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BIOLOGY OF THE WHITE SHARK

A SYMPOSIUM

MEMOIRS OF THE
SOUTHERN CALIFORNIA ACADEMY OF SCIENCES
VOLUME 9

(24 May 1985)



MEMOIRS OF THE SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

The MEMOIRS of the Southern California Academy of Sciences is a series begun in 1938 and published on an irregular basis thereafter. It is intended that each article will continue to be of a monographic nature, and each will constitute a full volume in itself.

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COVER: White shark, Carcharodon carcharias, at Dangerous Reef, south Australia. Photo by Al Giddings, Ocean Images, Ltd. ©

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National Marine Fisheries Service, Northeast Fisheries Center, Narragansett Laboratory, Narragansett, Rhode Island 02882-1199.

The Areal Distribution and Autoecology of the White Shark, Carcharodon carcharias, off the West Coast of North America

A. Peter Klimley

Abstract.—The areal distribution and autoecology of the white shark, Carcharodon carcharias, off the west coast of North America by A. Peter Klimley. Southern California Acad. Sci., Memoirs, Vol. 9, 1985. Capture information for 109 white sharks caught along the western coast of North America suggests the following life history pattern. Adult females give birth to pups during late summer and early fall south of Point Conception and the pups remain inshore at that time. As the pups grow larger, they move north of Point Conception to live both inshore and near offshore islands. As females continue to grow, they move back to south of Point Conception but offshore, probably to give birth to young. It is argued that the areal distribution of the white shark off the west coast is governed by the availability of pinniped prey for the large members of the species, and possibly the need of pupping grounds with few predators and food competitors.

Although the white shark, *Carcharodon carcharias*, commonly preys on pinnipeds (Ainley 1979; Ainley et al. 1981), causes substantial mortality on the sea otter (Ames and Morejohn 1980), and has attacked man along the western coast of North America (Follett 1966, 1974; Miller and Collier 1980), little is yet known about its areal distribution, habitat, feeding habits, and other behavior. In the following paper I will analyze capture records to describe this species' areal distribution and autoecology.

Methods

I have compiled 109 records of white sharks captured off the western coast of North America. Such reports often contain the size, weight, and sex of the shark as well as the location of capture, gear deployment depth, bottom depth, distance from the coast, and gear type. The catch records were obtained from three sources: 1) the scientific literature (Starks 1917; Walford 1931; Bonham 1942; Fitch 1949; Le Mier 1951; Pike 1962; Royce 1963; Follett 1966), 2) catalogues and field notebooks of ichthyological collections (California Academy of Sciences, the Natural History Museum of Los Angeles County, and Scripps Institution of Oceanography), and 3) collection records of Sea World, San Diego.

Since the number of sharks caught in a particular area could be highly dependent upon the types of gear used and the locations at which the gear was deployed (i.e., distance from coast, fishing depth, and bottom depth), an attempt was made to obtain this information and include it in the figures presented. Possible biases were taken into account in forming any conclusions based on the capture records. Also an attempt was made to determine whether the numbers of sharks captured in different geographical locations could be due to differences in the fishing effort or to the presence or absence of investigators to report such captures. Finally, the

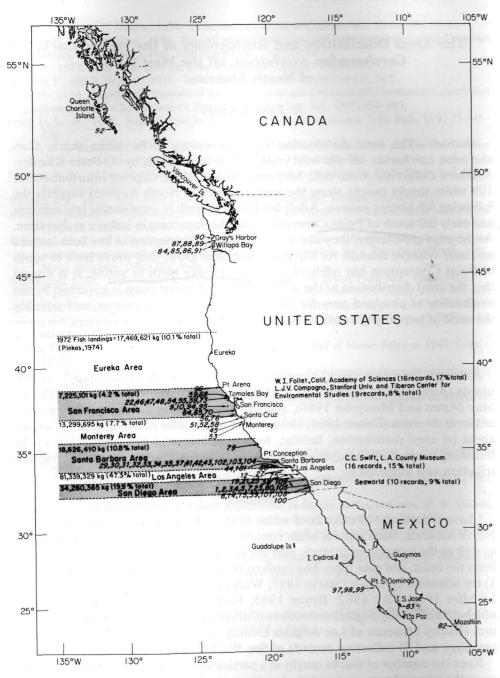


Fig. 1. Locations of white shark captures along the western coast of North America. Captures identified by number given in Appendix I. As an index of fishing effort, commercial fish landings included for six areas (alternately stippled or clear) along the coast of California. In the upper lefthand corner of each area, catch weight and its percent of the total catch are given in parentheses. As an index of investigator interest, names of investigators (and their institutions) providing 8% or more of the record total are added to right of coastline. The record number and its percent of the total number of records shown in parentheses.

relative use of different gears in these areas was also given since geographical variability in catches might be the result of such gear differences.

Results

Areal Distribution

The 109 capture records are presented in Appendix I. Records were comprised of the date and time of the capture, the captured shark's distance from both the shore and the coastline, the depth at which the shark was caught, the depth of the bottom, the capture method and the fisherman's identity, the shark's length, weight, sex, and stomach contents, and the source of the report. The records, identified by numbers to the left of the coastline, are shown on a chart of the northeastern Pacific from Queen Charlotte Island to Mazatlan (Fig. 1). Captures from adjacent geographic locations were pooled.

White sharks have been eaught as far north as the southern end of Queen Charlotte Island off the Alaskan coast (see capture record 92) and as far south as Mazatlan, Mexico (see 82). The northernmost capture probably reflects the northern limit of the white shark's distribution accurately since considerable commercial fishing is carried out farther north in the Bering Sea and unusual catches are generally reported in the scientific literature. On the other hand, the southernmost capture probably does not reflect the southern limit since less such fishing is carried out south of Mazatlan and unusual catches are less apt to be documented due to the paucity of fish biologists in this area. Larger numbers of captures were reported in four geographical areas: 1) from Gray's Harbor to Willapa Bay, 2) from Tomales to Monterey Bay, 3) near Santa Barbara, and 4) near San Diego.

