

DYNAMICS OF WHITE SHARK/PINNIPED INTERACTIONS IN THE GULF OF THE FARALLONES,
1970 TO 1983.

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ABSTRACT

Three types of evidence delineate seasonal and annual trends in the occurrence of white sharks at the Farallon Islands, California, from 1970 to 1983: 74 sightings of sharks attacking pinnipeds, 91 sightings of pinnipeds with recently inflicted shark-bite wounds, and 23 sightings of white sharks in non-attack situations. Seasonal occurrence along the adjacent mainland coast is inferred by 14 sightings of pinnipeds there with recently inflicted wounds, 1976 to 1983. In the Gulf of the Farallones, white sharks occur seasonally at sites in conjunction with peaks in the number of preferred prey (seals): the Farallones in the fall/winter and the adjacent coast in the spring/summer. Subadult pinnipeds are far more vulnerable to sharks than are adults; white sharks also prey more on seals than on sea lions. Seals are more vulnerable to shark predation than are sea lions, perhaps because of the method white sharks use to capture their mammalian prey and the way in which seals (vs. sea lions) swim and rest in the water.

The number of white shark sightings increased annually during the 14-year study period but the rate of increase leveled off coincident with a leveling off in the rate of increase in the number of immature elephant seals. The killing of four large white sharks in Farallon waters during fall 1982, which drastically reduced shark sightings, and the increasing size of white sharks seen at the islands, 1971 to 1980, indicated that the same, seasonally resident individuals may have been frequenting the Farallones.

We speculate that in the Gulf of the Farallones white sharks move seasonally inshore and offshore in response to seasonal concentrations of

preferred prey (seals as opposed to sea lions). We also note that the timing of the breeding seasons of seals are such that contact of recently weaned individuals with large white sharks is at a minimum, and speculate that this may not be entirely a coincidence; indeed, the timing of breeding seasons of seals may have evolved, in part at least, as a means to reduce white shark predation.

INTRODUCTION

The great white shark (Carcharodon carcharias) is a major predator on pinnipeds in California (Ainley et al. 1981; Le Boeuf et al. 1982), but the effects of predator on prey and prey on predator in shaping respective natural history patterns are largely unknown. At the Farallon Islands, California, the Point Reyes Bird Observatory (PRBO) operates a year-round research program. PRBO's intensive studies on pinnipeds, and its systematic daily surveys of the island's shores and inshore waters, have unintentionally provided considerable information on predator/prey interactions between pinnipeds and white sharks. Based on a recent but somewhat preliminary analysis (Ainley et al. 1981), we concluded that 1) the presence of white sharks at the Farallones was seasonal, peaking in the late fall; 2) beginning in 1972, the frequency of white shark sightings increased annually (to 1979); 3) white sharks were probably most attracted to the islands by a particular prey, the northern elephant seal (Mirounga angustirostris), rather than just to pinnipeds in general; and 4) the increase in shark sightings was likely the result of increasing numbers of elephant seals rather than to an environmental variable such as sea surface

temperature. Sharks prey on a higher percentage of elephant seals despite greater numbers of California sea lions (Zalophus californianus) and three other less numerous but increasingly abundant pinnipeds at the Farallones: northern sea lion (Eumetopias jubatus), northern fur seal (Calorhinus ursinus), and harbor seal (Phoca vitulina) (Huber et al. 1978; PRBO unpubl. data 1979-1983).

In this paper we further explore the seasonality of white shark occurrence at the Farallones and the apparent prey selectivity of the shark. Based on seasonal and annual changes in population dynamics of the predator and prey, we also speculate on how natural history patterns of these animals may be interrelated. We extend our data and comments to the larger Gulf of the Farallones area.

METHODS

The Farallon Islands (San Francisco Co.) are due west of San Francisco's Golden Gate, but the closest mainland points are Bolinas Point and Point Reyes, in Marin County 30 km away. The Gulf of the Farallones lies between the islands and the mainland, from Point Reyes to Devil's Slide (Fig. 1). The islands teem with marine bird and mammal life (DeSante and Ainley 1980; Huber et al. 1978). Large numbers of marine birds and pinnipeds also reside along the northern half of the Gulf's mainland shore including one of the largest populations of harbor seals on the Pacific West Coast, i.e. well over 2000 animals (PRBO unpubl. data).

Since 1968, PRBO has maintained a research station on Southeast Farallon, an island about 41 hectares (100 acres) in area. Every day,

except during heavy rain, we have censused birds and surveyed inshore waters; we have censused pinnipeds weekly since 1972 (elephant seals since 1970). Biologists have spent the majority of their time out-of-doors in various kinds of observational activity. It is during these activities that the observations we report on here were made. The number of biologists and their activities have not changed significantly since 1972 because a number of long-term projects are in progress. In almost every instance of shark/pinniped interaction, we were first alerted by a flock of gulls hovering in the vicinity (Ainley et al. 1980); gulls are least numerous at the island from September to January. Since 1972, we have collected daily water samples to determine sea surface temperature and salinity. Censuses and observation of harbor seals at Double Point, Marin County, have been made 2-10 times per month since 1976 by Allen.

In the following sections, a subadult elephant seal, indentifiable by size, is equivalent to "juvenile" (1-4 years of age) as defined by Le Boeuf et al. (1974:371). A subadult sea lion, also indentifiable by size, is any animal not an adult (also probably ≤ 4 years of age). The size of both seals and sharks was estimated by visual comparison with the wing span of gulls (ca. one meter) hovering nearby.

RESULTS AND DISCUSSION

The seasonality of white shark occurrence at the Farallones has continued beyond 1979 (Ainley et al. 1981). This was evident in direct observations of white sharks independent of pinniped interaction (Table 1), where the peak occurred October through December; in observations of shark

"attacks" on pinnipeds (Table 2), where the peak occurred in October and November; and in the frequency of occurrence of pinnipeds with recent shark-bite wounds, where the peak occurred September through December (Table 3). In contrast, as indicated by the occurrence frequency of fresh wounds on harbor seals, the peak of shark/pinniped interaction along nearby mainland shores, at Double Point, occurred March through June (Table 3). To accept a relationship here, one has to assume that the wounds on seals at Double Point were also inflicted by white sharks because we have few direct observations of interaction. It is known that harbor seals are an important prey of white sharks in California waters (Le Boeuf et al. 1982), and the wounds we observed were often quite large, which would indicate white sharks. Furthermore, few other shark species in these waters are known to feed on harbor seals to a significant degree. Blue sharks (Prionaca glauca) and sevengill sharks (Notorynchus sepioides) take them occasionally, apparently as carrion; sleeper sharks (Somniosus pacificus) probably take seals in the Arctic, but in central California the species lives in such deep water that it may not have much chance to eat live seals (L. Compagno, pers. comm.). Unfortunately, no data are available to compare the wounding frequency of harbor seals at Double Point with those at the Farallones because the species was not abundant at the islands and was not easy to view there at close range. Like harbor seals at Double Point, sea otters (Enhydra lutris; also in coastal waters of central California) are attacked by white sharks most frequently during the early summer (Ames and Morejohn 1980).

Direct observation of white sharks, including both attack and

non-attack situations, indicated a much sharper seasonality at the islands than did the occurrence of recently inflicted wounds on pinnipeds ($\chi^2 = 27.144$, df 11, $P < .005$). Thus, a significant proportion of pinnipeds hauling out at the Farallones with fresh wounds probably encountered sharks elsewhere particularly from March through August. It is likely that these individuals encountered sharks near the mainland.

Considering the ages of pinnipeds that had fresh shark-bite wounds, it appeared that young animals were bitten more often than older ones (Table 3). There was no difference in the age ratios of bitten animals, elephant seals as compared to California sea lions ($\chi^2 = .2080$, $P > .97$; the sample size for other species was too small for comparison). For both observed attacks and wounded animals, the age ratio of elephant seal victims was virtually identical to the average age ratio in their population (1 adult to 4.4 subadults, 1971-1983) during September to December when the peak of shark activity occurred ($\chi^2 = .0087$ for wounded animals; $\chi^2 = .0109$ for animals observed in attacks). Among sea lions, however, subadults were wounded disproportionately to their representation in the population (1 adult to 2.3 subadults) during September to December ($\chi^2 = 3.5092$, $P = .06$). These comparisons are much more instructive using sea lions as the example, because very few adult elephant seals were present at the Farallones during the peak of shark activity. We conclude that young pinnipeds fell victim to white sharks much more readily than adults.

In our earlier analysis (Ainley et al. 1981), based on identifying the pinnipeds being eaten by sharks and the proximity of attacks to specific haul-out areas, we tentatively concluded that elephant seals were the most

sought-after mammalian prey of white sharks at the Farallones. The data in Table 2 reveal how such a conclusion could be drawn: 26 elephant seals have been positively identified as being attacked by sharks compared to only seven sea lions even though four times as many sea lions haul out at the islands during the fall. If sharks had no preference for prey and if attacks occurred proportional to pinniped population size, we would expect to have identified about 100 sea lions in shark/pinniped interactions. The data in Table 3 support Table 2. Although 49 California sea lions have been observed with fresh shark wounds, compared to only 34 elephant seals, relative to the number of animals present (September to December) three times as many elephant seals (1.92% of the population) as sea lions (0.68%) were wounded. The difference is significant (footnote b in Table 3).

We conclude that in the vicinity of the Farallones, elephant seals were more vulnerable than sea lions, and that regardless of species, subadult animals were more vulnerable than adults. We have also learned, however, that white sharks do prey on sea lions to a greater degree than we had thought earlier.

