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BIOLOGY OF THE WHITE SHARK



MEMOIRS OF THE
SOUTHERN CALIFORNIA ACADEMY OF SCIENCES
VOLUME 9
(24 May 1985)

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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

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FOREWORD

On 7 May 1983 a symposium entitled "Biology of the White Shark (*Carcharodon carcharias*)" was held during the annual meeting of the Southern California Academy of Sciences at California State University Fullerton. The rationale behind the symposium was three-fold: 1) to present a series of timely and informative scientific papers dealing with the biology of this much mythologized and little-understood animal; 2) to enable North American researchers working on white sharks to meet informally and discuss their research and future plans; 3) to publish a symposium volume on the biology of the white shark.

Sixteen papers were presented during the symposium and asterisks denote the names of authors who have contributed to this volume. Leonard Compagno began with an overview of white shark biology and anatomy followed by Shelton Applegate and Luis Espinosa who presented two papers dealing with the fossil history of the white shark and implications concerning the habits and present status of the recent species. Peter Klimley* and Wes Pratt* and Jack Casey* presented papers on the distribution of white sharks along the California coast and in the western North Atlantic, respectively. Leighton Taylor* presented a paper on historical and contemporary records of white sharks in Hawaii. Three papers dealing with white shark physiology were presented by Frank Carey* (body temperature and capacity for activity), Scott Emery* (hematology, cardiac and gill morphology), and Joel Cohen* and Samuel Gruber* (visual system with emphasis on retinal structure) followed by Gregor Cailliet* who presented information on age and growth. Richard Huddleston presented a paper on stomach and spiral-valve contents of juvenile white sharks. The behavior of white sharks was detailed in four papers presented by John McCosker* (attack behavior and predator/prey strategies), Timothy Tricas* (feeding ethology), Donald Nelson (telemetry of white shark behavior), and David Ainley* (white shark/pinniped interactions at the Farallon Islands). Robert Lea* presented an update on shark attacks off California and Oregon. Bernard Zahuranec offered the concluding remarks. Eleven of the 16 contributed papers appear in this volume.

We gratefully acknowledge the following for their help in planning and executing the meeting and publication of this volume: Margaret Barber (Southern California Academy of Sciences) for her patience and assistance with the myriad of details concerning scheduling, abstracts, etc; Lon McClanahan and Steve Murray (California State University Fullerton), local chairmen, for arranging facilities; Bernard Zahuranec (Office of Naval Research, Washington, D.C.) for his interest and the support of the ONR and AIBS for providing travel funds; and the Southern California Academy of Sciences for providing travel funds and support for this publication.

This symposium volume on the biology of the white shark is far from the final word on the subject. Rather it is a summary of current scientific information from some of those working in the field. In view of many of the wild claims and statements that have pervaded the popular literature in recent years, it is our hope that this volume will dispel some of the unsubstantiated speculation concerning *Carcharodon*, disseminate the available biological data on the subject, and serve as a foundation for further scientific research on the great white shark.

Distribution of the White Shark, *Carcharodon carcharias*, in the Western North Atlantic

John G. Casey and Harold L. Pratt, Jr.

Abstract.—Distribution of the white shark, *Carcharodon carcharias*, in the Western North Atlantic by John G. Casey and Harold L. Pratt, Jr. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. The white shark, *Carcharodon carcharias*, based on 380 recorded sightings, is principally distributed in neritic waters of the Western North Atlantic from the Gulf of Mexico to Newfoundland. Occurrences range between surface temperatures of 11° and 24°C. The species is rare throughout most of the Western North Atlantic. We have recorded relative abundances in the New York Bight as high as 1:210 of all sharks landed. An examination of stomachs from 54 young white sharks showed a diet comprised primarily of demersal fishes. Larger white sharks feed on marine mammals in this area. Sizes of examined specimens ranged from 122 cm (12 kg) to 497 cm (1247 kg). Lengths in the sightings file ranged from 105 cm to 945 cm. A length-weight curve based on 200 sharks is provided.

The white shark, *Carcharodon carcharias*, has been a focus of terrifying tales by seafarers throughout history. In recent years the species has received worldwide attention in several motion pictures and a plethora of popular articles. Despite widespread publicity by the media, the fact remains that the white shark is one of the lesser known large sharks of the world's oceans. Details of its distribution and abundance in the Western North Atlantic have been poorly documented. Observations typically consist of one large white shark being dramatically caught or engaged by a sport or commercial fisherman. Because of confusion with basking sharks, *Cetorhinus maximus*, and other lamnids, identifications have not always been accurate, even when the shark was landed. Moreover, there is a dearth of published information about white sharks in the Mid-Atlantic Bight (Fig. 1) although several are caught or seen there every year. Bigelow and Schroeder (1948) list Western North Atlantic reports and sources, and Templeman (1963) summarizes the literature on white shark occurrence in the Canadian Atlantic. Because this apex predator plays a role in the ecology of whales (Carey et al. 1982), is actively pursued by recreational fishermen and infrequently but dramatically interacts with man, we have combined pertinent records from the literature and recent accounts from fishermen with our first-hand observations to clarify the range and distribution of the white shark along the Atlantic coast of North America.

Materials and Methods

Information on white sharks came from three primary sources: (1) records from the literature; (2) sharks collected by the authors and associates of the Oceanic Gamefish Task; and (3) white shark sightings from a file established by the authors (Fig. 1). The geographical area covered by the data extends from northern Cuba

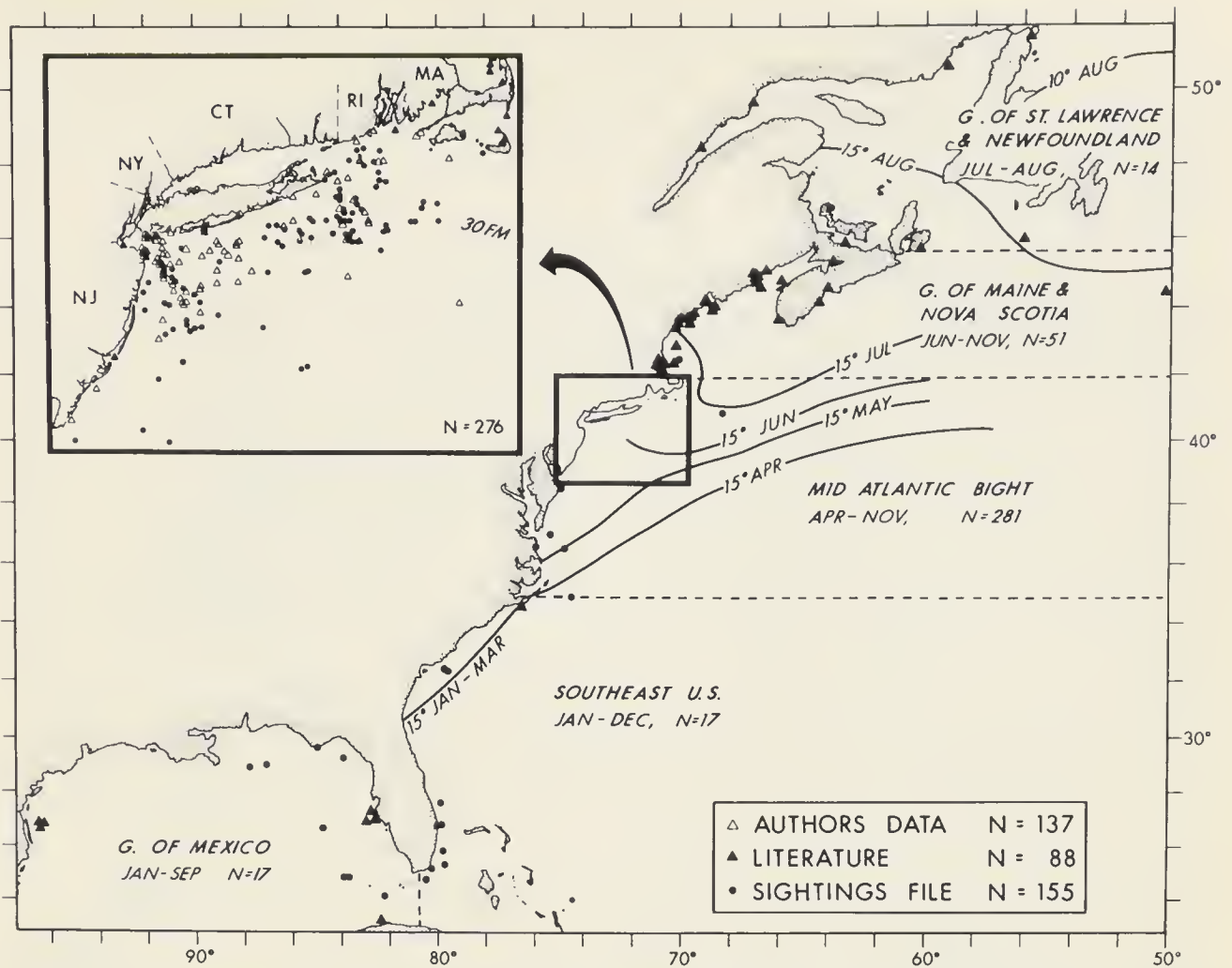


Fig. 1. Distribution and seasonal occurrence of white sharks off the east coast of North America. *Authors' data* are sharks we examined between 1960 and 1983. Reports from the *Literature* refer primarily to scientific publications covering the period 1800–1982. Our sightings file is mainly written or telephoned reports from fishermen (1979–1983) with some newspaper and magazine articles (1945–1983). Some symbols represent more than one shark at the same location. The mean position of the 15°C surface isotherm during spring and summer is from Robinson et al. (1979).

to northern Newfoundland. We divided the study area into the following five regions: Gulf of Mexico (North of 22°00'N lat.; West of 80°20'W long.), Southeast U.S. (22°00' to 35°00'N lat.; West of 50°00'W long.), Mid-Atlantic Bight (35°00' to 42°00'N lat.; West of 50°00'W long.), Gulf of Maine and Nova Scotia (42°00' to 45°30'N lat.; West of 50°00'W long.), Gulf of St. Lawrence and Newfoundland (45°30' to 52°00'N lat.; West of 50°00'W long.).

We have summarized confirmable literature records of white sharks in the Western North Atlantic from Putnam (1874), Coles (1919), Piers (1934), Schroeder (1938, 1939), Scattergood (1959, 1962), Springer (1939), Bigelow and Schroeder (1948, 1953, 1958), Baughman and Springer (1950), Scattergood, Trefethen, and Coffin (1951), Day and Fisher (1954), Scattergood and Coffin (1957), Scattergood and Goggins (1958), Leim and Day (1959), Skud (1962), Templeman (1963), Clark and von Schmidt (1965), Mundus and Wisner (1971), Arnold (1972), and Guitart and Milera (1974). Typically these records are notes on small numbers of stranded or incidentally captured sharks that have come to the attention of biologists. We did not include records if the identity of the sharks was doubtful, or if the reports lacked pertinent details on size, location, and date of capture.

“Authors’ data” include white sharks which we and our colleagues caught or personally examined. Many white sharks were taken over the years at sportfishing tournaments along the Mid-Atlantic Bight. Others were caught from research and commercial fishing vessels by a variety of methods including longline gear, gill net, rod and reel, and harpoon.

The “sightings file” was formally initiated in 1979 as a way to deal with newspaper articles, popular, and visual accounts originating from our 2500 cooperative shark taggers and others who were sending us unsolicited information. We made a request for white shark reports and sightings in our 1979 newsletter “The Shark Tagger” (Casey, Pratt, and Stillwell 1979). Most of our cadre of taggers are active fishermen, skilled in identification of common sharks. Each white shark report in the “sightings file” was given a subjective reliability index from 0 to 9 with highest rank going to those in which sharks were landed or documented with photographs. In cases where the shark was not landed, fishermen were interviewed in person or by telephone to verify their observations. Dubious reports were not included in the analysis. Large white sharks (>3 m) are easily confused with basking and other sharks. Reporters were objectively asked a series of identification questions relevant to his or her sighting. If the sighting was very brief, or could not be verified as a white shark by characteristics of morphology or behavior, then the sighting was given a low reliability index and subsequently deleted. The same strategy was employed with smaller white sharks (<3 m) which may be confused with the porbeagles (*Lamna nasus*) and mako (*Isurus oxyrinchus*).

All measurements given in this report are total lengths (TL). We define total length as a straight line measurement along the body axis from tip of snout and intersecting a perpendicular line dropped from the tip of the upper caudal lobe (Bigelow and Schroeder 1948). The lengths of white sharks reported in the literature from the late 1800’s and early 1900’s for the most part were recorded in feet of total length. These measurements were probably made in a straight line from the snout to the tip of the upper caudal lobe. Other literature and sightings’ length measurements were made following the curves of the body. For this paper, we assumed all total lengths to be similar to our measurement. For our purposes, males and females were considered mature at total lengths greater than 426 cm (14 ft) and 487 cm (16 ft), respectively (Pratt, unpub. data). When data on sex were not available, individuals greater than 457 cm (15 ft) were considered mature.

Three data sources were used to construct a length-weight relationship. Sharks measured by the authors from the Western North Atlantic were combined with length-weight information from world record rod and reel catches for the period 1958 through 1982 (World Record Gamefishes—International Gamefish Association, Fort Lauderdale, Florida); and records of Australian white sharks from 1938 to 1972 provided by the Game Fishing Club of South Australia (E. Palmer, South Australia, pers. comm.). All lengths which had been measured as fork length (i.e., tip of snout to fork of tail) were converted to total lengths using a regression derived from the authors’ data: $TL = (FL - a)/b$ where TL = total length (cm), FL = fork length (cm), $a = -6.8357$, $b = 0.9517$ ($n = 79$, and $r = 0.998$).

Results and Discussion

A total of 380 individual white shark records was obtained from: published accounts (88), the authors’ data (137), and the NMFS sightings file (155). Ap-

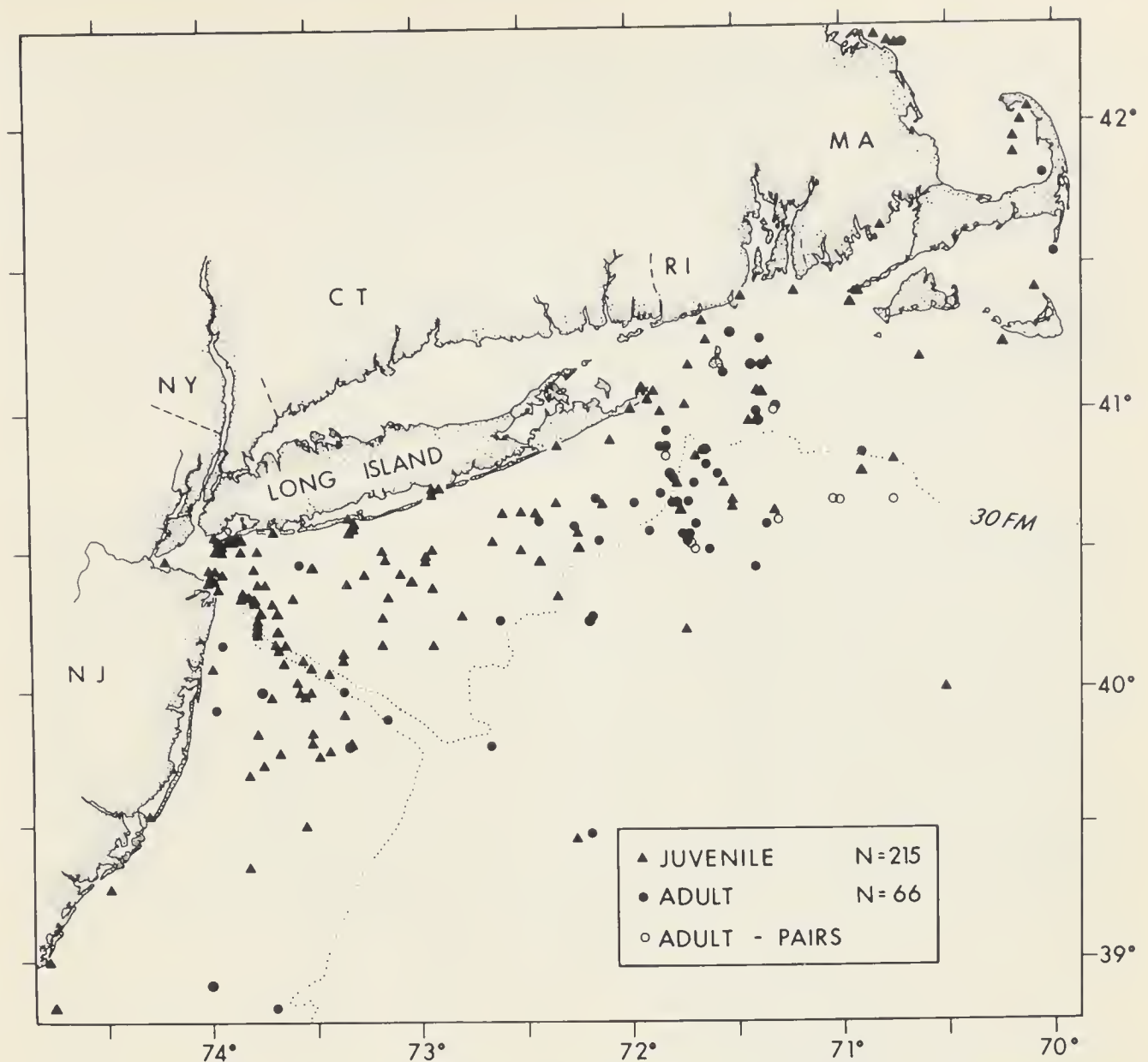


Fig. 2. Distribution of adult and juvenile white sharks between New Jersey and Massachusetts. All sources pooled $n = 281$.

proximately 50 additional records were considered unreliable and deleted from published accounts and the sightings file.

Nearly all the records are from continental shelf waters (<200 m) with many captures and sightings from near shore where depths were less than 75 m (Figs. 1–2). The number of white sharks reported along the North American coast was lowest in the most northern and southern parts of the range, i.e., the Gulf of St. Lawrence region and the Gulf of Mexico-Southeast U.S. regions, respectively. The highest number of occurrences were recorded from the Mid-Atlantic Bight.

Seasonally, white sharks were reported from January through September in the Gulf of Mexico; in every month but August off the southeastern U.S.; from April through December in the Mid-Atlantic Bight; from June through November in the Gulf of Maine; and during July and August in the Gulf of St. Lawrence-Newfoundland region (Table 1).

The seasonal occurrence of the white shark is at least partly influenced by surface temperature. Miles (1971) suggests that the world distribution of white sharks is restricted to water temperatures between 12° and 25°C. Squire (1967) reported

Table 1. Seasonal occurrence of white sharks in the Western North Atlantic.

Regions (see Fig. 1)	Numbers reported in each month												Total	
	J	F	M	A	M	J	J	A	S	O	N	D		X ^a
Gulf of St. Lawrence and Newfoundland							2	11					1	14
Gulf of Maine and Nova Scotia						4	10	22	3	4	3		5	51
Mid-Atlantic Bight				2	9	91	72	76	17	7	2	3	2	281
Southeast U.S.	1	1	2	1	4	1	1		2	1	1	1	1	17
Gulf of Mexico	3	7	1			3			1				2	17

^a Month not reported.

white sharks during all months of the year in Monterey Bay, where mean monthly temperatures ranged from 10.2° to 14.4°C. A sonic tagging experiment conducted by Carey et al. (1982) has demonstrated vertical movements of a large white shark through temperatures ranging from 17.8° to 5°C during its daily swimming activities. The mean spring and summer position of the 15°C isotherm in the Western North Atlantic (Robinson, Bauer, and Schroeder 1979) is shown in Figure 1. Most of the available evidence indicates that the white shark is a temperate species despite the apparent tolerance by the adults to a wide range of temperatures. Water temperatures reported in 73 cases of white shark occurrence in our data ranged from 11° to 24°C with 75% of the occurrences where surface temperatures were between 15°C and 22°C. The 15° isotherm in Figure 1 is therefore a rough indication of the seasonal white shark distribution in the northern latitudes.

If temperature is a major factor influencing the distribution of the white shark, it appears that larger individuals tolerate a wider range of temperatures and occupy a broader geographical range. Although white sharks over 300-cm TL have been reported in every region in Figure 1, individuals less than 200-cm TL are common only in the Mid-Atlantic Bight. Of the 135 white sharks less than 200-cm TL in our data base, four were taken in the Gulf of Maine, one was taken in the Southeast region, and the remaining 130 were taken in the Mid-Atlantic Bight. Apparently, young sharks have a lower tolerance for cooler waters that limits their distribution north of Cape Cod, and they may have an intolerance to higher temperatures that limits their distribution off southeastern United States.

From all available evidence the white shark is more abundant on the continental shelf between Cape Hatteras and Cape Cod (35°00'N, 43°00'N) than in any other region in the Western North Atlantic. More young white sharks have been caught there than in any area of comparable size in the world.

Historically a low percentage of white sharks have been taken in recreational and commercial fisheries directed toward large sharks, tunas and swordfish (Table 2). Springer (1960) did not report the actual number of white sharks caught in the Florida fishery but gave a ratio of 27 white sharks to 100,000 of all sharks. The numbers in the remainder of the table are actual numbers of large sharks caught.

Because white sharks are unevenly distributed over a broad geographical range, any attempt to estimate their abundance can only be expressed in general terms. Pelagic longline catch data representing 2.1 million hooks from commercial sword-

Table 2. Ratio of white sharks to other species of large^a Atlantic sharks.

Data source	Period	Primary area	Primary gear	No. white sharks		Ratio white : all sharks
				No. all sharks		
Springer (1960) (Commer. Shark Fishery)	1935-1950 (All months)	Florida	Longline	27/100,000		1:3704
Hoey & Casey ^b (Commercial Swordfishery & NMFS Research Cruises)	1957-1982 (All months)	N.W. Atlantic	Longline	45/105,123		1:2336
Casey (1977) ^c (Bayshore, NY Tour)	1965-1977 (June)	W. Long Island, NY	Rod and reel	26/5465		1:210
Casey (Unpub) (Brielle, NJ Tour)	1981-1983 (June)	Northern New Jersey	Rod and reel	5/334 ^d		1:67

^a Species of sharks which, as adults, generally exceed 183 cm and 50 kg.

^b Manuscript in review—includes catch data from commercial swordfish and research longline logs in the area from the Grand Banks into the Gulf of Mexico. In this data base, 36 of the 45 white sharks were caught by the authors in the Mid-Atlantic Bight during 1961-1972 (i.e., 36 white sharks/4954 all sharks; ratio 1:138).

^c From 1978 through 1983 one additional white shark out of 1843 sharks was caught during this tournament (i.e., 27 white sharks/7308 all sharks; ratio 1:270).

^d Does not include unreported sharks released during this tournament. Ratio of white sharks to all sharks, therefore, overestimated.



Fig. 3. Ten juvenile white sharks caught off New Jersey in 1964.

fish and research cruise effort in the Atlantic included records on the capture of only 45 white sharks.

The swordfish effort covered a 17-year period (1963 to 1980) and was distributed from the Grand Banks to the Gulf of Mexico, primarily beyond the 600-m isobath (John J. Hoey, Southeast Fisheries Center, Miami, Florida, pers. comm.). Several longline captains we interviewed recalled catching white sharks on only two or three occasions in 20 years. Although adult white sharks might consistently break free of longlines set in oceanic waters, it seems likely that young whites would be caught if they were more common offshore. Rhule [Ruhle] (1969) provides a description of pelagic longline gear. Our research effort (1963–1983) utilized the same type of pelagic longline gear and was fished beyond the continental shelf (depths >200 m) and in shallow coastal waters and bays primarily in the Mid-Atlantic Bight. Of the 45 white sharks caught on longline, nearly all were taken on the continental shelf, several within a few kilometers from shore. The evidence that young white sharks are neritic in this region is strengthened by the relatively high numbers of sharks caught with rod and reel during annual fishing tournaments held in New York and New Jersey (Table 2).

The higher abundance of white sharks in the Mid-Atlantic Bight may, in part, be explained by other factors including: (1) a disproportionate amount of field work by biologists compared to other regions; (2) more intensive recreational and commercial fisheries in this region; and (3) a closer working relationship between

Table 3. Stomach contents from juvenile white sharks (22 to 82 kg) from the New York Bight 1961–1965.

Item	Frequency of occurrence	Per cent occurrence
Pelagic fishes		
Menhaden, <i>Brevoortia tyrannus</i>	7	24.1
Bluefish, <i>Pomatomus saltatrix</i>	2	6.9
Butterfish, <i>Peprilus triacanthus</i>	1	3.4
Demersal fishes		
Searobins, <i>Prionotus</i> sp.	13	44.8
Hakes, <i>Urophycis</i> sp.	3	10.3
Skates, <i>Raja</i> sp.	3	10.3
Flounders, Pleuronectidae	2	6.9
Silver hake, <i>Merluccius bilinearis</i>	1	3.4
Smooth dogfish, <i>Mustelus canis</i>	1	3.4
Unidentified fish	11	37.9
Invertebrates		
Crabs, <i>Cancer</i> sp.	2	6.9
Starfish, <i>Asterias</i> sp.	1	3.4
Snails, Gastropoda	1	3.4
Other		
Bluefish offal	4	13.7
Garbage	2	6.9
No. examined = 54		
No. with food = 29		

the authors and fishermen in the Mid-Atlantic Bight who are aware of our interest in white sharks.

Regardless of their size, white sharks are more likely to occur singly or as scattered, unassociated individuals over several square kilometers. For example, in the 20 years that 150 boats have fished a two-day tournament at Bay Shore, Long Island, the same boat has never caught more than one white shark, and four individuals is the maximum number landed at this tournament in any year (Casey 1977).

There are, however, circumstances under which white sharks have aggregated in the same area. With respect to young sharks, we observed one such aggregation by catching 10 individuals on approximately ½ mile (1 km) of longline (32 hooks) in August 1964 off Sandy Hook, New Jersey (Fig. 3). These sharks ranging in size from 132 to 198 cm were caught in 9 m of water approximately ¼ mile (0.5 km) from a well attended bathing beach. We also caught young white sharks within 2 or 3 km of the beaches at Rockaway and Coney Island, New York, during the early and mid 1960's but chose not to publicize our activities in the interest of public relations.

One possible explanation for the aggregation of young white sharks off Sandy Hook was that recreational boats were fishing for bluefish (*Pomatomus saltatrix*) on Shrewsbury Rocks approximately 7 miles (11 km) south of Sandy Hook. As the boats travelled northward along the beach at the end of the day, bluefish were

being cleaned and the heads and entrails were thrown overboard. Some of the young white sharks contained bluefish heads that had obviously been discarded by fishermen.

Although in this case an opportunistic food source may have had a concentrating effect, the distribution of young white sharks in the inshore zone in the Mid-Atlantic Bight is not unusual and is more likely influenced by other factors including the distribution of natural prey. An examination of the stomachs of 54 young white sharks from the Sandy Hook-Western Long Island area showed they fed on a variety of items, primarily demersal fishes (Table 3). Adult white sharks are more likely to contain mammals such as porpoises (Arnold 1972), whales (Carey et al. 1982; Pratt, Casey, and Conklin 1982), and pinnipeds (Ainley et al. 1981; Brodie and Beck 1983).

With respect to adult white sharks congregating in the same area we are aware of two well documented incidents, both involving dead whales. In 1979 at least five large white sharks (305 to 457 cm) were observed feeding on a dead whale in the area between Montauk Point and Moriches, New York (8 to 20 mi from shore). Details of this occurrence are provided by Pratt et al. (1982), and Carey et al. (1982). In a similar incident, at least eight large white sharks were attracted to a dead whale floating off Block Island, Rhode Island, between August 5 and August 23, 1983. Three of these (497, 484, and 480 cm) were harpooned, and are among the five largest male sharks we have examined. Two (518 and 610 estimated TL) were tagged by Captain Charles Donilon as they swam near his vessel, and three others were seen or harpooned and lost as they fed on the whale. A similar concentration of white sharks around a whale off Rhode Island in 1960 is reported by Ellis (1975).

On eight occasions pairs of large white sharks have been observed swimming close together (Fig. 2). Although adult white sharks of both sexes occur in the Mid-Atlantic Bight, fishermen were unable to determine the sexes of these paired individuals. Nor did they report any activity that could be interpreted as mating or courtship behavior. Among the Carcharhinidae it is not unusual for adult males and females to remain segregated except during mating periods (Springer 1960, 1967; Pratt 1979). The occurrence of adults of both sexes in the same region and the presence of large individuals swimming together may be evidence of mating activity in the Mid-Atlantic Bight. Two of the three large adult males we examined in 1983 had fresh lesions presumably made by other sharks. Whether these were bites relating to mating activity or an indication of territorial behavior is uncertain.

The occurrence of small and intermediate size white sharks in continental shelf waters of the Mid-Atlantic Bight suggests this area serves as a nursery area for juveniles. Here, they may find protection from predators since there is no evidence that small white sharks are preyed upon by other sharks, including adults of the same species. Given that even small white sharks are in excess of 20 kg, they would not serve as normal prey for other species of sharks which occur in the Mid-Atlantic Bight region. Large dusky (*Carcharhinus obscurus*) and tiger sharks (*Galeocerdo cuvieri*) are possible exceptions.

The size range for measured sharks in the literature was from 145 cm to 640 cm (TL). The lengths and weights of white sharks examined by the authors ranged from 122 cm (12 kg) to 497 cm (1247 kg). Lengths reported in the sightings file ranged from 105 cm to 945 cm. Several authors (Gilbert 1973; Randall 1973;

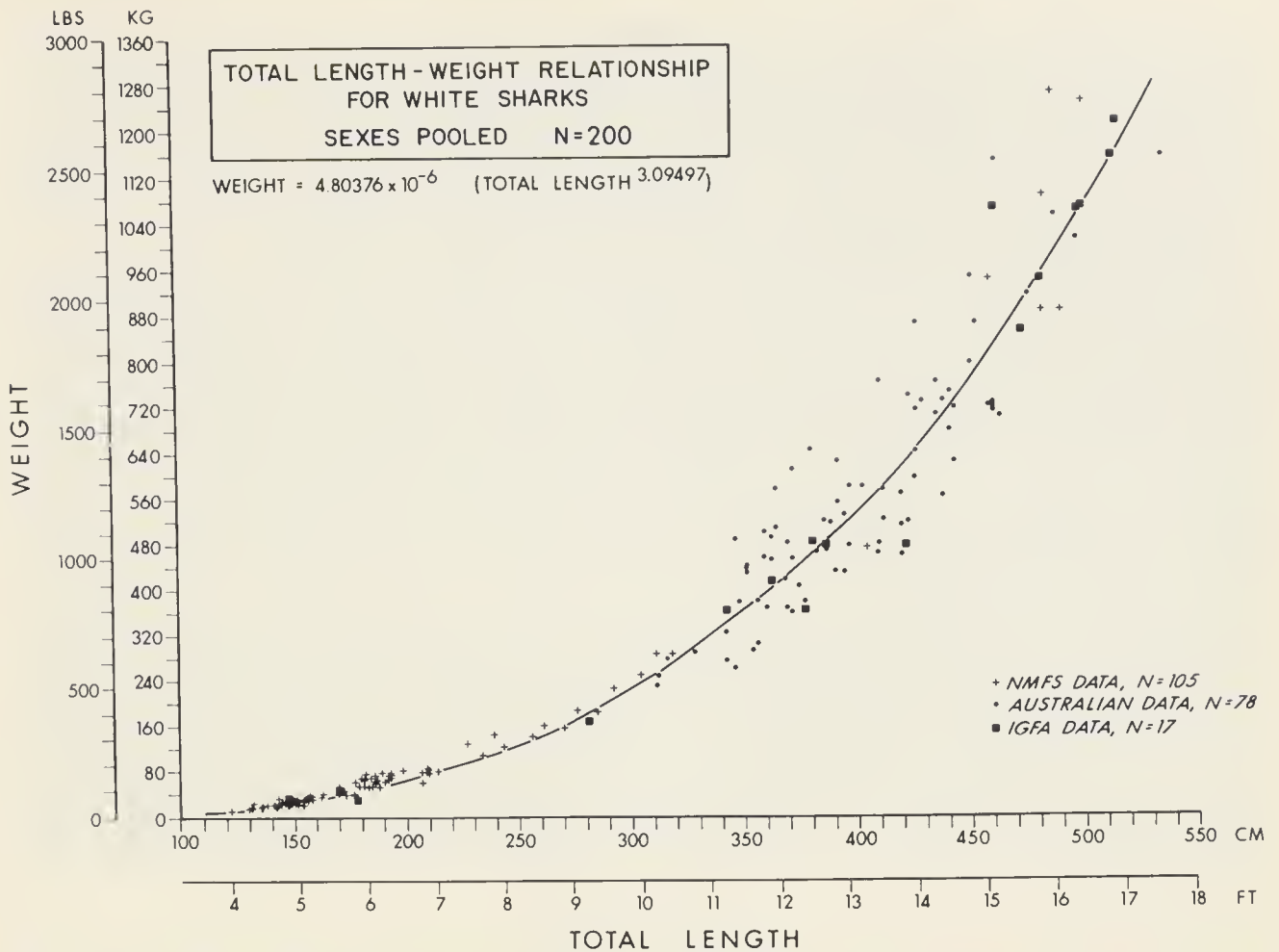


Fig. 4. Length-weight relationship for the white shark (sexes pooled). Regression is line of best fit for all data.

Ellis 1975) reporting on the maximum size attained by white sharks found no reliable record of a white shark exceeding a 640 cm (21 ft) specimen taken off Cuba in 1945 (Bigelow and Schroeder 1948).

Although we reviewed newspaper accounts and have received reports from fishermen claiming they have seen white sharks between 760 and 945 cm (25–31 ft), we have been unable to confirm any report of white sharks longer than the Cuban specimen. To our knowledge, the next largest white sharks reliably measured from the Atlantic were a 518 cm (17 ft) female harpooned off Montauk, New York, in 1964 (Mundus and Wisner 1971), and a 562 cm (18.4 ft) female which was landed after becoming entangled in a gill net near Prince Edward Is. in July 1983 (Thomas Hurlbut, Dept. of Fisheries, New Brunswick, pers. comm.). The total length of this latter specimen was calculated from a measured fork length of 526 cm (17.3 ft).

Bigelow and Schroeder (1948) estimated the size at maturity to be about 396 to 426 cm which appears conservative from our observations. The one large female white shark (406 cm) we examined had no developing ova, and therefore was immature. Based on the criteria for maturity of 457 cm, the 380 records include 92 adults and 288 juveniles. Information on sex was reported for 17 adults (12 males; 5 females) and 184 juveniles (87 males; 97 females).

The lengths and weights of the five largest white sharks we personally examined were adult males of 497 cm (1247 kg); 484 cm (1263 kg), 480 cm (1086 kg), 480 cm (886 kg) and 457 cm (943 kg). The five smallest individuals we have examined

from the Atlantic were 136 cm (18 kg), 132 cm (23 kg), two 130 cm specimens each weighing 16 kg, and one 122 cm (12 kg). The latter specimen—caught off Long Island, New York, in September 1983—we believe to be the smallest free-swimming white shark on record. (R. Markham of Mira Loma, California, kindly sent us a 122 cm (16 kg) white shark caught in a gill net off Catalina Is. on August 25, 1983. This is the smallest specimen reported from the Pacific.)

The length-weight curve (Fig. 4) indicates the white shark is very robust, its weight increasing an average of 456 kg (207 lb) for every 30 cm (1 ft) of length between 415–549 cm (15 and 18 ft). There was no significant difference in the length-weight relationship for the three data bases, or for males and females in the smaller sizes (122–325 cm) (analyses of covariance test of homogeneity of slopes $P < 0.05$). In the adults, females are expected to be heavier than males of the same length, but information on the sex of individuals over 325 cm was not sufficient for comparison.

Although the weight of white sharks is of interest to fishermen and scientists, suitable scales and equipment for weighing large individuals are often not available. Estimates of weight based solely on length are questionable because weights of sharks of the same length can vary considerably due to differences in girth. Based on a total of 119 records (sexes combined) that included measurements of length, girth, and weight, the weight of white sharks can be calculated using the relationship:

$$WT = \frac{(TL)(G^2)}{C}$$

where: WT = weight in pounds
 TL = total length in inches
 G = girth in inches
 C = constant:
 747 (<8 ft, n = 24)
 862 (8–14 ft, n = 65)
 933 (14–16 ft, n = 30)

The mean difference between the observed and predicted weight was –1.4 lb (SD 11.5) for juveniles less than 8 ft, –10.9 lb (SD 151.9) for immature sharks 8 to 14 ft, and –7.5 lb (SD 183.6) for adults 14–16 ft.

The capture of several white sharks, large or small, in any area gives rise to public concern that the population is increasing and represents a danger to swimmers and a detriment to the economy of resort communities. From our field studies, review of historical data, and discussions with fishermen over many years, these occurrences are more logically explained by changes in distribution related to food or environmental conditions than by an increase in abundance. Although the presence of large sharks should not be taken lightly, the white shark has not lived up to its sinister reputation off New Jersey and New York where only one shark attack (that by an unknown species) has come to our attention during the past 20 years (Sgt. Jack Malone, Manasquan, New Jersey, Police Dept., pers. comm.).

Acknowledgments

We would like to thank the fishermen, friends, and colleagues too numerous to mention who have contributed sightings and information about white sharks to support this study. Those who were particularly helpful include Robert Conklin (Riverhead, New York) for supplying data and biological samples; taxidermist Jeffrey Schneider (Babylon, New York) who provided several fresh specimens including the smallest white shark recorded; taxidermist Rocky Markham (Mira Loma, California) who sent the small Pacific specimen; Ernest Palmer and William Coombs (South Australia) who provided length-weight data from the Game Fishing Club of South Australia; members of the Bay Shore Tuna Club (New York) and Jersey Coast Shark Anglers (New Jersey) and fishermen Mike Albronda, Mark Marose, Ernest Celotto, Gregory Dubrule, Ken and Gloria Hayn, and Frank Mundus who allowed us to examine their catches. Carl Darenberg, Sr., Carl Darenberg, Jr., and Nicholas Shepis (Montauk, New York) provided vital logistical support that enabled us to examine several fresh specimens. Hal Lyman, Jack Woolner (Mass.), and Sgt. George Batt (R.C.M.P. Alberta, Can.) provided data on the Prince Edward Island specimens. We also thank NMFS scientific staff, Narragansett, including Charles Stillwell, who measured and assisted in examining several specimens, and Patricia Hadfield, Nancy Kohler, and Gregg Skomal for assisting in compiling and analyzing the data.

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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

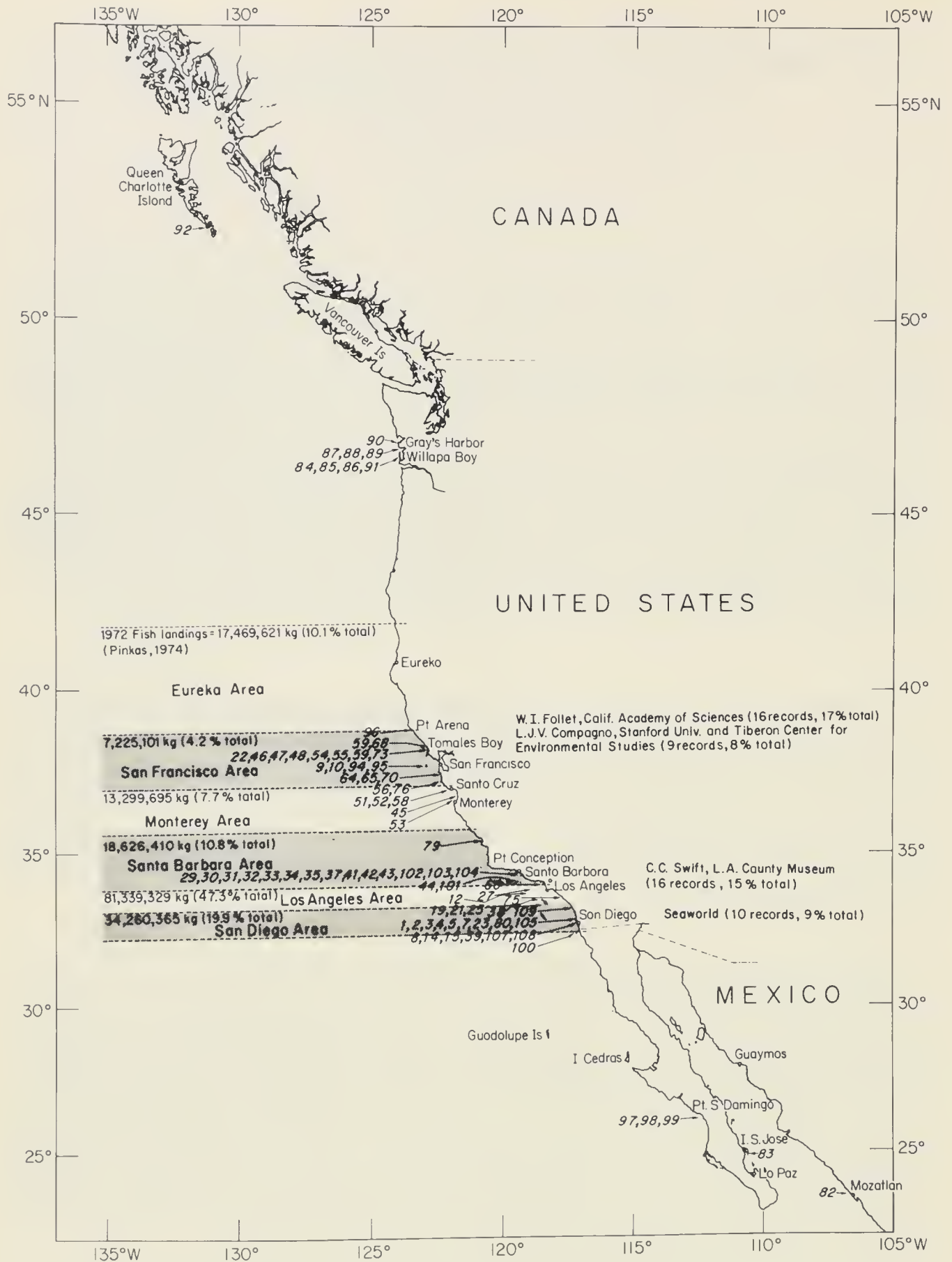


Fig. 1. Locations of white shark captures along the western coast of North America. Captures identified by number given in Appendix I. As an index of fishing effort, commercial fish landings included for six areas (alternately stippled or clear) along the coast of California. In the upper lefthand corner 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 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 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

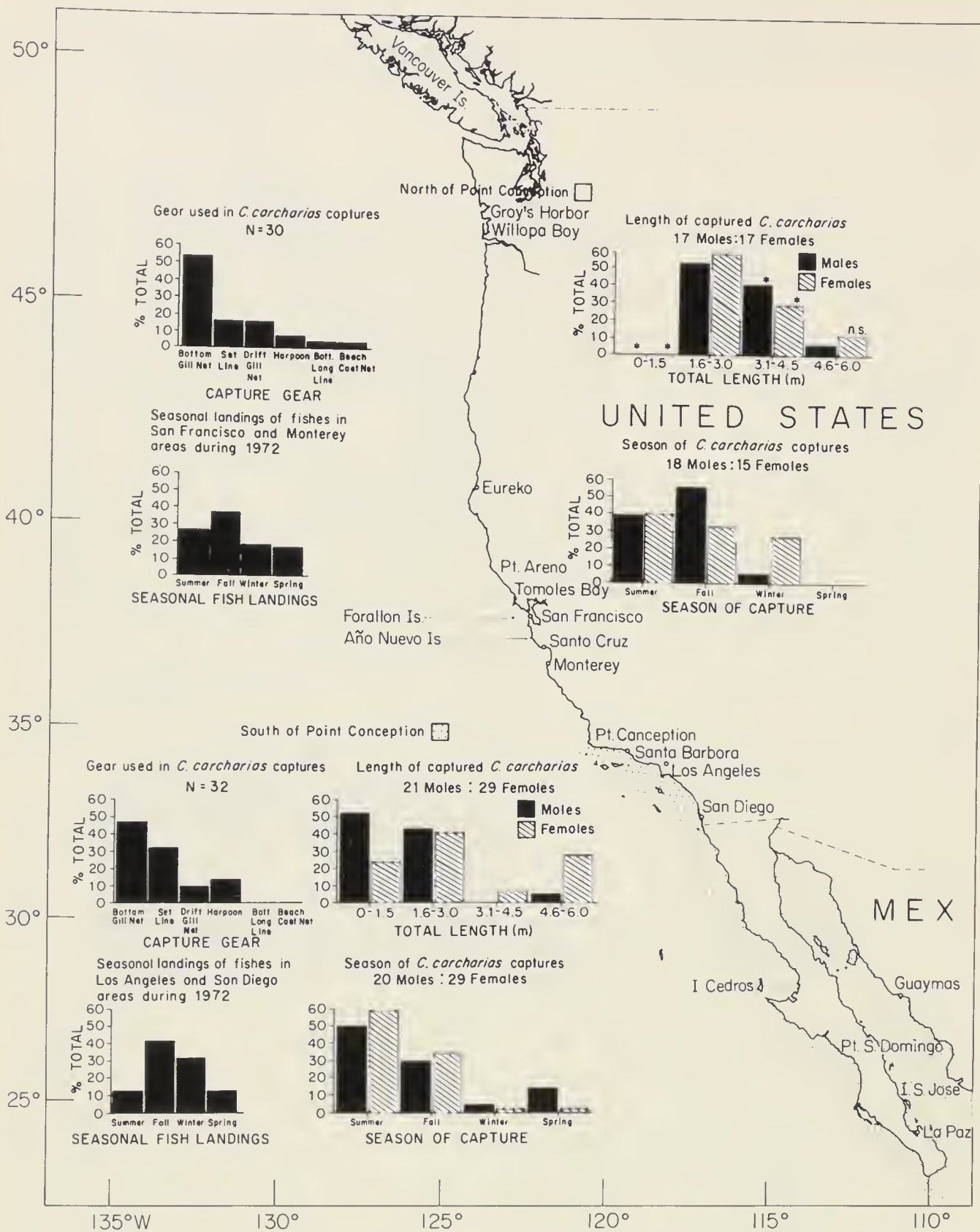


Fig. 2. Sets of four histograms given for north (upper) and south (lower) of Point Conception. Beginning with the upper lefthand histogram and moving in a clockwise manner, percentages of the total catch given for: 1) six gear types, 2) male (solid) and female (cross-hatched) white sharks in four size 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); ○ Fall (N=28); □ Winter (N=5);
 △ Spring (N=2)
 SEX: Male (N=38); ♀ Female (N=37)

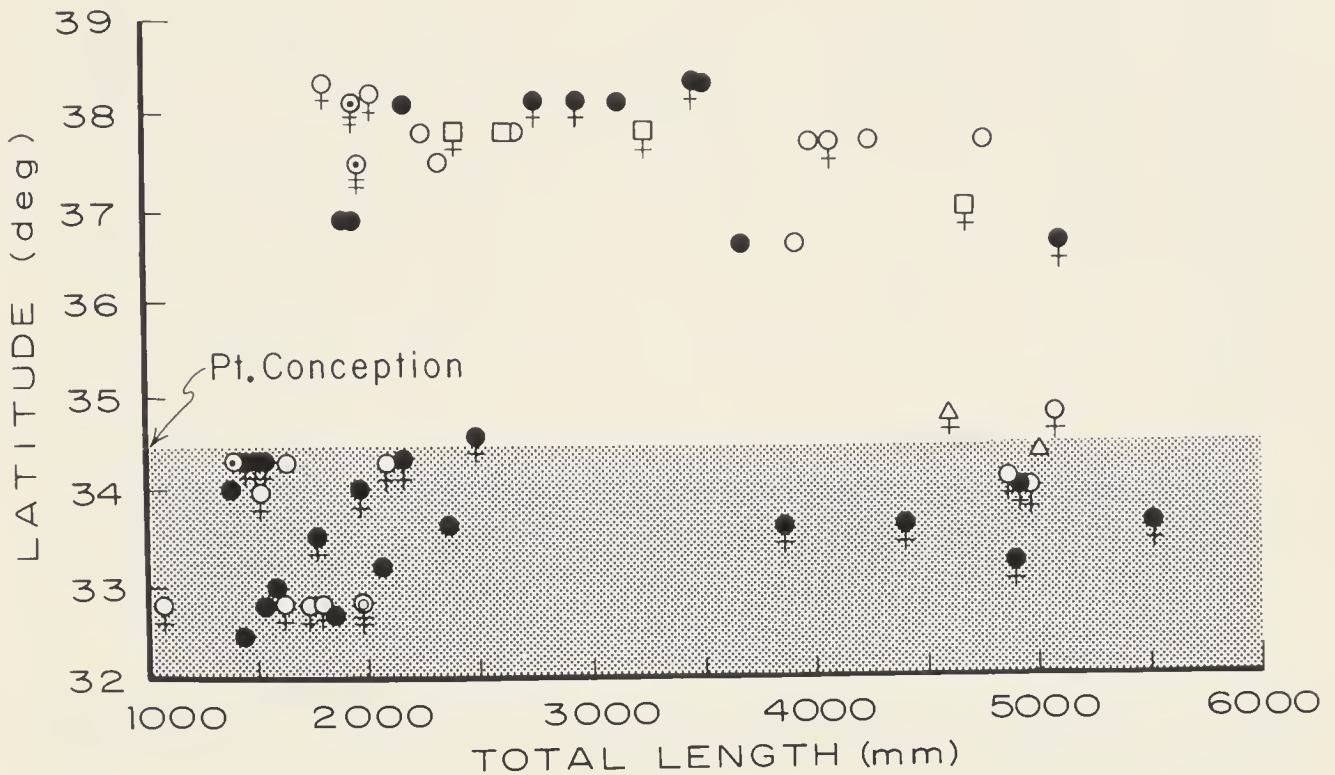


Fig. 3. White sharks of different sizes are plotted as a function of latitude. The season during which the shark was captured indicated by the shade and shape of the symbol. The sex of the shark designated by the presence or absence of an attached cross. The number of captures in parentheses. Multiple 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); ○ 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.