Are the higher numbers of sharks caught in these areas due to higher densities of sharks or other factors such as greater fishing effort or the presence of observant ichthyologists? Although an indicator of fishing effort was not available for the entire western coast of North America, such an indicator was available for the coast of California. Commercial landings of fish species in 1972 were reported by Pinkas (1974) for six areas: 1) the Eureka Area, 2) the San Francisco Area, 3) the Monterey Area, 4) the Santa Barbara Area, 5) the Los Angeles Area, and 6) the San Diego Area. Unfortunately, effort could not be integrated over the entire period from 1934 to 1983 during which captures were reported, however, effort was measured for a year lying midway between the peaks in annual captures during 1958 and 1976. The weight of landings for each area and the percentage of the total landings represented by this weight are given in the upper lefthand corners of each area. These percent values, a measure of relative effort, if correlated with the percentages of the total captures reported for the areas, would suggest that the varying numbers of captures from zone to zone were due to varying fishing effort. This was not so. For instance, the landing of fishes in the San Francisco Area was the smallest, constituting only 4.2% of the total of landings along the California coast; however, the 17 catch reports in this area was the second largest total, constituting 26.6% of the total number of white sharks reported captured along the California coastline. On the other hand, the largest landing, 47.3% of the total catch, was in the Los Angeles Area where only five catch reports, or 7.8% of the total, were recorded. In the four remaining zones the capture percentages were: 1) 3.1% for the Eureka Area, 2) 7.8% for the Monterey Area, 3) 28.1% for the Santa Barbara Area, and 4) 26.6% for the San Diego Area. These were also

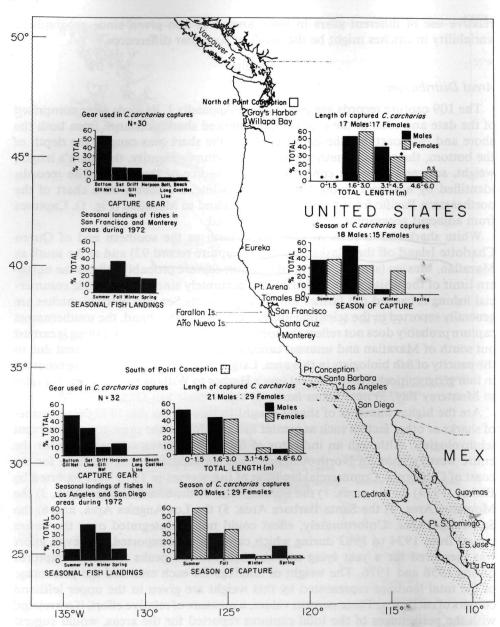


Fig. 2. Sets of four histograms given for north (upper) and south (lower) of Point Conception. Beginning with the upper lefthand histogram and moving in a clockwise manner, percentages of the total catch given for: 1) six gear types, 2) male (solid) and female (cross-hatched) white sharks in four size classes, 3) male and female white sharks during four seasons, and 4) fish landings during 1972 for four seasons. Landings for north of Point Conception pooled from the San Francisco and Monterey areas; landings for south of Point Conception pooled from the Los Angeles and San Diego areas. The asterisks above bars in length histograms indicate statistically significant differences between the relative number of sharks in that size class north and south of Point Conception. A non-significant difference indicated by n.s.

not correlated with fishing effort. Although the numbers of captures in the different zones can not be attributed to differences in effort, it is possible that the high numbers of captures reported, in particular in the San Francisco Area, could be due to the presence there of investigators interested in documenting such captures. Those sources providing eight or more percent of the reports are presented in Figure 1 to the right of the locations of their institutions. William Follett of the California Academy of Science and Leonard Compagno, originally at Stanford University and later at the Tiburon Center for Environmental Studies were both at locations near San Francisco, and they accounted for 25% of the total number of reports. Camm Swift of the Natural History Museum of Los Angeles County took records of the small white sharks captured by Bruce Henke near Santa Barbara prior to 1977, and Seaworld has done this since 1977. In recent years Seaworld has probably increased fishing effort for smaller white sharks in Southern California by offering substantial monetary rewards for captured white sharks to be placed on exhibit.

Size Segregation

Do juvenile and adult white sharks occupy different geographical areas as do many other shark species (e.g., Squalus acanthias [Ford 1921; Jensen 1965], Negaprion brevirostris [Springer 1950], and Prionace glauca [Suda 1953])? Size segregation appears characteristic of the white shark. If reports are separated into those north and south of Point Conception (the transition zone from the Californian to the Oregonian zoogeographic zones), juvenile white sharks 0-1.5 m in length were caught south but not north of Point Conception (Fig. 2). The percent total of males (solid) and females (clear) are shown in the upper righthand histograms of the lower set of four histograms for south of Point Conception (stippling along coastline) and the upper four histograms for north of Point Conception. Shark sizes are separated into only four classes because the sample size is small. The number of males in the 0-1.5 m size class in relation to those pooled from the larger size classes south of Point Conception differed significantly from that north of Point Conception (Chi-Square, Yate's Correction, P < 0.001). Females were also significantly more common south of Point Conception (Chi-Square, Yate's Correction, P < 0.024, Fisher's Exact Probability Test, P = 0.05). Two of the small sharks caught south of Point Conception (records 30 and 31) possessed umbilical scars possibly indicative of recent birth. Males and females in the 1.6-3.0 m size class were caught both south and north of Point Conception. However, in the next largest size class, 3.1-4.5 m, significantly fewer males (Chi-Square, Yate's Correction, P < 0.05, Fisher's Exact Probability Test, P = 0.002) and females (Chi-Square Test, Yate's Correction, P < 0.025) were caught south than north of Point Conception. This indicates, I believe, a northward movement along the coast of white sharks as they grow larger. Although males and females in the largest size class, 4.6-6.0 m, were caught both north and south of Point Conception, there was a higher percentage of females south than north of Point Conception (although the difference is not statistically significant). This high percentage was unexpected due to the absence of females in the next smaller size class for south of Point Conception. It could be that females move southward to give birth to the small sharks caught south of Point Conception. However, conflicting with this possibility was that none of the large females caught were pregnant and these

females were usually caught offshore, widely separated from the smaller sharks close to the coast (see later Fig. 3). However, one of the smallest sharks, 1397 mm, was caught offshore near Santa Cruz Island. The absence of small sharks offshore might be due to the lack of fishing effort there with bottom gill nets. The absence of pregnant females at intermediate distances from the coast might be due to the smallness of the capture sample. On the other hand the small percentages of males in the 4.6–6.0 size classes might reflect more determinate growth in males than females.

The difference between the sizes of sharks caught south and north of Point Conception appears not to be the result of differences in the types of fishing gear or the depths at which they are deployed in the two areas. It could be that small sharks were not caught north of Point Conception because fishermen were not setting gill nets in shallow water as is commonly done in southern California. Unfortunately, fishing effort for different gear types was not available in the scientific literature dealing with the coast of California. The gear types with which the white sharks were captured, however, were usually recorded in the capture report. The percentages of the total of captures for the different gear types (bottom gill net, set line, drift net, etc.) are presented in the upper lefthand histograms for south and north of Point Conception. In both areas the largest percentages of white sharks were caught with bottom gill nets (46.9% for south and 53.3% north of Point Conception). Since many juveniles in the 0-1.5 m size class were captured with this gear type south of Point Conception (see Appendix I), white sharks of the same size should have been captured in northern California if they were there. The slight differences in the design and mesh sizes of different bottom gill nets were ignored in this comparison. White sharks in the 3.1-4.5 m size class were caught most often with bottom gill nets and set lines (see Appendix I). Since effort with the former gear type was so similar for both areas and with the latter type was greater south of Point Conception (see Fig. 2), it is unlikely that the higher percentage of sharks caught in this size class south than north of Point Conception was due to a difference in fishing effort. Finally, white sharks in the 4.6-6.0 m size class were caught most frequently by gill net and harpoon. It is possible that the greater harpoon fishing effort in southern California (12.5% of the records) compared to that in northern California (6.7%) might explain in part the larger numbers of large females captured off southern California.

