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DISTRIBUTION, ABUNDANCE, AND HABITS OF PELAGIC SHARKS IN THE CENTRAL PACIFIC OCEAN

BY DONALD W. STRASBURG

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ABSTRACT

The distribution and abundance of the central Pacific pelagic sharks was investigated by longline fishing methods during 1952–55. In this period more than 6,000 sharks were caught; these belonged to 12 species. Great blue, whitetip, and silky sharks predominated. Bonito, thresher, mackerel, and other species were uncommon or rare.

Several significant facets of the biology of the common sharks were evident. The wide-ranging great blue shark made pronounced seasonal migrations during which sexual segregation occurred and reproduction probably took place. Vertical distribution of the great blue shark was limited in the north by the 45°–69° F. isotherms, and it was truly an oceanic species. The whitetip and silky sharks were denizens of the Tropics, and showed no particular migratory tendencies; the former was oceanic but the latter tended to be neritic.

In equatorial waters, great blues and whitetips were more abundant in warm years, and the silky more abundant in cold years. The species considered here fed principally on small fish and squid. The great blue shark was virtually harmless to the tuna catch. Only 1 percent of the catch was damaged where it abounded, as compared with 20 percent damaged in regions where the whitetip and silky sharks were dominant. In the great blue shark both the behavioral and geographical types of sexual segregation were found, and sexual segregation itself was related to latitude, shark length, and season.

DISTRIBUTION, ABUNDANCE, AND HABITS OF PELAGIC SHARKS IN THE CENTRAL PACIFIC OCEAN

By **Donald W. Strasburg**, ***Fishery Research Biologist***, BUREAU OF COMMERCIAL FISHERIES

The Pacific Oceanic Fishery Investigations (POFI) of the United States Fish and Wildlife Service is authorized to investigate the high seas fishery resources of the tropical and subtropical Pacific Ocean. A large part of POFI's research program has dealt with the biology of tunas, the stocks of which have been sampled extensively by longline fishing. In addition to tuna, spearfish, and other species of commercial importance, an incidental product of longlining has been the capture of numerous pelagic sharks. Information on the occurrence of these sharks is of importance to both the biologist and the commercial fisherman because of the sharks' competitive and predatory relation to tuna and also because of the damage sharks inflict on hooked tuna. Apart from discussions in systematic and general works (Bigelow and Schroeder, 1948, Englehardt 1913, Norman 1949, and Norman and Fraser, 1949) and the usually fragmentary data in faunal reports, little is known of the biology of high seas sharks, and any information on their abundance, distribution, and habits is of practical and academic interest.

This report is primarily based on the shark catches recorded during the years 1952 through 1955. During this period the POFI ships *John R. Manning*, *Charles H. Gilbert*, and *Hugh M. Smith* conducted 26 longline cruises, which obtained sharks in the central Pacific between 50° N. and 20° S. latitude, and 110° W., and 175° E. longitude (fig. 1). During the same period of years, four privately owned, commercial vessels, the *Cavalieri*, *Commonwealth*, *North American*, and *Oceanic*, operating in conjunction with POFI, made a total of eight cruises to the Line Islands area. Data from all the above cruises were utilized only when the shark catches were recorded by species. Although a considerable portion of these data have routinely been listed in reports by workers concerned primarily with tuna (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955; Shomura and Otsu, 1956; Iversen and Yoshida, 1956), it seems advisable to provide a summary of the catch and effort for the various cruises (table 1).

METHODS

The longline gear used by POFI as a tool for sampling the abundance of tunas (and sharks) has been described by Niska (1953) and Mann (1955). A unit or basket of longline gear consists of 210 fathoms of mainline supporting a number of hook droppers, usually 3 fathoms in length, and buoyed at its end by floats attached to 5-, 10-, or 15-fathom floatlines. Numerous baskets are joined together to form a set, each basket being placed in the water in a slack condition so that the 210-fathom mainline sags and subtends a distance of only about 150 fathoms between floats. The number of droppers per basket was typically 6, 11, or 13, although experimental gear employing 14, 15, and 21 droppers was occasionally used during the period under consideration. Bait consisted of frozen herring, sardines, or squid. Setting of longlines usually started at dawn and required about an hour. Recovery commenced at noon and was usually completed in 4½ hours. The last basket set was the first one retrieved.

In their classic treatise on North Atlantic sharks Bigelow and Schroeder (1948) frequently refer to nomenclatorial confusion resulting in nonacceptability of shark records. This confusion has several causative factors, chief of which is the lack of large preserved specimens available for systematic study. Further complicating the situation is the existence of several sets of names for sharks, e. g., one set for Atlantic species, another

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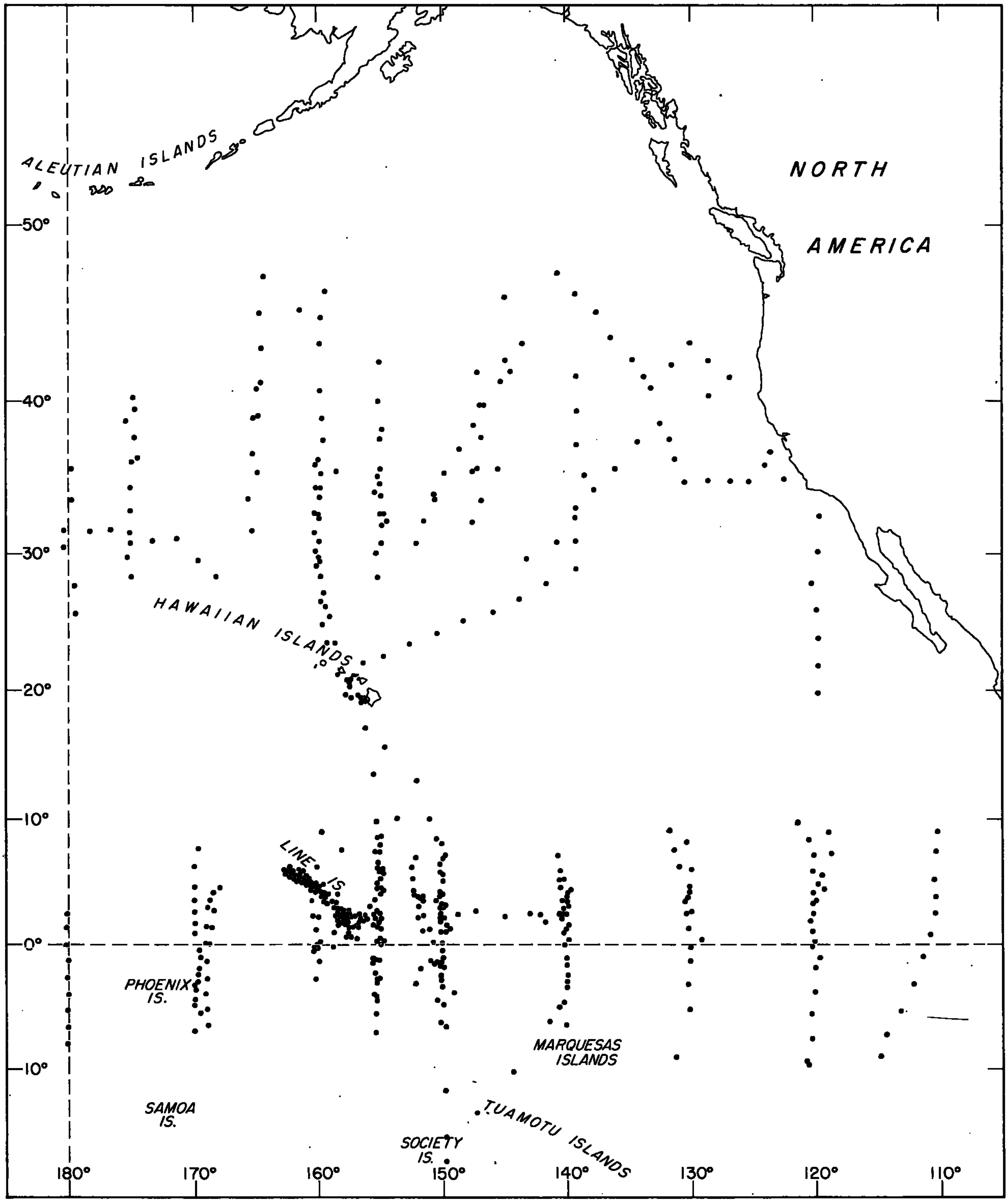

FIGURE 1.—Location of longline stations from which the sharks reported on were obtained.

TABLE 1.—*POFI and commercial longline cruises yielding identified sharks during the period 1952–55*

Vessel	Cruise	General operational area [1]	Date	Number of stations	Total hooks	Shark catch			
						Great blue	White-tip	Silky	Other
John R. Manning	11	Equator at 159° W., 169° W., 180°.	January–March 1952	27	6,960	51	71	31	1
	12	Equator at 140° W., 150° W	August–September 1952	18	4,560	13	59	5	8
	13	Equator at 150° W., 169° W	October–November 1952	27	7,620	20	131	19	0
	14	Equator at 140° W., 150° W	January–March 1953	33	8,850	25	140	25	3
	15	Equator at 150° W., 170° W	April–June 1953	28	9,521	47	109	42	9
	16	Equator at 155° W., 160° W	July–August 1953	26	8,811	47	47	139	5
	17	Line Islands	October–November 1953	6	2,418	2	2	48	1
	18	Equator at 155° W., Line Islands.	December 1953	14	7,140	15	76	92	5
	19	22° N.–36° N., 145°.–160° W	January–March 1954	18	14,014	91	3	0	11
	20	Line Islands	May–June 1954	27	15,764	32	108	268	3
	21	Hawaiian Islands	July 1954	5	2,052	7	4	0	0
	22	22° N.–47° N., 159° W.–177° W.	September–October 1954	16	11,869	170	1	0	6
	23	22° N.–37° N., 157° W.–180°	December 1954–February 1955.	18	13,415	131	0	0	4
	24	Line Islands	March–April 1955	10	6,422	15	32	79	7
	25	28° N.–41° N., 158° W.–175° W	May–June 1955	18	8,318	229	0	0	23
	26	30° N.–47° N., 122° W.–152° W	July–September 1955	38	19,609	719	0	0	16
	27	Line Islands	October 1955	11	6,928	11	9	121	9
	28	do	November–December 1955	5	3,955	7	25	35	0
Charles H. Gilbert	1	Equator at 120° W., 130° W	May–June 1952	14	3,360	16	32	16	0
	10	Hawaiian Islands	March 1953	3	623	4	2	0	0
	15	South of Baja California, and Equator at 110° W., 155° W.	February–April 1954	32	15,271	323	31	51	8
	20	Line Islands	March–April 1955	14	9,054	43	14	130	9
	23	36° N.–47° N., 145° W.–165° W	September–October 1955	8	4,147	54	0	0	1
Hugh M. Smith	18	Equator at 120° W., 130° W	October–November 1952	23	5,520	59	83	28	2
	19	Line Islands	January–February 1953	8	2,160	6	3	68	1
	29	22° N.–42° N., 139° W.–156° W.	May–June 1955	30	15,600	218	0	0	14
Commonwealth	1	Line Islands	July–August 1954	11	5,500	2	28	54	3
	3	do	May 1955	11	3,537	6	1	28	18
	4	do	July–August 1955	12	4,095	7	1	102	5
	5	do	September–October 1955	10	4,210	10	5	55	3
North American	1	do	January–February 1954	27	21,283	30	19	258	31
	2	do	March–April 1954	40	35,965	58	86	347	23
Cavalieri	1	Equator at 140° W., 150° W	August–September 1952	26	11,454	42	65	3	8
Oceanic	1	Line Islands	June 1954	9	3,762	2	0	132	6
Total					303,767	2,512	1,187	2,176	243

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[1] The term "Equator" denotes fishing in the equatorial area, and not necessarily along 0°. The position of the Line Islands is bounded roughly by 0°–10° N. latitude and 155° W.–165° W. longitude.

for northwest Pacific species, a third for Hawaiian forms, etc., a situation comparable to that found for other pelagic fish such as the tunas, marlins, and flying fishes. For comparative purposes it is thus necessary to note the identification sources and procedures and the disposition of the material upon which this report is based.

The principal references used in making the identifications were Bigelow and Schroeder's treatise (1948), supplemented by the reports of Roedel and Ripley (1950), Roedel (1953), and Schultz et al. (1953). On early cruises sharks were brought aboard, identified, measured, and frequently photographed. Occasionally jaws, patches of skin, embryos, and entire adult specimens were preserved, and laboratory examination of this material has since confirmed the recorded field identifications with the reservations that the names "thresher" and "hammerhead" are based on 3 and 2 species, respectively. As biologists and fishermen became better acquainted with the various species fewer sharks were landed, and identification was often based on the gross aspects of the animals as they lay in the water alongside the vessel. There is thus a possibility of an occasional error in identification, particularly with *Isurus glaucus* and *Lamna ditropis*, which are rather similar in appearance. Specimens of each species considered are to be shipped to the United States National Museum to serve as a permanent record.

The vernacular names of sharks are used throughout the remainder of this study. These names and their currently accepted scientific equivalents are as follows:

Whitetip shark	*Pterolamiops longimanus* (Poey).
Blacktip shark	*Carcharhinus melanopterus* (Quoy and Gaimard).
Silky shark	*Eulamia floridanus* (Bigelow, Schroeder, and Springer).
Great blue shark	*Prionace glauca* (Linnaeus).
Soupfin shark	*Galeorhinus zyopterus* Jordan and Gilbert.
Bonito shark	*Isurus glaucus* Müller and Henle.
Mackerel shark	*Lamna ditropis* Hubbs and Follett.

Thresher shark	*Alopias pelagicus* Nakamura. *Alopias superciliosus* (Lowe). *Alopias vulpinus* (Bonnaterre).
Hammerhead shark	*Sphyrna lewini* (Griffith). *Sphyrna zygaena* (Linnaeus).

Representative length-frequency distributions of the three most common pelagic sharks are shown in figure 2; these will acquaint the reader with the size of the sharks encountered. Insofar as possible common names have been taken from the list proposed by the American Fisheries Society (1948). For those species not covered by this list, vernacular names were derived from Bigelow and Schroeder's treatise (1948). Latin names follow the latter authors except for the carcharhinid genera lacking spiracles. Here Springer's revision (1950, 1951) has been employed with the result that the former *Carcharhinus longimanus* and *C. floridanus* are now referred to *Pterolamiops* and *Eulamia* respectively. Identification of *Sphyrna lewini* was made in accordance with Fraser-Brunner's synopsis of the hammerhead sharks (1950).