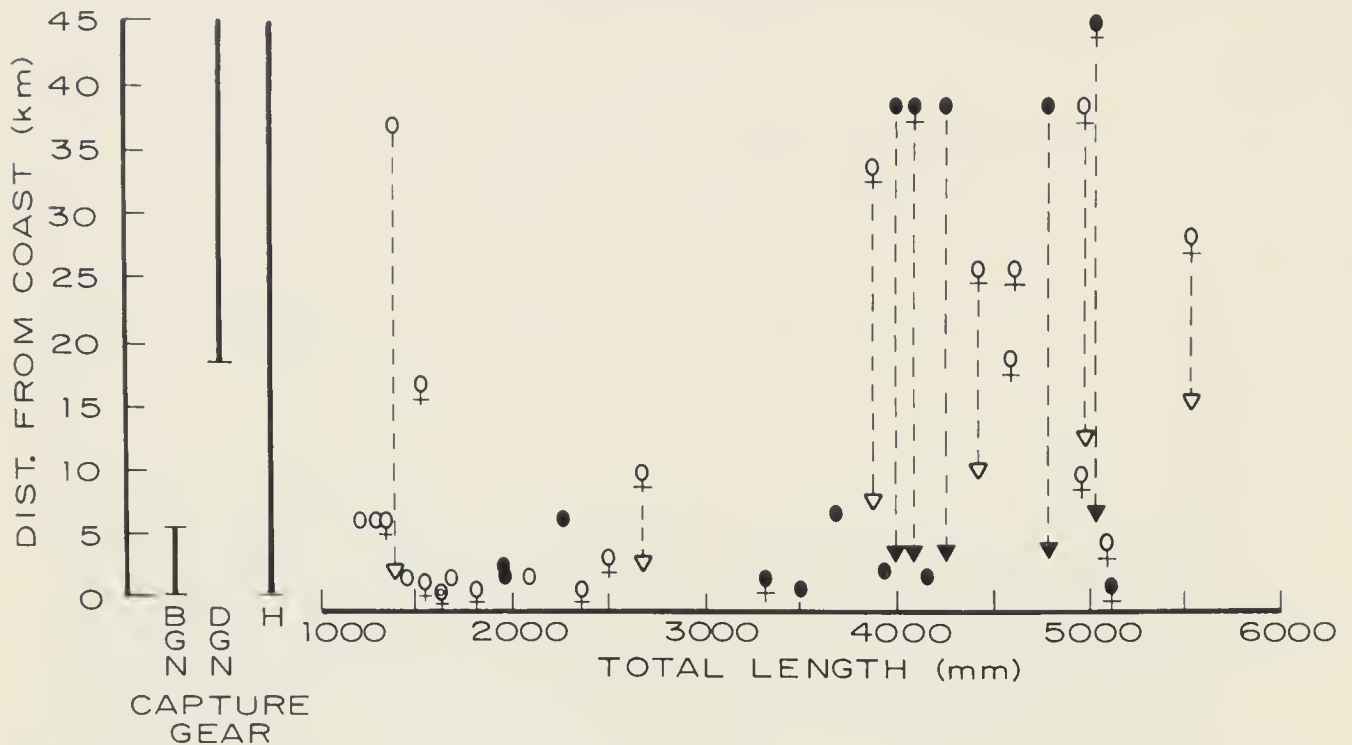


Fig. 4. The distance from coastline and shore at which white sharks of different sizes were captured. Note distinction between the distance from the coastline (circle) and distance from the shore (triangle connected by dashed line). These two distances only included when the former was greater than the 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 $38^{\circ}30'N$) and south of Point Conception ($34^{\circ}20'$). Although males remain north of $37^{\circ}N$ 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); ○ S of Pt. Conception (N=15)
 SEX: Male (N=20); ♀Female (N=18)

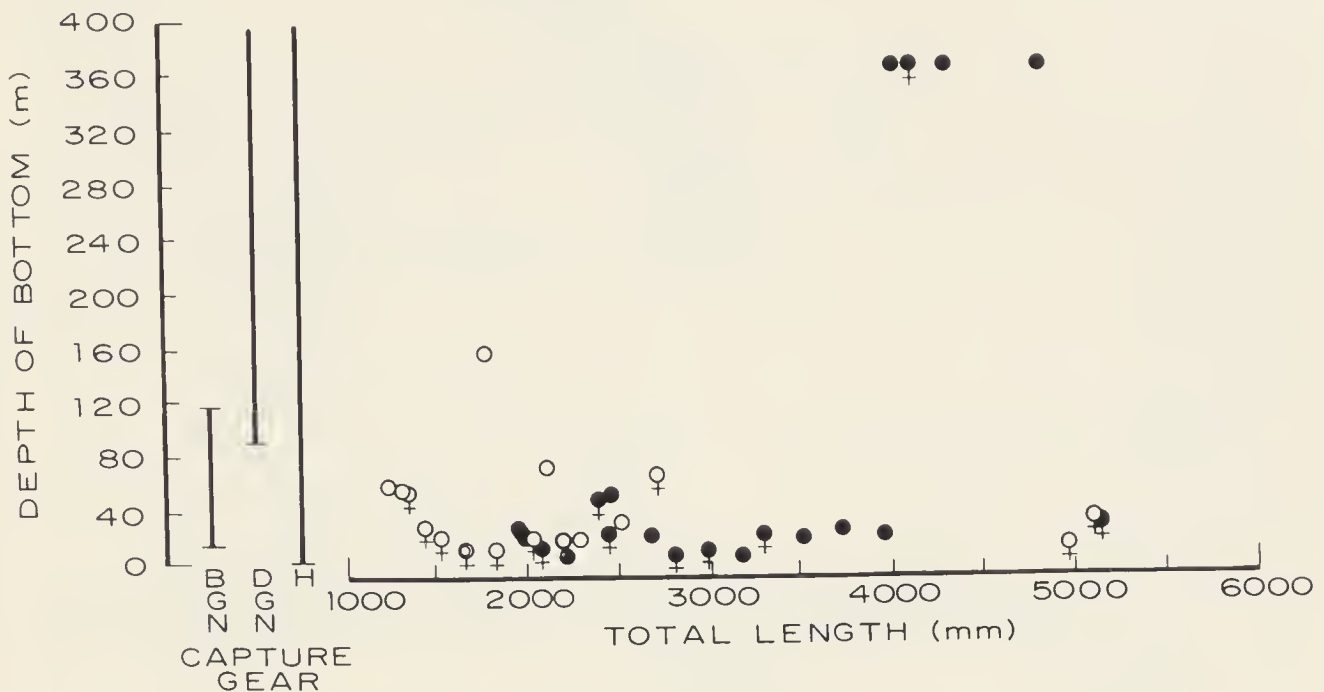


Fig. 5. Bottom depths over which white sharks of different sizes were captured.

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

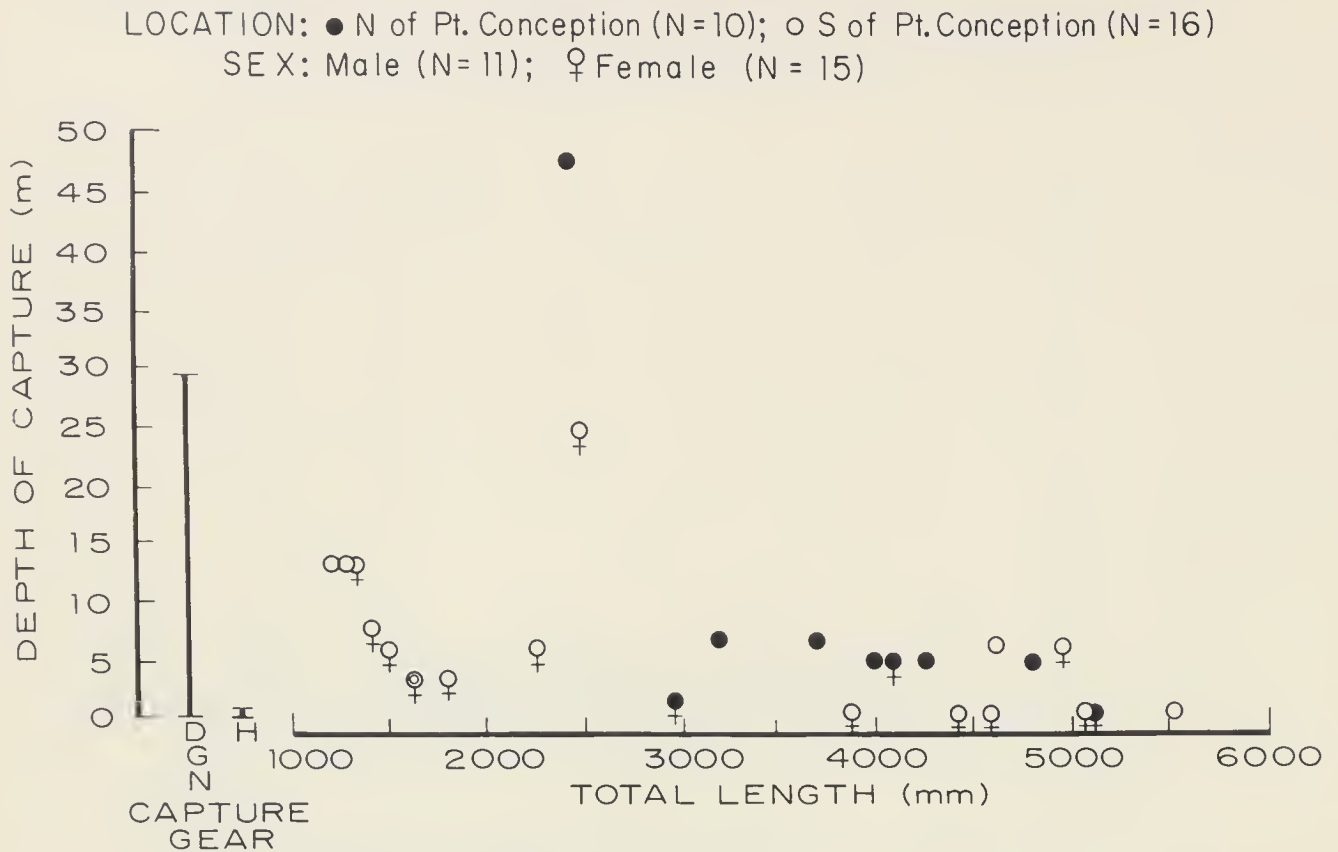


Fig. 6. Depths at which white sharks of different sizes were captured.

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 medirostris*, 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 zygoterus*, 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

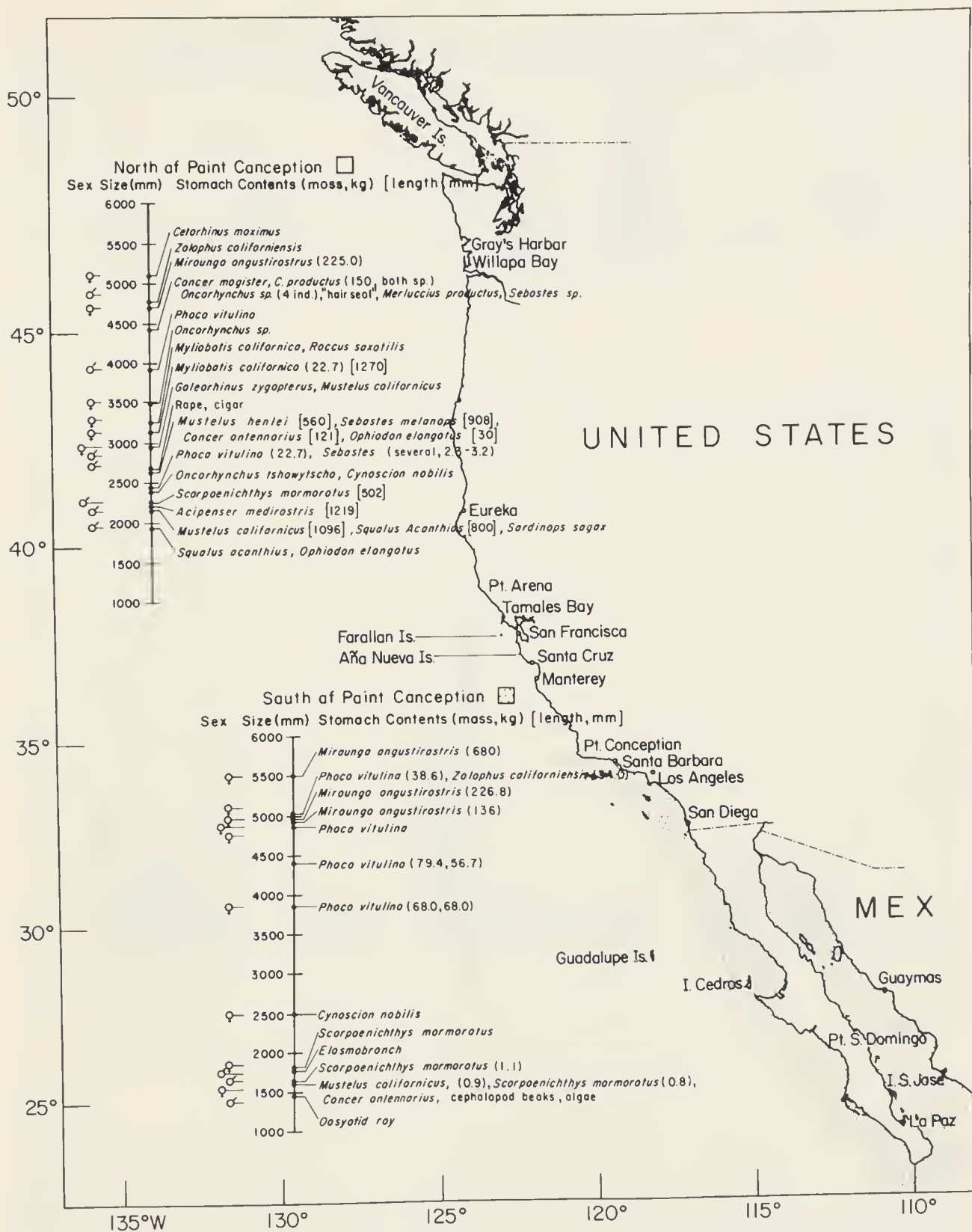


Fig. 7. Stomach contents of white sharks caught north and south (stippled) of Point Conception. The mass (parentheses) and length (brackets) given after identities of dietary items to right of shark length scale; the sex of the shark given to the left of the scale.

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

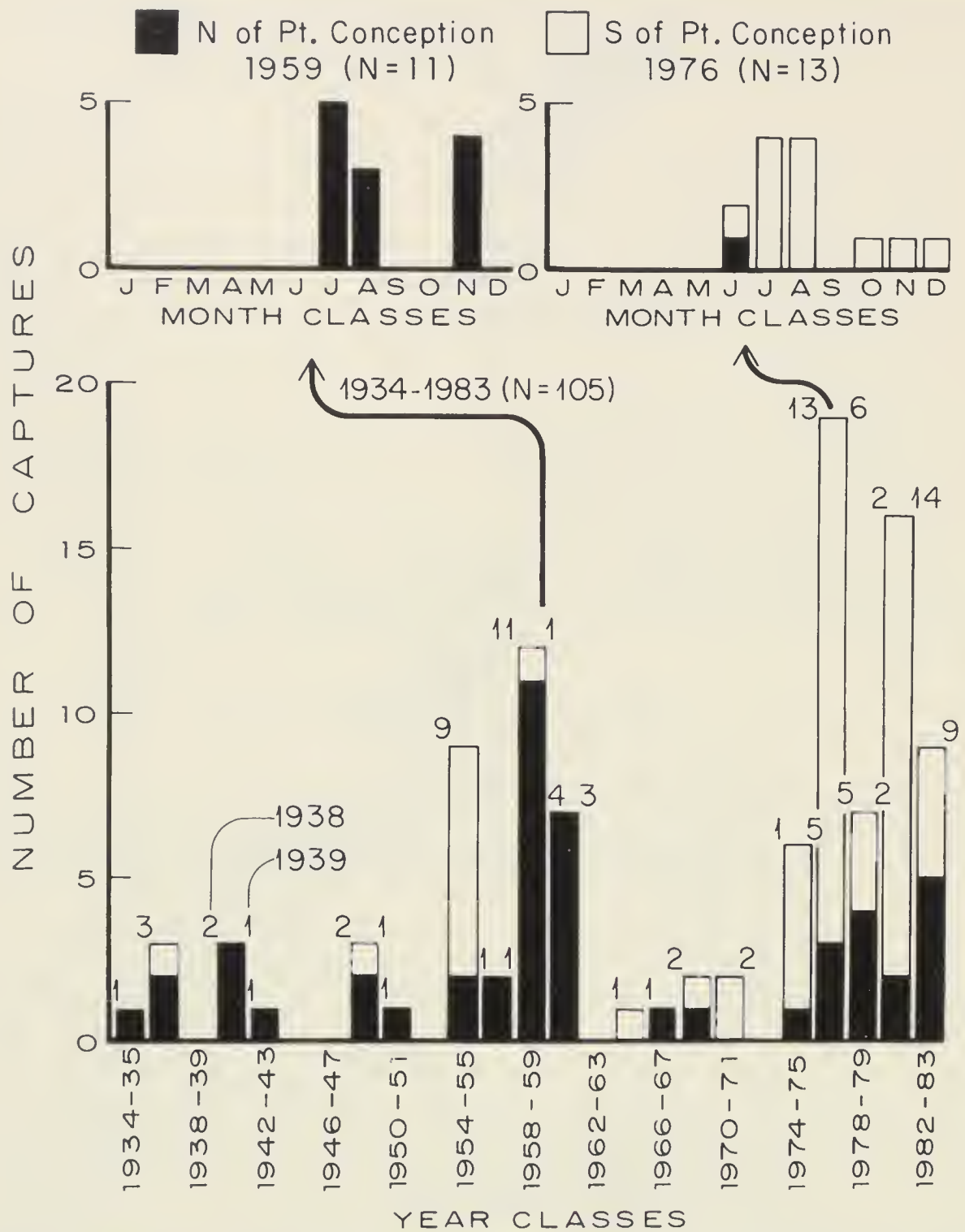


Fig. 8. Numbers of white sharks captured biennially from 1934 to 1983 (below) and monthly (above) during 1959 (lefthand) and 1976 (righthand) along the western coast of North America. Solid part of histogram bar indicates the number of captures north of Point Conception, the clear part south of Point 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

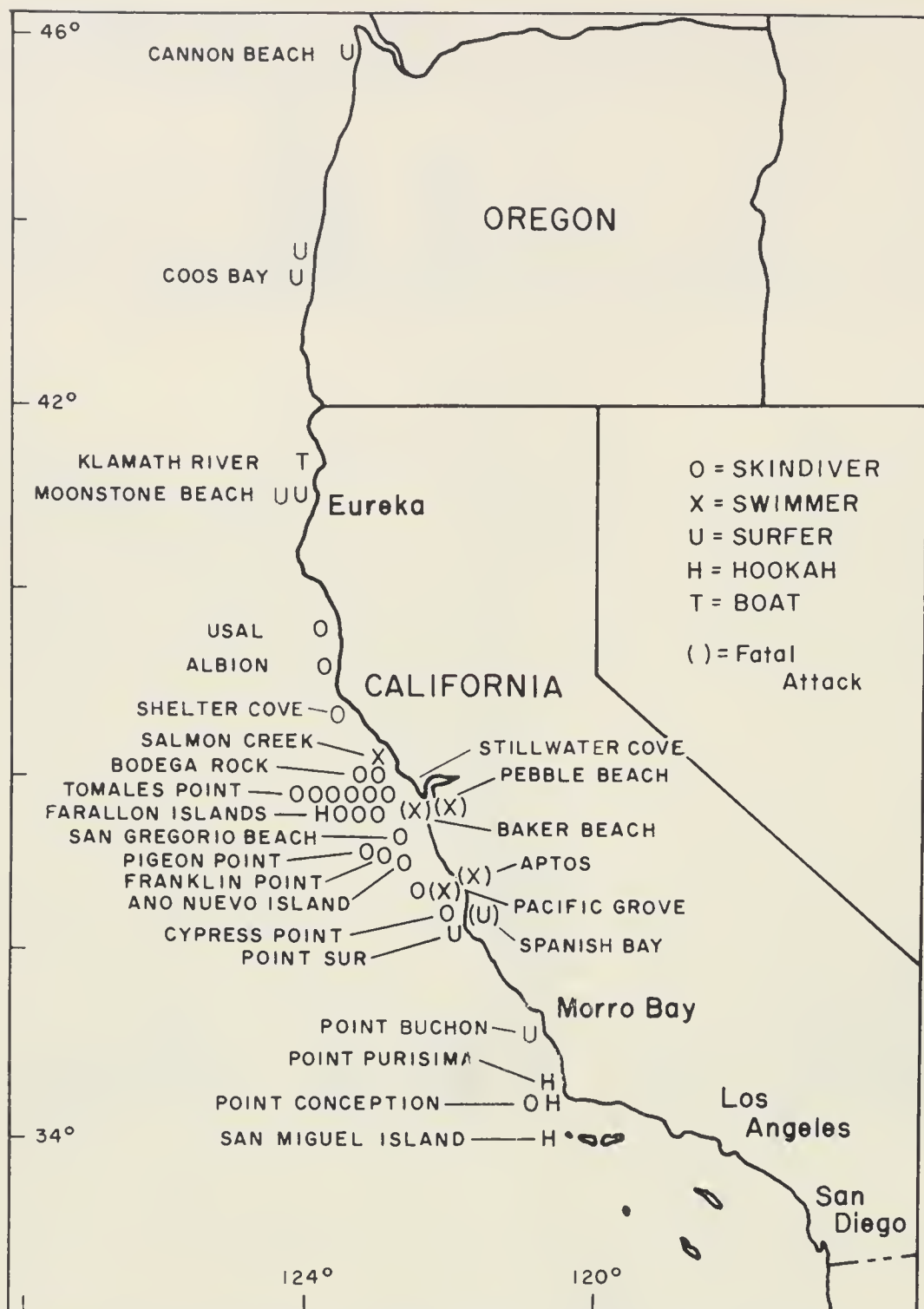


Fig. 9. Attacks by white sharks on humans along the western coast of North America. Records prior to 1979 taken from Miller and Collier (1979); those from 1980 to 1983 obtained from Lea (pers. comm.).

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.

Month	1		Obs./ flight	2	3		Kills/seals cens.	4
	Shark obs.	Flights			Attacks on man	Pinn. 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.).

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.

Years	Indic.					
	1 Attacks on man	Pinn. kills*	Pinn. cens.*	Kills/pinn. cens.	3 Seal bites	4 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.).

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").

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	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	684.9	F	not examined	Metzger
10	10-5-82	2200	2.9	38.0	366.0	4.5	set line	Pemperton	4775		M	<i>Zalophus californiensis</i>	Metzger
11	9-24-81			16.7				Desherow	1524	22.7	F	not examined	Zumwalt
12	6-28-76	1330		3.7	31.1	0	harpoon	Weeren	5080	2152.3		stomach everted	Swift
13	7-23-75		9.3	25.7		0	harpoon	Hawthorne	4409	612.3	F	<i>Phoca vitulina</i>	Le Boeuf
14	5-X-68								1854	54.9	M	not examined	Sea World
15	10-X-71							Tomlinson	1981		F	not examined	Sea World
16	9-7-75		11.3	37.8					4966	1560.4	F	<i>Mirounga angustirostris</i>	Le Boeuf
17	9-X-X								4877	1428.8	F	<i>P. vitulina</i>	Sea World
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	<i>M. angustirostris</i>	Le Boeuf
20	7-29-X							Fromhold	2946	385.6		not examined	Nelson
21	6-24-75		7.4	33.3		0	harpoon	Mansur	3861	635.0		<i>P. vitulina</i>	Le Boeuf
22	10-5-79						gill net	Bertelli	1829	90.7		not examined	Nelson

Appendix I. Continued.

No.	Date	Time hrs	DFS km	DFC km	BD m	SD m	Cap. meth.	Fisherman	Len. mm	Wt. kg	S	Stomach contents	Source
23	8-3-81		1.9	1.9			gill net		1676	45.4		not examined	Nelson
24	10-24-81								1473	25.9	M	not examined	Cailliet
25								Wilson	2133	136.1	F	not examined	Nelson
26	4-16-80		5.6	44.5			gill net	Barker	5029	1587.6	F	<i>Z. californiensis</i> , <i>P. vitulina</i>	Johnson
27	4-30-82		9.2	9.2	9.2	5.5	gill net	Williams	4942	907.3	F	<i>M. angustirostris</i>	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				14.6	5.8	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
39	11-4-71							Tomlinson	1085		F	not known	Swift
40	12-17-76			0.7	9.2		gill net	Caywood		48.5	F	not known	Swift
41	8-9-76				14.6		gill net	Henke	2170		F	unident.	Swift
42	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	F	not known	Swift
44	7-12-59			2.8	27.5	24.5	gill net	Castagnola	2492	145.2	F	<i>Cynoscion nobilis</i>	Follett
45	1-23-59	1400		0.5	27.5	0	harpoon	Tomlinson	5105	1279.1	F	<i>Cetorhinus maximus</i>	Follett
46	7-25-59	0730			5.5	5.5	drift net	Konatich	3143	283.5	M	<i>Myliobatis cali-</i> <i>fornica</i>	Follett
47	7-25-59	0730			5.8		drift net	Konatich	2775	109.3	F	none	Follett
48	7-2-60	1900			5.8	1.2	set line	Spenger	2960	190.1	F	<i>Galeorhinus zygo-</i> <i>terus</i> , <i>Mustelus</i> <i>californicus</i>	Follett
49	11-13-59							Vella	2673	171.1	M	<i>S. marmoratus</i>	Follett

Appendix I. Continued.

No.	Date	Time hrs	DFS km	DFC km	BD m	SD m	Cap. meth.	Fisherman	Len. mm	Wt. kg	S	Stomach contents	Source
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	Cardinalli	1924	65.6	M	<i>Squatulus acanthias</i> , <i>Ophiodon elongatus</i>	Follett
53	7-31-59	0530		6.5	23.8	6.4	drift net	Olivieri	3683	380.1	M	none	Follett
54	7-30-59	1620			5.8		drift net	Konatick	2184	98.9	M	<i>Mustelus californicus</i> , <i>S. acanthias</i> , <i>Sardinops sagax</i>	Follett
55	8-21-79						gill net	Bertelli	1956	88.7	F	none	Follett
56	2-X-77						beach cast	Helm					Follett
57	10-25-78			1.8	20.0		tram. net	Salter	3930	544.3	M	<i>P. vitulina</i>	Morejohn
58	8-28-59	0300		1.8	18.3		gill net	Carniglia	1959	54.4	M	none	Follett
59	10-7-60							Konatick	1965	69.9	F	none	Follett
60	12-27-60				20.1		gill net	Crivello	2419		F	<i>Onchorhynchus tshawytscha</i> , <i>C. nobilis</i>	Follett
61	1-2-61				20.1		gill net	Crivello				<i>Mustelus californicus</i> , <i>Morone saxatilis</i>	Follett
62	12-28-60				20.1		gill net	Crivello	2651	180.5	M	<i>Mustelus henlei</i> , <i>Cancer antennarius</i> , <i>O. elongatus</i> , <i>Sebastes melanops</i>	Follett
63	6-X-81							Mueller	1290	16.1	M	not examined	Cailliet
64	11-8-81							Renardez	2340	86.2	M	not examined	Compagno
65	11-8-81								1990	78.0	F	not examined	Compagno
66	8-27-81	1600					set line	Follett	1976	42.2	F	not examined	Follett
67	9-24-81								1590	37.6	M	not examined	Cailliet
68	10-16-66				9.2		gill net	Spenger	2044	68.0	F	none	Compagno
69	8-25-56								3505	408.2	F	<i>Onchorhynchus</i> sp.	Compagno
70	11-1-68						gill net		2340	72.6	M	not examined	Compagno

Appendix I. Continued.

No.	Date	Time hrs	DFS km	DFC km	BD m	SD m	Cap. meth.	Fisherman	Len. mm	Wt. kg	S	Stomach contents	Source
71	8-22-75						gill net	Johnson	1990	78.0	F	none	Compagno
72	X-X-35							Strobbecca	1981			not examined	Compagno
73	11-13-59							Vella		183.7	M	not examined	Compagno
74	11-9-59							Vecca		101.6		not examined	Compagno
75	8-1-75			0.1	45.5		gill net	Sea World	2362	138.8	F	pinniped	Le Boeuf
76	2-3-77								4700		F	<i>M. angustirostris</i>	Le Boeuf
77	9-25-78			1.6					4150			<i>P. vitulina</i>	Le Boeuf
78	X-X-55								3048		M	not examined	Miller, 1981
79	11-29-48				47.6	47.6	gill net	Thomas	2438	181.4		<i>P. vitulina</i> , <i>Sebastes</i> sp.	Fitch, 1949
80	8-21-48			0.9			set line	Ramsower	1543		F	not examined	Fitch, 1949
81	X-X-36						set line	Follett	1676	42.2	M	not examined	Follett, 1966
82	1-25-64								1960		M	not examined	Kato, 1965
83	8-2-81	1.8	9.2		62.2		long line	Cuevas	2685		F	not examined	Michael
84	4-28-36						gill net	Pederson	2235	155.1		<i>Acirpenser medios-</i> <i>tris</i>	Bonham, 1942
85	9-1-36						gill net	Moore	3962	362.9		<i>P. vitulina</i>	Bonham, 1942
86	9-5-40						gill net	Moore		997.2	M	not known	Bonham, 1942
87	8-X-41						gill net	Ogren		226.8		not known	Bonham, 1942
88	8-X-41						gill net	Oblad		453.6		not known	Bonham, 1942
89	8-X-41								3658	408.3		not known	Bonham, 1942
90	8-16-49	0.9	0.9				gill net	Fuller	3302	317.5	F	not known	Le Mier, 1951
91	9-1-50							Nelson	4420	907.2		<i>Cancer magister</i> , <i>Cancer productus</i> , <i>Oncorhynchus</i> sp., "hair" seal, <i>Mer-</i> <i>luccius productus</i> , <i>Sebastes</i> sp.	Le Mier, 1951
92	10-24-61								3429	453.6		not known	Pike, 1962
93	10-24-61								4674			not known	Royce, 1963
94	10-5-82	2.9	38.0		366.0	4.5	set line	Pemperton	4267	601.0	M	not examined	Metzger

Appendix I. Continued.

No.	Date	Time hrs	DFS km	DFC km	BD m	SD m	Cap. meth.	Fisherman	Len. mm	Wt. kg	S	Stomach contents	Source
95	10-5-82		2.9	38.0	366.0	4.5	set line	Pemperton	3988	567.0	M	not examined	Metzger
96	8-X-82			0.3	16.8		gill net		3480		M	not examined	Metzger
97	7-4-80			5.6	54.9	11.9	drift net	West	1295		M	not examined	Johnson
98	7-17-81			5.6	54.9	11.9	drift net	West	1219		M	not examined	Johnson
99	7-17-81			5.6	54.9	11.9	drift net	West	1321		F	not examined	Johnson
100	8-12-76			1.4			gill net		1448	25.9	M	none	Sea World
101	7-3-78		0.9	37.0			gill net	Henke	1397	17.2	M	none	Sea World
102	8-16-78						gill net	Henke	1473	25.8	M	fish head, dasy- atid ray	Sea World
103	7-25-81						gill net	Henke	1422	23.1	M	none	Sea World
104	7-29-81						gill net	Henke	1549		F	not known	Sea World
105	8-3-81								1600	36.3	M	not known	Sea World
106	6-17-82						gill net	Quinn	1778	52.6	M	elasmobranch	Sea World
107	X-X-74				152.4			Mechado	1473	25.9	M		Sea World
108	11-3-76				152.4		gill net	Nichols	1750	372.9	F	not examined	Sea World
109	8-13-76			1.8	73.2		gill net	Miller	2083		M	not examined	Sea World
NIA	6-5-83		18.5	27.8			gill net	Tibbles	4420				Sea World
NIA	6-27-83			0.2			tram. net			90.7			Lea
NIA	6-3-84		2.2	2.2	36.6	35.6	tram. net	Tomlinson	2133		F	<i>Bursa californica</i> , <i>Myliobatis cali- fornica</i>	Ainley McConnaughey
NIA	6-4-84		2.2	2.2	36.6	27.5	tram. net	Tomlinson	2286		F	<i>Sebastes</i> sp.	McConnaughey
NIA	5-19-84	0830		2.8	33.5	0	harpoon	King	1320	18.1	F	<i>Myliobatis californica</i> , engraulid	Seigel
NIA	6-20-84						tram. net	Carpenter	3048				Ainley
NIA	7-21-84	1800		1.9	1.2	0.6	gill net	Churchman	1864		M	<i>Squalus acanthias</i>	Ainley
NIA	8-24-84			37.0					5334	1452.0	F	not known	Lea
NIA	10-12-84	1030	0.9	0.9			set line	Poole	2000		F	none	Seigel

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White Sharks in Hawaii: Historical and Contemporary Records

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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 (Kaeppeler 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.); *Triacnodon 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

related to *Carcharhinus amblyrhynchos* or *Carcharhinus melanopterus*. The Hawaiians believed that deceased family members would find reincarnation in animal form (aumakua), often as a shark. The aumakua could be found in specific areas of the reef and could be relied upon for fishing assistance and protection. It seems likely that this belief involved a smaller territorial species rather than a large shark such as the great white.

A tattooing motif of small triangles encircling the ankle of a Hawaiian protected by an aumakua is said to have its origin in an incident which would also argue against the white shark as aumakua: a woman swimming across a bay on the Island of Hawaii was attacked by a shark who began to bite off her foot. She recognized the shark as her aumakua and shouted its name. The shark then released her and said "I'm sorry, I didn't realize it was you. Whenever I see the anklet of scars which I have made, I will recognize and protect you."

The Hawaiians also built *heiau*, or temple platforms, near the shore in areas where sharks seasonally aggregated. Legends tell of Hawaiian men and women swimming freely with these sharks and having the ability to predict the time of the sharks' return from year to year. It seems likely that this species is also *Carcharhinus amblyrhynchos* because large aggregations have been observed to recur regularly and predictably over the past eight years in a number of study sites in Hawaiian islands, including Laysan and French Frigate Shoals (this aggregating behavior is reported on in a separate manuscript).

The largest common shark species in Hawaii is the tiger shark, the teeth of which frequently occur in artifacts. This species has been implicated in human attack in modern Hawaii and might be the "man-eating shark" which Hawaiians referred to as *niuhi*. Kamakau (1976) relates a special method of fishing for *niuhi*:

"A fisherman sailed far out on the ocean until the land looked level with the sea, that was the place for shark fishing. When all was ready, the prow of the canoe was turned into the current so that the upswell of the current would be behind the canoe. The net containing the decomposed pig mixed with pebbles and broken kukui nut shells was tied to the starboard side of the canoe at the forward boom. Then the net was splashed into the sea and poked with a stick until the grease ran through the pebbles and shells. A shark would scent the grease, his dorsal fin would break through the surface of the sea, and it would snap its teeth close to the canoe. The large sharks were the *niuhi*; they could be tamed like pet pigs and be tickled and patted on the head. The fisherman would pat the shark on the head until it became used to being touched. Then he rested his chin on the head of the shark and slipped a noose over its head with his hands, turning his palms away from the shark lest it see their whiteness and turn and bite them. When the snare reached the gills, the fisherman eased it downward to the center of the body and tightened the noose. If it were a big shark there would be a furious tugging and battling."

It seems more likely that the large *niuhi* described in this account is a tiger shark rather than a great white shark. Large tigers are known to be quite tractable and can be handled relatively easily as demonstrated by film makers in such films as "For Your Eyes Only." Tiger sharks are also known to occur a considerable distance offshore (Tricas et al. 1981).

Table 1. Hawaiian artifacts containing teeth of great white sharks (examined by author).

Description	Museum and catalog no.	Maximum tooth size (mm)	Illustration	Remarks
1. Jawbone handle; single tooth	Cambridge 22.921	25 x 21	LT*; Fig. 177, Kaeppler 1978	Pre-Cook
2. Curved handle; single tooth	British Museum 1944 Oc.2-705	40 x 45	LT	Pre-Cook
3. Curved handle; single tooth	Cambridge 1920.803	31 x 28	LT	Pre-Cook
4. Curved handle; single tooth	Oxford Balfour I.15-II62 1896.29.43	35 x 27	LT	Post-Cook?
5. Curved handle	Oxford PR IV.53 1884.23.16	30 x 37	LT	Post-Cook?
6. Curved handle; single tooth	Dubling 1880.1613	—	Fig. 179, Kaeppler 1978	Pre-Cook
7. Curved handle; single tooth	Sydney H 111	—	Fig. 180, Kaeppler 1978	Pre-Cook
8. Semi-circle; two teeth simple handle	British Museum 2043	37 x 36	LT; Brit. Mus. PS057672	Pre-Cook
9. Semi-circle; two teeth; compound handle	British Museum HAW 186	35 x 35	LT; Brit. Mus. 061329	Pre-Cook
10. "Cricket bat"; twenty-two teeth	Cambridge 25.366	24 x 24	LT; Fig. 176, Kaeppler 1978	Pre-Cook
11. Curved handle; single tooth	British Museum HAW 191	19 x 19	LT	Post-Cook Iron blade simulating great white shark tooth
12. Curved handle; single tooth	British Museum 1944-Oc2-706	38 x 35	LT	Post-Cook
		38 x 40	LT	Worked ivory simulating great white shark tooth

* LT = Author has 35 mm color transparency of artifact.

I feel that the legends that are most likely to involve white sharks are those in which supernatural or spiritual powers are attributed to the shark. For example, there is a legend about the mother of Kamehameha I, who, during her pregnancy, craved the eye of the niuhi, "the bravest of sharks," and a shark which was sometimes called "chief." A priest predicted that she would give birth to a chief "whose anger would flash through his eyes and whose great power would be compared to the niuhi" (Pukui et al. 1972). Although it has been assumed by some that the niuhi in this instance is the tiger shark, it seems that such attributes would be more likely recognized in the great white.

While consideration of Hawaiian folk legend permits only speculation about the species of shark involved, an examination of Hawaiian artifacts provides much more concrete evidence. In an attempt to identify which shark species were utilized by the Hawaiians before western contact, I examined artifacts in various museums; those which were found to contain the teeth of great white sharks are summarized in Table 1.

Data on Hawaiian artifacts is scant indeed. However, those labelled "pre-Cook" are generally recognized to have been collected on Cook's expedition and are assumed to have been constructed before western contact influenced Hawaiian culture.

Hawaiians actively fished for sharks using large wooden hooks tipped with whalebone, specially made nets, and by noosing individuals (Buck 1964). I assume that the white sharks whose teeth are contained in these artifacts were probably caught by hook and line. It is unlikely that the Hawaiians would have traded these teeth with other Polynesian cultures or salvaged the teeth from beached carcasses. Some teeth included in the artifacts are quite large and indicate that white sharks of a total length of about 5 m (by extrapolation from the curve provided by Randall 1973) were available to the Hawaiians.

It has generally been reported by anthropologists that the typical curved-handled utensil bearing a single shark tooth (Fig. 1) was a weapon used in close infighting. However, after handling these artifacts, I feel that they could also have been used as utensils for delicate work such as trimming or carving.

It is noteworthy that there are two post-Cook artifacts which contain replicas of great white shark teeth. One of these is an iron blade. The other is a carefully worked piece of ivory complete with serrations; great care was taken to simulate a great white shark's tooth. It is possible that these are collector's attempts to restore the original artifacts, but one might also speculate that there was something significant to the Hawaiians about the tooth of this species. Such significance might be strictly utilitarian, or it might be related to the strong spiritual powers that the Hawaiians attributed to the great white shark.

No ichthyological specimens of *Carcharodon* from Hawaii exist in the collections of B.P. Bishop Museum, Honolulu; California Academy of Sciences, San Francisco; or the U.S. National Museum of Natural History. However, a review of local newspaper files and the final reports of several shark abatement programs in Hawaii revealed nine records of great whites in Hawaii since 1926.

Table 2 summarizes contemporary records; Balazs and Kam (1981) searched local records back to 1886 and found no reports of white sharks until 1926 when the fatal attack on W. J. Goins was noted. A second attack involving a white shark took place on 8 March 1969. Licius Lee, a 16-year-old surfer, suffered a



Fig. 1. Hawaiian implement containing a *Carcharodon* tooth held in place by bone pins. Tooth size (maximum enamel height = 27 mm) suggests the shark was at least 3 m total length (based on Randall 1973). Photo by author; Pitt Rivers Museum, Oxford University: Balfour I.15 II.62-1896.29.43.

laceration on his right leg requiring 23 stitches when a white shark bit the tail of his surfboard while he was paddling off Makaha, Oahu. The shark was not captured, but experienced observers (Dr. Richard Wass and Dr. Albert Tester 1969) attested to the identity of the species after examining the bite marks. Another notable record is the 13-foot 4-inch specimen captured off Honolulu Harbor on 8 March 1961 which was displayed alive in a Honolulu oceanarium for 24 hours. This is believed to be the first display of a living great white shark.

Although eight of the nine sharks reported in Table 2 were landed by fishermen, no formal deposition of their remains has been made. No samples exist in the collections of local museums and I have been unable to identify private individuals who may have kept souvenirs of their capture.

Discussion

Although it has been definitely demonstrated that *Carcharodon carcharias* has occurred in Hawaii historically and in recent years, it is certainly a rare species in Hawaiian waters. Only five white sharks were captured during two shark abatement programs (Ikehara 1961; Norris and Harvey 1969), and no specimens were collected in the 1967–69 Cooperative Shark Research and Control Program during which 13,594 hooks were set around the main Hawaiian Islands. The fishing program conducted by Gary Naftel and myself in the waters off Oahu, Maui, and Kauai, in which 1000 hooks were set, also failed to produce *Carcharodon*, as did a 2000 hook program in the Northwestern Hawaiian Islands at French Frigate Shoals, Pearl and Hermes Reef, and Maro Reef.

Sharks do enter the fresh fish market in Hawaii as incidental products from other fisheries but shark fishing effort in recent years has been concentrated in

Table 2. Contemporary records of great white sharks in Hawaii.

Date	Locale	(No. reported) length in feet	Source	Remarks
May 18, 1926	Kahuku, Oahu	(1) 12.5'	Anonymous, 1926	Stomach contained remains of W. J. Goins
1958-1960	Windward Oahu	(3) 10'10"-11'5"	Ikehara, 1960	Caught during abatement program
March 8, 1961	Off Honolulu Harbor	(1) 13'4"	Anonymous, 1961 Frank Inoue, pers. comm.	Displayed alive in oceanarium for one day
January 20, 1966	Kawaihae Bay, Hawaii	(2) not reported	Norris & Harvey, 1969	Caught during abatement program
March 8, 1969	Makaha, Oahu	(1) 12' (estimated)	Anonymous, 1969	Attacked surfboard; swam away
May 3, 1969	Kawaihae Bay, Hawaii	(1) not reported, male	Norris & Harvey, 1969	Caught during abatement program

state supported abatement programs. Typical catch per unit effort for these programs was approximately 3 sharks per 100 hooks set for tiger sharks, a species comparable in size to a great white shark. Although it is possible that the longline fishing method does not accurately portray the number of great white sharks because of their size, the fact that three specimens larger than ten feet have been caught in this manner argues that it is a successful fishing method.

The size of the sharks caught in Hawaiian waters and the size of the sharks whose teeth are included in Hawaiian artifacts (based on Randall 1973) all exceed the length at which the dietary shift to marine mammals has taken place (McCosker, this volume). At sizes in excess of 2.5 meters, white sharks are assumed to feed primarily on pinnipeds and other marine mammals.

Hawaii as a subtropical volcanic archipelago is quite different from those continental areas where white sharks are common. Primary productivity and fish standing crop are lower in Hawaii than in those areas and there are no large concentrations of pinnipeds. However, there is a native phocid, the Hawaiian monk seal (*Monachus schauinslandi*), now limited to the Northwestern Hawaiian Island chain. It is an endangered species numbering less than 1500 individuals. While there is no tangible evidence that the seals ever occurred in the main Hawaiian islands, recent work on Hawaiian midden material and on fossil birds suggest that the colonizing Polynesians may have rapidly exterminated defenseless species such as flightless birds and perhaps the Hawaiian monk seal. It may be possible that great white sharks were more abundant in Hawaii during a period when monk seals may have colonized the high islands.

