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# PREDATORY BEHAVIOR OF THE WHITE SHARK (*CARCHARODON CARCHARIAS*), WITH NOTES ON ITS BIOLOGY

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ABSTRACT: The feeding behavior of the white shark (*Carcharodon carcharias*) was studied at Dangerous Reef, South Australia. Cinematographic analyses of shark feeding patterns show that a single bite action is comprised of a uniform sequence of jaw and head movements. The components are: 1) snout lift, 2) lower-jaw depression, 3) palatoquadrate protrusion, 4) lower-jaw elevation, and 5) a bout-ending snout drop. Durations for a complete bite action ranged from 0.750 to 1.708 s ($\bar{x}$ = 0.985 s) for a 3.5 m (TL) subject. Various approach behaviors to baits were also documented.

The stomach contents of nine white sharks captured in northern and central California waters consisted entirely of fish prey associated with inshore and pelagic habitats. Records of the stomach contents of 24 additional sharks were combined and analyzed, and indicated fish to be the most frequent prey items, while marine mammals were also common. Analysis of prey type in relation to shark size shows small sharks (<3 m) feed primarily on fish prey, while larger sharks feed on marine mammals, especially pinnipeds.

Cursory field experiments and observations indicate sharks detect and are attracted to electric fields. Telemetric studies of white shark thermal biology show that they are warm-bodied, approximately 4-5°C above ambient water temperature.

Length-weight records for 127 sharks were analyzed and found to have the relationship: $W = 3.8 \times 10^{-6} L^{3.15}$, where W is weight in kg and L is length in cm. The largest reliable record for a white shark is that of a 6.4-m, 3324-kg specimen captured near Cojimar, Cuba, in 1945.

A hypothesis is proposed to explain the "bite and spit" paradox related to attacks on pinnipeds and humans. Comments concerning the risk associated with contemporary surfboard design are included.

## INTRODUCTION

The white shark (*Carcharodon carcharias*) (Fig. 1) is the largest piscivorous marine fish in the world and is well known for its aggressive behavior and potential threat to humans (Fast 1955; Collier 1964; Follet 1974; Ellis 1975; McCosker 1981). It is circumglobal in distribution, but most commonly inhabits the coastal temperate waters of North America, South Africa, and South Australia.

