 5 litters at Johnston was 2.8 embryos (range: 2 to 4).

Fecundity depends not only on the percentage of pregnant females and litter size, but also on how often litters are produced. Females holding full-term embryos and those that have recently given birth do not possess ripe ova. Assuming a 1-year gestation period, a minimum of 2 years is then required for the reproductive cycle. A 2-year cycle is probably the rule for Hawaiian C. milberti and C. menisorrah because, as mentioned, about half (42% of the C. milberti and 63% of the C. menisorrah) of the mature females captured were pregnant. Completely healed mating scars underlying fresh bite wounds found on some recently impregnated females are evidence that more than a single litter is produced. The total number of litters borne by the average female, however, cannot be estimated because the life-span is unknown.

Litter size and length at maturity are correlated for C. milberti and C. menisorrah. Hawaiian C. milberti mature at a smaller size than do their conspecifics in Florida and have smaller litters. Size

at birth, however, is about the same in Hawaii and Florida. Eniwetok and Johnston C. menisorrah mature at a smaller size and, likewise, have smaller litters than do their Hawaiian conspecifics. Size at birth is unknown for C. menisorrah at Eniwetok and Johnston. When the relationship between litter size and length of the mother was examined for all pregnant C. milberti caught in Hawaii, a highly significant (P less than .001) positive regression was found. Larger mothers, thus, produce a greater number of offspring. Backus, et al. (1956) found the same relationship for Carcharhinus longimanus, though Springer (1960) was unable to demonstrate it for C. milberti in the Atlantic.

CHAPTER IV.  
HORIZONTAL DISTRIBUTION

A. Distribution in the Hawaiian Islands

C. milberti

C. milberti is the most abundant shark around the main Hawaiian islands. Of the 1,727 sharks captured in the Cooperative Shark Research and Control Program, 789 were of this species. Although the abundance is not uniform, it is difficult to make inter-island comparisons because different methods were used for capture. The methods can, however, be grouped into 2 major categories: sets made parallel to the depth contours (all hooks at similar depths) as was done in standard fishing, and perpendicular sets at right angles to the depth contours (hooks at ever-increasing depths). Variety and freshness of baits, seasonality, different fishing depths, different bottom characteristics, etc., all serve to obscure the comparison so the estimates of relative abundance are, necessarily, rough approximations. Tester (1969) concluded that catch rate is reduced with continued fishing so only data from the initial set in an area were used for the estimates. Catch/100 hooks for each island is listed in Table 4. C. milberti appears to be most numerous around Molokai and Lanai and least abundant at Kauai and Penguin Banks. The other Hawaiian areas show intermediate abundances which are

TABLE 4. -- Catch/100 hooks for Carcharhinus milberti on initial sets of the longline

Location	Area	Parallel Sets	Perpendicular Sets
Kaula	17	4.2	--
Niihau	18, 19	4.9	11.0
Kauai	20, 24, 26, 27	2.5	9.7
Oahu	1-16	5.6	--
Penguin Banks	30	2.8	--
Molokai	31, 37	15.3	15.3
Lanai	42, 43	---	17.4
Maui	44, 55, 56	6.9	10.4
Kahoolawe	61	--	11.1
Kona Coast, Hawaii	72, 73, 74, 76	4.2	--
	Average	5.7	12.6

relatively uniform.

C. menisorrah

C. menisorrah has a restricted distribution within the Hawaiian Islands. It is most abundant at Kaula where it was captured in large numbers on longlines and handlines. Many individuals ranging in size from juveniles to mature adults were observed while SCUBA diving at depths of 5 to 18 fathoms. In one narrow channel about 7 fathoms deep, I counted 19. The only other islands where the species was frequently caught are Niihau, Molokini, and along the east coast of Kahoolawe. Additionally, one adult was caught on a longline off Waimea, Kauai and one juvenile was taken on a handline from the Alika in area 4 on the west coast of Oahu. Dr. John A. Maciolek also captured 3 juveniles at the artificial reef on the west coast of Oahu and Mr. Victor R. Faughnan caught a newborn pup off Kewalo Basin on the south coast of Oahu. While diving, I observed a sub-adult at Kaena Point, Oahu, a sub-adult at Mokuhooniki Island, east Molokai, and an adult at Keahole Point on the west coast of Hawaii. Thus, C. menisorrah occurs throughout the Hawaiian Islands, but uncommonly in most areas.

B. Localized Distribution

C. milberti

Eight circuits of standard fishing furnish enough data to look at the Oahu distribution of C. milberti in some detail.

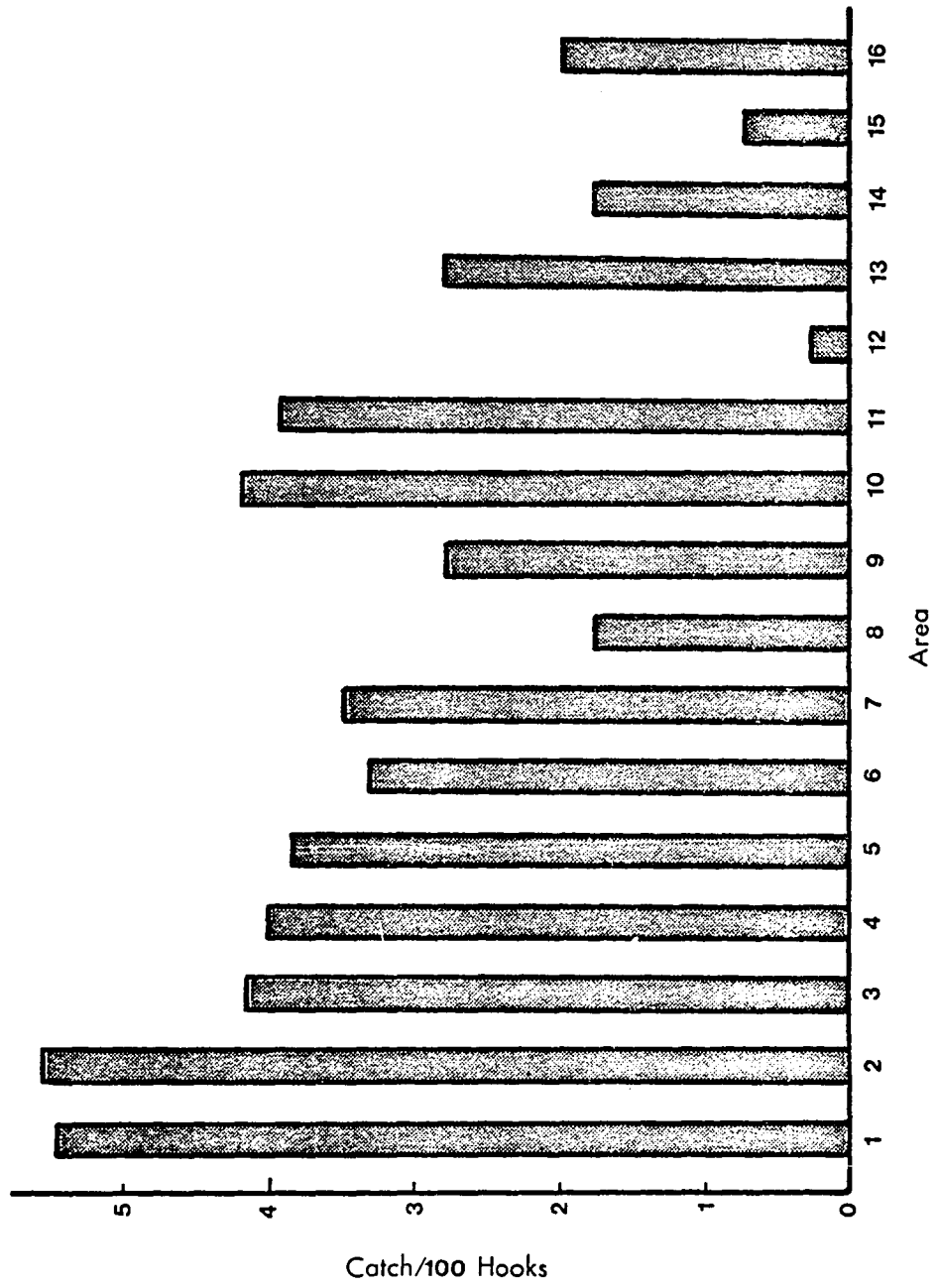
Coastal abundance is illustrated in the following table:

Oahu Coast	Number of Hooks	Sharks Caught	Catch/100 Hooks
North	1,727	48	2.78
South	2,270	76	3.35
East	3,341	89	2.66
West	1,704	67	3.93

An analysis of variance with a randomized block design (to eliminate the effect of variation between circuits due to seasonal trends and fishing mortality) and an arc-sine data transformation revealed that coastal differences were not significant. A chi-square value of 7.09 was calculated from a 2 x 4 contingency table which, again, is not quite significant. The means for the south and west coast (leeward areas), however, were somewhat greater than for the north and east coasts. They would probably be even larger had it not been for the large amount of experimental fishing confined to the leeward areas which removed individuals that would otherwise have been vulnerable to standard fishing. A total of 976 hooks was set experimentally within the depth range of C. milberti on the south shore and 31 individuals were captured. Six C. milberti were caught on 191 hooks fished experimentally on the west coast.

Catch/100 hooks is illustrated for the 16 areas around Oahu in Fig. 23. Excluding area 12 (inside Kaneohe Bay) where the catch is

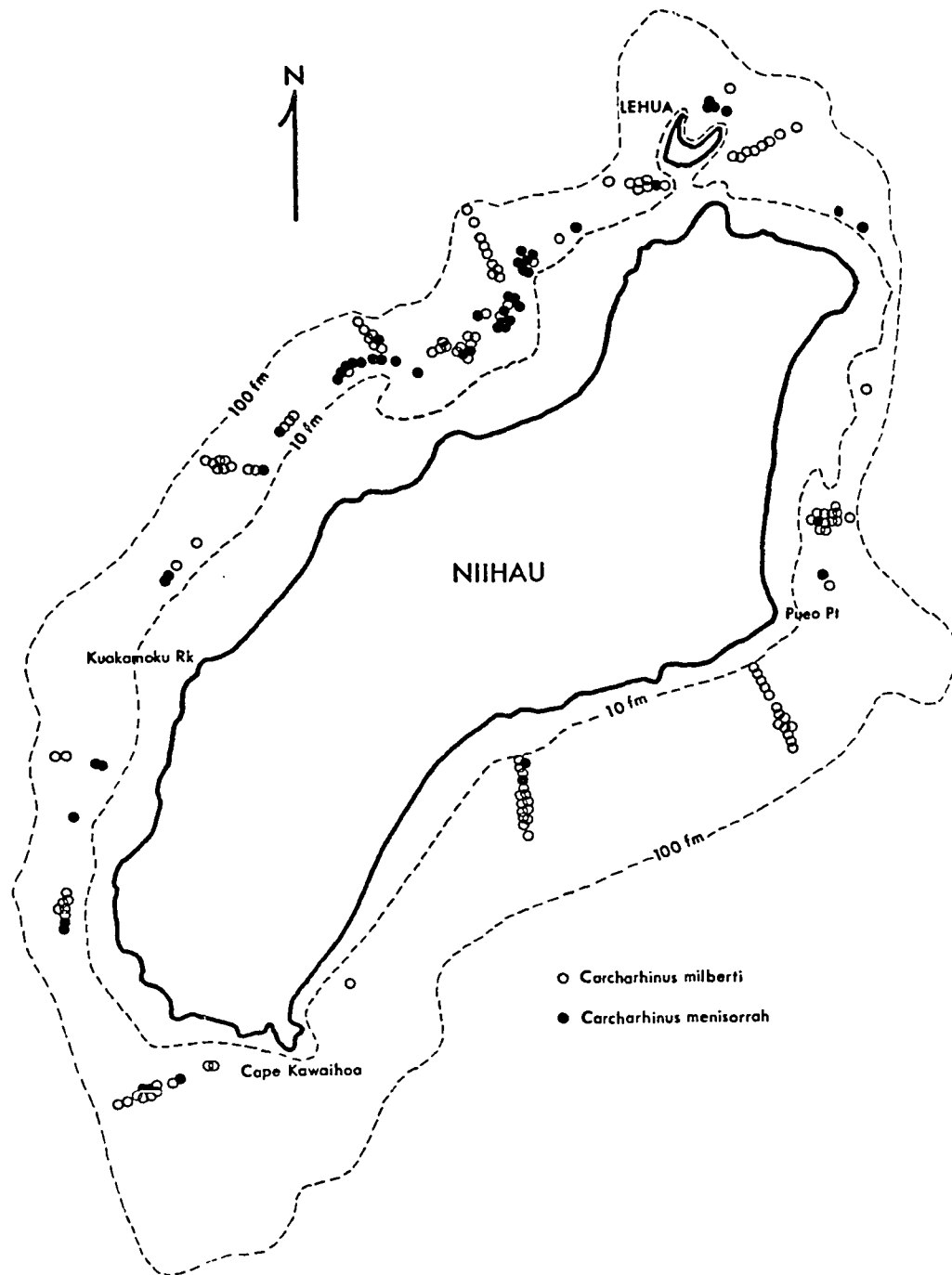
Figure 23. Catch/100 hooks for Carcharhinus milberti in the 16 areas around Oahu based on 8 circuits of standard fishing.



obviously less, an analysis of variance test similar to the one described above for coasts revealed that the areas differed significantly ( $P$  less than .005). C. milberti was most abundant in area 2 between Pearl Harbor and Barbers Point (5.56/100 hooks) and area 1 between Diamond Head and Pearl Harbor (5.43/100 hooks). The species was least abundant in area 12 inside Kaneohe Bay (0.26/100 hooks) and area 15 between Makapuu Point and Koko Head (0.70/100 hooks). Continuing with the analysis, areas 1-5 were compared by planned comparison techniques using lambda coefficients with areas 6-16 (excluding area 12). Areas 1-5 are contiguous from Diamond Head to Kaena Point and can be considered leeward when normal tradewinds are blowing. The mean catch/100 hooks for the leeward areas (4.60) differed significantly ( $P = .008$ ) from the mean for the remaining areas (2.65/100 hooks).

Fishing effort was also concentrated around the entire perimeter of Niihau (Fig. 24). It is a narrow island whose long axis lies at a slight angle to the north of prevailing tradewind direction. The southeast coast is more exposed (windward) with respect to the northwest coast (leeward). The catch/100 hooks (all sets combined) for C. milberti was 7.98 (53 sharks/664 hooks) on the windward coast and 5.06 (70 sharks/1,384 hooks) on the leeward coast. Analysis with a 2 X 2 contingency table yields a corrected chi-square value of 6.2 ( $P = .01$ ) indicating the difference in catch ratio is significant. The value for the windward coast might have been lower if it had been fished as heavily as

Figure 24. Location of capture for 123 Carcharhinus milberti and 51 Carcharhinus menisorrah caught on longline gear at Niihau.



the leeward coast. Despite this possibility, the Niihau population of C. milberti does not appear to show the preference for leeward areas that was found for the Oahu population.

There are insufficient data for analysis of the coastal distribution of C. milberti around other islands. However, catch rates encountered on the leeward sides of Molokai (south coast), Lanai (west coast), and Kahoolawe (east coast) were even higher than initial catch rates off leeward Oahu.

#### C. menisorrah

C. menisorrah appears to prefer the leeward side of Niihau (Fig. 24). When data from all sets were analyzed, the catch/100 hooks for the leeward side was 2.96 (41 sharks/1,384 hooks) as opposed to only 1.51/100 hooks (10 sharks/664 hooks) for the windward side. With greater fishing effort on the windward side, the figure would probably have been even smaller. Analysis with a 2 x 2 contingency table yields a corrected chi-square value of 3.34 indicating the difference is almost significant ( $P = .07$ ).

Captures and observations of C. menisorrah in other Hawaiian areas also indicate a preference for leeward areas. The species is common at Molokini which is protected by Maui. Of the 5 individuals captured around Oahu, 4 were taken off the west coast and 1 off the south coast. Both are leeward areas. The individual observed while diving off Kaena Point was also on the leeward side. One of the other 2

C. menisorrah observed while diving was at Keahole Point on the leeward side of Hawaii. The other was sighted off windward Molokai at Mokuhooniki Island. C. menisorrah is also common at Kaula which is too small to offer much lee. Thus, there are exceptions to the apparent preference for leeward areas.

#### C. Distribution by Sex and Maturity

Sharks were divided into 3 maturity (size) groups: adults or mature individuals, sub-adults (precaudal length greater than 80 cm), and juveniles (precaudal length less than or equal to 80 cm).

#### C. milberti

Standard longline, light longline and handline catches around Oahu are presented for the sex-maturity groups of C. milberti in Table 5 and Fig. 25. Mature sharks of both sexes were significantly more numerous (2.51/100 hooks) in the leeward areas between Diamond Head and Kaena Point (areas 1-5) than they were in the remaining areas excluding Kaneohe Bay (0.91/100 hooks). A corrected chi-square value of 33.3 (P less than .005) was calculated from a 2 x 2 contingency table.

Sub-adult C. milberti showed a relatively uniform distribution around Oahu with slightly larger populations in areas where juveniles were common. Juveniles, however, were restricted to windward coasts. They were captured in all areas along the north and east coasts of the island (except inside Kaneohe Bay), but in none of those along the

TABLE 5. -- Oahu catch of Carcharhinus milberti on standard longline, light longline and handline gear.

Area	Times Handlined	Light Longline Sets	Standard Longline Sets	Juveniles <sup>a</sup>	Sub-adults <sup>b</sup>	Mature Males	Mature Females	Total
1	3	6	8	0	13	5	7	25
2	7	6	8	0	11	1	13	25
3	8	3	8	0	8	4	9	21
4	10	5	8	0	9	0	14	23
5	8	6	8	0	5	4	14	23
6	5	3	8	1	5	2	12	20
7	2	4	8	7	11	2	5	25
8	4	4	8	7	10	2	2	21
9	8	2	8	10	10	2	1	23

<sup>a</sup> Precaudal length less than 80 cm.