There has been one reported sighting of a white shark within the range of the Hawaiian monk seal at Laysan Island, Northwestern Hawaiian Islands (by commercial fisherman Gary Naftel and National Marine Fisheries biologist John Naughton). However, no tangible evidence for the occurrence of *Carcharodon* in the Northwestern Hawaiian Islands exists despite fishing efforts from 1976 to 1980.

Humpback whales, *Megaptera novaeangliae*, are regular visitors to Hawaii from November to May and give birth to calves in Hawaiian waters during this period. It is interesting to note that almost all of the sharks recorded in Table 2 were collected or observed during the period when Humpbacks are present in Hawaiian waters.

All of the white sharks recorded from Hawaii are adults; no juveniles have been collected here. This suggests that there is no resident population of white sharks in Hawaii, but rather that the Hawaiian records represent vagrants or commuters from one area of the Pacific to another (a recent record of a healthy female elephant seal tagged at Ano Nuevo Island off California and found basking on the beach on Midway Island at the northwestern end of the Hawaiian chain is of note here).

Conclusion

While *Carcharodon carcharias*, the great white shark, was contemporaneous with the ancient Hawaiian culture, contemporary records suggest that this species is an irregular visitor to Hawaiian waters. The white shark should be considered a rare species and is probably not resident in Hawaii. Its presence here may be correlated with the occurrence of monk seals and humpback whales.

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Preliminary Studies on the Age and Growth of the White Shark, *Carcharodon carcharias*, Using Vertebral Bands

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and David A. Ebert

Abstract.—Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands by Gregor M. Cailliet, Lisa J. Natanson, Bruce A. Welden, and David A. Ebert. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. Radiography and silver nitrate staining were used to delineate calcified bands on vertebral centra of the white shark (*Carcharodon carcharias*) from the eastern Pacific. For age and growth estimates, vertebrae and body size measurements were used from 21 white sharks taken since 1936. Three readers reached a consensus on band definition, number, and diameter. The total length-centrum diameter relationship was linear. Birth marks (17–21 mm diameter) were detectable in all radiographs and verified in our smallest newborn shark (1290 mm TL), which had no calcified bands. Our three largest white sharks were between 4942 and 5079 mm TL and had between 13 and 15 band pairs. These band counts were used to construct a preliminary von Bertalanffy growth curve and compared favorably with an independently produced back-calculated growth curve.

Despite the notoriety of the white shark, *Carcharodon carcharias*, its basic biology is not well understood. The major difficulty in studying the white shark results from a combination of its large size, its mobility, and the rarity with which it is encountered. What is known about its distribution and abundance has been gathered from shark attacks, beachings, and incidental catches by fishermen (Bigelow and Schroeder 1948, 1953; Hart 1973). Through analysis of the resulting specimens, other pieces of information have been gathered about its size, maximum length and weight, length at birth, morphology, reproduction, and feeding habits (Pratt et al. 1982). However, there is virtually nothing known about its age composition, growth rate, longevity, age at maturity, fecundity, or gestation period.

The white shark is comparable in size only to large marine mammals and to three other species of sharks, the whale, basking, and megamouth sharks, all of which are filter feeders (Taylor et al. 1983). The white shark, being one of the largest predatory fishes, must influence the species composition of its prey communities. A more thorough understanding of its life history characteristics would be essential to fully evaluate its role as an apex predator and to determine its population size, distribution, and dynamics.

Considering the diversity of elasmobranch fishes (Compagno 1981), limited work has been done on their life histories (Holden 1977), especially the large, pelagic species (Stevens 1975; Cailliet et al. 1983b; Cailliet and Bedford 1983; Pratt and Casey 1983). However, what has been done suggests that elasmobranchs typically have relatively slow growth rates, live to be quite old, mature late in

Table 1. White shark catch dates, locations, sexes, sizes, band counts, and centrum diameters of each band from x-radiographs.

Catalog number	Source	Sex	Location	Date	Centrum diameter of bands							
					0+	1+	2+	3+	4+	5+	6+	
2	1	M	Baja (?)	6/81	17.6							
14	2	?	Ventura	7/76	17.4							
11	1	?	Southern California	8/80	19.3							
15	2	?	Ventura	7/76	18.3							
22	5	M	Bodega Bay	8/83	17.5							
8	3	M	Southern California	8/81	18.7	23.1						
9	3	M	Southern California	9/81	16.7	21.5						
7	4	F	Malibu	9/36	17.3	25.0						
10	4	F	Central California	10/79	18.5	25.5						
4	5	F	Half Moon Bay	?	17.6	22.3	27.9					
12	2	?	Ventura	9/77	20.2	23.5	28.3					
13	2	?	Ventura	7/76	18.6	22.0	26.5					
3	5	M	Half Moon Bay	7/68	17.4	24.0	29.4					
20	4	F	Marin Co.	10/76	16.6	22.6	27.2	32.8				
6	4	F	Unknown	?/59	17.0	21.0	27.0	30.8				
1	6	M	Moss Landing	9/78	20.1	27.0	30.0	33.0	36.6	40.0	45.0	
21	7	M	Anacapa Island	6/83	19.0	23.0	28.4	34.0	38.4	43.0	48.0	
17	2	M	Southern California	5/82	20.0	26.0	30.4	33.6	37.4	42.6	46.0	
19	2	F	Off Los Angeles	4/80	16.2	23.8	28.4	32.0	33.8	39.4	44.0	
16	2	F	NW Santa Barbara Isl.	6/76	16.8	20.4	27.2	30.6	38.0	41.6	48.0	
18	2	F	Off Pt. Dume	8/82	17.0	23.0	27.2	31.2	36.0	39.2	44.0	
		\bar{X}			18.0	23.9	28.2	32.3	36.7	41.0	45.8	
		S.D.			1.21	1.69	1.24	1.26	1.67	1.66	1.83	

1. West, San Pedro. 2. Los Angeles County Museum. 3. Sea World. 4. California Academy of Sciences. 5. Compagno. 6. Moss Landing Marine Laboratories. 7. Anacapa Island.

* Calculated total length from total length-centrum diameter regression.

life, have low fecundities, and have long gestation periods (Holden 1973, 1974, 1977).

Recently, a great deal of interest has surrounded sharks in general in California waters. One reason is the publicity due to shark attacks on man (Miller and Collier 1980). Another reason is the increase in the commercial utilization of sharks (Cailliet and Bedford 1983). As these fisheries have expanded, we have studied the life histories of many species of California elasmobranchs using vertebral bands to estimate ages and construct growth curves, which we combine with other life history information such as state of maturity and fecundity (Cailliet et al. 1983a, b). Few specimens of the white shark have been made available for study

Table 1. Continued.

Centrum diameter of bands									Number of bands		Size
7+	8+	9+	10+	11+	12+	13+	14+	15+	Consensus	Range	
									0	0	1290
									0	0-1	1365
									0	0-1	1469*
									0	0	1500
									0	0	1670
									1	1-2	1473
									1	1	1590
									1	0	1676
									1	1	1832*
									2	2	1990
									2	2	2099
									2	2	2258
									2	2	2340
									3	3	2134
									2	3	2775
50.0	53.0	58.0							9	7-9	3930
52.0	54.4	58.0	61.0	64.8	68.0	75.0			13	13	4591
49.0	53.4	56.0	60.8	66.0	68.0	70.8			13	10-13	4609
48.0	51.6	54.4	56.2	59.0	66.6	67.6	70.0		14	12-14	5029
54.0	56.2	59.6	64.0	68.0	72.2	76.6	80.0		14	13-14	5079
48.8	50.4	56.4	64.0	69.4	71.6	74.8	76.0	80.0	15	15	4942
50.3	53.2	57.1	61.2	65.4	69.3	73.0	75.3	80.0			
2.28	2.04	1.84	3.20	4.01	2.47	3.68	5.03				

since it is rare in commercial catches and has never served as the target for a fishery. Over the past few years, we have been collecting as much fresh material from the white shark as possible and have been surveying the museum collections in California for older dried or preserved material. Here, we report our preliminary results on age and growth processes in the white shark.

Materials and Methods

Vertebral centra, obtained from California museums and specimens from shark researchers and fishermen, were used to estimate individual ages of white sharks. For all but two specimens, total length (TL: distance from tip of snout to end of stretched tail) in mm was used as the body size parameter. For two others (numbers 10 and 11), we estimated TL from the linear regression we derived between

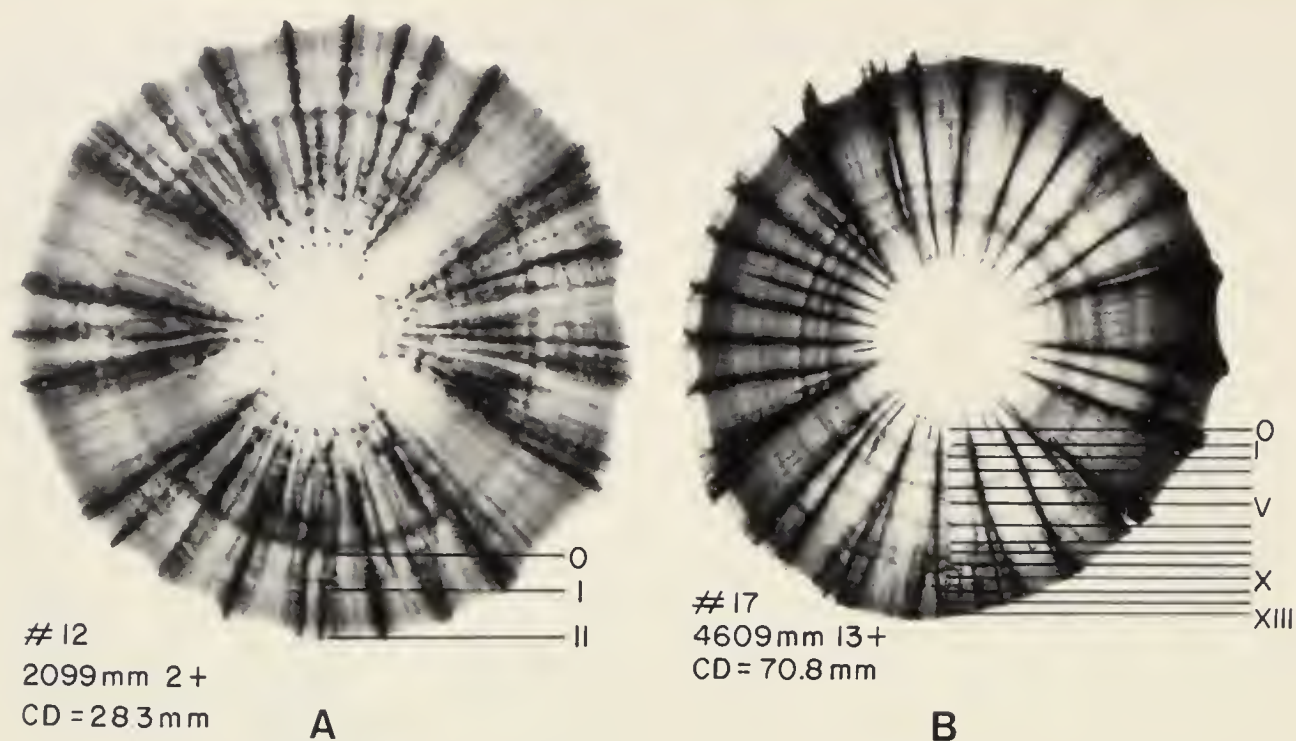


Fig. 1. X-radiographs of centra from white sharks. (a) is from a small (2099 mm TL) individual, sex unknown, which was estimated to be 2 years old; and (b) is from an adult (4609 mm TL) individual, sex unknown, which was estimated to be 13 years old.

centrum diameter and TL. Whenever possible, information on sex, reproductive condition, and feeding habits was noted.

For all specimens, a section of the vertebral column was removed and either frozen in a plastic bag, dried, or fixed in formalin and preserved in isopropyl alcohol. Vertebrae anterior to or directly under the first dorsal fin were taken. A piece of the vertebral column was cleaned using a combination of steps. First, the haemal arch, lateral processes, and most of the connective tissue were removed to expose the surface of the centrum. Then, several centra were soaked for approximately five minutes in distilled water, followed by soaking in bleach to further facilitate removal of connective tissue from the centrum. For larger centra, a longer soaking time was needed, and immersion intervals ranged from one-half hour to six hours. The vertebrae were then soaked in a concentrated solution of formic acid for two to four minutes to remove any remaining traces of bleach and to etch the centrum surface.

The primary technique used to estimate age from vertebral centra was x-radiography (Cailliet et al. 1981, 1983a). The cleaned centra were x-rayed whole using a Hewlett-Packard Faxitron Series x-ray system (Model No. 43805N) with Kodak Industrex M film (Readypack M-2). In one case, the x-radiograph did not produce clear bands, and the vertebral centra had to be cut in half transversely, extraneous tissue ground away with a dremel tool, and then x-rayed. In all cases, discernible bands could be distinguished.

A second band enhancement technique was used to corroborate the band counts derived for larger sharks. This second technique was a modified version (Cailliet et al. 1983a) of the one first described by Von Kossa and adopted by Stevens (1975). It basically involves replacing calcium salts in the centrum with silver, providing distinct silver-impregnated bands which become quite dark after illu-

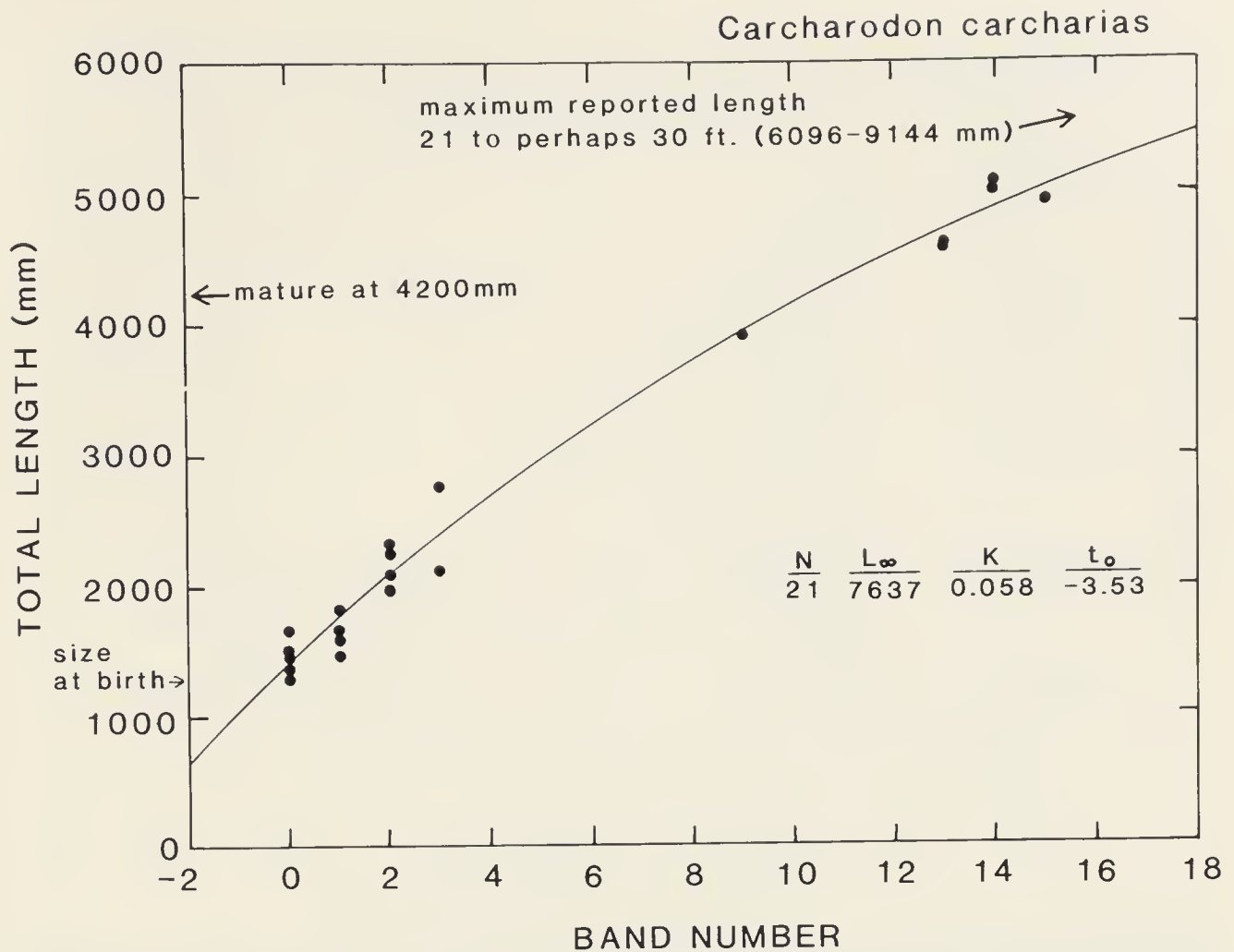


Fig. 2. Von Bertalanffy growth curve for 20 white sharks in which age was estimated from radiographs. Sexes were combined for calculation of the von Bertalanffy parameters. References used for size at birth, size at maturity, and maximum size were Bigelow and Schroeder 1948, 1953; Hart 1973).

mination under ultraviolet light. These centra were rinsed in distilled water for approximately fifteen minutes, then immersed in a 1% silver nitrate solution, and immediately placed in a chamber where they were illuminated by an ultraviolet light source. The length of light exposure ranged from 3 to 15 minutes, depending upon centrum size. The centrum was then rinsed again in distilled water to remove excess silver nitrate. Vertebrae were soaked in a 5% sodium thiosulfate solution for two to three minutes, removing excess silver and fixing the chemical substitution. The final step was storage in 70% isopropyl alcohol.

The x-radiographs were viewed through a dissecting microscope or, for the larger ones, directly over a fluorescent viewing glass, both with transmitted light. The silver-nitrate-impregnated vertebrae were viewed directly with illumination focused laterally on the centrum.

For both techniques, procedures for counting the concentric growth zones were standardized. We defined rings as the narrowest type of circular pattern and bands as wider circular patterns, made up of several of the narrower rings (see Cailliet et al. 1983a). We chose to count only bands because they provided consistent, repeatable counts and measurements. The more numerous finer rings were not used because of the variability in their numbers and dimensions among vertebrae from the same specimen. Thus, one year's growth was interpreted to be a pair of dark and light bands. For x-radiographs, the white band was interpreted as summer

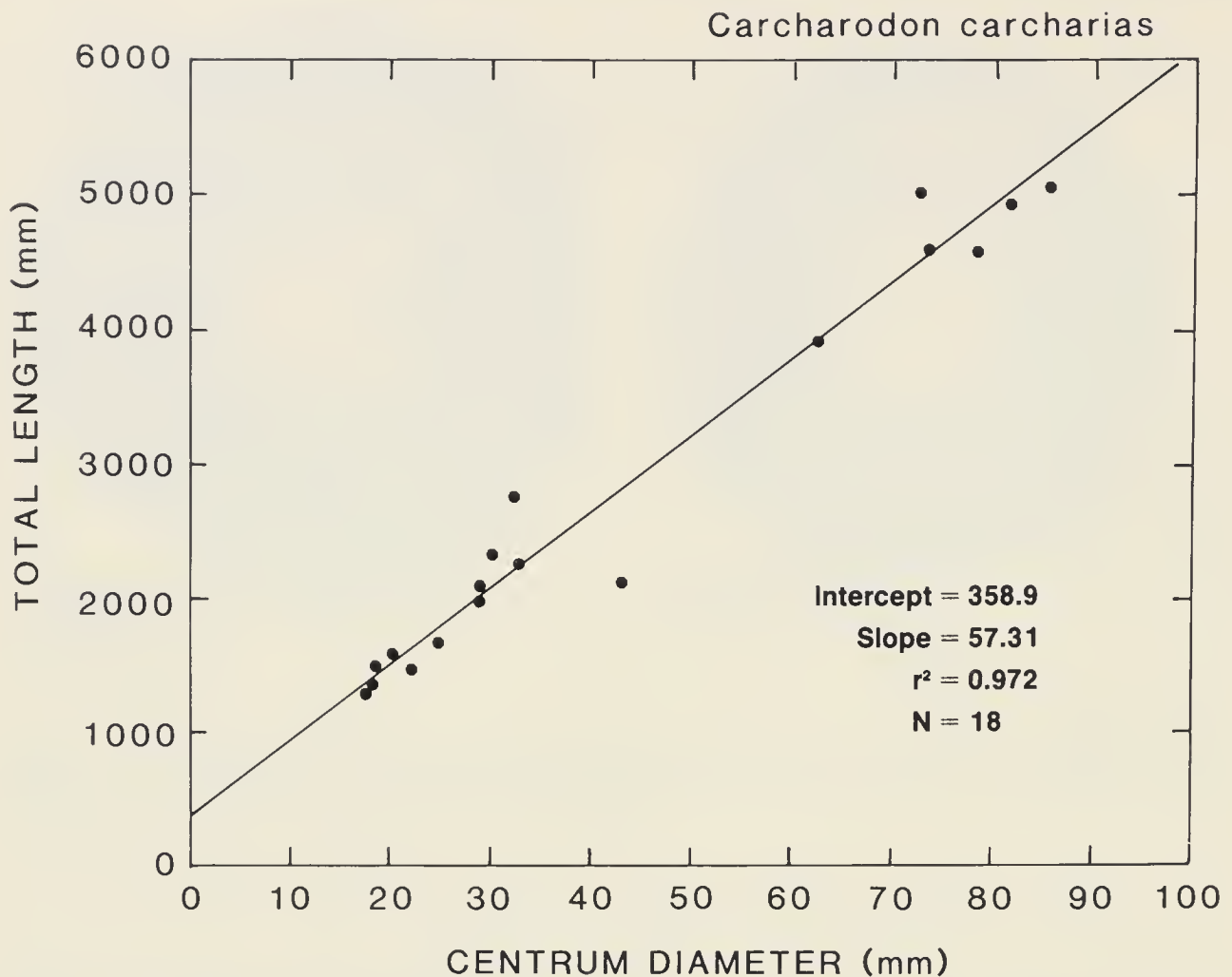


Fig. 3. Regression of centrum diameter and total length (mm) for 18 white sharks. Regression equation given was used to predict total length from centrum diameters in back calculation.

growth, in which more calcification occurs (see Fig. 1), and for silver-nitrated vertebrae, summer growth appeared as a dark band.

To ensure the accuracy of band counts, three observers made replicate, independent counts of the pairs of bands on each centrum. For an estimate to be accepted, counts from at least two of the three observers had to be identical. In no case was this criterion not satisfied.

Centrum diameters of 20 specimens were measured across the midlateral axis to the nearest mm with vernier calipers. A linear regression between the centrum diameter and TL (both in mm) was calculated and plotted for 18 of these 20. Individual summer band diameters were measured to the nearest mm on all vertebrae. These diameters were then used, with the regression equation, to predict what the total lengths of individual sharks had been in previous years of life, and these estimated total length measurements were then used to back-calculate total lengths. This was used to test for Rosa Lee's phenomenon of differential growth within an individual's history and to compare this growth curve with the one estimated from the individually collected and analyzed vertebral centra (Ricker 1975).

For simplicity and the widest applicability of this preliminary age information, we fit our data to the von Bertalanffy (1938) growth equation using methods for calculating the parameters L_{∞} , K , and t_0 from Allen (1966). These parameters were calculated for all individuals combined because several specimens had not

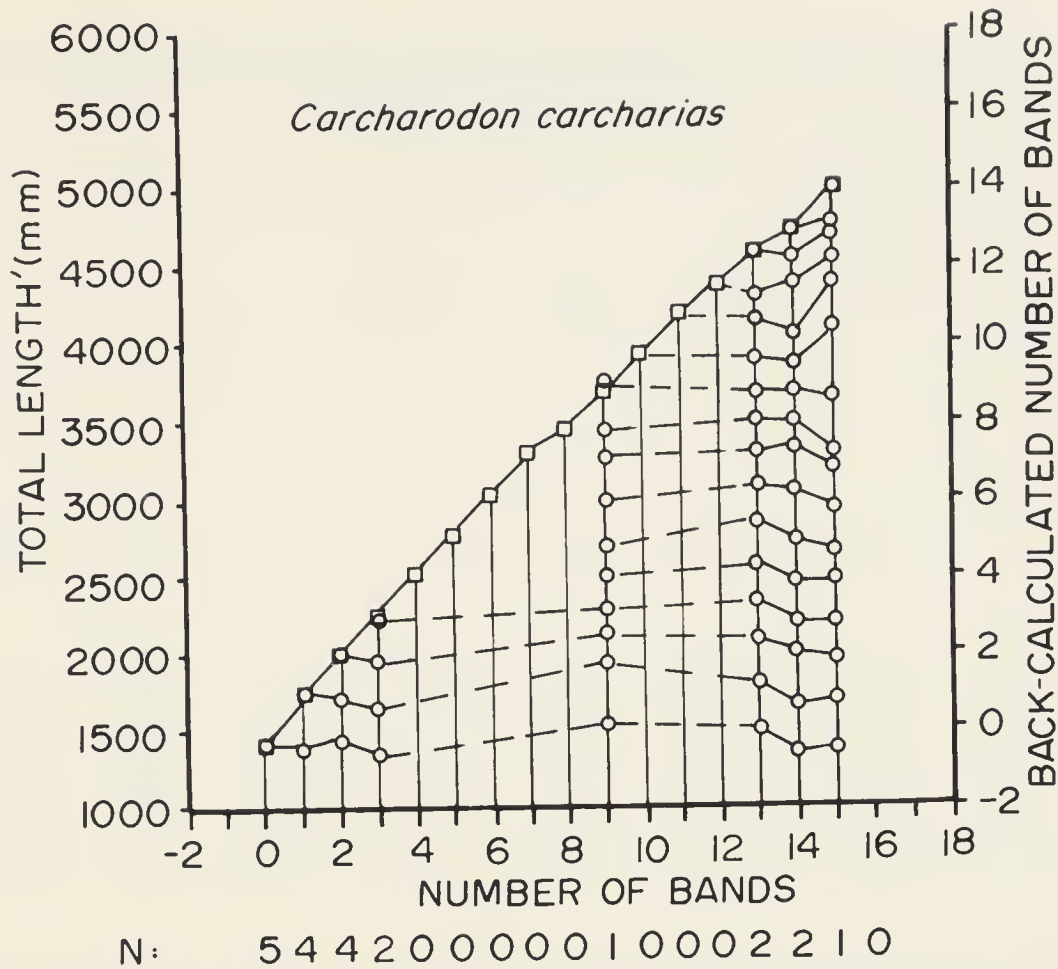


Fig. 4. Growth curve for 21 white sharks using back-calculated total lengths from centrum diameter. N indicates the number of specimens used for each age. Solid line connecting squares represents a growth curve using mean values of back calculated total lengths derived from band diameters. Solid lines connecting dots represent back calculations of adjacent ages for which we have data, while dashed lines connect dots between more distant ages, for which we do not have data.

been sexed, and the sample size for either known sex was quite low. We also compared the size and age at birth and first maturity and the maximum size reported in the literature with those values estimated from our growth curves.

Results and Discussion

Vertebrae from a total of 21 white sharks were obtained for study (Table 1). Catch dates for these specimens ranged between September 1936 and August 1983, with the majority being taken during the last ten years. All were captured from late spring (April) through early fall (October). All of the white sharks studied were caught off California, with one exception from Baja California. Eight of the specimens were males, eight were females, and the sex was unknown for the remainder. The specimens ranged in size from free-living juveniles as small as 1290 mm TL to adults as large as 5079 mm TL. White sharks have been reported to reach maximum lengths of 30 to 36½ feet (11,133 mm) TL worldwide (Jordan and Evermann 1896; Bigelow and Schroeder 1948, 1953), but these records have been disputed (Randall 1973). The largest white shark reliably measured was 21 feet (6400 mm) TL (Bigelow and Schroeder 1948). However, many authors feel that white sharks reach 25 to 30 feet (7600 to 9100 mm) TL (Miller and Lea 1972; Hart 1973; Randall 1973; Eschmeyer et al. 1983). Thus, our sample does not contain sufficient representatives of the larger size classes. However, the largest

Table 2. Mean back-calculated total lengths of *Carcharodon carcharias*.

Estimated age (years)	N	Band number							
		0	1	2	3	4	5	6	
0	5	1408.7							
1	4	1396.0	1741.2						
2	4	1433.6	1693.6	1986.8					
3	2	1338.2	1627.1	1933.4	2204.9				
4									
5									
6									
7									
8									
9	1	1528.9	1927.6	2100.9	2274.2	2482.3	2678.7	2967.6	
10									
11									
12									
13	2	1494.2	1783.1	2066.0	2320.4	2557.4	2843.4	3083.2	
14	2	1320.8	1644.4	1973.8	2176.0	2441.8	2707.6	3025.4	
15	1	1349.8	1696.4	1939.1	2170.2	2447.6	2632.5	2909.5	
	\bar{X}	1407.0	1717.0	1994.4	2230.9	2488.1	2735.5	3015.8	
	S.D.	69.87	105.26	71.71	74.84	96.62	97.10	106.05	

specimen reported for California waters was about 30 feet (9150 mm) TL (Jordan and Evermann 1896; Eschmeyer et al. 1983), and the largest actually measured were 18.5 ft (5639 mm) TL (Compagno, pers. comm.) and 16 $\frac{2}{3}$ feet (5100 mm) TL (Hart 1973; Miller and Lea 1972; Eschmeyer et al. 1983). Therefore, we have some representatives of the locally occurring larger size classes of this species.

Although both techniques produced discernible bands, the x-radiography technique was used to estimate age in all specimens and for centrum width measurements for back-calculation purposes (Fig. 1), because it was consistent and could be done more rapidly. The silver nitrate impregnation technique was used to check the larger, more difficult-to-read vertebrae.

For all vertebrae, at least two of the three independent readers agreed in their band counts. Discrepancies in age estimates were more common in larger specimens, but in no case was it more than three years (Table 1). In the majority of estimates (67%), all three readers agreed, with 19%, 9.5%, and 5% of the readings differing by 1, 2, or 3 years, respectively. There was no apparent effect of preservation or freezing on age estimates.

The von Bertalanffy growth curve for the 21 white sharks we aged rose gradually and slowly approached the estimated asymptotic length (L_{∞}) of 7636 mm TL (Fig. 2). The smallest specimens all exhibited only a birth mark, which was defined as 0 bands, while the oldest specimen (15 bands) was among the largest, but not the largest of the specimens (4942 mm TL). The other two largest specimens were estimated to be 14 years old (Table 1). To assess consistency of band identification, we calculated mean age-specific diameters and their standard deviations. In all cases, the means were quite similar and had low standard deviations (Table 1).

The combined asymptotic length of 7636 mm TL is very close to the generally agreed-upon maximum size of approximately 25 to 30 feet (7636–9150 mm) TL,

Table 2. Continued.

Band number								
7	8	9	10	11	12	13	14	15
3256.5	3429.9	3718.8						
3285.4	3481.9	3661.0	3886.4	4146.4	4296.6	4579.7		
3314.3	3481.9	3661.0	3840.1	4036.6	4377.4	4533.4	4701.0	
3187.2	3279.6	3626.3	4065.4	4377.5	4504.6	4689.5	4758.8	4990.0
3273.8	3439.5	3664.8	3903.7	4148.7	4370.5	4583.2	4720.3	4990.0
131.36	118.19	106.07	184.68	231.93	142.59	212.69	290.82	0

and is within the range of maximum reported sizes in the literature (Jordan and Evermann 1896; Bigelow and Schroeder 1948, 1953; Roedel and Ripley 1950; Randall 1973). Using a growth rate estimate of 218 mm per year, calculated from the last six years of growth in Table 2, it would take approximately 12 years for a fish to grow from 4590 mm TL to the asymptotic length of 7636 mm TL, and this fish would be approximately 27 years old. This approach is questionable, however, because we have not collected any specimens approaching this size, and growth rates will probably slow down in later years. Thus, the maximum age attained by the white shark still remains unknown.

Our estimate of size at birth, derived from the von Bertalanffy growth model (approximately 1250 mm TL) agrees well with values of free-living young reported in the literature (Bigelow and Schroeder 1948, 1953; Hart 1973; Eschmeyer et al. 1983) of between 3 and 5 feet (915–1525 mm) TL. There may be differences in size at birth with size of female or location, thus the wide variation in the literature.

Our very low t_0 value (-3.53) suggests a relatively long gestation period, considerably longer than the 0.5 years proposed by Holden (1974). With so few data points, any additional points could radically alter the t_0 estimate (see Gulland 1983). Thus, until a more adequate data base is developed, the gestation period will remain unknown.

White sharks reportedly range in size at maturity between 12 and 14 feet (3660 and 4270 mm) TL (Bigelow and Schroeder 1948, 1953; Hart 1973). Given our age estimates, this would correspond to an age at maturity of approximately 9 to 10 years. Using our asymptotic length of 7636 mm TL, white sharks apparently mature at a size which is about 48 to 56% of their asymptotic length, which is a bit lower than Holden's (1977) generalization of 60–90%. Using age at first maturity versus our preliminary projected age at asymptotic length, the figures would

be much lower, reaching maturity at between 33 and 37%. Of course, more observations, especially of older and larger sharks will need to be obtained before a more definitive statement can be made.

The relationship between centrum diameter and total length of those white sharks measured was linear, and the regression was statistically significant ($r^2 = 0.972$, $P < 0.001$; Fig. 3). Thus, total lengths can legitimately be estimated from centrum diameters to produce a back-calculated growth curve (Table 2). The resulting curve (Fig. 4) is almost identical to that produced independently by individual vertebral band counts. There are quite a few gaps in the back-calculated curve produced by the lack of specimens within a given size class, thus making it difficult to assess whether or not Rosa Lee's phenomenon occurred. However, from those lines which were connected, Rosa Lee's phenomenon does not appear to be a major consideration.

Few verification and validation techniques are applicable to the white shark because of the small number of available samples, and the difficulty involved in capturing, tagging, and marking these large animals. However, we have compared estimated growth rates with those reported by H. L. Pratt (pers. comm.) for Atlantic specimens and Ainley et al. (this volume) for sharks from Pacific waters. Pratt (pers. comm.) found slower growth in Atlantic specimens, calculating growth rates of 200 mm per year compared to our estimate of 250–300 mm/year for the younger and 218 mm/year for the older Pacific coast specimens. For example, they estimated that a 16-foot (4750 mm TL) white shark would be approximately 20 years old, which is older than our age estimate of 13–14 years. There is variability associated with such an estimate, and growth characteristics may certainly be different from one region to another as was proposed for the blue shark, *Prionace glauca*, in the Atlantic (Stevens 1975) and the eastern Pacific (Cailliet et al. 1983b; Cailliet and Bedford 1983).

Ainley et al. (this volume) estimated growth of individuals which were observed attacking pinnipeds off the Farallon Islands. Using calculated total lengths based on visually estimated heights of dorsal fins, assumed to be of the same individuals, they estimated growth to be 500 mm per year, which is approximately twice our growth estimate of 250–300 mm per year for individuals aged 0–15 years. However, since these growth rates are based on long range visual estimates of dorsal fin heights by different observers, they are most likely neither accurate nor precise.

Conclusion

In conclusion, our preliminary data and the available literature indicate that the white shark attains large sizes and has gradual growth rates and a relatively long life span. Therefore, as first postulated by Holden (1973, 1974, 1977), it is quite possible that this combination of life history traits could make this species susceptible to overexploitation from both direct and incidental fishing pressure. Ainley et al. (this volume) show evidence that the removal of just four white sharks greatly reduced and possibly eliminated the entire local population of white sharks off the Farallon Islands.

Before any definitive statements can be made concerning the life history of this species, more samples of all sizes and sexes over a wider geographical range are needed. In addition, more detailed analyses of age and growth, especially validation of age estimates, and information about their reproduction, population

abundance, distribution, and migratory patterns is necessary before we can begin to understand this poorly known, widely feared and certainly misunderstood top predator of the world's oceans.

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Visual System of the White Shark, *Carcharodon carcharias*, with Emphasis on Retinal Structure

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Abstract.—Visual system of the white shark *Carcharodon carcharias*, with emphasis on retinal structure by Samuel H. Gruber and Joel L. Cohen. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. The retina of the white shark *Carcharodon carcharias* was examined under the light microscope. Identification, counts, and measurement of retinal neurons provided evidence for diurnal vision in this species. The presence of cone photoreceptors suggests retinal mechanisms of acute, photopic, color vision. The increase of retinal cones from periphery to center indicates that different areas of the retina are specialized for day and night vision. Comparison of the retinas of white and lemon shark, *Negaprion brevirostris*, indicates that both species have extended periods of visual activity, but that the lemon shark is relatively more adapted to nocturnal vision.

Sharks are usually thought of as having poor eyesight (Walls 1942). This view stems from a long history of anatomical studies in which the retinas of benthic, temperate species such as *Scyliorhinus* were subjected to histological investigation (Neumayer 1897). Most of the classical North European histologists of the time concluded, as Schultze (1866) first suggested, that sharks lacked cone photoreceptors and were thus visually deprived. Still, Neumayer (1897) reporting on the retina of *Scyliorhinus* noted that “*Die Zapfen-Zellen sind etwa um ein Drittel kuerzer als die staebchen-Zellen . . .*” (the cone cells are $\frac{1}{3}$ shorter than the rod cells). Such reports notwithstanding, many comparative visual scientists even today still believe that sharks are visually handicapped because they lack cone cells (for review see Gruber and Cohen 1978).

The significance of cones to vision was first expressed by Schultze (1866) when he formulated the duplicity theory of vision. Schultze noted that the retinas of nocturnal vertebrates were dominated by rod photoreceptors while diurnal species had a preponderance of cones. Animals with both rods and cones, i.e., with duplex retinas, were afforded an expanded period of visual activity. Until recent times, the shark was considered visually handicapped because its visual activity is restricted to night time, caves, or the deep sea. Beginning in the 1960's in our laboratory and in several others (Gruber et al. 1963; Ali and Anctil 1974; Anctil and Ali 1974; Stell 1972; Hamasaki and Bridges 1965), the shark eye was subjected to contemporary analytical techniques and a profile of shark vision emerged which was quite different from the 19th century view.

First, most sharks possess a duplex retina (Table 1). Physiological and behavioral experiments established that some species possess day-vision mechanisms and even color vision (for review see Gruber and Cohen 1978). Behavioral studies showed that sharks such as the lemon and bonnethead were active in the daylight hours (Myrberg and Gruber 1974; Gruber and Myrberg 1977). So it is clear that visual function in sharks needed reevaluation in the light of these new findings.

Table 1. Distribution of duplex retinas in the elasmobranchs: recent studies.¹

Taxa	Source	Rod-cone ratio/remarks
Squaliformes		
Orectolobidae		
<i>Ginglymostoma cirratum</i>	Hamasaki and Gruber (1965)	7-12:1
<i>G. cirratum</i>	Wang (1968)	13:1
Alopiidae		
<i>Alopias vulpinus</i>	Gruber et al. (1975)	5:1
Lamnidae		
<i>Carcharodon carcharias</i>	Gruber et al. (1975)	4:1 electron optics
<i>Isurus oxyrinchus</i>	Gruber et al. (1975)	10:1
Carcharhinidae		
<i>Carcharhinus falciformis</i>	Gruber et al. (1963, 1975)	11:1
<i>C. longimanus</i>	Gruber et al. (1975)	10:1
<i>C. plumbeus</i>	Gruber et al. (1975)	13:1
<i>C. perezi</i>	Gruber et al. (1963)	—*
<i>Mustelus canis</i>	Stell and Witkovsky (1973)	100:1
<i>M. canis</i>	Dowling (unpublished observ.)	— electron optics
<i>Negaprion brevirostris</i>	Gruber et al. (1963)	12:1
<i>N. brevirostris</i>	Wang (1968)	12:1
<i>Prionace glauca</i>	Gruber et al. (1975)	8:1
Sphyrnidae		
<i>Sphyrna lewini</i>	Anctil and Ali (1974)	Few cones
<i>S. mokarran</i>	Gruber et al. (1963)	—
Squalidae		
<i>Squalus acanthias</i>	Stell (1972)	50:1 electron optics
Rajaformes		
Rhinobatidae		
<i>Rhinobatos productus</i>	Dunn (1973)	
Torpedinidae		
<i>Narcine brasiliensis</i>	Ali and Anctil (1974)	12:1
Dasyatidae		
<i>Dasyatis akajei</i>	Tamura et al. (1966)	—
<i>D. americana</i>	Gruber et al. (1963)	—
<i>D. navarrae</i>	Niwa and Tamura (1975)	—
<i>D. sayi</i>	Hamasaki and Gruber (1965)	5:1
Paratrygonidae		
<i>Paratrygon motoro</i>	Ali and Anctil (1974)	7:1

* Dashes indicate data not available.

¹ Taken from Gruber and Cohen 1978.

But even at the level of gross morphology it seems unreasonable from the point of view of evolutionary efficiency to expect animals with such unique and in some cases highly developed eyes to possess rudimentary vision.

If the reader accepts the possibility of "good" diurnal vision in sharks, and permits us to use visual data from the lemon shark as a guide, it will be possible to speculate on the visual capabilities of the white shark. Using anatomical data and reports of the natural feeding behavior (this symposium) we suggest that the eye of *C. carcharias* is well developed for diurnal color vision, is not as specialized for nocturnal vision as the eye of the lemon shark and that vision may play a more important role in the life of the great white compared to the lemon shark.

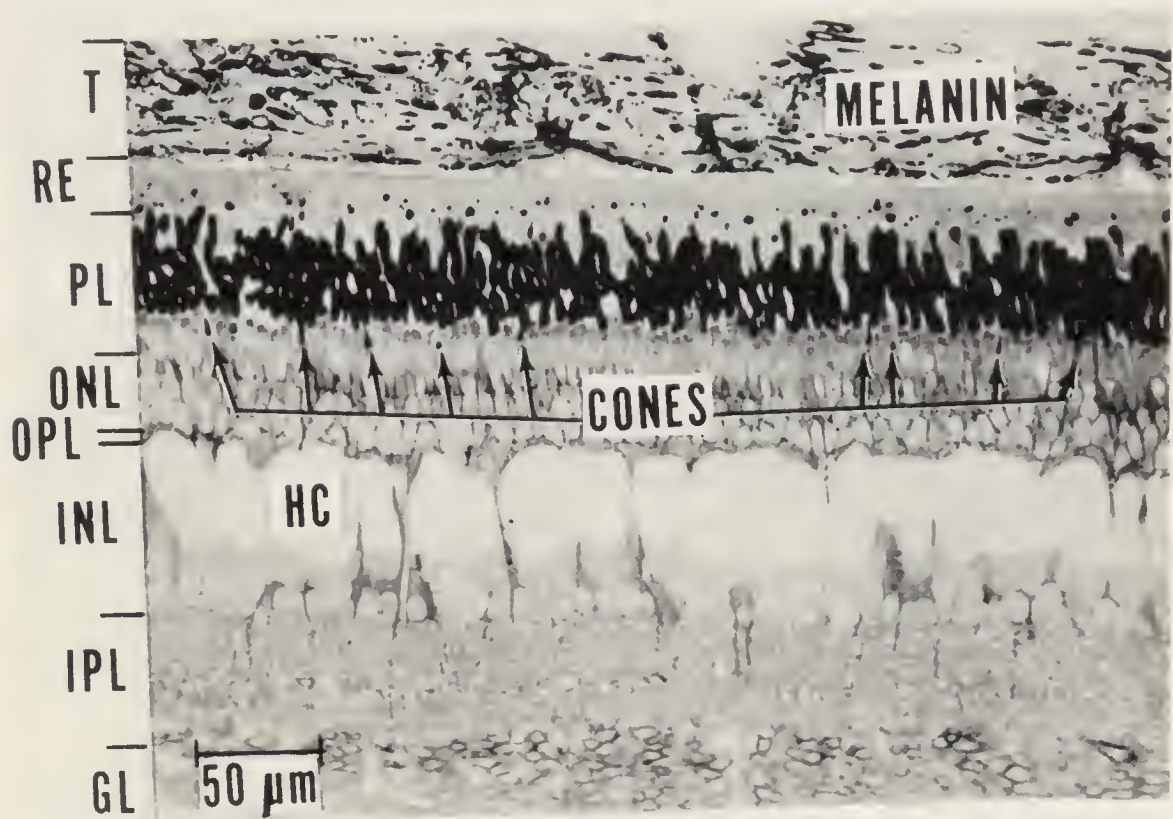


Fig. 1. Light micrograph of the retina of the white shark *C. carcharias*. Transverse plastic section cut at $1.5 \mu\text{m}$ and stained with paraphenyldiamine. Both rods and cones can be seen in the photoreceptor layer. Abbreviations: GL = ganglion cell layer; HC = horizontal cell; INL = inner nuclear layer; IPL = inner plexiform layer; ONL = outer nuclear layer; OPL = outer plexiform layer; PL = photoreceptor layer; RE = retinal epithelium; T = Tapetum.

Material and Methods

Eyes were obtained from two animals on 27 June 1971. The specimens were collected by rod and reel several miles east of Long Island, New York, during the Bayshore Mako Tournament. Eyes of the smaller shark, a 137 cm total length (TL), 19 kg male, were prepared for light microscopy. Eyes of the larger animal, a female of 154 cm TL, 32 kg, were prepared for electron microscopy. Both sharks were young, immature specimens.

By prior arrangement, any angler landing a white shark was instructed to call on the radiotelephone. The biologists, in a high speed skiff, located the broadcast signal with a radio-direction finder and proceeded to the catch boat at full speed. Thus, we were able to remove the eyes from a living (anesthetized) specimen and immediately fix them for electron microscopy.