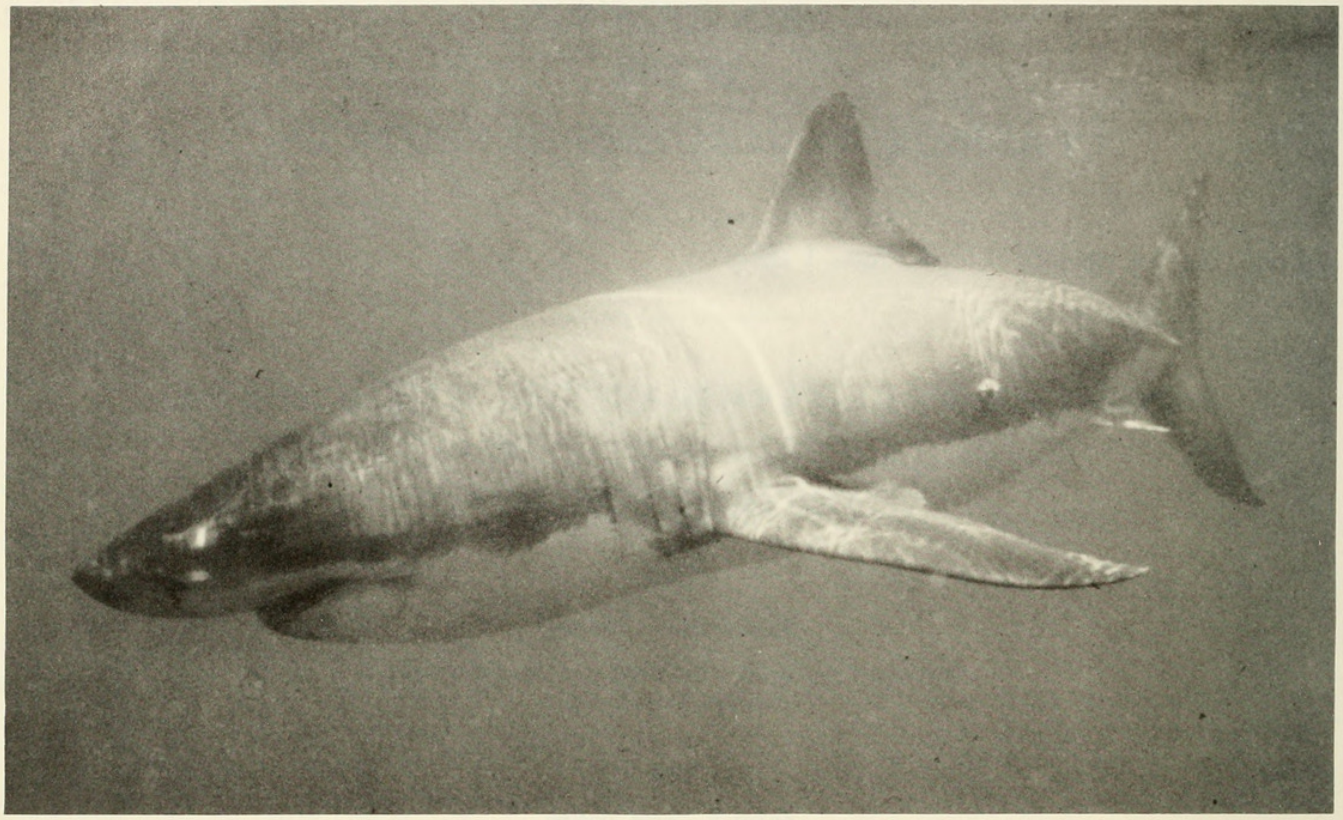


FIGURE 1. Tagged male white shark swimming near the surface at Dangerous Reef, South Australia. Photo by Al Giddings.

In spite of its size and fearsome reputation, surprisingly little is known about the natural history and behavior of this large fish. Almost all published information on the general biology of white sharks comes from anecdotal observations and notes obtained from commercial fishing or whaling operations (Squire 1967), regional species lists and range extensions (Bigelow and Schroeder 1948; Day and Fisher 1954; Royce 1963), and newspaper articles on captures by fishermen or accounts of attacks on humans.

The predatory behavior and feeding mechanics involved in prey capture by white sharks has remained, until the recent application of scuba and high speed photography, essentially unknown. Previous studies on the feeding morphology of other species of sharks were based largely on anatomical data where muscle and supportive tissue functions were inferred from examination of preserved specimens (Luther 1909; Haller 1926). This approach provided functional insight, based largely on articulations and spatial arrangements of skeletal tissues and head musculature. In some cases, however, the inflexibility of preserved materials has led to misinterpretations of the true mechanics of jaw protrusion and feeding in sharks (see Compagno 1977). Whereas examination of fresh pliant specimens may be more appropriate for functional analyses, they still provide only speculative data on sequential and temporal relationships of structures involved in feeding activity. Moss (1972) provided a qualitative analysis of feeding mechanisms in living carcharhinid sharks using observational, photographic, and electrical muscle stimulation techniques. Studies on the temporal and sequential mechanics of feeding behavior in sharks are still lacking, however, when compared to the more thorough cinematographic studies on teleostean fishes (Osse 1969; Liem 1978; Lauder 1980).

Because white sharks are rarely captured, documentation of their food habits is scattered throughout the literature. Most records come from notes on the stomach contents of dead fish (Schroeder 1938; Bonham 1942; LeMier 1951; Scattergood 1962) or from fortuitous observations of feeding in the field (Day and Fisher 1954; Pratt et al. 1982). More complete accounts are provided on the relationships of white sharks to pinnipeds (Ainley et al. 1981; and Le Boeuf et al. 1982) and sea otters (Ames and Morejohn 1980). There still remains, however, the need for a comprehensive collation of the prey items tak-

en by this predator so that a more complete assessment of predator-prey relationships can be made.

This paper presents new data obtained during a recent expedition to South Australia that relate to white shark predatory behavior and general biology. We analyze the feeding mechanics of white sharks in the field by use of cinematographic techniques and provide information on their sensory biology and thermal physiology. In addition, we have synthesized previously published and unpublished data on the length-weight relationships, predator-prey interactions, and general behavior of this shark. Based upon what is known about the predatory behavior of white sharks, we present a new interpretation of the curious pattern of non-feeding attacks upon marine mammals and humans.

## Study Area and Methods

White sharks were studied in the field during a ten-day period in January 1980, in waters near Dangerous Reef, South Australia. The reef consists of two small, low islands approximately 16 km east of Port Lincoln (Fig. 2). Sharks were attracted to the 20-m vessel, *Nenad,* using tuna and meat byproducts as bait. Sharks feeding on baits both at and below the surface were photographed using Actionmaster 500 cameras and 7247 Kodak color reversal film exposed at shutter speeds of 24 and 200 frames per second. Frame-by-frame analyses were performed on a Movieola 16-mm film editor.

Stomach content and morphological data from nine sharks on record at the California Academy of Sciences were analyzed. These data were then combined with other published records and further examined. To prevent multiple entries of a record into the analyses, only well-documented reports that included information on capture locality, number of sharks sampled, measured lengths and weights (no estimations), and specific prey types were used.