<sup>b</sup> Precaudal length greater than or equal to 80 cm.

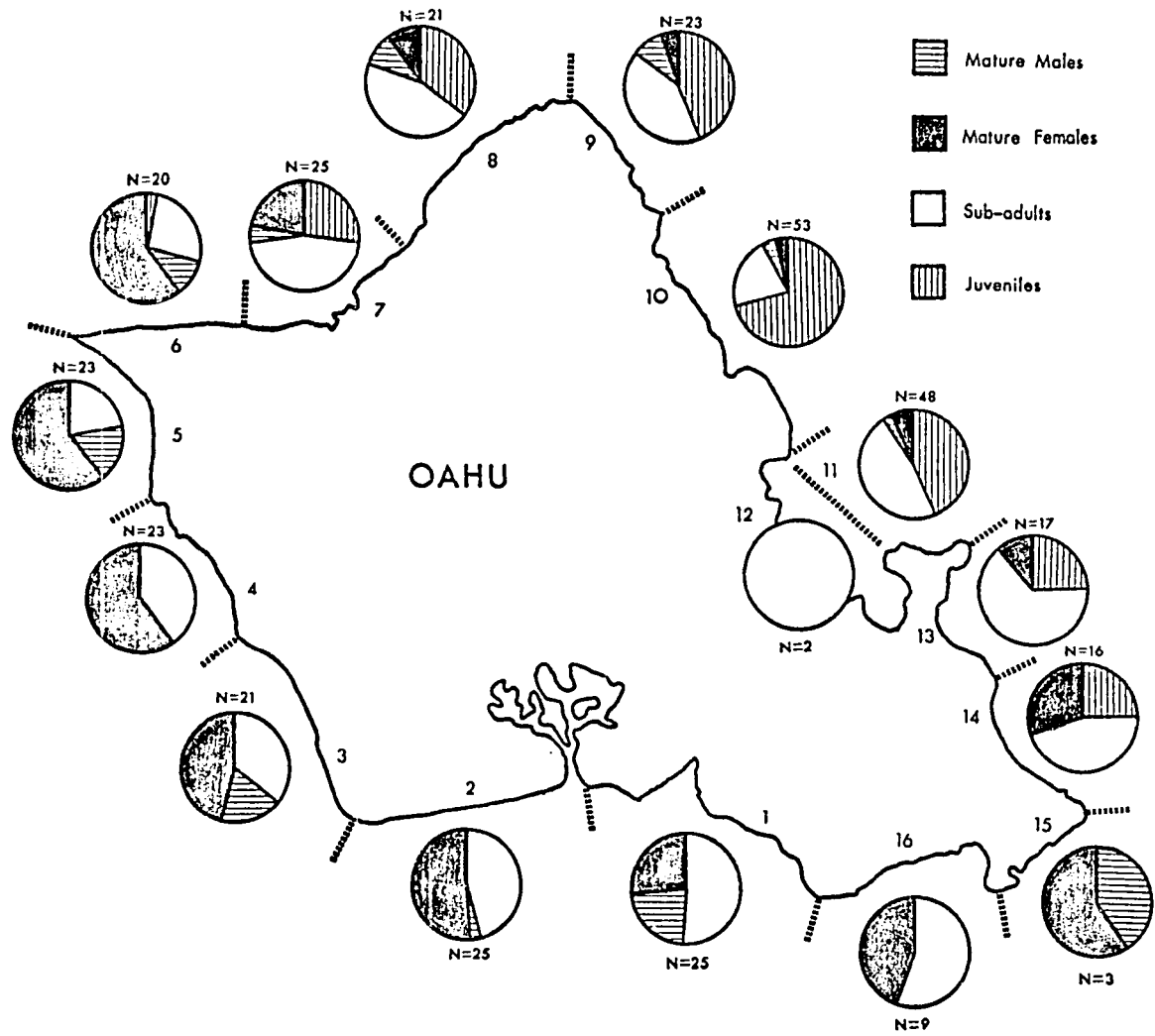
TABLE 5. -- cont.

Area	Times Handlined	Light Longline Sets	Standard Longline Sets	Juveniles <sup>a</sup>	Sub-adults <sup>b</sup>	Mature Males	Mature Females	Total
10	6	3	8	37	12	2	2	53
11	5	4	8	20	22	2	4	48
12	2	3	7	0	2	0	0	2
13	3	1	8	4	11	0	2	17
14	1	3	8	4	7	0	5	16
15	2	2	8	0	0	1	2	3
16	0	3	8	0	5	0	4	9
Totals	74	58	127	90	141	27	96	354

<sup>a</sup> Precaudal length less than 80 cm.

<sup>b</sup> Precaudal length greater than or equal to 80 cm.

Figure 25. Proportions of the total catch of Carcharhinus milberti for each Oahu area consisting of the indicated sex-maturity group. Total catch for each area is listed in parentheses and is the sum of all sharks caught on standard longline, light longline and handline gear.



south and west coasts. Handlines were used on more occasions in areas where no juveniles were caught (40 times) than in areas where they were caught (34 times) so the limited distribution of juveniles was real.

The distribution of pregnant females carrying full-term embryos correlates with the distribution of juveniles. Twenty-three per cent (5 of 22) of the mature females captured off the north and east coasts were carrying embryos averaging at least 50 cm total length. Only 8% (5 of 63) of those captured on the south and west coasts were carrying large embryos.

At Niihau, adults were uniformly distributed around the island. Nothing can be said about females with full-term embryos, because none were captured. There were, however, very few young C. milberti at Niihau. Of 101 individuals whose state of maturity could be ascertained, none were juveniles and only 9 were sub-adults. With the exception of area 1 off Oahu, no region was as extensively fished as the waters surrounding Niihau. The slight possibility exists, however, that juveniles were restricted to very localized areas where, by chance, there was no fishing effort.

Little can be said about the distribution of sex-maturity groups around the other Hawaiian islands. On 2 occasions, however, large numbers of pregnant females were caught. During September 1967, while fishing off Kawaihae, Hawaii, 7 of the 7 mature females caught were pregnant. Previous and subsequent sets in the same area did not

show a large proportion of pregnant females. During 2 consecutive days of fishing (September 1968) near Kolo Harbor, Molokai, 17 of the 19 mature females caught were pregnant. In neither of the above cases were most of the females carrying full-term embryos, nor were substantial numbers of juveniles taken, so it is not implied that these are nursery areas.

### C. menisorrah

Adult and sub-adult C. menisorrah at Eniwetok and in the Hawaiian Islands showed no significant preferences for a particular area or coast. The distribution of juveniles, however, is restricted. At Eniwetok, no juveniles were caught within the lagoon. Tester (pers. comm.) captured juveniles on the seaward sides of the atoll, however, and I observed them there while diving.

Only one juvenile C. menisorrah was captured around the southern end of Niihau though handlines were used at various depths and locations on 6 different nights. By contrast, 108 juveniles were captured to the north between Kuakamoku Rock and Pueo Point. Another concentration of juveniles was discovered at Molokini, off the south coast of Maui. Unlike the situation at the north end of Niihau where adults and immature individuals occur together, no adults were captured or observed at Molokini. The largest number of juveniles observed anywhere, however, was at Kaula. While anchored at night in approximately 20 fathoms, 4 or 5 sharks were always in view under the lights of the boat. Using one

handline, 21 juveniles were caught in 2 hours. The rate of capture was limited by the time it took to tag and measure the sharks, not by their numbers or reluctance to bite the baited hook.

#### D. Seasonal Variation in Horizontal Distribution

Seasonal migration has been observed for many sharks. Clark and von Schmidt (1965) give evidence for migration of Carcharhinus limbatus off the Florida coast; and Holland (1957) states that Squalus acanthias shows migration in the eastern North Pacific. Pelagic species like Prionace glauca also migrate seasonally (Strasburg, 1958).

Springer (1960) has shown that C. milberti makes extensive migrations along the eastern coast of the United States.

It is believed that neither of the study species migrates between islands in Hawaii though the evidence is purely circumstantial since the tagging study was inadequate. It will be shown in Chapter VII that the adult population of C. milberti around Oahu was significantly reduced with a relatively small amount of effort. It seems likely that much greater effort would be required to result in a similar reduction if sharks were migrating to Oahu from the surrounding islands.

Two explanations might account for a lack of migration in Hawaii. The seasonal temperature variation is only about 4°C which is much less than occurs along mainland coasts and may not be large enough to elicit migration. Also, no long shallow stretches of bottom along which

migration can occur extend in a north-south direction. C. milberti and C. menisorrah generally occur within a few fathoms of the bottom so would be unlikely to strike off across the deep, open channels between islands.

#### E. Conclusions

C. milberti appears to be abundant around all the islands, but occurs in greatest numbers at Molokai and Lanai. Around Oahu, it is most numerous in the leeward areas from Diamond Head to Kaena Point. No juveniles, however, were captured in these areas; they were found only off the north and east coasts. At Niihau, the situation is different. Adults occur more commonly on the windward side, while sub-adults and juveniles are rare everywhere.

C. menisorrah is abundant at Kaula and occurs commonly at Niihau, Molokini and Kahoolawe. Few C. menisorrah were captured and observed off the larger islands. When they were, the areas were generally leeward. At Niihau, the catch rate for adults was greater on the leeward side than on the windward side though the difference was not quite significant. Juveniles occur only around the northern half of Niihau, while adults are distributed around its entirety. At Molokini, however, no adults were caught--only juveniles.

There are certain areas where both C. milberti and C. menisorrah occur in large numbers as juveniles but where adults either do not occur,

or are relatively uncommon. The north and east coasts of Oahu are examples for C. milberti, and Molokini is such an area for C. menisorrah. Springer found areas where juvenile C. milberti are common in the western North Atlantic and termed them nursery areas. He reports that females which have given birth do not remain long in the nursery areas and do not feed actively while there, and that adult males are never found in these areas. Female C. milberti with full term embryos were most abundant in the same areas where juveniles occurred, strongly suggesting that the nursery areas on Oahu are on the north and east coasts. Molokini is probably a nursery area for C. menisorrah, but there are no data on pregnant females to support this.

Excepting inshore-offshore movements described in the following chapter, Hawaiian C. milberti and C. menisorrah probably make no seasonal migrations nor do they move extensively between the main islands separated by deep channels.

CHAPTER V.  
VERTICAL DISTRIBUTION

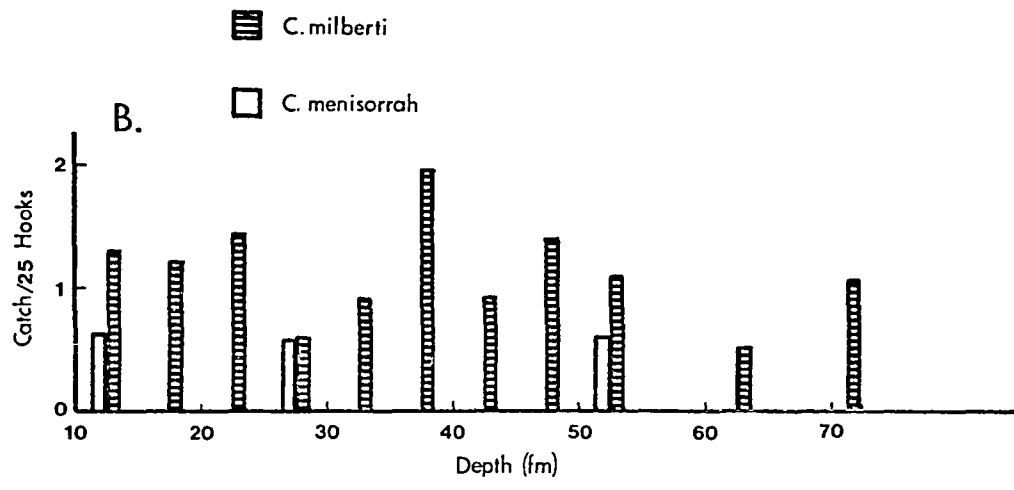
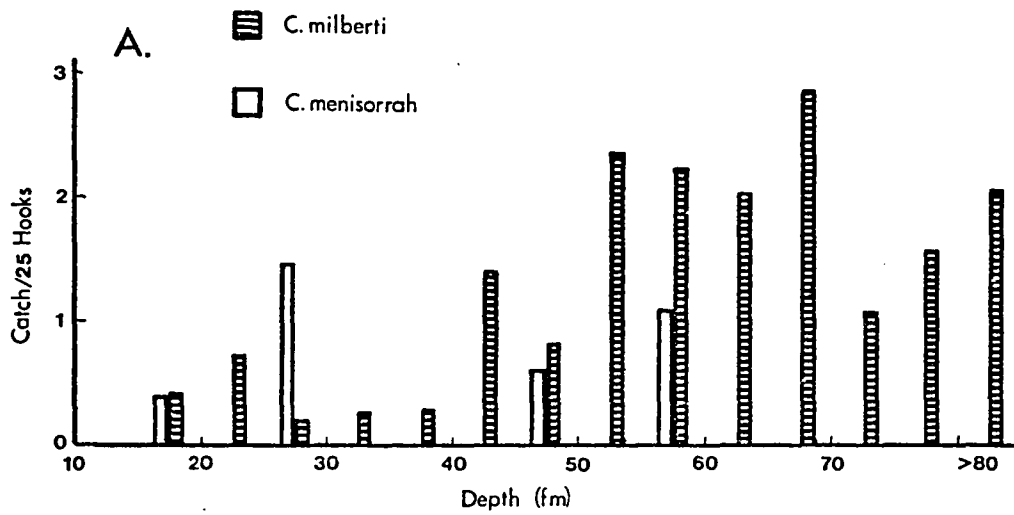
A. General

Both C. milberti and C. menisorrah are inshore sharks commonly occurring within a few fathoms of the bottom. There are no records of either species being captured in water deeper than 150 fathoms in the Pacific. In the Atlantic, however, Springer (1960) reported the capture of an adult male C. milberti at a depth of 30 fathoms in 600 fathoms of water and captures of 2 adult females at 50 fathoms in water deeper than 600 fathoms.

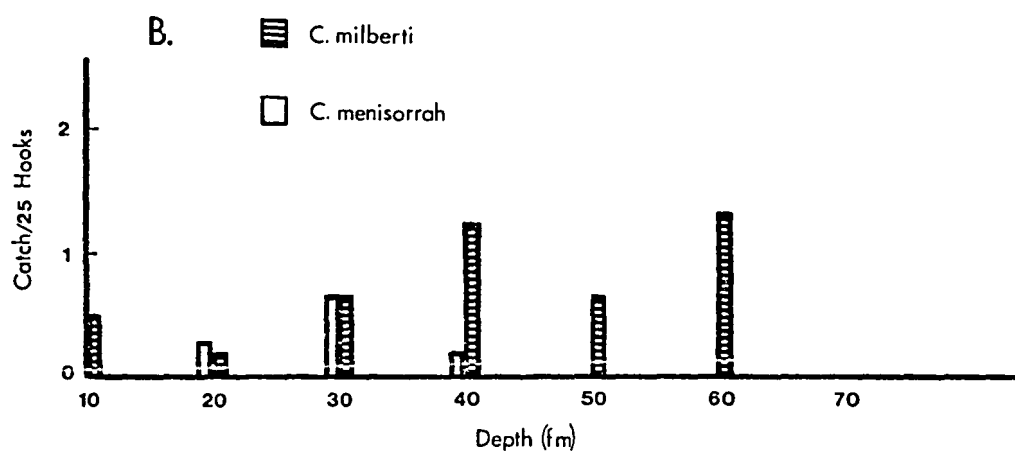
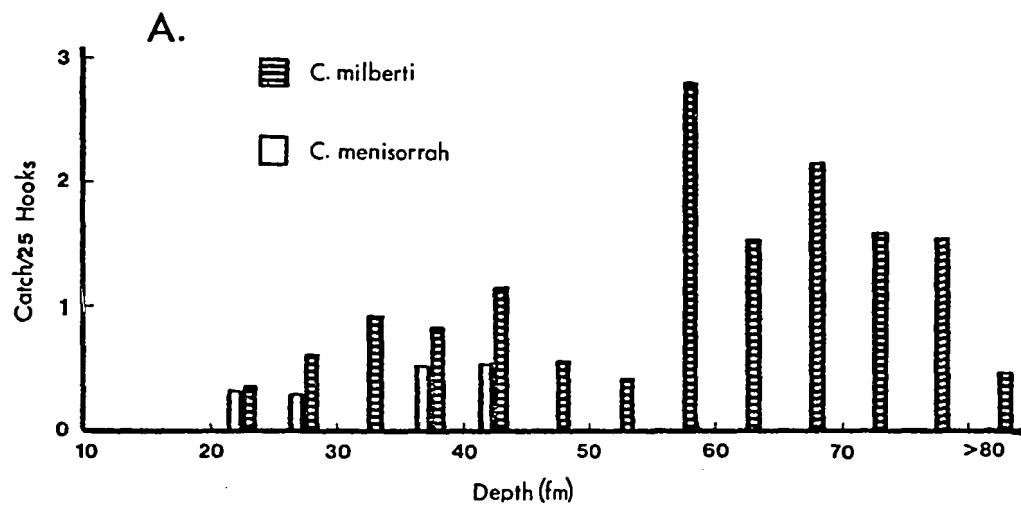
As part of our fishing program, 3 sets (2 off Oahu and 1 off Niihau) were made in water deeper than 100 fathoms with the hooks set to fish at approximately 20 fathoms. No C. milberti or C. menisorrah were caught. However, when the longline was set in 65 fathoms off the windward side of Oahu with the hooks at 20 fathoms, 2 immature C. milberti were captured. Both species were observed on the surface at night under the lights of the Alika while anchored at depths of 15 to 35 fathoms.