Both male and female white sharks were caught more frequently during the summer and fall seasons (lower righthand histograms for south and north of Point Conception in Fig. 2). Seasons in the histograms consist of three month periods with summer from June to August and fall from September to November. Again the catch records for different seasons are presented as percentages of the total number of males and females captured. Does this summer–fall peak truly reflect a greater abundance of white sharks, or does it only reflect greater fishing effort at this time? Although the peak north of Point Conception is paralleled by large landings of fishes in the San Francisco and Monterey Areas (lower lefthand histogram in the upper half of Fig. 2), the peak south of Point Conception is not paralleled by high seasonal landings in the Los Angeles and San Diego Areas during the summer but is during fall (see lower lefthand histogram in bottom half of Fig. 2). The landings were compiled by Pinkas (1974) from landings during 1972. There appears to be a real increase in abundance of both male and females

SEASON: • Summer (N = 40); o Fall (N = 28); □ Winter (N = 5); △ Spring (N = 2) SEX: Male (N = 38); ♀ Female (N = 37)

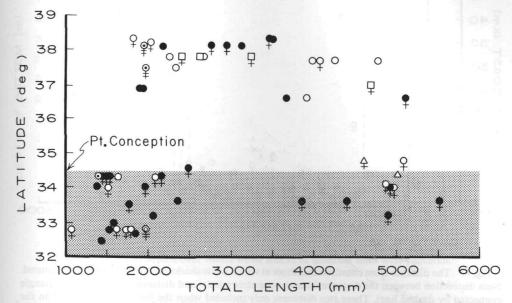


Fig. 3. White sharks of different sizes are plotted as a function of latitude. The season during which the shark was captured indicated by the shade and shape of the symbol. The sex of the shark designated by the presence or absence of an attached cross. The number of captures in parentheses. Multiple captures of similarly sized sharks at the same location indicated by concentric symbols. Note that small males and females were caught south of Point Conception (stippling) during summer (solid circles) and fall (clear circles).

in the summer. Since the males and females caught at this time are mostly in the 0-1.5 m size class, this peak may be due to birthing. The decreases in capture percentages for males and females south of Point Conception during winter are not paralleled by a decrease in fish landings, indicating possibly a decrease in white shark abundance at this time. Although a disproportionate decrease in females caught north of Point Conception occurs at this time probably indicating a decrease in female abundance, no such decrease occurs in the catch of males. It is possible that the large females move southward at this time. In spring decreased percentages of sharks caught in the two areas appear explicable by decreases in fishing effort at that time.

The movement of the white shark northward as they grow with the females returning southward as adults is best seen when size, sex, season of capture, and location of capture are all plotted together for sharks caught off only the California coastline (Fig. 3). Small males and females were caught south of Point Conception during the summer and fall. Rather than these points forming a line with a 45 degree slope, as would indicate that the sharks were slowly moving northward as they grew larger, they form a 90 degree slope, as would indicate a sudden movement northward from Ventura County (34°20′N) to Monterey Bay (37°N) at a size of ca. 2000 mm (see Fig. 2). This movement probably occurs in the late

LOCATION: • N of Pt. Conception (N=14); o S of Pt. Conception (N=22); SEX: Male (N=20); ¶ Female (N=16). Circle on dashed line indicates distance from coast, arrow distance from shore.

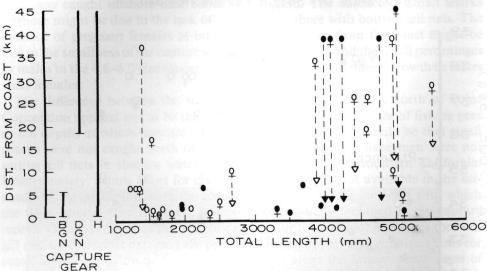


Fig. 4. The distance from coastline and shore at which white sharks of different sizes were captured. Note distinction between the distance from the coastline (circle) and distance from the shore (triangle connected by dashed line). These two distances only included when the former was greater than the latter. Also included to the right of the ordinate are the ranges of distance over which fishing with bottom gill nets (BGN), drift gill nets (DGN), and harpoons (H) occurs. If the range exceeds that of the ordinate, the upper horizontal bar excluded.

summer and fall, judging from the equal numbers of summer and fall captures along the coastline from Monterey to Tomales Bay (37° to 38°30′N) and south of Point Conception (34°20′). Although males remain north of 37°N as they grow to a size of 4775 (record 10 in Appendix I), females appear to move southward as they reach a size of ca. 3800 mm. This is reflected in the downward trend of the capture points in Fig. 2 at sizes over 3800 mm. Notice that all of the white sharks but one caught south of Point Conception (stippled) in this size range were females.

These large females caught south of Point Conception were not inshore where the juveniles were usually captured but offshore near islands. The distances from the coast at which white sharks were captured south and north of Point Conception are plotted in Figure 4. The females from south of Point Conception greater than 3800 mm in length, excluding capture record 27, were caught closer to an island than to the mainland. On the other hand, both females and males of this size were caught adjacent to offshore islands and inshore in northern California. White sharks smaller than 3800 mm were generally caught close to shore. Included to the left of the ordinate are bars indicating the range of depths fished with different gears along the California coastline. The range of depths over which bottom gill nets (BGN) were most often deployed was obtained from Charles Haugen of the California State Department of Fish and Game in Monterey. The ranges of depths over which drift gill nets (DGN) were deployed and harpooning (H) was carried out were obtained from Rondi Reingart of the Department of Fish and Game,

LOCATION: • N of Pt. Conception (N = 23); o S of Pt. Conception (N = 15) SEX: Male (N = 20); Premale (N = 18)

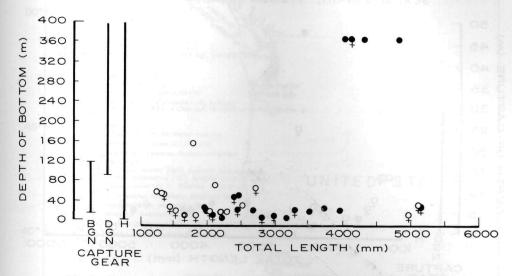


Fig. 5. Bottom depths over which white sharks of different sizes were captured.

Long Beach. Because of the large number of species fished for at different depths, it was not possible to get a depth range for set lines. It is clear from the depth ranges for the three other gear types that the entire distance range was being sampled.

The coastal and insular nature of the white shark is reflected by the relatively shallow depths at which these sharks were captured (Fig. 5). All but five of the white sharks, for which the depth of the bottom was recorded, were in less than 80 m with the median depth 20.6 m. Sharks, however, were caught in water as shallow as 5.5 m and as deep as 366.0 m. Yet even the four sharks caught in deep water were caught at the slope from southeastern Farallon Island. There were no differences in the depths of water in which male and female sharks were caught. The ranges of water depths over which fishing was carried out are shown again to the left of the ordinate for the different types of gear. It is possible that the absence of captures in water of depths greater than 80 m was because of the absence of the particularly effective bottom gill net fishing at these depths. Drift gill net and harpoon fishermen were less apt to report the bottom depth at the time of a shark capture because gear was not deployed along the bottom. However, in support of the rarity of sharks in depths greater than 80 m is their scarcity at depths of from 80 to 120 m where bottom gill net gear was at times deployed.