For electron microscopy, the anterior segment including cornea, lens, ciliary body, and vitreous humor were discarded and small pie shaped pieces of retina ($3 \times 6 \text{ mm}$) attached to the sclera were placed in individual vials of chilled fixative consisting of 5% glutaraldehyde and 0.1 M phosphate buffer. Some sections were directly fixed in osmium tetroxide for one hour and dehydrated through a series of alcohols on the fishing boat. The glutaraldehyde-fixed sections were post fixed in OsO_4 two days later. Sections were embedded in Epon plastic and cut on a microtome with a diamond knife. Thick sections (1.0 to $1.5 \mu\text{m}$) were stained

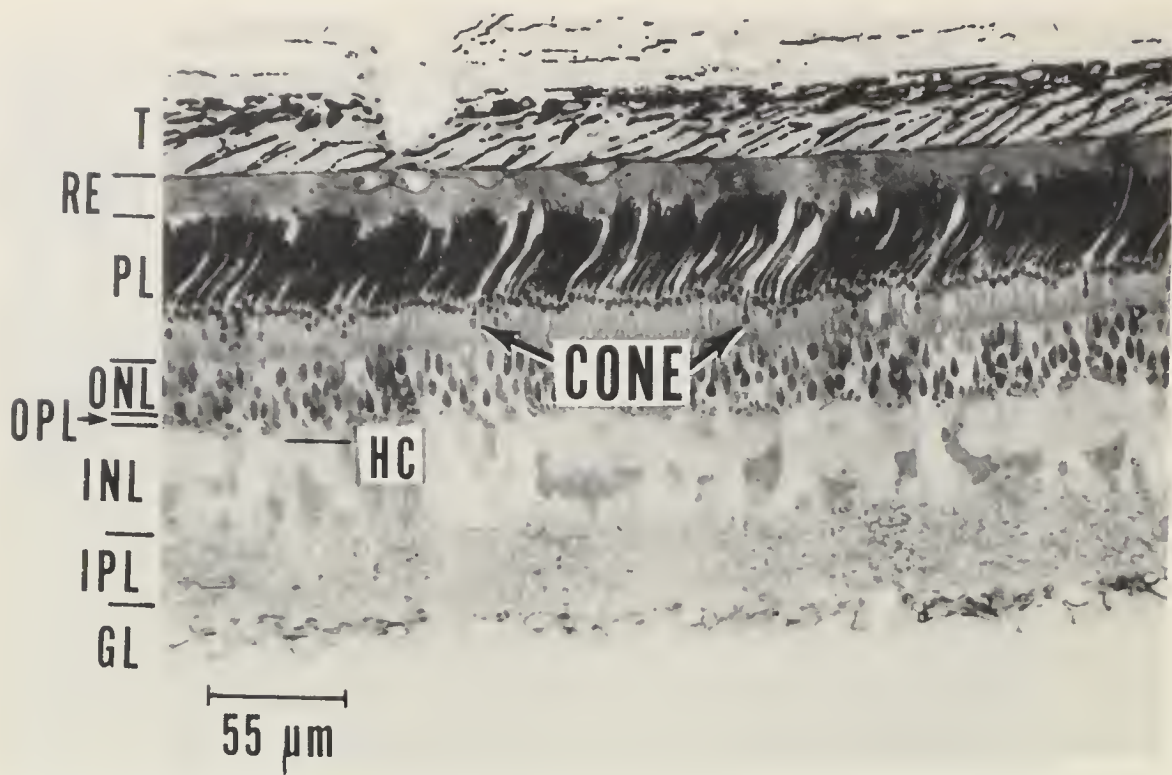


Fig. 2. Light micrograph of the retina of the lemon shark *Negaprion brevirostris*. Histology and abbreviations as in Fig. 1. Note the orientation of the tapetal plates (T layer) relative to the rods and cones (PL layer).

with paraphenyldiamine. Thin sections were stained with uranyl acetate and lead citrate.

Thick sections were viewed and photographed under a Zeiss Photomicroscope II light microscope. Thin sections were viewed under a JEM-7 transmission electron microscope.

For standard light microscopy, eyes were removed from a previously captured white shark, dead for approximately 1 hour. The anterior segment was removed from one eye and slits made in the cornea of the second. Both eyes were fixed in Kolmer's fluid (saturated $K_2Cr_2O_7$ solution, glacial acetic acid, 10% formalin, 4:1:1) for 48 hours, washed in running water, dehydrated, embedded in paraffin, and cut at 10 μm . Sections were stained with Mallory's trichrome, and photographed under a Zeiss Photomicroscope II. Further details can be found in Gruber et al. (1975).

Counts and measurements of the photoreceptors were made in two ways: 1) 22×28 cm photographic prints of the sections were made and dimensions were measured by photographing and printing a calibrated ruled slide at the same magnifications. 2) Measurements were made directly from the slides using an Olympus research microscope with an attached drawing tube. The image of the retina was optically superimposed through the drawing tube onto a Summagraphics "Bit Pad." The digitizing table was interfaced with a DEC Minc 11 computer which was programed to calculate histological dimensions.

Results

The retina of the white shark is organized around the standard vertebrate pattern of seven cellular and two synaptic layers. Between the choroid and retina lies the

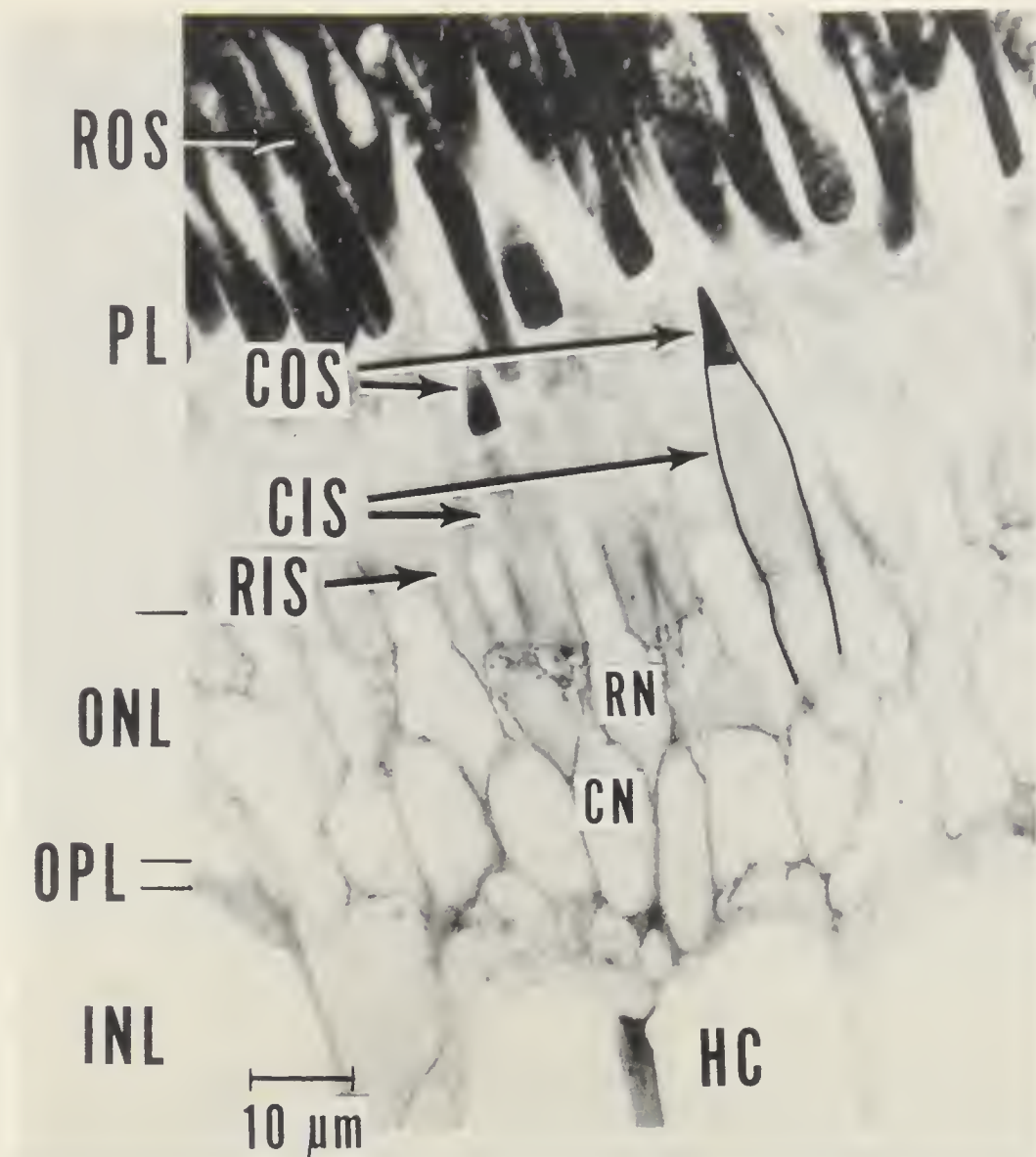


Fig. 3. Light micrograph of the outer layers of the white shark retina showing details of the rods and cones. Abbreviations and histology as in Fig. 1 except higher magnification. New abbreviations: CN = cone nucleus; CIS = cone inner segment; COS = cone outer segment; RN = rod nucleus; RIS = rod inner segment; ROS = rod outer segment.

tapetum lucidum, a tissue composed of endothelial cells and adapted for reflecting light back through the retina. Figure 1 shows that the tapetal plates of the white shark lie parallel to the retina while those of the lemon shark are arranged at an angle of about 45° to the incident light (Fig. 2). Screening pigments consisting of light absorbing melanin granules can be seen between the tapetal plates in both species (Figs. 1 and 2).

The outermost layer of the retina is the retinal epithelium which comprises about 6% of the entire retinal thickness in the white shark (Fig. 1).

The next layer consisting of the outer and inner segments of the rods and cones is the photoreceptor or bacillary layer (Fig. 3). It makes up about 25% of the retinal thickness. The retina of the white shark possesses both rods and cones but their proportions vary in different parts of the retina. For example, in one section of the central retina 5 cones and 49 rods were counted. A section of the same size taken at the periphery was cone-free, but contained 38 rods (Fig. 4). There appears to be a continual increase of cones from periphery to central retina but further

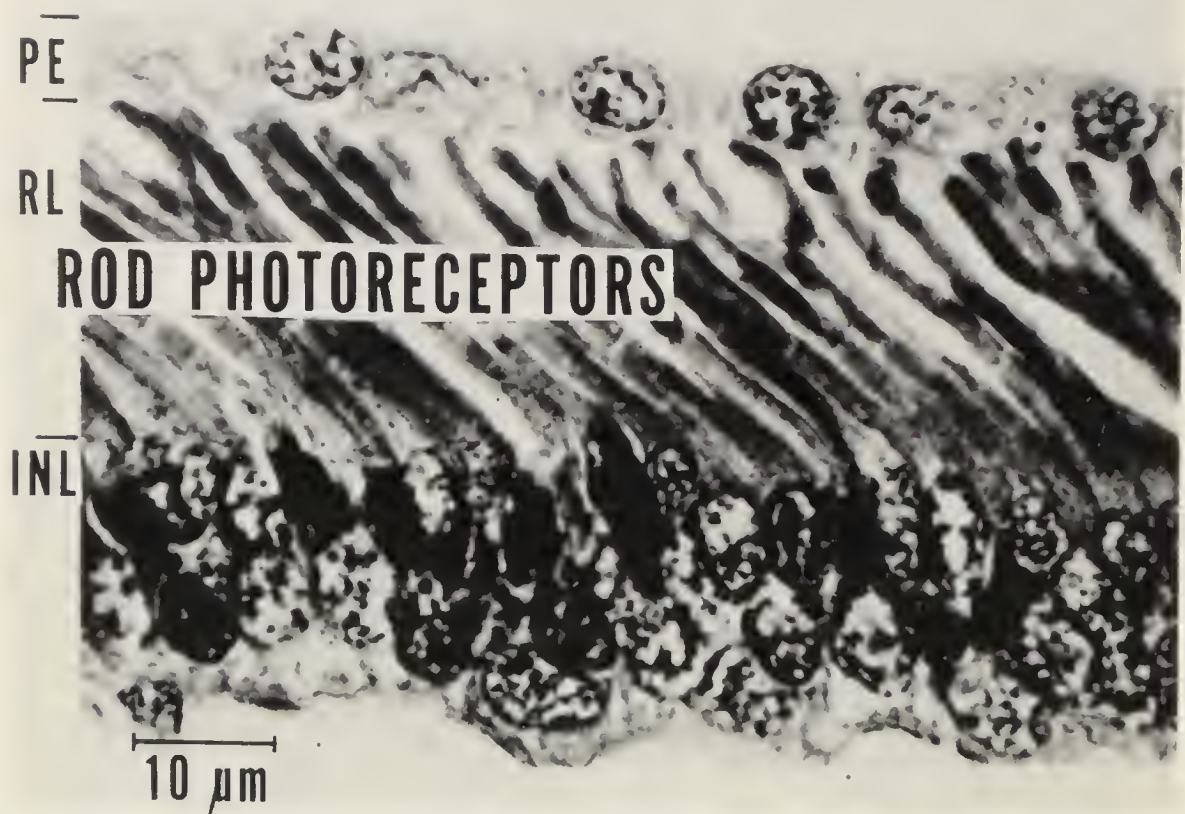


Fig. 4. Light micrograph of the outer layers of the periphery of the white shark retina. Transverse paraffin section is cut at 8–10 μm and stained with Mallory's trichrome. Abbreviations as in Fig. 1. Note the complete absence of cone photoreceptors in the periphery.

studies are needed to quantify the rod : cone ratios. The highest ratio of rods to cones observed in the present study was 10:1 (Fig. 5). Approximately 70 rods and 55 cones were measured in paraffin sections. The rod dimensions were: outer segment = $25.17 \pm .7 \mu\text{m}$ standard error of the mean (SE); inner segment = $20.74 \pm .4 \mu\text{m}$ SE. The cone dimensions were: outer segment $8.44 \pm 1.8 \mu\text{m}$ SE; inner segment $13.29 \pm 1.6 \mu\text{m}$ SE. Table 2 shows these values which have been increased by 30% to account for shrinkage from paraffin embedding. We made independent measurements of photoreceptors in plastic mounted retinas and confirmed that the shrinkage of paraffin section was about 30%.

The outer nuclear layer (ONL) is composed of the cell bodies and nuclei of the rods and cones (Figs. 1–6). We were not able to observe any segregation of rod or cone nuclei into sublayers; however, there were usually two and occasionally three layers of nuclei in the ONL (Fig. 3). The ONL comprises about 10% of the retinal thickness in plastic mounted sections.

The outer plexiform layer (OPL) contains synaptic connections between the photoreceptors and neurons of the inner nuclear layer (INL). It is bounded on the distal side by the ONL and on the proximal side by the INL (Fig. 3). The OPL accounts for about 1% of the retinal thickness in the white shark.

The INL contains cell bodies of the horizontal, bipolar, amacrine and a few percent of the ganglion cells (Fig. 1–6). This is the thickest layer encompassing some 26% of the retina in the white shark. This layer is remarkable for the size of the horizontal cells (HC) which are in turn arranged into three layers (Fig. 6). HCs having the largest cross-sectional area occupy the outermost layer (Fig. 1). In a sample of 10 white shark HCs the largest cross-sectional dimension averaged

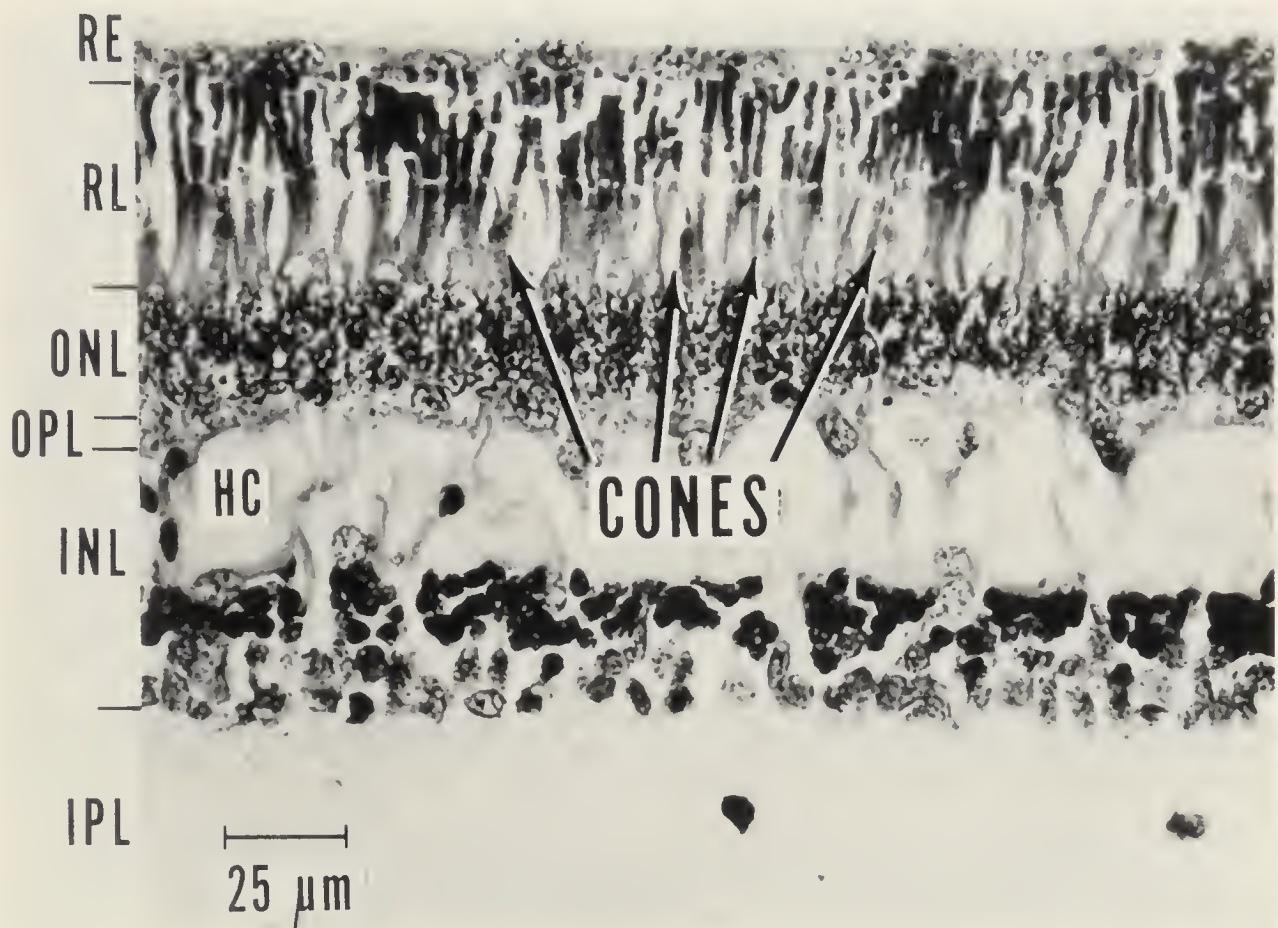


Fig. 5. Light micrograph of the central retina of the white shark. Histology as in Fig. 4 but lower magnification. Abbreviations as in Fig. 1. At least 6 cone photoreceptors can be seen in RL.

42.4 μm . This is about $1.5\times$ the size of lemon shark HCs and many times greater than HCs of other vertebrates. The cell bodies of the other neurons of the INL lie beneath (proximal to) the horizontal in a layer of 4 to 5 cells. Some neurons (presumably bipolars) send processes to the OPL between adjacent HCs.

The inner plexiform layer (IPL) contains synapses of bipolar, amacrine, and ganglion cells (Figs. 1, 2, and 6). It is an extensive layer in the white shark comprising some 17% of the retinal thickness. The IPL is unremarkable except for the few displaced ganglion cells found therein (Fig. 6). The size distribution of normal and displaced ganglion cells is similar with 10–20 μm diameter cells predominating in both (Table 3). However, giant ganglion cells—up to 50 μm diameter—are often displaced into the IPL (Fig. 6).

The most proximal (i.e., functionally closer to the brain) layer of the retina is the ganglion cell layer (Figs. 1, 2, and 6). The cell bodies and axons of retinal ganglion cells can be found there up to the vitreal-retinal boundary. The myelinated axons of the ganglion cells coalesce to form the optic nerve. Table 3 shows the size distribution of ganglion cells in the retina of the white shark. The ganglion cell layer in the white shark is about twice as thick as its counterpart in the lemon shark and comprises 15% of the retinal thickness (compare Figs. 1 and 2).

Discussion

Based upon an earlier examination of the retina (Gruber et al. 1975; Gruber and Cohen 1978) we believe that the white shark is a diurnal species. More detailed

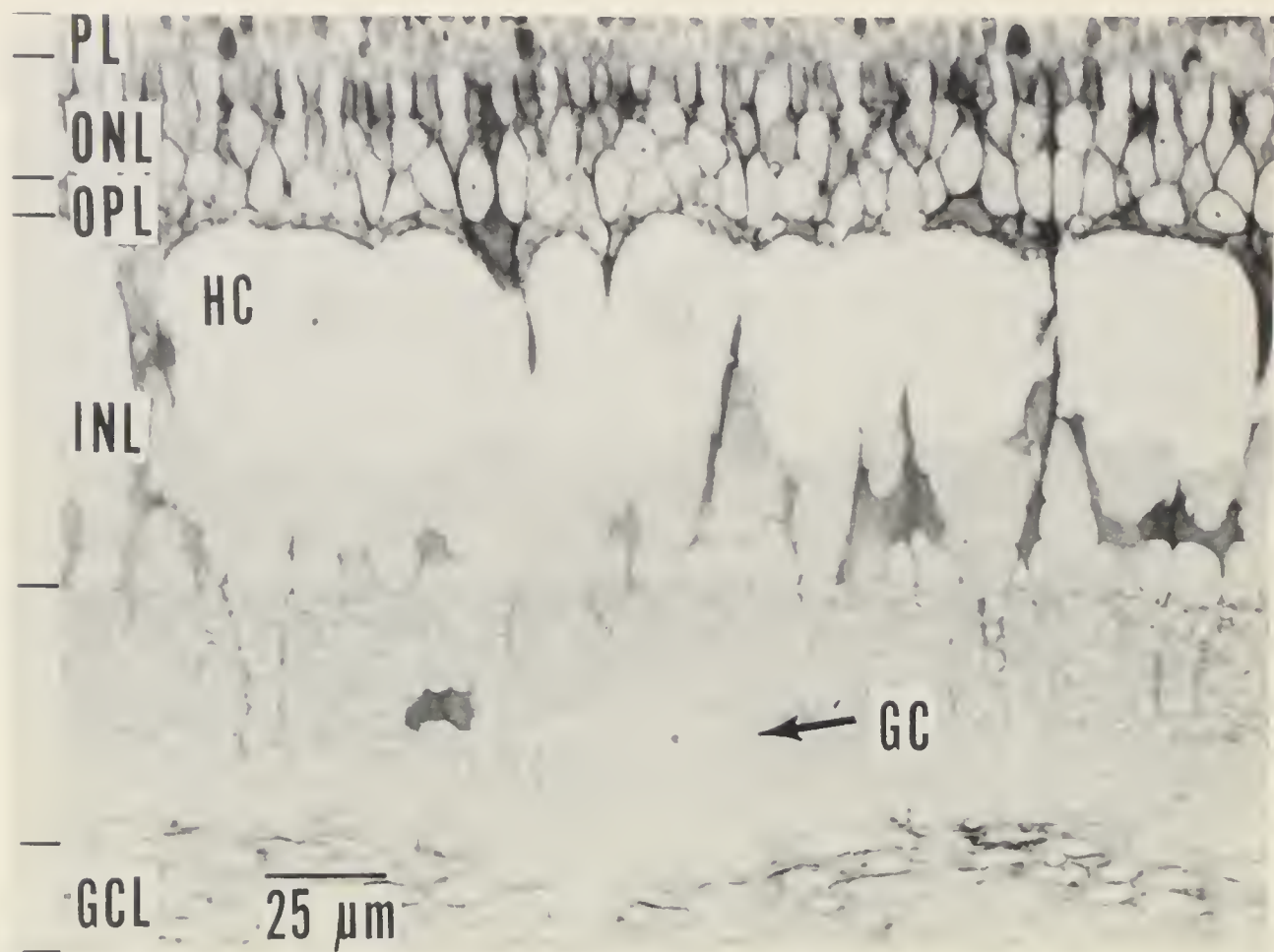


Fig. 6. Light micrograph of the inner layers of the white shark retina. Histology and abbreviations as in Fig. 1. Note the giant displaced ganglion cell (GC) in the IPL.

observations made during the present study have supported our thesis that the eye of the white shark is well adapted for day vision.

Besides our earlier work, the only other report on lamnid eyes appears to be that of Rochon-Duvigneaud (1943). He showed that the retina of the mackerel shark *Lamna cornubica* (= *nasus*) is amply provided with cones and possesses a tapetum very similar in structure to that of the white shark. Thus, the most important criterion for diurnal vision, the possession of cone photoreceptors has been confirmed in all genera of the Lamnidae, i.e., in the white, mackerel, and shortfin mako *Isurus oxyrinchus* (Rochon-Duvigneaud 1943; Gruber et al. 1975; Gruber 1977; Gruber and Cohen 1978).

The most important new evidence favoring diurnality in the white shark is the finding of increased numbers of cone receptors toward the central retina. Such an increase suggests that the retina is divided into areas specialized for diurnal and nocturnal vision. As in humans and some other vertebrates the periphery functions best during the night or other dim light conditions. In fact, the periphery of the white shark is devoid of cones and cannot function in bright light. Conversely, the central retina, more directly on the optical axis appears to be adapted for diurnal, acute, color vision. The increase of cones in the central retina is reminiscent of a retinal structure known as the *area centralis*. The *area centralis* is usually characterized by a dense packing of photoreceptors in the central retina. The increased number of cones in the white shark central retina might represent a rudimentary *area centralis*. The only other mention of an *area centralis* in

Table 2. Comparison of retinal dimensions in white and lemon sharks.

	Retinal thickness ¹	Pigment epithelium	Photoreceptor layer				Outer nuclear layer	Outer plexiform layer	Inner nuclear layer	Inner plexiform layer	Ganglion cell layer
			Rod outer segment	Rod inner segment	Cone outer segment	Cone inner segment					
Great White Shark	284.5 (100)	17.0 ² (6)	38.0 ³ (13)	31.4 (11)	12.8	20	25.9 (9)	3.5 (1)	73.4 (26)	47.4 (17)	44.0 (15)
Lemon Shark	212.25 (100)	16.9 (8)	43.2 (20)	23.7 (11)	7 ⁴	5	25.7 (12)	5.5 (2)	42.9 (21)	41.5 (20)	18.4 (8)

¹ Most data based on the average of seven different measurements from both species. All measurements are μm . Numbers in parentheses are % of retinal thickness.

² Data based on two measurements.

³ Data from white shark photoreceptors based on approx. 50 measurements but corrected for shrinkage (see text).

⁴ Data from lemon shark cones based on 4 measurements.

elasmobranchs is that of Franz (1931). He observed a thickening in the retina of *Mustelis* characterized, not by densely packed receptors, but rather by an increase of ganglion cells.

The ratio of receptors to ganglion cells in the central retina was 1:7. In the periphery, the receptor-ganglion cell ratio was 1:38 and no cones were evident. This is further evidence indicating that the central retina of the white shark is adapted for diurnal vision. The increased convergence of rods onto ganglion cells at the periphery is a nocturnal specialization and is predictable since only rod receptors are found there.

We have compared the retina of the white shark to that of the lemon shark because of convenience since we have much retinal material from our earlier studies on lemon sharks. However, this comparison does not provide a great contrast in retinal types. Both retinas are amply provided with cone receptors and the retinal layers are similar (Table 2). Similarity in retinal morphology is expected since both species are active during daylight hours. For example, we observed that lemon sharks can be captured on hook and line equally well by day or night. Also, aerial observations and telemetry-tracking confirmed that lemon sharks are active in the daytime (Nelson and Gruber 1983; Gruber 1982). From information presented at this symposium, the white shark appears to be diurnally active and has been observed to feed in the daytime. However, the lemon shark may be more nocturnal than the white shark. Measures of its metabolic rate (Nixon and Gruber 1983) indicate that both activity and oxygen consumption of the lemon shark peak shortly after midnight. Also field observations suggest that the lemon shark is slightly more active at night (Gruber et al. 1984).

Table 3. Size frequency of normal and displaced ganglion cells in the retina of the white shark.

	Cell diameter (μm)				
	0-10	11-20	21-30	31-40	41-50
Normal	8	32	6	2	0
Displaced	1	6	2	1	2

Comparison of the retinas of both species provided two further pieces of evidence suggesting that the lemon shark was more visually adapted to dim light relative to the white shark. These concerned photoreceptor length and tapetal structure.

Receptor measurements in both shark species showed that the lemon shark has ROSs nearly 10% longer than those of the white shark. We interpret this finding as evidence that the lemon shark's retina is more nocturnally organized than the retina of the white shark. A second, more tenuous indication concerns the ONL. The ONL of the lemon shark contains three to four rows of receptor nuclei whereas the white shark has two, and occasionally three rows of receptor nuclei (compare Figs. 1 and 2). This suggests that receptor density is greater in the lemon sharks. Since the ratio of rods to cones is similar in both species the existence of 30–50% more receptors in the lemon shark retina should provide greater visual sensitivity and thus favor nocturnal vision in this species. However, only by directly comparing flat mounted retinas on an equal area basis can this question be settled.

The second important observation is that the *tapetum lucidum* appears to be better organized in the lemon shark. The *tapetum lucidum* is an optical structure organized to reflect light back through the retina once it has entered the eye. The tapetal plates of the lemon shark appear to be aligned differently in different parts of the eye. Figure 2 shows that the guanine plates are set at an angle to the retina. This organization is similar to that found in the closely related blue shark *Prionace glauca*. Denton and Nicol (1964) demonstrated that tapetal plates throughout the blue shark eye change their angle of orientation toward the central retina and remain roughly perpendicular to the light that can reach them. Thus, at night, light is reflected back through the optical path of entry, significantly reducing glare from otherwise tapetally scattered light.

In the white shark (Fig. 1) tapetum plates appear to be perpendicular to the retina everywhere in the eye. Thus the white shark tapetum is apparently not as well organized for optical processing as that of the lemon shark. We interpret this finding as further evidence that the lemon shark eye is more nocturnally adapted than that of the white shark.

To summarize: We have shown that the retina of the white shark has the structural organization to function both at night and during the daytime. The most important finding in this study is that the number of cone photoreceptors increases from none at the *ora serrata* and extreme periphery to many in the central retina. This suggests a functional difference: The periphery is adapted for scotopic vision; the central retina is adapted for photopic vision. Comparison of the retinas of lemon and white shark indicated that the white may be a more diurnal species. Indeed, physiological data show that the lemon shark is quite nocturnal.

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Through his extensive records, Jack Casey of NMFS confirmed our identification of the two white shark specimens studied and for this we are grateful. Finally, we thank Ruth Perou for critically reading and correcting the manuscript and Shelley McCarthy for providing the typescript.

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Hematology and Cardiac Morphology in the Great White Shark, *Carcharodon carcharias*

Scott H. Emery

Abstract.—Hematology and cardiac morphology in the great white shark, *Carcharodon carcharias* by Scott H. Emery. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. The great white shark (*Carcharodon carcharias*) is warm-bodied. Hemoglobin and hematocrit values for white sharks are higher than the values reported for most elasmobranchs and teleosts and similar to the levels found in many mammals and birds. Cardiac morphology in the white shark more closely parallels that of warm-bodied tuna than of non-lamnoid elasmobranchs. Heart and blood parameters in the white shark reflect the greater metabolic requirements of this warm-bodied species when compared to ectothermic elasmobranchs.

The great white shark, *Carcharodon carcharias*, has been shown to possess large, cutaneous, lateral blood vessels and countercurrent heat exchangers in the swimming musculature, similar to those found in the shortfin mako (*Isurus oxyrinchus*) and porbeagle (*Lamna nasus*) (Carey and Teal 1969). In a telemetry experiment Carey et al. (1982) found muscle temperatures of a white shark to be as much as 6°C above water temperatures, suggesting that this species, like other lamnids, is functionally endothermic. The endothermic condition strongly suggests, in turn, that this species may exhibit enhanced metabolic capacities in comparison with ectothermic species of vertebrates.

The aerobic metabolic scope of a fish is determined at the point where energy demands exceed the supply of oxygen. The oxygen supply capabilities are limited by one or more of the following factors: the amount of oxygen transferred from the water through the gills per unit time; the carrying capacity of the blood for oxygen; and the ability of the circulatory system to deliver oxygen to the actively metabolizing tissues. In this paper, I concentrate on the latter two topics, by presenting information on aspects of erythrocyte hematology and cardiac morphology related to aerobic metabolism. The hematological factors discussed include hemoglobin levels (the major carrier of oxygen in the blood) and hematocrit levels, along with size determinations of mature erythrocytes. The information relating to the circulatory system concentrates on the relative size, shape, and muscularity of the cardiac pump, all of which have been used as indirect indicators of relative activity levels within different major vertebrate groups (Stahl 1965; Tota 1978; Schmidt-Nielsen 1979).

Methods

Sharks were obtained from June 1978 until August 1983 from three sources: sportsmen's catches landed during fishing tournaments; commercial gill netters; and fish capture via harpoon; all from Long Island, New York. Each fish was weighed and fork length recorded at dockside.

Unclotted blood samples were obtained from 5 individual sharks. Samples were collected in 20 ml syringes using 18 gauge needles inserted into the sinus venosus

following careful opening of the pericardial cavity. Blood was immediately transferred to standard EDTA tubes.

Hearts from 17 white sharks were carefully removed from the pericardial cavity, and gently massaged to remove excess blood. Blood and hearts were packed in ice pending transport to the laboratory for subsequent analyses. All blood samples were analyzed within 8 hours.

Hemoglobin (hgb) values were measured spectrophotometrically (as whole blood) on either a Model D or S plus Coulter Counter, hematocrits (hct) on either a MSE or IECMB microcentrifuge (spun 3 minutes at 11,000 rpm). Mean corpuscule hemoglobin concentrations (MCHC) were calculated by the formula:

$$\text{MCHC} = \frac{\text{Hemoglobin (g/100 ml)}}{\text{Hematocrit (vol \%)}} \times 100$$

Blood smears were made (Wright's Stain), and mean mature erythrocyte sizes measured under the oil immersion (100 \times) lens of a compound microscope with an ocular micrometer. A total of 100 individual cells were measured (25 cells from four individuals) to calculate the mean size for erythrocytes.

Heart aortas were carefully trimmed to the conus artericusus, and the heart was weighed to the nearest 0.05 g, with and without the atrium.

To estimate heart chamber size (ventricular volume), fresh ventricles were carefully filled with water injected through the atrioventricular opening, after the proximal portion of the conus had been clamped closed. Water was injected until the ventricular valves closed shut. The ventricle was placed in an empty beaker and the clamp removed. The heart was inverted and gently massaged to remove the major part of the water from the inner, spongy tissue layer. Water volume was measured in graduated cylinders. The entire process was repeated 3 times for each heart and a mean value taken. Variations between readings were never larger than 10% of the mean value.

The thickness of the outer cortical and inner trabecular heart muscle was measured on ventricles preserved in 10% buffered formalin. Estimates of relative amounts of each layer based upon measurements of tissue section surface areas using the techniques of Santer and Greer Walker (1980) provided only qualitative

Table 1. Hematological parameters, *C. carcharias* (\pm SD).

Fish wt. (kg)	Hemoglobin (g/100 ml)	Hematocrit (vol %)	MCHC %	Mature erythrocyte (μ m)
18.1	13.8	36.0	38.3	21.8 \pm 1.9 \times 16.7 \pm 1.5
28.6	16.2	49.0	33.1	21.2 \pm 1.8 \times 15.9 \pm 1.5
141.5	8.2*	22.0*	37.3	21.1 \pm 1.3 \times 16.6 \pm 1.1
170.1	14.3	36.0	39.7	21.5 \pm 1.5 \times 16.5 \pm 1.0
183.7	15.2	37.0	41.1	—
	13.5 \pm 2.8	36.0 \pm 9.0	37.9 \pm 3.0	21.4 \pm 1.6 \times 16.4 \pm 1.3

* Sample may have been diluted with pericardial fluid.

Table 2. Comparative hematology of select vertebrates (\pm SD).

Organism	Hgb (g/100 ml)	Hct (vol %)	MCHC (%)	Erythrocyte size (μ m)	Reference
<i>C. carcharias</i>	13.5 \pm 3.1	36.0 \pm 9.6	37.9 \pm 3.0	21.4 \pm 1.6 \times 16.4 \pm 1.3	Johansson-Sjobeck & Stevens (1976)
<i>Prionace glauca</i>	5.7 \pm 0.3 (SE)	27.7 \pm 1.8 (SE)	25.7	22.8 \times 15.0	
<i>Squalus acanthias</i>	3.8	18.9	20.1	22.7 \times 15.2	Kisch (1951)
<i>Thunnus thynnus</i>	14.9-19.8	41.0-52.8	29.2-32.8	10.5 \times 7.5	Alexander et al. (1980)
<i>Cypselurus oligolepsis</i>	10.7	34.5	21	9.6 \times 7.2	Glazova (1976)
<i>Lophius piscatorius</i>	3.1	16.8	18.5	13.6 \times 9.6	Kisch (1951)
Frog	7.8	29.3	27	24.8 \times 15.3	Wintrobe (1974)
Alligator	8.2	30	27	23.2 \times 12.1	Wintrobe (1974)
Pigeon	12.8	42.3	30	13.2 \times 6.9	Wintrobe (1974)
Dog	13.6 \pm 1.6	44.3 \pm 1.4	31.0 \pm 1.4	7.0	Wintrobe (1974)
Human (female)	14.0 \pm 2.0	42.0 \pm 2.0	34 \pm 2	7.2-7.9	Wintrobe (1974)
Chimpanzee	12.05 \pm 1.88	38.32 \pm 5.47	31.3 \pm 2.5	7.4	Wintrobe (1974)

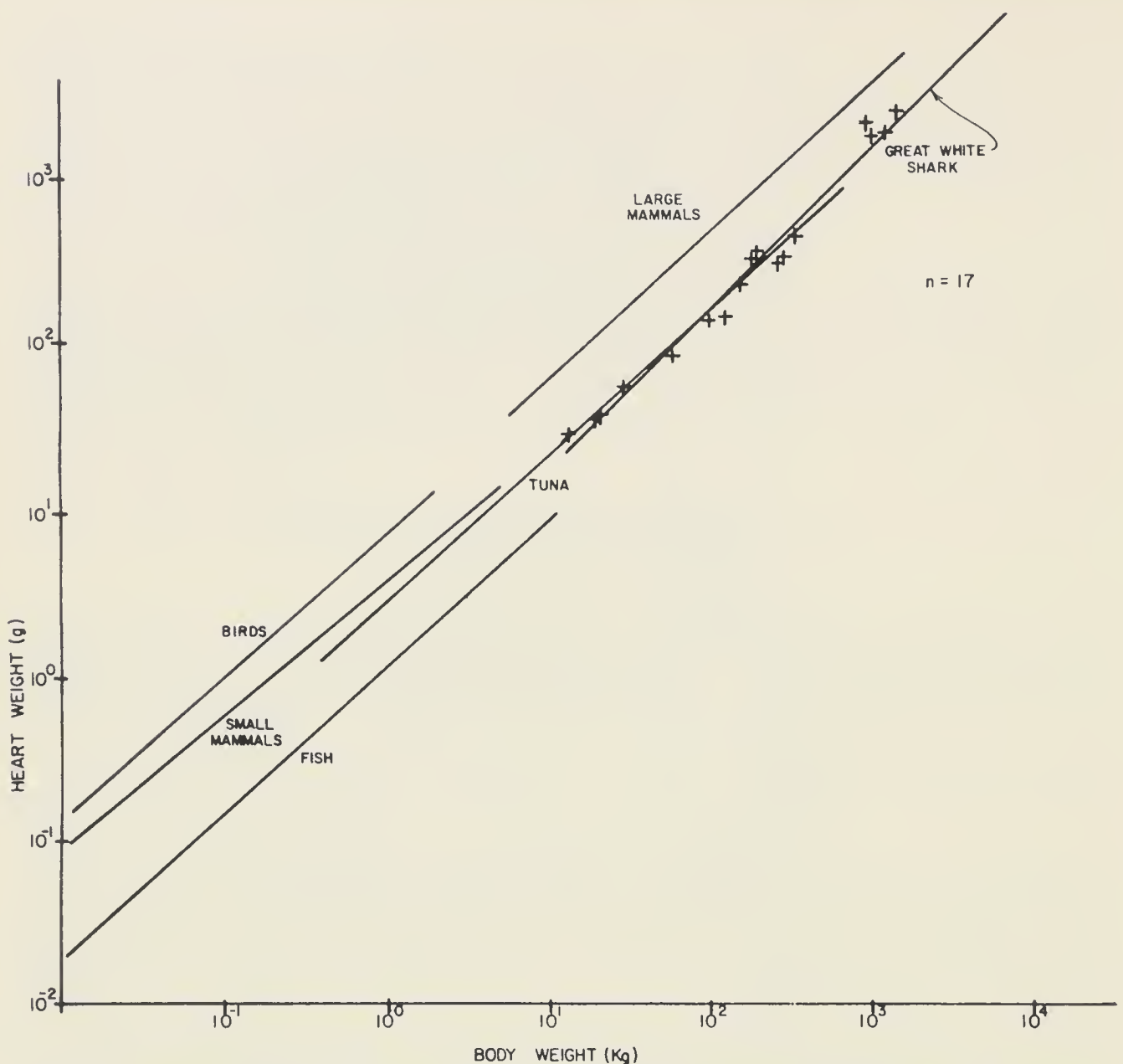


Fig. 1. The relation between heart weight and body weight for different groups of animals. Regression line equations, with $y = \log_{10}$ heart weight (g), and $x = \log_{10}$ body weight (kg) are as follows: Birds: $y = 0.89x + 0.93$; large mammals: $y = 0.87x + 1.02$; small mammals: $y = 0.85x + 0.58$; tuna $y = 0.90x + 0.47$; sea fish $y = 0.89x + 0.08$ (Poupa et al. 1981). Great white shark: $y = 0.98x + 0.29$ ($n = 17$; $r = 0.99$).

ratios, which were largely unreproducible. Sections run through graded ethanol dehydrations in preparation for staining exhibited high levels of tissue shrinkage, rendering results obtained suspect. Sections cut directly from formalin-preserved specimens exhibited minimal tissue shrinkage, but the lack of visual contrast between the outer and inner layers precluded anything approaching precise surface area determinations.

A satisfactory estimate of the amount of cortical and trabecular muscle was obtained by injecting a solution of methylene blue stain into 11 formalin-preserved ventricles (conus again clamped shut) so that the dye perfused the inner spongy tissues thoroughly. Excess stain was removed through the conus and the ventricle sectioned transversely at the level of the atrioventricular junction (Santer and Greer Walker 1980). The use of the dye, injected in a way mimicking *in vivo* blood flow into the ventricle, resulted in a section exhibiting a clear line of demarcation between the inner layer (dark blue) and the outer layer (unstained).

Table 3. Outer cortical tissue layer/inner spongy tissue layer ratios from the heart ventricle of *C. carcharias*.

Fish wt. (kg)	Tissue surface area ratio (%)
12.1	42.6
17.7	40.5
28.6	26.7
54.2	41.4
95.9	31.6
170.1	26.7
183.7	42.5
285.8	39.2
287.1	40.5
941.2	27.8
1084.1	36.8
Mean \pm SD	36.0 \pm 6.5

Surface areas were determined from tracing photographs of the sections using a Lasico Model N-30 Planimeter.

Results and Discussion

Hemoglobin levels in 5 white sharks ranged from 8.2 g/100 ml to 16.2 g/100 ml, with a mean value of 13.5 ± 3.1 (SD) g/100 ml (Table 1). Hematocrits ranged from 22.0 to 49.0 vol %, with a mean of 36.0 ± 9.6 (SD) vol %. MCHCs had a mean of 37.9 ± 3.0 (SD) %. These values are higher than have been reported for other species of elasmobranch fish to date (Glazova 1976; Johansson-Sjoberck and Stevens 1976; Kisch 1951; Larsson et al. 1976). Mean sizes of mature erythrocytes (21.4 ± 1.6 (SD) \times 16.4 ± 1.3 (SD)) are within the reported ranges for elasmobranchs (Saunders 1966a, b; Kisch 1951).

Hematological parameters from selected elasmobranch and teleost fishes, amphibians, reptiles, birds, and mammals are presented in Table 2 to facilitate comparisons between major vertebrate groups. White shark hemoglobin and hematocrit levels are similar to those found in mammals, birds, and warm-bodied tuna. Few ectothermic vertebrate species exhibit values as high. These results provide evidence that the oxygen transport capabilities of the white shark may be within the ranges documented for large mammals and tunas. Gibson and Carey (1982) propose that high hemoglobin levels may be a necessary part of the temperature elevating mechanism in large fishes like tunas and lamnid sharks. My results for the white shark appear to support this hypothesis, though the total number of large teleosts and elasmobranchs examined to date is too scanty for definite conclusions.

Results of the heart weight to body weight analysis are presented in Figure 1, along with regression lines for other vertebrate groups, adopted from Poupa et al. (1981). The slopes of the regression lines for all groups except the white shark are essentially parallel (0.85–0.90), with the heart weights of the warm-bodied groups being relatively larger than for those of small sea fishes. The slightly steeper slope of the white shark regression line (0.98) is likely a function of the relatively small sample size involved (17). Carey et al. (1985) have shown that the slope of the regression line for the Atlantic shortfin mako is more in keeping with those

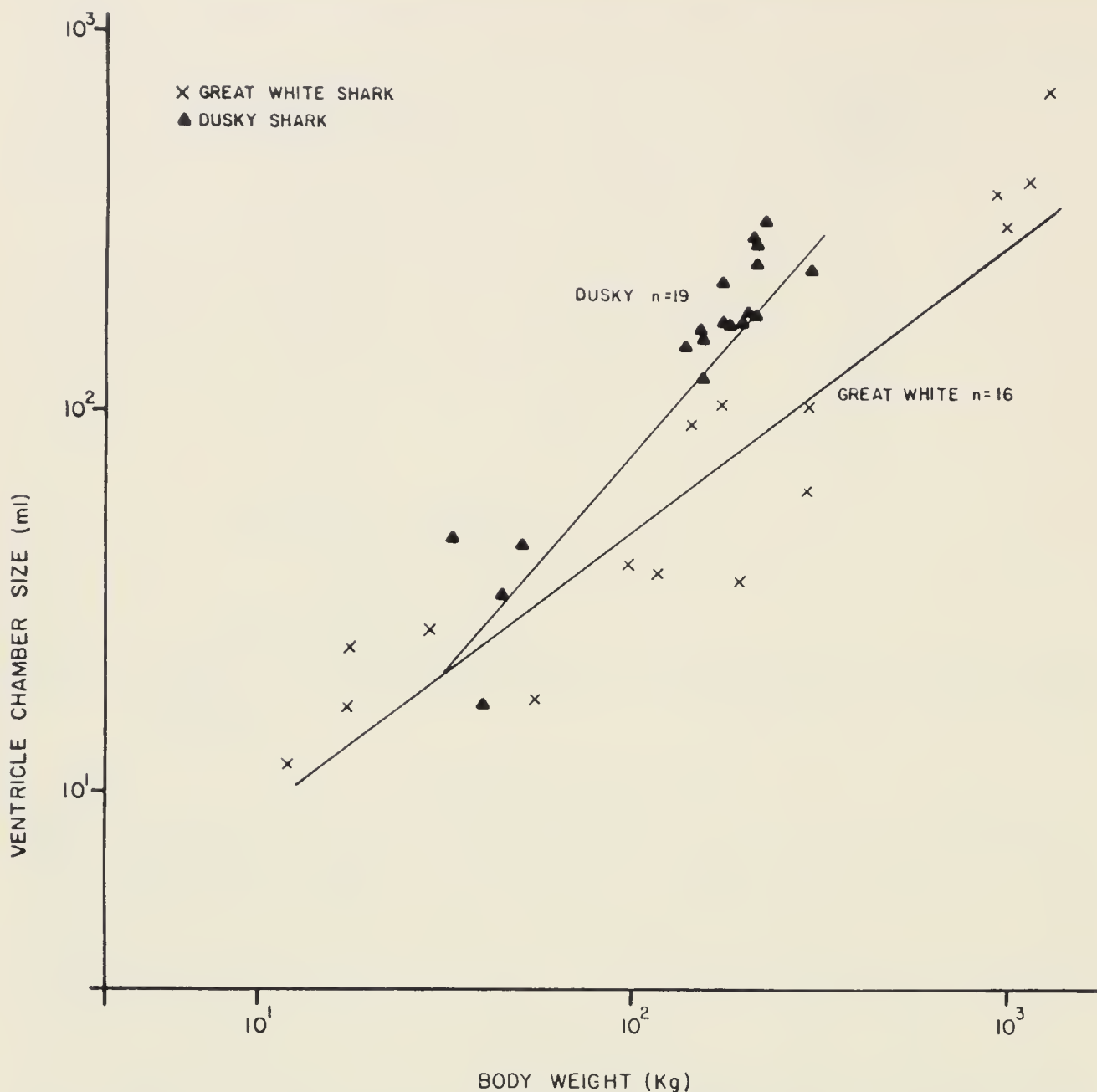


Fig. 2. The relation between heart ventricle chamber size and body weight for the great white shark and the dusky shark. Regression line equations, with $y = \log_{10}$ heart ventricle chamber size (ml) and $x = \log_{10}$ body weight (g) are as follows: Dusky shark: $y = 1.18x - 3.91$ (no. = 16; $r = 0.94$). White shark: $y = 0.77x - 2.13$ (no. = 19; $r = 0.94$).

of the other groups shown in Figure 1. It is evident from Figure 1 that the heart of the white shark is larger than are the hearts of most fishes at a given body weight. Stahl (1965) has demonstrated that more active species of mammals exhibit larger hearts than less active species. Poupa et al. (1981) have demonstrated a similar difference in the heart sizes of highly active bluefin tuna in comparison with other species of marine teleosts. Larger hearts, therefore, appear to be a general characteristic of more active species of vertebrates.