Data comparing the depth distribution of C. milberti and C. menisorrah are given for mature males and females in Fig. 26, for sub-adults in Fig. 27, and for juveniles in Fig. 28. The data were

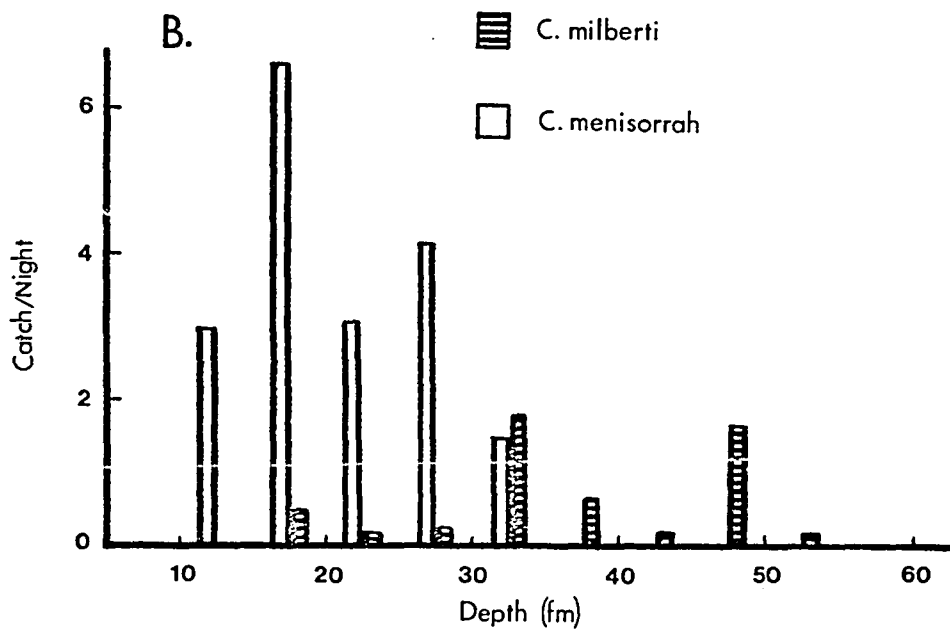
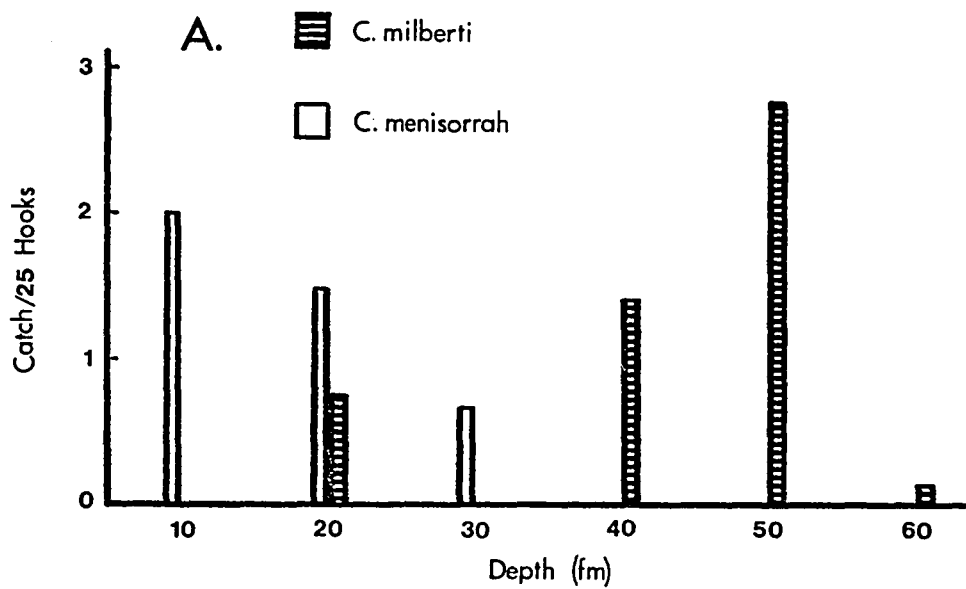
- Figure 26. A. Depth distribution of mature male Carcharhinus milberti and Carcharhinus menisorrah in Hawaii. Data are catch/25 hooks fished within the 5-fathom interval on perpendicular sets of the longline.
- B. Depth distribution of mature female C. milberti and C. menisorrah in Hawaii.



- Figure 27. Depth distribution of sub-adult (precaudal length greater than or equal to 80 cm) Carcharhinus milberti and Carcharhinus menisorrah.
- A. Catch/25 hooks fished within the 5-fathom interval on perpendicular sets of the longline.
  - B. Catch/25 hooks fished within the 10-fathom interval on the light longline.



- Figure 28. Depth distribution of juvenile (precaudal length less than 80 cm) Carcharhinus milberti and Carcharhinus menisorrah in Hawaii.
- A. Catch/25 hooks fished within the 10-fathom interval on the light longline.
  - B. Catch/night within the 5-fathom interval on handline gear.



compiled from 3 methods of fishing: perpendicular sets of longline gear, parallel sets of light longline gear and spot fishing with handline gear.

Adults and sub-adults were vulnerable to perpendicular sets of the longline. In this procedure all 9 baskets of gear were tied together and set perpendicular to the depth contours. Under a typical set, depths ranged from 15 to 80 fathoms with extremes of 8 and 110 fathoms. A total of 32 perpendicular sets were made, 16 of them in areas where C. menisorrah is common. One hundred and twenty-nine C. milberti were caught, but only 16 C. menisorrah so the conclusions concerning depth preferences of adult and sub-adult C. menisorrah suffer from lack of data.

Because the 32 sets did not begin and end at the same depths and because the slope of the bottom under each set was different, the data were analyzed on a catch-per-unit-effort basis. Depths between 10 and 100 fathoms were divided into 5-fathom intervals and the number of hooks fishing within each interval was determined. Sharks caught within each interval were totaled and are plotted as catch/25 hooks in Figs. 26 (adults) and 27A (sub-adults). To calculate mean depth of capture ("preferred depth"), each depth was multiplied by its corresponding catch-per-unit-effort and divided by the total catch/25 hooks for all depths. When calculating confidence intervals and standard deviations which are dependent on sample size, the catch/25 hook values were adjusted so their total equaled the actual number of individuals in the

sample.

Catch data from the light longline provides information on the vertical distribution of sub-adult and juvenile sharks. Sixty-four C. milberti and 10 C. menisorrah were caught on this gear which was set parallel to the depth contours at depths between 10 and 65 fathoms. Catch/25 hooks on the light longline at 10-fathom intervals is plotted in Fig. 27B for sub-adults and Fig. 28A for juveniles. Again the catch ratios were adjusted so the total equaled sample size when standard deviations and confidence limits were calculated.

The handline results are a final source of data concerning vertical distribution. Fifty-eight C. milberti and 146 C. menisorrah were caught by this technique, and all were juveniles. The data are difficult to quantify on a per-unit-effort basis because the number of lines in use and the time spent fishing varied, depending on the catch-rate, weather, etc. The minimum effort for a night of handlining consisted of 2 hours of fishing with 2 handlines. This was also the usual effort, but if sharks were biting, the effort was increased. The data are presented as average catch/night at 5-fathom intervals in Fig. 28B. As with the longline and light longline data, a correction for sample size was used when calculating confidence intervals and standard deviations.

The vertical distribution data are summarized in Table 6.

#### B. Depth Distribution of C. milberti

Mature male C. milberti were caught in Hawaii at depths ranging

TABLE 6. -- Summary of depth distribution data for Hawaiian Carcharhinus milberti and Carcharhinus menisorrhah. The values are number of individuals captured, mean depth (fathoms) of capture, the 95% confidence interval for the mean and the standard deviation of the mean.

Sex-maturity Group	Method of Capture	<u>C. milberti</u>				<u>C. menisorrhah</u>			
		N	Mean Depth	C. I.	S. D.	N.	Mean Depth	C. I.	S. D.
Adult Males	Longline	45	61.0	+5.4	18.1	8	38.9	+13.3	15.9
Adult Females	Longline	47	37.3	+5.1	17.5	4	30.6	+30.5	19.2
Sub-adults	Longline	37	57.5	+5.4	16.1	4	34.2	+14.3	9.0
Sub-adults	Light Longline	33	41.5 <sup>a</sup>	+5.7	16.1	3	29.3	+19.7	7.9
Juveniles	Light Longline	31	43.0	+4.0	11.0	7	16.7	+7.4	8.0
Juveniles	Handline	58	36.7	+2.6	9.9	146	21.0	+1.0	6.1
Total		251				172			

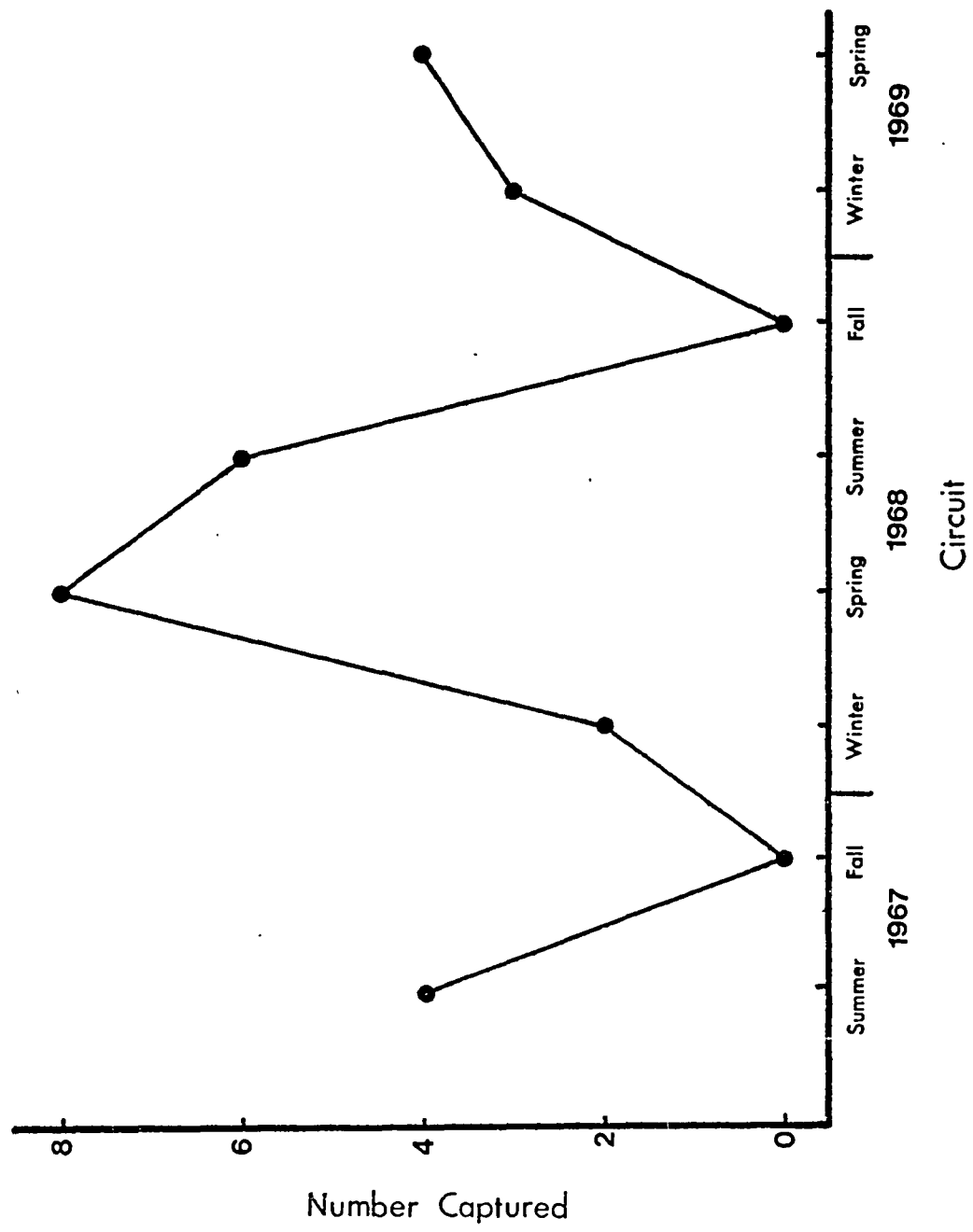
<sup>a</sup> This mean is biased because the light longline was not set at depths exceeding 65 fms.

from 15 to 152 fathoms. The mean depth of capture for 45 individuals caught on perpendicular sets of the longline was 61.0 fathoms. Mature females ranged in depth from 5 to 102 fathoms with a mean of 37.3 fathoms for 47 individuals caught on perpendicular sets. The difference between the mean depths of capture for adult males and females is highly significant ( $P$  less than .01).

Obviously, either the males or females or both must alter their depth distribution to simultaneously occupy the same depths during the mating season. The perpendicular-set data on depth distribution are too few to show seasonal variation, but there is evidence from another source for the shoreward migration of males during the late spring. Data from the 8 circuits of standard fishing, which was done in relatively shallow water (about 25 fathoms), show that most of the mature males were caught during the spring and summer quarters (Fig. 29). None were caught during the fall quarter. Since the mating season for C. milberti encompasses the months of July, August and September, it is concluded that males move to the shoaler depths occupied by the females shortly before this period. They return to deeper water during the late summer.

Springer (1960) reports the range of depth for adult C. milberti in the Atlantic to be from the "shallows just offshore" to 135 fathoms with the highest concentrations at depths of 10 to 30 fathoms. It is common to depths of 50 fathoms and the males are generally found deeper. His

Figure 29. Mature male Carcharhinus milberti captured during the 8 circuits of standard fishing around Oahu.



findings are similar to those for Hawaiian C. milberti though the distribution of Hawaiian sharks is centered in deeper water.

Sub-adult C. milberti were caught at depths ranging from 8 to 82 fathoms in Hawaii. Two estimates of preferred depth can be made. The mean depth of capture for the 37 individuals caught on the perpendicular sets was 57.5 fathoms. Thirty-three sub-adults caught on the light longline showed a distribution centered around 41.5 fathoms, but this is a biased estimate of preferred depth. The light longline was never set deeper than 65 fathoms, so a substantial portion of the depth range of sub-adult C. milberti was not fished with this gear.

Juvenile C. milberti were caught at depths ranging from 1 to 60 fathoms. Two estimates of their preferred depth are also available. The distribution of 31 individuals caught on the light longline was centered around 43.0 fathoms. The mean depth of capture for 58 juveniles caught on handlines was 36.7 fathoms.

In order to define the pupping depth for C. milberti, depths of capture for all pregnant females carrying full-term embryos (averaging at least 60 cm total length) were examined. Of the 6 females in this condition, 4 were caught at depths between 19 and 22 fathoms. The other 2 were captured at 51 and 74 fathoms. Additionally, Mr. Victor R. Faughnan captured a pregnant female with full-term embryos in Honolulu Harbor at a depth of only 5 fathoms. The depths of capture for the 16 smallest juveniles (precaudal lengths less than 54 cm) ranged from 18

to 40 fathoms, considerably narrower than the 5- to 74-fathom range of the full-term females. No juveniles were captured in very shallow areas such as Honolulu Harbor or Kaneohe Bay. The average depth of capture was 32.4 fathoms, a little shallower than the average depth for all mature females but not significantly so. The pupping depths for Hawaiian C. milberti appear to lie within the shallow end of the range normally habituated by mature females.

Springer (1960) reports that the nursery grounds for Atlantic C. milberti are shallow, inshore waters and bays. The young are found at depths of 5 to 25 fathoms throughout the summer and early fall. When the water becomes cooler, they move offshore to depths as great as 75 fathoms.

The vertical distribution of Hawaiian C. milberti can be summarized as follows. During the fall and winter months, adult males are found in deeper water than females. In the late spring, the mature males move inshore and join the females for the mating season. Sub-adult C. milberti generally occur at depths intermediate to those of the adults. Juveniles (especially newborn individuals) are found at lesser depths than the sub-adults. Pupping areas are at the shallow end (20 to 40 fathoms) of the depth range for mature females. Hawaiian C. milberti prefer greater depths than their Atlantic conspecifics. This may be a consequence of the steeply sloping bottom around the Hawaiian Islands with little area at relatively shallow depths. Along the east coast of the

United States, the continental shelf extends far offshore resulting in a vast expanse of shallow bottom.

### C. Depth Distribution of C. menisorrah

Mature male C. menisorrah were captured at depths ranging from 15 to 58 fathoms in Hawaii. While diving, I observed them as shallow as 2 fathoms. The mean depth for the 8 individuals caught on perpendicular sets was 38.9 fathoms.

Depths of capture for mature Hawaiian females ranged from 13 to 50 fathoms. They, too, were observed at much shallower depths by divers. The mean for 4 individuals was 30.6 fathoms and does not differ significantly from that of the males.

Depths of capture for sub-adult C. menisorrah caught on the longline ranged from 10 to 42 fathoms. The mean depth of capture for the 4 individuals caught on perpendicular longline sets was 34.2 fathoms. The mean for the 3 sub-adults captured on the light longline was 29.3 fathoms.

Juvenile C. menisorrah were observed close to the surface during the day by divers and at night from the Alika. The deepest depth at which they were captured was 30 fathoms. Two estimates of their preferred depth are also available. The mean depth of capture for 7 juveniles on the light longline was 16.7 fathoms. For 146 individuals caught on handlines, it was 21.0 fathoms.

In summary, it appears that the adults are most common at depths of 30 to 40 fathoms and that mature males may prefer water slightly deeper than mature females though the difference is not significant. Sub-adults also show preferences within this range while juveniles occur more commonly at shallower depths of about 20 fathoms.

At Eniwetok, Fanning and Johnston, the lack of a large vessel with power equipment for hauling the fishing gear restricted fishing to shallower depths (generally less than 20 fathoms). Consequently, no quantitative data are available. Throughout its range, C. menisorrah is usually restricted to the deeper waters of lagoons and channels and to the seaward side of fringing reefs and flats (Hobson, 1963). At Fanning, C. menisorrah was common over the fringing reef on the seaward side of the atoll at depths greater than 3 fathoms. Inside the lagoon, however, the species was not observed or captured though depths were as great as 6 fathoms. C. menisorrah also occurs in the deeper areas at Eniwetok. Adults of both sexes were frequently captured inside the lagoon at depths of 5 to 20 fathoms. However, only a few sub-adults and no juveniles were caught there. Rather, they occurred outside the seaward reef at similar depths.