Two types of ultrasonic telemetry packages, constructed by the senior author, were used in this study to monitor shark body and ambient water temperatures. All transmitter circuits consisted of a crystal-controlled oscillator (carrier frequencies = 31.700 or 32.768 kHz) gaited by a thermistor-controlled pulse circuit sensitive from 10°C to 33°C. The first tag consisted of a single transmitter with a thermistor probe

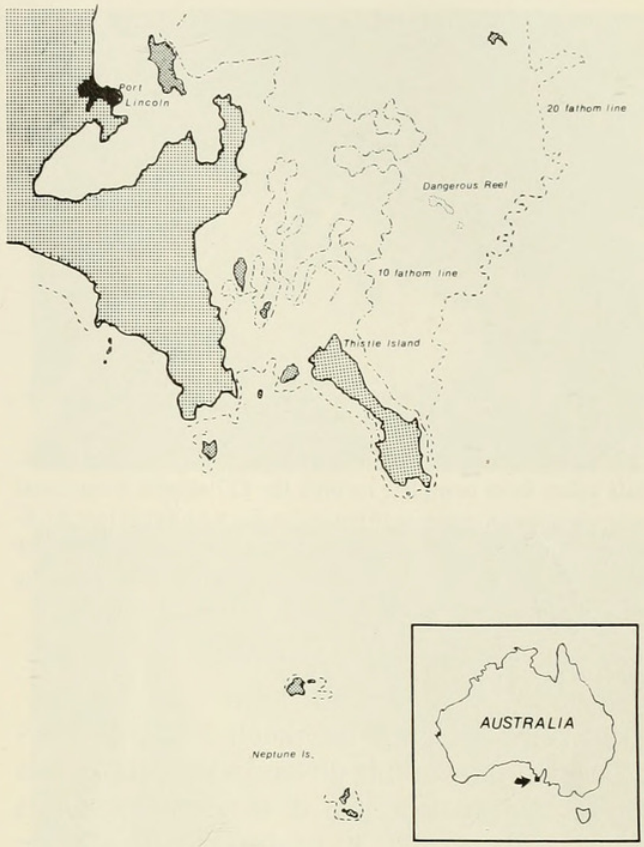



Figure 2. The study area, Dangerous Reef, South Australia.

(embedded on the surface of the transmitter housing) that monitored ambient water temperature around the animal. Its dimensions were 4.6 × 3.2 × 2.0 cm, and it weighed approximately 60 g in air. The second unit consisted of a cylindrical package with two transmitters of different carrier frequencies. One transmitted temperature data from a thermistor in contact with the surrounding water, the other from a thermistor embedded under the barb of a dart at the end of a 31 cm-long wire leader. Total package dimensions were length 17 cm × diam. 3.2 cm, with a weight of approximately 100 g in air.

The water temperature sensing package was applied from underwater using scuba (and a cage). A stainless steel dart was attached to an applicator tip on the end of a speargun shaft, and shot 3 cm deep into the shark's mid-lateral musculature. The dual-temperature sensor package was applied externally to another shark from the swimstep of the research vessel via barb and applicator pole. Signals were tracked with a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. Absolute maximum range of the transmitter-hydrophone system under ide-

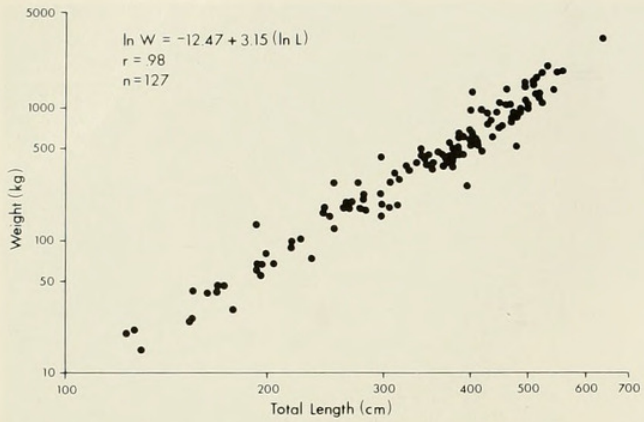



FIGURE 3. Length-weight relationship for the white shark. Data taken from complete records for 127 sharks. Functional (geometric mean) regression equation given on figure (see Ricker 1973 for discussion). Non-transformed power equation for relationship is $W = 3.8 \times 10^{-6} L^{3.15}$, where W = weight in kg and L = total length in cm.

al conditions was approximately 1500 m. However, practical working distances were much less due to transmission loss in the shallow waters around the reef (20–30 m deep). Ranges were estimated by relative audible strength calibrated prior to tracking sessions.