The vulnerability of young pinnipeds is probably a function of experience; many are probably naive about sharks or about maintaining a vigilance for danger in general. On the other hand, the smaller (young) pinnipeds may be of a size more manageable by sharks, and thus size of prey relative to size of predator may in some way factor into the sharks' seeming preference for small animals. Why elephant seals were more vulnerable than sea lions is more difficult to surmise. It may have to do with differences in behavior, and in support of this was the interesting

difference in the part of the body where pinnipeds of different types were bitten (Table 4). Among seals that survived a shark attack, shark-bite wounds were located more on the upper body whereas in surviving sea lions, bites occurred mostly on the lower body and hind flippers. .

The way in which white sharks were observed to attack a pinniped helps to explain these wounding patterns. On four occasions we had exceedingly good views of an attack, and by chance saw the entire sequence of events. In all cases, the shark bit the pinniped (all elephant seals) from behind. The victim was apparently disabled or in a state of shock because, though still alive, it did not swim away. From one to five minutes later, the shark bit again, this time actually to consume the victim. In one case an estimated five-meter long shark, five minutes after the initial disabling bite (from below and the rear) bit off and swallowed about two-thirds of the immature seal. Interestingly, most humans bitten by a white shark have been bitten on the legs or feet, and the shark usually approached unseen from the rear or below (Miller and Collier 1981). Also, harbor porpoise (Phocoena phocoena) successfully captured by white sharks are also attacked initially on the rear of the body (tail stock; Arnold 1972).

If we assume that a shark can approach a pinniped usually only from the latter's "blind" side, which would generally be from below and the rear, and the shark then administers its initial one-bite attack, a seal would be less likely to escape than a sea lion. This is because phocids (seals) propel themselves using their lower body and hind flippers whereas otariids (sea lions and fur seals) propel themselves using their front flippers. Thus, by attacking a pinniped from the rear, a white shark is more likely

to be successful in securing its prey if it attacks a phocid as opposed to an otariid. It is important to note that the data in Table 4 were based on pinnipeds that got away: seals that were initially bitten on the upper body as opposed to sea lions that were initially bitten on the lower body, and thus in both cases were not disabled. Whether or not a shark can visually distinguish between a seal and sea lion or distinguish by other means between the low frequency waves generated by the different motion of a swimming seal as opposed to a sea lion are points for speculation.

Another factor that likely increases the vulnerability of seals is their solitary nature when away from the beach. Sea lions, on the other hand, tend to occur in herds especially when resting. Thus only one sea lion need see a shark for the entire group to be alerted. When resting or sleeping in deep water, phocids "lie" vertically with their nose out of the water; sea lions lie horizontally, often in physical contact with other individuals, often with their heads under water except when breathing. This difference probably allows a shark to approach a seal more easily than a sea lion, and it may explain why so few sea lions were bitten on the face and neck (Table 4).

The number of attacks on pinnipeds and of sightings of sharks independent of attacks continued to increase at the Farallones after 1979, the last year of observations for our initial report (Ainley et al. 1981). The number of attacks observed in the fall/winter period continued to be directly proportional to the peak number of young elephant seals present during the fall (October or November, 1970 to 1981; Fig. 2). However, the annual rate of increase in the number of young elephant seals hauling out

has slowed (Fig. 3), and, interestingly, so did the rate of increase in the number of shark sightings per year (attack and non-attack situations). The rate of increase in other pinniped populations at the Farallones did not slow (Ainley et al. 1982; PRBO unpubl. data). Further supporting the importance of elephant seals in determining the occurrence of sharks at the Farallones during fall, a regression of shark sightings to the number of subadult elephant seals 1970 to 1981 yielded a correlation coefficient ($\underline{r}$) of .900, whereas regressions against the peak number of subadult sea lions and to the total pinnipeds present each fall yielded $\underline{r}$ -values of only .800 and .843, respectively. All correlation coefficients were statistically significant. The analysis could not be extended to 1982 because on 2 October of that year a commercial vessel caught four white sharks within 100 m of shore at Southeast Farallon. All sharks were 4-5 m in length. To that date, consistent with patterns in previous years, only two attacks and one non-attack sighting of a white shark had been made; later during that fall/winter period, only four attacks and four non-attack sightings were logged. The total shark sightings for the 1982-83 fall/winter period was only 11 incidents, compared to 12 in 1980-81 and 17 in 1981-82.

The killing of the four sharks at the islands has possibly upset our study, but their capture and the subsequent reduction in shark activity did indicate some interesting points. First, it became apparent that only about five or six different, large white sharks were responsible for the level of activity we observed in recent years. In fall 1976, we knew that at least three different white sharks were present (Ainley et al. 1981). Second, the fact that capture of the four sharks significantly reduced

shark sightings and shark/pinniped interactions (Fig. 4) indicated that the individual sharks were somewhat "resident" during the fall. Had sharks from a larger pool of individuals merely come and gone at random, we would have expected that the capture of four would have had little effect on sighting frequency. A week after capturing the four sharks, the same commercial vessel returned, and fished for but caught no sharks in spite of the fact that one shark was seen by us between visits of the vessel. This indicates that it may be relatively easy to "overfish" a local concentration of large white sharks.

Data on the size of sharks observed supported the hypothesis that individual sharks were resident around the islands during fall, and that the same sharks were likely involved year after year. Plotting the estimated length of sharks observed by year indicated a gradual increase in size (Fig. 5). The plateau in maximum size at 3-4 meters during 1974-1976 was probably an artifact of biological conservatism to avoid exaggeration. The sudden increase in the maximum size of sharks in 1977 likely resulted from the realization that overly conservative observations from shore were not accurate. This realization was encouraged when a 5.5 meter long shark surfaced next to our four meter long landing skiff. This was an incident which had not occurred since 1974 but which has occurred three times since 1978. The more instructive trend in Fig. 5 is probably the size of the smallest white sharks seen each year. Since 1977 we have seen no white sharks smaller than three meters, and the minimum size increased thereafter at least into 1981. Based on these trends, we hypothesize that the growing food source at the islands may initially have been discovered by small,

subadult white sharks that returned as larger and larger individuals year after year. It may not be coincidence that the growth rate of white sharks indicated in our data (i.e., plus or minus 50 cm per year) is comparable roughly to the rate calculated by G. Cailliet et al. (Moss Landing Marine Lab, this volume) on the basis of more exact techniques.

In our earlier analysis (Ainley et al. 1981), we concluded that sea surface temperature (SST) had little bearing on the occurrence of white sharks at the Farallones. Since then, however, we have heard several times, particularly in the news media, that anomalously warm waters off California in 1982-83 would likely lead to increased white shark activity/abundance in coastal waters. We thus looked again at our data, combining 1970-1979 with 1980-82 data. During this period anomalously warm water occurred in 1972-73 and again in 1976-77. The data still indicate no relationship between anomalous SST and the frequency of shark sightings: 35 shark sightings were recorded during months when SST was above average whereas 53 occurred during months when SST was below average. Furthermore, the frequency of sightings was not anomalously high in either 1972-73 or 1976-77 (Fig. 4).

During the fall/winter period, the frequency of shark sightings at the Farallones corresponded much better with the mean number of subadult elephant seals present ($r = .960$) than it did with the mean monthly SST ($r = .686$), which peaked about a month earlier than shark sightings and seal numbers (Fig. 6). Only one shark sighting was logged during the spring when seal numbers reached their other annual peak and SST reached the annual low. The correspondence between frequent shark sightings when SSTs

were warm in the fall and infrequent sightings when SSTs were cold in the spring is probably meaningless given that sharks during spring appeared to prey more on harbor seals along the adjacent coast where water temperatures are not much different than at the Farallones (Scripps Inst. Oceanogr., unpubl. data on SST at shore stations). The apparent increased white shark activity along the coast during spring happened to correspond with the single annual peak in the numbers of harbor seals hauled out (Fig. 7). [As already noted, though white sharks prey on sea otters along the central California coast throughout the year, predation on them apparently also peaks during the spring, May and June (Ames and Morejohn 1980)]. Based on the above data, we conclude that within the temperature limits of central Californian coastal waters, including anomalously warm conditions, water temperature was not a factor associated with white shark predation.

SPECULATIONS

Our data indicated that the occurrence of large white sharks in coastal waters of central California was influenced strongly by the population dynamics of two species of seals, which appeared to be preferred prey. In the fall, the sharks apparently moved to a site (e.g. Farallones) occupied by large numbers of young elephant seals, and were not present at that site during those parts of the year when large numbers of adult seals were present. The sharks then seemed to be more abundant elsewhere; in the Gulf of the Farallones they apparently occurred then in coastal waters where harbor seals reached an annual peak in abundance. It would be interesting to know whether the movement to coastal areas during spring and early

summer was also influenced by other factors such as the breeding or migrational activities of the sharks. There is no indication, however, that female white sharks drop their young in the area, as indicated by the fact that no white sharks smaller than about two meters have been captured in the Gulf of the Farallones vicinity (L. Compagno, pers. comm.). Few other data are available as a basis for further speculation.

Conversely, it is interesting to speculate how shark predation may have influenced the population dynamics of the white shark's preferred prey. The elephant seal is unusual among pinnipeds in California in that females give birth and pups are weaned during late winter. Other pinnipeds wean their young during summer. Most of the population of the northern elephant seal breeds on islands well offshore, and only in recent historical times have they bred at sites inshore (Le Boeuf and Bonnell 1980). Thus, except *no-use to seals mainland* during the past 40 years, if a white shark were to seek young elephant seals for food they would have to do so with any significant chance for success in offshore waters near to seal breeding sites. If pups venturing to sea for the first time are especially vulnerable to white shark predation, then it would certainly be advantageous for them to achieve independence and to overcome their initial naivete when the sharks are mostly elsewhere. It would follow that a female elephant seal at the Farallones is more likely to produce a pup that survives to adulthood if she gives birth and weans her pup during late winter/early spring. In contrast, the coastal harbor seal, which is another important prey of large white sharks, weans pups during the late summer/early fall in California, when at least in the Gulf of the Farallones, white sharks may be elsewhere

(i.e., offshore). Whether or not these events in the natural history of the two seals and the white shark really are interconnected remains for a great deal more work and observation to be completed.