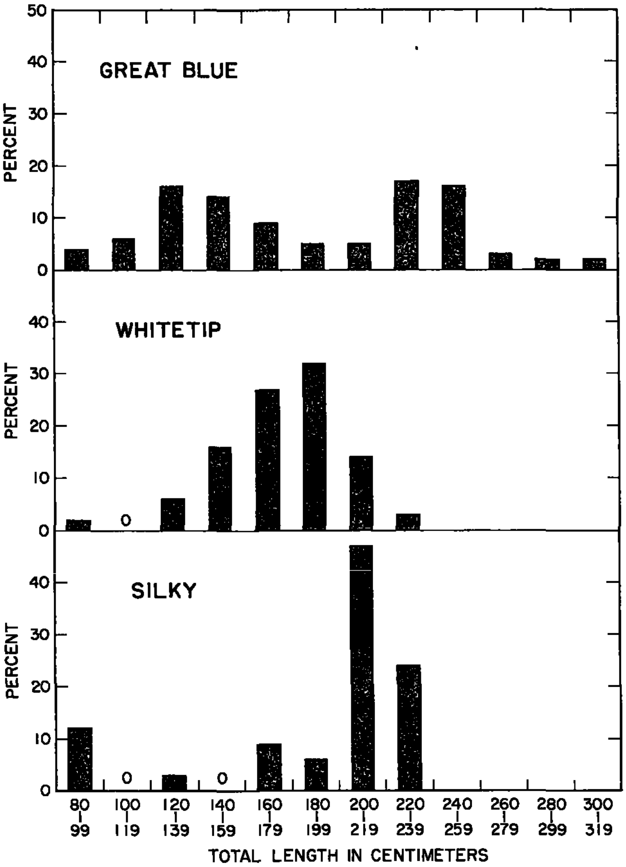

Figure 2.—Typical length-frequency distributions of pelagic sharks commonly occurring in longline catches in the central Pacific. Based on 106 great blue, 63 whitetip, and 34 silky sharks.

It was thought desirable to express shark abundance in terms of fishing effort, as average catch per hundred hooks per day for a certain unit of area. The operational region was accordingly divided into quadrates measuring 5 degrees on a side, and catch and effort were calculated for each areal unit. Iversen and Yoshida (1956) and Murphy and Shomura (1955) found differences in efficiency between two types of gear in catching yellowfin tuna, but all gear types were here considered equally efficient in catching sharks. It frequently happened that longline fishing stations were conducted along specified meridians or parallels, and these were also the boundaries of quadrates. Usually, the line drifted with the current so that fishing was restricted to one or the other of the quadrates, but when operations actually extended over two quadrates, the entire catch was assigned to the quadrate in which most fishing appeared to take place. This assignment took into account set and drift of the current, time spent in each quadrate, and vessel course and speed. Similarly, stations occupying parts of more than 1 day were assigned the date on which most fishing was conducted. For ease in presentation the data summarized by 5-degree quadrates have been regrouped on a 10-degree basis and are used in this form throughout most of the analyses.

The author wishes to thank all POFI scientific and vessel personnel for their efforts in landing and handling the sharks on which this report is based. Collection of shark data was begun at POFI by Dr. William F. Royce.

GENERAL RANGE AND ABUNDANCE

The distribution and abundance of the central Pacific pelagic sharks considered here are summarized in figures 3 and 4. It is apparent that high seas sharks are widely distributed as a group and that their abundance, expressed as average catch per hundred hooks per day, is usually less than that of tuna (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955; Shomura and Otsu, 1956; Iversen and Yoshida, 1956). On the other hand the present data indicate a greater abundance of sharks than do those of Nomura et al. (Shomura and Murphy, 1955).

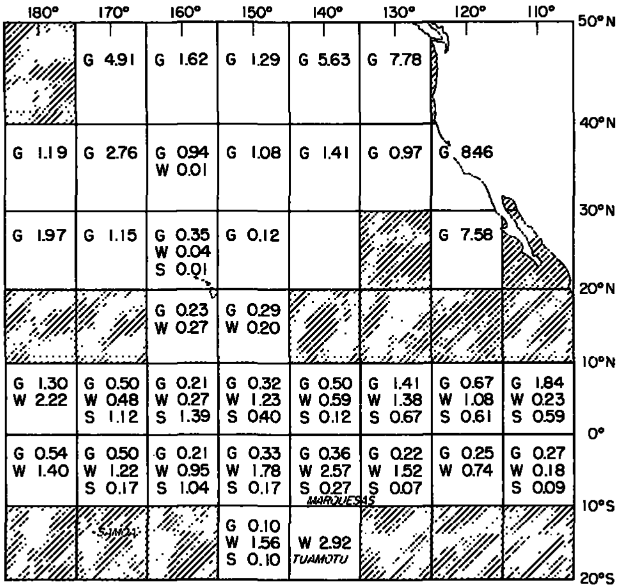

Figure 3.—Distribution and abundance of three common pelagic sharks. Abundance expressed as average catch per hundred hooks per day; hatched areas not sampled. *G*=great blue, *W*=whitetip, *S*=silky shark.

Inspection of figures 3 and 4 shows that the great blue shark is wide ranging throughout the area considered whereas certain of the other species occur within rather narrowly circumscribed limits. In addition, the great blue is easily the most abundant shark in terms of POFI's longline catch, for its 2,512 records constitute about 41 percent of the entire shark catch. Its area of greatest abundance lies north of 20° N. latitude in the eastern part of the Pacific.

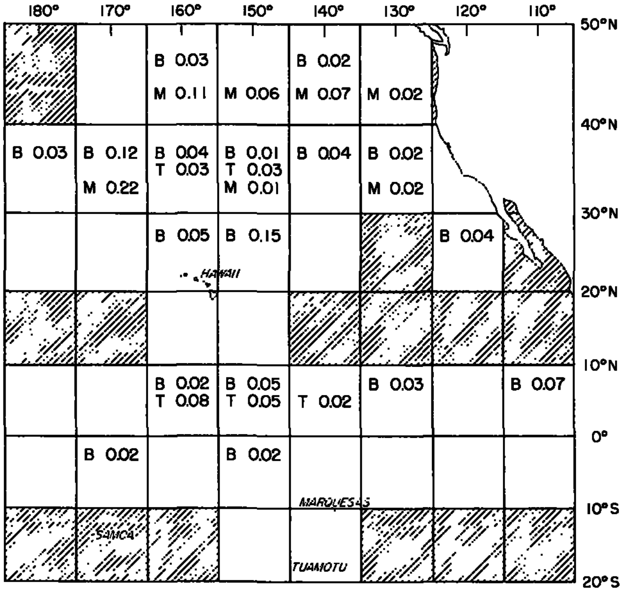

Figure 4.—Distribution and abundance of three uncommon pelagic sharks. Abundance expressed as average catch per hundred hooks per day; hatched areas not sampled. *B*=bonito, *T*=thresher (3 species), *M*=mackerel shark.

The bonito shark has almost the same range as the great blue shark (fig. 4), but as only 74 of the former were taken the catch was almost negligible when reduced to an effort basis. The present data indicate no centers of abundance for the bonito shark although Bigelow and Schroeder (1948: 129–130) list its Atlantic counterpart as a tropical and warm-temperate species which is particularly common in the Canary and Bahamas Islands (between 20° N. and 30° N. latitude).

The silky and whitetip sharks are equatorial species, the range of the former being practically restricted to a band about 10 degrees (600 miles) on either side of the Equator, whereas that of the latter is bounded roughly by 20° N. and 20° S. latitude (fig. 3). The total catch south of 10° N. latitude consisted of 4,157 sharks of which 2,175 (52 percent) were silkies and 1,173 (28 percent) were whitetips. Despite the fact that the catch contained nearly twice as many silkies as whitetips, in terms of catch-per-hundred-hooks in the open ocean areas the whitetip is actually the more abundant of the two species (fig. 3), thus confirming Hubbs' (1951) observation that it is common in the equatorial Pacific. As implied by Bullis (1955) and pointed out by Mather and Day (1954) and Backus et al. (1956), the whitetip rather than the great blue is probably the most abundant warm-water pelagic shark.

It is of interest that the silky shark was not reported from the Pacific until the tentative identification in 1953 (Murphy and Shomura, 1953b), and its presence there was confirmed in 1956 (Iversen and Yoshida).

The region of maximum abundance for the silky shark is centered around the Line Islands area (between 0° and 10° N. and 155° W. to 165° W.), which is also the center of abundance of equatorial yellowfin tuna (Sette 1955). Whitetip concentration is more diffuse, the species being more strictly oceanic (Bigelow and Schroeder, 1948), and not congregating near land (most longlining in the Line Islands was conducted quite close to land). It has been postulated that the whitetip's oceanic existence represents a general avoidance of reduced salinities (Bigelow and Schroeder, 1948), but Backus et al. (1956) found the whitetip occurring over a wide salinity range and alternatively suggested that land avoidance may simply be the result of unfavorable food competition with faster-moving neritic species.

The catch data for the mackerel shark consist of 28 records, 26 of which are from north of 35° N. latitude indicating that this shark is a temperate- or cold-water form (fig. 4). Not shown in figure 4 is a single record from the Line Islands which is most likely based on a misidentified bonito shark.

Little can be said of the distribution and abundance of central Pacific thresher sharks except that they are uncommon (only 127 were taken) and have a tendency to congregate near land in the equatorial region as is shown later. All three species (*Alopias pelagicus*, *A. superciliosus*, and *A. vulpinus*) were taken within about 300 miles of Christmas Island in the Line Islands group, but the identity of the boreal records shown in figure 4 could not be determined.

No distributional charts were prepared for soupfin, hammerhead, or blacktip sharks as only 8, 4, and 2 specimens, respectively, were taken. The soupfins were obtained off the coast of southern California, 1 hammerhead (*Sphyrna lewini*) came from the area bordered by 0°–5° N., 120°–125° W., another (*S. zygaena*) was from 0°–5° N., and 110°–115° W., and 2 others, identified only as "hammerheads," were obtained just east of the Line Islands. The 2 blacktips were taken near shore in the Marquesas Islands, and this species should not be regarded as oceanic (Schultz et al. 1953: 15).

VARIATIONS IN SHARK ABUNDANCE WITH LATITUDE AND SEASON

Geographical variations in abundance were examined by plotting average catch per unit of effort for 10-degree bands of latitude, and temporal variations were studied by recording the data by season. The northern seasons (spring, Mar. 21 to June 20; summer, June 21 to Sept. 20; autumn, Sept. 21 to Dec. 20; winter, Dec. 21 to Mar. 20) were used with the assumption that antipodal season-reversal would not be significant in the latitudinal distribution considered. For the uncommon species (bonito, mackerel, thresher hammerhead, soupfin, and blacktip sharks), seasonal subdivision resulted in so few records per season that very little was indicated. As a consequence this section deals with the three abundant species, the great blue, the whitetip, and the silky.

In the Pacific, heavy concentrations of great blues occur only north of about 20° N. latitude (figs. 3, 5). Since the southern limits of our sampling lay between 15° S. and 20° S. it is not possible to say whether similar concentrations also exist in the Southern Hemisphere. In the Atlantic large numbers of great blues have been reported from both high and low latitudes (Bigelow and Schroeder, 1948), and the species is particularly numerous off the west coast of South Africa at about 30° S. latitude (Smith 1950).

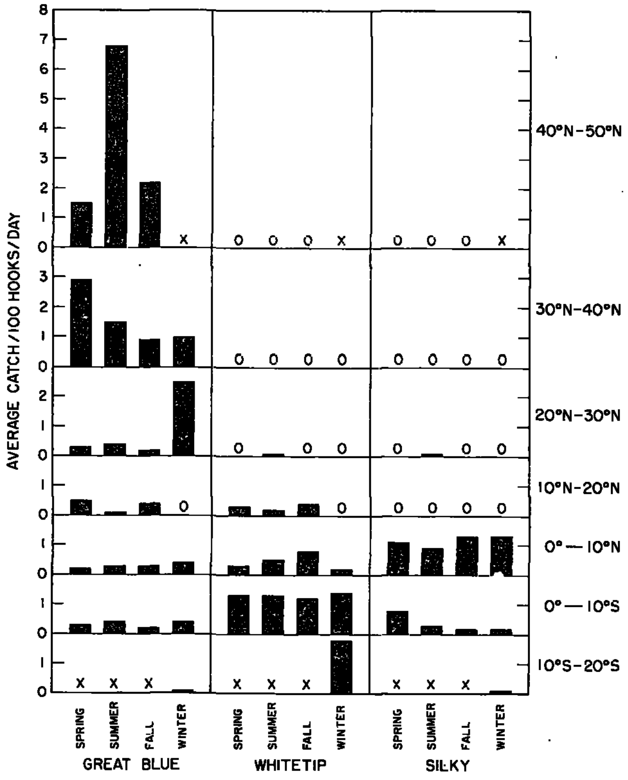

Figure 5.—Abundance of pelagic sharks by latitude and season. Based on 2,512 great blues, 1,187 whitetips, and 2,176 silkies. X=no fishing effort, O=no catch.

When the seasonal aspects of great blue distribution are considered (fig. 5), it appears that fluctuations are small or absent in the warm waters between 20° N. and 20° S. Between 20° N. and 30°

N. the species is most common in the winter, from 30° N. to 40° N. in the spring, and from 40° N. to 50° N. in the summer. These varying spatial and temporal concentrations indicate a north-south migration of this species, and judging from the relative constancy of its numbers in the Tropics, we deduce that temperature changes are their basis.

As pointed out by Shomura and Otsu (1956) there exists in the North Pacific a latitudinally shifting transition zone between the relatively cold Aleutian Current and the relatively warm North Pacific Current. This zone lies between latitudes 31° N. and 36° N. in the winter, and between latitudes 41° N. and 46° N. in the fall (fig. 6). Shomura and Otsu (ibid.) indicate that albacore move north and south with the advance and retreat of this zone, and the present data show that great blue sharks do also. Most of the larger catches of the great blue were made in or just south of the transition zone in water with surface temperatures ranging from 56° to 74° F., depending on the season (fig. 6). This range of surface temperatures cannot be considered as limiting their geographical occurrence because many great blues were taken from deeper, cool water in the Tropics (see p. 344).

Returning to figure 5, seasonal migrations of the great blues apparently extend only as far south as 20° N., although the absence of these sharks from the winter catch between 10° N. and 20° N. may indicate that migration also occurs there. With the onset of autumn a return southern migration presumably takes place, but this may occur outside the fishery since it is not evident from the catch data. It would seem that the number of northern migrants is augmented from populations extralimital to this study, otherwise it is difficult to explain the disparity between summer abundance at 40° N.–50° N. and spring abundance at 30° N.–40° N.