The depth distribution of C. menisorrah at Johnston differs from the above pattern. Both adults and immatures were frequently caught and observed on shallow reef flats within the lagoon at depths of less than 6 fathoms. An aggregation of 12 to 15 adults was observed in water

less than 1 fathom deep off the north end of Sand Island. Four of them were caught and all were pregnant. Juveniles were caught in a dredged boat channel only 2 fathoms deep.

There is evidence that C. menisorrah moves into shallower water after dark at Eniwetok. Three pairs of perpendicular sets from depths of 3 to 16 fathoms were made in each of 3 areas. One set of each pair was made during the day and the other at night. Four sharks were caught during the day at an average depth of 14.5 fathoms. Ten were caught at night at an average depth of 9.1 fathoms. The difference between depths was significant ( $t = 2.26$ ,  $P = .04$ ). Randall (1967) has observed that Galeocerdo also moves into shoaler water after dark.

#### D. Conclusions

The various sex-maturity groups of Hawaiian C. milberti and C. menisorrah do not have narrowly restricted depth ranges. Rather, the individuals of each group commonly occur within a 30- to 40-fathom range. The mean depth of capture for each of the sex-maturity groups of C. milberti was deeper than that of the corresponding group of C. menisorrah. The mean depth of capture for mature male C. milberti differed significantly from that of the mature females. No significant differences in depth preference were found for the sex-maturity groups of C. menisorrah. The sex-maturity groups of C. milberti are spread over a wider range of depth than C. menisorrah and, consequently, show

less overlap.

## CHAPTER VI.

### PHYSICAL FACTORS AFFECTING DISTRIBUTION

#### A. Temperature

During the 2 years of this study, surface temperatures in the fishing areas ranged from 23.0 to 28.1°C. The averages for each quarter were: spring, 25.23°C; summer, 26.89°C; fall, 26.88°C; and winter, 24.26°C. Temperatures at the fishing depth averaged about 0.8°C less than surface temperatures and ranged between 22.8 and 27.0°C.

Surface temperatures in areas where C. menisorrah is common did not differ significantly from those in other Hawaiian areas.

Temperature is not responsible for the discontinuous distribution of C. menisorrah in Hawaii.

The average temperatures for the 4 coasts of Oahu were: north, 25.61°C; south, 25.93°C; east, 25.64°C; and west, 25.81°C. These differences are small and statistically insignificant and are unlikely to account for coastal preferences shown by the sex-maturity groups of C. milberti.

#### B. Salinity

Except for inclosed areas such as Kaneohe Bay, surface salinities around the Hawaiian Islands ranged from 34.17 to 35.17<sup>0</sup>/<sub>00</sub>. The

seasonal averages for all areas fished were: spring (53 samples),  $34.57^{\circ}/_{\text{oo}}$ ; summer (8 samples),  $34.36^{\circ}/_{\text{oo}}$ ; fall (15 samples),  $34.64^{\circ}/_{\text{oo}}$ ; and winter (42 samples),  $34.67^{\circ}/_{\text{oo}}$ . The summer value is significantly less than the others but this is probably because it was derived from samples taken mostly in one area. Salinities measured at the fishing depth showed little variation from those at the surface. They averaged  $0.03^{\circ}/_{\text{oo}}$  higher.

The average surface salinity in areas where C. menisorrah is abundant (Kaula, Niihau, Molokini and Kahoolawe) was  $34.66^{\circ}/_{\text{oo}}$  while it was  $34.59^{\circ}/_{\text{oo}}$  in other Hawaiian areas. The difference is not significant. None of the salinity differences measured are likely to affect the distribution of C. milberti or C. menisorrah.

### C. Turbidity

Depths at which the Secchi Disc became invisible ranged from 1.2 to 38 m with an average of 24.6 m for all islands. Average visibilities for the 4 coasts of Oahu were: north, 22.4 m (8 observations); south, 19.0 m (5 observations); east, 18.7 m (14 observations); and west, 25.5 m (10 observations). As expected, the windward side (east coast), where the water is the roughest and the runoff from the land the greatest, has the most turbid water. The leeward side (west coast), where the water is the calmest and the rainfall least, has the clearest water. None of the above differences, however, are statistically

significant and it is unlikely that the Oahu distribution of the sex-maturity groups of C. milberti is related to turbidity.

The visibility in areas where C. menisorrah was abundant averaged 31.9 m (22 observations) as opposed to 21.7 m (56 observations) in other Hawaiian areas. This difference is highly significant (P less than .001) indicating a strong correlation between the distribution of C. menisorrah and clear water. This relationship is supported by data and observations from other sources as well. Three C. menisorrah were captured on an artificial reef off Waianae and one was observed while diving near Kaena Point, both locations are on the west coast of Oahu where the water is the clearest. Keahole Point, Hawaii and Mokuhooniki, Molokai, the other 2 areas where C. menisorrah was observed, also have exceptionally clear water. The apparent preference of this species for leeward areas, where the water is generally less turbid, is further corroboration.

The association between C. menisorrah and clear water may be related to vision. In Chapter VII it is hypothesized that C. menisorrah feeds almost entirely on organisms swimming in the water column. A substantial proportion of the diet of C. milberti, however, consists of benthic organisms. Perhaps vision is used to a greater extent when capturing prey that is swimming off the bottom.

Attempts to maintain captive sharks in the large tank at Kewalo indicate that C. milberti and C. menisorrah show different tolerances

for water of poor quality--a factor which may be related to turbidity. Four attempts were made to keep C. menisorrah. The first 3 groups of sharks died 1 to 4 weeks after they were placed in the tank. During this period, the water was turbid (visibility about 1 m) due to suspended diatoms and other algae. In the summer of 1969, the Propalite sunscreen was erected over the tank and a new pump with over twice the capacity of the old one was installed. The water cleared up (visibility 12 to 15 m) immediately. Five more C. menisorrah were placed in the tank. One died 5 weeks later, but the other 4 fed well and remained in good condition for many months thereafter. The obvious conclusion is that the last group of sharks was able to live in the tank because of improved water quality. While it is doubtful that turbidity per se was responsible for the death of the first 3 groups of sharks, factors associated with it such as a decreased amount of dissolved oxygen, metabolic waste products, and suspended organic material, may have been lethal. These factors may exist to a limited extent in areas like Honolulu Harbor and Pearl Harbor where C. milberti occurs. The ability of this species to tolerate water of poorer quality was also demonstrated by captive individuals. Four to 8 C. milberti were maintained in the large tank throughout the period discussed above and they remained healthy.

The inverse relationship between turbidity and the field distribution of C. menisorrah may be a response to an aspect of water quality related

to turbidity. Pollution resulting from centers of human habitation is a remote possibility. In Hawaii human populations are low or non-existent in areas where C. menisorrah is abundant. This is also true for many of the areas in the tropical Pacific where the species commonly occurs.

#### D. Current

Measurements of current velocity were not made during this study, but inferences concerning the effects of current on the distribution of C. milberti and C. menisorrah can be drawn from an analysis of the data on horizontal distribution. Laevastu and Avery (1964) report that currents are strong around the major points of Oahu and relatively weak in the intervening areas. Fig. 23 shows that C. milberti was least abundant in the areas on either side of Makapuu Point and Kahuku Point (areas 8, 9, 14 and 15). The species was abundant in areas 2 and 3 which encompass Barbers Point, but when setting in these areas, an effort was made to fish well away from the point because strong currents were encountered here during the first circuit of standard fishing which resulted in displaced and tangled gear. Currents are relatively weak in areas 1, 4 and 10 where C. milberti was abundant. Thus, evidence from the Oahu distribution of C. milberti suggests the species is relatively abundant in areas where currents are weak and uncommon where currents are strong.

Data concerning the relationship between current velocity and the

distribution of C. menisorrah are lacking except for general observations. The species is abundant off the northern end of Niihau where currents are strong. At Eniwetok, it is abundant in the deep channels between the lagoon and open ocean where strong tidal currents occur. C. menisorrah does not avoid areas where currents are strong and it may prefer such areas.

#### E. Bottom Characteristics

Warfel and Clague (1950) found that Galeocerdo is most commonly caught over a sandy bottom in the Philippine Islands. Galeorhinus australis is found over rough or foul bottom (Olsen, 1961), and Carcharhinus galapagensis prefers rugged terrain (Limbaugh, 1963). Bottom characteristics are also likely to influence the distribution of C. milberti and C. menisorrah which probably spend most of their lives within a few fathoms of the bottom.

Data on bottom characteristics are difficult to obtain, especially over a large area such as that covered by one or more sections of the longline used in the present study. With the exception of observations made while diving, there are no data on bottom composition under individual sets. Charts detailing this characteristic at depths of 10 to 100 fathoms do not exist for the Hawaiian Islands. However, fathometer traces depicting the bottom contour under each section of gear are available for analysis.

Two classes of bottom contour, smooth and rough, were arbitrarily defined from an examination of the fathometer traces for each section of longline gear. To qualify as "smooth" bottom, the depth trend (increasing or decreasing depth) must not reverse more than twice by an increment of 1 or more fathoms and the depth under the entire section must have a range no greater than 5 fathoms. To qualify as "rough" bottom, the cumulative depth change (increase plus decrease in depth) must total at least 10 fathoms for each of the 3 baskets in the section. Additionally, the traces for all baskets in the section must be similar before the bottom under a particular section is termed smooth or rough. This is to insure that the smooth or rough relief is extensive and not just an isolated area straddled by only a portion of the gear.

While diving, I observed 2 bottom types at Niihau which satisfy the above requirements for smooth bottom. The most extensive were expanses of flat sand over which were scattered a few live coral heads and pockets of coral rubble. This bottom was barren and supported a low biomass of fishes and larger invertebrates. The other type of smooth bottom at Niihau was a hard substratum of basalt. Macroscopic brown algae was usually abundant, and scattered about were live coral heads, small cracks, and some extensive areas of fine rubble, all of which served to increase the biomass. This hard substratum, however, was less extensive and occurred more often in shallower water (less than 15

fathoms).

Two types of rough bottom were also observed at Niihau. One consisted of a jumble of large boulders and low ledges on which grew widely scattered heads and patches of coral. This bottom supported a large population of fishes, but it did not occur extensively and was never observed at depths greater than 15 fathoms. The most common bottom of high relief around Niihau was basaltic and was composed of numerous ledges, canyons and steep drop-offs with sandy channels and patches at the bottom. Coral was abundant, especially in the shallower areas, and fishes and larger invertebrates were numerous. Most of the C. menisorrah observed were over this kind of bottom. The bottom around Kaula, where C. menisorrah was observed in greatest numbers, was similar to this. Basaltic ledges and canyons extend to depths of at least 40 fathoms in some areas off Niihau, especially around the northern end. Molokini, a nursery area for C. menisorrah, is known for its underwater cliffs and steep drop-offs covered with live coral. The bottom off Kahoolawe in the area where C. menisorrah was caught is also rugged.

The fathometer traces from the 17 Niihau sets made parallel to shore were examined in an attempt to distinguish between the bottom preferences of C. milberti and C. menisorrah. Fifteen sections were found which satisfied the requirements for smooth bottom. Twenty C. milberti and 20 C. menisorrah were caught on these sections. Only 4 sections satisfied the requirements for rough bottom. Two C. milberti

and 7 C. menisorrah were captured on these. When the data are converted to catch-per-unit-effort, both species averaged 1.33 individuals caught per section set over smooth bottom. Over rough bottom C. menisorrah was more numerous (1.75/section) while C. milberti was less numerous (0.50/section). The catch ratios over smooth and rough bottom do not differ significantly for either species. It is unfortunate that more sets were not made over rough bottom because a larger sample size might have revealed a significant difference.

Comparison of the mean depth of capture for C. milberti at Niihau, Kaula and Kahoolawe with other Hawaiian areas also suggests a relationship between this species and smooth bottom. Though differences were not significant, the preferred depths of each of the sex-maturity groups captured on perpendicular sets of the longline gear (mature males, mature females and sub-adults) were 7 to 9 fathoms deeper in areas where they are sympatric with C. menisorrah than in areas where C. menisorrah does not occur. One explanation for the above is that shoaler depths have a rougher terrain in areas frequented by C. menisorrah and that smooth bottom occurs in relatively deeper water.

The relationship between C. menisorrah and rugged bottom contour holds for juveniles more often than for adults and may be a necessary characteristic of a nursery area. During the latter part of

the shark program, we always tried to find a ledge when anchoring at Niihau in preparation for a night of handlining for sharks, because experience had shown that juvenile C. menisorrah were most often associated with bottom of high relief. Juveniles were caught (with one exception) only around the northern end of Niihau. Much of the bottom in this area falls under the rough classification as defined above. There is little rough bottom around the southern half of Niihau and only one juvenile was captured there. Juveniles were also abundant at the edge of the drop-off at Molokini and over the rugged bottom at Kaula.

The association with rough bottom also holds for juvenile C. menisorrah at Eniwetok. Only adults and sub-adults were found inside the lagoon where the bottom is mostly flat and sandy with an occasional patch-coral reef jutting up toward the surface. Juveniles occurred outside the lagoon in the deeper portions of surge channels where the bottom is hard and of rugged relief and along the often vertical submarine cliffs.

Most of the bottom around the larger Hawaiian Islands is flat and sandy. Though there are numerous exceptions (e.g., the area around Moku Manu Island and Kaena Point, Oahu), a major portion of this bottom would fit into the smooth category as defined above. C. milberti is the most abundant shark in all of these relatively smooth areas. Most of the bottom along the north and east coasts of Oahu where the nursery areas of C. milberti are located is smooth. Analysis of the faunal

composition of the diet of C. milberti (Chapter VII) yields further evidence for the association with smooth bottom.

Atlantic C. milberti also prefer a smooth bottom. Along the eastern coast of the United States, the species "is ordinarily not common in areas of coral reefs or where the bottom is rough" according to Springer (1960).

Composition of the substratum is correlated with bottom relief. Rugged bottom is generally hard consisting of coral or basalt. Level bottom may be hard or soft. When visual observations were possible, it was usually found to consist mostly of soft sand or mud.

The surface area of the smooth bottom within the preferred depth range of C. milberti may also influence distribution. From a map of Oahu, the following average distances between the 10- and 100-fathom depth contours were calculated for each coast: north, 3,575 m; south, 1,475 m; east, 2,511 m; and west, 998 m. An analysis of variance revealed that the mean distances (and, therefore, the surface areas) differ significantly ( $P$  less than .005). When the means for the north and east coasts are combined and compared with the combined means for the south and west coasts, the difference is even more significant ( $P$  less than .001). Juvenile C. milberti were caught only along the north and east coasts. An expansive shallow area, thus may also be a requisite for a C. milberti nursery area.

## CHAPTER VII.

### BIOLOGICAL FACTORS AFFECTING DISTRIBUTION

#### A. Competition

##### 1. General

Interspecific competition may be a widely occurring phenomenon in the natural environment and probably limits the population size and distribution of many species. The literature on competition among sharks is meager. Backus, et al. (1956) believe the offshore distributions of Galeocerdo cuvieri, and other large carcharhinids in the warmer regions of the Atlantic, are limited by the range of Carcharhinus longimanus. When C. longimanus migrates south in the winter in response to a cooler temperature, G. cuvieri extends its range to include part of the offshore environment occupied by C. longimanus during the warmer months. Strasburg (1958) studied pelagic sharks in the Pacific and found Carcharhinus falciformis to be common near shore and C. longimanus to be more common offshore though they both eat the same food. He concluded that C. falciformis has a competitive advantage because it is a faster swimmer and, thus, better able to catch small fish and squid. This ability enables it to exclude C. longimanus to the more offshore areas where food is not as plentiful.

Larkin (1956) defines competition as the "demand of more than

one organism for the same resource which is in limited supply." For sharks, either space or food could be limiting. Observations of territorial defense may indicate that space is a factor. Rapson (1961) states "Sharks may develop a proprietary right to certain areas of water...and some brushing attacks of sharks are probably of this proprietary type." Nelson (1969b) reports that unusual swimming postures, particularly for C. menisorrah and a hammerhead, have been noted by divers just prior to attack. He says "These postures are distinctly different from the shark's normal swimming posture and, in some respects, appear similar to the "threat" postures displayed by certain fishes during courtship and territorial defense."

I have no data indicating that sharks are territorial or that space is limiting in any way. Food is the most likely resource in limited supply. The distribution of C. milberti and C. menisorrah may be influenced by competition with other inshore sharks so the discussion will be broadened to include these species.

## 2. Stomach-Content Analysis

Five members of the family Carcharhinidae commonly occur in inshore Hawaiian waters at depths of less than 50 fathoms. In order of abundance (from catch records) they are: Carcharhinus milberti, Galeocerdo cuvieri, C. galapagensis, C. menisorrah, and C. limbatus. All are fairly large sharks maturing at total lengths of about 150 cm or

more and all are strictly carnivorous and, thus, potential competitors for food. Stomach contents of each species were examined to determine the extent of overlap in diet. A summary of these data is presented in Table 7. Because space does not permit a detailed list, the food items are grouped into larger categories for simpler comparison. Appendix E furnishes a complete list of the genera and species of prey found in the stomachs of each species. The data, especially the percentages of empty stomachs, are biased to the extent that they were gathered only from sharks hungry enough to take a baited hook.

The diet of Galeocerdo cuvieri differs markedly from the other 4 species. It is highly variable and includes several unique items. The other carcharhinids are primarily piscivorous, but fish make up only about half the diet of G. cuvieri. It eats fewer cephalopods, but more crustaceans, especially large ones like spiny and slipper lobsters. It also eats sharks, turtles, birds, cetaceans, and terrestrial mammals (which have probably fallen or washed into the sea). Other inshore sharks eat few or none of these items. The numerous indigestible items (cardboard, sticks, plastic bags, tin-foil, etc.) also attest to the indiscriminant food habits of G. cuvieri.