Our data indicated that Farallon waters were populated by only a few white sharks, probably semi-resident on a seasonal basis year after year. The data also indicated that it was easy for this population to be overfished. In a world where the continued existence of large terrestrial predators (other than man) is rather tenuous, given that virtually all large felids and canids are considered endangered, we wish to propose that white sharks could also attain, quite easily, a similar endangered status.

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FIGURE CAPTIONS

- Figure 1. Map of the Gulf of the Farallones.
- Figure 2. The number of attacks on pinnipeds at the Farallon Islands as a function of the fall peak in the number of immature elephant seals; Farallon Islands, 1971 to 1982 [attacks = $42.6 (\text{no. seals}) + 122.4$; $r = .900$].
- Figure 3. Trends in the number of subadult elephant seals at the Farallon

Islands during each fall/winter month, September - January; curves for October and November are described by second degree polynomial equations, where z is the number of animals and x is the year; October: $z = -68.7 + 95.2 x - 4.3 x^2$, $r = .964$; November: $z = -22.3 + 81.7 x - 3.4 x^2$, $r = .949$.

Figure 4. The trend in the number of white shark sightings at the Farallon Islands 1970-71 to 1981-82 (annual periods extend from July through June); the curve is described by the equation, z (sightings) = $-1.8 + 1.7 x - .02 x^2$ ($r = .943$). The open circle designates sightings in 1982-83, when four large sharks were killed at the Farallones by fishermen.

Figure 5. The estimated lengths of white sharks (as a function of the estimated distance between caudal and dorsal fins) seen at the Farallon Islands, 1972-73 to 1982-83.

Figure 6. The proportion of white shark sightings by month compared to the mean monthly sea surface temperature (°C) and the mean monthly numbers of subadult elephant seals, Farallon Islands, 1971-72 to 1982-83.

Figure 7. Changes in the seasonal inshore vs offshore occurrence of white sharks compared to seasonal cycles in the abundance of inshore vs offshore prey: harbor seals at Double Point and immature elephant seals at the Farallon Islands, respectively; shark presence is reflected in the proportion of recently bitten seals by month.

Table 1. Observations of white sharks independent of pinniped interactions,
Farallon Islands 1970-1983.

	Month												Total
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
No. sightings	0	0	1	8	4	5	3	2	0	0	0	0	23

Table 2. The number of observations of sharks preying on pinnipeds by month and, when known, the age and species of pinniped; Farallon Islands, April 1970-March 1983.

Prey	Months												Totals
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
Elephant seal													
Adult							2						2
Non-adult		2	5	4	1	2							14
Unknown				4	5				1				10
Sea lion													
Adult								1					1
Non-adult	1							1	1				3
Unknown			2		1								3
Pinniped species	1	2	5	14	12	4	2	1					41
Totals	2	4	12	22	19	6	4	3	2	0	0	0	74

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

A. Peter Klimley

Abstract.—Capture information for 109 white sharks caught along the west coast of the North America suggests the following life history pattern. Adult females give birth to pups during late summer and early fall south of Point Conception where the pups remain inshore at that time. As the pups grow larger, they move north of Point Conception to live both inshore and offshore near islands. As females grow even larger, 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 west 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; and Follett, 1966), 2) catalogues and field notebooks of ichthyological collections (California Academy of Sciences, the Los Angeles County Museum, and Scripps Institution of Oceanography), and 3) collection records of Seaworld, 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. These biases were incorporated into 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 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 Table 1. 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 caught 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 interested fish biologists? 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. Although, unfortunately, effort could not be integrated over the entire period from 1934 to 1983 over which captures were reported, 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 were 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 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 Fig. 1 to the right of the locations of their institutions. William Follett of the California Academy of Science and Leonard Compagno, at one time 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 captures. Cam Swift of the Los Angeles County Museum 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 captures of white sharks to be kept in the Seaworld shark exhibit.

TUNA FISHERY
DIFFERENT

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 size 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 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.). 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 appear 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 for along the coast of California. The gear types with which the white sharks were captured, however, were usually recorded by the source of 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 Table 1), 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 Table 1). 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 north than south 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) than 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 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 males caught north of Point Conception occurs at this time probably indicating a decrease in male abundance, no such decrease occurs in the catch of females. In spring decreased percentages of sharks caught in the two areas appear explicable by decreases in fishing 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 (symbol with cross) were caught south of Point Conception (stippling) during summer (solid circles) and fall (clear circles). 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 deg 20 min N) to Monterey Bay (37 deg N) at a size of ca. 2000 mm (see Fig. 2). This movement probably occurs in the late summer and fall, judging from the equal numbers of summer and fall captures along the coastline from Monterey to Tomales Bay (37 deg to 38 deg 30 min N) and south of Point Conception (34 deg 20 min). Although males remain north of 37 deg N as they grow to a size of 4775 (record 10 in Table 1), 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 (circles) at which white sharks were captured south (clear) and north (solid) of Point Conception are plotted in Fig. 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) were carried out were obtained from Rondi Reingart of the Department of Fish and Game in Long Beach. Due to 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 along the dropoff near South 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 due to 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 they were not deploying their gear 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 specific, but it is also possible that 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 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 white shark supports this movement northward as they grow into adults and return to offshore islands as adult females. The dietary items for male and female white sharks of different sizes caught south and north of Point Conception are shown in Fig. 7. Stomachs of white sharks less than 2000 mm in length contained bony fishes (cabezon-S. marmoratus and lingcod-O. elongatus), cartilaginous fishes (gray smoothhound-M. californica, spiny dogfish-S. acanthias, and a dasyatid ray), crustaceans (spot-bellied rock crab-C. antennarius), and cephalopods. Intermediate size white sharks from 2000 to 4000 mm were caught primarily north of Point Conception with bony fish (additionally, Pacific sardine-S. sagax, green sturgeon-A. mediodorsalis, king salmon-O. tshawytscha, white seabass-C. nobilis, black rockfish-S. melanops, and striped bass-Roccus saxatilis), cartilaginous fishes (addit., brown smoothhound-M. henlei, soupfin shark-G. zygopterus, and bat ray-M. californica), a pinniped

(harbor seal-P. vitulina), and a crustacean. Large sharks greater than 4000 mm in length fed on pinnipeds (addit., northern elephant seal-M. angustirostris and California sea lion-Z. californiensis, bony fishes (addit., Pacific hake-M. productus), cartilaginous fishes (addit., basking shark-C. maximus), and crustaceans (addit., market crab-C. magister). The increasing importance of pinnipeds over fishes in the diets of white sharks as they grow larger 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 offshore on islands south of Point Conception, white sharks probably remain offshore there where prey is available.

Lastly, 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 Fig. 8. Although there is considerable variability in records on both the annual and biennial scales, the numbers of captures appear to be increasing, in particular, since 1974. Two biennial frequency peaks exist, 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, and this was probably due to the public interest aroused from the showing of the motion picture "Jaws" throughout the United States in 1975. Furthermore, since this time Seaworld has offered rewards to fishermen capturing small white sharks be kept in captivity, and these have 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 being only in the larger cities), the frequencies of white sharks 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. com.) and occurred from 1926 to 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 Bay (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 after dying from lacerations inflicted by white sharks. The cause of these wounds was demonstrated to be the white shark from the presence of tooth fragments in the wounds and tooth penetrations and scratches on the bones of the otters (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 along the shoreline 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 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 to the possibility 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 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 2. 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). Higher frequencies of sharks were spotted from May to October with the peak frequency in August. The attacks on man by the white shark from 1926 to 1983 (Miller and Collier, 1980; Lea, pers. com.), all except for one north of Point Conception, 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) to five and two kills 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 prey other than pinnipeds. Anyway, the fall peak does not 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 March to July and not during the late summer and fall as most other indices.

Is the overall increase in shark captures since 1974 reflected in these indices of white shark abundance? Are there peaks similar 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 3. 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 are so low. There do, however, appear to be broader peaks in attacks correlated with the capture record peaks from 1959 to 1961 and 1974 to 1976. Although the number of pinniped kills increased over a period of from 1970 to 1978 at the Farallon Islands (Ainley et al., 1981), the increase is not evident if attacks on pinnipeds 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 per censused seals, and thus could be due to an increasing pinniped population size with a static shark population size. 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 west 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 the 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) was less than 174 cm. The location of its capture was not given. Furthermore, few very large sharks were in the sample of Bass et al. (only four of the sharks were greater than 324 cm). Of these 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 are very different than that of white sharks off the west 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 west 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 these large sharks were caught in areas of peak pinniped densities such as surrounding San Francisco, Año Nuevo Island, and Morro Bay. Large white sharks were caught in Southern California offshore, near islands with pinniped rookeries. Four out of six sharks greater than 3500 mm were captured at near islands. These islands 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).

The northeastern Atlantic white sharks 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 comprised larger percentages. This would be expected from our finding 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 Agulhas 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 feed on moribund whales than small fishes. Along the western coast of North America, large white sharks 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 by myself 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 were not there from September to January when temperatures increased over the same temperature range.

It is striking that white shark pups are birthed most commonly off the coast of Baja California 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 due to 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 were obtained from the scientific literature, catalogues and 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 remain inshore and move offshore. This northward movement may occur rather abruptly as the sharks reach a size of ca. 2000 mm in length. Females return to Southern California, yet to offshore islands possibly to give birth to young. 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 the larger members of the species and possibly the proximity of pupping grounds with fewer predators and competitors.