A set of cursory experiments were performed to test the sensitivity of sharks to weak electric fields. Sharks attracted to the boat by chum were presented two pieces of bait, approximately one meter apart, suspended on the surface from lines attached to the end of 7-m bamboo poles. Two saltwater electrodes, similar to those used by Kalmijn (1978), were attached to one bait (the experimental). Electrodes consisted of one-meter lengths of 6.3 mm inside diameter tygon plastic tubing filled with a 3% seawater-agar gel. One end of each tube was open to the water, while at the other end a 32-mm stainless steel pin with wire lead was inserted. Lead wires (+ and −) were connected to a Grass S-6 stimulator. The two saltwater electrodes were attached behind the experimental bait and spaced 10 cm apart. The control consisted of bait only. The experimental bait was presented in two different experiments that used 1) pulsed (2.2 volts at source, 5 Hz, 1.9 ms duration) current, and 2) constant (0.5 and 2.2 volts at source, DC) current electrical fields. Each test sequence began when a shark visually oriented to and approached the baits. Once the shark was within 2 m of the baits, the stimulator was turned on and choice of bait fed upon recorded. Relative positions of the control and experimental baits were randomly determined to control for extrinsic cues.

## Results and Discussion

SIZE.—The length-weight relationships of 127 white sharks, based on records at the California Academy of Sciences and those of published and contributed sources, are shown in Fig. 3. The largest shark record we found was that of a 6.4-m-long (21 ft), 3324-kg (7302-lb) individual captured off Cojimar, Cuba, in 1945 (Guitart and Milera 1974). The maximum size previously reported for a white shark originated from an incorrect record of an 11.1-m individual from Port Fairy, Australia, reported by Günther (1870). Randall (1973) re-examined the jaws of this specimen and concluded that the correct total length was approximately 5 m, well within the size distribution of sharks currently on record. The purported capture of a 9-m (29.5-ft) white shark said to be from Vila Franca, Azores, is probably erroneous (see Ellis 1983). The smallest published record was a 125-cm (49-in), 20-kg (44-lb) specimen reported by Smith (1951). Robert Johnson (pers. comm.) has advised us of three juveniles captured off Baja California that ranged from 130 to 135 cm (51 to 53 in) total length and weighed less than 18.2 kg (40 lb).

Remarkably, we found no well-documented records of female white sharks with fetuses or pups. Bigelow and Schroeder (1948) reported embryos ranging in length from 20 to 61.6 cm, but gave no further source information. One female taken near Alexandria, Egypt, was reported to have nine embryos, each 0.61 m (2 ft) long and weighing 49 kg (108 lb). This erroneous weight probably represents a total for all nine embryos, and translates to a more reasonable mean of 5.4 kg (12 lb) for each fish. We can only speculate about this lack of pregnant females in the capture record. Females may pup in less frequently sampled areas, such as remote geographic regions, oceanic waters, or deeper pelagic habitats. Although it is possible that females fast while pregnant, this would not completely account for the phenomenon, because many of the largest females on record were taken by harpoon rather than with bait and hook. Perhaps pregnant females undergo spontaneous parturition when hooked or harpooned and therefore eliminate key embryonic evidence before they are landed. More critical examination of the reproductive tract of