Perhaps of greater importance to the fish than actual ventricular mass are the relative muscularity and shape of the cardiac pump. High metabolic rates characteristic of endotherms necessitate a more highly developed vascular system for delivery of blood to the tissues. Such vessels must be small (arteriole/venule to capillary-sized) to effectively transfer oxygen. Consequently, resistance to blood flow is potentially greater in endotherms than in ectotherms. This increased resistance must be overcome by the power of the cardiac pump.

All elasmobranchs and many teleosts possess a ventricle composed of two distinct tissue layers: an outer cortical layer, receiving oxygen-rich blood from the gills via the coronary artery; and an inner, trabeculated (spongy) layer receiving its major supply of oxygen from oxygen-poor blood returning from the tissues (Satchell 1971). It is the outer layer which supplies most of the contractile force during systole. Hence, the relative amount of cortical to spongy layer will be larger in more active species of fish. Tota et al. (1983) have qualitatively estimated cortical to spongy layer surface area ratios in tuna ventricles to be greater than 35 to 40%, well in excess of the estimates made by Santer and Greer Walker (1980) for a large number of non-tunas. Cortical to spongy layer ratios of the ventricles from 11 white sharks averaged 36.0 ± 6.5 (SD) (Table 3). Consequently, it would appear that white sharks do exhibit an unusually thick, muscular ventricle, similar to the ventricles of the endothermic tunas. This expanded development of the cortical layer is qualitatively similar to that seen in the left ventricle of the mammalian heart (Tota 1978).

The shape of the ventricle is known to be important in determining its ability to generate force. To maintain a given ventricular pressure a narrow chamber (small volume) requires less myocardial tension than would a more rounded chamber (La Place's Law, from Tota 1978). My co-workers and I are presently investigating chamber sizes (ventricular volumes) in a number of pelagic elasmobranch species. To our knowledge, there are no published accounts of chamber sizes of fishes available for comparison from the literature. In Figure 2, I present a log/log plot of ventricular volume to body weight in white sharks, along with preliminary data from our study of chamber size in the dusky shark (*Carcharhinus obscurus*) a large, pelagic, but ectothermic shark species. At a body weight of 10^2 kg, \hat{Y} (estimated ventricle chamber volume) of the dusky shark is 97.7 ml, almost twice the \hat{Y} for the great white shark (52.5 ml). Over a wide range of body sizes, ventricular volumes in the white shark are much smaller than ventricular volumes for similar sized dusky sharks, suggesting that the white shark's ventricle is more characteristic of a high-pressure pump, better adapted for maintaining the large ventricular pressures found in endotherms.

The great white shark has proven to be, so far at least, impossible to maintain in captivity. Consequently, it may be a long time before any direct studies of metabolic rates and scope are conducted on this species. In the absence of such physiological information, it is necessary to turn to comparative studies of morphology and erythrocyte hematology to gain insight into this species' relative metabolic capacities. The large heart of the great white in comparison with most poikilothermic vertebrates is one indirect indicator of a highly active species. The expanded development of cortical muscle layer within the ventricle of the white shark is similar to the situation seen in the warm-bodied tunas, as well as in mammals and birds and is a second indirect indicator of a high energy physiology. The shape of the ventricle, as evidenced by chamber size measurements, is indicative of an organ adapted to a physiology designed to function under high blood pressures characteristic of endotherms. And, perhaps most significantly, hemoglobin and hematocrit levels in the white shark are equal to, and in some instances greater than, the average values found in a number of mammals and birds. Taken together, these characteristics are suggestive of a high resting metabolic rate and large aerobic metabolic scope, more similar to those of mammals and birds than to most teleost or elasmobranch fishes.

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Feeding Ethology of the White Shark, *Carcharodon carcharias*

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Abstract.—Feeding ethology of the white shark, *Carcharodon carcharias* by Timothy C. Tricas. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. Approach and attack behaviors of white sharks, *Carcharodon carcharias*, to bait were documented in the field using cinematographic techniques. The five different approach behaviors were: 1) underwater approach, 2) surface approach, 3) inverted approach, 4) normal underwater pass, and 5) side roll.

Feeding attacks made on food items at the surface involved a pronounced elevation of the head and protraction of the upper jaw out of the oral cavity to inflict the bite. The components that form the feeding action are: 1) snout lift, 2) lower-jaw depression, 3) palatoquadrate protrusion, 4) lower-jaw elevation, and a bout-ending 5) head drop. Time for a complete bite (that included a snout drop) averaged .985 s for a 3.5 m (TL) shark, while a bite action (not including the snout drop) was made in a mean time of .443 s. Maximum gape and palatoquadrate protrusion occurred at mean times of .167 and .307 s, respectively. Sharks also occasionally engulfed small bait by simple depression of the lower jaw.

While feeding actions were clearly stereotyped in their sequence of occurrence, significant temporal differences exist between sharks for total feeding-bout time, between acts for each shark, and between acts among sharks. These results are discussed in light of the current paradigms used to distinguish and classify stereotypic behaviors.

A major factor for the evolutionary success of sharks as predators in marine ecosystems is the diversity of feeding mechanisms found within the group. From a morphological standpoint, this functional diversity in feeding is determined largely by the structural characteristics of the upper jaw (palatoquadrate), lower jaw (mandibular), and suspensorium (hyomandibular) cartilages. Because of the relatively simple structure of the elasmobranch jaw, the spatial arrangements of these three components and their articulations to the cranium are also important in the expression of actions that characterize different feeding modes (Moss 1972, 1977).

Almost all previous studies on feeding adaptations in sharks entailed descriptions of skeletal, connective, and muscle tissues from dead specimens (e.g., Luther 1909; Haller 1926), and few have addressed the functional morphology of the shark jaw in contexts other than those used for comparative or phylogenetic applications (e.g., Compagno 1973, 1977). From a behavioral point of view, little is known about jaw movements in relation to predation. Studies that deal with preserved specimens provide only inferential data on feeding mechanics and therefore little is known on sequential and temporal relationships of the structures involved in feeding. In the best known exception, Moss (1972) studied the feeding mechanisms of living and fresh-collected carcharhinid sharks using electrical mus-

cle stimulation and cinematography. He showed that within a species, upper jaw protraction can occur in different ways that relate to feeding on prey of different sizes and disposition. Although the existence of variable feeding modes within species is well known (Springer 1961; Budker 1971; Tricas 1979, 1982) information on behavioral stereotypy for specific feeding patterns is tentative.

This paper presents an ethological analysis of the feeding behavior of white sharks, *Carcharodon carcharias*, and examines the sequential and temporal variability of feeding actions and their components. This species is the largest flesh-eating shark in the world and exhibits feeding displays amenable to close observation and analyses. Its predatory and attack behaviors are of particular relevance since it feeds on a variety of marine mammals (including some endangered species) and is also known to attack humans.

Methods

The feeding behavior of white sharks was documented during January 1980 in waters near Dangerous Reef, South Australia (approximately 136°13'E, 34°47'S). Topside observations were made from the deck of a 20-m-long vessel anchored in 20–30 m of water just off the north shore of the two small islands. Underwater observations were made using scuba and protective steel cages. Water surface temperature was approximately 21°C. Sharks were attracted using tuna and meat by-products as chum. Behaviors associated with feeding were photographed using Actionmaster 500 ciné cameras and 7247 Kodak color reversal film shot at either 24 (normal) or 200 (high speed) frames per second. A more general analysis of the feeding behavior is presented elsewhere (Tricas and McCosker 1984). Additional feeding behaviors were photographed with 35 mm still cameras. To determine sequential and temporal characteristics of the behaviors, frame by frame analyses of movie films were performed on a digital Moviola film editor.

Documented feeding behavior was separated into two groups: 1) behaviors used to approach, and 2) attack patterns used to bite and engulf baits. Qualitative descriptions of approach patterns were obtained by direct observation and review of film footage. Attack behavior was further analyzed by subdivision into acts that composed an attack pattern. The definition of these behavioral subunits was based upon two criteria. First, an act must show points of initiation and termination that could be measured on a temporal scale. Second, and more subjective, was that each act must have appeared to characterize individual neuro-muscular actions. This qualification was based largely on descriptions of muscle control of jaw movements from other studies (e.g., Moss 1972).

Standard parametric and non-parametric statistical tests were performed on data from the film analyses for time durations of the attack behavior and its component acts. For estimates of variability, a coefficient of variation (CV) was generated for durations of feeding bouts and each act.

$$CV = \frac{SD \times 100}{\bar{X}},$$

where \bar{X} = mean duration and SD = standard deviation. A high CV value indicates a relatively high degree of temporal variability for a behavior.

An index of stereotypy (ST) was also determined for feeding action patterns and component acts where,

$$ST = \frac{100}{CV + 1}.$$

This index described the relative degree of temporal constancy for the act or action pattern considered. High values indicate a relatively high degree of stereotypy. The use and limitations of these indices were discussed by Barlow (1977).

Results

Approach Behaviors

Sharks approached baits in five distinct ways depending on bait size, location relative to the surface, and motivational state of the sharks. Three modes were most commonly used to advance on bait floating on the surface.

1) *Underwater approach*.—Most attacks at the surface were made from this approach pattern. In this behavior, sharks swam just below the surface until approximately 1 m from the bait and then attacked by deflecting the head upward and emerging out of the water to either swallow or bite baits.

2) *Surface-charge*.—Sharks often approached bait by swimming partially above the surface. This approach was characterized by a rapid rush towards the bait and created considerable surface disturbance (i.e., splashing) before the attack was actually made.

3) *Inverted approach*.—When advancing towards bait at the surface, sharks often rolled over 180 degrees and swam with ventral side up. Generally, sharks that showed this type of approach were in relatively low states of excitement and had been feeding in the area for some time.

Sharks took submerged bait in two additional approach modes.

4) *Normal underwater pass*.—This approach pattern consisted of swimming below the surface (> 1 m) towards the bait at a normal speed.

5) *Side roll*.—Sharks directly approached baits under the surface, but rolled approximately 60 degrees from normal, took the prey, and returned to an upright swimming attitude.

Ethology of the Attack

Underwater attacks.—Within the various approach modes, sharks exhibited different patterns of attacks on food items once within striking range. In attacks made from approaches to bait suspended beneath the surface (approximately > 1 m), the mouth was opened by a slight elevation of the snout and full depression of the lower jaw. This feeding pattern was relatively subtle and involved no protrusion of the upper jaw. Although most commonly observed underwater, this form of attack was coupled at times with all five different approach modes. Some sharks occasionally displayed upper jaw protrusion during bites made underwater. These usually occurred when sharks vigorously bit large pieces of bait, or snapped their jaws while abreast of the cages.

Surface attacks.—The most aggressive and observable attack behavior occurred when sharks took bait at the surface from underwater or surface-charge approaches. Sharks approached just below the surface until approximately 1 m away

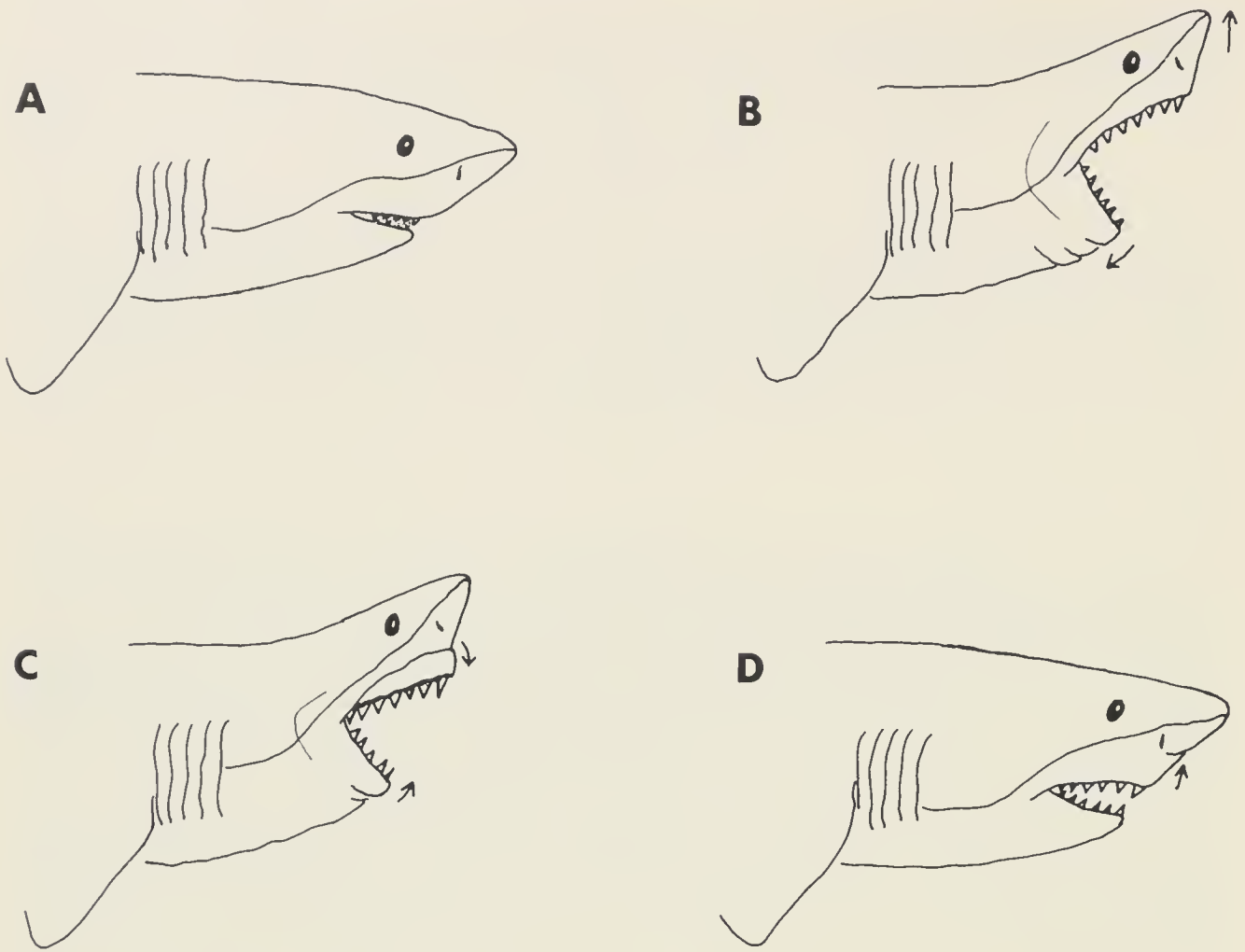


Fig. 1. The surface attack behavior pattern. A) Shark just prior to initiation of feeding action. Snout and lower jaw are at normal resting position. B) Snout lift and lower jaw depression result in maximum gape. C) Palatoquadrate protrusion rotates upper jaw forward and downward exposing upper teeth. Lower jaw moves forward and upward. D) Snout drop, which occurs at the end of a feeding bout, results in return of upper jaw to its normal juxtaposition beneath the cranium. Arrows indicate direction of jaw movements.

from the bait and lunged out of the water to attack. The most frequent and vigorous attacks involved elevation of the head and protrusion of the upper jaw from the oral cavity thus swallowing (small) or biting (large) baits with its jaws. This pattern has been observed when sharks attacked pinnipeds and humans (Tricas and McCosker 1984).

The "surface attack" involved five discrete behavioral acts coupled in a fixed sequence of occurrence (Figs. 1 and 2).

1) *Snout lift*.—The initiation of a feeding action was marked by elevation of the head by flexion just posterior to the occiput.

2) *Lower-jaw depression*.—This act involved a drop of the lower jaw, occurred concurrently with the snout lift, and resulted in expansion of the mouth.

3) *Palatoquadrate protrusion*.—Once the mouth was fully opened, the upper jaw disassociated from its sub-cranial position and rotated forward and downward out of the oral cavity. This initiated the closing action of the mouth and fully exposed the teeth of the upper jaw.

4) *Lower-jaw elevation*.—Concurrent with palatoquadrate protrusion, the lower jaw began an antero-dorsal (upward) motion. These two acts collectively closed the jaws.

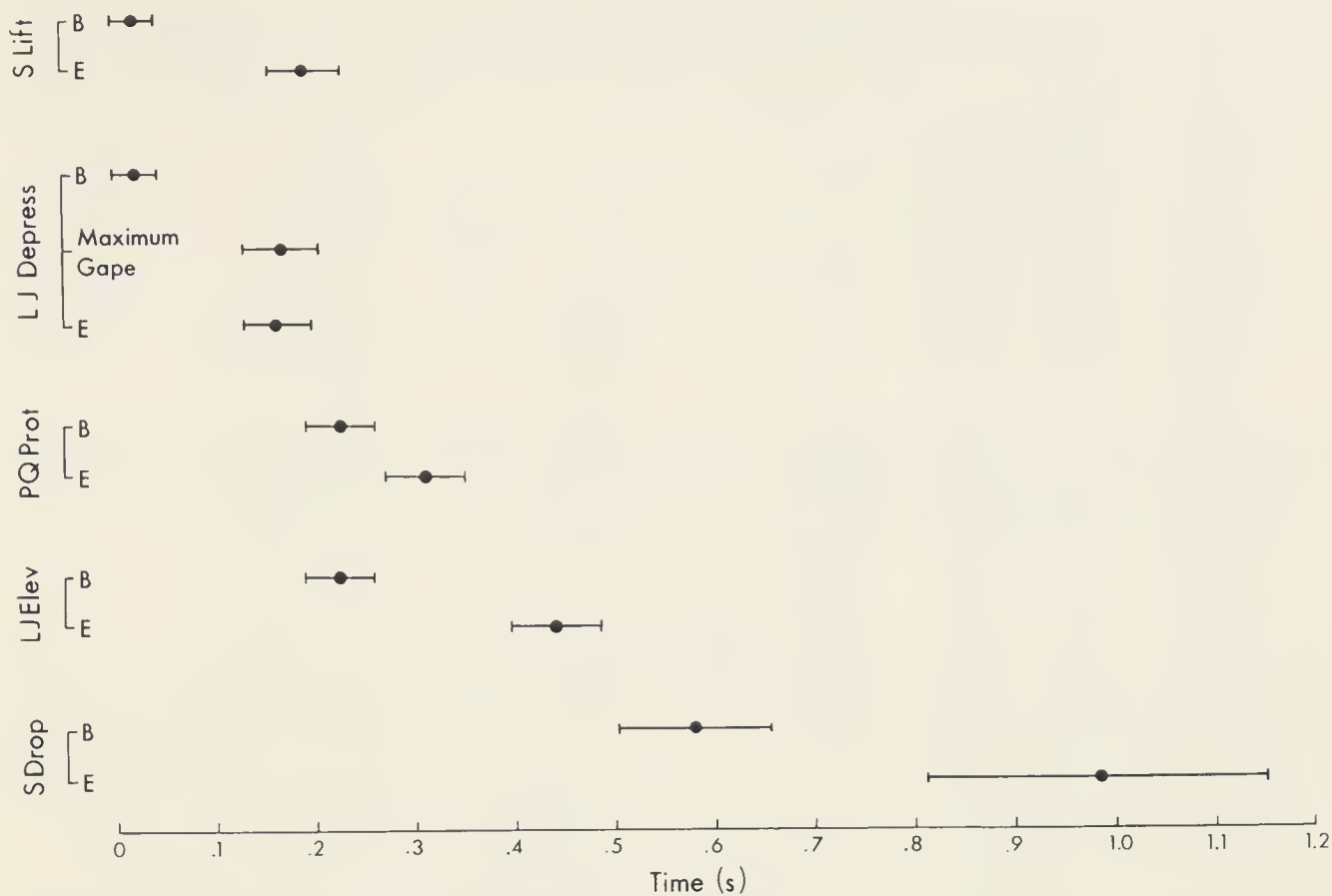


Fig. 2. Timing of feeding actions for eleven bites made by a 3.5 m (TL) white shark (#2). Mean times indicated by points. Horizontal lines show 95% confidence limits. Legend: B = begin, Depress = depression, E = end, Elev = elevation, LJ = lower jaw, Max = maximum, PQ Prot = palatoquadrate (upper jaw) protrusion, S = snout.

5) *Snout drop*.—The occurrence of this act marked the termination of a feeding bout. The snout drop was characterized by lowering of the head and snout, and a retraction of the palatoquadrate cartilage to its original position ventral to the cranium. During multiple-bite bouts, the snout remained elevated until the last bite was inflicted.

Variability in durations for a complete bite action between three sharks is shown in Table 1. Mean times ranged from .264 to .740 s and were significantly different (Kruskal-Wallis non-parametric one-way analysis of variance test, $P < .005$). These subjects also showed different levels of stereotypy with the smallest shark being the least variable in duration for a complete bite. Comparisons of mean durations and stereotypy for each act for two sharks are given in Table 2. The ranked sequence for mean duration of each act is shown in Figure 3, and was the same for both sharks. The act of shortest duration was palatoquadrate protrusion, while snout drop was the longest. Variability within acts however was not similar between individual sharks as indicated by index of stereotypy ranks shown in Figure 3. Of the four sequence-linked acts (exclusive of the snout drop), palatoquadrate protrusion showed the least variability for shark #2, while the most for shark #4. Snout drop showed the greatest variability thus lowest stereotypy in duration for both sharks, which reflects its non-integral part in a bite action.

While the sequence of acts did not vary among different sharks, significant durational differences exist between acts within each shark (Table 2) and between

Table 1. Stereotypy (ST) of "surface attack" feeding pattern for 3 white sharks. Snout drop act not included in analysis due to variability in its occurrence. Shark total lengths (TL) are estimates.

Shark ID no. and (TL)	Number of bites	Range	Mean	SD	CV%	ST
2 (3.5)	20	.210-1.540	.540	.331	58.5	1.7
4 (3.0)	7	.225-.295	.264	.028	10.8	8.5
5 (3.5)	4	.542-1.083	.740	.239	32.3	3.0

some acts among sharks as seen in Table 3. In the latter case, no significant differences were detected in mean duration for the lower jaw depression or palatoquadrate protrusion acts.

Discussion

This study focuses on two aspects of white shark predatory behavior that deal with interactions after prey detection. The first classifies different modes of approach in terms of the shark's spatial orientation to the location of the prey. The second addresses proximate patterns of prey capture and consumption, and describes different behavioral, spatial, and temporal characteristics of biting. A complete understanding of white shark predatory behavior must include other relevant aspects that relate to motivation, search patterns, prey detection and recognition, prey selection, and capture. Some of these were addressed by Tricas and McCosker (1984).

Although approach and capture patterns are intimately linked, it is appropriate to separate them for analysis since each is composed of distinct independent behaviors. For example, sharks that took bait by the highly aggressive 'surface attack' pattern, often advanced on prey from either surface charges or underwater approaches. Similarly, different capture behaviors were observed among sharks

Table 2. Comparisons of stereotypy for individual feeding acts for two white sharks. Mean act durations for each shark are significantly different (Kruskal-Wallis test).

Act	Range (s)	Mean (s)	SD	CV	ST
Shark #2 (TL = 3.5 m, n = 11)					
Snout Lift	.083-.208	.171	.054	31.9	3.1
LJ Depress	.083-.292	.140	.057	40.7	2.4
PQ Prot	.083-.125	.084	.001	.8	54.9
LJ Elev	.167-.292	.220	.046	20.9	4.6
Snout Drop	.292-1.041	.405	.230	56.8	1.7
<i>P</i> < .001					
Shark #4 (TL = 3.0 m, n = 7)					
Snout Lift	.090-.170	.118	.027	22.7	4.2
LJ Depress	.070-.145	.113	.029	25.3	3.8
PQ Prot	.040-.085	.064	.019	29.6	3.2
LJ Elev	.095-.150	.121	.020	16.3	5.8
Snout Drop	.055-.240	.159	.073	45.7	2.1
<i>P</i> < .025					

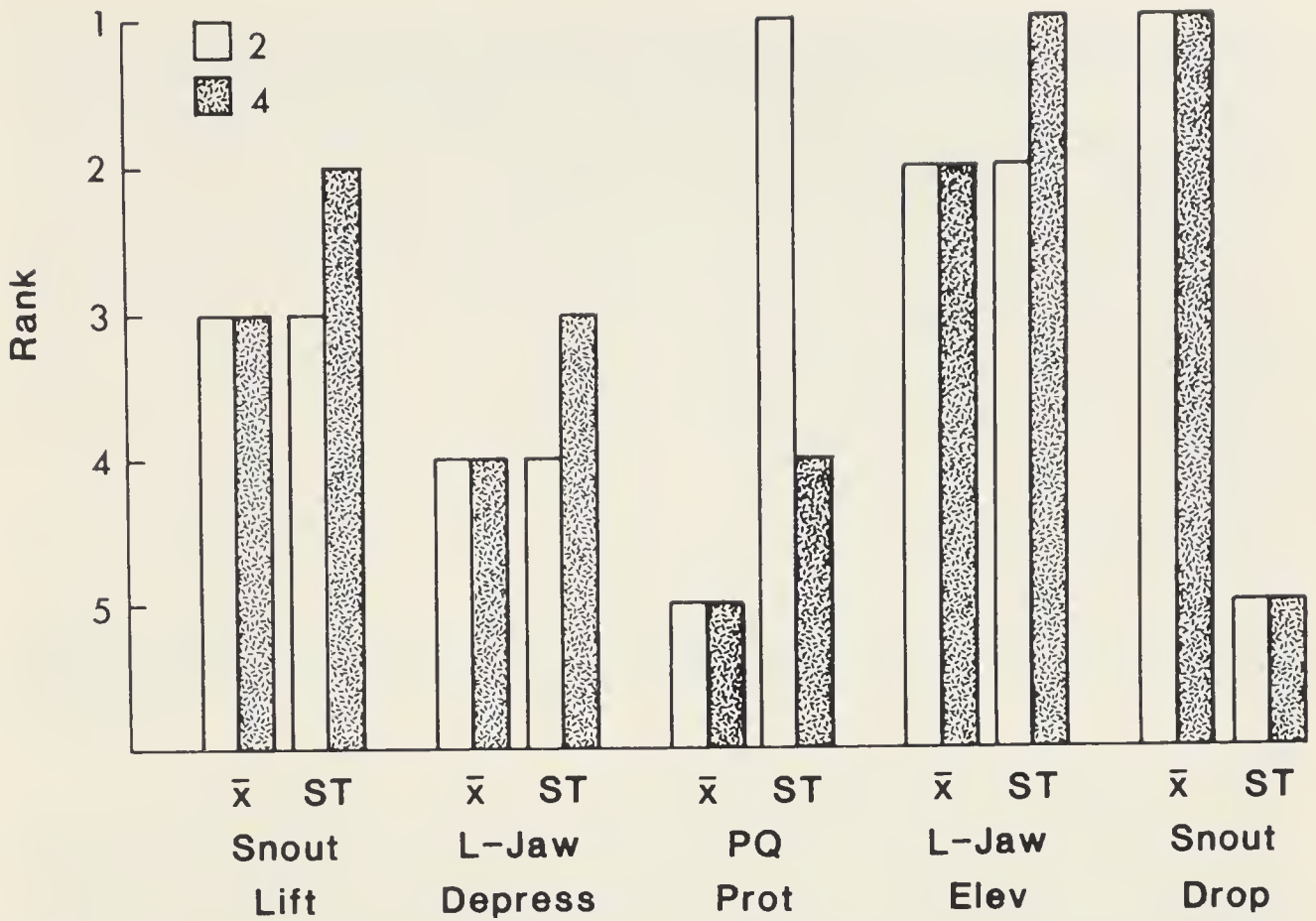


Fig. 3. Comparison of ranked mean durations (\bar{x}) and indices of stereotypy (ST) for acts that compose the surface feeding attack behavior. Shark #2 = open bars; shark #4 = shaded bars.

that used the same approach mode. This was evident when some sharks approached from underwater but engulfed prey by either a slight opening of the mouth or a full surface attack.

Sets of these behaviors were shown both among different sharks and within the same individuals. Generally, the most vigorous attacks were made when sharks first arrived at the baiting site and were probably in a hunger-motivated state. After numerous feedings by an individual, the active bite attack behavior (that involved upper jaw protrusion) often transgressed to the simple swallowing of pieces of bait. This change in attack behavior may be due to satiation. Some of the same sharks also rolled ventrally to approach and ingest small pieces of bait ingested by lower-jaw depression alone. Pratt et al. (1982) observed white sharks feeding on a large whale carcass by first turning (= approaching) ventral-surface-up to set the teeth and then rolling upright to cut a clean mouthful of blubber. This behavior was observed three times (probably among different sharks) and was seen only during attacks at the waterline. They also observed an attack from an upright swimming position (= the surface attack). Unfortunately, very large baits were not available in the present study to experimentally scrutinize differences in feeding actions between large and small prey. It appears however that specific approach and attack behaviors may be a function of motivational, prey size, and prey position factors.

In spite of the variability in linkage of specific approach and attack behaviors, some associations were more frequent than others. The most common co-occurrence was the underwater approach and the surface attack. A similar recurrent

Table 3. Comparison of mean durations of feeding acts that comprise a "surface attack" in two white sharks (#2 and #4). Probabilities given for parametric (analysis of variance) and non-parametric (Mann-Whitney U-test) tests. Observations: shark #2, $n = 11$; shark #4, $n = 7$. Legend: ns = not significant; * = $P < .05$, ** = $P < .025$, *** = $P < .001$; m = modified analysis of variance for unequal means (see Sokal and Rohlf, 1969). Act legend as for Figure 2.

Act	F	Probability	
		Anova	U-test
S Lift	7.72 m	*	**
LJ Depress	.84	ns	ns
PQ Prot	2.63 m	ns	ns
LJ Elev	39.51 m	*	***
S Drop	10.91 m	**	***
Max Gape	6.29 m	*	**

association was observed when sharks fed on submerged baits after approaching by normal underwater passes and using a simple lowering of the jaw to engulf the bait.

The Surface Attack—A Patterned Behavior

The need for defining shark behaviors is clear, but because they are rarely addressed in quantified ways they are often difficult to characterize and compare. The problems associated with identification of action patterns and their behavioral "units" are not new and the solutions still in debate. Barlow (1968, 1977) reviewed the terminological problems and proposed the term "modal action pattern" (MAP) which avoids the interpretive and semantic constraints inherent in the long-used term "fixed action pattern" and other classifications that infer instinctive or innate origins of behaviors. Of the many properties proposed by behaviorists to identify motor patterns, a set of major criteria can be defined (see Schleidt 1974; Barlow 1977 for review). The action pattern must 1) appear stereotyped, 2) be a product of central nervous system processes rather than a simple reflex, 3) once triggered be independent of environmental feedback, 4) generally have a more variable taxic component used for orientation prior to expression of the action pattern, and 5) be widely distributed among individuals of a population (i.e., be heritable).

The surface attack behavior and its components are clearly stereotyped in nature. The sequence of each act was invariably linked to the preceding one, and the order of occurrence was fixed. Within individual sharks, each component had a narrow range of non-overlapping temporal limits. Strict spatial relationships between acts also exist, although it was not possible to measure these because of varying observational perspectives and the lack of suitable scaling during film analyses.

The apparent positive relationship between shark size and increasing time duration of bites and individual acts (Tables I and II) may be a result of biomechanical phenomena related to movements of increasing mass, and such physical limiting factors may set constraints on the evolution of certain predatory modes. It is also possible that durational differences between sharks for specific acts were due to the use of different muscle groups that cause the same feeding expression. For example, palatoquadrate protraction could result from various combinations of quadratomandibularis, preorbitalis, and levator hyomandibuli/palatoquadratii

muscle actions in relation to food position, size, or density (see Moss 1972). Electromyographic monitoring during feeding would provide information on muscle activity involved in specific feeding actions.

The complete attack action pattern involved sets of numerous muscles (see Moss 1972) and is not a simple reflex. Once elicited, the behavior continued to its completion often in the presence of obstructions (e.g., cages, boat, poles, lines) and there was no overt indication of guidance of the behavior by sensory feedback. This observation by itself however does not eliminate possible involvement of proprioceptive feedback. Possible input by proprioceptors on the patterning of acts could be tested by local narcotization of these sites around the mouth and snout, and changes in feeding action patterns observed.

Additional arguments for designation as a MAP could be made if the action pattern could be evoked by direct stimulation of a releasing center in the shark's brain. Demski (1977) showed that biting and mouthing were produced by electrical stimulation of the inferior lobe of the hypothalamus in the nurse shark, *Ginglymostoma cirratum*. Unfortunately, no ethological description of the behavior was provided.

Action patterns are generally associated with orientation movements or taxes that serve to position the animal for delivery of the behavior (see Eibl-Eibesfeldt 1970). Much of the variability for the behavior is expressed in the taxic phase and often is the primary means of adapting to various environmental situations. For the white shark, the orienting movement is seen in the various approach behaviors to the prey, each of which has particular advantages in different situations. For example, the underwater approach is much more likely to result in a surprise attack on a basking pinniped than is a thrashing surface approach. Use of the most appropriate mode also allows the shark to position the head to deliver the most effective bite.

The surface attack behavior was observed in at least six different sharks in this study, in different white sharks by Pratt et al. (1982), and has also been widely recorded (although not analyzed) by commercial and popular cinematographers. Based upon the widespread documentation, it is very likely that this attack behavior occurs in all members of the species (i.e., is "species typical").

Adaptiveness of Predatory Behaviors

The diversity of approach and attack behaviors seen in *Carcharodon* may serve an ontogenetic function to maximize predatory success. In their summary of the food habits of white sharks, Tricas and McCosker (1984) found that individuals less than about 3 m (TL) fed primarily on fish prey while larger sharks preferred marine mammals. The authors attributed this separation of food habits to differences in tooth morphology and suggested that each tooth shape was better adapted for feeding on the different prey types. Correlations of specific attack behaviors with various prey might also be predicted. The predominant posterior-ventral location of bite wounds on pinnipeds (Tricas and McCosker 1984; McCosker, 1985) suggest attacks to be directed from beneath and behind a floating or basking prey. Similar approach patterns were reported on humans (Miller and Collier 1980) and porpoises (Arnold 1972), and generally involve jaw protrusion as in the surface attack behavior. For smaller sharks, protrusion of the upper jaw may be less efficient than a quick drop of the lower jaw to engulf small

fish prey. Rapid depression of the lower jaw may also function to engulf benthic prey through suction created by buccal expansion. Suction feeding has been reported for other species of sharks (Moss 1977; Tricas 1982), and may be the primary means by which small white sharks engulf benthic fish like the cabezon *Scorpaenichthys marmoratus* (see Tricas and McCosker 1984).

There is evidence that first attacks on large mammals function to wound or kill rather than feed, and reduce risk of injury to the shark from a struggling or fighting prey (Tricas and McCosker 1984; McCosker 1985). Once prey is rendered harmless, subsequent feeding attacks often involve behaviors of prolonged contact like head shaking or twisting. Selective pressures to maximize predatory success must also direct evolution of these ancillary behaviors and undoubtedly contribute to the overall pattern and strategy of the feeding attack for white sharks.

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Temperature, Heat Production and Heat Exchange in Lamnid Sharks

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Abstract.—Temperature, heat production and heat exchange in lamnid sharks by Francis G. Carey, John G. Casey, Harold L. Pratt, David Urquhart, and John E. McCosker. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. Lamnid sharks have an unusual ability to warm their bodies above water temperature. We present the currently available muscle and viscera temperature data for 5 species of these sharks and compare ability to raise their body temperature. An adequate set of temperature data is available for the short fin mako, but only a few measurements have been made on the other lamnids. Because these sharks are difficult to obtain, and when caught, are often in poor condition, further temperature data will accumulate only slowly. We therefore supplement the temperature measurements with information on anatomical features related to metabolic heat production and heat conservation. These include relative heart size, the amount and distribution of red muscle, the number of vessels in the lateral cutaneous rete, and the weight of the suprahepatic rete relative to that of the visceral mass it serves. From this anatomical information we rank the sharks: *Isurus paucus*, *I. oxyrinchus*, *Carcharodon carcharias*, *Lamna nasus*, *L. ditropis*, in order of an increasing ability to elevate their temperatures. This ranking is consistent with the existing temperature data. We also note a relationship of muscle temperature to environmental temperature, with the greatest elevations in body temperature found in sharks from the coldest water.

The lamnid sharks have specialized masses of vascular tissue, the rete mirabile (Muller 1841; Burne 1923) which act as heat exchangers and enable them to maintain their tissues at temperatures significantly warmer than the water. Elevated body temperatures have been reported for several species of these sharks. Expressed as the difference between the maximum tissue temperature and the ambient water temperature, muscle temperature elevations averaged 5°C and had a maximum of 9°C for the short-fin mako, *Isurus oxyrinchus* Rafinesque 1809, and 7.0, 9.2, and 11.3°C for three porbeagles, *Lamna nasus* (Bonnaterre, 1788) (Carey and Teal 1969a). The Pacific salmon shark, *Lamna ditropis* Hubbs and Follett 1947, is reported to be 11°C warmer than the surrounding water (Rhodes and Smith 1983). Temperature elevations of 4 to 6°C have been found in the white shark, *Carcharodon carcharias* (Linnaeus, 1758) (Carey et al. 1982; Tricas and McCosker 1984). The viscera and brains of lamnid sharks are also warm (Carey et al. 1981; Block and Carey 1983). The presence of a retial system in the muscle (Bone and Chubb 1983) and gut (Eschricht and Muller 1837) of the thresher shark, *Alopias vulpinus* (Bonnaterre, 1788) indicates that it may also be warm, but no information on this species is presented here.

The ability to maintain a high temperature is certainly one of the interesting

features of these sharks and must be important in their ecology and evolution, but it will be a difficult and lengthy process to improve the temperature data. We have had access to an abundance of mako, but the other species are difficult to obtain. Furthermore, although the lamnid sharks are powerful and vigorous predators, they are also delicate animals and are often in poor condition or dead when caught. Some of the measured temperatures are probably from moribund specimens and lower than normal. In these circumstances we felt it useful to compare anatomical features related to the ability of these sharks to generate and conserve metabolic heat. We use this anatomical information to supplement the temperature measurements and rank the species of lamnid sharks according to their potential ability to elevate their body temperatures.

Methods

Most sharks were obtained by longline fishing gear in the North Atlantic (steel leaders, mackerel baits set at depths of 10 to 60 meters). A live longfin mako, *Isurus paucus* Guitart Manday, 1966, was taken off Daytona, Florida in April 1978. Two *I. paucus* were given to us by Captain Phil Ruhle of Newport, Rhode Island. Much of the *I. oxyrinchus* data came from a collection of 20 specimens made from the Polish Research Vessel, *Wieczno* near Cape Hatteras in March 1983. Muscle tissue from a fetal mako was given to us by Dr. John Stevens, of CSIRO, Hobart, Australia. Specimens of *Carcharodon carcharias* were made available to us by J. Seigel and C. Swift of the Natural History Museum of Los Angeles County and by the Connecticut Museum of Natural History. Other specimens were donated by fishermen G. Dubrule and E. Celetto of Noank, Connecticut, C. Stulz and W. Latham of Williamstown, N.J., and by R. Mayo, Barnstable, Mass. Specimens of *Lamna ditropis* were donated by D. Rhodes, University of Alaska, and by T. Hansen, San Francisco, California. Specimens of *Lamna nasus* were given to us by Captain M. Bartlett of the F/V Penobscott Gulf, who also donated a number of mako sharks.

Temperature measurements were made with thermistors mounted in 16 gauge needle tubing. The sharks were lifted aboard and a deck hose placed in their mouths to quiet them during the temperature measurement. Maximum muscle temperature was found by probing with the thermistor needle for the highest reading in the red muscle at the level of the rear of the dorsal fin. Maximum tissue temperatures were usually referred to surface water temperature, but sometimes were referenced to the coldest tissue in the shark, such as the heart or deep caudal muscle (Carey et al. 1981). There are only a few specimens in common between those whose temperatures appear in Table 1 and those in the anatomical tables.

To determine longitudinal distribution of red muscle, sharks were cut into segments each with a thickness $\frac{1}{10}$ the distance between the fourth gill slit and the rear of the second dorsal fin. The region between the second dorsal and the caudal fin was also cut into segments of the same length, resulting in a total of 11 segments from the mako and porbeagle and 12 from *Carcharodon*, which has a longer caudal peduncle. The anterior ends of the segments were photographed and the areas of red muscle and of total muscle, exclusive of fin musculature, were measured by digitizing the photographic prints.

For the *Isurus paucus* and *Lamna ditropis* specimens examined early in the

Table 1. Temperatures of sharks.

Species	Water temperature (°C)	Maximum temperature elevations °C above water			
		Muscle	Liver	Stomach	Spiral valve
<i>Isurus paucus</i>	23.1	-0.4			
<i>Isurus oxyrinchus</i>					
Avg	20.2	4.0	2.4	2.7	4.2
SD	3.1	2.5	1.7	2.2	2.8
n	38	38	14	10	11
<i>Carcharodon carcharias</i> *					
	18.0	5.0			
	21.0	4.0			
<i>Lamna nasus</i>					
	11.0	9.2			
	10.2	5.8			
	6.6	11.3			
	15.5	8.7			
	6.5	7.0			
	12.7	9.9	4.9	5.5	9.0
	14.0	6.8	2.7	4.3	6.0
Avg	10.9	8.4			
SD	3.2	1.8			
<i>Lamna ditropis</i> †					
	8.0	11.0			
	8.0	11.0			
	8.0	8.0			

* Temperatures measured by acoustic telemetry Tricas and McCosker 1984, Carey et al. 1981.

† Rhodes and Smith 1983.

study, the amount of red muscle was estimated from a single section at the level of the rear of the dorsal fin by tracing the outlines of the tissue on mylar film which was then cut out and weighed. These species were not available for the more complete analysis that was used subsequently, but we were able to examine sections of a small *L. ditropis* to confirm in a qualitative fashion that the distribution of red muscle was the same in this species as in the porbeagle.

The lateral cutaneous rete which serves the axial muscle was sampled at the level of the first dorsal fin by taking a plug of muscle which included the lateral cutaneous vessels, the rete and a portion of the red muscle. The samples were preserved in 10% formalin. The thin walled veins are often completely flattened dorso-ventrally and not visible, but the contracted arteries show clearly as discs or thick-walled rings in cross section. The number of arteries along a vertical line drawn through the rete was used to compare species. To enumerate the arteries, a parasagittal section was taken across the rete at the point of its maximum vertical dimension and number of vessels. This position began a few mm medial to the cutaneous vessels and extended 10 to 15 mm along the rete in a medial direction. Hand-cut sections were stained briefly in Verhoeff's stain (Humanson 1962) to differentiate the arteries. A line of an optical reticule was superimposed on the rete in a vertical orientation and the arteries along the line from top to bottom

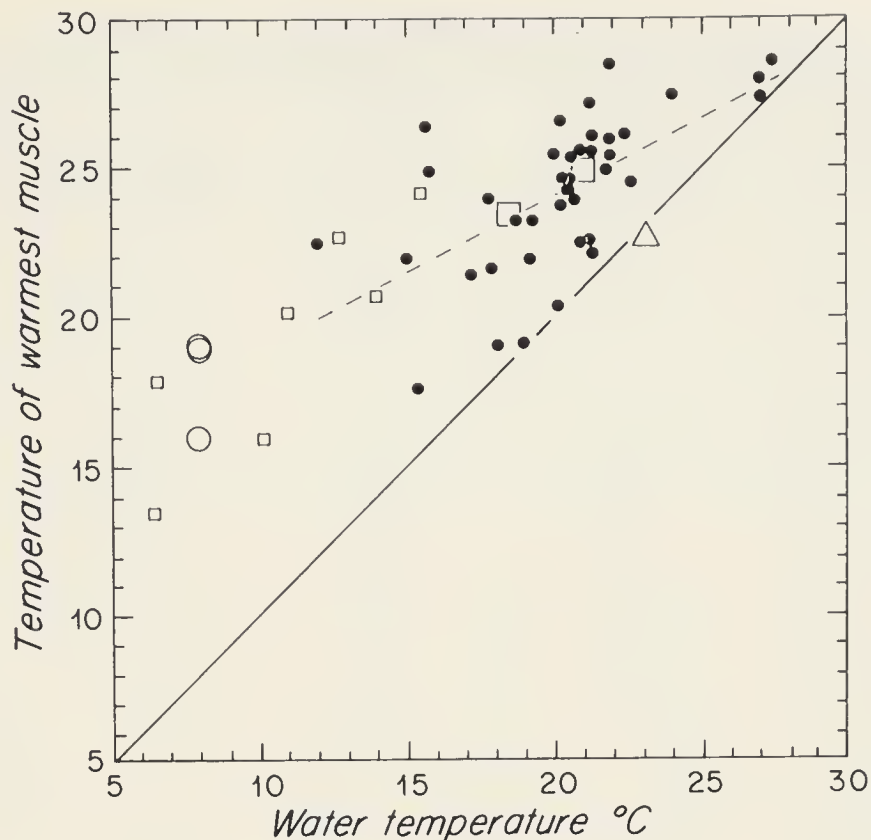


Fig. 1. Temperature in the warmest muscle of lamnid sharks compared to water temperature. Diagonal line gives position of zero temperature elevation. (Δ) *Isurus paucus*. (\bullet) *I. oxyrinchus*, with dashed line for regression equation: $T_{\text{muscle}} = 13.8 + 0.513 T_{\text{water}}$. (\square) *Carcharodon*, the point at 21°C is from Tricas and McCosker 1984. (\square) *Lamna nasus*. (\circ) *L. ditropis*, from Rhodes and Smith 1983.

of the rete were counted 10 to 40 times over a distance which took in several myomeres. Counts could be repeated to within 5 or 10%, but variation along the rete with an increase in arteries near the intersection of myosepta increased the standard deviation to 10 or 20%. This method of sampling across the entire depth of the rete was felt to be indifferent to the major distortion of this tissue, which was compression in the vertical direction.

The heart (atrium, ventricle, and conus arteriosus) was dissected out, slit, washed free from blood, and preserved in 10% formalin. Five specimens were weighed fresh to determine shrinkage and all preserved samples were weighed ashore.