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Figure Captions

Fig. 1. Locations of white shark captures along the western of North America. Captures identified by numbers given in Table 1. 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 mass and its percent of the total catch is given in parenthesis. 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 parenthesis.

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.

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 color 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 parenthesis. Multiple captures of similarly sized sharks at the same location indicated by concentric symbols.

Fig. 4. The distance from coastline and shore at which white sharks of different sizes are 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.

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

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

Fig. 7. Stomach contents of white sharks caught north and south (stippled) of Point Conception. The mass (parenthesis) 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.

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.

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. com.).

Table Captions

Table 1. Capture information for white sharks caught along the western coast of North America. DFS: distance from shore; DFC: distance from the coastline; BD: bottom depth; SD: shark depth; S: sex; X: missing date; NIA: not included in analysis.

Table 2. 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. com., 3) population censuses and kills of pinnipeds from Ainley et al., 1981, and mortality of sea otters from Ames and Morejohn, 1980.

Table 3. 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. com., 2) population censuses and kills of pinnipeds from Ainley et al., 1981, 3) bite scars on northern elephant seals from LeBoeuf et al., 1982, and 4) mortality of sea otters from Ames and Morejohn, 1980.

Fig. 1

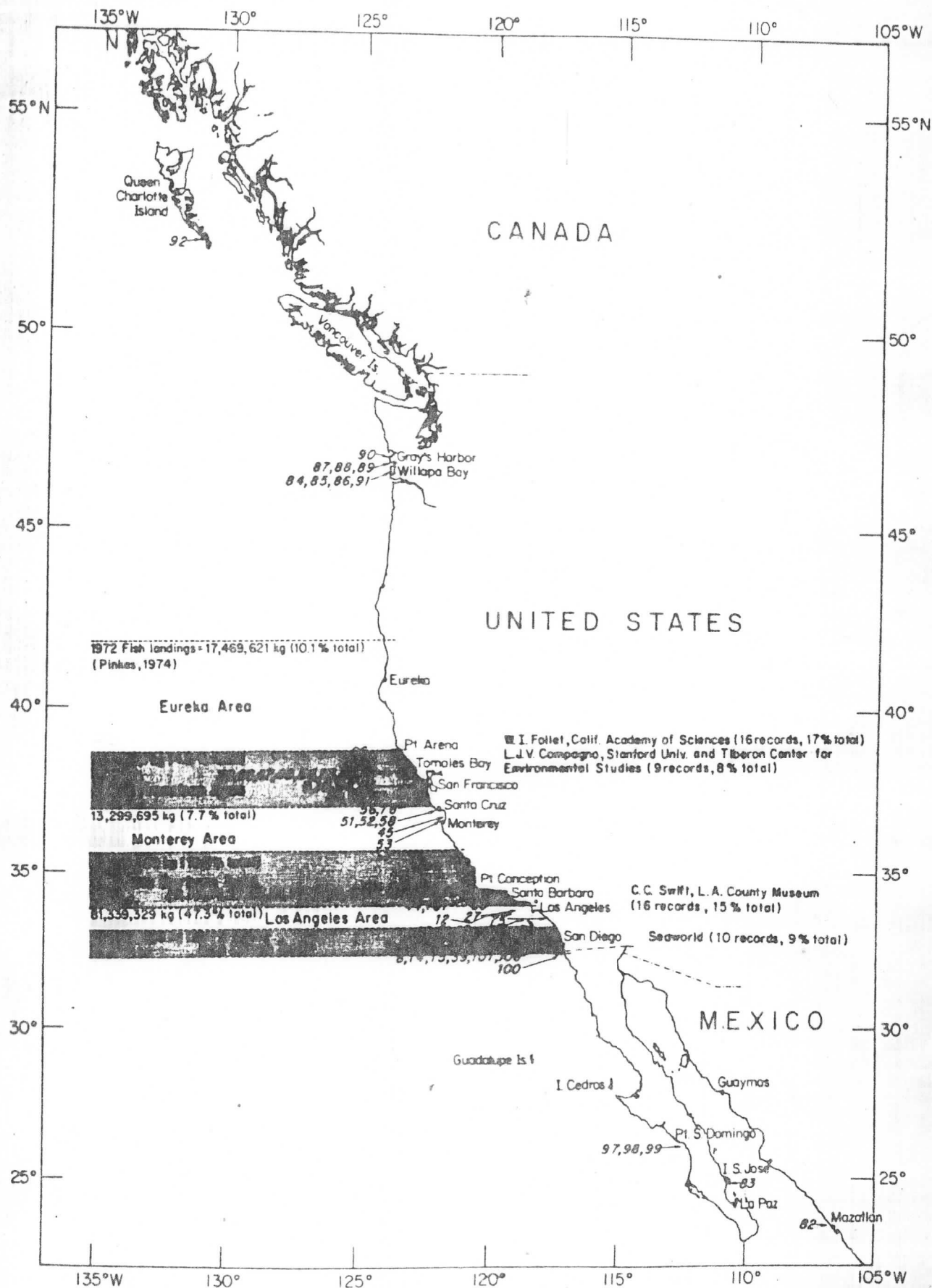
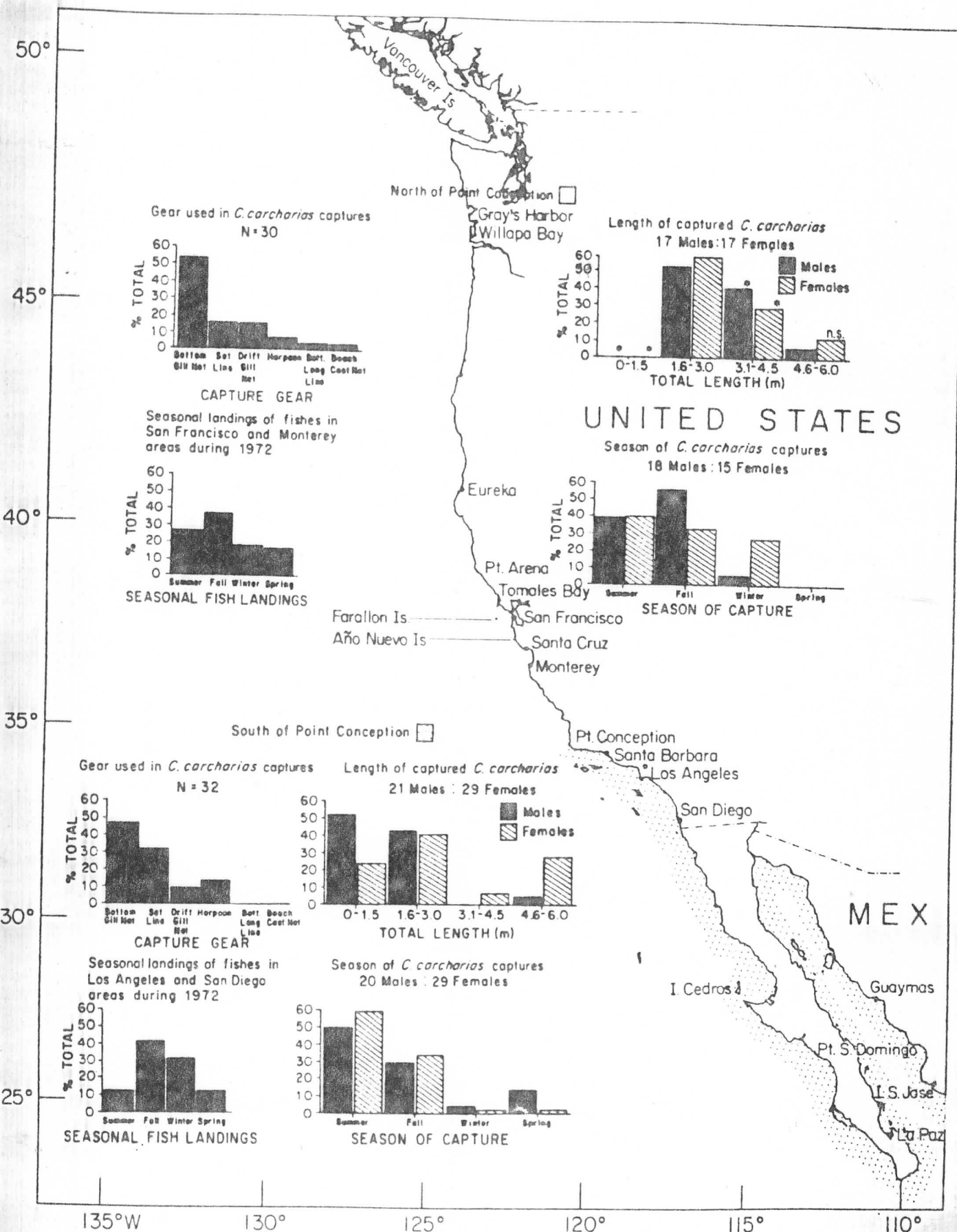
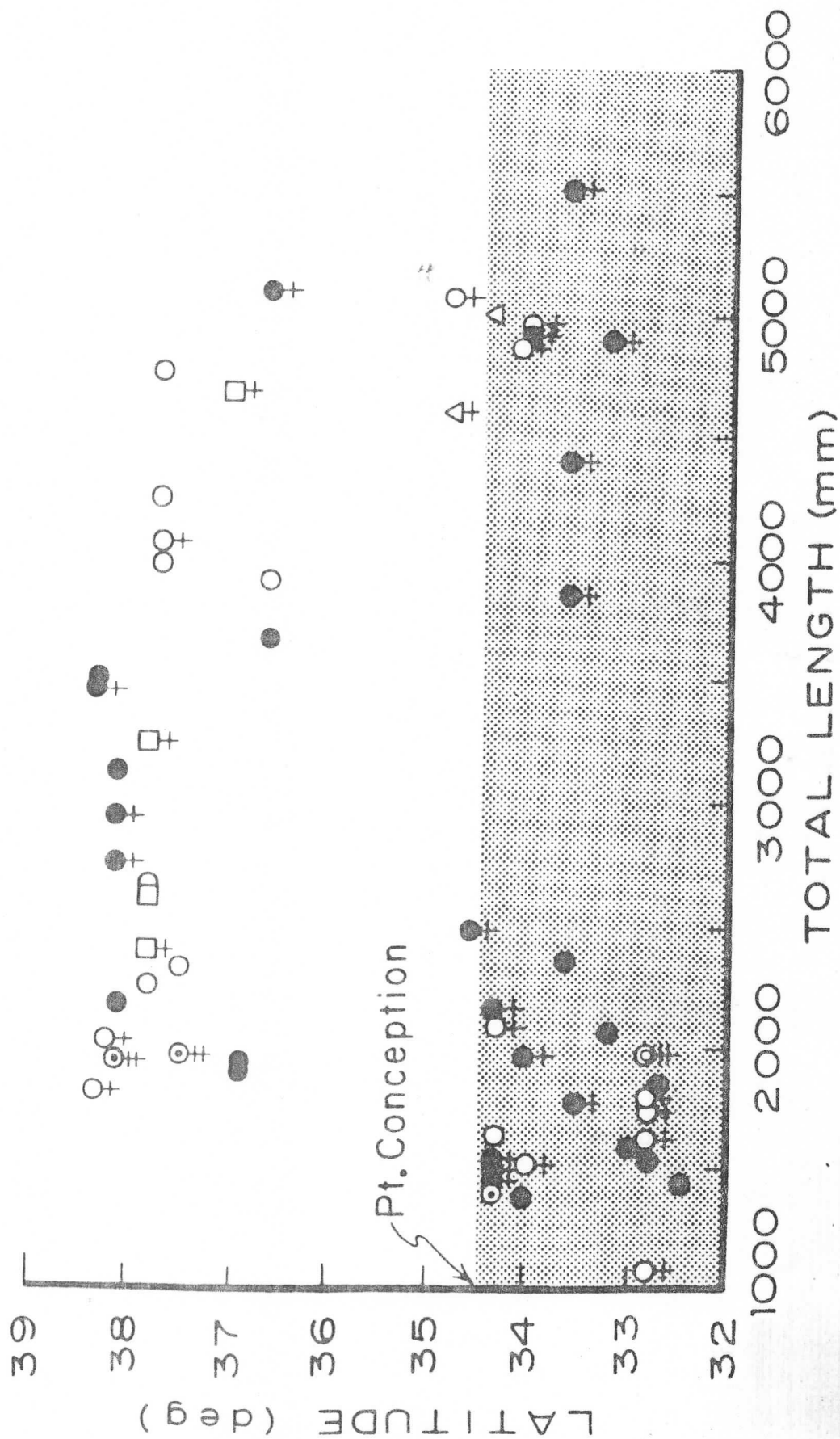
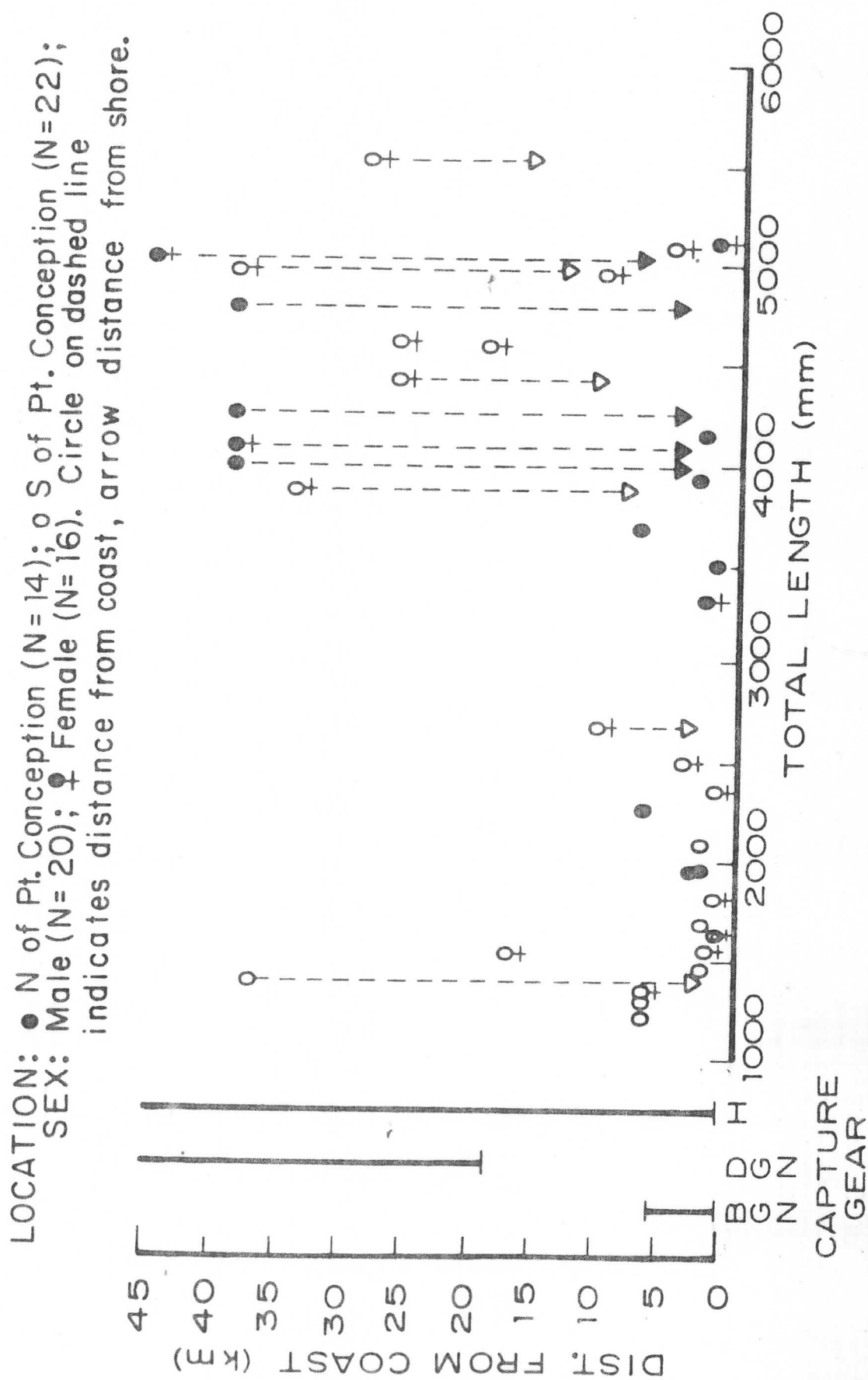