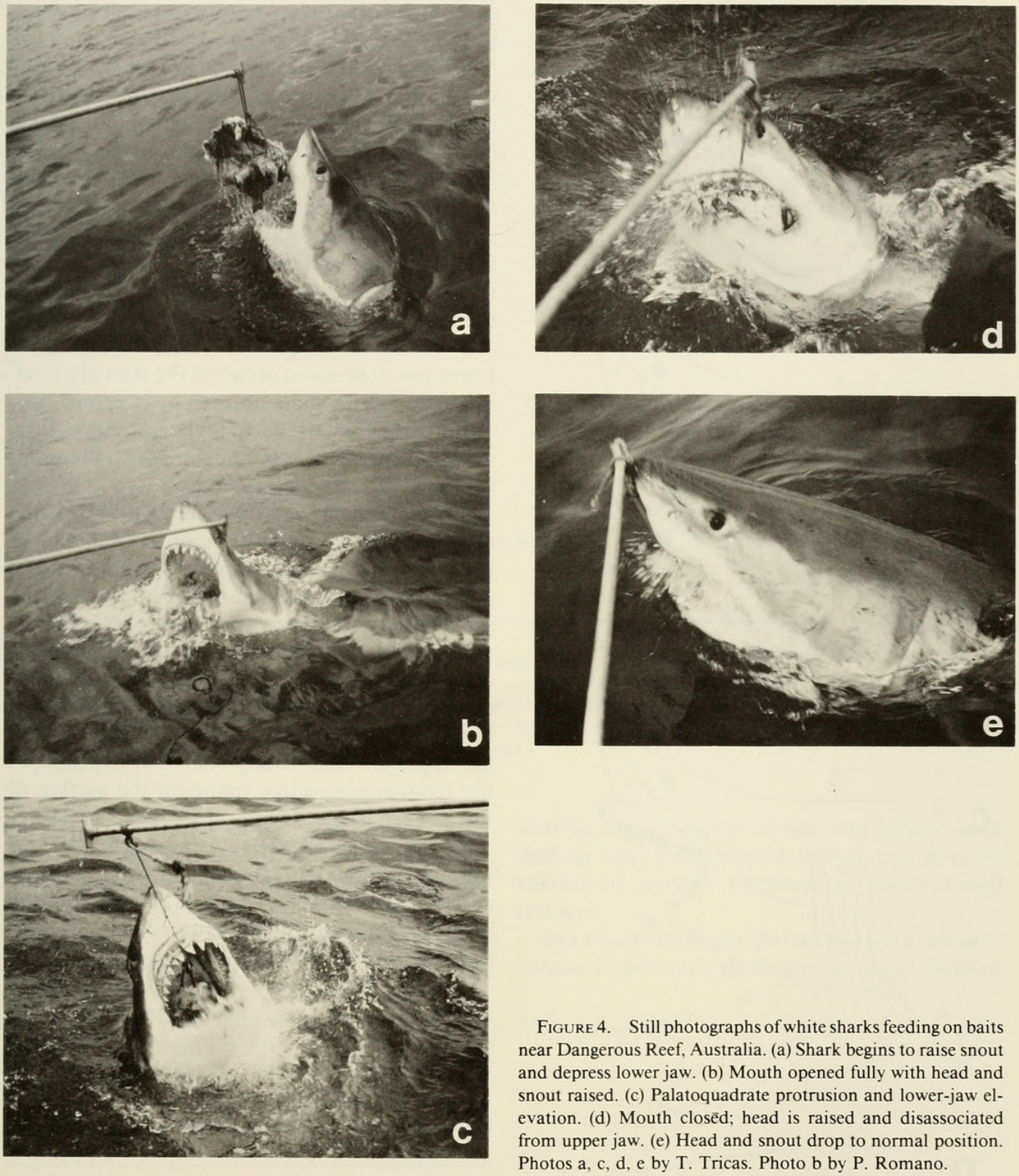
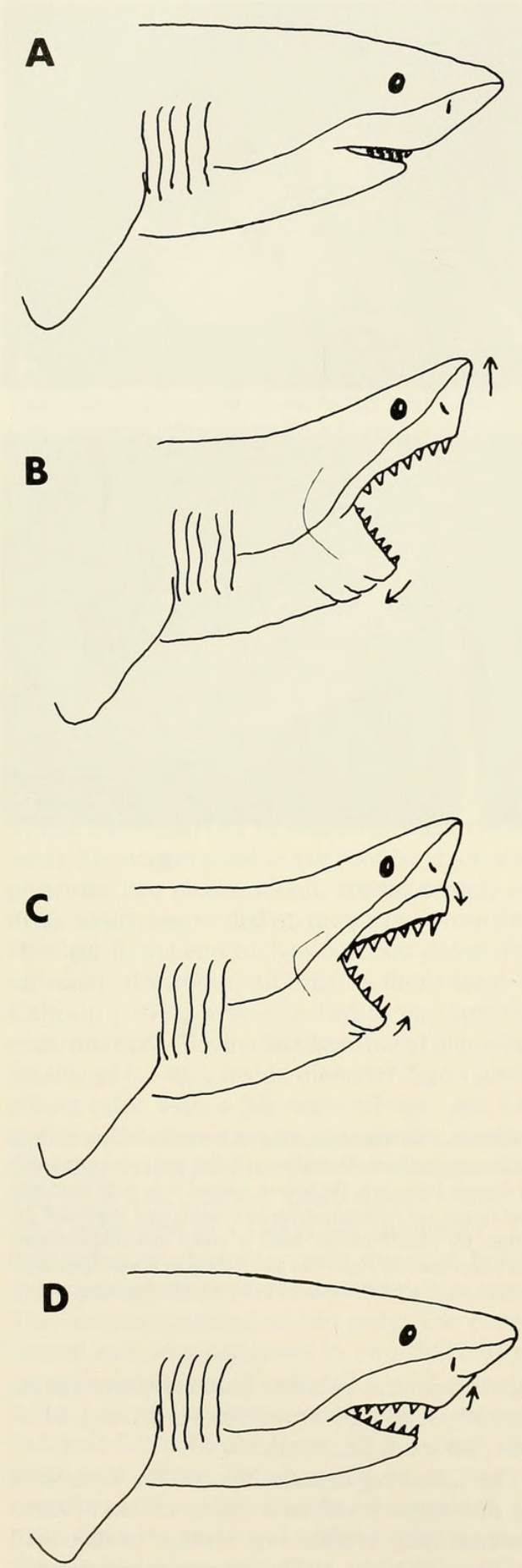



FIGURE 4. Still photographs of white sharks feeding on baits near Dangerous Reef, Australia. (a) Shark begins to raise snout and depress lower jaw. (b) Mouth opened fully with head and snout raised. (c) Palatoquadrate protrusion and lower-jaw elevation. (d) Mouth closed; head is raised and disassociated from upper jaw. (e) Head and snout drop to normal position. Photos a, c, d, e by T. Tricas. Photo b by P. Romano.

freshly landed specimens might provide useful insight to this enigma.