Only minor differences exist between the diets of the 4 members of the genus Carcharhinus. All eat mostly fish and some cephalopods. Considerably more than half of the stomachs of each species were empty.

Little can be said about the diet of Carcharhinus limbatus because

TABLE 7. -- Stomach contents of Hawaiian Galeocerdo cuvieri, Carcharhinus limbatus, C. galapagensis, C. milberti and C. menisorrhah. Number of individuals is enclosed in parentheses. The percentages listed in the body of the table are number of stomachs containing the listed food item times 100, divided by the number of stomachs containing food.

	<u>G. cuvieri</u>	<u>C. limbatus</u>	<u>C. galapagensis</u>	<u>C. milberti</u>	<u>C. menisorrhah</u>
Number examined	(210)	(27)	(155)	(541)	(92)
Empty stomachs	(29) 14%	(22) 81%	(90) 58%	(298) 55%	(65) 71%
Stomachs containing food	(181) 86%	(5) 19%	(65) 42%	(243) 45%	(27) 29%
Food Items					
Fish	(90) 50%	(5) 100%	(46) 71%	(170) 70%	(25) 93%
Large Fish <sup>a</sup>	(55) 30%	(1) 20%	(14) 22%	(36) 15%	(7) 26%
Small Fish <sup>b</sup>	(28) 15%	(3) 60%	(21) 32%	(114) 47%	(15) 56%
O. Tetraodontiformes	(64) 35%	(1) 20%	(7) 11%	(11) 5%	(1) 4%
O. Anguilliformes	(6) 3%	(1) 20%	(3) 5%	(12) 5%	- -
O. Perciformes	(12) 7%	- -	(13) 20%	(42) 17%	(4) 15%

<sup>a</sup> Total length greater than 30 cm (1 foot)

<sup>b</sup> Total length less than 30 cm (1 foot)

TABLE 7. -- (Continued) Stomach contents of Hawaiian sharks.

	<u>G. cuvieri</u>	<u>C. limbatus</u>	<u>C. galapagensis</u>	<u>C. milberti</u>	<u>C. menisorrhah</u>
Crustacean	(47) 26%	- -	(6) 9%	(44) 18%	(1) 4%
Spiny lobster	(24) 13%	- -	- -	(2) 1%	- -
Slipper lobster	(21) 12%	- -	(2) 3%	(3) 1%	- -
Crab	(5) 3%	- -	- -	(7) 3%	- -
Shrimp	- -	- -	(1) 2%	(5) 2%	- -
Stomatopod	(1) 1%	- -	(2) 3%	(15) 6%	- -
Cephalopod	(20) 11%	(1) 20%	(18) 28%	(66) 27%	(5) 19%
Ray	(7) 4%	- -	(3) 5%	(3) 1%	- -
Shark	(19) 10%	- -	(2) 3%	(5) 2%	- -
Turtle	(20) 11%	- -	- -	- -	- -

TABLE 7. -- (Continued) Stomach contents of Hawaiian sharks.

	<u>G. cuvieri</u>	<u>C. limbatus</u>	<u>C. galapagensis</u>	<u>C. milberti</u>	<u>C. menisorrah</u>
Bird	(42) 23%	- -	- -	- -	- -
Cetacean	(13) 7%	- -	(1) 2%	- -	- -
Terrestrial mammal	(38) 21%	- -	(1) 2%	(1) 1%	- -
Indigestible items	(32) 18%	- -	(2) 3%	(2) 1%	- -

few were captured and a high percentage of those that were had empty stomachs. That it primarily eats fish is indicated by Baughman and Springer (1950) and Clark and von Schmidt (1965) for specimens caught in the Gulf of Mexico.

Distinctive characteristics of the diet of Carcharhinus galapagensis are primarily correlated with the larger size of this species. C. milberti and C. menisorrah mature at precaudal lengths of 100 to 115 cm while C. galapagensis matures at a precaudal length of about 165 cm. A greater proportion of its diet consists of large fish and it eats more tetraodontiforms (especially Diodon hystrix), sharks, rays, and cetaceans. Excepting the generally larger size of its prey, the diet of C. galapagensis is similar to that of C. milberti.

There is a significant difference in the relative number of empty stomachs (P less than .01 using Chi-square in a 2 x 2 contingency table) between C. milberti (298/541, or 55%) and C. menisorrah (65/92, or 71%).

C. menisorrah appears to eat more fish than C. milberti though the difference is not significant. Of the stomachs that were not empty, 93% of the C. menisorrah and 70% of the C. milberti stomachs held fish remains. Both species eat mostly small fish, especially common reef fishes of the order Perciformes. Further breakdown of the perciforms into family, genus and species reveals no particular preferences for either shark.

C. milberti appears to eat more crustaceans and cephalopods than C. menisorrah, though again, the difference is not significant. The bulk of the crustacean remains which could be identified from C. milberti stomachs were large stomatopods. Only one C. menisorrah was caught with crustacean remains in its stomach and they could not be identified.

Stomach-content data from C. menisorrah captured at Eniwetok, Johnston, Palmyra, Fanning, and Marcus are listed in Table 8. The data from these areas are consistent and, when combined, are similar to those from Hawaii.

Diets of sharks are related to their distribution and feeding behavior. C. menisorrah eats relatively more fish (most of which swim above the bottom) while C. milberti eats more crustaceans and cephalopods (primarily benthic). This suggests that C. milberti frequently feeds on organisms in contact with the bottom while C. menisorrah tends to feed on organisms in the water column.

Large stomatopods comprised the greatest proportion of identifiable crustaceans found in the stomachs of C. milberti. Townsley (1953) characterizes the typical habitat of Lysiosquilla maculata (the probable identity of the stomatopod) as soft sand or mud. This correlates with evidence presented in Chapter VI that C. milberti tends to frequent more level, and in most cases, softer bottom than C. menisorrah.

TABLE 8. -- Stomach contents of Carcharhinus menisorrh from Pacific areas other than Hawaii. Number of individuals is enclosed in parentheses. The percentages listed in the body of the table are number of stomachs containing the listed food item times 100, divided by the number of stomachs containing food.

	Eniwetok	Johnston	Fanning & Palmyra	Marcus	All areas combined
Number examined	(87)	(18)	(47)	(5)	(157)
Empty stomachs	(67) 77%	(12) 67%	(33) 70%	(3) 60%	(115) 73%
Stomachs containing food	(20) 23%	(6) 33%	(14) 30%	(2) 40%	(42) 27%
<hr/>					
Food Items					
<hr/>					
Fish	(20) 100%	(6) 100%	(12) 86%	(2) 100%	(40) 95%
Large fish <sup>a</sup>	(6) 30%	(2) 33%	(1) 7%	(1) 50%	(10) 25%
Small fish <sup>b</sup>	(10) 50%	(3) 50%	(1) 7%	(1) 50%	(15) 38%
O. Tetraodontiformes	- -	(1) 17%	- -	- -	(1) 3%
O. Anguilliformes	- -	- -	- -	(1) 50%	(1) 3%

<sup>a</sup> Total length greater than 30 cm (1 foot)

<sup>b</sup> Total length less than 30 cm (1 foot)

TABLE 8. -- cont.

	Eniwetok	Johnston	Fanning & Palmyra	Marcus	All areas combined
O. Perciformes	(8) 40%	- -	- -	(1) 50%	(9) 21%
Cephalopod	- -	- -	(1) 7%	- -	(1) 3%
Garbage	- -	- -	(1) 7%	- -	(1) 3%

Observations regarding the food habits of Hawaiian C. milberti agree with those of Springer (1960) who states more concisely that the species "is a discriminating feeder; that it is a bottom feeder; and that it feeds on small bottom fish and invertebrates rather than the large ones."

Field observations, as well as those of sharks in captivity, support the hypothesis that C. milberti feeds on or very close to the bottom while C. menisorrah feeds higher in the water column. While handlining for sharks at night, juvenile C. menisorrah were often observed swimming near the surface and were caught on handlines with the baits dangling just under the boat, 15 to 20 fathoms above the bottom. C. milberti, however, was seldom observed on the surface and only a very few juveniles were caught there.

In the tank at Kewalo Basin, C. milberti generally swam right on the bottom with the lower lobe of its caudal almost touching the substratum. C. menisorrah, however, cruised 40 to 50 cm off the bottom. Experiments to determine if C. menisorrah has a tendency to feed nearer the surface than C. milberti were inconclusive--possibly because of the narrow depth range (1.5 m) of the tank.

### 3. Bait Preferences

Bait preference studies yielded information perhaps related to diets. Sharks were offered a choice between baits placed on alternate hooks and records were kept of the baits on which each species was

caught.

When skipjack tuna was paired with chunks of porpoise, Steno (Table 9A), C. milberti showed a significant preference for tuna ( $P=.04$ ) while Carcharhinus galapagensis showed a highly significant preference for porpoise ( $P$  less than .005). These results are consistent with stomach-content data. Unfortunately, this choice was not offered at Kaula, Niihau or Kahoolawe so there is no information on the reaction of C. menisorrah to porpoise.

The data in Table 9B and 9C are based on 11 sets during which a variety of baits was used. No single bait pair yielded sufficient data for analysis so several pairs were combined. Skipjack and Kawa-kawa, Euthynnus yaito, were given equal status as one member of the bait pair and termed "tuna." Both are relatively fast swimmers and inhabit the more pelagic waters so are unlikely to be preyed upon frequently by inshore sharks. The other choice was termed "inshore fish." These were fish caught incidentally while fishing for sharks and while spearfishing. The species used most often were jacks (Caranx sexfasciatus and C. melampygu), barracuda (Sphyraena barracuda), squirrelfish (Myripristis spp), moray eels (Gymnothorax spp), parrotfish (Scarus spp), and snappers (Pristiopomoides microlepis and Aprion virescens). On some of the sets, the inshore-fish member of the bait pair consisted of only one species. Usually, 2 or more species were

TABLE 9. -- Number of sharks caught on the listed baits when offered a choice between the two. (Chi-square values are corrected for continuity.)

A. Skipjack vs. Porpoise

	Skipjack	Porpoise	Chi-square
<u>Carcharhinus milberti</u>	10	2	4.08*
<u>Carcharhinus galapagensis</u>	1	13	8.64*

B. Tuna vs. Inshore fish (both choices fresh or fresh frozen)

	Tuna	Inshore Fish	Chi-square
<u>Carcharhinus milberti</u>	17	25	1.16
<u>Carcharhinus menisorrah</u>	6	11	.94
<u>Carcharhinus galapagensis</u>	4	7	.36

C. Tuna vs. Inshore Fish (stale tuna)

	Tuna	Inshore Fish	Chi-square
<u>Carcharhinus milberti</u>	17	15	-
<u>Carcharhinus menisorrah</u>	1	12	7.69**
<u>Carcharhinus galapagensis</u>	8	16	2.04

used because not enough of one was available.

Most sharks prefer fresh food to that which is stale or decaying (Springer, 1960). For this reason the data used in the comparison between tuna and inshore fish were divided into 2 groups: one in which both choices were fresh or fresh frozen (5 sets) and the other in which the tuna had become stale (6 sets). The only significant preference was that shown by C. menisorrhah for inshore fish when it was fresher than tuna. Though other differences were not significant, both C. menisorrhah and Carcharhinus galapagensis were captured more often on inshore fish than on tuna even when the choices were equally fresh. Therefore, it seems likely that both species prefer inshore fish to tuna. The results of this comparison for C. menisorrhah and C. galapagensis verify Springer's observation that sharks prefer fresh food because preferences for inshore fish were more pronounced when stale tuna was the other member of the bait pair.

When the choices were of equal freshness, C. milberti too seemed to prefer inshore fish. However, this preference was not shown when inshore fish was fresher than tuna.

Other bait pairs were offered in 4 additional sets (Table 10), but the only species caught in substantial numbers were C. milberti and Galeocerdo cuvieri. When skipjack was compared with whole cats in 2 sets, the 3 C. milberti captured were taken on skipjack while 8 of the 13 G. cuvieri were caught on cats. Fresh akule, frozen squid and

TABLE 10. -- Number of sharks caught on the listed baits when offered a choice between the two. (Chi-square values are corrected for continuity.)

Skipjack vs. Cat

	Skipjack	Cat	Chi-square
<u>Carcharhinus milberti</u>	3	-	1.33
<u>Galeocerdo cuvieri</u>	5	8	.30

Akule vs. Shark Chunks<sup>a</sup>

	Akule	Shark	Chi-square
<u>Carcharhinus milberti</u>	11	1	4.07*
<u>Galeocerdo cuvieri</u>	1	5	2.83

<sup>a</sup> Squid was also used as bait on these sets and the number of hooks holding each bait were uneven--hence the peculiar chi-square values.

chunks of fresh shark were compared in 2 other sets. A significant preference for akule was shown by C. milberti while G. cuvieri was caught most often on shark chunks. These results are consistent with the stomach-content analysis and indicate that overlap in food preferences of C. milberti and G. cuvieri is not great.

#### 4. Feeding Adaptations in Tooth Structure

A correlation between diet and tooth structure exists for the 5 species of sharks whose stomach contents were examined. The upper teeth of these species are illustrated in Fig. 30.

Galeocerdo cuvieri has similar teeth in both the upper and lower jaws. These sturdy teeth are deeply notched and arranged in a single functional band in both jaws. This arrangement and tooth structure is particularly well adapted for sawing off chunks of food. Much of its diet was found to consist of large items which must be cut into pieces and which are often quite hard (turtle shells, mammal bones, large crustaceans).

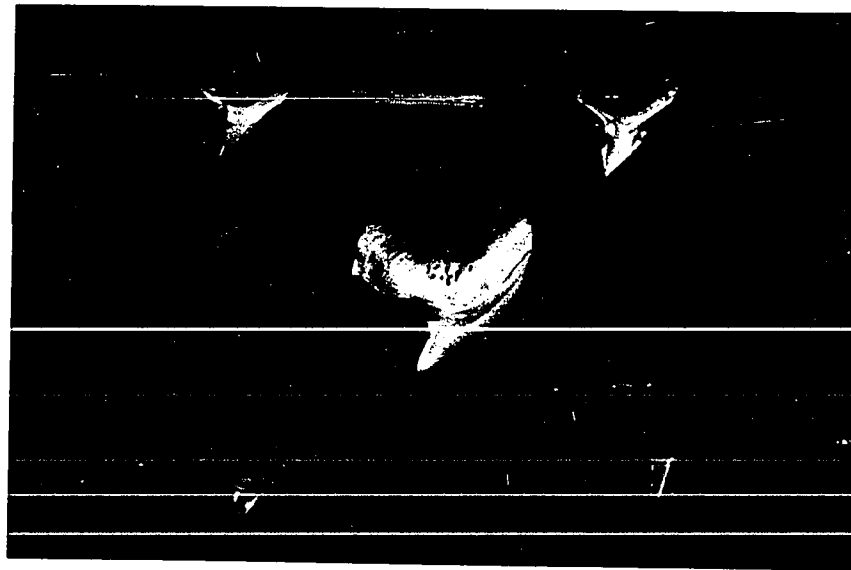
The other 4 species have dissimilar teeth in the upper and lower jaws. The lower teeth of all 4 are adapted for grasping. They are broad-based, but narrow quickly to a thin, sharply pointed spike directed towards the interior of the mouth. The teeth in the upper jaw are arranged in a single band adapted for cutting and are unique for each Hawaiian member of the genus Carcharhinus. All are bladelike,

Figure 30. Upper teeth (fourth series) of inshore Hawaiian carcharhinids. From left to right and starting at the top, the teeth belong to Carcharhinus milberti, C. galapagensis, Galeocerdo cuvieri, C. menisorrh, and C. limbatus. A. anterior view  
B. posterior view.

A



B



but they range from narrowly to broadly triangular. C. limbatus and C. menisorrah possess narrowly triangular teeth in their upper jaw. They are broad-based but the cusp is narrow and sharply pointed with numerous serrations. The upper teeth of C. galapagensis and C. milberti are broadly triangular and bordered with serrations. Minor differences in shape and serration pattern enable one to differentiate between the members of the narrowly triangular and broadly triangular pairs.

The 4 members of the genus Carcharhinus prey on generally smaller and softer animals than does Galeocerdo cuvieri. Though comparisons show no statistically significant differences, the percentages in Table 7 indicate that C. galapagensis and C. milberti, which have sturdy, broadly triangular upper teeth, prey more heavily on crustaceans which have hard shells and that C. limbatus and C. menisorrah, with narrowly triangular teeth in the upper jaw, tend to restrict their diets to cephalopods and fish which are softer.

Differences in tooth structure, thus, may serve to reduce competition. However, dietary differences as indicated by stomach-content and bait-preference analysis are not great and it might still be argued that competition is occurring provided the food resource is limited.

##### 5. The Food Resource--Limited or Unlimited?

Reef fishes are numerous and sharks are frequently surrounded

by them. But are they really "available" in the sense that they can be readily preyed upon? Healthy fish of most species are quicker and more maneuverable than sharks and, therefore, difficult to catch. Many remain near the shelter of coral or rocky crevices into which they can escape if threatened. Only dead, injured or moribund fishes are easily captured, and it is prey of this type for which the sensory systems of sharks seem particularly adapted. Hobson (1963) reports that sharks are able to track down wounded fish at some distance by following an olfactory corridor and that rapid, erratic movement excites and attracts them. Their hearing is most sensitive to pulsed sounds at frequencies similar to those produced by wounded or struggling fish (Nelson, 1969a). Sharks are able to detect fish under stress purely by olfaction (Tester, 1963).