Fig. 2

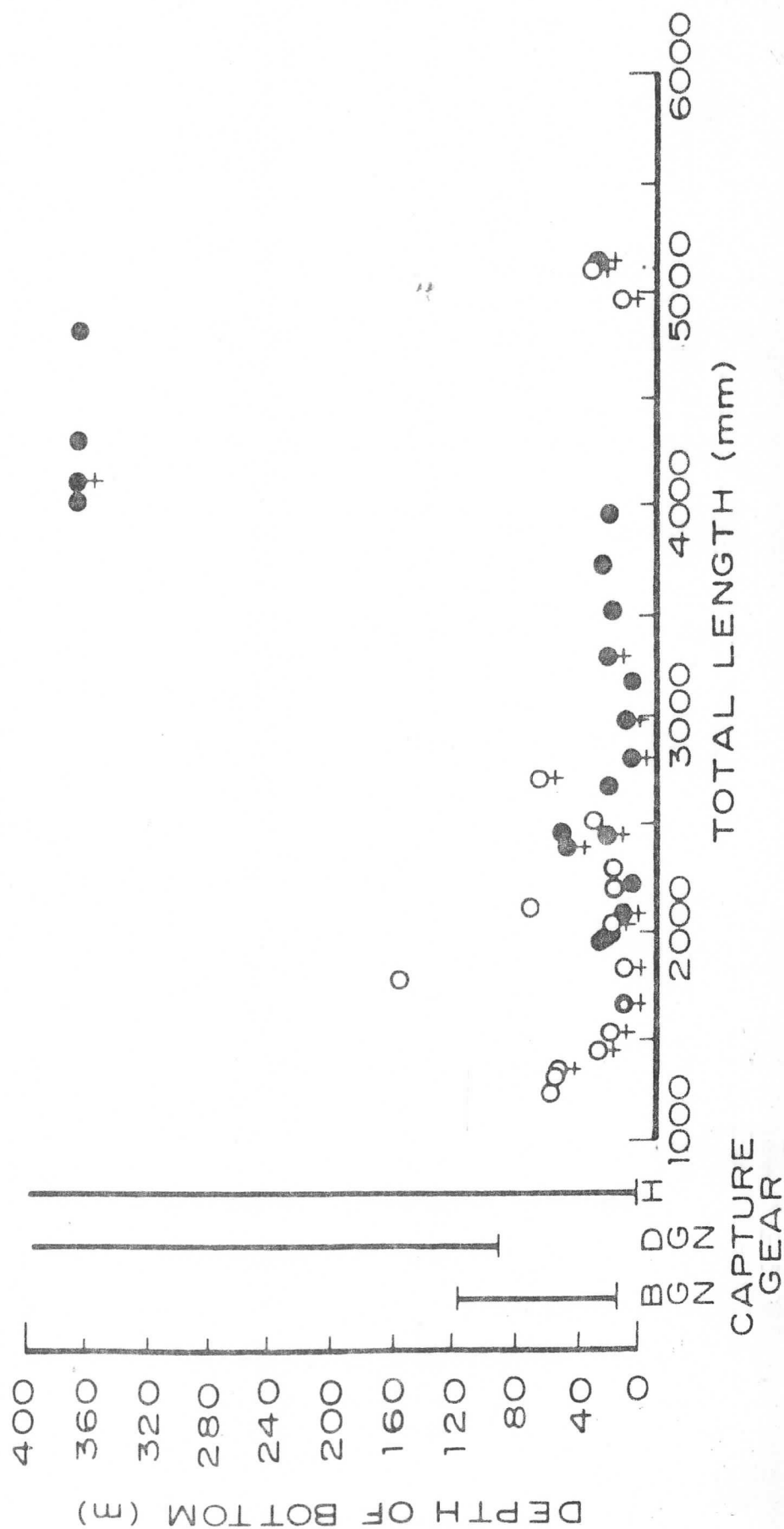


SEASON: ● Summer (N=40); ○ Fall (N=28); □ Winter (N=5);
 △ Spring (N=2)
 SEX: Male (N=38); ♀ Female (N=37)