White sharks were caught at shallow depths (Fig. 6). Only two out of the 26 sharks for which capture depths were recorded were at a depth greater than 15 m. Captures were most common at depths around 5 m; however, captures of large sharks by harpoon at the surface were also common. It is possible that surface swimming is age related, or smaller white sharks were not harpooned on the surface because they are less easy to see or ignored when seen due to their small size. Surface swimming has been observed by the author frequently in the blue

LOCATION: • N of Pt. Conception (N=10); o S of Pt. Conception (N=16) SE X: Male (N=11); ♀ Female (N=15)

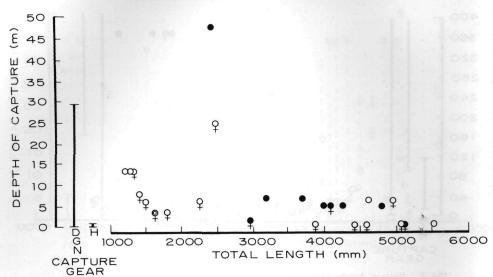


Fig. 6. Depths at which white sharks of different sizes were captured.

shark, *Prionace glauca*, and less frequently in the scalloped hammerhead, *Sphyrna lewini*. The rarity of sharks at depths greater than 15 m might reflect less fishing effort at those depths.

Dietary information for the female white sharks supports a movement northward as they grow into adults and a return southward to offshore islands. The dietary items for male and female white sharks of different sizes caught south and north of Point Conception are shown in Figure 7. Stomachs of white sharks less than 2000 mm in length contained bony fishes (cabezon-Scorpaenichthys marmoratus and lingcod—Ophiodon elongatus), cartilaginous fishes (gray smoothhound-Mustelus californica, spiny dogfish-Squalus acanthias, and a dasyatid ray), crustaceans (spot-bellied rock crab—Cancer antennarius), and cephalopods. Intermediate size white sharks from 2000 to 4000 mm were caught primarily north of Point Conception. They had been feeding on bony fish (additionally, Pacific sardine—Sardinops sagax, green sturgeon—Acipenser mediostris, king salmon—Oncorhynchus tshawytscha, white seabass—Cynoscion nobilis, black rockfish—Sebastes melanops, and striped bass—Morone saxatilis), cartilaginous fishes (brown smoothhound-Mustelus henlei, soupfin shark-Galeorhinus zygopterus, and bat ray-Myliobatis californica), a pinniped (harbor seal-Phoca vitulina), and a crustacean. Large sharks greater than 4000 mm in length fed on pinnipeds (northern elephant seal-Mirounga angustirostris and California sea lion—Zalophus californiensis), bony fishes (Pacific hake—Merluccius productus), cartilaginous fishes (basking shark—Cetorhinus maximus), and crustaceans (market crab—Cancer magister). The increasing importance of pinnipeds over fishes in the diets of larger white sharks probably affects their distribution. Since pinnipeds haul out both inshore and offshore north of Point Conception, white sharks may move into both of these areas to capture prey. Since pinnipeds haul out only

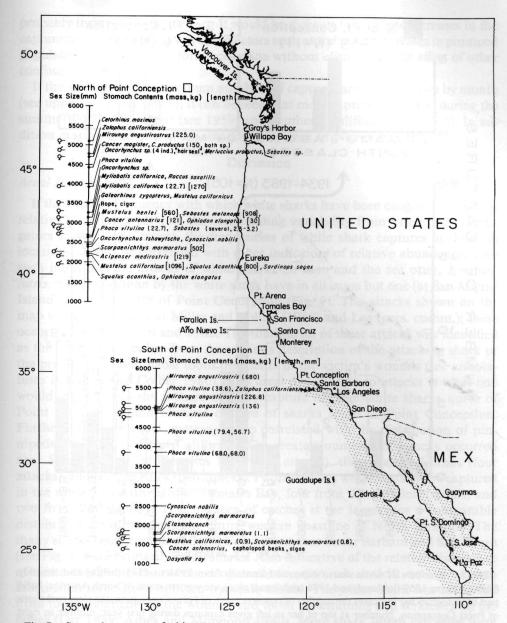


Fig. 7. Stomach contents of white sharks caught north and south (stippled) of Point Conception. The mass (parentheses) and length (brackets) given after identities of dietary items to right of shark length scale; the sex of the shark given to the left of the scale.

offshore on islands south of Point Conception, white sharks probably remain offshore there where prey is available.

Finally, the frequency with which white shark captures are being reported is increasing. The numbers of white sharks captured during two-year periods from 1934 to 1983 are presented in Figure 8. Although there is considerable variability in records on both the annual and biennial scales, the numbers of captures appear

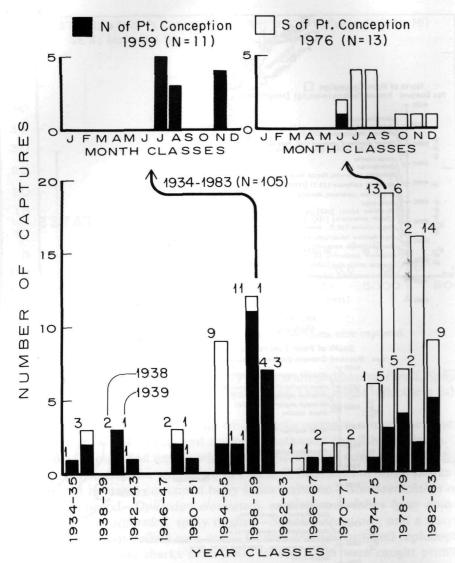


Fig. 8. Numbers of white sharks captured biennially from 1934 to 1983 (below) and monthly (above) during 1959 (lefthand) and 1976 (righthand) along the western coast of North America. Solid part of histogram bar indicates the number of captures north of Point Conception, the clear part south of Point Conception. Number at top of bar to left gives captures during first year; number to right captures during the second year of biennial class.

to be increasing, in particular, since 1974. There are biennial frequency peaks, 1958–1959 and 1976–1977. The reports in the former peak were primarily from northern California, and this prevalence was probably due to the interest of William Follett in recording capture events at that time. The reports comprising the latter peak were primarily from southern California, probably due to the public interest aroused from the motion picture "Jaws" in 1975. Furthermore, since then Sea World has offered a reward for small white sharks for exhibition; this has

probably increased fishing effort. It would be difficult to attribute increases in the capture rate of white sharks to other factors such as the recent increases in pinniped populations along the California coastline without eliminating the effect of other confounding variables.

If the years with the maximum numbers of captures are broken down by month (see upper inserts in Fig. 8), it can be seen that most captures occurred during the summer both in northern (see 1959) and southern California (see 1976). In addition, during 1959 there was an additional peak in November.