Observations made of the captive sharks at the Kewalo facility indicate they do not often prey upon healthy fish. On numerous occasions live fish were released into the tank. If they swam in an erratic manner or were slightly injured, they were immediately attacked and eaten. If they were healthy and swam normally, they remained unmolested except on rare occasions when the sharks were already excited by the presence of food. Under these circumstances, a shark would sometimes snap at a healthy fish, perhaps mistaking it for the source of the olfactory stimulus. Each time such an incident was observed, however, the fish proved more agile than the shark and escaped harm.

The diet of sharks is, of course, not restricted to wounded and moribund fishes. Bullis (1961) observed numerous Carcharhinus longimanus feeding on schools of small tuna on one occasion and, at a later date, a single individual biting off mouthfuls of fish from a densely packed ball of threadfin shad. Eibl-Eibesfeldt and Hass (1959) reported seeing Carcharhinus melanopterus and C. menisorrhah herding healthy fishes against a shoreline to facilitate capture. C. milberti and C. menisorrhah are probably opportunistic feeders. They prey on sick or injured organisms whenever they are encountered. In situations where capture is feasible (e. g. when the prey is sleeping or otherwise exposed) they also prey on healthy animals. If unhealthy and injured fish are the usual prey of sharks, the food supply may be limiting. Certainly, they occur uncommonly, though there is no way to measure their abundance.

Springer (1967) feels that sharks get plenty to eat and argues that sharks store food reserves in their livers which usually comprise 10 to 25% of the weight of large sharks. Sharks with livers as large as these must be well fed. In the light of Springer's argument, livers of C. milberti and C. menisorrhah were weighed. Juveniles were found to have relatively small livers comprising only about 3% of their body weight. The livers of the largest adults, however, comprised 9% (C. milberti) to 12% (C. menisorrhah) of the body weight. Adult C. menisorrhah generally had heavier livers (even though a greater percentage of this species had empty stomachs) than adult C. milberti of comparable size

and mature females of both species had slightly heavier livers than males of equal size. There is wide variation in liver size for individuals of the same size and sex, especially among the larger sharks.

The livers of the 2 species under consideration in this study are at the low end of the 10 to 25% range found by Springer (1967). Nevertheless, they seem large enough to indicate that both acquire an adequate amount of food.

#### 6. Distribution of Hawaiian Sharks

Hobson (1963) found Carcharhinus melanopterus to be common in the shallow waters of the reef flats and lagoon of Eniwetok at depths of 0.2 to 8 fathoms. C. menisorrah is most abundant in deeper areas of the lagoon and along the outer reef slope. These are typical habitats for the 2 species throughout the Pacific where their distribution is sympatric. At Johnston, however, where there are no C. melanopterus, C. menisorrah frequents the very shallow water over the reef flats at depths in which it is never found at Eniwetok. Adults were caught at depths of less than 0.5 fathoms and juveniles were captured inside the lagoon in water as shallow as 2 fathoms. Randall (pers. comm.) observed a similar depth distribution for C. menisorrah at Marcus Island which also lacks C. melanopterus. These observations indicate that C. menisorrah can and does occupy the very shallow waters inside lagoons and on reef flats, but is usually restricted from doing so by the

presence of C. melanopterus which must, therefore, be the better shallow-water competitor.

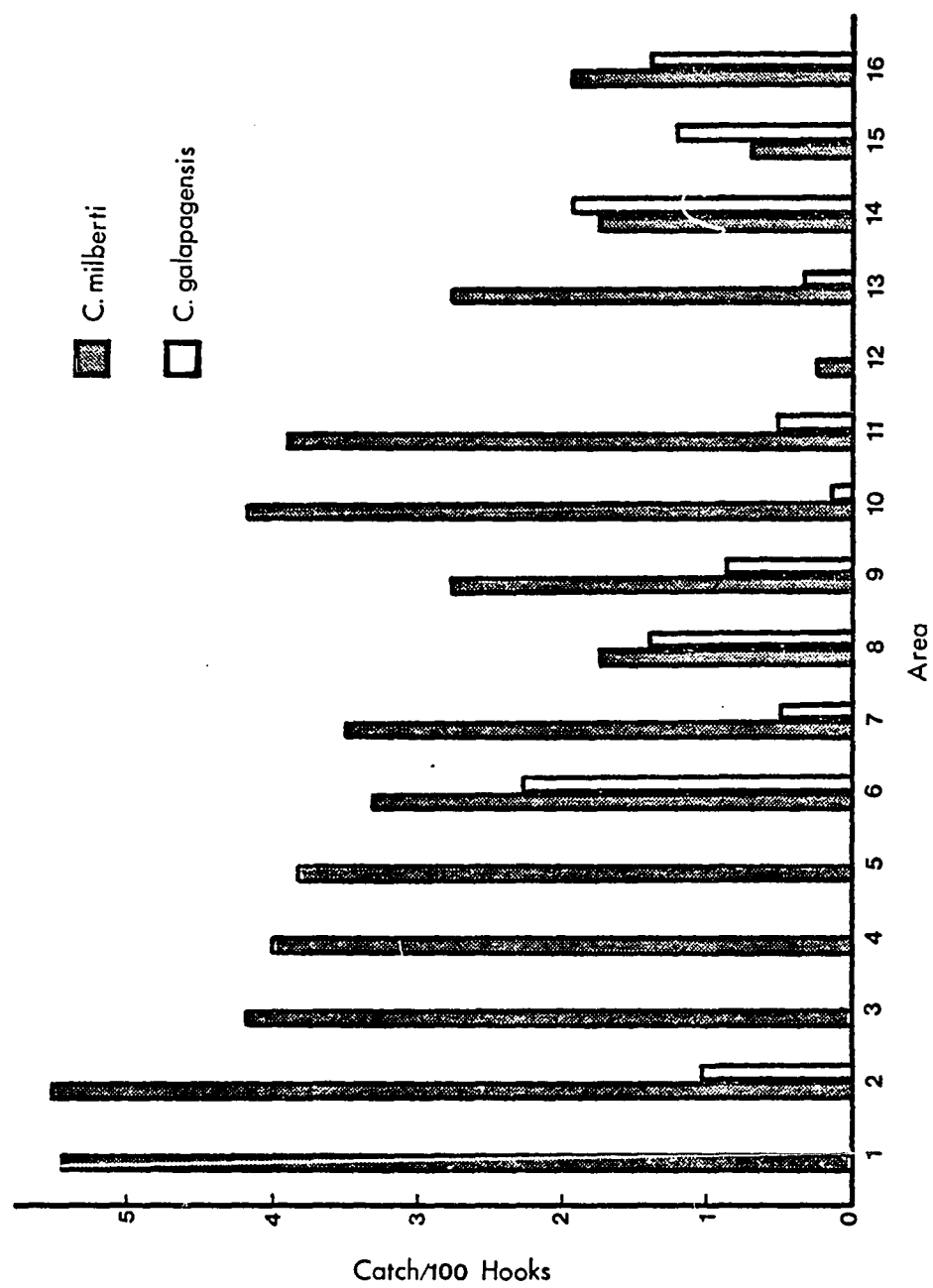
The distribution of C. milberti at Niihau may also be influenced by competition though the evidence is not as unequivocal as in the above instance. It was noted in Chapter IV that the catch-per-unit-effort for C. milberti was significantly greater off the windward coast of Niihau. For Oahu, however, the catch-per-unit-effort was significantly greater in leeward areas. There are no data concerning the coastal preferences of C. milberti around other Hawaiian Islands so it is unknown whether competition with C. menisorrhah has displaced a large portion of the C. milberti population to the windward side of Niihau or if other factors (e.g., bottom composition) are responsible.

Carcharhinus limbatus and Carcharhinus galapagensis have diets similar to C. milberti and C. menisorrhah and can be classed as potential competitors. In Hawaii C. limbatus is relatively uncommon. It is most abundant in the more sheltered areas on the lee sides of the larger islands and in places like Kaneohe Bay, and is generally found over sandy or coral encrusted bottom of low relief. Thus, its distribution does not broadly overlap that of C. menisorrhah. While C. limbatus is often geographically sympatric with C. milberti, it is generally found at shallower depths (5 to 30 fathoms) resulting in a relatively allopatric distribution.

Little can be said about competition between C. menisorrah and Carcharhinus galapagensis which has a ubiquitous Hawaiian distribution but is particularly abundant at Kaula and Niihau. The species is widely distributed throughout the Pacific and the Atlantic and appears to prefer the coasts of oceanic islands (Garrick, 1967). Limbaugh (1963) states that C. galapagensis prefers clear water and rugged terrain which is compatible with observations at Kaula and Niihau. One habit separates this species from the other inshore members of the genus Carcharhinus in Hawaii. It is often found near the surface over very deep water. One experimental set at Niihau was made in water deeper than 100 fathoms with the hooks fishing near the surface. The entire catch consisted of 5 C. galapagensis. This shark is also caught occasionally by fishing boats trolling on the surface for marlin, tuna, etc. several miles offshore.

Because Carcharhinus galapagensis is the third most abundant shark in Hawaii, its Oahu distribution is well known. The histogram comparing the abundance of C. galapagensis and C. milberti around Oahu (Fig. 31) shows that where one species is abundant, the other occurs in relatively low numbers. The negative correlation was found to be significant ( $P=.02$ ) when Spearman's rank correlation coefficient was calculated. The data indicate that C. galapagensis prefers rugged terrain and areas where currents may be strong because it is most common around Kaena Point, Makapuu Point, and Kahuku Point. Thus,

Figure 31. Catch/100 hooks for Carcharhinus milberti and Carcharhinus galapagensis in the 16 areas around Oahu based on 8 circuits of standard fishing.



while C. milberti and C. galapagensis are both common around Oahu, they tend to occupy different habitats. It is unknown if this is the result of competitive displacement. There is no large area or island in Hawaii occupied by only one of the species where we could see if its habitat preferences were widened to include those of the other species. The distribution might also be the result of predation by C. galapagensis on C. milberti. This possibility will be discussed below, but it is probable that the observed distributions are merely the result of preferences for different physical factors.

#### 7. Intraspecific Differences in Diet

To this point, the discussion has been confined to interspecific competition. Competitive relationships between sex-maturity groups within a species are also important and may be partly responsible for differences in their depth distribution. Diets among sex-maturity groups are now examined for similarities and differences.

There are sufficient data for comparison of the diets of mature C. milberti males and females (Table 11). Chi-square tests using 2 x 2 contingency tables revealed that significantly fewer males with empty stomachs were captured (P less than .02) and that they ate a greater proportion of crustaceans (P less than .02). There were no major differences in the fish species composition of the diets.

Stomach content data for C. milberti were also broken down

TABLE 11. -- Stomach contents of mature Hawaiian Carcharhinus milberti. Number of individuals is enclosed in parentheses. The percentages listed in the body of the table are number of stomachs containing the listed food item times 100, divided by the number of stomachs containing food.

	Males	Females
Number examined	(100)	(189)
Empty stomachs	(45) 45%	(115) 61%
Stomachs containing food	(55) 55%	(74) 39%
<hr/>		
Food items		
<hr/>		
Fish	(36) 65%	(58) 79%
Large fish <sup>a</sup>	(14) 25%	(13) 18%
Small fish <sup>b</sup>	(20) 36%	(33) 45%
O. Tetraodontiformes	(4) 7%	(5) 7%
O. Anguilliformes	(3) 5%	(5) 7%
O. Perciformes	(9) 16%	(16) 22%

<sup>a</sup> Total length greater than 30 cm (1 foot)

<sup>b</sup> Total length less than 30 cm (1 foot)

TABLE 11. -- cont.

	Males	Females
Crustacean	(14) 25%	(9) 12%
Spiny lobster	(1) 2%	(1) 1%
Slipper lobster	(2) 4%	- -
Crab	(1) 2%	(5) 7%
Shrimp	(3) 5%	- -
Stomatopod	(3) 5%	(1) 1%
Cephalopod	(12) 22%	(21) 29%

according to the 3 major maturity groups (Table 12). Juveniles appear to eat fewer fish and cephalopods than the matures and sub-adults, but more crustaceans, especially stomatopods. The fish they eat are smaller than those eaten by larger individuals.

The data (Table 13) used for comparing the diets of the maturity groups of C. menisorrah are rather sparse so the differences do not even approach the level of statistical significance. Adults appear to have a greater proportion of empty stomachs than younger individuals. Juveniles appear to subsist almost totally on fish while adults eat substantial numbers of cephalopods in addition to fish. Again, as would be expected, larger individuals tend to eat larger fish.

## B. Predation

### 1. Hawaiian Predators

Porpoises and sperm whales are known shark predators (Springer, 1967). Occasionally, smaller sharks are also eaten by large bony fishes. R. Brock (pers. comm.) found a whole Triaenodon obesus of about 65 cm total length in the stomach of a large moray eel, Gymnothorax javanicus. Other sharks, however, are the primary shark predators. Bigelow and Schroeder (1948) report finding sharks in the stomachs of Carcharodon carcharias. Springer (1967) found that the 5 largest sharks occurring in Florida's inshore waters commonly prey on other sharks.

TABLE 12. -- Stomach contents of the maturity groups of Hawaiian Carcharhinus milberti. Number of individuals is enclosed in parentheses. The percentages listed in the body of the table are number of stomachs containing the listed food item times 100, divided by the number of stomachs containing food.

	Matures	Sub-adults	Juveniles
Number examined	(289)	(211)	(41)
Empty stomachs	(162) 56%	(110) 52%	(25) 61%
Stomachs containing food	(127) 44%	(101) 48%	(16) 39%
<hr/>			
Food items			
<hr/>			
Fish	(93) 73%	(71) 70%	(9) 56%
Large fish <sup>a</sup>	(27) 21%	(9) 9%	- -
Small fish <sup>b</sup>	(52) 41%	(54) 53%	(9) 56%
O. Tetraodontiformes	(9) 7%	(2) 2%	- -
O. Anguilliformes	(8) 6%	(3) 3%	(1) 6%
O. Perciformes	(25) 20%	(13) 13%	(2) 13%

<sup>a</sup> Total length greater than 30 cm (1 foot)

<sup>b</sup> Total length less than 30 cm (1 foot)

TABLE 12. -- cont.

	Matures	Sub-adults	Juveniles
Crustacean	(23) 18%	(18) 18%	(4) 25%
Spiny lobster	(3) 2%	- -	- -
Slipper lobster	(3) 2%	- -	- -
Crab	(6) 5%	(2) 2%	- -
Shrimp	(3) 2%	(1) 1%	(1) 6%
Stomatopod	(4) 3%	(8) 8%	(2) 13%
Cephalopod	(33) 26%	(31) 31%	(1) 6%
Shark	(1) 1%	(3) 3%	- -
Ray	(3) 2%	- -	- -
Terrestrial mammal	(1) 1%	- -	- -
Garbage (inedible)	(3) 2%	- -	- -

TABLE 13. -- Stomach contents of the maturity groups of Hawaiian Carcharhinus menisorrah. Number of individuals is enclosed in parentheses. The percentages listed in the body of the table are number of stomachs containing the listed food item times 100, divided by the number of stomachs containing food.

	Matures	Sub-adults	Juveniles
Number examined	(36)	(18)	(39)
Empty stomachs	(29) 81%	(12) 67%	(24) 62%
Stomachs containing food	(7) 19%	(6) 33%	(15) 38%
<hr/> <b>Food items</b> <hr/>			
Fish	(5) 71%	(6) 100%	(14) 93%
Large fish <sup>a</sup>	(4) 57%	- -	(3) 20%
Small fish <sup>b</sup>	(1) 14%	(4) 67%	(10) 67%
O. Tetraodontiformes	(1) 14%	- -	- -
O. Anguilliformes	- -	- -	- -
O. Perciformes	(2) 29%	(1) 17%	(1) 7%
Crustacean	- -	- -	(1) 7%
Cephalopod	(3) 43%	(1) 17%	(1) 7%

<sup>a</sup> Total length greater than 30 cm (1 foot)

<sup>b</sup> Total length less than 30 cm (1 foot)

Sharks captured with shark remains in their stomachs are the primary source of data on shark predation in Hawaii. Other sources are catch records of sharks caught on hooks already holding another shark and sharks caught on hooks baited with shark flesh.

Stomach content analysis implicates the 2 largest inshore Hawaiian sharks, Galeocerdo cuvieri and Carcharhinus galapagensis as the major predators. Of the G. cuvieri stomachs that were not empty, 10.5% contained the remains of sharks (Table 7). If there was any question that the remains in the stomachs were of sharks eaten off the longline, the data were not used in calculating the above value so it is probably too low. Shark remains were also found in 3.1% of the C. galapagensis stomachs and 1.6% of the C. milberti stomachs. Larger samples would probably show that Carcharhinus limbatus and C. menisorrhah are occasional shark predators, too.

Several Galeocerdo cuvieri and Carcharhinus galapagensis were captured on longline hooks on which another shark had previously been caught ("sharkbait"). The commotion caused by a shark struggling on a hook is attractive and the fact that these hooked sharks are immobilized makes them easy prey. Of 210 G. cuvieri captured on the longline, 59 (28.1%) were caught with another shark head on the leader or with a head still attached to the hook in their stomach. C. galapagensis was the only other species taken on hooks fortuitously baited with live sharks. Of 155 individuals, 9 (5.8%) were captured on "sharkbait."

Two sets were made in the Molokai-Maui area employing chunks of shark, frozen squid, and fresh akule in a bait preference study. The apparent preference of Galeocerdo cuvieri for shark chunks ( $P=.09$ ; 5 of 6 caught on shark) was noted above.

It appears that smaller sharks are subject to the heaviest predation. Those found in stomachs generally had precaudal lengths ranging between 45 and 115 cm. Springer (1960) believes that adult C. milberti in Florida are subject to little predation because of their size. This is probably also true for adult C. milberti and C. menisorrah in Hawaii.

## 2. Effects of Interspecific Predation on Distribution

Springer (1960) feels that heavy predation by Carcharhinus leucas is responsible for the exclusion of C. milberti from the Gulf of Mexico. Adult C. leucas appear to prefer shark flesh to any other food and their optimal depth range is shallow enough to broadly overlap the nursery areas of C. milberti.