FEEDING ETHOLOGY.—The following section is based on our observations and the analyses of films taken of white sharks feeding on bait at Dangerous Reef, Australia. Although baited situations can only simulate natural conditions, the feeding behaviors observed in these sessions represented natural patterns because white sharks normally take prey at the surface (Ainley et al. 1981; personal observations).

The following descriptions of the structures and mechanics involved in biting actions of white sharks employ terminology similar to that used by Moss (1972, 1977). Cinemaphotographic analysis of 36 feeding bouts revealed five basic




components that constitute a single feeding action.

**1) Snout Lift:** This movement involves an upward lifting of the snout and head, and initiates the feeding action (Figs. 4a and b, 5b). The degree of snout lift ranged from a slight upward movement to a pronounced elevation that produced an acute angle behind the head (30–40° above the longitudinal body axis). The intensity of snout lift varied in relation to size of bait, angle of approach to the bait, and possibly to level of motivation (e.g., hunger).

**2) Lower-Jaw Depression:** Like the snout lift, lower-jaw depression occurs at the start of a feeding action. It is characterized by a ventro-posterior movement of the tip of the lower jaw (Figs. 4a and b, 5b). This motion, along with the snout lift, fully extends the gape.

**3) Palatoquadrate Protrusion:** Closure of the mouth is marked by disassociation of the upper jaw from its original juxtaposition ventral to the cranium, and subsequent protrusion out of the oral cavity. The upper jaw rotates in an antero-ventral direction, while the snout remains at its elevated position (Figs. 4c, 5c). During palatoquadrate protrusion the teeth become fully exposed and are directed downward. Eversion of the upper jaw was readily visible by exposure of the reddish connective tissue on the surface of the jaw cartilage.

**4) Lower-Jaw Elevation:** Concurrent with the initiation of palatoquadrate protrusion, the lower jaw begins an antero-dorsal (upward) motion (Figs. 4c, 5c). These movements collectively produce the closing action of the jaws.

**5) Snout Drop:** After single-bite feeding bouts the snout returns to its normal pre-feeding position. This results from a drop of the head and snout, and a retraction of the palatoquadrate cartilage to its position immediately ventral to the cranium (Figs. 4e, 5d). During multiple-bite bouts,

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FIGURE 5. Components of a feeding action 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. These two components comprise the actual bite. (D) Snout drop entails retraction of palatoquadrate cartilage to its normal juxtaposition beneath cranium. Snout drop occurs at the end of a feeding bout and is not an essential component of the biting action. Arrows indicate direction of jaw movements.