Discussion

Areal Distribution

If the relative frequency with which white sharks have been caught reflects their relative abundance (despite the confounding variability from interested investigators in the larger cities), the frequencies of white shark captures at different locations should be correlated with other indicators of relative abundance. Two such indicators are attacks of white sharks on man and the sea otter, Enhydra lutris. Attacks on man by the white shark have in all cases but one (at San Miguel Island) occurred north of Point Conception (Fig. 9). The attacks shown on the map were obtained from Miller and Collier (1980) and Lea (pers. comm.); these occurred between 1926 and 1982. The shark in all of these attacks was identified as the white shark either from the victim's description of the attacking shark or the presence of identifiable tooth fragments in the victim's wounds (see annotations in Miller and Collier 1980). This areal distribution to attacks is what one would expect from the inshore-offshore capture of large white sharks north of Point Conception and offshore capture of sharks south of Point Conception. Furthermore, this attack pattern is also correlated with the distribution of pinnipeds along the coast of California. The greatest numbers of attacks occurred near San Francisco at Tomales Point (six attacks), the Farallon Islands (four attacks), and Bodega Rock (two attacks). Fourteen large white sharks were captured in the same area with eight at Tomales Bay, four from the Farallon Islands, and two from Bodega Bay. This number of catches is the largest for a comparable distance of coastline along the entire western coastline of North America. The many sharks caught south of Point Conception near Santa Barbara and San Diego (see Fig. 1) were primarily small sharks. Also indicative of the relative abundance of white sharks are the numbers of dead sea otters which drift onto the beach killed from lacerations inflicted by white sharks. The white shark was identified from tooth fragments in the wounds and tooth penetrations and scratches on the bones (Orr 1959; Ames and Morejohn 1980). More shark bitten carcasses were recovered north than south of Point Sur (Ames and Morejohn 1980). However, it is possible that this difference could be due not to a greater abundance of sharks north of Point Conception but to other confounding factors. Since access by the public to the coastline is restricted along some sections and not others of the coastline, search effort in the two areas may not be equivalent. Furthermore, since the populations of sea otters have not been yet censused along the entire coastline. it is possible that the population sizes in the two areas are not equal. In a more recent compilation of sea otter mortality from 1968 to 1982 from Point Sal to Point Año Nuevo by Jack A. Ames of the California State Department of Fish and Game, Monterey (pers. comm.), the highest frequency of sea otter mortality



Fig. 9. Attacks by white sharks on humans along the western coast of North America. Records prior to 1979 taken from Miller and Collier (1979); those from 1980 to 1983 obtained from Lea (pers. comm.).

was off Monterey with slightly lower peak frequencies at Morro Bay and San Simeon, south of Monterey. However, these data are also confounded by the before-mentioned two factors. An additional problem with such data as an indicator of white shark relative abundance is the limited range of the sea otter. It appears that the distribution of shark attacks along the coast of California parallels that of the capture records, and this correlation may give greater credence that the abundance of larger white sharks is highest along the coastline near San Francisco.

Is the seasonal increase in white shark captures along the west coast during

Table 1. Indicators of seasonal abundance of the white shark off the western coast of North America: 1) aerial survey from Squire 1967, 2) attack data from Miller and Collier 1980, and Lea, pers. comm., 3) population censuses and kills of pinnipeds from Ainley et al. 1981, and 4) mortality of sea otters from Ames and Morejohn 1980.

		1		2		3	1 1	4
Month	Shark obs.	Flights	Obs./ flight	Attacks on man	Pinn. kills*	Pinn. censused*	Kills/seals cens.	Sea otter kills
December	10	33	0.30	4	muncy	Buildies		2
January	8	36	0.22	3	5	410	0.0122	5
February	1	30	0.03	2				4
March	2	49	0.04	0				9
April	1	45	0.02	1				6
May	12	38	0.32	5	2	2701	0.0007	7
June	10	48	0.21	0				11
July	14	37	0.38	7				6
August	27	45	0.60	4				4
September	6	22	0.27	7				4
October	9	34	0.26	2	30	2067	0.0145	0
November	4	28	0.14	4				2

^{*} Taken from Table 1 in Ainley et al. 1981 with winter (late Dec.-Feb.), summer (late March-early July), and fall (late Aug.-mid Dec.).

summer and fall due to increased fishing at those times, or is it corroborated by other indirect measures of white shark relative abundance not influenced by fishing effort? Four such indices are presented in Table 1. From 1948 to 1950 Eric Durden, San Francisco, flew surveys across Monterey Bay for the basking shark fleet at Monterey and San Luis Obispo Bays. During these flights he logged white sharks as well as basking sharks swimming at the surface of the Bay. I have included on a monthly basis mean numbers of sharks per flight from numbers of sharks observed and flights taken (see Table 1 in Squire 1967). More sharks were spotted from May to October with the peak in August. White shark attacks on man from 1926 to 1983 (Miller and Collier 1980; Lea, pers. comm.) were most frequent from July to September. One of the two peak frequencies was in August. These time periods are similar, although slightly offset, from the summer-fall (June to Nov.) periods during which larger white sharks were caught most often north of Point Conception (see Fig. 2). The July-August peaks also correspond closely to the July-August monthly peaks in white shark captures in 1959 and 1976 (see Fig. 8).

A third indicator of seasonal abundance is pinniped kills by white sharks at the Farallon Islands recorded from 1970 to 1978 by Ainley et al. (1981). Thirty pinniped kills were recorded in the fall (late August to mid-December). Five and two kills were recorded in winter and spring, respectively. This fall peak could result from a constant number of white sharks feeding more often when the pinniped population was larger. This possibility would be excluded by using the frequency of pinniped kills per pinnipeds censused. The frequency of pinnipeds killed per those censused in the fall of 0.0145 was only slightly larger than that in winter of 0.0122, yet considerably larger than that in summer of 0.0007. However, it is still possible that the white sharks could change their prey preference during the summer, switching to other food. At any rate, the fall peak does not

Table 2. Indicators of annual abundance of the white shark off the western coast of North America: 1) attack data from Miller and Collier 1980, and Lea, pers. comm., 2) population censuses and kills of pinnipeds from Ainley et al. 1981, 3) bite scars on northern elephant seals from Le Boeuf et al. 1982, and 4) mortality of sea otters from Ames and Morejohn 1980.