LOCATION: ● N of Pt. Conception (N=23); ○ S of Pt. Conception (N=15)
 SEX: Male (N=20); ♀Female (N=18)



LOCATION: ● N of Pt. Conception (N=10); ○ S of Pt. Conception (N=16)
 SEX: Male (N=11); ♀ Female (N=15)

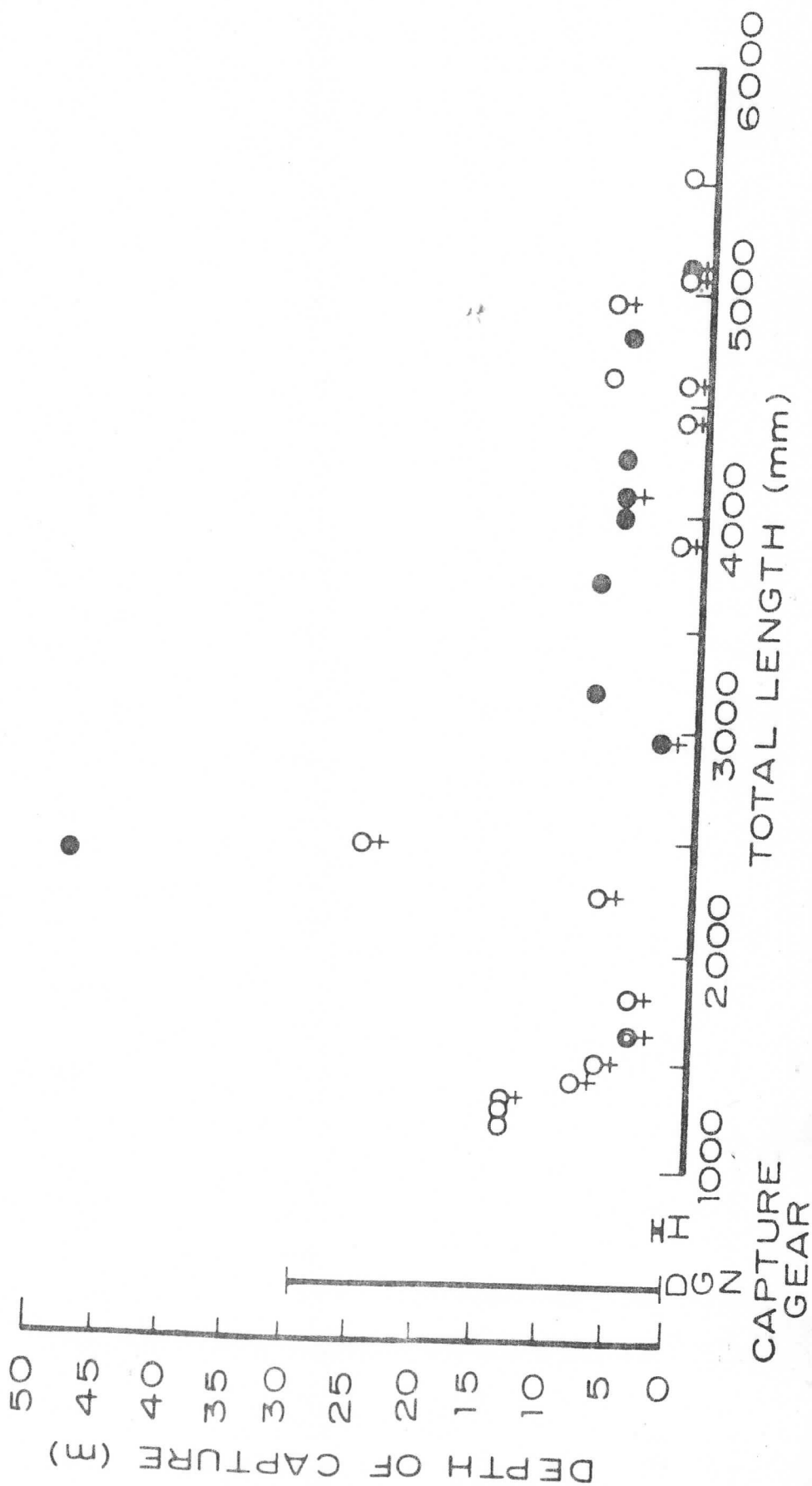


Fig. 7

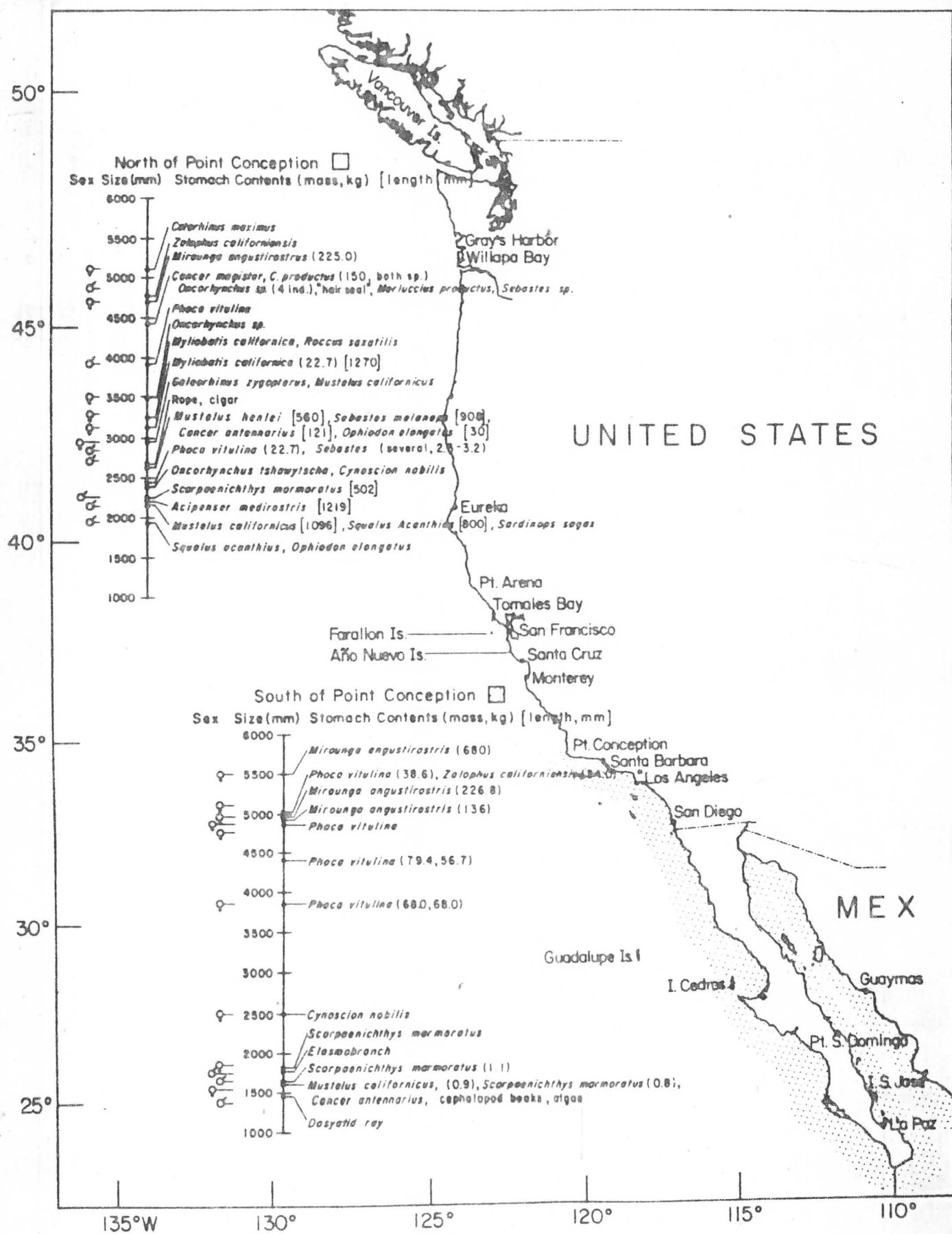


Fig. 8

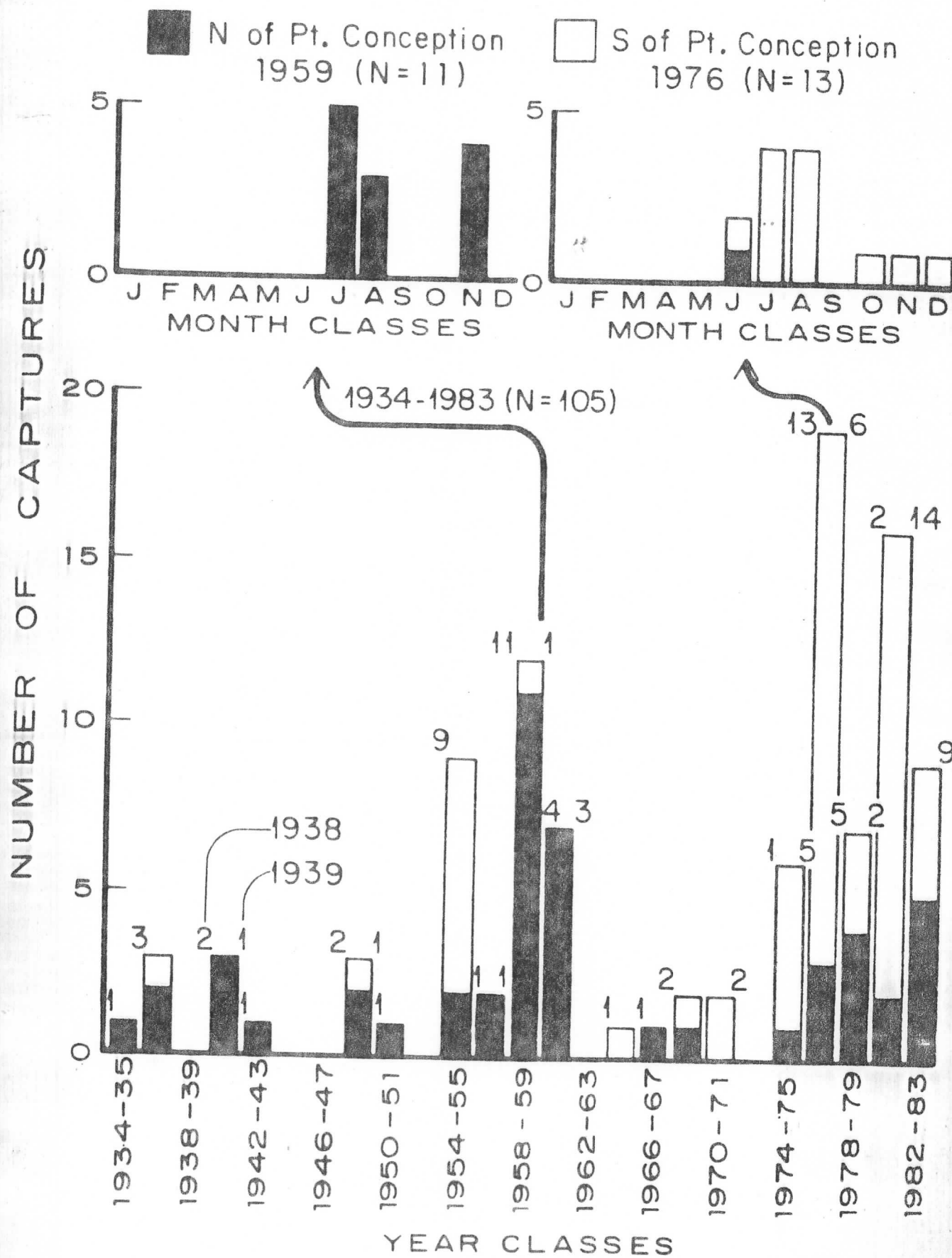


Fig. 9



Table 1. Capture information for white sharks, *Carcharodon carcharias*, caught along the western coast of North America. DFS: distance from shore; DFC: distance from coast; ED: bottom depth; and SD: shark depth; S: sex; X: missing date; N/A: not included in analysis.

No.	Date	Time hrs	DF km	DFS km	ED m	SD m	Cap. Meth.	Fisherman	Len. mm	Wt. kg	S	Stomach Contents	Source
1	10-30-55	1530		0.4	6.1	3.1	set line	Flechsigs	1886		F	Scorpaenichthys Marmoratus	Flechsigs
2	10-31-55	1530		0.4	6.1	3.1	set line	Flechsigs	1632		M	S. marmoratus, Can- ger antennarius, Muscelus californi- cus, algae, squid beaks	Flechsigs
3	10-31-55	2100		0.4	6.1	3.1	set line	Flechsigs	1629		F	S. marmoratus	Flechsigs
4	11-3-55	1300		0.4	6.1	3.1	set line	Arebalo			F	not examined	Flechsigs
5	11-6-55	1100		0.4	6.1	3.1	set line	Tuthill	1626		M	none	Flechsigs
6	11-9-55							anon.					Flechsigs
7	11-12-55	1000		0.4	6.1	3.1	set line	Limbaugh				none	Flechsigs
8	11-4-55				15.2		set line	Tomlinson	2000		F	not examined	Flechsigs
9	10-5-82	1500	2.9	38.0	366.0	4.5	set line	Pemperton	4089	664.9	F	not examined	Flechsigs
10	10-5-82	2200	2.9	38.0	366.0	4.5	set line	Pemperton	4775		M	Zalophus californi- ensis	Metzger
11	9-24-81			16.7				Deshrow	1524	22.7	F	not examined	Zumwalt
12	6-28-76	1330		3.7	31.1	0	harpoon	Weeren	5080	2152.3	F	stomach everted	Swift
13	7-23-75		9.3	25.7		0	harpoon	Hawthorne	4409	612.3	F	Rhoca vitulina	LeBoeuf
14	5-X-68								1654	54.9	M	not examined	Seaworld
15	10-X-71							Tomlinson	1981		F	not examined	Seaworld
16	9-7-75			11.3	37.8				4966	1560.4	F	Microungia angustis- costalis	LeBoeuf
17	9-X-X								4877	1428.8	F	P. vitulina	Seaworld
18	8-21-76		18.5			0	harpoon	Langham	4572			not examined	Nelson
19	6-13-76		14.8	27.8		0	harpoon	Weeren	5525	2041	F	M. angustirostris	LeBoeuf
20	7-29-X							Frankhold	2946	385.6		not examined	Nelson
21	6-24-75		7.4	33.3		0	harpoon	Mansur	3861	635.0		P. vitulina	LeBoeuf
22	10-5-79						gill net	Bartelli	1829	90.7		not examined	Nelson
23	8-3-81		1.9	1.9			gill net		1676	45.4	M	not examined	Nelson
24	10-24-81								2133	136.1	F	not examined	Calliet
25								Wilson	5029	1587.6	F	Z. californiensis,	Nelson
26	4-16-80		5.6	44.5			gill net	Barker				P. vitulina	Johnson
27	4-30-82		9.2	9.2	9.2	5.5	gill net	Williams	4942	907.3	F	M. angustirostris	Seigel
28	5-20-82		25.9	25.9		6.1	gill net	Peters	4609	1224.7	M	not examined	Swift
29	10-15-76						gill net		1650		M	not known	Huddleston
30	9-3-77						gill net	Henke	1408		M	not known	Swift
31	9-3-77						set line	Henke	1414			not known	Swift
32	9-18-77						gill net	Henke	2099	73.5	F	not known	Swift
33	7-15-76				14.6	5.8	gill net	Henke	1500	29.5	F	not known	Swift
34	7-15-76						gill net	Henke	2258			not known	Swift