There is also the likelihood that the increase in numerical abundance in the areas to the north is the result of females giving birth to young. Large numbers of very small great blues were captured by longline in the areas during the spring, summer, and autumn. The smallest of these were about a foot and a half in total length, exactly the same size as large embryos (p. 354), and there can be little doubt that they were born shortly before capture. Unfortunately, length measurements were not routinely recorded for sharks and it is impossible to state what percentage of the popu-

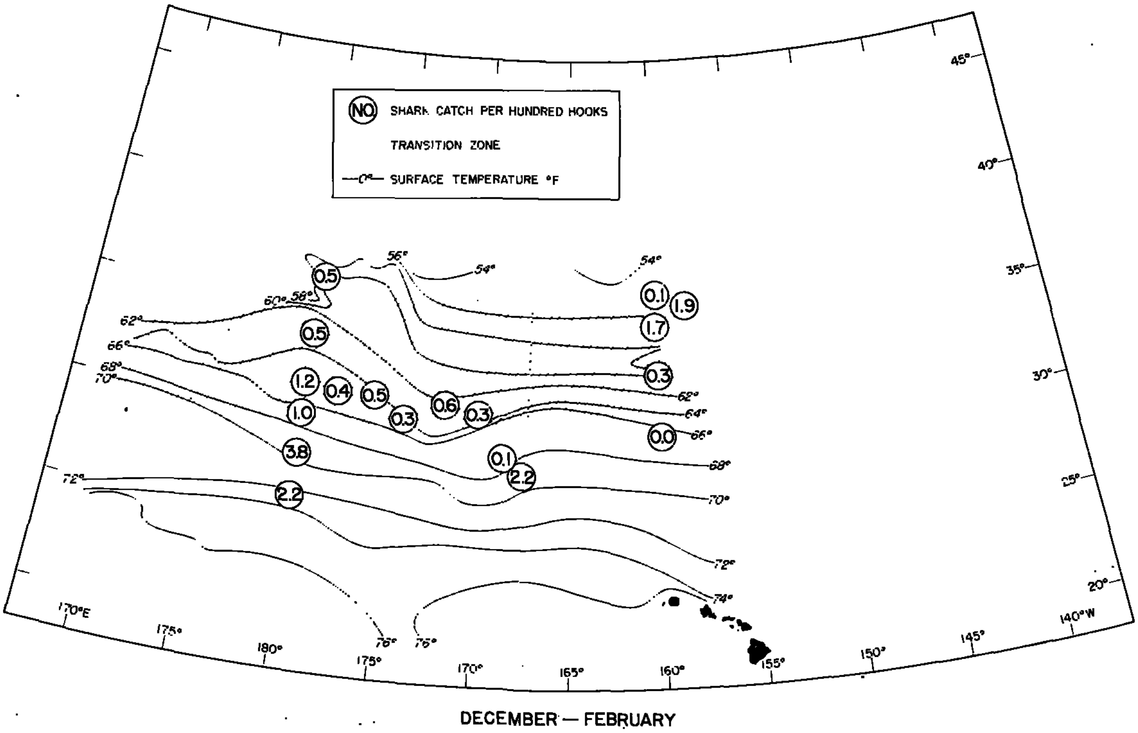

FIGURE 6a.—Relation between the great blue shark catch rate and position of transition zone, December–February. (After Shomura and Otsu, 1956.)

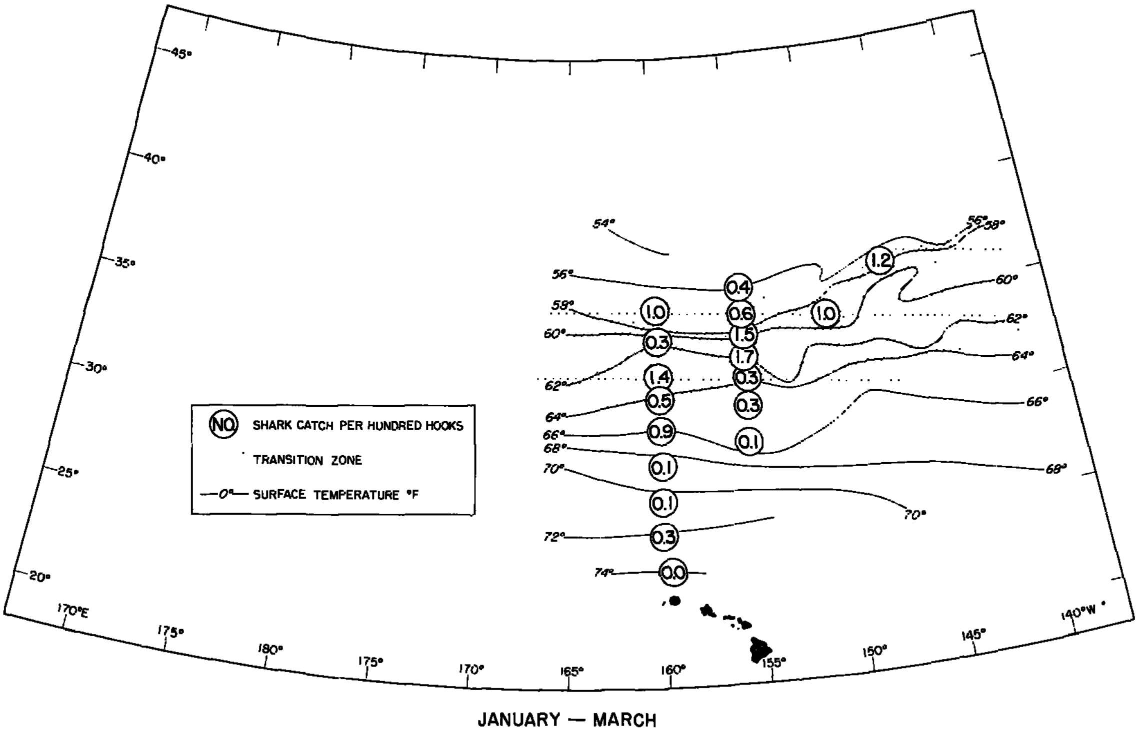

FIGURE 6b.—Relation between the great blue shark catch rate and position of transition zone, January–March. (After Shomura and Otsu, 1956.)

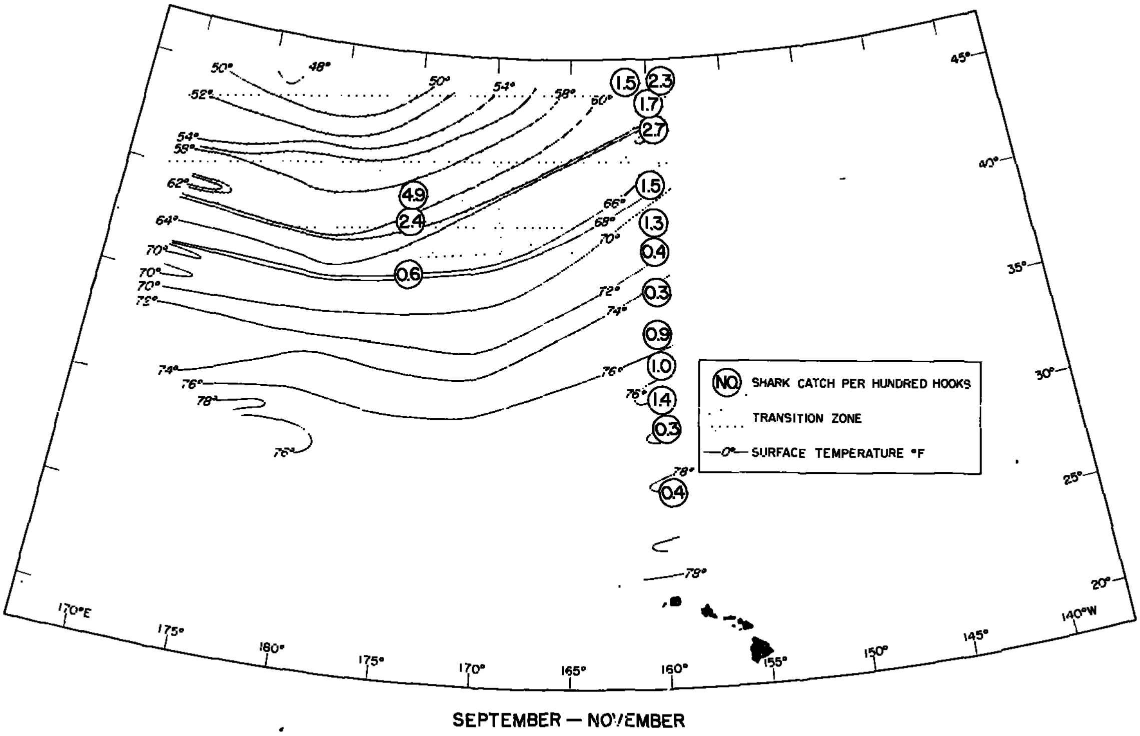

FIGURE 6c.—Relation between the great blue shark catch rate and position of transition zone, September–November. (After Shomura and Otsu, 1956.)

lation was newly born. The fact that small great blues were rarely encountered in warmer waters suggests that migrations may be a reproductive phenomenon having a close relation to the position of the transition zone.

The present data are inadequate for a discussion of the longitudinal aspects of migration.

The whitetip and silky sharks, occurring as they do solely within the Tropics, do not exhibit marked fluctuations in abundance. Figure 5 indicates that, within the limits of our sampling, whitetip numbers are greatest between 0° and 10° S., whereas the area of maximum silky concentration lies between 0° and 10° N. In neither region is there much change in numbers during the year. The significance of the large winter catch of whitetips between 10° S. and 20° S. cannot be determined until more seasons are represented in the catch data. Peripheral to these areas of concentration there is some evidence of seasonal fluctuations, the whitetip being more numerous in the summer to the north, and the silky more numerous in the spring to the south. Finally, the most northerly records of each species were obtained in the summer.

DISTRIBUTION BY DEPTH

Although the use of chemical sounding tubes to ascertain the fishing depth of the longline (Graham and Stewart[1]) is now standard procedure on POFI cruises, such information was not available for the majority of the cruises on which this report is based. The vertical distribution of sharks has accordingly been evaluated from the relative depth of the hook of capture. The use and applicability of this method have been discussed by Murphy and Shomura (1953a, 1953b, 1955) and Shomura and Murphy (1955), and the treatment employed here is similar to that used by these authors. Hooks were classified as shallow, intermediate, and deep, but because the number of hooks per basket varied between cruises it was necessary to weight each category in inverse proportion to the number of hooks involved. The arrangement of hooks within a basket for the three types of longline used and the relative hook depths are illustrated in figure 7. Table 2 summarizes hook number, relative depth, and relative weight for the three types of gear considered.

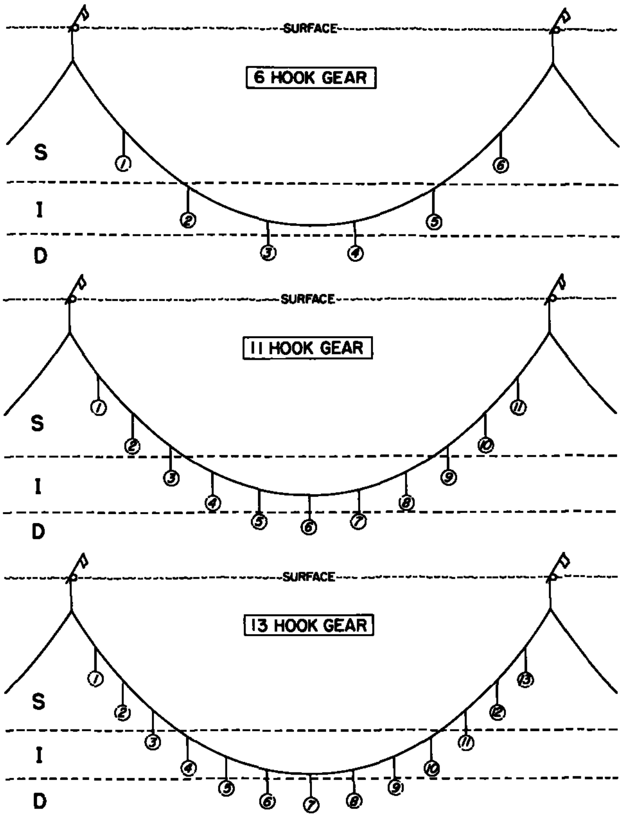

FIGURE 7.—Arrangement of a unit (basket) of each of the three types of longline employed in this study, showing floatlines, mainline, hook-bearing dropper lines, and the general lay of the gear with respect to the surface. Relative hook depths are indicated as shallow (*S*), intermediate (*I*), and deep (*D*).

TABLE 2.—*Depth assignment of hooks*

Type of gear	Relative depth and hook number			Relative weight applied to depth categories
	Shallow	Intermediate	Deep	
6-hook	1, 6	2, 5	3, 4	1:1:1
11-hook	1, 2, 10, 11	3, 4, 8, 9	5, 6, 7	¾:¾:1
13-hook	1, 2, 12, 13	3, 4, 10, 11	5, 6, 7, 8, 9	1:1:⅘

The actual depths implied by shallow, intermediate, and deep have been estimated from the data of Murphy and Shomura (1953a), Iversen and Yoshida (1957) and Stewart and Graham,[2] for 6-, 11-, and 13-hook gear, respectively. Although the depth categories are not strictly comparable between the three gear types, the following ranges are illustrative of the depths sampled:

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[1] Estimating the maximum fishing depth of longline gear with chemical sounding tubes, by Joseph J. Graham and Dorothy D. Stewart. U. S. Fish and Wildlife Service. (Manuscript.)

[2] Unpublished data in files of Pacific Oceanic Fishery Investigations.

shallow, 160 to 280 feet; intermediate, 280 to 430 feet; and deep, 370 to 500 feet. Pooling of results from different kinds of longline gear was minimized by selecting data by latitude and gear type. All catch records from north of 30° N. latitude were derived from 13-hook gear, whereas the majority of records south of 20° N. latitude were based on 6-hook gear, with a few catches from 11- or 13-hook baskets. Between 20° N. and 30° N. latitude the catches from only 11- and 13-hook gear were analyzed. Shark catch expressed as percentage occurrence on shallow, intermediate, and deep hooks is presented graphically in figure 8.

The great blue is wide-ranging and as such would be expected to be broadly eurythermal (fig. 3). The depth distribution data shown in figure 8 are at variance with this in that they show the species as being taken mainly on shallow hooks in the northernmost parts of its range, and mostly on deep hooks south of the Equator. Numerous observations of free-swimming great blues confirm this depth distribution picture, for the species was frequently seen swimming at the surface in the north but never so in the Tropics (not even in pursuit of a hooked and bleeding tuna). This shift in vertical distribution is possibly an example of "tropical submergence," and implies a narrower degree of eurythermality for the species. Lines of evidence supporting this idea are as follows.

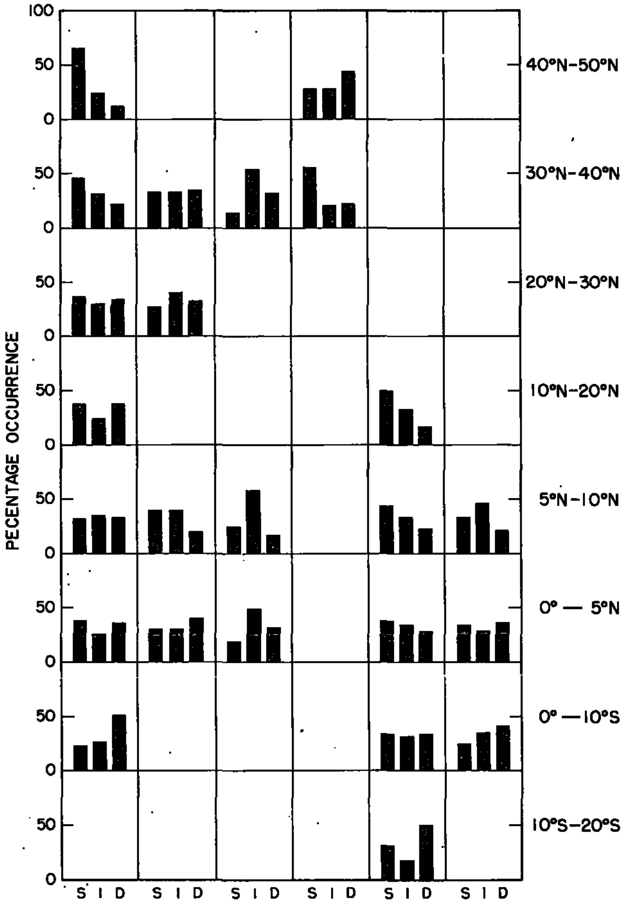

FIGURE 8.—Vertical distribution of pelagic sharks by latitude. Histograms depict percentage occurrence on shallow (S), intermediate (I), and deep hooks (D). Data are based on following catches: 1,318 great blues, 33 bonitos, 486 whitetips, 311 silkies, 27 mackerels, and 62 threshers.