				Indic.		
	1	-10019 /s	2		3	4
Years	Attacks on man	Pinn, kills*	Pinn. cens.*	Kills/pinn. cens.	Seal bites	Sea otter kills
1982	3					
1981	0					
1980	1				17	
1979	2				7	5
1978	0	12	1507	0.008	9	6
1977	1	7	1140	0.006	8	7
1976	3	4	965	0.004	3	3
1975	4	6	665	0.009		5
1974	5	3	610	0.005	1	6
1973	0	2	356	0.006	*	6
1972	3	1	278	0.004		9
1971	0	0	170	0		7
1970	0	1	95	0.011		2
1969	2					3
1968	Nova 1					1
1967	0					
1966	1					
1965	0					
1964	121 6 1					
1963	0					
1962	1					
1961	2					
1960						
1959	2 2					
1958	0					
1957	0					
1956	0					
1955	1					
1954	0					
1953	0					
1952	offe Tom in					

^{*} Taken from Table 1 in Ainley et al. 1981 with winter (late Dec.-Feb.), summer (late March-early July), and fall (late Aug.-mid Dec.).

fit nicely with the other three indices of relative abundance. Sea otter mortality, the fourth additional index of relative abundance, was not correlated to the other indices. Otter mortality was high from December to July and not during the late summer and fall as most other indices. It is also possible that the seasonal differences in these indicators (which vary in their geographic ranges) may reflect the movements of sharks from one location to another.

Is the overall increase in shark captures since 1974 reflected in these indices of white shark abundance? Are there peaks corresponding to the two biennial peaks of captures in 1958 to 1959 and 1976 to 1977? Four additional indices of white shark abundance are presented in Table 2. An overall increase in attacks on man

is not evident since 1974. It is difficult to exclude the possibility that the variations in attack frequency are not due to chance, since the number of attacks in any one year is so low. Broader peaks in attacks appear correlated with the capture record peaks from 1959 to 1961 and 1974 to 1976. Although the number of pinniped kills increased between 1970 and 1978 at the Farallon Islands (Ainley et al. 1981), the increase is not evident if attacks are expressed as a function of pinnipeds censused. Although Le Boeuf et al. (1982) showed an increase in shark bites on elephant seals from 1976 to 1980, the frequency of bites was not expressed in terms of censused seals. This could be due to an increasing pinniped population, with a static shark population. Sea otter mortality due to white sharks appears to have remained relatively constant since 1971. Overall, it is difficult to argue strongly that white shark abundance is increasing along the California coast with the meager and indirect evidence available.

Size Segregation

Is the life history pattern of the white shark off the western coast of California indicated by capture records similar to those patterns in other geographical areas? Many capture records exist for sharks caught off the northeast coast of North America (Schroeder 1938, 1939; Bigelow and Schroeder 1953, 1958; Scattergood and Coffin 1957; Scattergood 1962; and Skud 1962) and off the southwestern coast of South Africa (Bass et al. 1975; Bass 1978). Do large females in these geographical areas move into warm temperate waters to give birth to pups in late summer and fall, and do the juveniles move into colder temperate waters as they grow larger? Pratt et al. (1982) suggested that white shark birthing along the eastern coast of the United States occurs in the New York Bight from the presence there of very large females and very small young. Yet those juveniles out of 36 sharks recorded in the scientific literature (see earlier references), were caught over a broad geographical range. A juvenile white shark of 1524 mm was caught off Sakonnet, Rhode Island (Bigelow and Schroeder 1953), a second of 1448 mm was caught near the Boston Light Ship (Bigelow and Schroeder 1958), and a third of 1905 mm was caught off of Boothbay Harbor (Bigelow and Schroeder 1958). Adults were caught only over a slightly larger range extending as far north as Campobello. The pupping area for South Africa is not known: only one of the 58 white sharks in Table 8 of Bass et al. (1975) is less than 174 cm. The location of its capture was not given. Furthermore, there were few very large sharks in the sample of Bass et al. (only four greater than 324 cm). Of the intermediate size sharks, the smaller individuals (<240 cm) were caught in cooler water (south of Durban) throughout the year, but north of Durban only during the winter months when water temperatures were lower. The larger individuals (>240 cm) were caught both north and south of Durban throughout the year in equal numbers. These distributional patterns were very different from those of white sharks off the western coast of North America.

Factors Controlling Distributional Patterns

I believe the availability of prey to large members of the species to be shaping the distributional pattern of the white shark; but, of course, within broad thermal limits. As I have shown earlier, white sharks greater than 3500 mm in length feed along the western coast of North America primarily on harbor seals, northern

elephant seals, and California sea lions. White sharks in this size range are caught both inshore and offshore in northern California. Pinnipeds are also present inshore (for pinniped relative abundances see Figs. 2,3,4, and 5 in Dohl et al. 1982) and offshore (see Fig. 8). Furthermore, the largest numbers of large sharks were caught in areas of peak pinniped densities such as near San Francisco, Año Nuevo Island, and Morro Bay. Large white sharks were caught offshore in Southern California, near islands with pinniped rookeries. Four of six sharks greater than 3500 mm were captured at or near islands which have large rookeries of harbor seals (see Fig. 74 in Bonnell et al. 1978), northern elephant seals (Fig. 58), and California sea lions (Figs. 13 and 38).

White sharks in the northeastern Atlantic have been reported to feed on harbor seals (Scattergood 1962), harbor porpoises, *Phocoena phocoena* (Arnold 1972), and a fin whale (Pratt et al. 1982). It is possible that the large number of white shark captures reported from the Gulf of Maine (12 records reported by Scattergood [1962] from 1959 to 1960) may also be due to the abundance of pinnipeds such as the harbor seal in this area. In the South African sample (Bass et al. 1975), composed primarily of intermediate size sharks, pinnipeds comprised only a small percentage of the diet, while bony fishes and sharks constituted larger percentages. This would be expected from other findings of such prey in the stomachs of intermediate size sharks (see Fig. 7). Fishing activities occur only over part of the geographical range of the white shark in South Africa and, for this reason, very small and large sharks are not caught. Large white sharks from 3048 to 5486 mm, and not small sharks, have often been observed in the vicinity of a seal colony of 7000 individuals in Algoa Bay (Compagno, pers. comm.). These sharks have been seen repeatedly to attack seals.

This argument of a prey dependent distribution to the white shark is possibly inconsistent with its ability to fast for a time period of up to 1.5 months, a duration determined from the caloric measurement of food ingested by a shark and a metabolic rate determined from differences in the temperature of the shark's muscle mass and the surrounding water (Carey et al. 1982). This, together with the large size of the shark and its ability to obtain large bites, led Carey et al. to the conclusion that the white shark is more likely to feed on moribund whales than small fishes. Large white sharks caught along the western coast of North America have not been found with whale flesh in their stomachs. These sharks generally feed on pinnipeds. It would be important to know how often individuals ingest pinnipeds so that the dependency on the availability of pinnipeds proposed here could be tested.

It does not appear that the distribution of the white shark is solely determined by temperature, judging from the different movements of sharks off North America and off South Africa. Bass (1978) also suggested that temperature was not an important factor off South Africa because large sharks (>275 cm TL) were caught off Natal from February to June when temperatures decreased. But they were absent from September to January during similar temperatures.

It is striking that white shark pups are birthed most commonly off the coast of Baja California north to Santa Barbara at the edge of the temperate zone. It is possible that the movement of females into this environment to deposit their pups is to optimize the survival of the pups. It is possible that the risk of predation is less in this environment in the absence of large white sharks. Furthermore, it

is possible that the pups receive a competitive advantage. The carcharhinid sharks which also feed on neritic bony fish are generally caught farther southward. The pinnipeds, which are also piscivorous, are also not generally present inshore where the pups live, but offshore near islands.