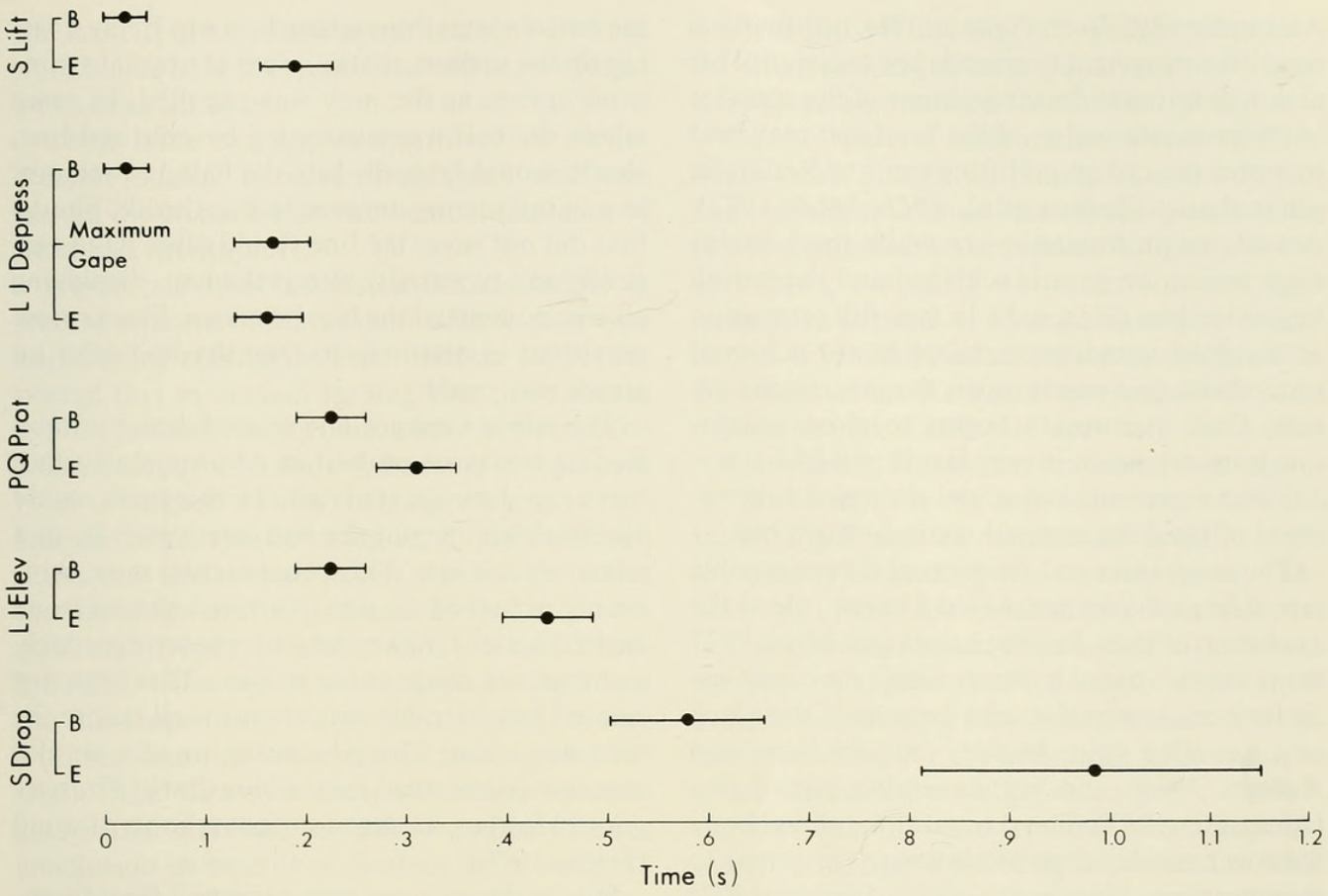


FIGURE 6. Timing of feeding actions for eleven consecutive bites made by a 3.5 m (TL) white shark. Mean times indicated by dots. Horizontal lines show 95% confidence limits. Key: B = begin, D = depression, E = end, Elev = elevation, LJ = lower jaw, PQ Prot = palatoquadrate (upper jaw) protrusion, S = snout.

the snout remains partially elevated prior to the next biting action (Fig. 4d). The retention of an elevated snout in these cases results in shorter time intervals between bites.

Mean durations for components of eleven complete successive feeding events recorded for one shark are shown in Figs. 6 and 7. Depression of the lower jaw was the fastest component ($\bar{x}$ = 0.140 s), and the snout drop duration the longest ($\bar{x}$ = 0.405 s). Total time for a complete biting action, including the snout drop, ranged from 0.750 s to 1.708 s ($\bar{x}$ = 0.985 s). Temporal analyses of film footage showed that the sequence of each feeding component fell in a fixed order with a non-overlapping range of time limits for each individual head and jaw movement. While each action showed a range in timing, minimal overlap was detected between events. The four components occurred within a mean time of 0.443 s, and never was a shark observed to partially complete a bite once the snout lift and lower-jaw depression actions were initiated. The snout drop, however, was not always an integral part of a feeding action, except at the termination of a feeding bout (as discussed above), and may be subject to sensory feedback or motivational changes.

Our observations on the mechanics of jaw protrusion in the white shark are similar to those of

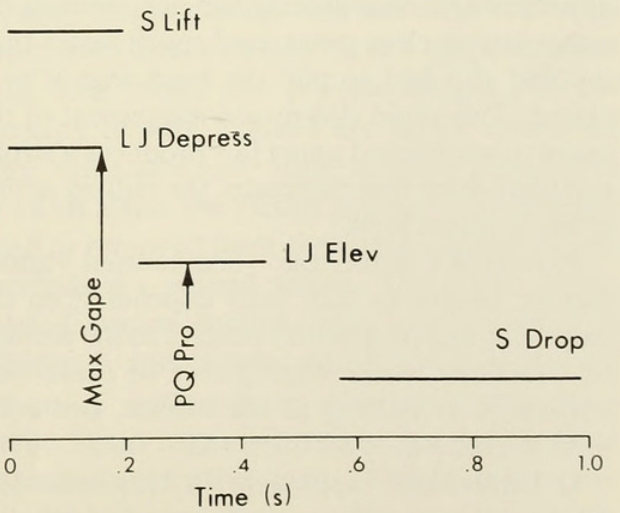


FIGURE 7. Range of durations for feeding events. Data from same shark as in Fig. 6.