Stewart and Graham[3] have calculated temperatures for the depth of capture of 1,200 great blue sharks taken north of 25° N. From their data the frequency of occurrence of great blues in 5-degree temperature categories was as follows:

Temperature:	*Frequency of occurrence great blue shark*
40° to 44° F	5
45° to 49° F	311
50° to 54° F	524
55° to 59° F	285
60° to 64° F	44
65° to 69° F	24
70° to 74° F	7

Ninety-nine percent of the above sharks were from temperatures between 45° and 69° F., and 86 percent were captured in or below the thermocline. These temperature data are biased to an unknown degree on the cold side (they were derived from estimated maximum hook depths), but they nevertheless indicate that temperatures between about 45° and 69° F. are preferred by the great blue shark. When the depths of the 45°–69° F. isotherms are examined by latitude (c. f. McGary et al., 1956; Cromwell 1954) it is seen that isotherms in the range 50°–69° F. follow the vertical distribution of the great blue (fig. 8). These isotherms either reach the surface or are very shallow between 40° N. and 50° N. latitude but gradually deepen to the south, ultimately lying as deep or deeper than the deepest hooks (this occurs between 20° N. and 30° N. where the isotherm depth range is roughly 500–800 feet). The 50°–69° F. isotherms continue at this depth as far south as the scope of this study except for a marked shallowing at about 10° N. latitude where they ap-

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[3] Unpublished data in files of Pacific Oceanic Fishery Investigations.

proach to within 200–600 feet of the surface. Their broad depth range here renders their shoaling insignificant, and the great blue's depth distribution does not show an accompanying shallowing.

Another factor which could account for the increased surface abundance of the great blue to the north is a pronounced seasonal increase in the food supply. Although no direct measures of the standing crop of shark forage (principally small fish and squid) are presently available, an idea of its potential magnitude can be obtained from variations in zooplankton abundance (McGary et al., 1956: 24–26). Between Midway Island and 40° N. latitude zooplankton volumes were about equal for oblique hauls from 0 to 40 meters, which sampled entirely above the thermocline, also for hauls made from the surface to 140 meters and hence, reaching or penetrating the thermocline; in addition, the average volume per haul was uniformly small (16–27 cubic centimeters per 1,000 cubic meters strained) at these latitudes. Between 40° N. and 45° N. latitude the shallow hauls yielded about 1.5 times as much zooplankton as the deeper hauls, and the volume of the catches increased to an average of 64 and 44 cc., respectively. From 45° N. to 50° N. latitude, the shallow hauls caught 1.75 times as much zooplankton as the deeper hauls, and average volumes increased to 168 and 98 cc., respectively. This marked increase in surface zooplankton toward the north is similar in general respects to the distributional picture seen in the sharks themselves.

The vertical distribution of bonito, mackerel, and thresher sharks, shown in figure 8, is based on few records and is probably not very reliable. Bonito and thresher sharks appear to be eurythermal, but three species are involved in the latter and the status of each is dubious. The only explanations offered for the apparent latitudinal shift in vertical distribution of the mackerel shark are (1) that the data may be misleading because of the small sample size (12 and 15 specimens), or (2) that both the shallow- and deep-hook catches were from about the same temperature. With reference to the data of McGary et al. (1956), it is seen that between 40° N. and 50° N. latitude at certain depths the isotherms are very steep so that both the deep and shallow hooks could fish in water of the same temperature.

In common with the other species occurring in the equatorial area, neither the whitetip nor the silky shark shows much latitudinal change in vertical distribution. The whitetip appears to be principally a surface dweller north of the Equator and more bathypelagic to the south, whereas the silky is almost uniformly distributed in depth to the north and is more deep-swimming to the south. The shoaling of the 60°–70° F. isotherms to 200–400 feet at about 10° N. latitude (Cromwell 1954) may explain the whitetip's shallow distribution in that general area, and similarly the deepening of isotherms south of 5° S. latitude could account for both sharks' deeper occurrence there.

VARIATIONS IN ABUNDANCE WITH LONG-TERM TEMPERATURE CYCLES

In the foregoing paragraphs frequent mention has been made of temperature as a factor regulating the spatial distribution of certain sharks. It is of interest, therefore, to examine abundance fluctuations in an area where temperatures are well known and relatively constant, and where shark numbers might be expected to vary directly or indirectly (through food chains, competition, etc.) with slight thermal changes. The region selected for this was the band of equatorial water extending from about 175° E. longitude to 110° W. longitude and bordered by 10° N. and 10° S. latitude. Shark catches from this region were segregated by species, year, and month, reduced to an effort basis, and plotted as anomalies between monthly means and the 4-year mean for each of the three common species. Similar data for surface temperature have been compiled by T. S. Austin, who has kindly made them available to this study. It should be noted, however, that the temperature anomalies are derived from a 6-year mean. Figure 9 shows the relation between shark abundance and temperature fluctuations.

As can be seen from figure 9, the years 1952 and 1953 were characterized by relatively warm surface temperatures (although quite variable in 1952), and 1954–55 by relatively cold conditions. The abundance of both whitetip and great blue sharks was greater during the warm years and lesser during the cold years, the same situation as found for yellowfin tuna.[4] Silky shark abund-

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[4] Murphy and Shomura, unpublished data.

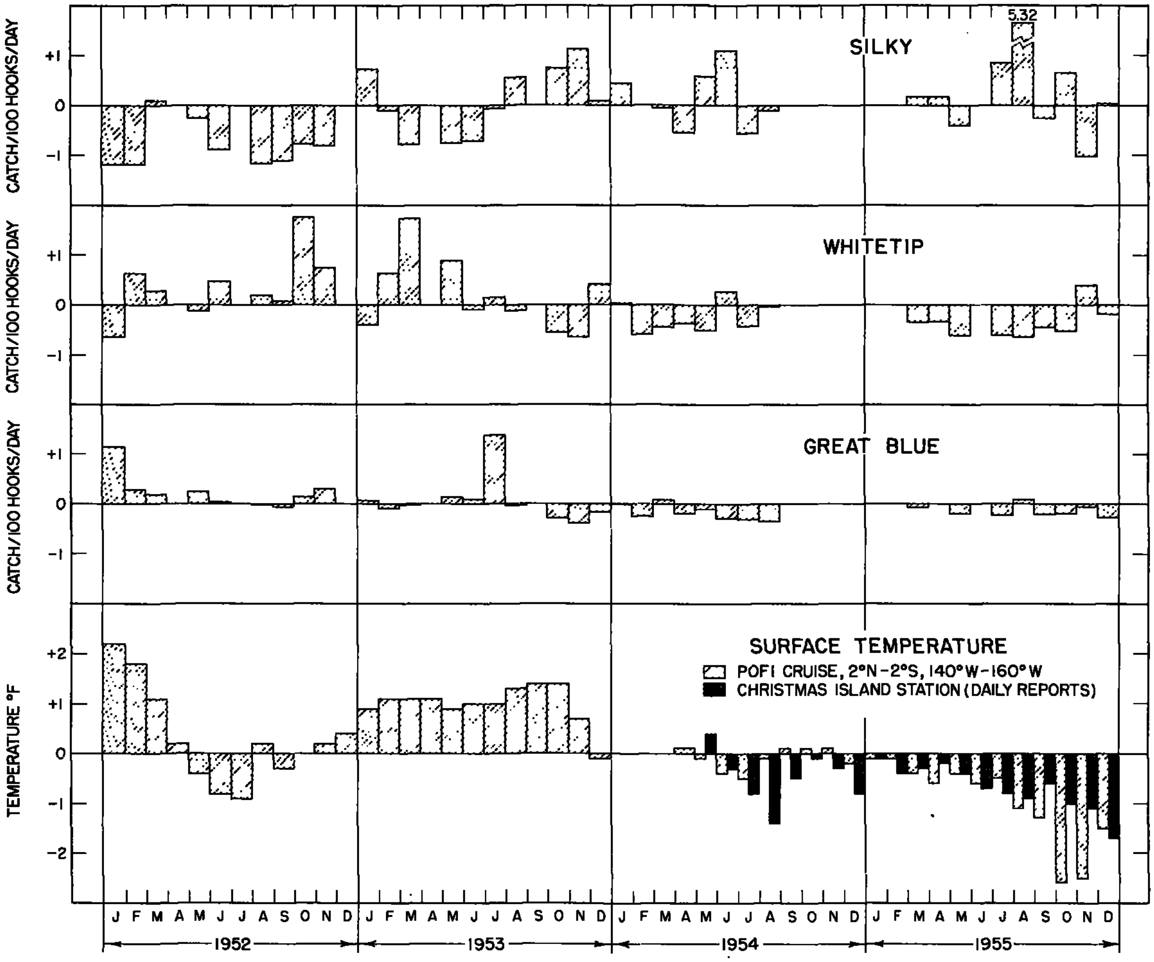

Figure 9.—Relation between shark catch and surface water temperature in the equatorial area. Shark histograms depict monthly deviations from 1952–55 means, based on entire catch between 10° N. and 10° S. latitude. Temperature histograms show monthly deviations from 1950–55 means.

ance, on the other hand, appears to be complementary to the other two, but why this should be so is difficult to understand. From the standpoints of latitudinal and depth distribution (figs. 3 and 8), the silky and the whitetip are similar although the silky shark has a narrower latitudinal range. One would assume, on an a priori basis, that the silky was more dependent on warm temperature than the whitetip, and would further deduce that a reduction in its numbers would be brought about by colder rather than warmer water.

Perhaps a portion of the irregularity in the catch data stems from sampling artifacts, for several types of longline gear were in use and fishing was both insular and oceanic. In several instances where whitetip and great blue abundance was anomalous with respect to temperature (notably the last 6 months of 1953) silky shark abundance retained its complementary relation to the other two species, and did not follow the temperature fluctuation. This may represent a behavioral interaction between the silky shark and one or more of the others. A similar situation involving these same sharks is discussed in a later section dealing with abundance versus distance from land.

VARIATIONS IN ABUNDANCE WITH LONGITUDE IN THE EQUATORIAL PACIFIC

A large portion of POFI's research program has been devoted to an evaluation of the fishery resources of the equatorial region of the central Pacific. Intensive sampling of fish stocks, plankton, and the physical and chemical environment has been undertaken, and a considerable body of knowledge of the interrelationships of these properties has been assembled. Physically the region is characterized by the easterly flowing Equatorial Countercurrent between 5° N. and 10° N. latitude, and by the westerly flowing South Equatorial Current to the south of this. Between 5° N. and the Equator there exists a zone of enrichment which reaches optimum conditions, biologically speaking, between 140° W. and 160° W. longitude. Here the sequence of trade winds, divergence, and upwelling brings nutrient-rich water into the euphotic zone, with a resultant increase in biological productivity. An increase in abundance in this area has been shown for zooplankton (King and Demond, 1953), tuna (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955), and sea birds (King and Pyle, 1957) so it would not be surprising to find a similar increase in the number of pelagic sharks.

To examine further the geographic variation in shark abundance the catch records for all species were reduced to terms of average catch per hundred hooks per day for 5-degree intervals of latitude and 10-degree intervals of longitude between 10° N. and 10° S. latitude, and 175° E. and 110° W. longitude (fig. 10). The 4,133 records considered include 2,174 silky, 1,151 whitetip, 641 great blue, and small numbers of bonito, thresher, hammerhead, and blacktip sharks. Because of the effects of land on species composition the species data were pooled.

In the region of the Equatorial Countercurrent (5° N. to 10° N. in the central Pacific) shark numbers generally decreased from east to west, the configuration of this decline being nearly identical to that found for zooplankton volumes (King and Hida, 1957). A difference between the zooplankton and shark abundance patterns is that the former peaks at 140° W. and declines east of that point, whereas shark abundance appears to be minimal at 140° W. and to rise to the eastward. Because of the generally close correlation between shark numbers and zooplankton volumes it would seem that basic food abundance, and not temperature or proximity to land (see p. 348) is the factor influencing shark distribution in the Countercurrent area. King and Hida (loc. cit.) state that the east-to-west decline in zooplankton parallels a decrease in surface enrichment caused by a slackening of wind and deepening of the thermocline.

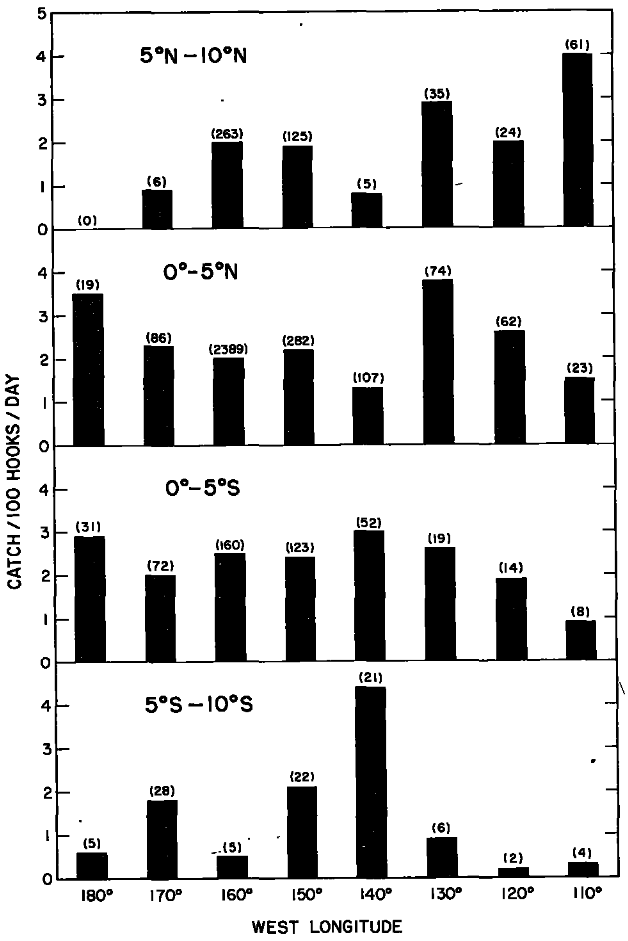

FIGURE 10.—Abundance of pelagic sharks in equatorial waters, all species combined. Each histogram depicts abundance for the area 5 degrees on each side of the numbered coordinate of longitude and within each 5-degree band of latitude. Numbers in parentheses represent actual catch.