The distributions of Galeocerdo cuvieri and C. milberti around Oahu are quite similar. Both are most abundant between Diamond Head and Barbers Point (areas 1 and 2) and least abundant in Kaneohe Bay and off Sandy Beach (areas 12 and 15). Juveniles of both species are most numerous on the windward coast between Kaneohe Bay and Kahuku Point. Relative abundances differ mainly off the west coast between

Barbers Point and Kaena Point where G. cuvieri occurs infrequently. Because C. milberti is relatively abundant in the same areas as G. cuvieri, it is concluded that G. cuvieri does not have a restrictive effect on the horizontal distribution of C. milberti.

Carcharhinus galapagensis and C. milberti tend to have different habitat preferences. This, plus the fact that C. galapagensis is only an occasional predator on other sharks, leads to the conclusion that it probably does not influence the distribution of C. milberti.

There is an inverse relationship between the occurrence of Galeocerdo cuvieri and that of C. menisorrhah. At Niihau and Kaula G. cuvieri is uncommon. Less than 10% of the sharks caught there were of this species and it ranked only fourth in abundance. The catch-per-unit-effort for G. cuvieri is also low in these areas. Around the other Hawaiian Islands, however, G. cuvieri made up about 25% of the shark fauna and ranked second in abundance to C. milberti.

Predation could account for the scarcity of C. menisorrhah in areas where G. cuvieri is abundant but the distribution is more likely the result of different habitat preferences. G. cuvieri seems to prefer turbid areas around high islands where fresh-water runoff may be heavy and where currents are not strong. Many were caught along the leeward coast of Kauai, especially near the mouth of the Waimea River where the water is generally calm and often turbid. They are also abundant outside Kewalo Basin, Honolulu Harbor and Pearl Harbor.

There are sewage outfalls in these areas and garbage and dead fish wash out of the harbors and are thrown from ships as they enter the channels. G. cuvieri probably frequents habitats like these because of the abundance of food.

Since Carcharhinus galapagensis and C. menisorrah have peak abundances in the same areas, predation by C. galapagensis probably does not influence the distribution of C. menisorrah.

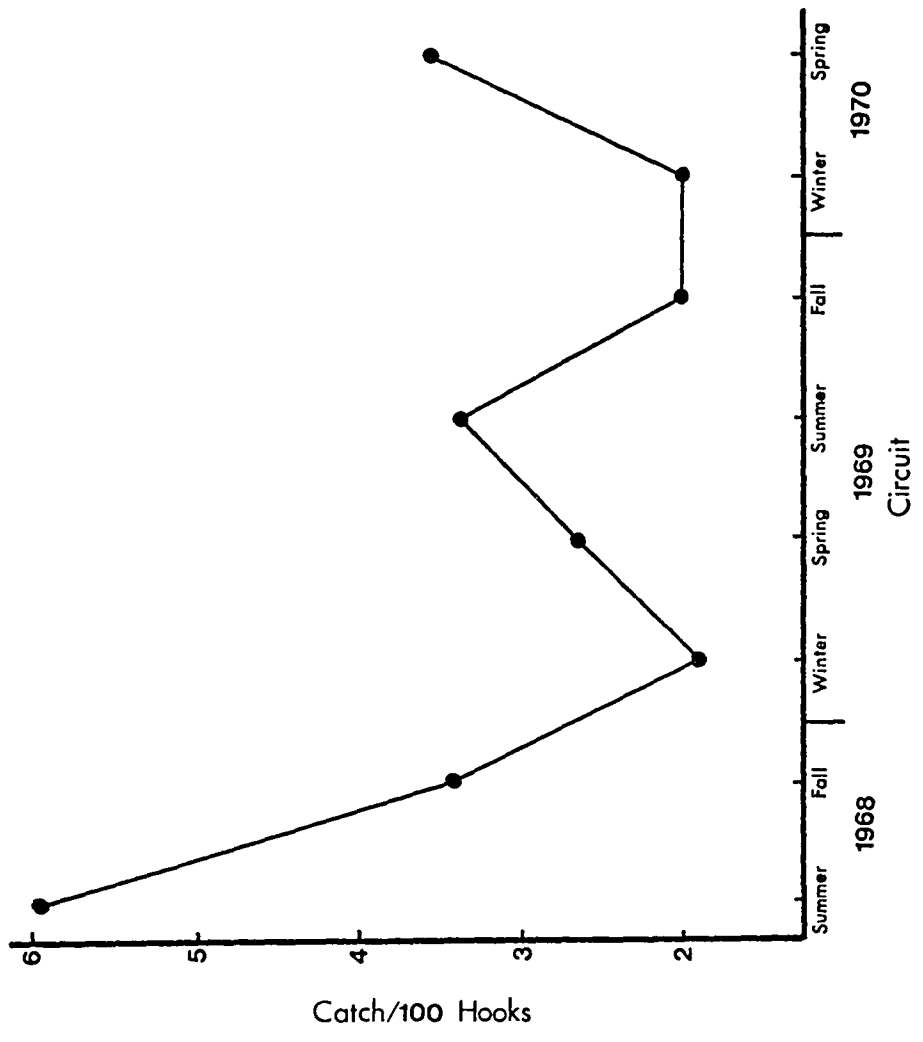
As a consequence of their distributions, it is concluded that Galeocerdo cuvieri is the primary predator of C. milberti. Because Carcharhinus galapagensis has the same habitat preferences as C. menisorrah, it may prey more heavily on C. menisorrah than does G. cuvieri. Although there is some evidence that predation is an important factor in the ecology of the study species, it probably does not limit their Hawaiian distribution.

### 3. Predation as a Limiting Factor

Springer (1967) thinks predation is responsible for limiting population size of the smaller (total length less than 175 cm) species of inshore sharks in the Florida region. The catch data indicate this may also hold for Hawaiian C. milberti.

Catch/100 hooks for C. milberti around Oahu showed an overall decline during the 8 circuits of standard fishing (Tester, 1969) which is illustrated in Fig. 32. The catch rate dropped initially and then came

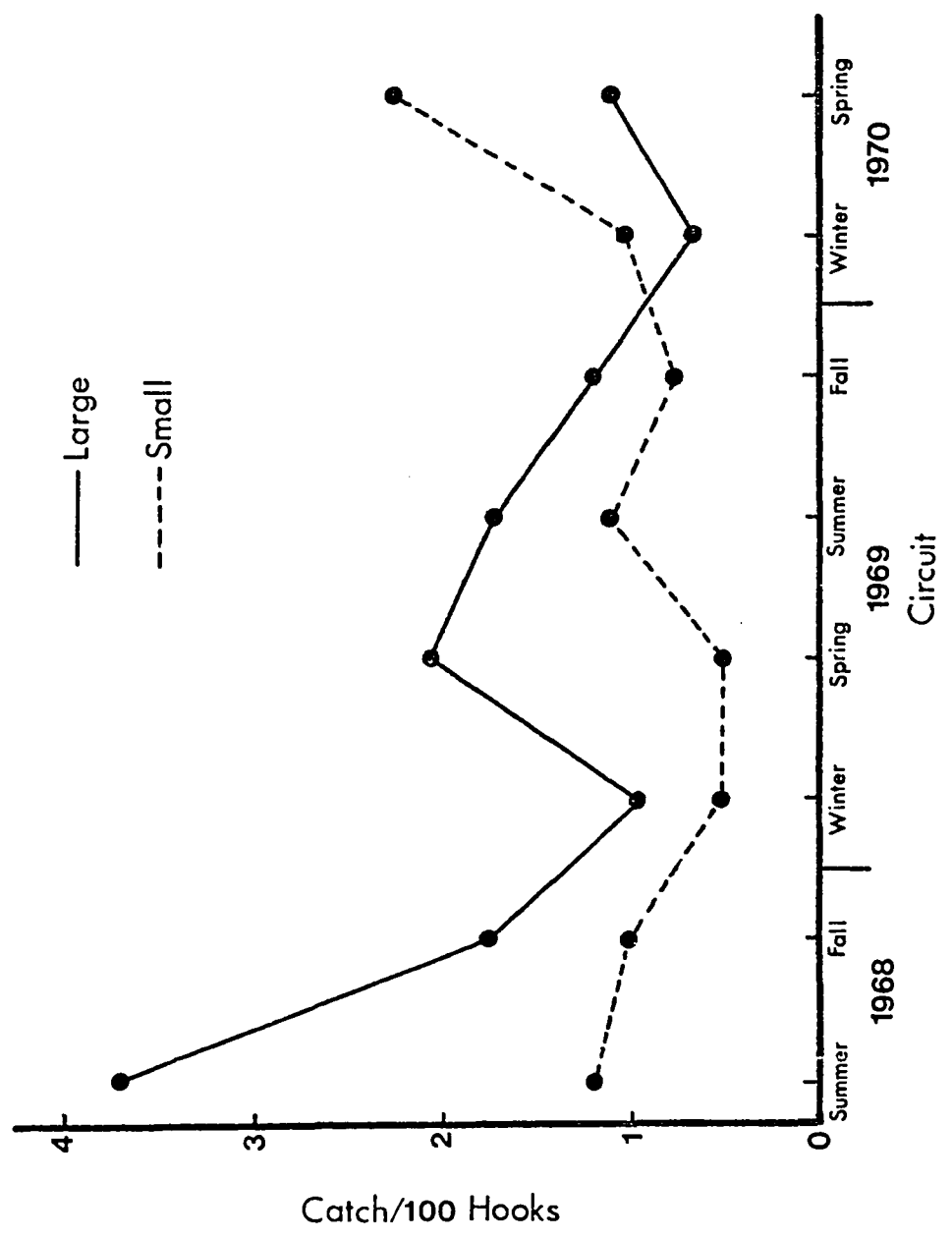
Figure 32. Catch/100 hooks for Carcharhinus milberti during the 8 circuits of standard fishing around Oahu. (Data from Tester, 1969)



up again during the spring and summer quarters. Only part of this increase can be attributed to the shoreward migration of mature males for mating purposes. Mature females are responsible for most of the remainder. Reasons for this are not clear. Possibly they also assume a shoaler distribution during this time, or perhaps their appetite increases as the water becomes warmer. During the fall and winter quarters, the catch rate showed another decline. On the last circuit, however, the catch rate increased to a value greater than those of previous quarters with the exception of the first. Mature sharks were not responsible for this rise. Rather, the catch consisted primarily of smaller individuals. This is shown clearly in Fig. 33 where the catch rate is plotted separately for "large" (precaudal length greater than 105 cm) and "small" (precaudal length less than 105 cm) C. milberti. "Large" individuals show the expected decrease in catch on successive circuits (with spring and summer increases). The catch rate for "small" C. milberti, however, remains relatively constant for the first 7 circuits and suddenly doubles during the final one.

"Small" C. milberti are of the size range most commonly found in the stomachs of Galeocerdo cuvieri whose numbers were also being reduced by the fishing effort. Catch/100 hooks for G. cuvieri fell (with winter increases) from a value of 2.33 to 0.52 during the 8 circuits of standard fishing around Oahu (Tester, 1969). It is postulated that the increased catch of young C. milberti during the final circuit was

Figure 33. Catch/100 hooks for large (precaudal length greater than 105 cm) and small (precaudal length less than 105 cm) Carcharhinus milberti during the 8 circuits of standard fishing around Oahu.



the result of a reduction in the amount of predation normally exerted by G. cuvieri. Unfortunately, the fishing program was terminated after 8 circuits so it is unknown whether the apparent increase of "small" C. milberti would have been substantiated by subsequent fishing.

There is a slight possibility that the increased catches of young C. milberti at the end of the fishing program were due to the use of a different bait. Because of a shortage of skipjack tuna, we were forced to use kawa-kawa, another tuna of similar size. It was pointed out in the discussion of bait preference studies, however, that sharks are unlikely to prefer one tuna over the other. Even if they do, this does not explain why larger numbers of immature individuals, only, were caught.

#### 4. Intraspecific Predation

Most sharks are cannibalistic to some extent. C. milberti and C. menisorrhah are probably no exception. Springer (1967) has speculated that cannibalism may be the factor limiting population sizes among some of the larger species of sharks. For a sample of C. milberti from Florida, he interpreted the scarcity of mature males and the low percentage of pregnant females (only about 20% of the mature females) as due to the females sometimes fatally injuring the males during courtship. Small percentages of pregnant females and uneven sex ratios, however, are not characteristic of Hawaiian populations of

C. milberti and C. menisorrah, so fatal injuries to males during courtship and mating rarely occur. Springer (1967) states that attrition in group feeding may also have a limiting effect on population size. As sharks become more numerous in an area, the likelihood of a "feeding frenzy," in which the participants are sometimes fatally injured, increases.

Sex-maturity group segregation functions to reduce intraspecific predation. C. milberti populations in the western North Atlantic possess nursery areas geographically isolated from areas frequented by adults (Springer, 1960). In Hawaii the isolation is not as complete. Only mature males are excluded from the nursery areas of C. milberti though the abundance of females is reduced. At Molokini mature C. menisorrah of both sexes are absent from their nursery area. Contact between the sexes of both species is reduced by the tendency for mature males to occur deeper than mature females during most of the year.

## CHAPTER VIII.

### CONCLUDING REMARKS

It has been shown that C. milberti occurs commonly in all Hawaiian areas that were fished (except Molokini), but with significant differences in abundance between leeward and windward shores of Oahu and Niihau. C. menisorrah, on the other hand, occurs abundantly only at Niihau, Kaula and Molokini. The primary objective of this investigation was to determine if differences in life history and ecology can account for differences in the distribution of the 2 species.

C. milberti and C. menisorrah are born and mature at about the same sizes, have similar fecundities and possess gestation periods of similar lengths. Although there may be differences in growth rate and seasonal differences in reproductive cycles, it seems unlikely that they could be responsible for the distributional differences between islands.

Interspecific competition, if it exists, probably has no great influence on inter-island distribution. Analysis of diet, bait preferences and tooth structure indicate that Galeocerdo cuvieri, Carcharhinus limbatus, C. galapagensis, C. milberti, and C. menisorrah probably do not compete strongly for food, the resource most likely to be present in limited supply. The diet of G. cuvieri is clearly distinguished from that of C. milberti and C. menisorrah by the larger size of its prey and the

relative lack of fish. The 4 members of the genus Carcharhinus are primarily fish eaters, with cephalopods ranking second in their diet. Adult C. galapagensis tend to eat larger fish (including tetraodontiforms and elasmobranchs) than do C. milberti and C. menisorrah. C. menisorrah appears to eat more fish than C. milberti, but fewer crustaceans and cephalopods. The apparently greater proportion of benthic organisms in the stomachs of C. milberti suggests that this species feeds on or very close to the bottom to a greater extent than does C. menisorrah.

The upper teeth of each species are distinctive and the structure correlates with their diet. Galeocerdo cuvieri has heavy, cutting teeth in both jaws and preys on large animals, often with a hard shell or skeleton, which must be cut into bite-size pieces. The other 4 carcharhinids possess both cutting and grasping teeth and generally eat smaller and softer animals.

Both study species are subject to predation--the main predators being other sharks. Galeocerdo cuvieri is the primary predator in Hawaii and is followed in importance by Carcharhinus galapagensis. Immature sharks are subject to the heaviest predation because of their smaller size. Predation on immatures appears to be an important factor in limiting the population size of C. milberti. Though predation may limit the absolute abundance of C. milberti and C. menisorrah within an area, it probably has little or no effect on horizontal distribution.

In evolutionary time, however, both competition and predation are likely to have played roles in establishing the observed distributions. Likewise, intraspecific competition and predation probably favored evolution of sex-maturity group segregation.

The Hawaiian distributions of C. milberti and C. menisorrah appear to be the result of associations with physical factors of the environment. C. milberti is found abundantly where water may be turbid, where currents are of low to medium velocity, and over a relatively smooth bottom consisting of sand and fine rubble. The amount of level or gently sloping bottom may influence the distribution of juveniles. Nursery areas occur off the north and east coasts of Oahu where there are broad expanses of smooth bottom. Physical factors generally associated with the smaller islands and islets in Hawaii appear to be important in limiting the distribution of C. menisorrah. Small islands get less rainfall and have little runoff so the surrounding waters are clean. Also, the shallow bottom surrounding them is generally rugged.

The associations described above hold for juveniles to a greater extent than for adults. In fact, these parameters appear to be requisites for nursery areas. It is concluded that the Hawaiian distributions of the study species probably result from associations, especially among juveniles, with particular bottom types, turbidities and current velocities.

The same factors also appear to affect the distribution of C. milberti and C. menisorrah on a global scale. It was noted in Chapter I that C. milberti usually occurs along continental coasts where the water is more likely to be turbid and the bottom smoother and more extensive. C. menisorrah, however, is most abundant around oceanic islands and atolls where the water is usually clear and the bottom rugged.

The cause for these associations is unknown. Does C. milberti frequent soft, level bottom because it is the habitat of stomatopods and other crustaceans which are a common part of its diet? Can C. milberti capture food more easily over smooth bottom where there is little cover? Does C. menisorrah prefer clear water because vision plays a dominant role in its feeding activity? Is this species found in the more rugged areas because fishes are more numerous in this habitat? Answers to these and similar questions are only speculative at the present time.

Appendix A. Scientific and common names of sharks mentioned in the dissertation.