35	8-16-78						gill net	Henke		36.3		not known	Swift
36	7-3-78		7.4	0.7	22.0		gill net	Henke		25.0		not known	Swift
37	11-X-76						gill net	Henke		45.4	F	not known	Swift
38	8-18-76							Langham	4900		F	not known	Swift

Table 1. 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; and SD: shark depth; S: sex; X: missing date; N/A: not included in analysis.

No.	Date	Time hrs	DFS km	DFC km	BD m	SD m	Cap. Meth.	Fisherman	Len. mm	Wt. kg	S	Stomach Contents	Source
1	10-30-55	1530		0.4	6.1	3.1	set line	Flechsigs	1806		F	<i>Scorpaenichthys marmoratus</i>	Flechsigs
2	10-31-55	1530		0.4	6.1	3.1	set line	Flechsigs	1632		M	<i>S. marmoratus</i> , <i>Cancer antennarius</i> , <i>Mustelus californicus</i> , algae, squid beaks	Flechsigs
3	10-31-55	2100		0.4	6.1	3.1	set line	Flechsigs	1629		F	<i>S. marmoratus</i>	Flechsigs
4	11-3-55	1300		0.4	6.1	3.1	set line	Aleballo			F	not examined	Flechsigs
5	11-6-55	1100		0.4	6.1	3.1	set line	Tuthill	1626		M	none	Flechsigs
6	11-9-55							anon.					Flechsigs
7	11-12-55	1000		0.4	6.1	3.1	set line	Limbaugh				none	Flechsigs
8	11-4-55				15.2		set line	Tomlinson	2000		F	not examined	Flechsigs
9	10-5-82	1500	2.9	38.0	366.0	4.5	set line	Pemperton	4089	684.9	F	not examined	Flechsigs
10	10-5-82	2200	2.9	38.0	366.0	4.5	set line	Pemperton	4775		M	<i>Zalophus californicus</i>	Metzger
11	9-24-81			16.7				Deshrow	1524	22.7	F	<i>Diemisis</i>	Zumwalt
12	6-28-76	1330		3.7	31.1	0	harpoon	Weeren	5080	2152.3	F	not examined	Swift
13	7-23-75		9.3	25.7		0	harpoon	Hawthorne	4409	612.3	F	stomach everted	LeBoeuf
14	5-X-68							Tomlinson	1854	54.9	M	<i>Diemisis</i>	Seaworld
15	10-X-71								1981		F	not examined	Seaworld
16	9-7-75		11.3	37.8				Tomlinson	4966	1560.4	F	<i>Micropogonias undulatus</i>	LeBoeuf
17	9-X-X												
18	8-21-76		18.5			0	harpoon	Langham	4877	1428.8	F	<i>P. vitulina</i>	Seaworld
19	6-13-76		14.8	27.8		0	harpoon	Weeren	4572			not examined	Nelson
20	7-29-X							Fromhold	5525	2041	F	<i>M. angustirostris</i>	LeBoeuf
21	6-24-75		7.4	33.3		0	harpoon	Mansur	2946	385.6		not examined	Nelson
22	10-5-79							Bertelli	3861	635.0		<i>P. vitulina</i>	LeBoeuf
23	8-3-81		1.9	1.9			gill net		1829	90.7		not examined	Nelson
24	10-24-81						gill net		1676	45.4	M	not examined	Calliet
25								Wilson	1473	25.9	F	not examined	Nelson
26	4-16-80		5.6	44.5			gill net	Barker	2133	136.1	F	<i>Z. californicus</i>	Johnson
27	4-30-82		9.2	9.2	9.2		gill net	Williams	5029	1587.6	F	<i>P. vitulina</i>	Seigel
28	5-20-82		25.9	25.9		5.5	gill net	Peters	4942	907.3	F	<i>M. angustirostris</i>	Swift
29	10-15-76					6.1	gill net		4609	1224.7	M	not examined	Huddleston
30	9-3-77						gill net	Henke	1650		M	not known	Swift
31	9-3-77						set line	Henke	1408		M	not known	Swift
32	9-18-77						gill net	Henke	1414			not known	Swift
33	7-15-76				14.6	5.8	gill net	Henke	2099	73.5	F	not known	Swift
34	7-15-76				14.6	5.8	gill net	Henke	1500	29.5	F	not known	Swift
35	8-16-78						gill net	Henke	2258			not known	Swift
36	7-3-78		7.4	0.7	22.0		gill net	Henke	36.3			not known	Swift
37	11-X-76						gill net	Henke	25.0		F	not known	Swift
38	8-18-76						gill net	Langham	45.4		F	not known	Swift