Between 5° N. and 5° S. (South Equatorial Current) there are two types of distributions in the biotic indices. One involves a gradual doming of abundance with maximal values occurring between 140° W. and 160° W., the other the reverse situation with minimal values occurring at these central longitudes, and increases to the east and west. King and Hida (1957) found the first type for yellowfin tuna and zooplankton, and it also occurs for sharks between the Equator and 10° S. (fig. 10). The second situation obtains for inorganic phosphate (King and Hida, loc. cit.) and for sharks between 5° N. and the Equator. It is difficult to reconcile these seemingly antithetical patterns, for one would presume the distribution of organisms high in the food chain to correspond closely to that of the nutrients below them. Perhaps the decline in shark numbers at 140° W. longitude is brought about by food competition between sharks and yellowfin tuna. As shown by Murphy and Shomura (1955), yellowfin are particularly abundant at this longitude between the Equator and about 7° N. latitude. South of the Equator there is close agreement between the longitudinal distributions of sharks, yellowfin tuna, and plankton.

SHARK DISTRIBUTION WITH RESPECT TO LAND

The effect of land or proximity of land on the distribution of a pelagic marine animal provides an interesting problem. For certain oceanic species the presence of land acts only as a barrier to movements, whereas others congregate about islands and other land masses to feed or to reproduce. It occasionally happens that oceanic fish abound in insular environments, either because of the islands' intrinsic nutritive richness or because they lie in the path of rich oceanic currents. The latter situation is apparently true for Christmas Island, a member of the Line Islands group. Here an atoll is located in the path of flow of enriched equatorial water, and maximum abundance of yellowfin tuna occurs in a narrow band extending from Christmas eastward for several hundred miles (Sette 1955).

The POFI longline surveys have provided information on the distribution of sharks in relation to nearness of land. Proximity to land was determined by measuring the distance between the noon position of a fishing station (recovery of longline gear usually started at noon) and the nearest portion of Christmas Island. Shark abundance in neritic situations is contrasted with that of the open ocean in figure 11.

Three distributional patterns are apparent for the sharks shown in figure 11. The thresher sharks (3 species) are definitely neritic, their abundance falling close to zero 40 miles from shore. The silky shark (noted as semipelagic, Springer 1950) occurs in moderate numbers on the high seas but is about twice as plentiful in the neritic region. Two sharks, the whitetip and the great blue, are truly oceanic species, and their numbers steadily increase as land is left behind.

The zone delimited by the categories 10–19 and 50–59 miles from land is essentially a region where the physical and ecological characteristics of the neritic and oceanic provinces intergrade. It is of interest that in this transitional area none of the sharks considered exists in the same degree of abundance as it does in more landward or seaward locales. Perhaps the intermediate nature of the physical environment favors neither the neritic nor the oceanic species, or perhaps abundance fluctuations represent biotic interaction between one or more sharks and other organisms. If the latter, then interaction is most likely in the realm of food competition, for predation and other immediately deleterious relationships are probably inconsequential for large sharks.

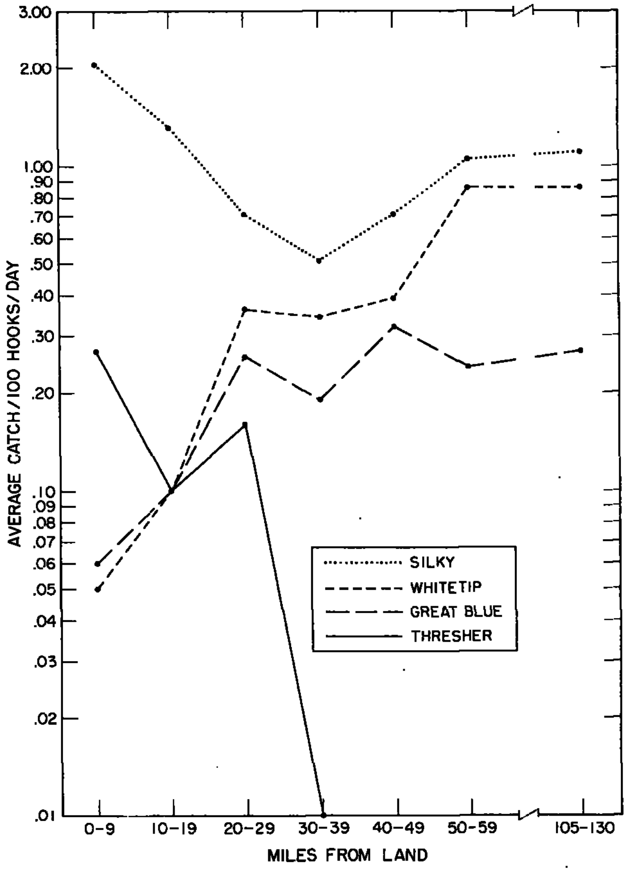

FIGURE 11.—Abundance of pelagic sharks with regard to distance from land. Data derived from Christmas Island area and region to eastward between 1° N. and 3° N. latitude. Based on 997 silky, 210 whitetip, 133 great blue, and 86 thresher sharks.

The species of sharks discussed here subsist principally on small fish and squid and have this diet in common with yellowfin tuna (Reintjes and King, 1953) and bigeye tuna (King and Ikehara, 1956). As to swimming speeds, it would appear almost certain that the tunas are much faster than the sharks, and that among the sharks themselves there may be considerable differences in speed. It has been suggested that whitetips are relatively slow swimmers compared to silky sharks (Backus et al., 1956), with the whitetip's cruising speed being estimated at about a mile an hour by Strasburg (1957). Also confirming this slowness is the fact that, although several silky sharks have been taken while trolling at 6 to 8 knots, only 1 whitetip was so captured during several thousand hours of trolling by POFI vessels. This lack of speed would place the whitetip in an unfavorable competitive position with both the yellowfin tuna and the silky shark, the abundance of each of which increases as Christmas Island is approached (see Shomura and Murphy, 1956 for yellowfin data). It appears, therefore, that the generally inverse relation between whitetip and silky abundance shown in figure 11 may represent a competitive interaction between the two.

FOOD HABITS OF PELAGIC SHARKS

The fact that sharks are broadly carnivorous is common knowledge, but the food of many of the pelagic species is not particularly well known. Unfortunately, the stomach contents of longline-caught sharks were not routinely examined by POFI, and as a consequence the ensuing discussion is not based on a large body of data. Another factor reducing the number of records is that more than half of the 265 stomachs examined were empty. A summary of the results of our food study is presented in table 3.

As evidenced by the information in table 3, pelagic sharks subsist mainly on small fish and squid. Bigelow and Schroeder (1948) and Backus et al. (1956) have shown that the whitetip and bonito sharks also consume large fish such as tuna, and this is also indicated by the present data. In the present case, however, it could not be determined whether tuna were only preyed on after they had been hooked. The more neritic silky shark included littoral forms such as *Diodon* and crabs in its diet, and other sharks did the same in suitable locales. One tendency not shown in table 3 is that a number of thresher sharks were foul-hooked by the tail. Their capture probably resulted from attempts to herd the dangling bait with their tails (Breder 1929).

Pelagic sharks as a group are opportunistic feeders, commonly taking almost any available food, and often ingesting articles of little or no nutritive value. Several species tend to congregate around ships, and have been seen to swallow such items as paper cartons, tin cans, and scraps of cloth, along with considerable amounts of

TABLE 3.—*Food of longline-caught sharks*

Shark species	Number of stomachs in which occurred—																									Number of empty stomachs	Number of stomachs examined
	Fish													Longline bait			Flying fish eggs		Cephalopods			Miscellaneous					
	Alepisaurus (Lancet fish)	*Neothunnus* (Yellowfin tuna)	*Katsuwonus* (Skipjack)	Unidentified tuna	Tuna-like fish	*Diodon* (Spiny puffer)	*Mola* (Ocean sunfish)	Bramids (Pomfrets)	Echeneids (Sucker fish)	Myctophids (Lantern fish)	Ostracids (Trunkfish)	Stingray	Unidentified fish	Herring	Sardines	Unidentified bait	Attached to feathers	Unattached	Squid	Octopus	Unid. cephalopods	Crabs	Shrimp	Sea bird (booby)	Blubber (?)		
Great blue	5								1	1	1		25	4	10		4	2	19	1	20	2	2	1	1	76	140
Whitetip	2	1		2				1				1	6	2	24				10	1	2					35	73
Silky						2							1		2				3			1				22	29
Bonito	1	1			1		1						1			1			2							6	13
Thresher	1		1										3	2					1							2	7
Blacktip													1													0	1
Hammerhead:																											
S. zygaena				1																						0	1
S. lewini													1						1							0	1
Total	9	2	1	3	1	2	1	1	1	1	1	1	38	8	36	1	4	2	36	2	22	3	2	1	1	141	265

garbage and fish scraps. The indiscriminate nature of this type of feeding suggests a low degree of visual (and olfactory?) acuity coupled with voracious feeding behavior, both of which are well known for sharks, and which would seem to belie their ability to capture squid, tuna, and sea birds unless these were moribund or dead. On the other hand, the author has seen a team of 2 or 3 whitetips slowly herd and capture squid around a surface light at night, and has also removed large pieces of tuna flesh from whitetip stomachs in areas where no fishing was taking place. Finally, a bigeye tuna (*Parathunnus sibi*) captured on a POFI longline cruise bore a pair of large U-shaped scars suspiciously resembling shark jaws in shape. The indications are that some pelagic sharks can be both fast moving and selective feeders, and perhaps the unpredictable rapacity of their feeding enables them to capture what would seem to be elusive, highly motile prey.

Some mention must also be made of a rather artificial food habit of sharks, namely the damage they inflict on longline-caught tuna. Other workers have noted that damage is virtually absent from the more northerly portions of POFI's investigative area (Shomura and Otsu, 1956) but averages about 20 percent of the longline catch in equatorial waters (Murphy and Shomura, 1955; Iversen and Yoshida, 1956). It is obvious that shark damage to hooked tuna is ultimately limited by both shark abundance and the availability of tuna, and that the interaction of these two factors coupled with the behavioral characteristics of sharks is what determines the extent of the damage. For the purposes of the present study all species of longline-caught tuna (*Neo-*

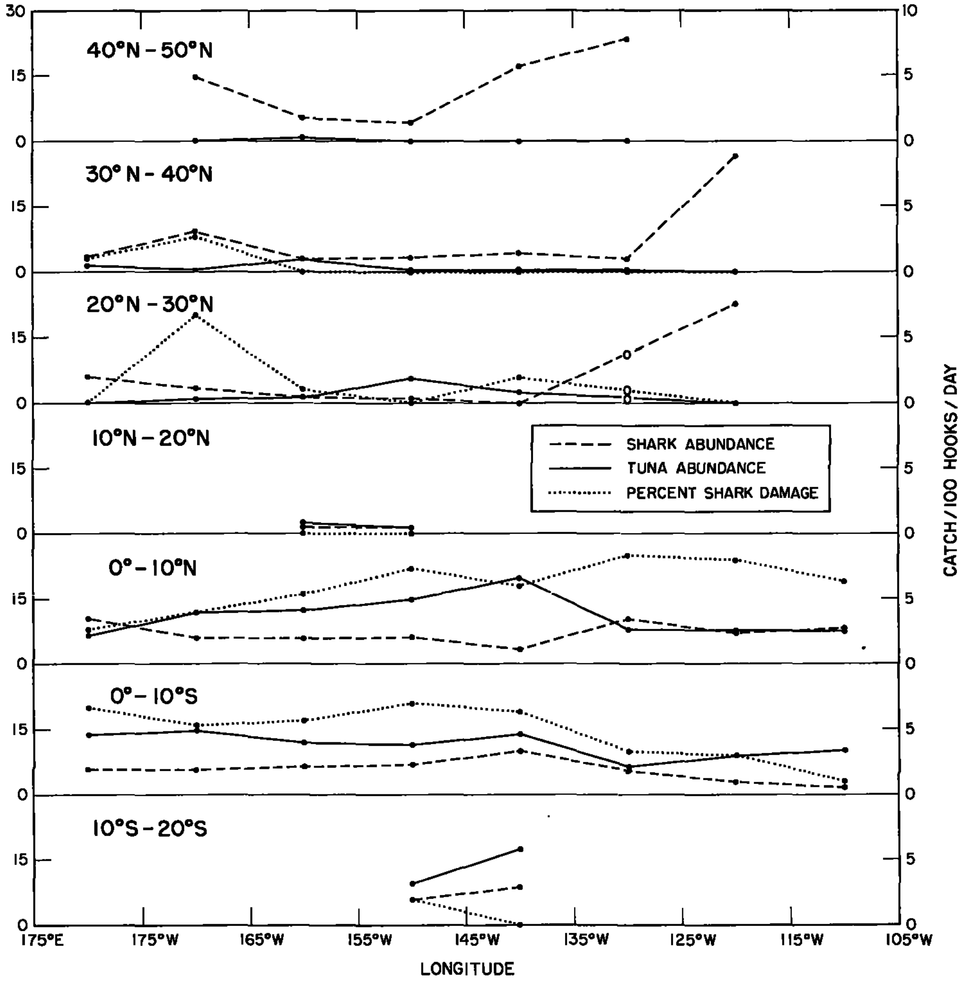

FIGURE 12.—Shark damage to tuna contrasted with shark and tuna abundance. 0=no sample.

thunnus macropterus, *Parathunnus sibi*, *Germo alalunga*, and *Katsuwonus pelamis*) are lumped as "tuna," and all shark species are combined.

North of about 30° N. latitude POFI's longline tuna catch has been minimal, and shark damage affected only about 1 percent of it (fig. 12, and Shomura and Otsu, 1956). Between 20° N. and 30° N. latitude tuna abundance increased whereas shark damage was only slight or moderate (fig. 12). The prominent peaking of shark damage between 20°–30° N. latitude and 165°–175° W. longitude is an artifact caused by a very small sample (1 damaged tuna out of 5 caught). In these northern areas the abundant shark is the great blue (fig. 3), and it would seem that this species is not particularly deleterious to the fishery, other accounts to the contrary (c. f. Bigelow and Schroeder 1948: 286).

In equatorial waters tuna abundance is equal to or greater than shark abundance (fig. 12), and shark damage is at its greatest here, frequently involving as much as 20 percent of the tuna catch. The principal culprits in this region are the whitetip and silky sharks, with the bonito being of much less importance (figs. 3 and 4, and numerous observations by POFI biologists). From the equatorial situation one might suppose a good positive correlation to exist between shark and tuna abundance, but this was not found by Iversen and Yoshida (1956). These authors found a strong relation between shark catch rate and shark damage on a monthly basis, but this breaks down, in part, when studied on a nonsecular basis. When tuna abundance is low there is a correlation (r=0.573) between shark abundance and shark damage (fig. 13), but when tuna abundance is high there is almost no relation between the two (r=0.019). A possible explanation of these phenomena is that an abundance of tuna probably indicates an abundance of forage organisms so that a large natural food supply (either tuna or forage) is available to the sharks. The sharks are well-fed and not interested in longline-caught fish. Conversely, a dearth of tuna and other forage animals would enhance the attractiveness of hooked tuna, and proportionally more of the catch would be eaten by sharks.