Conclusions

Capture information for 109 white sharks caught along the west coast of North America was obtained from the scientific literature, catalogues, field notebooks from ichthyological collections, and collection records of an oceanarium. This information suggests that large females move southward to give birth to pups during late summer and early fall. As the pups grow larger they move north of Point Conception where they live both inshore and offshore. This northward movement may occur rather abruptly as the sharks reach a size of ca. 2000 mm in length. Females return to islands offshore of Southern California probably to give birth. All sizes of sharks are caught in mid-water; large sharks are also caught at the water's surface. It is argued that the distribution of the species is controlled by the availability of large prey for large sharks and possibly the proximity of pupping grounds with fewer predators and competitors.

Acknowledgments

I would like to thank the many investigators who provided capture records: in particular, William Follett of the California Academy of Sciences and Camm Swift of the Los Angeles County Museum. The identities of those who contributed records are included in Table 1. Richard Rosenblatt of Scripps Institution of Oceanography read the manuscript and offered useful comments. This work was made possible by a contract (N00014-83-K-0299) with the Office of Naval Research and a grant from the Foundation for Ocean Research, San Diego.

Appendix I. Capture information for white sharks, Carcharodon carcharias, caught along the western coast of North America. DFS: distance from shore; DFC: distance from coast; BD: bottom depth; SD: shark depth; S: sex; X: missing date; NIA: not included in analysis. Note distinction made between not knowing whether the contents of the shark's stomach were examined (designated "not known") and knowing that they were not examined ("not examined").

	nts Source	Flechsig	Can- Flechsig	45,	or-	quid		Flechsig	Flechsig	Flechsig	Flechsig	Flechsig	Flechsig	Metzger	r- Metzger		Zumwalt		Le Boeuf	Sea World	Sea World	sti- Le Boeuf		Sea World			Nelson	Le Boeuf	
	Stomach contents	Scorpaenichthys marmoratus	S. marmoratus, Can-	cer antennarius,	Mustelus califor-	nicus, algae, squid	peaks	S. marmoratus	not examined	none		none	not examined	not examined	Zalophus califor-	niensis	not examined	stomach everted	Phoca vitulina	not examined	not examined	Mirounga angusti-	rostris	P. vitulina	not examined	M. angustirostris	not examined	P. vitulina	
	S	Г	Z					Н	ц	M			щ	ц	M		ц		H	M	H	H		ц		ц			
Wt.	kg													684.9			22.7	2152.3	612.3	54.9		1560.4		1428.8		2041	385.6	635.0	100
Len.	mm	1806	1632					1629		1626			2000	4089	4775		1524	5080	4409	1854	1981	4966		4877	4572	5525	2946	3861	
	Fisherman	Flechsig	Flechsig					Flechsig	Arebalo	Tuthill	anon.	Limbaugh	Tomlinson	Pemperton	Pemperton		Desherow	Weeren	Hawthorne		Tomlinson				Langham	Weeren	Fromhold	Mansur	
	Cap. meth.	set line	set line					set line	set line	set line		set line	set line	set line	set line			harpoon	harpoon						harpoon	harpoon		harpoon	THE R. P. LEWIS CO., LANSING, MICH.
SD	ш	3.1	3.1					3.1	3.1	3.1		3.1		4.5	4.5			0	0						0	0		0	
BD	ш	6.1	6.1					6.1	6.1	6.1		6.1	15.2	366.0	366.0			31.1											
DFC	km	0.4	0.4					0.4	0.4	0.4		0.4	;	38.0	38.0		16.7	3.7	25.7			37.8	*			27.8		33.3	
DFS	km													2.9	2.9				9.3			11.3			18.5	14.8		7.4	
Time	hrs	1530	1530					2100	1300	1100		1000		1500	2200			1330											
	Date	10-30-55	10-31-55					10-31-55	11-3-55	11-6-55	11-0-55	11-12-55	11-4-55	10-5-82	10-5-82		9-24-81	92-86-9	7-23-75	89 X S	10-X-01	9-7-75		X-X-6	8-21-76	6-13-76	7-29-X	6-24-75	
	No.	-	7					"	4	٧ ٠	, 4	0 1	- o	0	10	2	Ξ	17	13	17	17	91		17	18	19	20	21	1

Appendix I. Continued.

No.	Date	Time	DFS	DFC	BD	SD III	Cap. meth.	Fisherman	Len.	Wt. kg	S	Stomach contents	Source
23	8-3-81		1.9	1.9			gill net	The state of the s	1676	45.4	k	not examined	Nelson
24	10-24-81								1473	25.9	M	not examined	Cailliet
25								Wilson	2133	136.1	ц	not examined	Nelson
9	4-16-80		5.6	44.5			gill net	Barker	5029	1587.6	ц	Z. californiensis,	Johnson
- 1	55.65			1	200							P. vitulina	
7.7	4-30-82		9.5	9.2	9.5	5.5	gill net	Williams	4942	907.3	ц	M. angustirostris	Seigel
~	5-20-82		25.9	25.9		6.1	gill net	Peters	4609	1224.7	M	not examined	Swift
_	10-15-76						gill net		1650		M	not known	Huddleston
_	9-3-77						gill net	Henke	1408		M	not known	Swift
31	9-3-77						set line	Henke	1414			not known	Swift
	9-18-77						gill net	Henke	2099	73.5	H	not known	Swift
	7-15-76				14.6	5.8	gill net	Henke	1500	29.5	Н	not known	Swift
10.70	7-15-76				14.6	5.8	gill net	Henke	2258			not known	Swift
	8-16-78						gill net	Henke		36.3		not known	Swift
	7-3-78		7.4	0.7	22.0		gill net	Henke		25.0		not known	Swift
	11-X-76						gill net	Henke		45.4	F	not known	Swift
	8-18-76							Langham	4900		H	not known	Swift
	11-4-71						gill net	Tomlinson	1085		H	not known	Swift
40	12-17-76			0.7	9.2		gill net	Caywood		48.5	H	not known	Swift
	92-6-8				14.6		gill net	Henke	2170		H	unident.	Swift
	8-17-77						gill net	Henke	1514		M	not known	Swift
43	7-27-76				25.6	7.3	gill net	Henke	1410	23.5	H	not known	Swift
	7-12-59			2.8	27.5	24.5	gill net	Castagnola	2492	145.2	H	Cynoscion nobilis	Follett
45	1-23-59	1400		0.5	27.5	0	harpoon	Tomlinson	5105	1279.1	H	Cetorhinus maximus	Follett
	7-25-59	0730			5.5	5.5	drift net	Konatich	3143	283.5	M	Myliobatis cali-	Follett
	S. Line											fornica	
47	7-25-59	0230			2.8		drift net	Konatich	2775	109.3	щ	none	Follett
48	7-2-60	1900			2.8	1.2	set line	Spenger	2960	190.1	Щ	Galeorhinus zygop-	Follett
								" Harrigana"				terus, Mustelus	Follett
	11-13-50							Vella	27.70		;	californicus	;

Appendix I. Continued.