The size of the suprahepatic rete was determined by weighing. The rete was dissected free from the esophagus and body wall, squeezed free of blood and preserved in 10% formalin. As with the heart, five specimens were weighed fresh, before preserving, to determine shrinkage. Both heart and suprahepatic rete specimens were wrapped in absorbent toweling and firmly squeezed by hand to reduce the amount of excess fluid before weighing. The weight of the suprahepatic rete was compared with the weight of the viscera it serves: the liver, stomach, intestine, and spiral valve. The latter three organs were washed free of their contents before weighing. Visceral weights were from both fresh and frozen specimens.

Results

The single specimen of longfin mako, *Isurus paucus*, caught alive, was in rather poor condition, but still making swimming motions when brought to the boat ($29^{\circ}20'N$, $80^{\circ}09'W$, 2 April 1978). All tissue temperatures were essentially the

Table 2. Red muscle and heart relative to body weight.

	Body weight (kg)	Heart weight (g)	Heart body wt × 1000	Area red muscle (cm ²)	Red muscle wt ² / ₃ × 1000
<i>Isurus paucus</i>					
	36.3	70.3	1.94	7.86	0.72
	56.7	89.4	1.58	9.62	0.65
<i>Isurus oxyrinchus</i>					
	5.0			4.28	1.46
	19.0	31.1	1.64	10.83	1.52
	25.0	58.9	2.36	15.90	1.86
	33.0	59.5	1.80	14.83	1.44
	36.3	70.3	1.94	7.86	0.72
	52.0	86.7	1.67	18.20	1.30
	53.0	80.7	1.52	17.03	1.21
	56.7	89.4	1.58	9.62	0.65
	75.0	106	<u>1.41</u>	22.52	<u>1.26</u>
Avg			1.74		1.27
SD, n			0.28, n = 28		0.36, n = 9
<i>Carcharodon carcharias</i>					
	12.2	27.0	2.21	6.80	1.28
	17.7	35.7	2.02	8.53	1.25
	23.6	38.0	1.61	6.86	0.83
	40.5			17.19	1.46
	118	149	1.25		
	227	352	1.55	54.20	1.45
	297	536	1.80	88.32	1.98
	1086	2010	1.85		
	1247	2660	2.13		
	1256	2324	<u>1.85</u>	267.00	<u>2.29</u>
Avg			1.81		1.51
SD, n			0.28, n = 9		0.45, n = 7
<i>Lamna nasus</i>					
	46.5	173	3.73	33.10	2.56
	88.5	233	2.63	38.00	1.91
<i>Lamna ditropis</i>					
	7.2	27.0	3.74	8.10	2.17
	37.2	148	3.98	23.05	2.07

same as the surface water temperature of 23.1°C: deep muscle near the tail, 22.6–22.7; red muscle beneath the dorsal fin, 22.7; brain, 22.6; eye, 23.0. The existing temperature data for all lamnid sharks are presented in Table 1 and Figure 1.

We have accumulated enough temperature data for the mako, *I. oxyrinchus*, to have some confidence in the degree to which this fish is independent of water temperature. The relationship of muscle temperature (T_m) to water temperature (T_w) for the data in Figure 1 and Table 1 is:

$$T_m = 13.8 + 0.513 T_w$$

$$r = 0.622, n = 38$$

Table 3. Suprahepatic and lateral cutaneous rete.

	Total weight (kg)	Liver (kg)	Gut (kg)	SHep rete (g)	SHep rete viscera ×1000	Arteries across lat. cut. rete	
						Avg.	±SD
<i>Isurus paucus</i>							
	36.3	3.1	2.9	60.4	10.07	6.5	1.50
	56.7			77.2		4.1	0.95
<i>Isurus oxyrinchus</i>							
	Avg				8.7	19.9	
	SD, n				2.3, n = 20	3.0, n = 22	
<i>Carcharodon carcharias</i>							
	12.2	1.2	0.6			25.6	2.92
	17.7	3.0	0.8	53.9	14.34	24.2	3.50
	23.6	2.8	0.8	68.2	18.66		
	40.5	6.0	1.9	98.6	12.48	27.7	2.70
	227	27.3	5.8	568	17.16	19.8	2.75
	297	38.9	8.7	514	10.80	24.3	2.56
	1086	247	31.8	1959	7.03	22.4	4.27
	1247	250	39.4	1881	6.50	30.1	4.36
	1256	205	33.4	2919	12.23	26.6	2.33
	Avg				12.4	25.1	
	SD, n				4.1, n = 8	3.0, n = 8	
<i>Lamna nasus</i>							
	46.5	3.2	1.6	95.0	20.0	41.6	4.7
	88.5	5.7	1.9	267	34.9	45.8	2.5
<i>Lamna ditropis</i>							
	7.2	0.5	0.3	20.9	27.9	68.9	3.6
	37.2	1.8	1.6	182	53.6	59.9	2.8

The probability that the slope of this line is 1.0 is <0.001. The 95% confidence limits are 0.23 to 0.73 on the slope and 9.4 to 18.3 on the intercept.

The porbeagle, *Lamna nasus*, presented here include several additional specimens obtained since an earlier publication (Carey and Teal 1969a). These porbeagle temperatures fit the equation:

$$T_m = 9.18 + 0.927 T_w$$

$$r = 0.86, n = 7, P < 0.05$$

The heart of *I. oxyrinchus* shrank 7.5% and the suprahepatic rete 10% on preservation in formalin and the preserved specimens are corrected by these factors. No correction has been made for the probable further shrinkage of the two museum *Carcharodon* specimens in isopropanol. The weights of heart appear in Table 2 and liver, gut, and suprahepatic rete in Table 3. The weights of heart, viscera, and suprahepatic rete of mako, *I. oxyrinchus*, which are omitted from the tables are shown in Figure 2.

The ratio of heart weight to body weight was used to compare the heart among different sized specimens of the 5 species of sharks in Table 2. Relative heart size is similar in *Isurus paucus*, *I. oxyrinchus*, and *Carcharodon carcharias*, but the heart is clearly larger in the *Lamna* species.

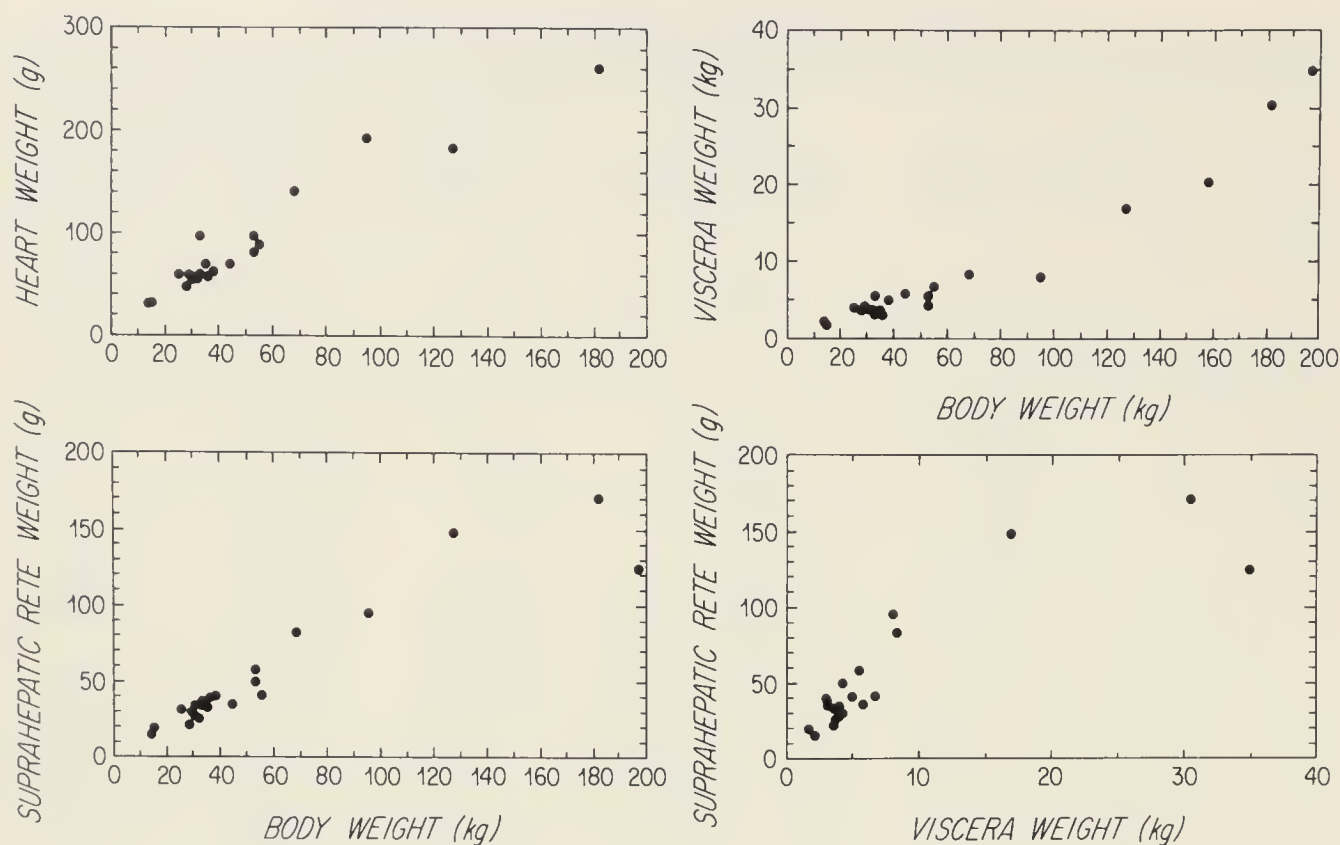


Fig. 2. Change in viscera, heart and suprahepatic rete with body size in mako, *I. oxyrinchus*. (A) Heart weight is an approximately linear function of body weight. (B) Viscera weight (liver and gut) may increase exponentially with body size. (C) Suprahepatic rete weight. (D) Suprahepatic rete appears to increase asymptotically with viscera weight, but a linear relationship was assumed for comparisons made in the text and in Table 3.

In Lamnid sharks the main red muscle mass forms a distinctive heavy band near the vertebral column. In *Lamna* it lies directly against the vertebral column (Fig. 3), but is not attached to the vertebrae over much of its length. An easily sliding fascia allows the medial surface of the red muscle to slide freely. In *Isurus oxyrinchus* the red muscle is more laterally located and separated from the vertebrae by intervening white muscle fibers. For part of its length the red muscle band is free along its medial border, but not as conspicuously free sliding as in *Lamna*. In *Carcharodon* the red muscle band is also separated from the vertebrae by white muscle but it is not noticeably free along its medial surface. Red muscle makes up 4% of the total axial muscle (exclusive of fin musculature) in *I. oxyrinchus* and *Lamna nasus* and 6% in *Carcharodon*. The longitudinal distribution of red muscle is shown in Figures 4 and 5. The red muscle is thickest at the level of the rear of the dorsal fin, but the three species show marked differences in longitudinal distribution of red muscle. The large visceral mass and a relatively thin body wall in *I. paucus* and *Carcharodon* (Fig. 3) affects the ratio of muscle types and another ratio, the red muscle area to total body weight raised to the $2/3$ power (to make a bulk term compatible with an area term), is included in Table 3 as an aid for comparison of the amount of red muscle in the different sharks.

All of the lamnid sharks have a lateral cutaneous rete supplying blood to the axial muscle but there are marked differences in this structure between species. The degree of elaboration of the muscle rete increases in the order: *Isurus paucus* < *I. oxyrinchus* ≤ *Carcharodon carcharias* < *Lamna nasus* ≤ *L. ditropis* (Table 4). The rete is poorly developed in *I. paucus*, with only a few layers of blood vessels

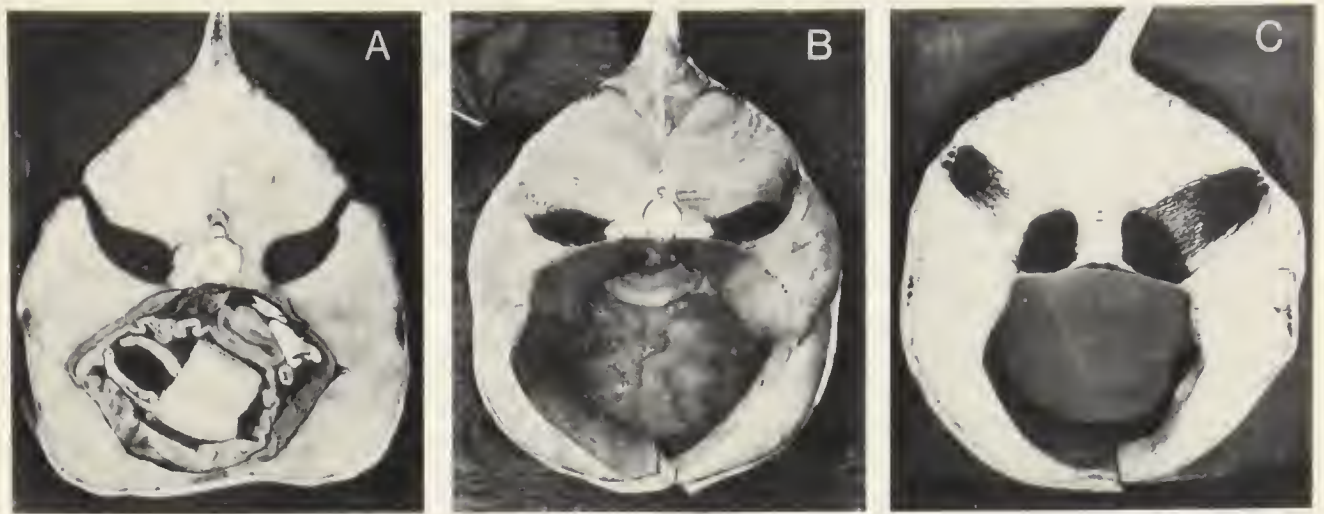


Fig. 3. Lamnid sharks cut in cross section at the level of the dorsal fin. (A) A 5 kg mako, *I. oxyrinchus*, cut while frozen, leaving the viscera in place with fish in the stomach. The lateral cutaneous rete is visible as a band of blood filled vessels running from beneath the skin to the red muscle. There is white muscle between the red muscle band and the vertebrae. (B) A 227 kg *Carcharodon*. The rete vessels run between white muscle fibers to the red muscle. Here also white muscle separates the red muscle from the vertebrae. The body cavity of *Carcharodon* is larger and the body wall thinner than in the other two species. (C) An approximately 40 kg porbeagle, *Lamna nasus*, with colored latex injected in the vascular system. This procedure inflates the vessels and makes them conspicuous. The red muscle is centrally located against the vertebrae.

interspersed with muscle fibers. *Isurus oxyrinchus* has a well developed rete which is unique in being a solid mass of blood vessels with no interwoven white muscle fibers, an arrangement which should make a most effective heat exchanger. In *Carcharodon* and *Lamna nasus* the vessel are in layers 2 to 10 vessels thick interleaved with muscle fibers. The rete in *Lamna ditropis* is similar to these, but with noticeably more arteries in the two specimens examined. Cross sections of the rete are shown in Figure 6.

The number of arteries in a vertical line across the rete varies along the length of the fish in a manner related to the bulk of red muscle it supplies (Fig. 5). At the level of the pelvic fins, there is no red muscle in *L. nasus* and the rete is reduced to intermittent bands one vessel thick. In *Carcharodon* which has a large amount of red muscle at this point there is a well developed rete. The elaboration of the rete in *I. oxyrinchus* also parallels red muscle distribution.

The visceral organs make up 12% of body weight in *I. oxyrinchus* and 20% in *Carcharodon*. The single intact *I. paucus* had a larger visceral mass than the average for *I. oxyrinchus* and the *Lamna* species had less. The liver and the alimentary tract receive the major portion of their blood supply through the suprahepatic rete. The size of this rete relative to the viscera it serves was much larger in the *Lamna* species and in *Carcharodon* than in *Isurus* (Table 3).

Discussion

The muscle of *Isurus oxyrinchus*, *Lamna nasus*, *L. ditropis*, and *Carcharodon carcharias* is substantially warmer than the water. Only *I. paucus* seems likely to have cold muscle. There are some problems with these temperature data. Because acute temperatures were measured at a time when the fish were highly stressed, the normal temperature elevation is probably underestimated. The data for *Car-*

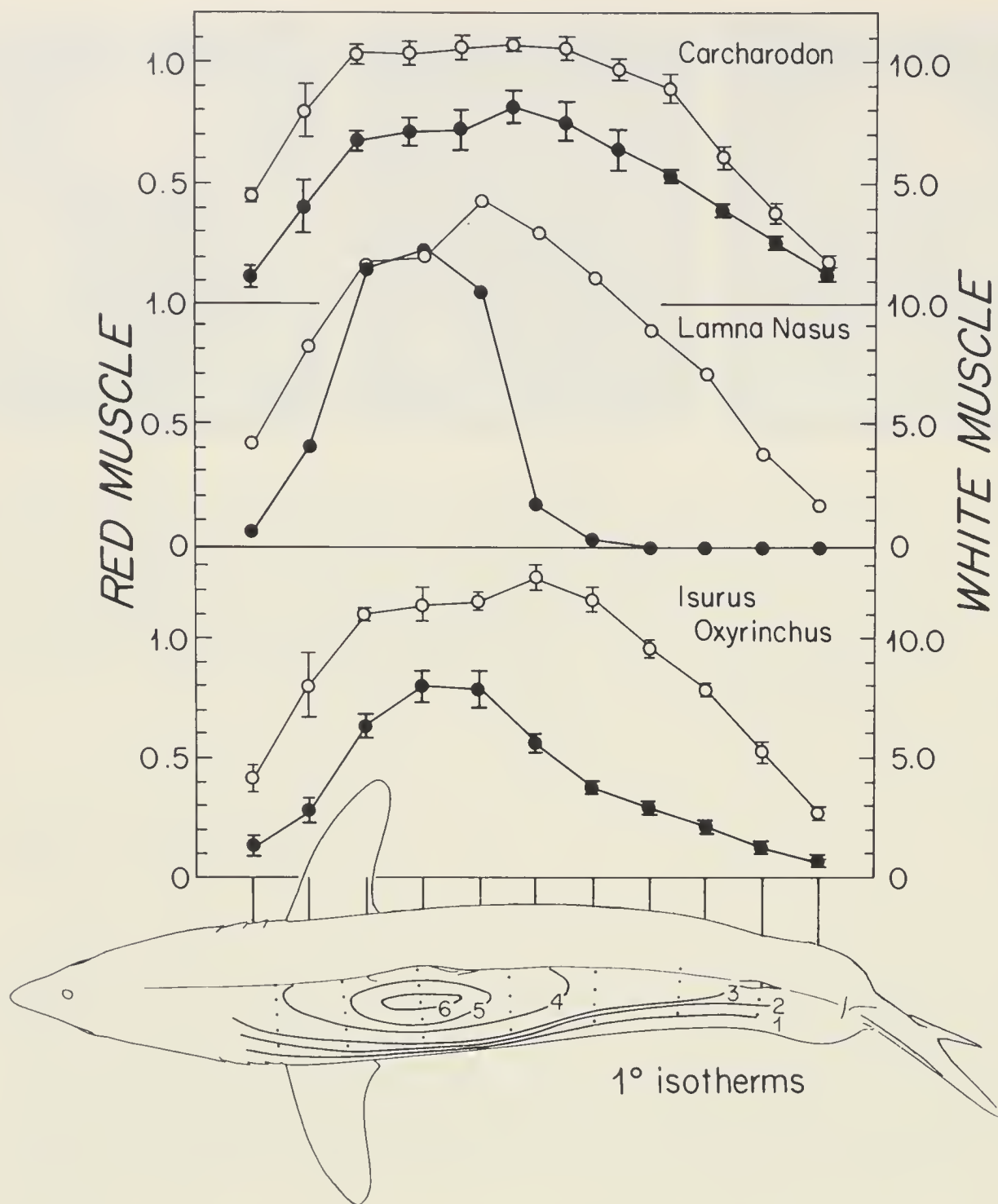


Fig. 4. Longitudinal distribution of axial muscle, measured at about 5% intervals between 27% and 85% fork length. The area of red and white muscle in each section is expressed as percent of total area in all sections. Note that the scale for red muscle is 10× that of white. Results from a single porbeagle and from 4 specimens each of mako and *Carcharodon* (Avg. ± S.D.). The high red muscle values for the 1256 kg *Carcharodon* (Figure 5) are omitted from this figure. The red muscle band in *Carcharodon* extends rather evenly back into the posterior region of the shark, while in *Lamna nasus* it is concentrated in the thickest region of the body under the dorsal fin. The mako, *I. oxyrinchus* is an intermediate case. The isotherm distribution in mako, shown at the bottom, closely approximates that of red muscle. ○ = White muscle, ● = Red muscle.

charodon in Figure 1 were from telemetry experiments and probably represent normal temperatures in undisturbed individuals. But while the thermistors were close to the region of highest temperature we are not sure they were actually in the warmest muscle.

From Figure 1 it appears that *Isurus oxyrinchus* can control the temperature

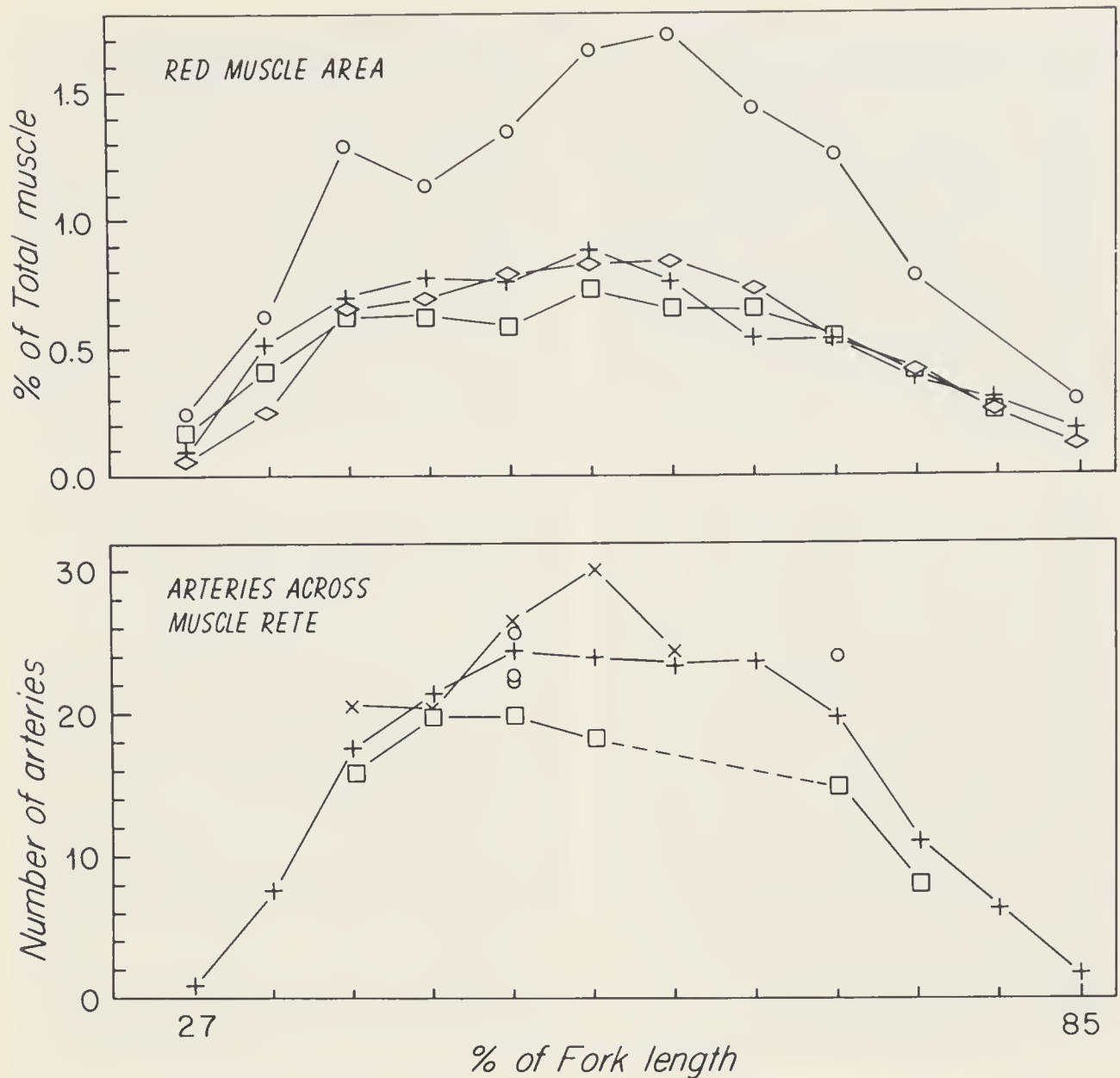


Fig. 5. Longitudinal variation of red muscle and rete arteries in *Carcharodon*. Upper panel: Red muscle from sharks weighing 23.6 (\square), 227 (+), 297 (\diamond) and 1256 (\circ) kg. The amount of red muscle in the largest shark was markedly greater than in the others. Lower panel: The number of arteries in the lateral cutaneous rete remains constant as the sharks increase in size (see Table 3). The rete is well developed over most of its length and should serve as an effective heat exchanger through most of the region where red muscle occurs.

of its muscle. Figure 1 almost certainly includes some data from moribund individuals with body temperature close to water temperature and such data increase the apparent dependence on water temperature. Temperature control in healthy sharks is probably better than indicated by the 0.5 slope of the regression line in Figure 1, but this is still a good degree of independence from water temperature. The data are not adequate to judge if any of the other species can control their muscle temperature.

While the question of temperature regulation can only be measured by measurements on living fish, we can infer something about the ability of the different species to elevate body temperature from anatomical measurements. In doing this we have assumed that in the relatively homogenous lamnid group, similar structures perform the same function in the same way, and that the size and elaboration

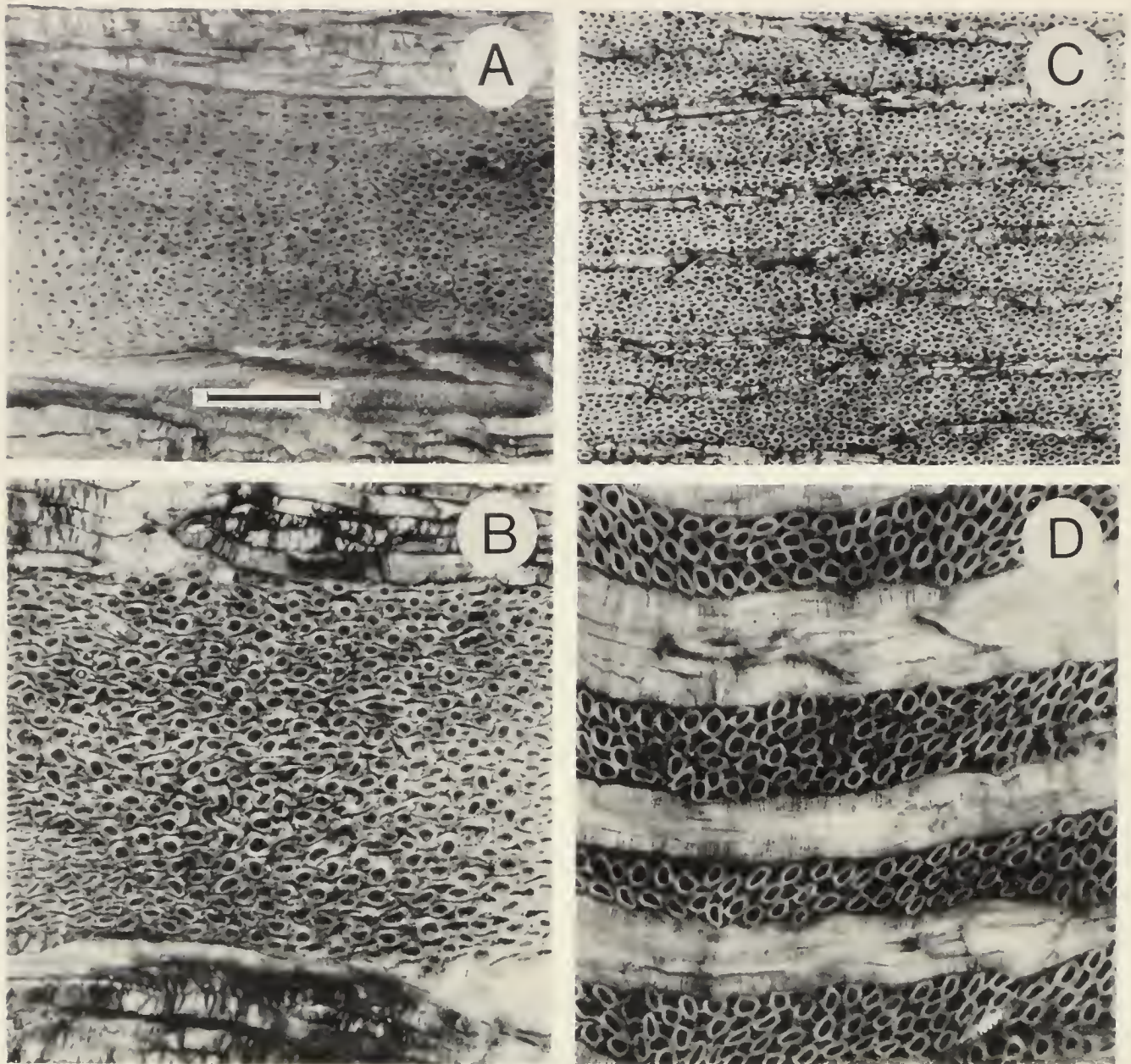


Fig. 6. Cross section of vessels in the lateral cutaneous rete of: (A) 14 kg mako, *I. oxyrinchus*, (B) 181 kg *I. oxyrinchus*, (C) 7 kg *Lamna ditropis* and (D) 46 kg *Lamna nasus*. The rete in mako is a homogenous slab of vascular tissue while in *Carcharodon* and *Lamna* the blood vessels are in layers interspersed through the white muscle. There is a clear increase in size of the vessels between the small and the large fish. All panels at same magnification. Calibration bar in panel (A) = 1 mm.

of an organ are related to its effectiveness. We have made comparisons from a limited amount of material. Our largest sample included 28 *Isurus oxyrinchus*, but of these the largest was less than 200 kg. The female of this species does not become sexually mature until it reaches a size of about 250 kg (Stevens 1983). Such large fish are seldom captured and may have quite different habits and thermal regimes from the smaller ones. With the caution that we lack large specimens of any species besides *Carcharodon* and have only a small number of specimens for species other than mako, we use anatomical features to supplement the available temperature measurements and rank the lamnid sharks for body temperature elevation.

The lamnid sharks have a large heart. We have assumed that heart size is related to cardiac output and the demand for oxygen and thus to heat production. Emery in this volume questions this assumption and suggests that ventricle size may not

be related to activity in elasmobranchs. With this caution in mind, we recklessly forge ahead and compare the heart weights of these sharks (Table 2). A linear relationship, the ratio of heart weight to body weight, fit the data in Figure 2 as well as the power function commonly used to relate metabolic rate to body size. Relative heart size is similar in *Isurus* and *Carcharodon*, but larger in *Lamna*. If heart size is any general indicator of metabolic rate, *Lamna* species may be capable of a greater rate of heat production than the other lamnid sharks.

Red muscle used in continuous swimming (Bone 1966), is prominent in the axial muscle of lamnid sharks. When compared at the region of greatest red muscle concentration, under the dorsal fin, the sharks rank *Isurus paucus* < *I. oxyrinchus* = *Carcharodon* < *Lamna nasus* ≤ *L. ditropis*. Red muscle is least abundant in *I. paucus* where its cross section area to body weight ratio is about half that of the other species (Table 2). When comparing the total amount of red fiber muscle over the length of the body, rather than by its cross section area under the dorsal fin, *Carcharodon* has the largest amount, 6% of the axial muscle (excluding the value for the largest shark). In *Lamna* and *I. oxyrinchus* red muscle makes up 4% of the muscle. If metabolic activity of red muscle in these species is equivalent, the red muscle of *Carcharodon* may be generating more heat. In this instance there is an apparent disagreement between the anatomical measurements and the temperature data. *Carcharodon* has a greater total amount of red muscle than the *Lamna* species, which appear to be the warmest sharks. These comparisons of red muscle are based on quantity of tissue. We have no assurance that the muscle of the different species is equivalent in metabolic activity.

The distribution of red muscle in these sharks is different. In *Lamna nasus* and *L. ditropis* the red muscle is concentrated in the thickest region of the body, while in *Carcharodon* it is more evenly distributed along the length of the fish. *I. oxyrinchus* presents an intermediate condition between the two (Fig. 3). The isotherm distribution in mako closely approximates that of the red muscle (Fig. 4). It seems likely that the temperature distribution in *Carcharodon* will also follow the red muscle, with the highest temperatures extending more caudally than in the mako. The lateral cutaneous rete which supplies blood to this muscle is well developed and could act effectively to exchange heat along its length (Fig. 5).

Red muscle made up 12.2% of the axial muscle in the 1246 kg *Carcharodon*, twice the amount of red muscle found in the smaller specimens. At this time we can not tell if this striking difference indicates a different degree of utilization of this tissue in large sharks or if it is just an individual variation. Fragments of the other two 1000 kg white sharks which we examined indicate they may also have had a similarly large amount of red muscle. The mako gets much larger, 500 kg, than the largest, 75 kg, specimen in which we measured red muscle area. It would be interesting to learn if in this species also there is a disproportionate increase in red muscle in the largest fish.

The distribution of red muscle in the lamnid sharks may tell us something about how they swim at cruising speed. The small amount of red muscle in *I. paucus* is probably associated with a slow speed. Sharks are denser than water (Bone and Roberts 1969) and must swim to keep from sinking. The very large pectoral fins in this species may provide the extra lift needed to maintain depth while swimming slowly.

Carcharodon has red muscle which extends two-thirds the length of the vertebral column. In *Lamna* the red muscle is concentrated in a region where it is locally uncoupled from the backbone, and swimming motions must be produced through posterior connections to the vertebrae and caudal fin. In a study of red muscle distribution in scombrids, Graham et al. (1983) found that the bulk of the red muscle was located anteriorly in the tunas, while most of it was in the posterior region of *Scomber* and *Sarda*. They related this to a difference in swimming style with thrust being developed almost entirely by tail movement in tunas while the other scombrids use carangiform swimming involving undulation of the body. The extension of the red muscle into the posterior region of *Carcharodon* suggests a more sinuous swimming motion, while *Lamna*, like *Thunnus*, may have a stiffer body propelled by movement of the caudal fin. *Carcharodon* has been filmed on a number of occasions. If suitable films of *Lamna* or *I. oxyrinchus* are available, it might be possible to tell if the style of slow speed swimming in these sharks differed in the manner indicated by distribution of red muscle.

The short-fin mako is known for its leaping struggle on hook and line, while the porbeagle is not considered a strong fighter (Ellis 1983, Bigelow and Schroeder 1953). The larger heart size and red muscle mass in *Lamna* may indicate a greater aerobic capacity and the mako probably relies on white muscle for the anaerobic exercises which delight the gamefisherman.

The deep-set red muscle of the lamnid sharks is supplied with blood through the lateral cutaneous rete. We have used the number of vessels in the rete as one indicator of its effectiveness as a heat exchanger. It would have been preferable to use a measurement of the effective area of contact between arteries and veins offered by the rete, but such characterization would have required information on vessel diameter, wall thickness, and length (Mitgard 1983). The vessels have contractile walls and in the material available for study, the state of contraction varied from relaxed to fully constricted. The rete was frequently compressed and distorted after preservation. This made it difficult to make meaningful estimates of vessel diameter or to compare vessel size between specimens. Because of these complications the number of arteries across the rete was used as an easily obtained number for comparing species.

An increase in vessel number is not an important factor in the growth in thickness of the lateral cutaneous rete. The number of arteries across the rete for *Carcharodon* weighing between 12 and 1200 kg was:

$$24.2 + 0.002 \text{ Body Weight}$$

and for mako between 1.3 and 180 kg:

$$19.1 + 0.015 \text{ Body Weight.}$$

The insignificant slope of this regression indicates that the number of vessels remains constant over a 100 fold range of body size. The diameter of the vessels, however, clearly grows larger with size of the fish (Fig. 6) and the same would of course be true of their length.

In *Isurus paucus* there are only a few vessels in the lateral cutaneous rete. With a poorly developed rete and small amount of red muscle, *I. paucus* probably cannot produce or retain much metabolic heat. This is consistent with our one measurement showing a lack of temperature elevation in this species. Its rete,

which is similar to the one in the thresher shark (Bone and Chubb 1983), might not allow much temperature elevation, but could significantly affect the rate of temperature change in the tissue when the fish passes through the thermocline. Such an increase in thermal inertia (Neil et al. 1976) would prolong the time for cooling and allow a fish to operate at temperatures many degrees above ambient for a useful length of time when it moved from warm surface water to cold deep water (Carey 1982).

The lateral cutaneous rete is well developed in *Carcharodon* and *I. oxyrinchus* and is most elaborate in the *Lamna* species (Table 3). Our indicators of heat production and conservation for the muscle rank the sharks: *I. paucus* < *I. oxyrinchus* = *Carcharodon* < *L. nasus* ≤ *L. ditropis*, in order of increasing ability to maintain an elevated muscle temperature. The salmon shark, *Lamna ditropis*, which seems to have the most elaborate muscle rete and a high concentration of red muscle, probably has the highest muscle temperature elevation.

The lamnid sharks have an unusual blood supply to the viscera (Eschricht and Muller 1841, Burne 1923). The normally small pericardial arteries become greatly enlarged, leave the heart chamber and penetrate the hepatic vein where they branch and rebranch to form a great arterial sponge filling the lumen of the vein. On the distal side of this rete the fine arteries coalesce into trunks which serve the visceral organs. The coeliac artery which normally provides blood to the viscera is reduced to a small vessel and most of the visceral blood supply is through the suprahepatic rete. The function of this rete as a heat exchanger is related to the area of interface it offers between venous and arterial blood. This may be as much as 4 m² for an 88 kg *Lamna nasus* (Carey et al. 1981). This is certainly a large area for heat exchange, indicating that on some occasions the organ exchanges heat with high efficiency for a large blood flow. We have not attempted further estimations of blood vessel area in the suprahepatic rete, but have used weight of the organ for our comparisons. The suprahepatic rete is well developed in all lamnid species, but particularly so in *Carcharodon* and *Lamna*. When the sharks are compared by the ratio: suprahepatic rete weight to visceral weight (Table 3), they rank: *Isurus paucus* = *I. oxyrinchus* < *Carcharodon* < *Lamna nasus* = *L. ditropis*. This ratio is strongly affected by weight of the liver, which is the major visceral organ. The liver serves in part as a storage organ and has a large and variable lipid content. Aasen (1961) gives an average of 8% of body weight for liver of *L. nasus*, with a maximum of 18%. In our *I. oxyrinchus* specimens liver varied from 5% to 14% of body weight. Excluding the liver to avoid this source of variation, and comparing the suprahepatic rete to the gut gives the same ranking for the sharks.

Temperature measurements show that lamnid sharks do have warm guts. The visceral temperatures of *I. oxyrinchus* are variable and often low when measured on deck, but during telemetry experiments they regularly maintained stomach temperature elevations of 8°C or more (Carey et al. 1981). The rete in *I. paucus* is similar in size to that in *I. oxyrinchus* and it seems likely that *I. paucus* is capable of a substantial elevation of its visceral temperature. *L. nasus* has warm viscera (Table 1). While no temperature measurements are available from *L. ditropis* or *Carcharodon*, the large size of the rete indicates that their guts should be quite warm.

Because popular interest in *Carcharodon* generates numerous attempts to film it and because it can be attracted to a boat and fed, it is a good candidate for a

telemetry experiment to monitor stomach temperature. Feeding it a transmitter imbedded in a bait would provide information on stomach temperature under natural conditions and could also tell us if stomach temperature rises after feeding and falls when digestion is complete. The stomach temperature of another warm fish, the bluefin tuna, cycles up and down with feeding and digestion (Carey et al. 1984) and it would be most interesting to learn if the lamnid sharks show similar fluctuations. We urge anyone planning an expedition to observe these sharks to consider trying this interesting experiment.

The anatomical information and temperature data are consistent with ranking the sharks *Isurus paucus*, *I. oxyrinchus*, *Carcharodon carcharias*, *Lamna nasus*, and *L. ditropis* in increasing ability to maintain an elevated temperature. Although the number of specimens was small and individual variation was large, we believe that this relationship will hold as more sharks are examined. The sharks rank in the same order with regards to their occurrence in cold water. *Isurus paucus* is a warm water species from the near tropical waters of Cuba, the Gulf of Mexico, and the Gulf Stream. It appears that its muscle is close to water temperature, but its viscera may be warmer. *Isurus oxyrinchus* occurs in warm waters, but also moves into temperate water. It is an active predator on squid, bluefish, and swordfish (Stillwell and Koehler 1982) and its muscle and viscera are warm. *Carcharodon* has a wide distribution throughout the oceans of the world. In muscle temperature it appears to be intermediate between *Isurus* and *Lamna* and the size of its suprahepatic rete indicates that it will rank between these sharks in visceral temperature also. The *Lamna* species are cold-water forms which occur in water cooler than 16°C. *Lamna nasus* is found at 5°C in the North Atlantic (Aasen 1961) and a specimen was captured near South Georgia in the South Atlantic in 1.7 to 3.2°C water (Svetlov 1977). It feeds on squid, hake, mackerel, cod, and other cold water species (Aasen 1961). Maximum temperature elevations of 9°C and 11°C have been found in its viscera and muscle. *Lamna ditropis* also lives in a cold habitat. It has been reported as far north as 60 degrees in the Bering Sea near Kamchatka (Sano 1960, 1962). Mr. J. O'Malley of New England Development Foundation Inc., Boston, reports that the fishing vessel Great Pacific caught two salmon sharks in March and April 1980 northeast of Akutan in the Aleutians. The sharks, which were identified from photographs, were taken from water that was 2.5°C or colder. The 11°C temperature elevations reported in the muscle of these sharks (Rhodes and Smith 1983) are as high as any recorded for the porbeagle and show that salmon sharks are indeed quite warm. From our anatomical comparisons it seems likely that the salmon shark can maintain even higher temperature elevations than the porbeagle.

The lamnid sharks can be compared with another group of warm fishes, tunas of the genus *Thunnus*. The large bluefin tuna, which passes from the tropics to near the Arctic in its annual migrations, controls its body temperature. The temperature elevation is much less in warm water than it is in the cold (Carey and Teal 1969b). The mako apparently has a similar, if less well developed, ability to control temperature (Fig. 1). The white shark is another large fish which occurs over a wide area of the oceans of the world. Its movement pattern brings it into inshore areas in the north during summer months and to unknown regions in the winter (Pratt and Casey, this volume). It encounters a wide range of water temperature but in a telemetry experiment lasting for 3 days, one white shark did not

appear to control its muscle temperature (Carey et al. 1982). It will be interesting to learn more about the body temperature of this fish and how it changes between warm and cold environments.

The tunas vary in their ability to maintain an increasingly elevated temperature in the order: *Thunnus atlanticus*, *T. albacares*, *T. alalunga*, *T. obesus*, *Thunnus thynnus* (Barrett and Hester 1964; Carey et al. 1971; Sharp and Vlymen 1978). In these fish an increased temperature elevation in the muscle is associated with an ability to enter colder water. *Thunnus atlanticus* is confined to warm water while the bluefin, *T. thynnus* moves readily into water as cold as 6°C. Like these warm tunas, the Lamnid sharks utilize their heat conservation ability to function in a cold environment rather than to achieve a high absolute temperature. The muscle of *I. paucus* has relatively ineffective heat exchangers, but its temperature is as warm as or warmer than the *Lamna* species because it lives in a warm environment.

Acknowledgment

This information on lamnid sharks was collected over a span of many years during which the senior author was supported by a number of grants from NSF, including OCE 8311520 and GB8150 and by contracts with NOAA-NMFS. We had the help of many people, but particularly thank Charles Stillwell, Nancy Kohler, and John Hoey, NOAA-NMFS, Narragansett, Rhode Island, who provided much of the data on visceral weights; W. I. Follett, John Mee, Sue Middleton, and Mike Hearne of the California Academy of Sciences for work on one of the *Lamna ditropis* specimens; George Benz of University of Connecticut for help in numerous dissections and all of the many volunteers who at one time or other got wet and filthy helping us at sea.

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Dynamics of White Shark/Pinniped Interactions in the Gulf of the Farallones

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Abstract.—Dynamics of white shark/pinniped interactions in the Gulf of the Farallones by David G. Ainley, R. Philip Henderson, Harriet R. Huber, Robert J. Boekelheide, Sarah G. Allen, and Teresa L. McElroy. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. Observational evidence delineates seasonal and annual trends in the occurrence of white sharks at the Farallon Islands, California, from 1970 to 1983. Seasonal occurrence along the adjacent mainland coast is inferred by similar evidence, 1976 to 1983. In the Gulf of the Farallones, white sharks occurred 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 were more vulnerable to sharks than adults; white sharks also preyed more on seals than on sea lions.

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 subadult 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 sharks may have been frequenting the Farallones.

We speculate on why seals appear to be more vulnerable to shark predation than sea lions, and also that in the Gulf of the Farallones white sharks move inshore and offshore in response to seasonal concentrations of preferred prey (seals as opposed to sea lions). We further speculate that the timing of breeding seasons of seals may be an evolutionary response, in part at least, to white shark predation.