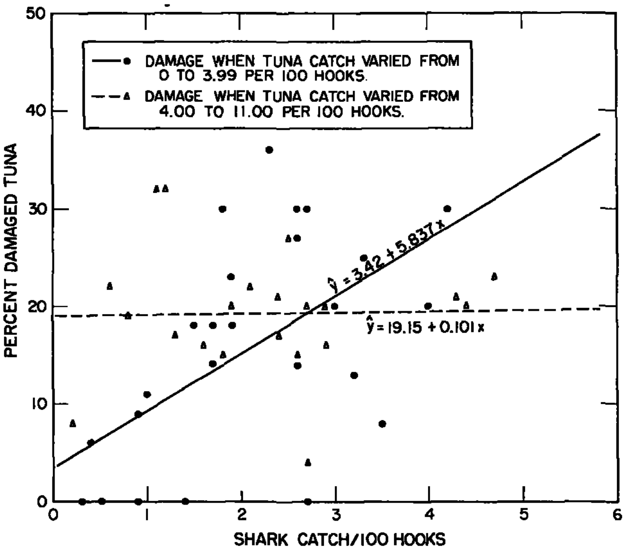

FIGURE 13.—Relation between shark damage of longline-caught tuna and shark abundance. Based on catch records of 8,797 tuna (of which 1,511 were damaged) and 4,133 sharks. All catches made between 10° N. and 10° S. latitude. When tuna catch low, b=5.837, p <0.01; when tuna catch high, b=0.101, p >0.5.

SEXUAL SEGREGATION

Among sharks there appear to be two basic types of sexual segregation or tendency to school by sex. In behavioral segregation individuals school with others of similar size, thus sorting the sexes in the case of a dimorphic species such as *Squalus acanthias* (Ford 1921). In what has been called geographical segregation (Backus et al., 1956) the sexes school separately because of differences in habits. Geographical segregation has been found for *Scyliorhinus canicula* by Ford (op. cit.), for the soupfin (Ripley 1946), for *Galeorhinus australis* by Olsen (1954), the great blue (Bigelow and Schroeder, 1948), and the whitetip (Krefft 1954; Backus et al., 1956). These authors have related geographical segregation to season, region, depth, distance from land, and degree of sexual maturity, with the underlying causative factor generally being regarded as reproductive in nature. In two cases (Olsen 1954; Backus et al., 1956) the existence of definite breeding grounds has been mentioned.

The present data are scanty as to sex of the sharks caught, but nevertheless they indicate that both behavioral and geographical segregation may occur in the same species. This study is primarily restricted to the great blue because sex was not recorded for adequate numbers of the other species. An inherent fault in the data is that because of the length of the longline gear (7 to 10 miles in each set) a single day's catch may actually contain samples from several schools.

Table 4 illustrates the degree of unisexual predominance in the catches from 36 longline stations where sharks were sexed and at least 4 specimens of a species were taken. In the great blue shark the sex ratio varied from about 1:1 to a tremendous preponderance of one sex. The data on the whitetip and the silky were not so extensive and did not show this degree of variability.

TABLE 4.—*Instances of unisexual predominance in shark catches* [1]

Species and number of specimens examined	Frequency of occurrence of predominant sex (in percent)					
	50-59	60-69	70-79	80-89	90-99	100
Great blue (283)	6	3	5	3	2	10
Whitetip (29)		1	2	1		1
Silky (11)				1		1

[1] Units are number of stations showing predominance. The smallest station considered yielded 4 sharks of any one species.

In determining whether preponderance of either sex was of the behavioral or geographical type of segregation the great blue shark data were analyzed in several ways. When the percentage of males was plotted by latitude (fig. 14), males comprised a smaller proportion of the northern catch than they did of the southern. This difference is most striking when the unisexual catches are considered, but it is also apparent in mixed catches and the entire catch (unisexual and mixed data pooled). There can be no doubt that latitudinal variation in sex ratio represents geographical segregation but the biological aspects of this phenomenon are not so easily classified.

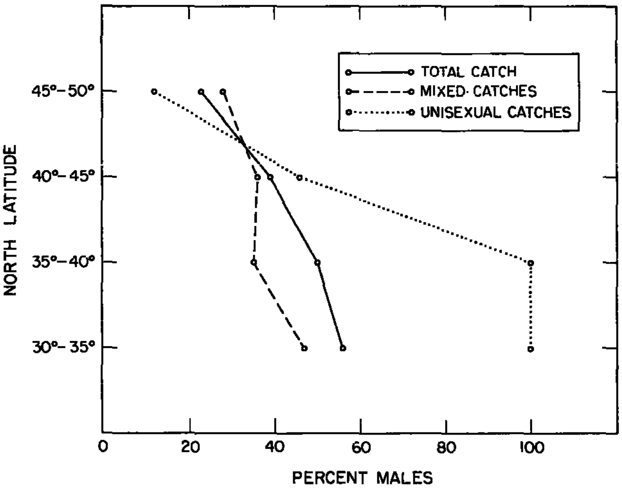

FIGURE 14.—Sex composition of great blue shark catch by latitude. Based on 255 records of which 184 were from mixed and 71 from unisexual catches.

If the mean total length of great blues is plotted by sex and latitude (fig. 15), it appears that in mixed catches (pooled from several stations) both sexes are about the same size at any latitude, and the mean length decreases to the north. The lengths of sharks from unisexual catches are slightly to considerably greater than those of mixed catches, but there is little relation between the lengths of males and females. If our catches actually represent schools then it is not illogical to presume that unisexual schools are derived from mixed schools by a behavioral size-sorting mechanism. Judging from the overlap between the standard deviations of mixed and unisexual school lengths, this mechanism becomes operative at lengths between about 110 and 160 centimeters. It is unlikely that segregation of such small sharks has a direct reproductive significance, for the smallest gravid females known were from 208 to 214 cm. in length (Bigelow and Schroeder, 1948, and in this paper p. 354).

Because the causative agent for behavioral segregation is thought to be size dimorphism between the sexes (Backus et al., 1956), it was reasoned that the difference between male and female lengths in individual mixed catches should be related to the sex ratio of the catch. This relation is shown in figure 16 which indicates that the greater the size difference between the sexes the greater the disparity in sex ratio. Where females are larger than the males most of the catch is male, and where males are larger than the females most of the catch is female. A similar situation obtains for the soupfin shark (Ripley 1946). Such a situation not only poses the question of why large sharks should be of opposite sex from the rest of the school, but it is also rather contrary to the principal tenet of behavioral schooling, that members of a school be of like size. The regression in figure 16 is significant (p=0.02) only when the two points to the extreme left are included.

The available data are too few to form more than an outline of the secular aspects of sexual segregation. They are derived from a sample of 255 great blues taken between 30° N. and 50° N. latitude over a period of several years. Both mixed and unisexual catches were made in the

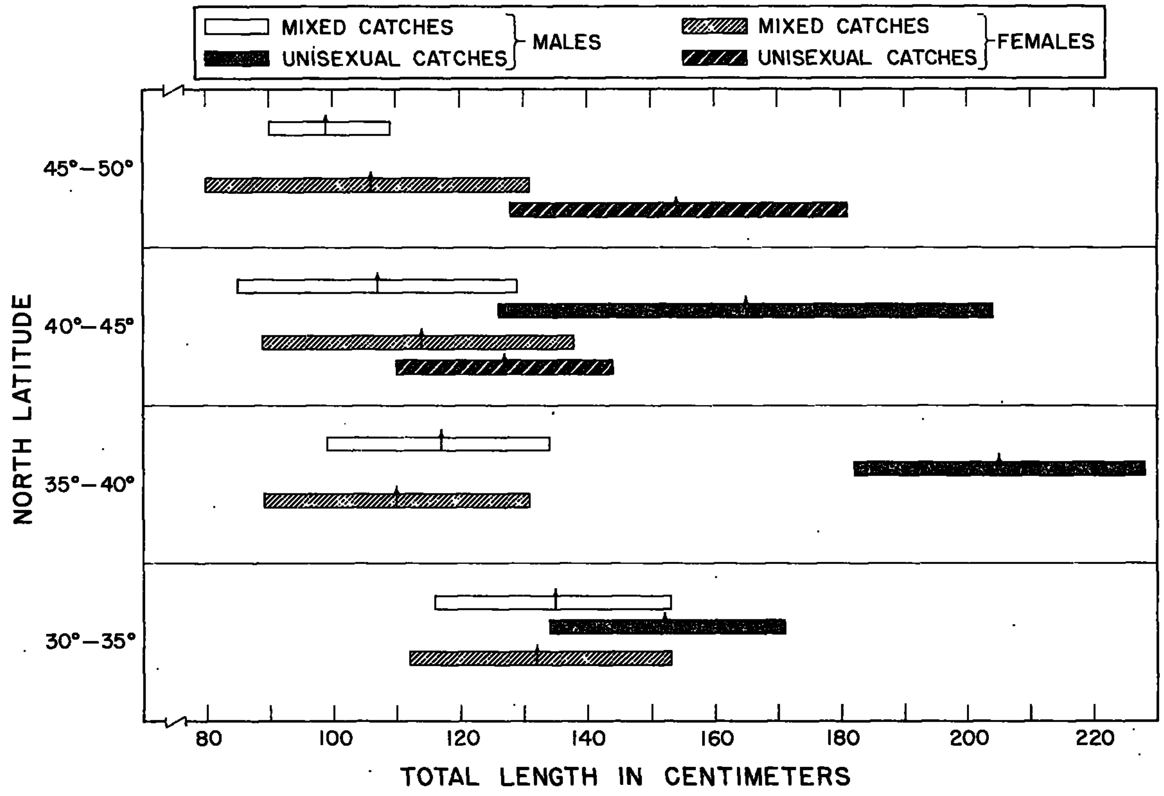

FIGURE 15.—Length composition of unisexual and mixed catches of great blue sharks at various latitudes. Vertical lines are means; blocks are one standard deviation on each side of mean.

summer and autumn but only mixed catches were taken in the winter and spring. On a percentage basis mixed catches contained the following proportions of males: spring 36 percent, summer 33 percent, autumn 22 percent, and winter 47 percent. The autumnal disparity in sex ratio is also of interest in that the two unisexual catches made in that season were composed of males. The low male ratio in summer mixed catches is similarly reflected in the unisexual data, for here only 2 all-male (versus 4 all-female) catches were made. From these sketchy data it appears that the great blue catch is composed of about equal numbers of both sexes in the winter, and that females gain predominance in the spring. Unisexual schools form during the summer and autumn and probably reassemble as mixed schools in the winter. The data are too few to present a latitudinal picture of these changes.

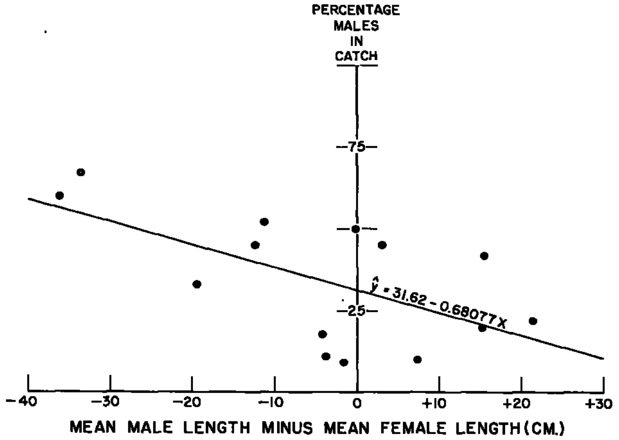

FIGURE 16.—Relation between sex and size composition of individual mixed great blue shark catches. Based on 172 sharks taken in catches containing from 5 to 24 individuals. Regression line fitted by method of least squares.

When the mean lengths of great blues are plotted by sex and season (fig. 17), it is evident that autumn is not only the period of greatest disparity in sex ratio but is also the time of greatest length difference between the sexes. Unfortunately, the data were necessarily derived from pooled mixed and unisexual catch records and are thus rather unreliable (in the case of unisexual records there is no particular reason for

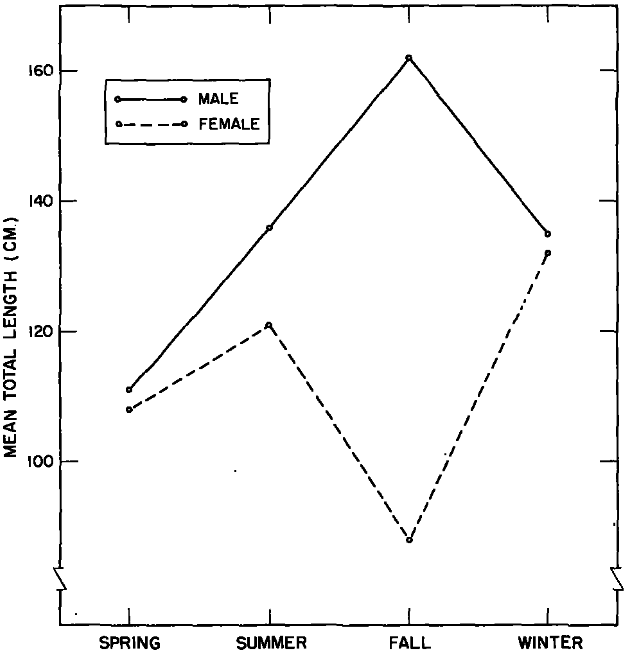

FIGURE 17.—Mean total length of great blue sharks by sex and season. Based upon 112 males and 143 females from mixed and unisexual catches taken between 30° N. and 50° N. latitude.

one school to resemble another in its length composition). The increase in mean length over the spring-to-fall interval probably reflects an availability fluctuation more strongly than growth.

REPRODUCTION

The available data on reproduction in the female are based on observations on the following: 18 great blues, 19 silkies, 32 whitetips, and 4 threshers (2 *A. pelagicus*, 1 *A. vulpinus*, 1 *A. superciliosus*). All of these except 6 great blues and 1 whitetip were taken in equatorial waters, with most specimens coming from the Line Islands area. Although the data are meager they are presented because of the general lack of knowledge of the reproductive habits of pelagic sharks.

Of the 12 great blue sharks from the equatorial Pacific the smallest gravid female measured 214 cm. and the largest 244 cm. Nongravid females from this region ranged from 188 to 243 cm. in total length. Embryos were found during February, March, May, August, October, and December, with the largest fetuses (22–28 cm.) occurring in March and May. Nongravid females as large or larger than the pregnant ones were encountered from January through August. The number of embryos per female ranged from 4 to 38, and in 1 litter of 18 their distribution was 8 on the left side and 10 on the right. There was no apparent correlation between embryo size and time of year.

The 6 nonequatorial great blue females were taken between 24° N. and 35° N. latitude. The 4 gravid specimens ranged from 208 to 247 cm. in total length and contained from 23 to about 40 embryos, the distribution of which was bilateral (16 on the left side and 17 on the right in 1 specimen). All 6 females were taken in January and February and here again there was no relation between embryo size and time of year. One female obtained in February gave birth to between 30 and 40 pups on deck (fig. 18), and these were the largest great blue embryos taken, suggesting that they were very near term. Further confirming this conclusion is the fact that their length range (34–48 cm.) approximates the foot-and-a-half length of the smallest longline-caught great blues. Also, the pups were very active at birth and appeared ready to fend for themselves. All emerged tail first.

All 19 female silky sharks were taken from the equatorial region, and of these 12 were gravid and 7 not. Both gravid and nongravid females were taken throughout the year, the range in total length of the former being 213 to 236 cm., and of the latter, 186 to 218 cm. The number of young observed varied from 2 to 11, with a mean value of 6.5 per female. The total length was recorded for 32 embryos and ranged from 37 to 66 cm., the upper extreme suggesting that the pups are quite sizeable when born. There again appeared to be no relation between embryo size and time of year. Uterine distribution of embryos was recorded for 2 females, one of which had 4 embryos on each side, the other having 2 on the left and 5 on the right. The single litter sexed contained 2 male and 7 female embryos.