<u>Carcharhinus albimarginatus</u>	Silvertip Shark
<u>C. altimus</u>	Bignose Shark
<u>C. falciformis</u>	Silky Shark
<u>C. galapagensis</u>	Galapagos Shark
<u>C. leucas</u>	Bull Shark
<u>C. limbatus</u>	Blacktip Shark
<u>C. longimanus</u>	Oceanic Whitetip Shark
<u>C. melanopterus</u>	Blacktip Reef Shark
<u>C. menisorrhah</u>	Gray Reef Shark
<u>C. milberti</u>	Sandbar Shark
<u>Carcharodon carcharias</u>	Great White Shark
<u>Galeocerdo cuvieri</u>	Tiger Shark
<u>Galeorhinus australis</u>	School Shark
<u>Mustelis canis</u>	Smooth Dogfish
<u>Negaprion brevirostris</u>	Lemon Shark

<u>Prionace glauca</u>	Blue Shark
<u>Scyliorhinus canicula</u>	Cat Shark
<u>Somniosus microcephalus</u>	Greenland Shark
<u>Sphyrna lewini</u>	Scalloped Hammerhead
<u>Squalus acanthias</u>	Spiny Dogfish
<u>Triaenodon obesus</u>	Reef Whitetip Shark

Appendix B. Key to common inshore Hawaiian Carcharhinid sharks\*

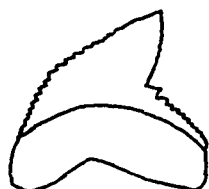
- 1 Teeth multi-cuspid, second dorsal almost as large as first, white tips on dorsal and caudal. . . . . Triaenodon obesus

The Reef Whitetip is a small shark (maximum size about 1.8 m) and is generally found in shallow water often resting on the bottom.

- Teeth unicuspid, second dorsal much smaller than the first . . . . . 2

- 2(1) Sides of caudal peduncle with low, hard keel, body with vertical bars or blotches, head blunt, similar notched teeth in upper and lower jaw. . . . . Galeocerdo cuvieri

The Tiger Shark is the largest shark commonly caught in Hawaiian waters and is the most dangerous as far as man is concerned. The teeth of this species are distinctive. Maximum size is about 4.5 m.



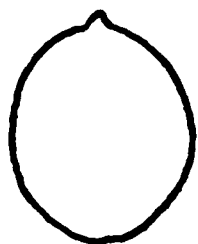
Tooth of G. cuvieri

- Body without vertical blotches, teeth of upper and lower jaw dissimilar. . . . . 3

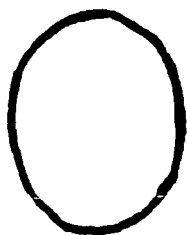
\* Modified from Kato, Springer & Wagner, 1967.

- 3(2) Ridge present between first and second dorsal . . . . . 6
- No ridge or only very slight ridge between dorsals . . . . . 4

Cross section of trunk between dorsals.



Shark with a ridge on back.



Shark without a ridge on back.

- 4(3) Snout quite pointed, ridge entirely absent, no broad dark band on trailing edge of caudal (particularly the lower lobe), teeth in upper jaw slender . . . . . Carcharhinus limbatus

The Blacktip Shark is generally found at depths of less than 30 fathoms and attains a maximum size of about 2.2 m.

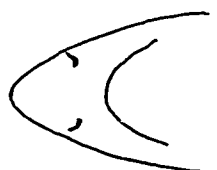
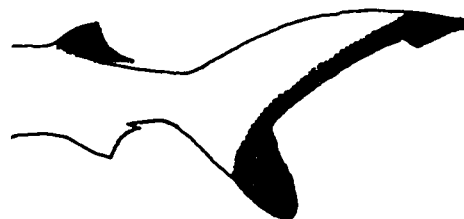
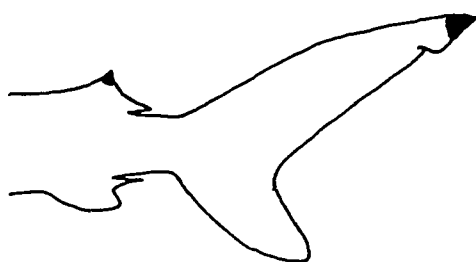
- Snout rounded . . . . . 5

- 5(4) Ridge may be slightly developed, no black on first dorsal, broad black band on trailing edge of caudal . . . . .  
 . . . . . Carcharhinus menisorrah

The Gray Reef Shark grows to a maximum length of 2.0 m and is common around the smaller islands and offshore islets.

- Distinct black tip on first dorsal with cream-colored band beneath it, no dorsal ridge . . . . .  
 . . . . . Carcharhinus melanopterus

The Blacktip Reef Shark is usually found in very shallow water and attains a total length of about 1.5 m.



C. limbatus

C. menisorrah

- 6(3) Distance from tip of snout to mouth greater than width of mouth, underside of pectoral tips, tips of second dorsal and anal, and extreme trailing edge of caudal may be black . . . . .  
 . . . . . Carcharhinus altimus

The Bignose Shark is generally found at depths greater than 40 fathoms and may attain a size of 2.8 m.

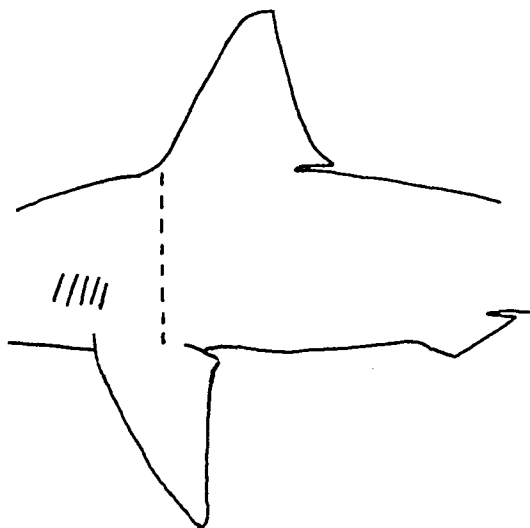
Distance from tip of snout to mouth less than width of mouth, no black tips on fins . . . . . 7

- 7(6) First dorsal large and located far forward, origin over pectoral axil . . . . . Carcharhinus milberti

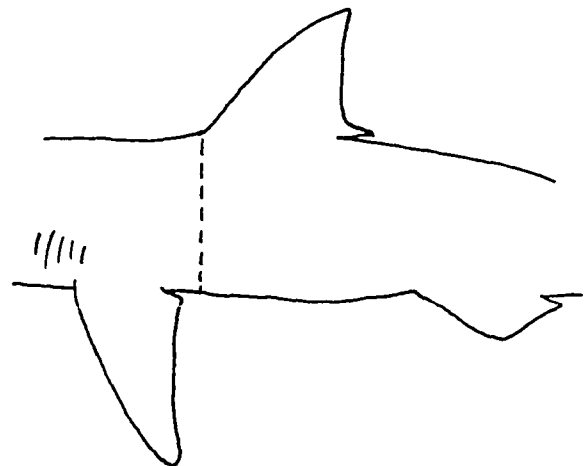
The Sandbar Shark is the most common inshore Hawaiian shark. Its maximum size is about 2.0 m.

First dorsal with origin posterior to rear margin of pectoral . . . . . Carcharhinus galapagensis

The Galapagos Shark is the largest "gray shark" in Hawaii attaining a maximum length of 3.0 m.



C. milberti



C. galapagensis

Appendix C. Growth data for captive sharks at the Kewalo Basin facility. The lengths are precaudal lengths (cm).

A. Carcharhinus milberti, male, captured off Molokai 9-14-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
9-14-68	72.	8-19-69	92.3
1-12-69	79.5	9-16-69	92.5
2-03-69	81.5	12-19-69	98.8
5-03-69	86.7	1-08-70	98.8
5-25-69	87.7		
6-16-69	88.8		

B. Carcharhinus milberti, male, captured off Oahu 11-9-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
11-13-68	48.2	6-16-69	64.6
1-12-69	54.6	8-19-69	70.8
2-03-69	56.0	9-11-69	72.0
5-03-69	61.3	12-19-69	79.7
5-25-69	63.6	1-08-70	80.1

C. Carcharhinus milberti, female, captured off Oahu 11-9-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
11-13-68	49.2	6-16-69	64.6
1-12-69	54.0	8-19-69	71.7
2-03-69	55.2	9-11-69	73.7
5-03-69	58.9	12-19-69	82.9
5-25-69	62.0	1-08-70	83.7

D. Carcharhinus milberti, female, captured off Oahu 11-9-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
11-13-68	50.2	8-19-69	74.4
1-07-69	54.3	9-11-69	76.1
2-03-69	56.7	12-19-69	85.0
5-03-69	64.2	1-08-70	85.6
6-16-69	68.4		

E. Carcharhinus milberti, male, captured off Oahu 11-9-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
11-13-68	50.5	3-18-70	87.5
1-12-69	56.2	4-08-70	88.2
2-03-69	57.3	6-10-70	92.5
5-03-69	63.5	7-31-70	94.8
5-25-69	66.2	10-15-70	97.6
6-13-69	67.1	11-09-70	98.7
8-19-69	74.6	1-07-71	100.3
9-11-69	75.8	3-11-71	102.8
12-19-69	83.3	6-11-71	104.0
2-22-70	85.7		

F. Carcharhinus milberti, female, captured off Oahu 12-27-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
9-24-69	138.6	1-08-70	140.2

G. Carcharhinus milberti, female, captured off Oahu 12-30-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
2-28-69	141.	9-24-69	141.7

H. Carcharhinus milberti, female, born in tank 9-24-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
9-25-69	51.2	2-22-70	65.2
10-06-69	51.5	3-18-70	67.5
10-13-69	52.1	4-08-70	70.0
10-20-69	52.2	6-10-70	75.9
11-26-69	54.9	7-31-70	80.0
12-02-69	56.2	10-13-70	85.5
12-08-69	56.4	11-05-70	86.3
12-12-69	57.0	1-07-71	90.0
12-16-69	57.5	3-11-71	93.2
		6-08-71	99.3

I. Carcharhinus milberti, female, born in tank 9-24-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
9-25-69	51.0	2-22-70	64.7
10-06-69	51.9	3-18-70	67.2
10-13-69	52.2	4-08-70	69.3
10-20-69	52.7	6-10-70	75.9
11-26-69	55.8	7-31-70	80.4
12-02-69	56.8	10-13-70	85.3
12-08-69	57.3	11-05-70	86.7
12-12-69	58.2	1-07-71	91.9
12-16-69	58.3	3-11-71	94.5
		6-07-71	100.5

J. Carcharhinus milberti, male, born in tank 9-24-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
9-25-69	47.8	3-18-70	59.7
10-06-69	48.7	4-08-70	62.0
10-13-69	49.1	6-10-70	68.2
10-20-69	49.8	7-31-70	73.5
11-26-69	50.6	10-13-70	79.0
12-02-69	50.6	11-05-70	80.1
12-08-69	50.6	1-07-71	83.6
12-12-69	50.8	3-11-71	87.8
2-22-70	57.8	6-11-71	94.2

K. Carcharhinus milberti, female, captured off Oahu 2-12-70.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
2-12-70	124.8	10-15-70	130.1
4-21-70	125.9	1-07-71	130.7
5-27-70	126.9	6-07-71	132.1

L. Carcharhinus milberti, female, captured off Oahu 11-9-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
11-13-68	50.7	2-03-69	57.4
1-07-69	55.7	3-21-69	60.3

M. Carcharhinus milberti, female, captured off Oahu 11-9-68.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
11-13-68	50.2	2-03-69	57.0
1-12-69	55.6	3-05-69	59.2

N. Carcharhinus menisorrah, male, captured off Niihau 6-22-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
6-24-69	63.0	12-19-69	68.6
8-19-69	63.3	1-08-70	68.5
9-16-69	64.2		

O. Carcharhinus menisorrah, male, captured off Niihau 6-22-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
6-24-69	67.5	6-10-70	79.1
8-19-69	70.1	7-31-70	80.3
9-16-69	71.4	10-13-70	82.3
12-19-69	74.8	11-05-70	83.1
2-22-70	76.9	1-07-71	83.7
3-18-70	77.1	3-11-71	85.6
4-15-70	77.8	6-11-71	86.6

P. Carcharhinus menisorrah, female, captured off Niihau 6-22-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
6-24-69	64.0	12-19-69	77.5
8-19-69	67.0	1-08-70	78.6
9-16-69	69.3		

Q. Carcharhinus menisorrah, female, captured off Oahu 9-20-69.

<u>Date</u>	<u>Length</u>	<u>Date</u>	<u>Length</u>
9-20-69	55.0	6-10-70	66.5
10-06-69	55.2	7-31-70	68.4
10-20-69	56.0	10-13-70	71.3
12-19-69	59.1	11-05-70	71.7
2-22-70	61.7	1-07-71	73.5
3-18-70	62.7	3-11-71	75.3
4-15-70	64.0	6-07-71	78.8

Appendix D. Computations for determination of mean functional tooth life. Data are from a male Carcharhinus milberti with a precaudal length of 97.6 cm when the teeth were first marked.

<u>X</u>	<u>Y</u>
0	8
7	5
19	3
25	1

X = number of days since teeth were marked.

Y = number of marked teeth still in position.

- 1) Because the regression line must pass through the point (0, 8), transformed Y-values (Y') are used in the calculations. Therefore, subtract 8 from each value.

<u>X</u>	<u>Y'</u>
0	0
7	-3
19	-5
25	-7

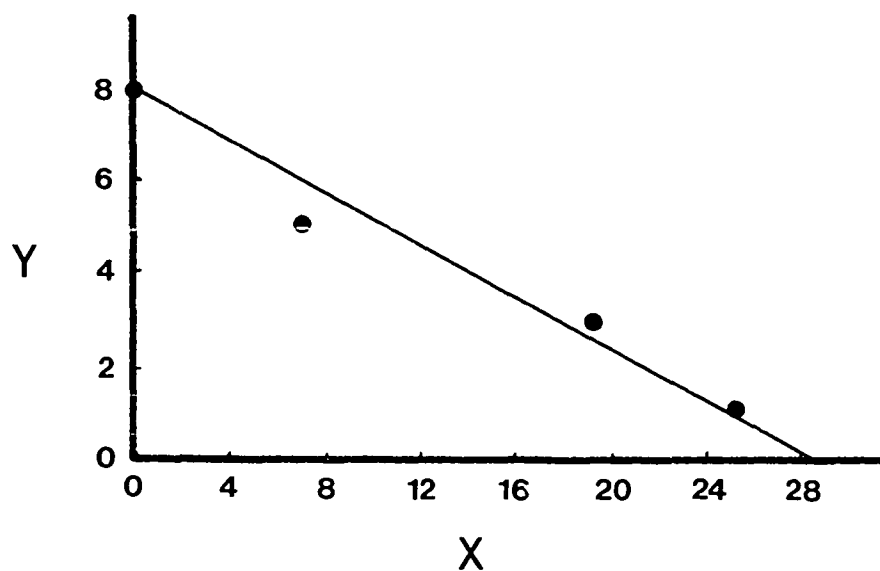
- 2) Calculate regression equation using Y'.

$$\hat{Y}' = -0.2812 X.$$

- 3) Find X when Y' = -8 (i. e. when Y = 0).

$$-8 = -0.2812 X$$

$$X = 28.4 \text{ days}$$



Appendix E. List of fishes taken from stomachs of sharks caught in Hawaii and the number of stomachs containing the listed item.

A) <u>Galeocerdo cuvieri</u>	
O. Tetraodontiformes	(64)
<u>Diodon hystrix</u>	43
<u>Arothron</u> spp	17
<u>Lactoria fornasini</u>	1
Balistidae	2
Monacanthidae	1
O. Anguilliformes	(6)
Muraenidae	4
O. Perciformes	(12)
Carangidae	3
<u>Seriola dumerilii</u>	1
<u>Trachurops crumenophthalmus</u>	1
Scaridae	1
Labridae	1
Istiophoridae	1
<u>Coryphaena hippurus</u>	1
Acanthuridae	1
<u>Mulloidichthys samoensis</u>	1
Flatfish	1

Other orders	(9)
<u>Fistularia petimba</u>	5
<u>Aulostomus chinensis</u>	2
<u>Sphyreana</u> spp	1
<u>Synodus</u> spp	1
B) <u>Carcharhinus limbatus</u>	
O. Tetraodontiformes	(1)
<u>Lactoria fornacini</u>	1
O. Anguilliformes	(1)
Muraenidae	1
Other orders	(1)
<u>Sphyraena</u> spp	1
C) <u>Carcharhinus galapagensis</u>	
O. Tetraodontiformes	(7)
<u>Diodon hystrix</u>	5
Monacanthidae	2
O. Anguilliformes	(3)
Muraenidae	2
O. Perciformes	(13)
Scaridae	2
Acanthuridae	2

<u>Naso</u> spp	2
Carangidae	1
<u>Trachurops crumenophthalmus</u>	2
<u>Decapterus maruadsi</u>	1
<u>Priacanthus cruentatus</u>	1
<u>Monotaxis grandoculis</u>	1
<u>Dascyllus albisella</u>	1
Other orders	(4)
<u>Stolephorus purpureus</u>	1
<u>Holocentrus</u> spp	2
<u>Synodus</u> spp	1
D) <u>Carcharhinus milberti</u>	
O. Tetraodontiformes	(11)
<u>Diodon hystrix</u>	6
Monacanthidae	3
Balistidae	1
<u>Lactoria fornasini</u>	1
O. Anguilliformes	(12)
Muraenidae	7
Congridae	2
O. Perciformes	(42)
Labridae	9

Scaridae	6
Acanthuridae	6
<u>Naso spp</u>	3
<u>Trachurops crumenophthalmus</u>	4
<u>Decapturus maruadsi</u>	2
Scorpaenidae	2
Mullidae	2
<u>Mulloidichthys samoensis</u>	2
<u>Priacanthus cruentatus</u>	2
<u>Pristipomoides microlepis</u>	1
<u>Zanclus canescens</u>	1
<u>Forcipiger longirostris</u>	1
<u>Chaetodon miliaris</u>	1
Other orders	(20)
<u>Fistularia petimba</u>	7
Holocentridae	1
Flatfish	3
Exocoetidae	2
<u>Synodus spp</u>	1
<u>Aulostomus chinensis</u>	1
Belonidae	1
Callionymidae	1

Dactylopteridae	1
E) <u>Carcharhinus menisorrah</u>	
O. Tetraodontiformes	(1)
<u>Lactoria fornasini</u>	1
O. Perciformes	(4)
Scaridae	1
<u>Naso</u> spp	1
<u>Chaetodon</u> spp	1
<u>Zanclus canescens</u>	1
Other orders	(3)
Holocentridae	3

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