The 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 long-term, intensive studies on pinnipeds, and its systematic daily surveys of the island's shores and inshore waters, have inadvertently provided considerable information on predator-prey interactions between pinnipeds and white sharks. In a recent preliminary analysis, Ainley et al. (1981) 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 (through 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

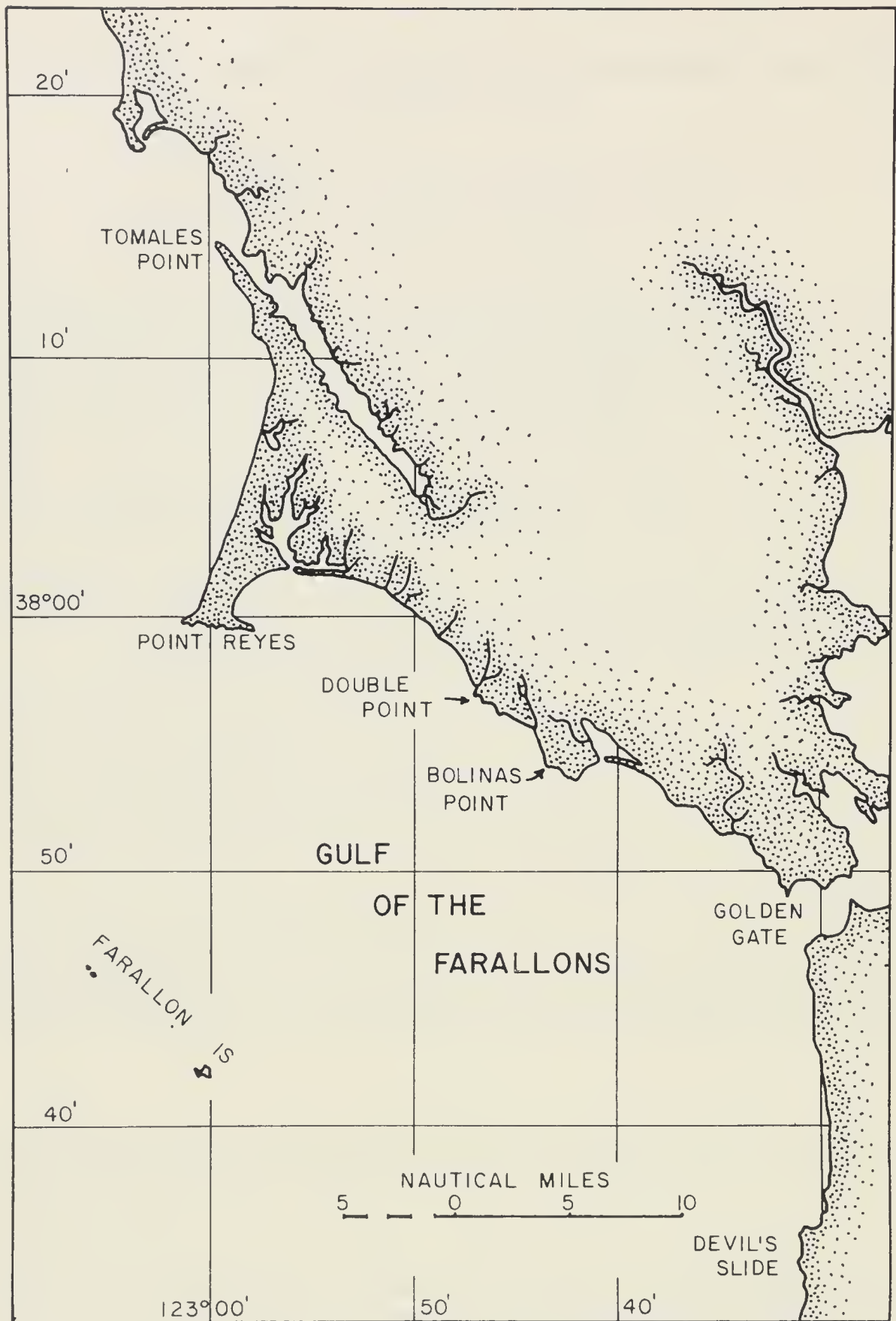


Fig. 1. Map of the Gulf of the Farallones.

numbers of elephant seals rather than to a change in 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 speculate on how natural history patterns of these animals may be interrelated. We extend our data and comments to the adjacent Gulf of the Farallones area.

Methods

The Farallon Islands (San Francisco County) 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. As described in DeSante and Ainley (1980), 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; Huber et al. 1978). 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 reported 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. While biologists' activities changed seasonally—studies emphasizing seabirds from March to August, avian migration including marine birds from August to November, and elephant seal reproduction from December to February—attention given to surrounding waters actually changed little. In almost every instance of shark/pinniped interaction, we were first alerted by a flock of gulls hovering in the vicinity (Ainley et al. 1981). Thus, because gulls are least numerous at the island from September to January (DeSante and Ainley 1980), the chances of noticing this type of shark activity are perhaps least during the fall. As will become clear below, however, other evidence was also available to indicate the presence of sharks. 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 S. G. Allen (unpubl. data).

In the following sections, a subadult elephant seal, identifiable 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 identifiable 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

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

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). We here define a “recent” shark-bite wound as one still bleeding and otherwise showing little evidence of having begun to heal. In contrast to the Farallon pattern, as also 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.

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

Table 3. Observations of pinnipeds by species and age class, with recently inflicted shark-bite wounds, Gulf of the Farallones 1970–1983.^a

Pinniped	Months												Totals
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
Elephant seal													
Adult						2	3	1					6
Non-adult			5	6	7	5			2	1	2		28
Ratio ^b	0.0	0.0	2.6	1.4	1.7	2.7	1.1	0.4	1.0	0.2	0.4	0.0	1.0
Harbor seal													
Adult	1								2	2	3	3	11
Non-adult	1	1										1	3
Ratio	0.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.6	0.9	1.0	0.7
California sea lion													
Adult			1	1	1	3		1					8
Non-adult	4	2	5	5	8	6	3	3	3		1	1	41
Ratio	0.6	0.2	0.4	0.4	0.8	0.9	0.3	0.4	0.3	0.0	0.1	0.2	0.4
Northern sea lion													
Adult		1	1				2	1				1	6
Non-adult		1							1				2
Ratio	0.0	2.0	4.9	0.0	0.0	0.0	3.2	1.6	1.2	0.0	0.0	0.8	0.8
Total observations													
Farallones	4	3	13	13	16	16	8	6	6	1	3	2	91
Mainland	2	1							2	2	3	4	14

^a Data for harbor seals are from Double Point, Marin County, 1977–1982; data for the other species are from the Farallon Islands.

^b The ratio gives the number of bitten animals per the average total animals of that species present during that month ($\times 100$). For September through December (the peak months of shark activity) an average 1.92% of 1304 elephant seals had wounds compared to an average 0.68% of 4591 California sea lions ($t = 3.55$, $P < .01$).

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

Table 4. The number of pinnipeds having fresh shark bite wounds by species and part of body bitten.^a

Pinniped species	Location of wound on body ^b					
	Face/neck	Pectoral region	Side/chest	Belly	Flank/rump	Rear flippers
Elephant seal	7	11	12	3	3	2
Harbor seal	2	1	3	2	5	2
California sea lion		6	5	3	24	8
Northern sea lion		1		1	6	1

^a Data on harbor seals from Double Point, Marin Co. (S. Allen, unpubl.); remaining data from the Farallones.

^b Area of body bitten is similar in the two sea lions ($\chi^2 = 1.663$, 4 df, $P > .900$) and in the two seals ($\chi^2 = 6.052$, 5 df, $P > .250$), but area is dissimilar between sea lions and seals ($\chi^2 = 36.270$, 6 df, $P < .005$).

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 (on the part of young elephant seals, increased vulnerability is a function of seasonal occurrence patterns coinciding with the presence of sharks). We 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 perhaps 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.

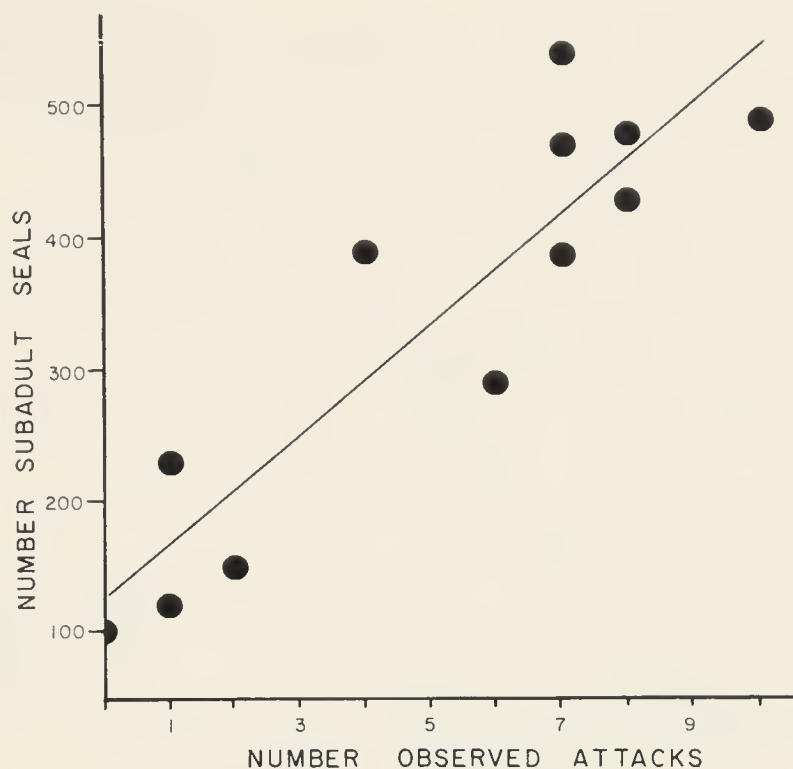


Fig. 2. The number of attacks on pinnipeds at the Farallon Islands as a function of the fall peak in the number of immature elephant seals; Farallon Islands, 1971 to 1982 [attacks = 42.6 (no. seals) + 122.4; $r = .900$].

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 subadult 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 for the moment that white sharks are indiscriminate feeders in the case of pinniped prey, and we also assume that a shark can approach a pinniped usually only from the latter's "blind" side, which would generally be from the rear, when the shark 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

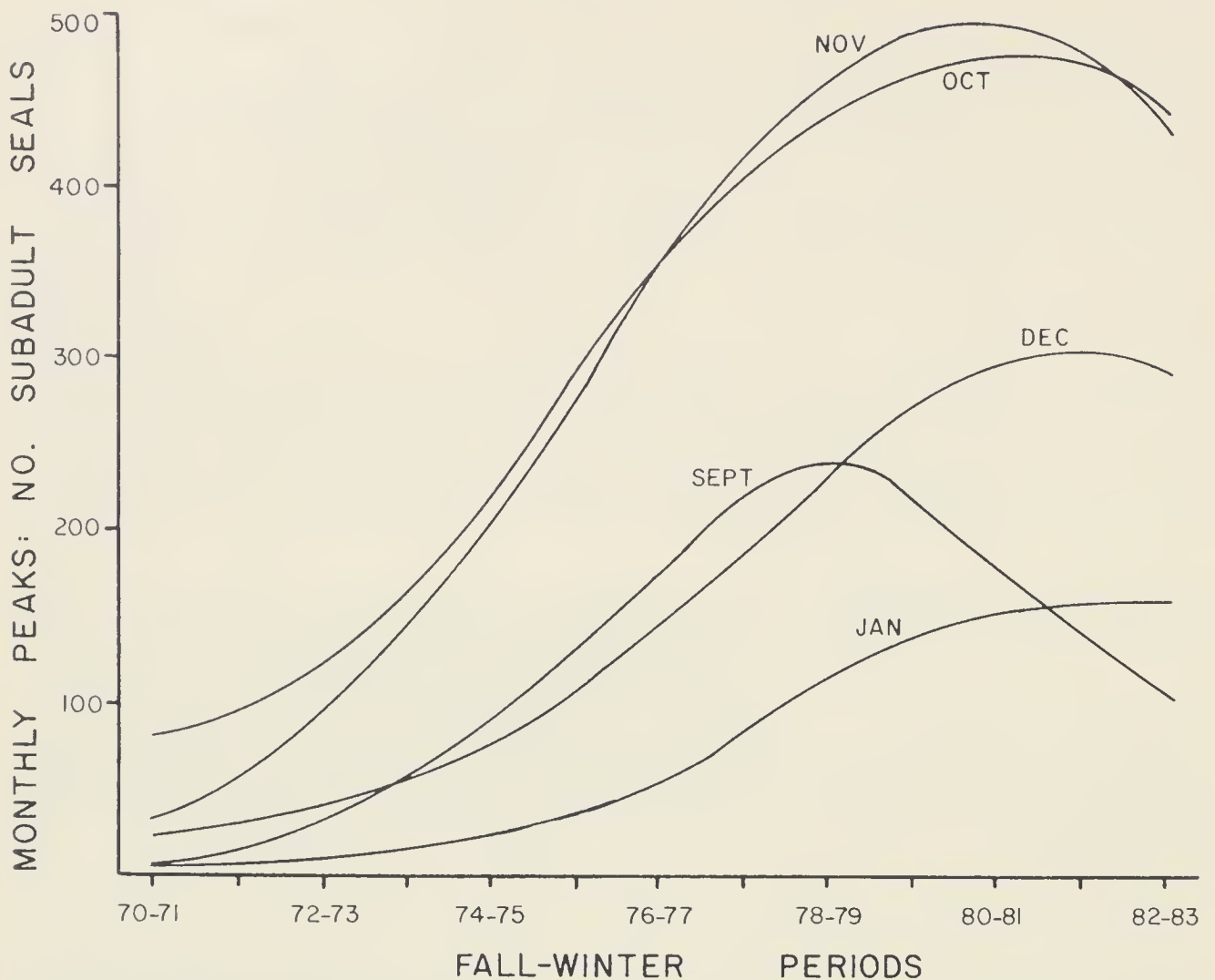


Fig. 3. Trends in the number of subadult elephant seals at the Farallon Islands during each fall/winter month, September–January; curves for October and November are described by second degree polynomial equations, where z is the number of animals and x is the year; October: $z = -68.7 + 95.2x - 4.3x^2$, $r = .964$; November: $z = -22.3 + 81.7x - 3.4x^2$, $r = .949$.

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 on the surface 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 may allow 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 reported in 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 1982; Fig. 2). However, the annual rate of increase in the number of young elephant

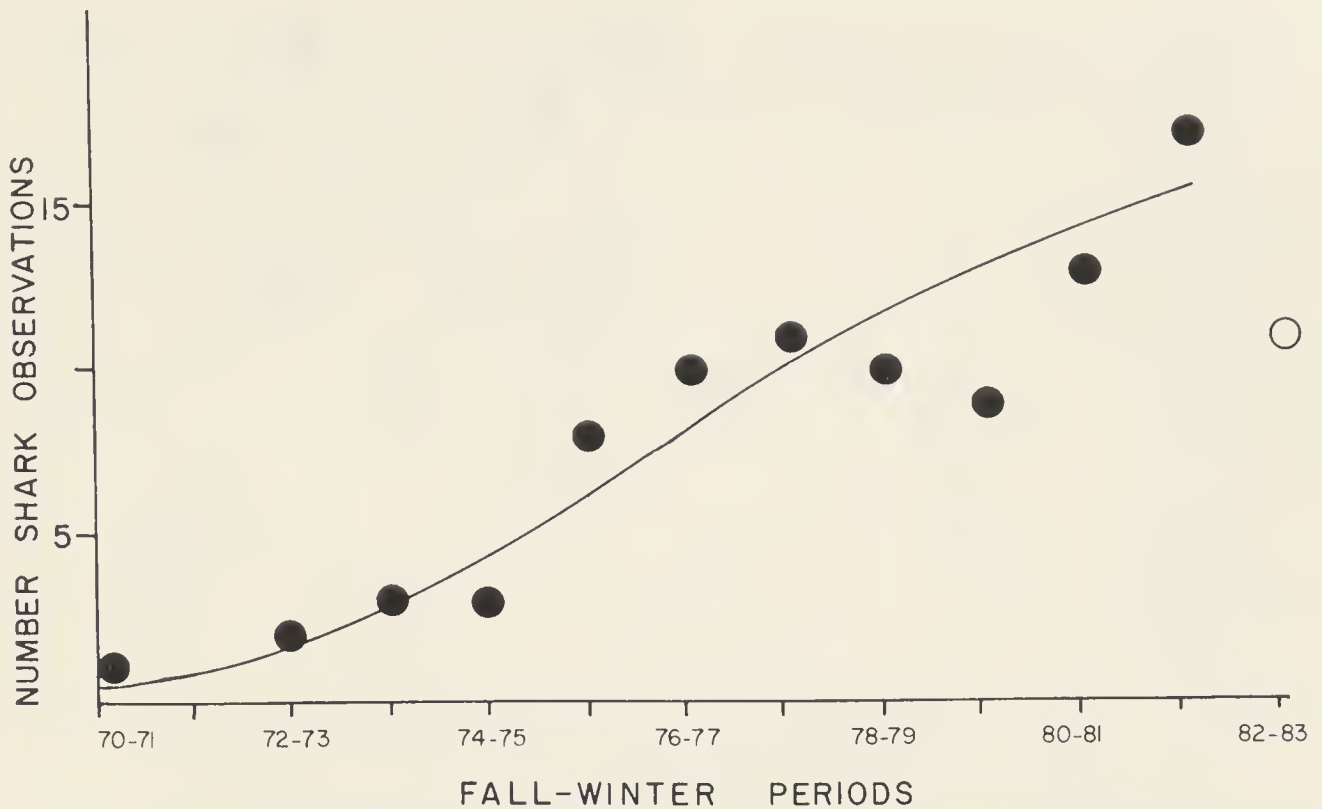


Fig. 4. The trend in the number of white shark sightings at the Farallon Islands 1970-71 to 1981-82 (annual periods extend from July through June); the curve is described by the equation, z (sightings) = $-1.8 + 1.7x - .02x^2$ ($r = .943$). The open circle designates sightings in 1982-83, when four large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

seals hauling out 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 change (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 (r) of .900, whereas regressions against the peak number of subadult sea lions and to the total pinnipeds present each fall yielded r -values of only .800 and .843, respectively. All correlation coefficients were statistically significant. The analysis was not 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 same fall/winter period, and not typical of patterns in previous years, 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. (During the fall/winters of 1983/84, only 7 incidents were observed in spite of continued growth in pinniped populations.)

The killing of the four sharks at the islands possibly nullified our study, but their capture and the subsequent reduction in shark activity did indicate some interesting points. First, it became apparent that only a few, and perhaps no more than 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

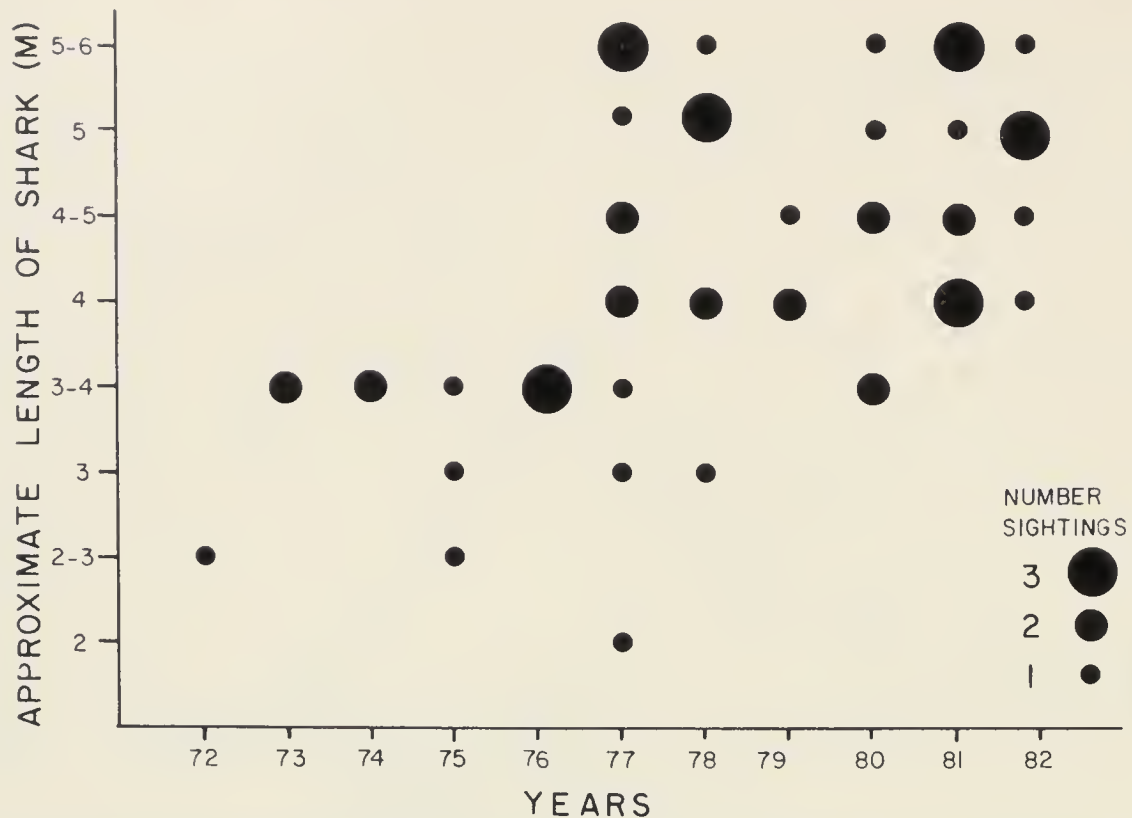


Fig. 5. The estimated lengths of white sharks (as a function of the estimated distance between caudal and dorsal fins) seen at the Farallon Islands, 1972-73 to 1982-83.

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

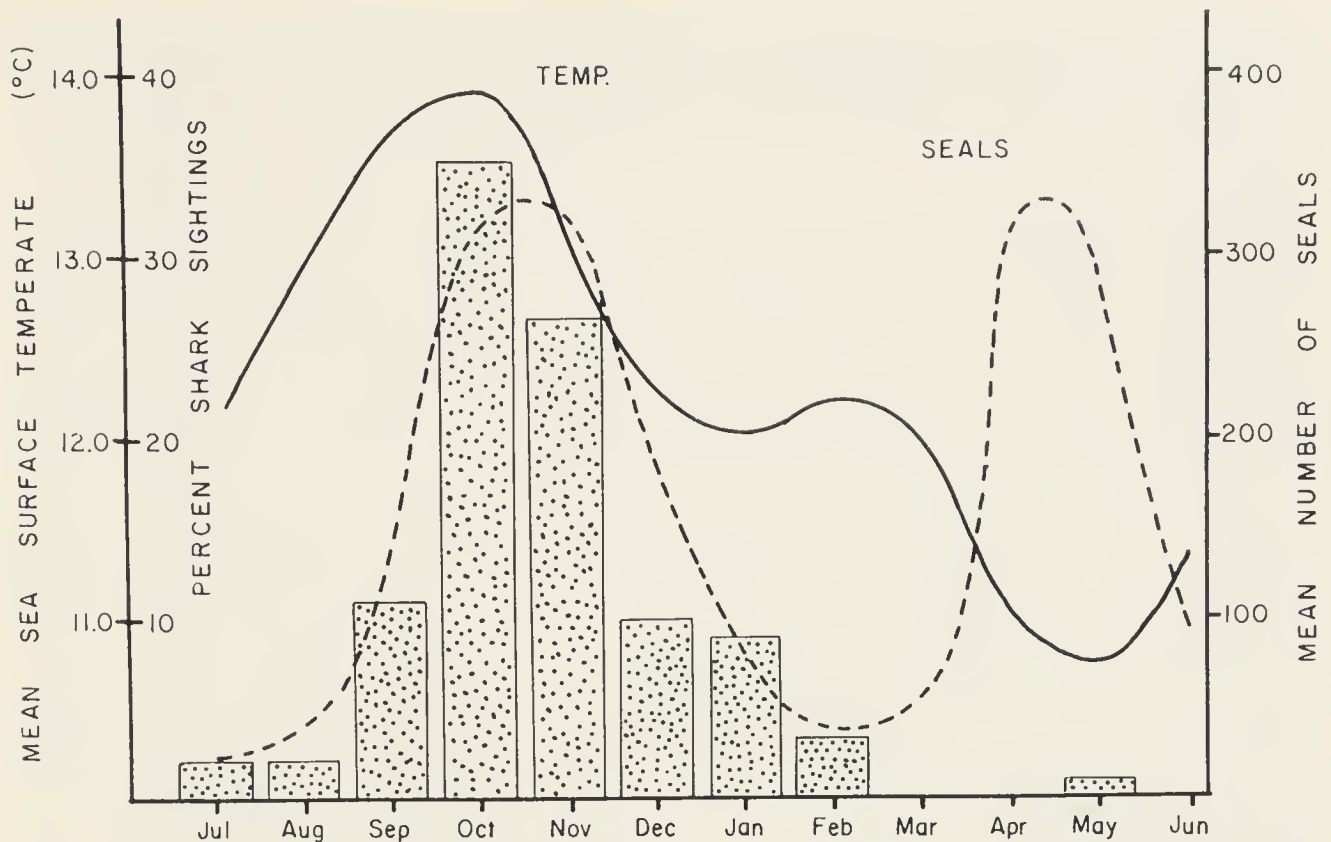


Fig. 6. The proportion of white shark sightings by month compared to the mean monthly sea surface temperature (°C) and the mean monthly numbers of subadult elephant seals, Farallon Islands, 1971-72 to 1982-83.

year) is comparable roughly to the rate calculated by Cailliet et al. (1985); on the basis of other 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). The anomalously low frequency of sightings in 1982-83 (and later), as indicated above, was the result of overfishing.

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

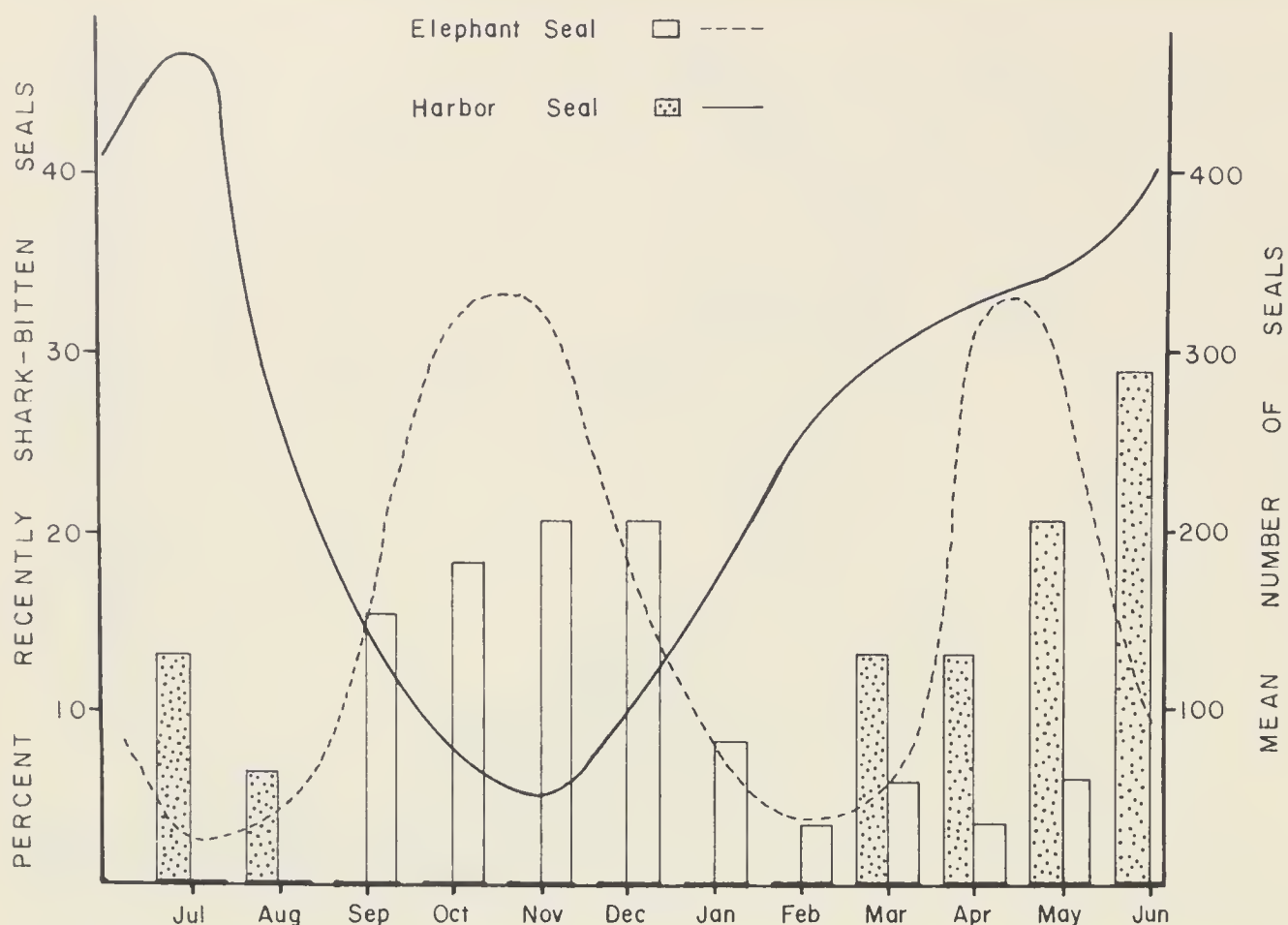


Fig. 7. Changes in the seasonal inshore vs offshore occurrence of white sharks compared to seasonal cycles in the abundance of inshore vs offshore prey: harbor seals at Double Point and immature elephant seals at the Farallon Islands, respectively; shark presence is reflected in the proportion of recently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

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). (It should also be noted that although 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.

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 give birth to their young in the area, as indicated by the fact that few 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. Thus, northern elephant seals raise their young at the same time of year, but in a different season than their subantarctic counterparts, *M. leonina*. Other pinnipeds in California 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). Except 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.

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White Shark Attack Behavior: Observations of and Speculations About Predator and Prey Strategies

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Abstract.— White shark attack behavior: observations of and speculations about predator and prey strategies by John E. McCosker. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. The predatory behavior of the white shark, *Carcharodon carcharias* (Linnaeus), is analyzed on the basis of literature records and field observations in southern Australia and northern California. Young white sharks are primarily piscivorous and possess narrower teeth than do the adults, which feed primarily on pinnipeds. Adult feeding behavior, sensory stimuli involved in the shark's prey search behavior, and prey avoidance strategies are discussed. The shark's bite-and-spit behavior is interpreted to be an adaptation to avoid injury from struggling pinniped prey. White shark predation on elephant seals, *Mirounga angustirostris*, at Año Nuevo Island and the Farallon Islands is described. White shark populations and attacks on humans in California are apparently increasing, along with the increase and range expansion of elephant seals; shark populations may further increase. Breath-hold diver behavior and the similarity in appearance of the silhouette of contemporary surfboards to that of a pinniped are presumed to be responsible for many attacks upon humans. Recommendations to avoid shark attack and suggestions for future research are presented.

Analysis of white shark predatory behavior has historically been limited to the opportunistic capture and evisceration of post-prandial individuals, a rare glimpse from shoreline or shipboard of a shark feeding, or the analysis of bite scars left upon normal white shark prey items or human victims. Since white sharks are uncommon, feed only occasionally, and present a life-threatening risk to the observer of shark behavior, it is therefore not surprising that little accurate information has been documented about this, perhaps the most dangerous of living fishes to mankind. The advent of modern self-contained underwater breathing apparatus, the improvement in underwater high-speed and high-resolution movie equipment, and the public's interest in the white shark since the advent of the films "Blue Water, White Death" and "Jaws" have recently presented research opportunities to study the predatory behavior of the white shark from within its own milieu.

Reviews of white shark biology are limited. Tricas and McCosker (1984) updated McCosker's (1981) and Ellis' (1975) general reviews and added original data and analysis based on 11 days of observation and experimentation during the 1980 Giddings' White Shark Expedition to South Australia. Their findings were discussed at the 1983 Fullerton White Shark Conference and it is upon those discussions, published and unpublished data, and recent observations that I have made along the California and south Australian coastlines that I have prepared this summary report.

Due to the paucity of data, much of what I propose in this report must be

considered speculative. At such time however, when a healthy white shark is maintained in a captive state, the opportunity will exist to test my hypotheses.

Ontogenetic Feeding Behavior

Carcharodon carcharias is the largest living flesh-eating elasmobranch, rivaled only by the tiger shark (*Galeocerdo cuvier*) of tropical seas. Their large size at birth, greater than 125 cm (Smith 1951) and 18 kg (Tricas and McCosker 1984), makes them formidable predators soon after birth. They are viviparous (Wourms 1977) and, although not yet verified, are probably oophagus, participating in intrauterine cannibalism as do *Odontaspis* spp. and certain alopiids (Gilbert 1981). *Carcharodon* prey items and dental morphology change with growth and are accompanied by a change in predatory behavior (Tricas and McCosker 1984; and other papers in this volume).

The white shark dental condition is unique in that teeth are both serrate and regularly triangular (particularly the central jaw teeth). However, juveniles and sub-adults (less than 3–4 m total length) have a longer and narrower tooth shape than do adults (see Tricas and McCosker 1984, Fig. 13, and discussions elsewhere in this volume). This condition allows them to grasp small bonyfishes and elasmobranchs, but lacks the cutting ability of the broader tooth of the adult. Like the relatively smaller mako (*Isurus* spp.), the young white shark is more capable of making the rapid turning movements involved with capturing moving fish prey than is the larger, apparently more ungainly adult white shark. Gut content analyses of young northern California white sharks (Tricas and McCosker 1984; W. I. Follett, pers. comm.) indicate that benthic fish are abundant prey items. The California bat ray (*Myliobatis californica*), spiny dogfish (*Squalus acanthias*), leopard shark (*Triakis semifasciata*), lingcod (*Ophiodon elongatus*), and cabezon (*Scorpaenichthys marmoratus*) were most abundant, and all inhabit shallow water habitats. Lingcod and cabezon are camouflaged, benthic, rocky reef and kelp bed associates, whereas the bat ray and other sharks typically frequent sand and mud bottom bays and estuaries. Prey within white shark stomachs were usually intact and suggest that the young sharks search, grasp, and swallow their prey entire. Observers of white shark feeding habits should be cautious in interpreting the prey species found in stomachs of sharks caught by fishermen; it has been my experience that sharks are often entrapped in gill nets while consuming net-caught halibut, flounders, and white sea bass, prey species which might not otherwise have been eaten. The state of digestion, or course, affords a clue to the method of prey capture.

The tooth shape of larger white sharks (ca. 4 m total length) broadens basally, providing a cutting and gouging ability which is well suited for feeding upon large, thick-skinned mammalian prey. Tricas and McCosker (1984) reported both fish and pinnipeds in adult white sharks, but suggested that certain fish prey might have been incidental to net capture. Le Boeuf et al. (1982) found only marine mammals in California white sharks, and it is noteworthy that all of their white shark specimens had been either harpooned or found as beach washups. They examined six individuals longer than four meters and a small, 2.4 m individual which had a 10 cm patch of pinniped pelage in its stomach. In California waters, elephant seals (*Mirounga angustirostris*) are commonly preyed upon by adult white sharks (Le Boeuf 1974) and apparently support a sizeable white shark population

at the Farallon Islands (Ainley et al. 1981) and at Año Nuevo Island (Le Boeuf et al. 1982). Adult male *Mirounga* are apparently more susceptible to white shark predation because they are excluded from desirable haulout sites by larger bulls.

The Farallon Islands and Año Nuevo Island, along the central coast of California, have been carefully monitored by scientists at the University of California, Santa Cruz, and the Point Reyes Bird Observatory, respectively. The Farallon Islands, in San Francisco County, are located 30 km west of San Francisco and lie along the edge of the continental margin and the California current. The largest island, Southeast Farallon (lat. 37°25'N, long. 123°0'W), is ca. 700 m long and has 10 major seal and sea lion haulout sites. The much smaller north islands have not been carefully studied and all references herein refer only to Southeast Farallon. Año Nuevo Island (lat. 37°05'N, long. 122°20'W), in San Mateo County, is a small, irregular rocky islet 600 m offshore and ca. 260 m × 400 m.

The frequency of shark attack has been well documented at the Farallon Islands (Ainley et al. 1981, 1985), but the lack of accurate shark population estimates and the inability to identify individuals disallows any calculation of feeding frequency by individuals. Carey et al. (1982) made a crude estimate of the duration between meals in their estimate of the metabolic rate of a 4.6 m white shark. They suggest that such a shark could survive for approximately 45 days on 30 kg of whale blubber, an adaptive behavior if in fact the sharks migrate or feed only occasionally. The Farallon Islands data (Ainley et al. 1981; and in this volume) indicate that white sharks may feed upon pinnipeds more often than Carey et al. suggest, but as yet no accurate study has been made. White sharks commonly prey upon the carcasses of floating cetaceans and basking sharks (*Cetorhinus maximus*). The observations of attacks upon basking sharks have all been made in association with harpooned individuals (Fast 1955; Limbaugh 1963; Squire 1967), thus its significance under normal circumstances is not known.

White sharks do prey upon naturally occurring whale carcasses and appear to feed until sated under such circumstances. In 1982 I observed a single white shark, ca. 4–5 m in length, feeding near shore upon a floating gray whale (*Eschrichtius robustus*) carcass in central California. No other shark species were observed in the close vicinity. Pratt et al. (1982) report that four and possibly as many as nine white sharks fed during a 30 hour period upon a floating fin whale (*Balaenoptera physalus*) carcass. No more than two white sharks were ever seen feeding together and blue sharks (*Prionace glauca*) and shortfin makos (*Isurus oxyrinchus*) were conspicuously absent, suggesting that feeding adult white sharks exclude other sharks and smaller conspecifics. On 17 January 1980, I witnessed a similar intraspecific encounter between two white sharks at Dangerous Reef, south Australia. The smaller, ca. 3.5 m male, was feeding upon a large floating piece of horsemeat bait when a larger, ca. 4 m, male swam to the bait, rapidly advancing upon the feeding shark and bit it on the nape using only its upper jaw teeth. (The shark's wounds, but not the attack event, were photographed.) The smaller shark, with only visible puncture wounds, rapidly fled while the larger began to eat and once apparently sated, departed. The smaller shark returned in two hours and remained at the periphery until the larger shark had left, at which point it fed upon the bait.

Other prey items of adult California white sharks include harbor seals (*Phoca vitulina*) (Fitch 1949), California sea lions (*Zalophus californianus*) (Le Boeuf et



Fig. 1. White shark attack scar on adult male California sea lion. Note the lower jaw puncture marks on the right foreflipper and lacerations from upper jaw teeth along the shoulder. Photo taken at Año Nuevo Island by Ray Bandar.

al. 1982), Steller sea lions (*Eumetopias jubata*) and, presumably, northern fur seals (*Calorhinus ursinus*). There have been numerous accounts (Snow 1910; Orr 1959; Ames and Morejohn 1980) of sea otters (*Enhydra lutris*) having been attacked by white sharks, although none has been found within a shark stomach. It has been suggested that white sharks do not consume sea otters; it seems more reasonable to conclude that the stomach contents of too few sharks have been examined from areas inhabited by sea otters. White shark prey records extralimital to California include the harbor porpoise (*Phocoena phocoena*) (Arnold 1972), a variety of elasmobranchs, and the blue whale (*Balaenoptera musculus*) (Ellis 1975).

Predator and Prey Strategies

On the basis of my underwater observations of 25 white sharks (2.5–5.5 m, total length) in Australian waters, I suggest the adult white shark is a relatively ungainly predator, and presumably unable to catch most smaller, more agile healthy prey species. It therefore must attack its prey by surprise, attempt to immobilize it at first contact, and then consume the incapacitated prey. The location of bite scars well evidences such behavior (see Figs. 1–2).

A likely attack scenario involving an adult white shark would consist of a pinniped prey at the surface, either resting on its dorsum or perhaps on its venter, ventilating its lungs after returning from a dive. Water depth at the attack site, in the case of the Farallones, is usually 4–12 m (Ainley et al. 1981). Attacks upon humans off California and Oregon (Miller and Collier 1981), and presumably upon most pinnipeds as well, have occurred beyond the edge of the kelp bed,



Fig. 2. Carcass of subadult male California sea lion displaying white shark bite. The shark's lower jaw teeth penetrated the right flank, indicating that the sea lion may have been in a prone posture when attacked from below. Photo taken along central California coast by Ray Bandar.

although white shark swim among but below the kelp canopy (pers. obs., and Al Giddings, pers. comm.). A white shark, swimming a few meters below the surface, would presumably be visually attracted to the silhouette of a pinniped or sea otter at the surface. Once prey is sighted, the shark rapidly ascends and at close range (ca. $\frac{1}{2}$ body length or less) begins one of a variety of modal action feeding patterns (cf. Tricas and McCosker 1984; Tricas 1985) according to prey size and posture.

The attack usually consists of a single massive bite from beneath and behind the prey which, in the case of pinnipeds, is typically upon the midbody, haunches, or flippers. Analysis of victims and carcasses indicate that white shark attacks rarely occur on the head region, indicating that frontal attacks are less successful and/or that head bitten seals do not survive (Le Boeuf et al. 1982; Ainley et al. 1985; and pers. observ.). Attacks upon the harbor porpoise (Arnold 1972) and upon humans display a similar pattern.

Although a variety of shark species and human behaviors were involved, Baldridge (1974) reported that 90% of attacks upon humans were at the surface and Miller and Collier (1981) listed 79%. Miller and Collier further note that only eight of 43 attack victims observed the shark before being attacked, and only three of 42 were frontal attacks. Feet and legs were most commonly attacked, followed by arms and hands, and the torso. Of the three recorded human white shark attack victims in Chile, two were taken mid-torso and the third on the foot (Egaña and McCosker 1984).

The behavior of sea otters and California sea lions appears to make them particularly vulnerable to such an attack strategy; when at the sea surface, sea lions spend much of their time with their fins in the air (Fig. 3), and sea otters



Fig. 3. Aggregation of California sea lions with flippers out of the water. This posture is presumably contributory to the attacks by white sharks from below and behind the prey. Photo by Brian Gibeson.

float on their backs while preening or feeding (Fig. 4). I suggest that certain behaviors such as the gregarious nature of sea lions and the occasional lateral "eskimo roll" made by sea otters might increase the chance of seeing an ascending shark, thereby avoiding attack.

The behavior of the shark just prior to and during the attack is noteworthy. Because of the location of the eyes and the extension of the upper jaw accompanying the snout lift during the bite (Tricas and McCosker 1984; Tricas 1985), it appears that the shark is unable to see the prey at the moment of strike, particularly if the prey has sensed the onrushing shark and is attempting to escape at the surface. Tricas and McCosker (1984) proposed that at that moment the shark depends extensively upon the ampullae of Lorenzini to locate the struggling prey. The amount and distribution of ampullae would support such a contention. Furthermore, analysis of high-speed film indicates that the shark's eyes are rolled posteriorly within the socket at that time, protecting the eye from the defensive struggles of the pinniped victim.

Controversy exists concerning the forcefulness of the attack; whereas many human and pinniped victims are lifted out of the water and boats are occasionally attacked with such force that they are stove in (Follett 1974), Miller and Collier (1981, p. 92) state that "most of the attacks (upon humans) were apparently slow, deliberate movements which could be described as an investigatory interaction." In all recorded north Pacific attacks upon humans, the victim was then released and the shark routinely retreated a short distance from the injured and immobilized prey, thereby allowing the victim to lapse into shock or bleed to death.

In the case of human victims, I suggest that the retreat behavior has previously been misinterpreted to indicate something "distasteful or offensive" about human flesh and/or neoprene wet suit material. It is commonly held that white sharks

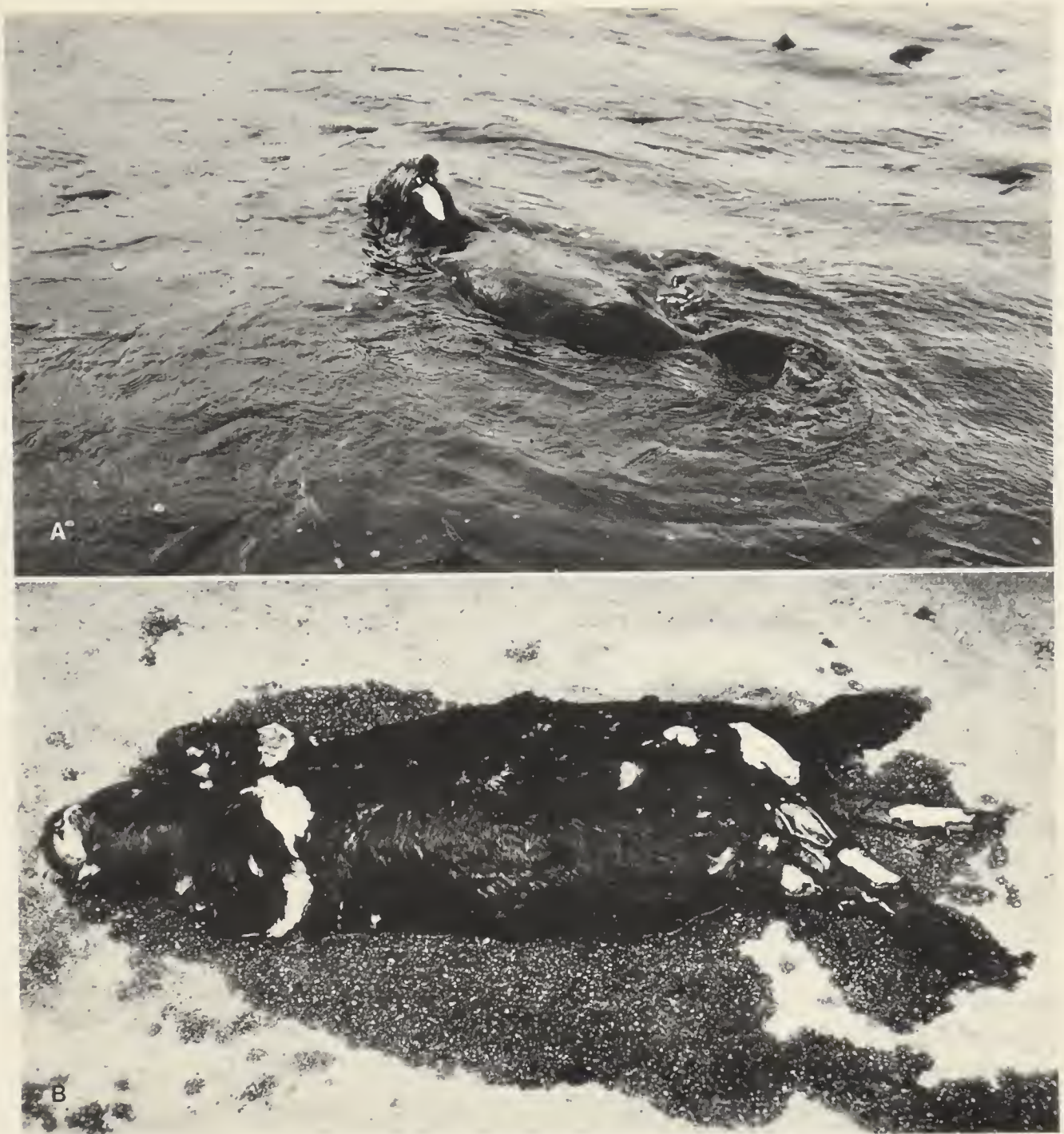


Fig. 4. Sea otters from the central California coast. A. Adult in normal feeding or preening posture along the edge of a kelp bed. Photo by J. E. McCosker at Monterey Bay. B. Lacerated carcass from which several white shark tooth fragments were removed, suggesting that the animal was bitten at the surface while lying on its back. Photo by Jack Ames at Pismo Beach.

are “man-biters,” but not “man-eaters,” a paradox when one considers the catholic nature of its diet. Rather, I interpret this “bite-and-spit” behavior to be adaptive in that it reduces the injury to the shark caused by the teeth and nails of a struggling pinniped. It is noteworthy that even the largest adult bull elephant seals, more than 4.9 m long and between 1800–2700 kg, were attacked at Año Nuevo Island (Le Boeuf et al. 1982) and the largest southern fur seal (*Arctocephalus doriferus*) bulls at Dangerous Reef, south Australia, had been attacked (pers. obs.).

A variety of sensory receptors, as well as vision and electric field detection, are perhaps involved in white shark prey location and will be mentioned briefly. Odor

is probably significant in the discovery of floating cetacean carcasses. Carey et al. (1982) and Pratt et al. (1982) suggest that dead whales may be a primary food source for white sharks in the western north Atlantic. In south Australia, the Giddings Film Expeditions of 1980 and 1983 were able to attract white sharks to a boat in 2½ and ca. 6 hours, respectively, using a blood and tuna emulsion that created a surface slick that extended for ca. five km.

Considering the speed and erratic swimming behavior of seals and sea lions, it is unlikely that odor plays a significant role in white shark predation upon healthy pinnipeds, except for the general odor that is associated with the vicinity of a rookery.

At present there is nothing to indicate that hearing is significantly involved in white shark predatory behavior. As stated above, white shark vision is important in locating prey, although the levels of sensitivity and diurnal shifts have yet to be investigated (cf. Gruber 1977).