Only 3 of the 32 female whitetips examined contained embryos, these 3 being equatorial specimens. A 210-cm. specimen was taken in April and contained 6 fetuses from 36 to 40 cm. in total length, a 196-cm. female obtained in May had five 20- to 28-cm. embryos, and a 195-cm. female taken in December contained 7 averaging 18 cm. in total length. These fragmentary data suggest a rather different developmental picture from that noted by

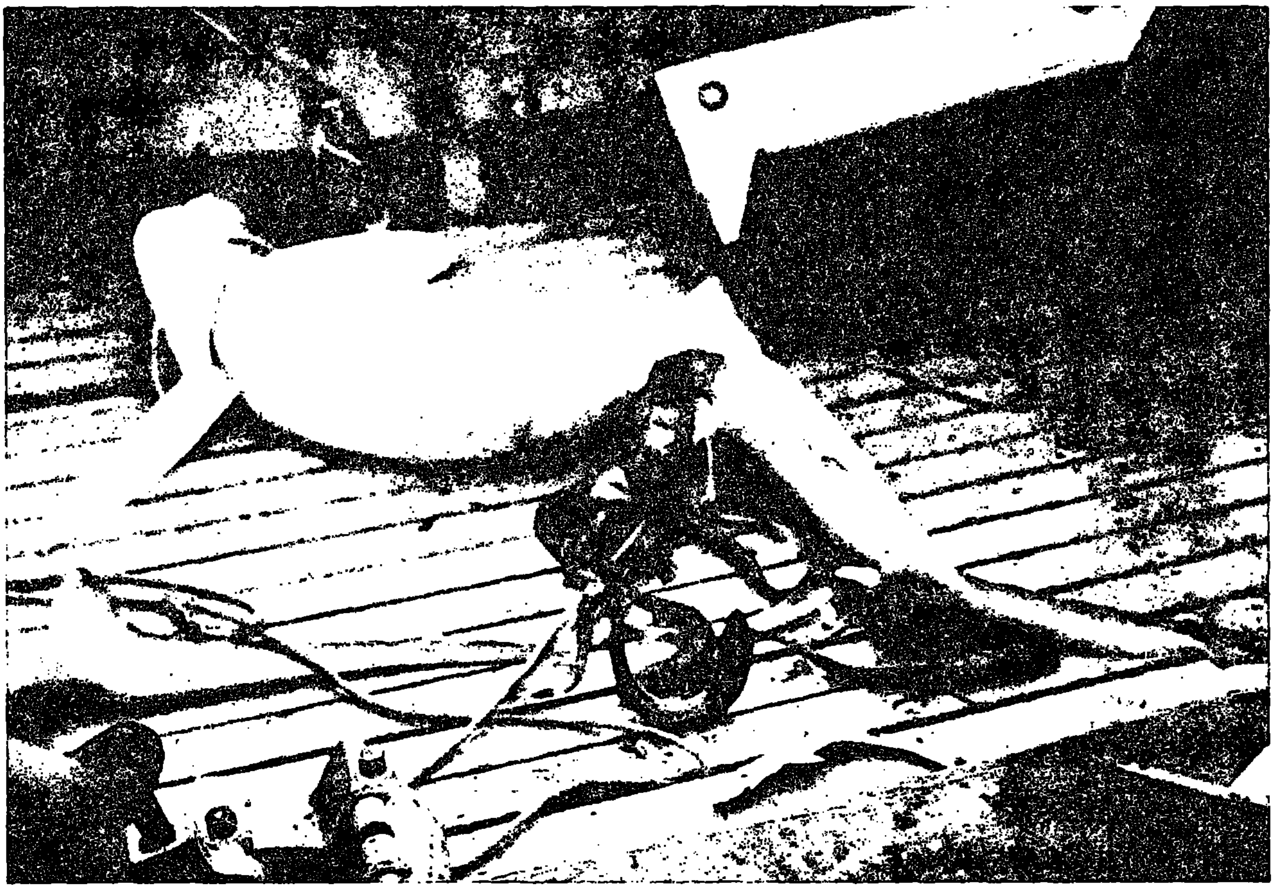

Figure 18.—Female great blue shark giving birth to young on deck of the *John R. Manning*. Nine young can be seen on deck while a tenth, still enveloped in its embryonic membranes, is just emerging.

Backus et al. (1956) for the whitetip of the Gulf of Mexico and the West Indies, as the central Pacific embryos were rather small at all times of the year. One Hawaiian and 28 equatorial whitetip females contained no young. These infertile females were taken throughout the year and ranged in length from 99 to 246 cm.; about one-fourth of this group were as large or larger than the gravid females.

With regard to thresher sharks, the single female *Alopias vulpinus* examined was captured on June 4, 1954, just to the west of Christmas Island (Line group). This thresher measured 315 cm. in total length and contained 2 fetuses, one of which was 114 cm. in total length. Also present were a number of eggs about 0.7 cm. in diameter. Two females of the rather uncommon *A. pelagicus* were examined, the larger (893 cm. total length) being taken on April 7, 1955, off Fanning Island (Line group), and the smaller (167 cm.) on May 4, 1953, at about 9° N. latitude and 150° W. longitude. The larger female contained the apparently typical number of 2 embryos (see Nakamura 1935), and the smaller one was not gravid. On June 7, 1954, a nongravid female of *A. superciliosus* was taken near Christmas Island. Its total length was 328 cm.

MORPHOMETRY AND TAXONOMY

In the early part of the shark investigation morphometric data were recorded for a number of specimens of each species. In order to make these data comparable to those of other investigators, measurements were standardized with those given by Bigelow and Schroeder (1948). Figure 19 depicts the methods used for measuring certain characters; other measurements follow. Eye diameter — greatest horizontal diameter; labial furrow length—length of outer labial furrow; gill slit height—height of gill opening when

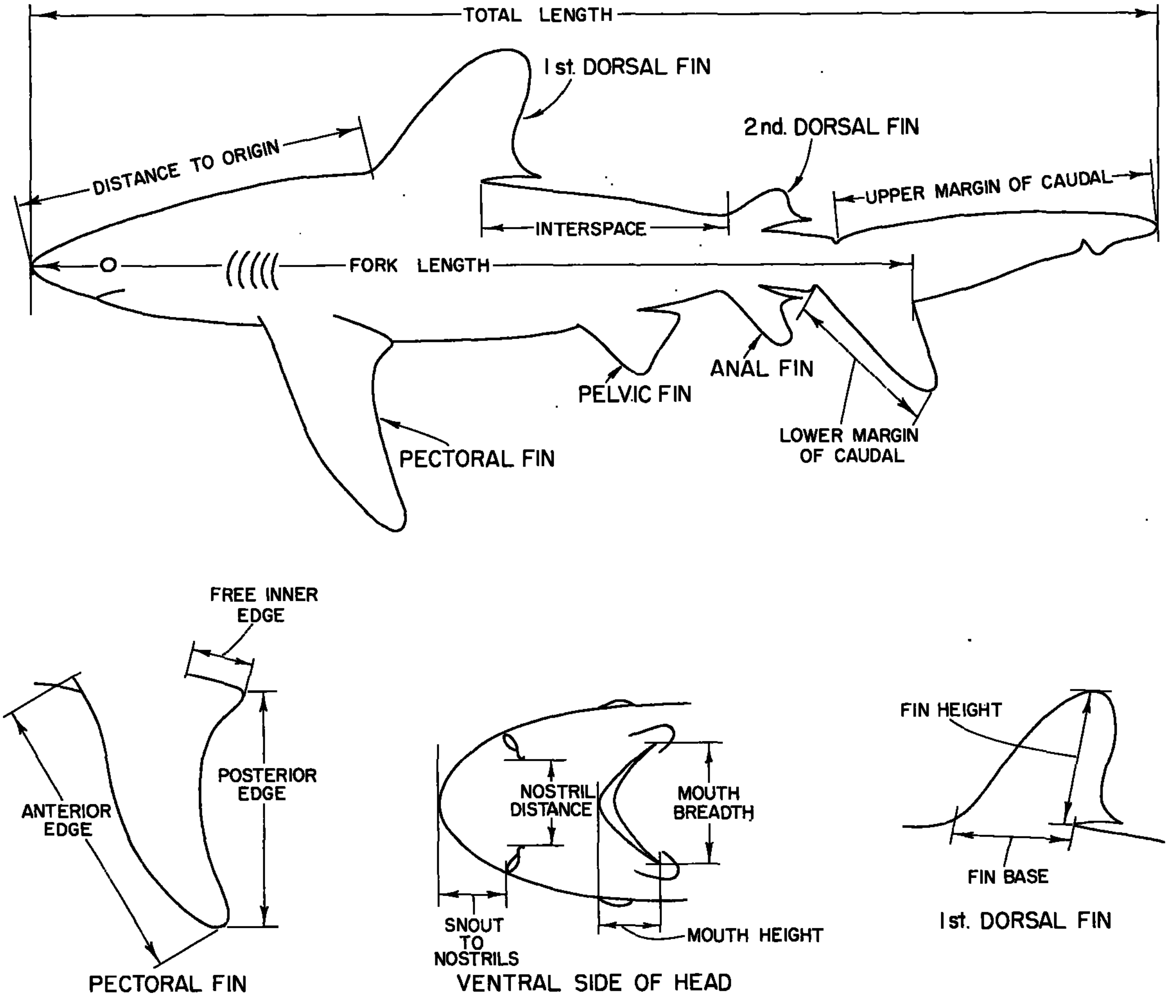

FIGURE 19.—Method of measuring sharks. All distances are straight lines between perpendiculars, with fish lying on belly when possible.

stretched just enough to prevent buckling of anterior edge; trunk breadth and height—maximum breadth and height at pectoral origin; lower margin of caudal—distance from rear edge of ventral precaudal pit to tip of lower caudal lobe; free clasper-distance from point where clasper leaves anal fin (lateral side) to tip of clasper.

Table 5 summarizes the morphometric data obtained in this study. For the common species the mean and the range are given for each character considered, although the range was not necessarily derived from individuals of maximal and minimal length. The original data were tabulated by sex, but with a very few exceptions overlapping was complete or nearly so, and it did not appear necessary to segregate the final data in this manner.

The volume of morphometric data available for whitetip, silky, and great blue sharks makes possible a comparison between the central Pacific and other forms. Morphometric data for Atlantic specimens were obtained from Bigelow and Schroeder's descriptions (1948) even though these were derived from only a few specimens. For all three species it appears that in the Pacific specimens the distance between the snout and all fins except the anal is greater than in Atlantic material, and also that the second dorsal, the anal, and the upper caudal lobe are smaller in the Pacific. In Pacific whitetips the lower caudal lobe and the various pectoral fin measurements are relatively greater than in the Atlantic, whereas in Pacific silkies and great blues these structures

Table 5.—*Shark morphometrics*

[Values expressed as hundredths of total length. Columns indicating range express the range for each character, and not the measurements of the largest and the smallest shark. See pp. 355–56 for measurement methods]