39	11-4-71				gill net	Tomlinson	1085		F	not known	Swift
40	12-17-76				gill net	Caywood		48.5	F	not known	Swift
41	8-9-76	0.7	9.2		gill net	Henke	2170		F	unident.	Swift
42	8-17-77	14.6			gill net	Henke	1514		M	not known	Swift
43	7-27-76				gill net	Henke	1410	23.5	F	not known	Swift
44	7-12-59	2.8	27.5	7.3	gill net	Castagnola	2492	145.2	F	Onoscion nobilis	Follett
45	1-23-59	0.5	27.5	24.5	gill net	Tomlinson	5105	1279.1	F	Cetorhinus maximus	Follett
46	7-25-59	0.5	5.5	5.5	harpoon	Konatchik	3143	283.5	M	Hylobatis californica	Follett
47	7-25-59	0.730	5.8		drift net	Konatchik	2775	109.3	F	none	Follett
48	7-2-60	1900	5.8	1.2	set line	Spenger	2960	190.1	F	Galeorhinus zygodon, ternus, Mustelus californicus	Follett
49	11-13-59					Vella	2673	171.1	M	S. marmoratus	Follett
50	11-9-59	5.6			gill net	Vella	2254	101.6	M	rope, cigar	Follett
51	8-10-59	0300	2.3	22.9	drift net	Carniglia	1943	61.7	M	not examined	Follett
52	8-7-59	0530	24.8		drift net	Cardinali	1924	65.6	M	Squalus acanthias, Squalus elongatus	Follett
53	7-31-59	0530	6.5	23.8	drift net	Olivieri	3683	380.1	M	none	Follett
54	7-30-59	1620	5.8	6.4	drift net	Konatchik	2184	98.9	M	Mustelus californicus, S. acanthias, Sardinops sagax	Follett
55	8-21-79				gill net	Bertelli	1956	88.7	F	none	Follett
56	2-X-77				beach cast	Helm	3930	544.3	M	P. vitulina	Follett
57	10-25-78	1.8	20.0		tram. net	Salter	1959	54.4	M	none	Morejohn
58	8-28-59	0300	1.8	18.3	gill net	Konatchik	1965	69.9	F	none	Follett
59	10-7-60				gill net	Crivello	2419		F	Anchoa hepsetus tschukotensis, C. nobilis	Follett
60	12-27-60				gill net	Crivello				Mustelus californicus, Roccus saxatilis	Follett
61	1-2-61		20.1		gill net	Crivello				Mustelus henlei, Cancer antennarius, O. elongatus, Sebastes melanops	Follett
62	12-28-60		20.1		gill net	Crivello	2651	180.5	M	not examined	Calliet
63	6-X-61					Mueller	1290	16.1	M	not examined	Compagno
64	11-8-61					Remarquez	2340	86.2	M	not examined	Compagno
65	11-8-61					Follett	1990	78.0	F	not examined	Compagno
66	8-27-61	1600			set line	Follett	1976	42.2	F	not examined	Follett
67	9-24-61				gill net	Spenger	1590	37.6	M	not examined	Calliet
68	10-16-66				gill net	Spenger	2044	68.0	F	none	Compagno
69	8-25-56	9.2			gill net	Johnson	3505	408.2	F	Onchorynchus sp.	Compagno
70	11-1-68				gill net	Johnson	2340	72.6	M	not examined	Compagno
71	8-22-75				gill net	Strobbe	1990	78.0	F	none	Compagno
72	X-X-35					Vella	1981	183.7	M	not examined	Compagno
73	11-13-59					Vecca	2362	138.8	F	not examined	Compagno
74	11-9-59					Seaworld	4700	101.6	F	not examined	Compagno
75	8-1-75	0.1	45.5		gill net	Seaworld	4700	101.6	F	not examined	Compagno
76	2-3-77	1.6					3048		M	P. vitulina	Follett
77	9-25-78									not examined	Follett
78	X-X-55									not examined	Follett
79	11-29-68	47.6	47.6		gill net	Thomas	2438	181.4	M	P. vitulina, Sebastes	Follett

80	8-21-48	0.9	set line	Ramsower	1543	F	ES sp.	Fitch, 1949
81	X-X-36		set line	Follett	1676	M	not examined	Follett, 1966
82	1-25-64				1960	M	not examined	Kato, 1965
83	8-2-81	1.8	long line	Ouevas	2685	F	not examined	Michael
84	4-28-36	9.2	gill net	Pederson	2235		<i>Actipenser medius-</i> <i>lins</i>	Borham, 1942
85	9-1-36		gill net	Moore	362.9		<i>P. vitulinus</i>	Borham, 1942
86	9-5-40		gill net	Moore	3962	M	not known	Borham, 1942
87	8-X-41		gill net	Ogren	226.8		not known	Borham, 1942
88	8-X-41		gill net	Oblad	453.6		not known	Borham, 1942
89	8-X-41				3658		not known	Borham, 1942
90	8-16-49	0.9	gill net	Fuller	3302	F	not known	Lewter, 1951
91	9-1-50	0.9		Nelson	4420		Cancer magister, Cancer productus, Oncorhynchus sp., "hair" seal, Mer- luccius productus, Sebastes sp.	Lewter, 1951
92	10-24-61				3429		not known	Pike, 1962
93	10-24-61				4674		not known	Royce, 1963
94	10-5-62	2.9	set line	Pamperton	4267	M	not examined	Metzger
95	10-5-82	38.0	set line	Pamperton	3988	M	not examined	Metzger
96	8-X-82	2.9	gill net		567.0	M	not examined	Metzger
97	7-4-80	0.3	gill net	West	3480	M	not examined	Johnson
98	7-17-81	5.6	drift net	West	1295	M	not examined	Johnson
99	7-17-81	5.6	drift net	West	1219	M	not examined	Johnson
100	8-12-76	5.6	drift net	West	1321	F	not examined	Johnson
101	7-3-78	1.4	gill net	Henke	1448	M	none	Seaworld
102	8-16-78	0.9	gill net	Henke	1397	M	none	Seaworld
		37.0	gill net		1473	M	fish head, dasya-	Seaworld
103	7-25-81		gill net	Henke	1422	M	tid ray	Seaworld
104	7-29-81		gill net	Henke	1549	F	none	Seaworld
105	8-3-81		gill net		1600	M	not known	Seaworld
106	6-17-82				1778	M	not known	Seaworld
107	X-X-74		gill net	Quinn	1473	M	elasmobranch	Seaworld
108	11-3-76	152.4		Mechago	1750			Seaworld
109	8-13-76	152.4	gill net	Nichols	372.9	F	not examined	Seaworld
NLA	6-5-83	1.8	gill net	Miller	2083		not examined	Seaworld
NLA	6-5-83	27.8	gill net	Tibbles	4420	M		Seaworld
NLA	6-27-83	0.2	tram. net		90.7			Seaworld

See
Anley

Table 2. 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. com., 3) population censuses and kills of pinipeds from Ainley et al., 1981, and 4) mortality of sea otters from Ames and Morejohn, 1980.

Month	Shark Obs.	1 Flights	Obs./ Flight	2 Attacks on Man	Pinn. Kills*	3 Pinn. Censused*	Kills / Seals Cens.	4 Sea Otter Kills
December	10	33	0.30	4				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.)

Table 3. 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. com., 2) population censuses and kills of pinnipeds from Ainley et al., 1981, 3) bite scars on northern elephant seals from LeBoeuf et al., 1982, and 4) mortality of sea otters from Ames and Morejohn, 1980.

Indic.	1	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		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	1					1
1967	0					
1966	1					
1965	0					
1964	1					
1963	0					
1962	1					
1961	2					
1960	2					
1959	2					
1958	0					
1957	0					
1956	0					
1955	1					
1954	0					
1953	0					
1952	1					

*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.)