The importance of the ampullae of Lorenzini to near field prey detection and movement is worthy of further study. Kalmijn (1971, 1982) has demonstrated the significance of electric and magnetic field detection by other elasmobranchs and shown that the electric fields detected are weaker than those generated by a moving vertebrate or invertebrate (cf. Boord and Campbell 1977). Tricas and McCosker (1984) performed cursory experiments which indicated that white sharks can correctly choose between dead baits with and without pulsed or constant currents. They further suggested that white shark attacks on boats are in response to the electric field created by the electrolysis devices located on the underside of boats.

White shark predation upon pinnipeds and sea otters in California appears to contribute to population control. At most any time, a visitor to Año Nuevo Island, Farallon Island, or Guadalupe Island (225 km west of central Baja California, lat. 29°11'N, long. 118°16'W) will encounter elephant seals, harbor seals, or sea lions with fresh or healing white shark attack scars, and may also discover pinniped carcasses along the shoreline with evidence of a massive white shark bite. Identification of the attacker as a white shark is not difficult due to the typical scar pattern and occasional presence of teeth or tooth fragments (cf. Le Boeuf et al. 1982; Ainley et al. 1981; Ames and Morejohn 1980).

The proportion of the population which has been bitten is often high. Data from Ainley et al. (1981) and Le Boeuf et al. (1982) indicate that it is a density dependent function, such that increasing elephant seal colonies are evidencing a proportional increase in shark attack. (It is important to note, however, that this evidence does not take account of attack victims that are successfully consumed.) This also may be biased by the dietary shift of a growing white shark; as the shark population increases, their numbers will not affect the seals until they shift from a primarily piscivorous diet to one of pinnipeds, thus incorporating a lag time of several years.

A mature elephant seal and white shark community may evidence an even greater proportion of attacks if one may draw a conclusion from Townsend's (1885) report that 19th century sealers observed that 25% of the female elephant seals at San Cristobal Bay, Mexico, bore "unmistakeable traces of the teeth of sharks." Few shark-bitten weaned pups are seen at Farallones or Año Nuevo, suggesting to Le Boeuf et al. (1982) that weaned pups rarely survive an attack.

Shark attack survivors of both sexes have a much reduced breeding success. Le Boeuf et al. (1982) note that at Año Nuevo, most injured females do not successfully give birth during the year of injury and fail to copulate as well. Ainley et al. (1981) found similar results at the Farallones, where only one of nine shark-injured mothers was able to wean her pup. If the mortality calculated at Año Nuevo Island is largely a result of white shark predation, then shark attacks must be more common than presently suspected. At Año Nuevo, Le Boeuf (1974) observed a 50% mortality of alpha bull elephant seals, and Reiter et al. (1978) found only 50% of weaned pups going to sea in the springtime return the following September; in neither case, however, were the authors able to ascribe a proportion of that mortality to white shark predation.

A related phenomenon has been observed in eastern Canada (Brodie and Beck 1983) whereby a decrease in the predatory shark population through a shift in commercial fishing practices has resulted in an increase in grey seal (*Halichoerus grypus*) abundance. Concomitant with a shift from incidental shark capture to a vastly more effective longline capture technique, grey seal pup abundance increased nine fold on Sable Island, off Nova Scotia (Mansfield and Beck 1977).

Although elephant seal population at the offshore islands are high in the spring, there is a seasonal reduction in shark attacks and presumably shark numbers. Earlier data suggested that sharks might fast periodically (Springer 1967) or migrate seasonally (Squire 1967). However, Ainley et al. (1985) observed a seasonal shift in white shark attack sites from the island to the mainland in northern California and a concomitant shift from elephant seal to harbor seal prey. Le Boeuf (pers. comm.) and Ainley et al. (1985) have hypothesized that the springtime pupping season of *Mirounga angustirostris* might have evolved, in part, so that weaned pups enter the water in the spring when predator pressure is lowest. Weaned pups depart rookeries in spring throughout the range.

White Shark and Human Interactions

There has been a marked increase in white shark attacks upon humans in central and northern California and Oregon waters since 1959 (Miller and Collier 1981; Lea and Miller 1985). Concurrently, there has been a significant increase in white shark attacks upon pinnipeds and sea otters as well as an increase in the abundance of white sharks (Miller and Collier 1981; Le Boeuf et al. 1982) which as adults prey nearly entirely upon them. I suggest that *Carcharodon carcharias* was historically more abundant than at present but, due to the activity of elephant seal, sea otter and fur seal hunters in the 19th century (Le Boeuf and Bonnell 1980), the shark population was dramatically reduced. The northern elephant seal population has made a rapid recovery in this century and has yet to achieve its population potential and expanded breeding range (cf. Le Boeuf 1977). Although it is at present difficult to establish a population estimate of *Carcharodon carcharias* in California and the vagaries of human behavior are difficult to predict, it is most likely that Californians will witness an increase in both white shark numbers and shark attacks upon humans.

Differences in human behavior along the California coast north and south of Point Conception may also be contributory to shark attacks. For example, all of the 14 white shark attacks upon surface swimming divers (primarily in search of abalone) have occurred in northern California. Abalone are present throughout



Fig. 5. Silhouette of a surfer lying prone on a short surfboard (right) alongside an adult female harbor seal (left). Photo, at Steinhart Aquarium by Al Giddings, Ocean Images, Ltd. ©.

the coast, but in southern California recreational abalone divers are allowed to use SCUBA. In northern California, abalone are, by law, only collected by breath-hold divers who spend the majority of their dive time at the surface, and divers therefore might be mistaken for pinnipeds.

White shark attacks upon surfboarders and paddleboarders have become a significant problem since 1972 and are also limited to the north coast of California and Oregon. Whereas surfing is a more popular activity in southern California, it is largely confined to long expanses of sand beaches, well away from pinniped aggregations and rookeries. Surfing along the northern California coastline is often conducted in the vicinity of rocky headlands and near pinniped rookeries. Fourteen attacks upon humans on surfboard have occurred since 1972 in the north Pacific, all north of Point Conception. A single white shark attack (in 1969) upon a surfer, has been recorded in Hawaii, at Makaha, Oahu (Balazs and Kam 1981). More intriguing, perhaps, is the observation by Tricas and McCosker (1984) that the design of modern surfboards is contributory to white shark attack. They note that "since the early 1970's, the trend in surfboard design has been toward an increase in floatation, reduction in board length, multiple posterior fixed rudders ('skegs'), and bifurcated 'v' tails. All of these modifications have enhanced the similarity between the silhouette of a surfer and that of a pinniped, and [they] suggest this may increase the possibility of attack." Figure 5 well exemplifies that similarity in silhouette.

With the increasing body of knowledge concerning white shark behavior, and the presumption that white shark abundance and attacks upon humans will continue to increase, what then might we do to avoid unpleasant experiences between

these two species? As yet, there is no adequate means of shark deterrence other than avoidance. The "buddy system" rigorously practiced by most American divers has saved the lives of many attack victims after the initial bite of the shark; in most cases, the victim has been rescued after the initial "bite-and-spit" and before the shark completes the attack. It is noteworthy that in Chilean waters, where divers often dive alone, two of the three attack victims since 1969 have been partially or entirely consumed by the white shark after the initial attack (Egaña and McCosker 1984).

Rookeries and other areas of white shark abundance should be properly identified so that recreational divers, swimmers, and surfers will be familiar with the potential risk.

Finally, any efforts to control white shark and/or pinniped numbers, as has been suggested by some, should be approached with utmost caution. Marine mammals are now protected by federal and international regulation and will probably continue to increase, approaching pre-exploitation levels. Without *Carcharodon carcharias* to affect their numbers, the pinniped populations will remain imbalanced. Future research concerning the predatory behavior of *Carcharodon carcharias* should be directly toward an accurate survey of population size and individual movements, as well as a comprehensive study of healthy captive animals.

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Shark Attacks off the California and Oregon Coasts: an update, 1980–84

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Abstract.—Shark attacks off the California and Oregon coasts: an update, 1980–84 by Robert N. Lea and Daniel J. Miller. *Southern California Acad. Sci.*, Memoirs, Vol. 9, 1985. In 1981 Miller and Collier reported on 47 unprovoked shark attacks which had taken place off California and Oregon from July 1926 to November 1979. Since that date, 12 shark attacks involving humans have taken place: two in 1980, one in 1981, four in 1982, one in 1983, and four in 1984. Encompassed in these 12 attacks were: six surfers, three skin divers, one paddle boarder, one scuba diver, and one swimmer. In ten of the twelve attacks the white shark was the species implicated. By geographic area: one attack occurred off southern California, four off central California, four off northern California, and three off Oregon.

In 1981 Miller and Collier reported on all shark attacks occurring off California and Oregon from 1926 through 1979. Their analysis included 47 unprovoked attacks: 45 off California and two off Oregon. Since 1979, 12 unprovoked shark attacks involving humans have taken place within this geographic area: two in 1980, one in 1981, four in 1982, one in 1983, and four in 1984. The 12 attacks involved six surfers, three skin divers, one paddle boarder, one scuba diver, and one swimmer. In five cases there was no injury to the victim, in two cases minor injury, in three cases major injury (hospitalization), and two attacks proved fatal. In ten of the 12 attacks the white shark, *Carcharodon carcharias* (Linnaeus), family Lamnidae, was the species of implication. In the other two attacks only the fact that a shark (of unknown species) was involved could be established.

As pointed out by Baldrige (1974), “considerable variance exists in published accounts of what happened, again clearly attesting to the difficulties in gathering meaningful information on shark attacks of the past.” This, coupled with the fact that ocean-water sports such as skin diving, scuba diving, surfing, paddle boarding, kayaking, wind surfing, etc. have increased in popularity during recent years, makes comparing early shark attack information with more recent data a difficult and somewhat questionable proposition.

By geographic area: one attack occurred in southern California (south of Point Conception), four off central California (between San Francisco Bay and Pt. Conception), four off northern California, and three off the coast of Oregon. A geographical listing of California-Oregon shark attacks is presented in Table 1; all attacks since 1926 are enumerated with a breakdown by county given. Forty-six of the fifty-nine (78 percent) shark attacks for California and Oregon can be attributed unequivocally to the white shark (Table 1). A summary of white shark

Table 1. California-Oregon shark attacks by county, 1926 through 1984.

	Number of attacks	Species involved			
		White shark	Blue shark	Species unknown	Other species
Oregon					
Clatsop Co.	1	1			
Tillamook Co.	2	2			
Lincoln Co.	0				
Lane Co.	0				
Douglas Co.	1	1			
Coos Co.	1	1			
Curry Co.	0				
California					
Del Norte Co.	0				
Humboldt Co.	2	2			
Mendocino Co.	3	3			
Sonoma Co.	5	5			
Marin Co.	7	7			
Alameda Co.	1			1	
San Francisco Co.	1	1			
Farallon Islands	5	5			
San Mateo Co.	6	6			
Santa Cruz Co.	2	1		1	
Monterey Co.	6	6			
San Luis Obispo Co.	4	1		3	
Santa Barbara Co.	3	3			
Southern Calif. Islands ¹	1	1			
Ventura Co.	0				
Los Angeles Co.	2		1	1	
Orange Co.	0				
San Diego Co.	6		1	3	2 ^{2&3}
Totals	59	46	2	9	2

¹ San Miguel Island (Attack No. 43—J. Worrel, 18 Dec 1976).

² Tiger shark (?) (Attack No. 11—R. Pamperin, 14 June 1959).

³ Hammerhead shark, *Sphyrna* sp. (Attack No. 12—V. Fleet, 28 July 1959).

attacks by month is given in Table 2. Also, a summary of attacks since 1969, indicating period between attacks, is presented in Table 3.

A chronological narrative of the twelve most recent shark attacks follows. Since the last four attacks occurred while this paper was in press an abbreviated summary of each of these incidents is given.

Table 2. White shark attacks by month ($\Sigma = 46$).

Jan	3	May	5	Sept	10
Feb	2	June	0	Oct	5
March	1	July	7	Nov	2
April	1	Aug	6	Dec	4

Table 3. Shark attacks since 1969 indicating date, days between attacks, and species implicated.¹

Attack no.	Victim	Date	Days since previous attack	Species white shark (W) other species (O)
25	Colby	20 July 69	358	W
26	Joslin	6 Sept 69	48	W
27	Ward	20 Oct 71	774	W
28	Himmrich	28 May 72	221	W
29	Gray	19 July 72	52	W
30	Kretschmer	9 Sept 72	52	W
31	Hancock	26 May 74	624	W
32	Kehl	26 July 74	61	W
33	Sanders	5 Aug 74	10	W
34	Webster	2 Sept 74	28	W
35	Greenlaw	2 Sept 74	—†	W
36	Holcomb	14 Sept 74	12	W
37	Johnson	28 Sept 74	14	W
38	Rebstock	23 July 75	298	W
39	Brown	9 Aug 75	17	W
40	Buckley	6 Dec 75	119	W
41	Shook	24 Aug 76	262	W
42	Kennedy	18 Oct 76	55	W
43	Worrell	18 Dec 76	61	W
44	Friedman	14 Aug 77	239	W
45	Dunah	5 Aug 78	356	O
46	Sloan	11 Mar 79	218	W
47	Doudt	26 Nov 79	260	W
48	Vikan	17 Oct 80	326	W
49	Cowan	27 Oct 80	11	W
50	Boren	19 Dec 81	418	W
51	Smith	7 Feb 82	50	W
52	Pulaski	24 July 82	167	W
53	Buchanon	29 Aug 82	36	O
54	Herder	19 Sept 82	21	W
55	Weldon	20 Aug 83	335	W
56	Conger	15 Sept 84	392	W
57	Cramer	17 Sept 84	2	O
58	Parsons	30 Sept 84	13	W
59	Rice	30 Sept 84	0	W

¹ See paragraph 2 (text) discussing comparison of early and recent shark attack data.

† Webster and Greenlaw were together at the time of attack; the two scuba divers were swimming at the surface.

Discussion

Shark Attacks, 1980–83

Attack no. 48.—Curt Vikan. 17 October 1980, 0930 h; California: Humboldt Co., Moonstone Beach, lat. 41°02.5'N, long. 124°07.5'W.

Curt Vikan was surfing off Moonstone Beach in 6 to 8 ft of water, approximately 100 yards offshore, at time of the encounter. Without warning his board was “ripped with tremendous force” from under him. Vikan was tethered to the surfboard with a leash and could only watch as the shark held his board out of water for several seconds; “the shark was kind of playing with my board in the



Fig. 1. Damaged section of Curt Vikan's surfboard. Photograph by Ronald Warner.

air.” During this brief period the shark's tail brushed against Vikan. Once the shark released the board, the surfer immediately caught a wave and paddled to shore. There was no injury to Vikan. A tooth fragment was found in the fin of the surfboard and identified by Dr. John DeMartini, Humboldt State University, as that of a white shark. Attack was to the rear of the surfboard; a small section of the board was bitten off (Fig. 1). Small amounts of blood were found embedded in the styrofoam of the board, apparently from the spongy tissue surrounding the teeth of the attacking shark. The shark was estimated as 12 plus ft by Vikan.

Moonstone Beach had been the site of a white shark attack four years earlier; William Kennedy (Attack No. 42), also a surfer, was attacked on 18 October 1976.

Attack no. 49.—Christopher Cowan. 27 October 1980, 1545 h; Oregon: Douglas Co., off Umpqua River, lat. 43°39.7'N, long. 124°12.8'W.

On the afternoon of 27 October 1980 Chris Cowan was surfing with two friends just south of the jetty at the entrance of the Umpqua River. The three surfers had been in the water approximately 25 minutes. Cowan was 150 m from shore and had just been thrown off his board by a large wave. Upon regaining the surfboard a heavy impact knocked Cowan from his board and he was aware of a strong tugging sensation on the leash that tied his foot to the surfboard. Upon release of tension, Cowan mounted his board and noticed that his left leg was injured and bleeding. He called to his companions that a shark was in the vicinity and began paddling rapidly toward shore.

His two surfing companions, still unaware that Cowan had been injured or of the presence of a shark, continued to surf. Upon reaching shore, Cowan sent a

messenger out on the jetty to warn his friends. Upon receiving the signal of distress the two surfers immediately headed for shore.

Cowan was driven to Bay Area Hospital in Coos Bay where four lacerations on the left leg above the knee were sutured; he was then released. The injury to Cowan is considered minor although the potential is obvious.

Examination of the surfboard (2.2 m in length and 50 cm in width; under surface of board uniform bright orange, upper surface bright yellow) revealed a number of tooth impressions. The damaged area of the board was on the left side and centered 64 cm from the rear. Tooth impressions were noted primarily on the lower surface of the board. In the area of damage equating with the mandibular symphysis, two rows of teeth were apparent. The upper surface of the board was damaged at the edge and along the circumference of the jaw outline; damage was much less severe than that to the bottom. The greatest width of the impression on the upper surface measured 360 mm. Cowan was wearing a black neoprene dry suit. We treat this case as involving the white shark.

Attack no. 50.—Lewis Boren. 19 December 1981, afternoon; California: Monterey Co., Spanish Bay, lat. 36°37.2'N, long. 121°57.1'W.

The Lewis Boren incident probably has received the most publicity of any California shark encounter since the fatal attack of Barry Wilson in October 1950 (Bolin 1954). Not only was the attack fatal, but the fact that Boren's body was not recovered for five days led to wild speculation by the media as to the fate of the victim and to the size of the attacking shark.

Lewis Boren had chosen to surf by himself on a cold and windy Saturday (19 December 1981) at Spanish Bay off Asilomar State Beach. He had last talked to friends about 1400 h before leaving to knee surf on his 5 ft 4 in. board. The following morning (20 Dec.), surfers Christian Kai and David Murphy, walking along Asilomar Beach found a surfboard with a portion missing along with the matching section; "the two pieces were about 15 yards apart." That afternoon the board was turned over to the Salinas Police Department who passed it on to the supervising ranger at Asilomar State Beach. On Monday (21 Dec.), a missing persons report was filed by one of Boren's friends concerned that Lew Boren had not been seen nor his vehicle moved from Asilomar State Beach in two days. On the morning of Tuesday, Dec. 22, we were able to examine the surfboard at the Monterey Marine Resources Laboratory. The board was yellow on both upper and lower surface, measured 163 cm in length and 61 cm in width. The removed portion was 774 mm from the tip of the board and measured 400 mm wide by 259 mm deep (Fig. 2). The approximate area of attack was to the left center side of the board. Damage to the upper surface was clean and symmetrical while that to the under surface quite ragged, exemplifying the differing functionality of the upper and lower jaws. Based upon the width of the jaw impressions and the individual triangular impressions on the under surface of the surfboard, we concluded the attacker to be a white shark of 17 to 19 ft. No tooth fragments were found embedded in the styrofoam but small areas of bloodstain were noted near the base of several impressions. Upon analysis, the blood "did not respond to human typing" (Sandi Pinar, California Department of Justice, pers. comm.). We have observed bloodstains in the styrofoam of other surfboards where no injury occurred and conclude that the pulpy gum tissue of the white shark is the source of these stains (see Vikan—attack no. 48, Weldon—attack no. 55).



Fig. 2. Surfboard of Lewis Boren. Photograph by RNL.

On Thursday, 24 December 1981, at 1100 h, a body was observed floating in a small cove approximately 1 km north of Spanish Bay. The corpse was recovered and taken to the Paul Mortuary, Pacific Grove, where the positive identification of Lewis Boren was made and an autopsy was ordered. Cause of death was listed as "severe trauma, left chest (shark bite)." No teeth or tooth fragments were recovered. Examination of the surfboard, victim's body, and wetsuit strongly suggest that Boren was in a prone position on his board, with arms outstretched at time of attack (Fig. 3). The initial attack to the board and surfer was violent and the victim most likely fell from his board at this time. A second minor attack or more likely a repositioning of the board in the shark's jaws then took place, evidenced by left jaw impressions 125 mm forward of the main damage to the board. It is noteworthy that although Lewis Boren's body remained in the water for over 115 hours, and obviously a large quantity of blood initially accompanied the victim, Boren was only bitten once.

Sea surface temperature, taken two days prior to the attack and 2.3 nautical miles north inside Monterey Bay, was 13.3°C; temperature at 18 m was 12.8°C. Secchi disc reading at this location was 19.5 m, indicating extremely clear water.

The previous fatal attack was to Robert Pamperin, on 14 June 1959, off La Jolla. The species of shark implicated in the Pamperin attack is under controversy. It has been suggested that the assaulter was a tiger shark, *Galeocerdo cuvieri* (Baldrige 1974); however, the white shark can not be ruled out. There is a question in some corners concerning the authenticity of the Pamperin attack.

Attack no. 51.—Donald "Harvey" Smith. 7 February 1982, 1100 h; California: Sonoma Co., Stillwater Cove, lat. 37°32.8'N, long. 123°18.0'W.

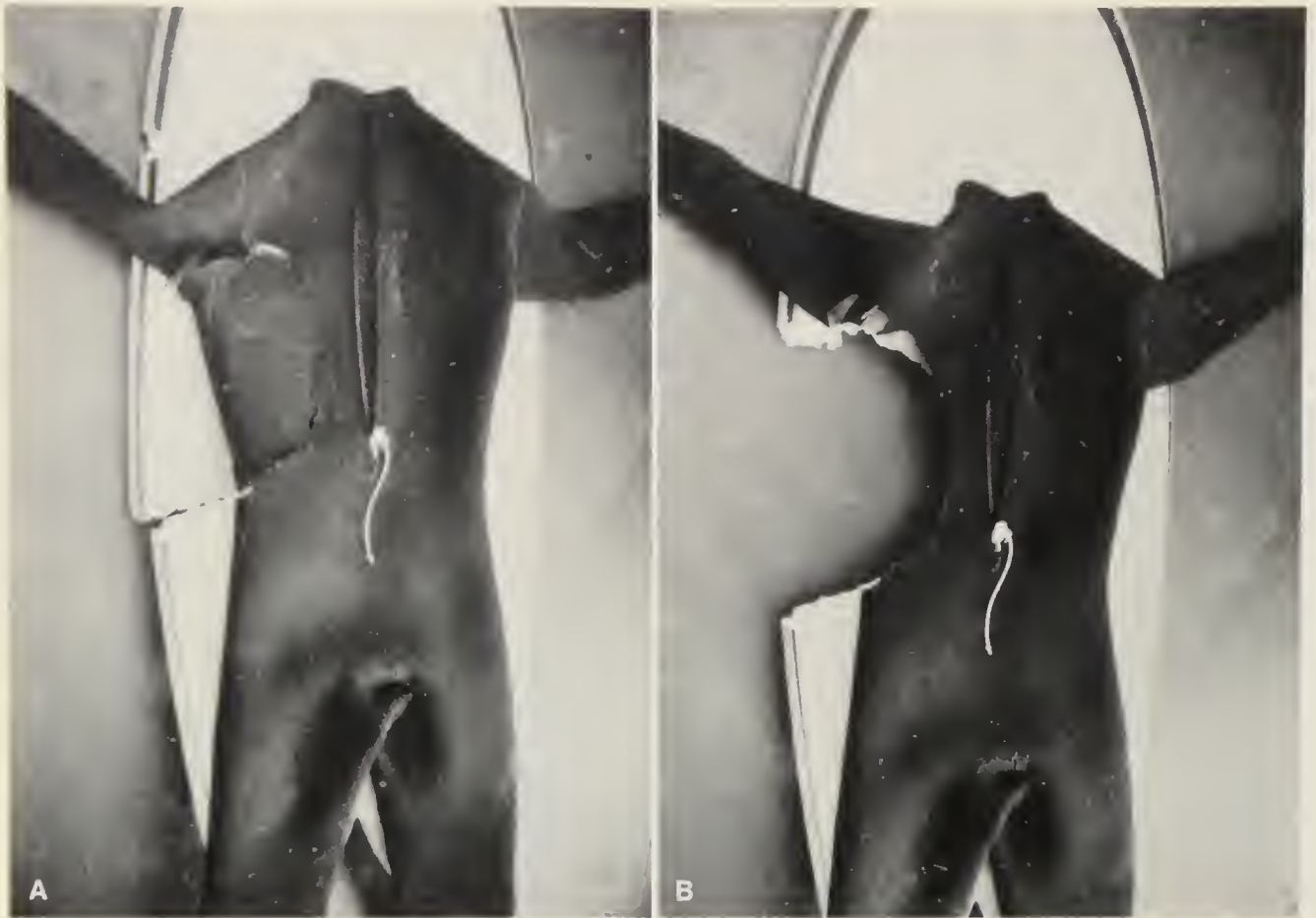


Fig. 3. Surf suit of Lewis Boren superimposed on surfboard. A. Section of board and suit positioned as prior to attack. B. Simulated position immediately following attack. Photographs by RNL.

Harvey Smith and Ken Shimizu were planning to scuba dive at Stillwater Cove, north of Fort Ross. They were in a 14 ft Achilles inflatable boat, approximately $\frac{1}{4}$ mile offshore and 30 yards outside a kelp bed. The Achilles was anchored in 50 ft, on a ledge which drops off rapidly to 80 ft, and near a large rock that "boils" at low tide. Upon anchoring, Smith entered the water and remained at the surface for several minutes. He then descended along the anchor line followed by Shimizu. At 40 ft Smith stopped and considered aborting the dive because of "very very bad visibility," estimated at 2–4 ft. Smith then sensed a strong tug on his calf, "it felt like my leg got tangled in an anchor line and I was being pulled by a boat," and turned to see the head of a shark. The shark first bit his right calf, released and then bit his ankle, taking Smith's fin in the process; "it let me go in about two seconds . . . there was very little pain." Smith rapidly ascended to the surface, swimming past Shimizu. Shimizu saw the shark and estimated it as ca. 8 ft; the shark was not observed again. First aid was immediately applied to Smith in the Achilles and emergency treatment was given by a Stillwater Cove Regional Park Ranger upon arrival at the beach. An air bandage was applied to Smith's profusely bleeding right leg and he was airlifted by helicopter to Sonoma Community Hospital in Santa Rosa for emergency medical care; Smith arrived within one hour from time of attack. The injury to Smith's right leg was major; surgery was required to repair nerve and tendon damage. The bite spanned ca. 15 inches from mid-calf to instep. The leg was bitten to the bone requiring a leg cast for six weeks. Several tooth fragments removed from Smith's leg were identified as those of a white shark by Dr. John McCosker, California Academy of Sciences.



Fig. 4. Casimir Pulaski with 3.57 m rescue board. Note crescentic impression from shark bite on forward left side of board. Photograph by RNL.

Attack no. 52.—Casimir Pulaski. 24 July 1982, 1100 h; California: San Luis Obispo Co., Point Buchon, lat. $35^{\circ}14.5'N$, long. $120^{\circ}54.6'W$.

Cas Pulaski and Terry Shubert had set out on long surfboards to paddle from Montaña de Oro State Park to Avila (ca. 13.5 naut. miles); both were wearing wet suits. After paddling for a period of 45 min to 1 hr, and near the Pt. Buchon buoy, Pulaski was suddenly knocked off his board into the water. Point Buchon buoy is ca. 1 naut. mile from nearest land and is anchored in 24 fm (144 ft). Pulaski's first thought was that a sea lion had playfully hit his board. When he surfaced, he saw the board "in the mouth of a shark." "The tail of the board

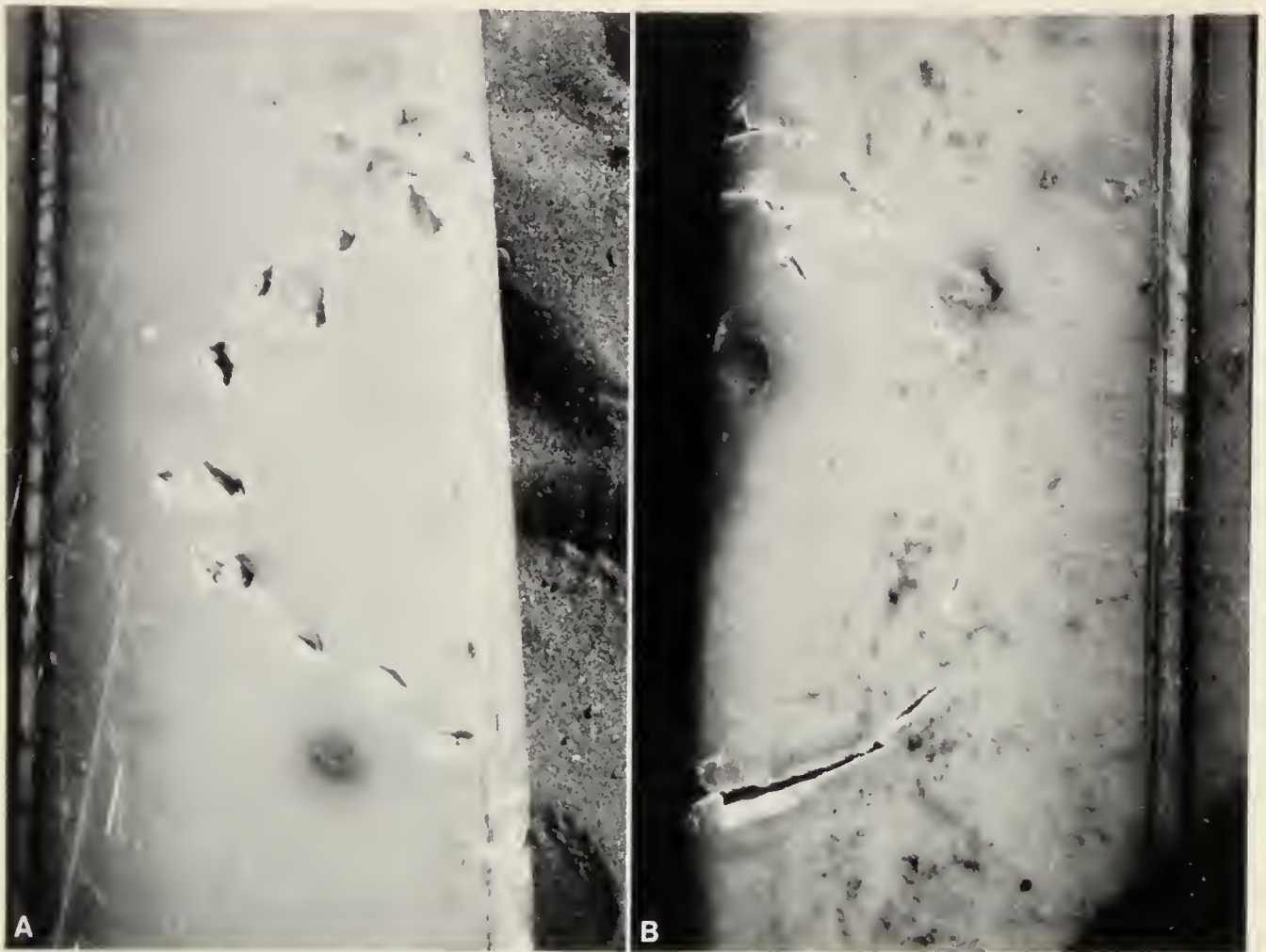


Fig. 5. Casimir Pulaski's rescue board. A. Tooth impressions on bottom of board. B. Tooth impressions on upper surface of board. Photographs by RNL.

stayed in one spot and the nose was being moved in a circle by the shark." The head of the shark "looked like a buoy out of water." Shubert, seeing the initial impact, first thought the board was hit by a whale. Pulaski climbed onto the aft section of the board while it was still being held by the shark. He slid forward on the wet surface and inadvertently struck the snout of the shark; "this was just an instinct reaction." Within seconds the shark let go, and with its head angled downward, departed. Pulaski headed immediately for shore but was greatly concerned about a follow-up attack. "I would take a couple of strokes, grip the board, wait a few seconds for the shark to return, then resume the process." After several minutes he realized the shark would probably not return and paddled with Shubert 15 minutes to reach shore.

We categorize this attack under the heading of "paddle boarding." The dimensions of Pulaski's O'Brien board are quite different from the modern surfboard: the board measured 3.57 m (11 ft 8.4 in.) in length and 57 cm (22.4 in.) in width and is used primarily for life guard rescue work. These dimensions are equivalent to those of Royaks, kayaks, and wind-surf boards.

The tooth impressions from the attack were to the left side of the board, 830 mm from the tip of board to center of bite. Width of bite measured 355 mm on the upper surface and 360 mm on the bottom of board (Figs. 4, 5A, B). The color of the board was a dull yellow.

There was no injury to Pulaski and no tooth fragments were found in the

styrofoam of the board. Based on tooth impressions in the board and the dimensions of the bite the attacking shark was identified as a white shark. Size was estimated between 4.5 to 5.5 m (ca. 15 to 18 ft).

Attack no. 53.—John Buchanan. 29 August 1982, 0930 h; California: San Luis Obispo Co., Morro Bay, lat. 35°22.3'N, long. 120°51.8'W.

John Buchanan was surfing on Sunday morning just north of Morro Rock. Buchanan was alone, with seven or eight other surfers approximately 50 yards to the north. He was on a Lightning Bolt surfboard, 6 ft 1 inch (1.85 m) in length, with red bottom and sides. The water was “pretty clean” and “7 or 8 ft” in depth.

Buchanon felt a jolt to the left front side of his board, looked down and “saw the head of an animal” between his hand and body; “The head was gray with a touch of brown . . . it looked smooth and somewhat pointed.” Buchanan fell into the water and began thrashing and swimming rapidly, primarily out of fear. He calmed himself, caught a wave, and swam to shore; Buchanan was not leashed to his board. The board did not wash ashore so another surfer swam out to retrieve it, unknowing of the incident which had occurred minutes before.

There was no injury to Buchanan. Two elongate impressions (ca. 50 mm each), one large circular indentation, and three small punctures were the only marks evident on the lower surface of the board. On the day before there had been two shark sightings at this beach. These could have been blue sharks (*Prionace glauca*), basking sharks (*Cetorhinus maximus*), or for that matter any other surface-dwelling shark. The species of shark that attacked Buchanan's surfboard is unknown.

Attack no. 54.—Michael J. Herder. 19 September 1982, 1430 h; California: Mendocino Co., Bear Harbor, lat. 39°55.0'N, long. 123°56.0'W.

Mike Herder and two friends were free diving for abalone off the northern California coast. They were diving from a Zodiac inflatable and several speared fishes (lingcod and rockfishes) were hanging over the side in the water. Sea lions and harbor seals had been noted about. Two of the divers had been swimming in the area for approximately 20 minutes while Herder was resting in the inflatable. Herder entered the water, depth ca. 15 ft, and started to descend. Within a few seconds, Herder felt “a bump or tug along the left side of my torso.” “At the time, I believed I was caught in kelp . . . I was suddenly hit hard from my left side. I felt as if I had been hit by a truck.”

Only one bite occurred, the shark shaking the victim violently three or four times; the attack lasted “less than 5 seconds.” The depth of attack was at ca. 12 ft (within 3 ft of bottom) and visibility was estimated at 2.5 ft. Two hours elapsed from time of attack to the time Herder received medical treatment at Garberville Hospital. Approximately 120 stitches were required for deep lacerations to the upper left thigh and buttocks (Fig. 6). Four and one-half months after the attack Herder competed in an 8.2 mile run.

From the time of attack to receiving medical treatment, Herder did not remove his wetsuit. It is our opinion that this measure functioned in the reduction of blood loss by providing pressure to the wounded area. This is a precaution divers and surfers should be aware of in the event of a shark attack.

A personalized account of this attack is presented by Herder (1983).

Attack no. 55.—Randy Weldon. 20 August 1983, 1000 h; Oregon: Tillamook Co., Cape Kawanda, lat. 45°12.0'N, long. 123°59.0'W.

Randy Weldon had been surfing at north Kawanda Beach for about one hour



Fig. 6. Sutured wounds of Michael Herder two days after attack. Photograph by Ronald Warner.

on the morning of 20 August. He was on a “6 ft thruster” (type of board), 20 inches in width, color basically off-white with black and purple stripes. Weldon was ca. 75 yards from shore in 8 to 15 ft of water; visibility was considered “good.” Weldon had just shifted from paddling in a prone position to sitting up on the board when the attack occurred. “I did not see the initial attack I received such a shock [tremendous impact] it threw me in the air. I landed in the water and went under a few inches and popped back up.” The shark held the board for several seconds, let go and then took a second bite. “After holding [the board] for another second or two it let go and disappeared into the ocean heading south-southwest.” Weldon, still leashed to his board, remounted the surfboard and “stroked very hard to shore.” After several strokes, the shark surfaced 8 to 12 ft off Weldon’s right and headed in a line that would have intercepted the path of the surfboard. “Then it went right back under and that’s the last I saw of it.”

There was no injury to Weldon in this incident. There were a number of tooth marks (20 plus) on both the upper and lower surfaces of the board (Figs. 7 and 8). The widest dimension of the semi-circular bite measured 41.3 cm; the depth of bite into the board was 19.5 cm. Distance from tip of the board to the most forward impression was 47 cm (pers. comm., Sid Cook, Argus-Mariner). Had Weldon been lying on the surfboard instead of sitting, he would undoubtedly have received major injury to the upper torso, probably resulting in fatality. The attacking shark was described as a “very large great white . . . [with] tan-brown upper body and dirty white underneath.” The *modus operandi* of the attack and



Fig. 7. Radiograph of damaged section of Randy Weldon's surfboard. Arrow indicates symphysis of upper jaw. Number 1 thru 4 manifest right upper jaw tooth impressions. Lower jaw tooth impressions also evident by this technique. Radiograph by Sid Cook, Barbara Watrous, and Gene Bonham.

the position and geometry of the tooth impressions in the surfboard indicate a large white shark.

It is interesting to note the similarity between this attack and the Curt Vikan encounter (Attack No. 48). Also, the fortuitous nature of this attack compared to the fatal case of Lewis Boren (Attack No. 50).

Shark Attacks, 1984

Attack no. 56.—Omar Conger. 15 September 1984, 0830 h; California: San Mateo Co., Pigeon Point, lat. 37°11.3'N, long. 122°24.0'W.

At 0745 h on Saturday, 15 September, Omar Conger and Chris Rehm swam out to free dive for abalone ca. one mile north of Pigeon Point. Both divers were wearing black wet suits and were sharing a blue and yellow surf mat. At 0830 h they were approximately 150 yards offshore in 15 feet of water, visibility was 3 to 5 ft; they had taken one abalone. The two divers were about 15 feet apart, Conger was resting vertically in the water (there was no splashing). At this point Rehm observed a large shark grab Conger from behind and while shaking him, pull the victim under water; "neither of us saw the shark before the attack." The shark surfaced, its dorsum completely out of the water, with Conger still in its

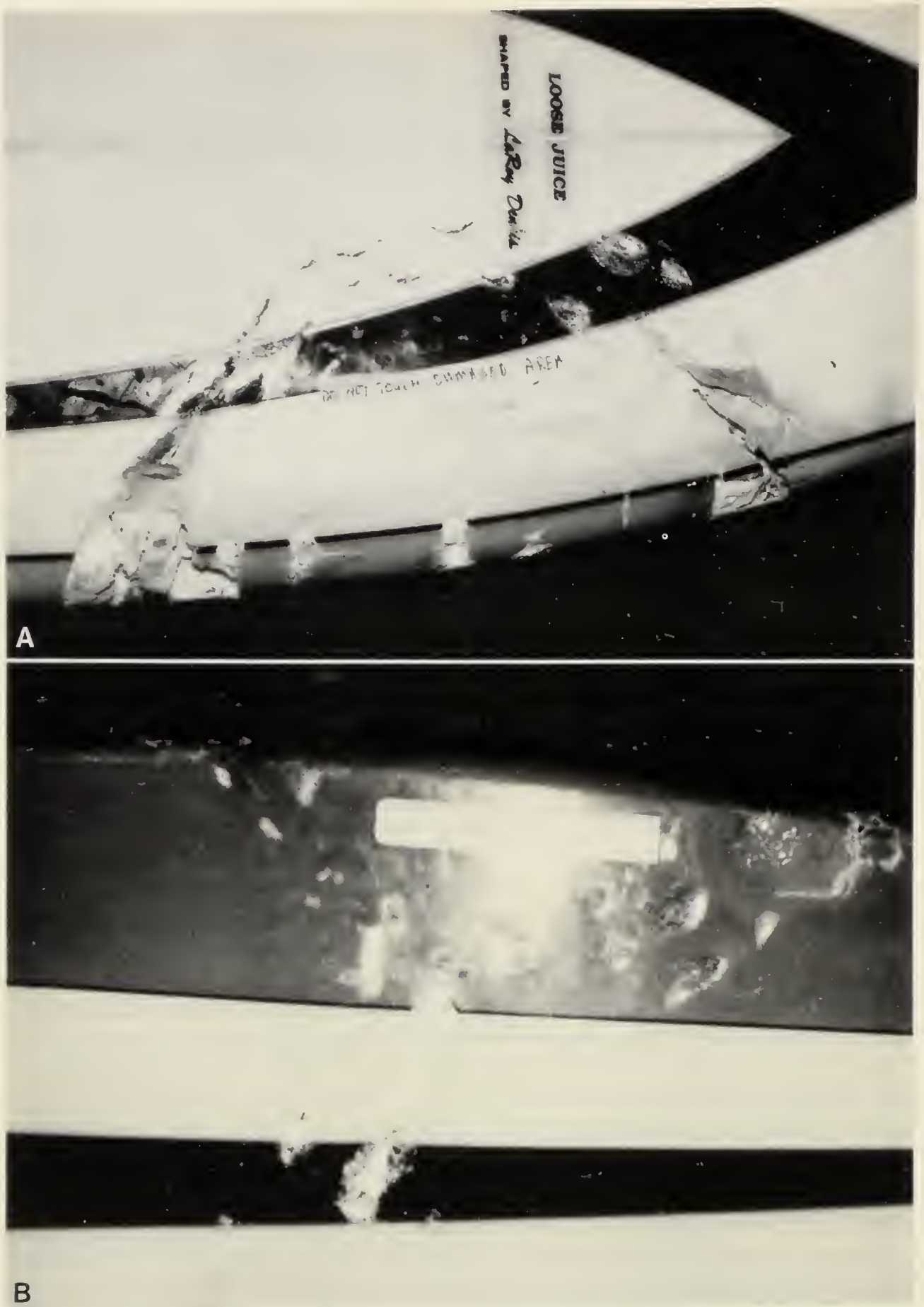


Fig. 8. Randy Weldon's surfboard. A. Tooth impressions on upper surface of board. B. Tooth impressions on bottom of board. Photographs by Sid Cook.

mouth. Swimming in the direction of Rehm the shark let go of Conger and submerged. Conger yelled "help me" and Rehm swam to his friend, lifted his head onto the surf mat, and headed directly to shore. Upon reaching shore, it was discovered the victim had no pulse and undoubtedly died by exsanguination

within minutes of the attack; both femoral vessels were severed. Extensive damage occurred to the buttocks and both legs; muscle mass was removed from this area. The attacking shark was a white shark estimated by Rehm to be 15 feet in length.

As stated by Baldridge and Williams (1969), “. . . very often a shark will strike its victim only once or twice, and then leave.

Attack no. 57.—Brian Cramer. 17 September 1984, 1530 h; California: San Diego Co., Mission Beach, lat. 32°47.0'N, long. 117°15.4'W.

Brian Cramer was wading in waist-deep water off Mission Beach and felt a grabbing and shaking to his right arm near the elbow. A crescentic-shaped wound, 7.5 to 10 cm in width, composed of four to five punctures, required stitches. Cramer was wading amongst a school of bait fish when he was hit; he could only identify the attacker as a fish (the water was murky). The “fish” was undoubtedly a shark, however the species involved is not determinable. The shape and dimensions of the wound suggest a small requiem shark (family Carcharhinidae). It is not unlikely that the attacking fish was a blue shark (James Stewart, Scripps Institution of Oceanography, pers. comm.). The injury to Cramer is considered minor.

Attack no. 58.—Paul Parsons. 30 September 1984, 1000 h; California: Marin Co., Tomales Point, lat. 38°13.8'N, long. 122°59.8'W.

Paul Parsons and Mike Eccles were free diving for abalone near Bird Rock, ca. one mile south of Tomales Point. They had gathered their limits and decided to explore a new area 150 yards northwest of Bird Rock for future diving. Upon moving to this new locale by Zodiac inflatable, Parsons made one dive, reached the bottom (30 ft), then surfaced. He felt uncomfortable with the area, “it was deep open water with little or no vegetation on the bottom.” He called for the boat which was 75 to 100 yds away, to pick up the two divers. Still uneasy at the surface, he decided to make another dive while the Zodiac approached. “I made another dive, reached the bottom, looked around and started for the surface.” Before reaching the surface, at between 10 and 5 ft, Parsons was struck from behind by a large shark. “I could see the shark’s eye on my right and attempted to hit it with my ab iron [abalone collecting tool] while he shook me. The shark let go of me, I came to the surface yelling shark!!” Parsons swam to the boat, was pulled in by his wife and brother, and the boat tenders then picked up Eccles. Paul’s wife, Peggy, an emergency trained registered nurse, applied pressure to the wounded area to control bleeding. The boat trip from the site of attack to Lawson’s Landing, inside Tomales Bay, took ca. 20 minutes. Another 20 minutes elapsed waiting for the rescue helicopter which transported Parsons to Sonoma Valley Hospital. Within one hour of the time of attack Parsons received full emergency medical treatment. He spent the first day in intensive care and four additional days in recovery before being released. Parsons suffered major wounds to his lower back, buttocks, and upper legs; in some areas damage was two inches deep. No tooth fragments were found by the attending physician. A white shark, estimated at 8 to 12 ft, is the species of implication.

The area proximal to Tomales Point has had the greatest incidence of shark attacks in California. Seven abalone divers (including Parsons) have been hit at this location; five suffering major injury. In the case of Parsons, as with a number of attack victims, luck has played a key role in the outcome. Almost immediate first aid and emergency medical treatment within a short period after the attack have swung the pendulum in favor of the attacked on more than one occasion.

Attack no. 59.—Robert Rice. 30 September 1984, 1530 h; Oregon: Tillamook Co., Cape Kawanda, lat. 45°11.0'N, long. 123°59.0'W.

On the afternoon of Sunday, 30 September, Robert Rice was surfing ca. one mile south of Cape Kawanda, at an area known to local surfers as "Turnaround." Rice had been in the water for ca. two hours and was 50 to 75 yds from shore. There were "good waves" and the sea surface was smooth; there was very little wind. Depth of water was 10 to 15 ft and it was clear, Rice could see the bottom. He was straddling his surfboard, a 6 ft, 4 in. Lance Collins thruster, basically yellow-green in coloration, when a large shark suddenly appeared and struck the board. The shark bit at the board twice then released it and swam away. Rice slid off his board into the water at time of impact. With the release of the surfboard by the shark, Rice climbed back onto the board and paddled directly to shore. Only 30 seconds prior to the attack Rice had been lying flat on his board. Had the attack taken place at that time the surfer would most likely have lost his right arm and shoulder; the scenario is obvious. Rice sustained no injury other than a small abrasion to his right foot, probably the result of a scrape against the rough surface of the shark. The attacking shark, unquestionably a white, was estimated at 12 to 15 ft. Cape Kawanda was the site of the Randy Weldon attack one year earlier.

Acknowledgments

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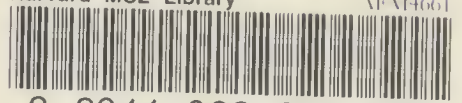
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