Item	Whitetip (8 males, 8 females)			*P. insularum*[1]	Silky (7 males, 5 females)			Great blue (17 males, 5 females)			Bonito (11 males, 2 females)			Mackerel (1 male, 1 female)	Thresher (*A. pelagicus*) (1 male, 2 female)	Thresher (*A. superciliosus*) (1 female)	Thresher (*A. vulpinus*) (1 female)	Hammerhead (*S. zygaena*) (1 male)	Hammerhead (*S. lewini*) (1 male)	Blacktip (1 male, 1?)
	Smallest	Largest	Mean	Type	Smallest	Largest	Mean	Smallest	Largest	Mean	Smallest	Largest	Mean	Mean	Mean					Mean
Total length (cm.)	72.0	243.1	116.0	213.0	87.7	227.0	192.7	121.7	304.5	234.3	125.1	257.9	205.9	96.0	290.2	327.7	317.0	266.3	301.8	143.2
Fork length	77.3	83.5	80.0	---	78.5	83.6	80.7	80.1	83.2	81.9	86.8	92.2	88.0	86.2	53.6	57.4	52.5	77.8	80.4	78.6
Snout—1 D	31.3	34.2	32.6	33.3	32.4	35.0	34.1	36.2	39.8	37.9	35.6	38.6	37.3	34.4	25.6	30.4	24.6	27.3	28.2	33.4
Snout—2 D	61.9	65.3	63.2	65.3	63.9	66.7	64.9	62.4	67.2	64.7	69.5	73.2	70.5	67.8	43.0	46.1	41.3	63.5	64.1	63.8
Snout—upper C	71.3	76.6	72.5	74.2	73.0	77.8	74.0	74.0	76.4	75.5	77.9	80.1	79.3	76.6	48.1	51.1	45.9	73.1	74.2	75.0
Snout—pectoral	20.9	24.2	22.5	22.5	20.7	23.7	22.0	19.8	25.0	22.1	23.5	28.0	26.3	29.8	14.4	15.8	14.6	19.8	19.6	20.5
Snout—pelvic	49.5	54.5	51.8	---	47.6	52.1	49.5	48.0	54.3	50.8	53.9	57.6	55.8	54.8	36.7	38.0	34.8	45.4	46.4	48.7
Snout—anal	61.8	66.2	63.8	---	61.8	65.8	64.0	61.4	67.5	64.0	70.2	74.1	71.7	67.6	44.6	48.9	43.7	59.8	61.4	63.6
Interspace 1 & 2 D	19.4	22.7	21.1	22.1	22.5	25.3	23.9	19.0	26.4	20.9	24.6	27.0	25.7	25.9	16.7	9.5	12.8	---	28.1	23.8
Interspace 2 D & C	5.4	7.9	6.4	6.0	6.6	7.9	7.1	7.1	10.0	7.7	7.7	9.0	8.4	7.8	4.1	4.6	4.5	8.5	8.2	7.2
Interspace A & C	3.9	5.1	4.5	3.8	5.3	7.3	6.5	6.9	10.0	7.4	7.2	9.3	7.8	7.8	3.0	2.7	3.1	7.8	7.8	6.5
Origin Pect.—pelvic	28.1	35.2	30.6	---	26.2	29.9	28.1	26.1	32.9	29.0	22.8	32.0	29.6	26.6	22.7	23.3	20.8	25.7	27.2	27.8
Origin Pelvic—anal	12.1	14.3	13.0	---	13.6	17.2	15.3	12.1	15.3	13.5	15.6	17.8	16.9	15.1	8.8	11.0	9.5	14.6	14.3	15.9
Snout—nostrils	2.5	3.4	3.0	---	3.4	4.7	3.9	3.4	4.9	4.2	4.3	5.4	4.8	5.2	2.8	3.1	2.8	---	4.1	3.2
Snout—mouth	6.1	7.3	6.8	---	6.5	8.4	7.1	7.9	10.4	8.6	6.2	7.2	6.6	6.7	4.2	4.5	4.1	4.5	4.1	6.4
Mouth breadth	8.8	10.1	9.3	---	7.4	8.9	8.4	3.0	7.7	6.4	6.4	7.9	7.1	9.5	3.4	4.2	3.6	7.4	7.2	8.8
Mouth height	4.1	6.1	4.9	---	4.1	6.0	4.9	3.0	4.9	3.8	5.4	6.9	6.1	5.6	2.3	2.4	2.0	3.4	4.7	5.4
Eye diameter	.9	1.8	1.3	---	.9	1.9	1.3	1.0	2.0	1.5	1.5	2.1	1.7	2.2	1.4	2.0	1.4	1.2	1.1	1.4
Nostril distance	5.6	6.0	5.8	---	5.1	5.8	5.3	3.3	3.8	3.5	3.3	4.6	3.7	3.8	1.2	1.5	1.2	20.5	20.7	5.4
Labial furrow length	0	2.2	.8	---	.4	1.1	.6	0	1.4	.6	0	3.7	2.1	1.6	1.9	.9	.6	---	.3	.6
Height gill slit 1	2.9	4.8	3.3	3.5	2.6	3.5	3.1	2.0	3.3	2.5	6.5	8.2	7.4	8.0	2.4	2.5	1.9	3.0	3.0	2.8
Height gill slit 2	3.4	4.7	3.8	3.8	2.9	4.0	3.3	2.1	3.7	2.9	6.5	8.2	7.3	7.5	2.6	2.7	2.1	3.2	3.2	3.1
Height gill slit 3	3.3	4.9	4.1.	4.1	2.9	4.4	3.5	2.3	3.7	2.9	6.3	8.0	7.2	7.5	2.7	2.9	2.2	3.2	3.4	3.2
Height gill slit 4	2.8	4.6	3.7	3.8	2.6	3.7	3.1	2.0	3.4	2.7	6.4	7.9	7.1	7.4	2.4	2.7	2.1	2.9	3.4	2.8
Height gill slit 5	1.9	3.8	2.7	2.7	1.9	3.0	2.4	1.3	2.7	1.9	6.7	8.1	7.4	6.8	1.7	2.4	1.8	2.0	2.4	2.2
Trunk breadth	12.0	14.6	13.1	---	11.2	13.1	12.1	9.0	12.1	10.4	10.9	14.4	12.4	16.2	7.1	7.1	7.9	9.0	10.3	12.0
Trunk height	7.8	14.8	12.4	12.1	10.5	12.2	11.4	8.5	12.6	10.6	11.8	15.3	13.7	18.3	10.3	9.2	9.3	11.6	11.4	11.6
Vertical height 1 D	10.0	14.4	12.9	---	7.5	9.4	8.5	6.2	9.3	7.6	8.6	10.1	9.6	9.8	6.2	7.5	6.6	12.4	12.6	9.0
Base 1 D	10.0	11.3	10.7	9.8	7.6	9.0	8.4	6.5	7.8	7.0	8.2	9.4	8.9	9.4	5.3	6.7	5.2	10.2	9.1	8.6
Vertical height 2 D	2.9	4.2	3.4	---	1.8	2.5	2.1	2.1	3.1	2.7	.9	2.0	1.4	1.7	.7	.6	.6	2.1	2.3	3.1
Base 2 D	3.0	3.9	3.4	3.0	2.1	2.8	2.4	2.6	3.8	3.5	.8	1.1	1.0	1.4	.6	.8	.6	2.5	2.3	3.6
Vertical height anal	3.3	6.0	4.3	---	2.3	4.0	3.2	2.5	4.3	3.4	1.0	2.2	1.6	2.0	1.1	1.3	.9	2.9	2.5	3.7
Base anal	3.5	4.7	3.9	4.2	2.8	3.3	3.0	3.1	4.3	3.7	.8	1.4	1.1	1.7	1.0	1.5	.8	3.8	4.0	3.9
Upper margin C	23.4	28.7	27.5	27.9	22.2	27.0	26.0	23.6	26.0	24.5	19.9	22.1	20.7	23.4	51.9	48.9	54.1	26.9	25.8	25.0
Lower margin C	12.5	14.7	14.0	14.1	11.4	13.5	12.6	11.1	14.0	12.2	15.2	17.4	16.2	16.6	7.0	---	6.6	12.7	12.8	11.6
Pect. ant. edge	21.5	26.1	23.8	18.3?	16.2	20.9	19.3	19.1	23.3	21.3	17.0	25.1	19.6	17.0	17.7	20.1	18.6	14.0	14.1	17.4
Pect. free inner edge	5.1	6.7	5.8	6.6	3.3	4.9	4.4	3.1	4.9	3.9	3.9	5.7	4.5	4.9	1.5	3.0	1.5	2.9	3.1	4.9
Pect. post. edge	19.1	23.4	22.4	17.4?	12.7	18.2	16.7	15.6	20.3	18.6	13.9	22.7	16.8	13.8	17.0	19.7	19.0	11.6	11.7	14.6
Free clasper	2.1	11.2	6.9	---	2.3	14.2	7.0	2.1	9.6	5.6	2.0	11.2	8.1	4.0	---	---	---	4.6	4.5	---

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[1] Data from Snyder (1904).

are generally smaller than in their Atlantic counterparts. The gill slit heights of Pacific specimens compare with the Atlantic forms as follows: Pacific great blues, larger; whitetips, smaller; silkies, about the same size.

The other species listed in table 5 either lacked Atlantic counterparts or were represented by an inadequate size range for comparative purposes. The present data for *Alopias pelagicus* are derived from a 354.3-cm. male and 2 females of 166.8 and 349.5 cm., total length. The mean values presented in table 5 agree fairly well with the measurements given by Nakamura (1935) for adult specimens from Taiwan, and where the means do not agree the range in our values (not given here) overlaps Nakamura's figures. Finally, our data for mackerel sharks (*Lamna ditropis*) are based on small specimens (95.8 and 96.1 cm., total length) and do not appear to be comparable to those of the Atlantic mackerel shark (*L. nasus*). For identification purposes it is of interest that our small *ditropis* have a basal lateral denticle on the teeth (as shown by Roedel and Ripley, 1950) but have relatively long snouts. The distance from the snout tip to the anterior edge of the eye is only slightly less than half the distance between the posterior edge of the eye and the first gill slit.

Another identification problem concerns the name to be used for the Pacific whitetip. Our data and those of other authors (Hubbs 1951, Krefft 1954) agree very well with descriptions of the Atlantic whitetip (*Pterolamiops longimanus*) given by Bigelow and Schroeder (1948) and Springer (1950), but there is a possibility that *P. insularum*, which was described from Oahu by Snyder (1904), actually represents the species under discussion. Snyder's measurements of the holotype have been converted to percentage values and listed in table 5 for comparative purposes, but these figures do not solve the problem. The principal differences between *insularum* and other Pacific specimens are in the morphology of the pectoral fin, with this structure being relatively small in *insularum*. This could be caused by either the type being an aberrant specimen, *insularum* being a distinct species, or doubtfully, by much different methods of measurement. It would seem that *longimanus* is the name to be applied to the whitetip reported on here unless future work reveals it to differ from the Atlantic form in some manner not considered at this time.

The length-weight relationships obtaining for the whitetip, silky, bonito, and great blue sharks are shown in figure 20. The data indicate that the whitetip, silky, and bonito sharks have nearly identical weights for any given length, but that the great blue is a lighter fish. In the original plots the data were segregated by sex, and in the

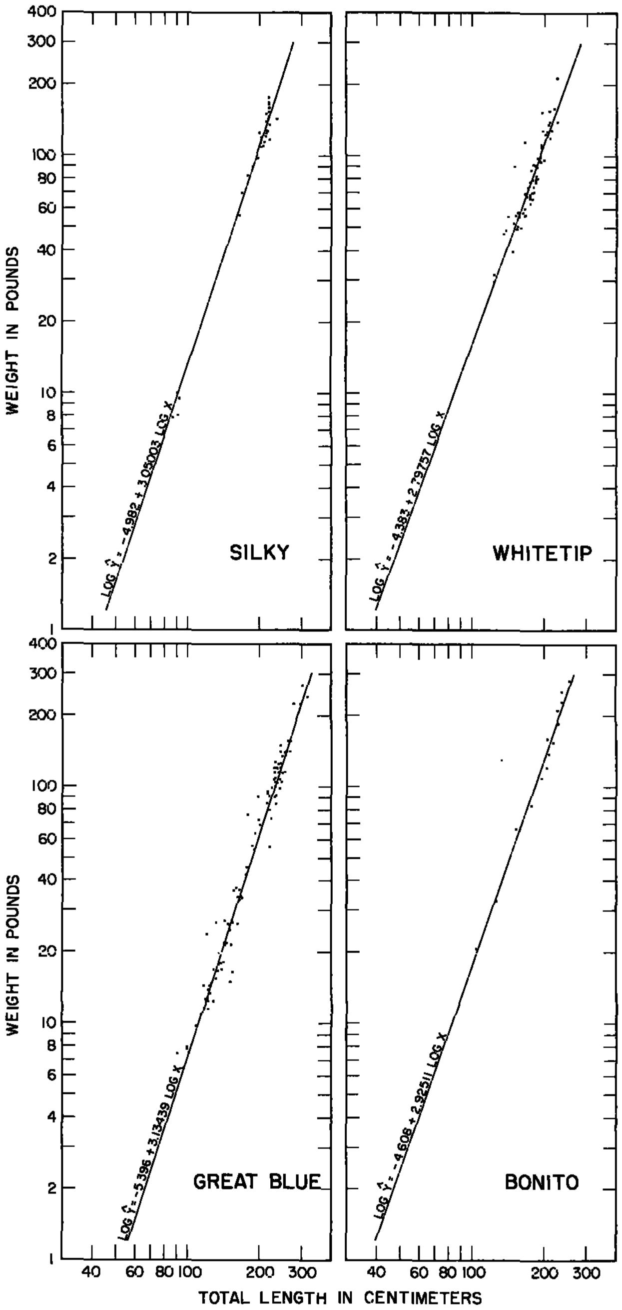

FIGURE 20.—Length-weight relationships for whitetip, silky, bonito, and great blue sharks.

great blue and whitetip sharks females were slightly heavier than males. This is to be expected, for some of the specimens were known to be gravid. The original data were also broken down by locale, but no differences in length-weight of the sharks were noticeable between those from the Line Islands, the Phoenix Islands, various isolated oceanic positions, and the west coast of Central America.

SUMMARY

1. This report is based on the catch records of 34 cruises made in the area between 50° N. and 20° S. latitude and 110° W. and 175° E. longitude during 1952–55. Of 6,118 sharks captured on longline gear, there were 2,512 great blues, 2,176 silkies, 1,187 whitetips, and 243 belonging to 9 relatively uncommon species.

2. The 12 shark species taken show considerable differences in range and abundance. The great blue and the bonito were wide ranging, the former being abundant, the latter uncommon; the whitetip and silky were abundant warm-water forms with the whitetip's range lying roughly between 20° N. and 20° S. latitude and the silky's more narrowly equatorial; the mackerel shark was uncommon and subarctic; the 3 species of thresher sharks were uncommon and equatorial, but may have broader ranges; and the soupfin, hammerhead (2 species), and blacktip were all rare in POFI's catches.

3. The great blue shark appeared to make pronounced northern migrations, probably reproductive in nature, during the warmer parts of the year. Migrations followed the advance and retreat of a transition zone between two major ocean currents. Whitetip and silky sharks were nearly uniformly abundant throughout the year. Their most northerly records were obtained in summer.

4. When the vertical distribution of sharks is analyzed by relative depth of hook-of-capture, the northern great blues are found to be taken principally by shallow hooks and the southern ones by deep hooks. The species apparently favors temperatures between 45° and 69° F. Perhaps also influencing the great blue's vertical distribution in boreal latitudes is the larger amount of food present on the surface. Bonito and thresher sharks were broadly eurythermal, whereas the mackerel appeared to be more nearly stenothermal. The whitetip was surface-dwelling north of the Equator and bathypelagic to the south; the silky shark was uniformly distributed at all hook depths.

5. In the equatorial region the great blue and whitetip sharks were more abundant during warm years than cold, but the silky shark appeared to be the opposite. This difference in abundance may represent a behavioral interaction rather than a temperature-induced phenomenon.

6. In the Equatorial Countercurrent (5° N. to 10° N.) overall shark abundance decreased from east to west between 110° W. and 175° E. longitude, paralleling the situation found for zooplankton volumes. Between 5° N. latitude and the Equator, total shark abundance was minimal at about 140°–150° W. longitude and higher on either side, whereas between the Equator and 10° S. latitude just the reverse occurred. The former situation is similar to that found for inorganic phosphate, the latter similar to that for tuna and zooplankton. The trophic relations obtaining in these situations remain to be demonstrated.

7. The silky and thresher sharks were more abundant near land, whereas the whitetip and great blue were more strictly oceanic, and declined in abundance near islands. There is some evidence for biotic interaction (food competition) between the silky and whitetip sharks in areas intermediate between the neritic and oceanic provinces.

8. All sharks examined were found to subsist principally on small fish and squid, and occasionally to ingest inedible objects. Some species probably capture live tuna on occasion.

9. In northern waters shark damage to hooked tuna averaged only about one percent of the catch, and the abundant shark there, the great blue, is regarded as rather harmless in this respect. In the equatorial area, damage amounted to about 20 percent, and was largely attributed to the silky and whitetip sharks. In this region damage was related to shark abundance only when tuna abundance was low. Shark and tuna abundance themselves were not correlated.

10. Several species of sharks tend to school by sex, and segregation of this type is known as behavioral when caused by size dimorphism between the sexes, or geographical when caused by other factors. The great blue, whitetip, and silky sharks

exhibit sexual segregation to the extent that catches may show a 1:1 sex ratio or may consist of solely one sex. For the great blue shark, males comprised an increasingly smaller proportion of the catch to the north, and the mean size of both sexes in mixed catches steadily decreased to the north, with both being about the same length at any latitude. In unisexual catches both sexes were larger than in mixed catches. In individual catches containing both sexes there was a tendency for a few large females to occur with numerous small males or vice versa. On a secular basis it appears that in the winter both sexes occur together in about the same ratio, females begin predominating in the spring, unisexual schools form in the summer and autumn, and reassembly of mixed schools takes place in the winter.

11. Gravid females of the great blue shark measuring from 208 to 247 cm. (total length) were taken throughout the year along with nongravid specimens of the same size range. The largest embryos were found in March and May but no pupping season could be demonstrated. The number of embryos ranged from 4 to about 40, with large pups (34 to 48 cm.) being of the same size as numerous longline-caught specimens. Gravid females of the silky shark, ranging from 213 to 236 cm., were taken throughout the year and were similar in size to nongravid specimens. The number of fetuses per female ranged from 4 to 11.

12. Detailed morphometrics were obtained from 16 whitetip, 12 silky, 22 great blue, 13 bonito, 2 mackerel, 5 thresher, 2 hammerhead, and 2 blacktip sharks. Pacific whitetip, silky, and great blue sharks differed from their Atlantic counterparts in having a greater distance between the snout and all fins except the anal, and also in having smaller anal, second dorsal, and upper caudal fins. Minor differences are shown for other characters, but none of these indicates a lack of conspecificity between the two oceans. The whitetip reported on is termed *Pterolamiops longimanus* on the basis of marked differences between it and the Hawaiian *P. insularum*.

13. Whitetip, silky, and bonito sharks have nearly identical length-weight relationships but the great blue is a lighter, more slender fish. No geographical differences were noted in length-weight.

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