		Time	DFS	DFC	BD	SD			Len.	Wt.			
No.	Date	hrs	km	km	m	ш	Cap. meth.	Fisherman	mm	kg	S	Stomach contents	Source
	11-9-59			5.6			gill net	Vella	2254	9.101	M	rope, cigar	Follett
	8-10-59	0300		2.3	22.9		drift net	Carniglia	1943	61.7	M	not examined	Follett
	8-7-59	0530		24.8			drift net	Cardinalli	1924	9.59	M	Squalus acanthias,	Follett
												Ophiodon elongatus	
	7-31-59	0530		6.5	23.8	6.4	drift net	Olivieri	3683	380.1	Σ	none	Follett
	7-30-59	1620			5.8		drift net	Konatich	2184	6.86	Σ	Mustelus califor-	Follett
												nicus, S. acan-	
												thias, Sardinops	
												sagax	
	8-21-79						gill net	Bertelli	1956	88.7	ഥ	none	Follett
	2-X-77						beach cast	Helm					Follett
	10-25-78			1.8	20.0		tram. net	Salter	3930	544.3	Σ	P. vitulina	Morejohn
	8-28-59	0300		1.8	18.3		gill net	Carniglia	1959	54.4	M	none	Follett
	10-7-60							Konatich	1965	6.69	IТ	none	Follett
	12-27-60				20.1		gill net	Crivello	2419		ī	Onchorhynchus tsha-	Follett
												wytscha, C. nobilis	
	1-2-61				20.1		gill net	Crivello				Mustelus cali-	Follett
												fornicus, Morone	
												saxatilis	
	12-28-60				20.1		gill net	Crivello	2651	180.5	M	Mustelus henlei,	Follett
												Cancer antennarius,	
												O. elongatus, Se-	
												bastes melanops	
	6-X-81							Mueller	1290	16.1	M	not examined	Cailliet
	11-8-81							Renardez	2340	86.2	Z	not examined	Compagno
	11-8-81			A					1990	78.0	H	not examined	Compagno
	8-27-81	1600					set line	Follett	1976	42.3	H.	not examined	Follett
	9-24-81								1590	37.6	Z	not examined	Cailliet
	10-16-66				9.2		gill net	Spenger	2044	0.89	ц	none	Compagno
	8-25-56								3505	408.2	ц	Oncorhynchus sp.	Compagno
	11-1-68						gill net		2340	72.6	Σ	not examined	Compagno

Appendix I. Continued.

Date	Time	DFS km	DFC km	BD m	SD m	Cap. meth.	Fisherman	Len.	Wt.	S	Stomach contents	Source
						gill net	Johnson	1990	78.0	H	none	Compagno
							Strobbeca	1981			not examined	Compagno
							Vella		183.7	Σ	not examined	Compagno
							Vecca		101.6		not examined	Compagno
			0.1	45.5		gill net	Sea World	2362	138.8	ц	pinniped	Le Boeuf
								4700		ц	M. angustirostris	Le Boeuf
			1.6					4150			P. vitulina	Le Boeuf
								3048		M	not examined	Miller, 1981
				47.6	47.6	gill net	Thomas	2438	181.4		P. vitulina, Sebas-	Fitch, 1949
											tes sp.	
			6.0			set line	Ramsower	1543		H	not examined	Fitch, 1949
						set line	Follett	1676	42.2	M	not examined	Follett, 1966
								1960		M	not examined	Kato, 1965
		1.8	9.2	62.2		long line	Cuevas	2685		H	not examined	Michael
						gill net	Pederson	2235	155.1		Acirpenser medios-	Bonham, 1942
											tris	
						gill net	Moore		362.9		P. vitulina	Bonham, 1942
						gill net	Moore	3962	997.2	M	not known	Bonham, 1942
						gill net	Ogren		226.8		not known	Bonham, 1942
						gill net	Oblad		453.6		not known	Bonham, 1942
								3658	408.3		not known	Bonham, 1942
		6.0	6.0			gill net	Fuller	3302	317.5	H	not known	Le Mier, 1951
							Nelson	4450	907.2		Cancer magister,	Le Mier, 1951
											Cancer productus,	
											Oncorhynchus sp.,	
											"hair" seal, Mer-	
											luccius productus,	
								3470	4536		Sebastes sp.	Dike 1962
								4674	0.001		not known	Rovce, 1963
		2.9	38.0	366.0	4.5	set line	Pemperton	4267	601.0	Σ	not examined	Metzger

Appendix I. Continued.

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Marine Biology Research Division, A-002. Scripps Institution of Oceanography, La Jolla, California 92093.

White Sharks in Hawaii: Historical and Contemporary Records

Leighton Taylor

Abstract.—White sharks in Hawaii: historical and contemporary records by Leighton Taylor. Southern California Acad. Sci., Memoirs, Vol. 9, 1985. Study of Hawaiian artifacts collected by the expeditions of Cook and Vancouver indicates the historical presence of white sharks in Hawaiian waters. Since 1926 there have been eight confirmed collections of Carcharodon carcharias in the Hawaiian Islands; three from the island of Hawaii and five from Oahu, including the public display of a living 13-foot specimen. Two attacks on humans by white sharks have been documented on Oahu. Carcharodon carcharias is definitely rare in Hawaii but it is not known whether it is a resident or a vagrant species. Abundance may be related to population levels of either the Hawaiian monk seal or the humpback whale.

Carcharodon carcharias is reported in the literature to be a widely-ranging species in temperate and subtropical zones. However, specific records have not been summarized for Hawaii. Therefore, it seems worthwhile to review the contemporary records of white sharks in Hawaii and to examine historical sources for indications of the presence of the species in the Islands.

Methods

The ancient Hawaiian culture was rich with oral tradition and complex folklore about sharks (Beckwith 1970; Kamakau 1976; Malo 1951; Pukui et al. 1972). I carefully reviewed these legends for possible mention of great white sharks. Artifacts collected by early European visitors to the Hawaiian Islands (Kaeppler 1978) were examined and the shark teeth included were identified to species using reference sets of teeth. Modern records of white sharks in Hawaii were sought by querying museums for holdings of white shark material from Hawaii, by reviewing the scientific and popular literature, and by interviewing local fishermen known to be reliable sources.

Results

Various shark species were of great cultural importance to Hawaiians in their religion, folklore, and as the source for strong cutting edges for tools and weapons. The particular species relating to various cultural aspects are not definitely known but can be considered to be among the following: *Carcharhinus* (six spp.); *Triaenodon obesus* (a common inshore species); *Galeocerdo cuvier* (the most abundant large species); and *Sphyrna lewini*.

There is a confusion of nomenclature between Hawaiian and scientific names and it is unclear which shark species match specific cultural contexts. Knowledge of the species and the folklore permits some speculation as to which species may be involved.

For example, the Hawaiian concept of Aumakua, or guardian species, may be