Alexander (1967) on *Squalus*. He too found a head lift component to precede jaw eversion. This action is initiated by contraction of the muscles at the posterior region of the head and may lead to a pronounced snout lifting prior to feeding in other sharks (Backus et al. 1956; Moss 1972). Actual jaw protrusion in the white shark begins after maximum gape is achieved and the mouth begins to close (Figs. 4, 5). In fact, full protrusion of the palatoquadrate cartilage is not achieved until about midway through the jaw closing action. Once the mouth begins to close, palatoquadrate extension is very fast ($\bar{x} = 0.083$ s, $n = 11$) and represents the actual downward movement of the fully exposed teeth during a bite.

The mechanics and function of the protrusible jaw in large sharks has played a major role in the evolution of their feeding habits (see Moss 1977 for review). Special hydrodynamic problems exist for non-demersal sharks because of their lack of a gas-filled swim bladder (but see Bone and Roberts 1969) and maneuverable paired fins (Alexander 1967). The general streamlined body form is considered an evolutionary response to this problem (Alexander 1967; Budker 1971; Thomson and Simanek 1977). The development of a protractile jaw has allowed large lamnid and carcharhinid sharks to retain a hydrodynamically efficient fusiform body and the capacity to take clean bites with a subterminal mouth. The rounded pattern of bites taken from prey too large to swallow whole comes primarily from the upward and forward rotation of the lower jaw that secures the mouth to the prey, and the downward and forward cutting rotation of the upper jaw. The detached hyostylic association of the upper jaw and chondrocranium also permits the upper jaw to close downward much faster than it could if it had to pull the head with it as it closed. This rapid downward movement of the massive unattached upper jaw produces a strong resultant force that facilitates the cutting action of the serrated teeth.

Predatory Behavior.—Sharks used various capture modes to take baits depending on the bait's size and its position relative to the surface. In situations where large pieces of meat were suspended or floating at the surface, two common approaches were observed.

**1) Underwater Approach:** In this behavior, sharks swam parallel to and approximately 0.5 m below the surface until less than 1 m away from the bait. In situations where bait was freely floating on the surface, sharks swam at normal swimming speeds as the prey was engulfed. In cases where the bait was suspended by pole and line, sharks would typically bite the bait and attempt to pull it under by depressing their heads. Sharks that did not sever the line would often hang vertically and repeatedly bite at the bait, displaying all components of the bite behavior. Sharks were persistent in attempts to take the bait after an attack was made.

**2) Surface Charge:** The second, less common feeding behavior on bait at or near the surface was a rapid accelerated rush. Here a shark would approach and engulf the bait as it swam by at a relatively fast rate. This behavior was most commonly observed on newly arrived sharks in an excited state. Unlike the underwater approach, a charge was made at the surface. This behavior created considerable disturbance well before the bait was taken. Charging behavior of a similar nature was described for the blue shark (*Prionace glauca*) feeding on dense surface schools of squid (Tricas 1979).

White sharks were also observed feeding underwater, and exhibited different predatory behaviors than when taking prey from the surface. Two additional modes are presented.

**3) Normal Underwater Pass:** This feeding behavior was observed when a shark approached a relatively small submerged bait. Sharks approached with the mouth opened wider than during normal swimming and raised the snout slightly when approximately 1 m from the bait. When the bait contacted the underside of the snout, the lower jaw depressed slightly and the bait was taken. In this behavior the snout lift and lower jaw movements were present, but not as pronounced as in surface feeding modes, and there was no protrusion of the upper jaw. The underwater pass appeared to be first mediated by vision prior to contact, and second by tactile sensory input when the snout touched the prey just prior to initiating a feeding action. Additional sensory systems (e.g., gustatory or electroreceptive) may also be involved in normal feeding situations at close ranges.

**4) Side-Roll:** A similar approach to a normal underwater pass occurred where a shark rolled onto its side just prior to engulfing the submerged prey. Here the shark maintained its horizontal approach until approximately 1–2 m away from

the bait. It then rolled aproximately 60° from normal, took the prey, and returned to an upright swimming attitude.

These latter two approaches involved no detectable change in swimming speed and employed the characteristic movement sequence of head and mouthparts.

Numerous observations on the variability in feeding patterns of sharks in relation to prey type and feeding conditions exist. Budker (1971) reported that in normal feeding situations sharks exhibit no body contortions when they consume small fish prey which are swimming at their own level or slightly below. This appears to be the case for white sharks taking small pieces of bait in normal underwater passes. He further states that there are only two situations that might require a different type of approach to a bait. These are either when a bait is attached to a hook and the shark must turn on its side to avoid the line with its snout, or when bait is floating and the shark must thrust its snout out of the water to get its mouth around the bait. We agree with his conclusion in regards to floating baits, with the addition that this includes natural feeding situations as well. This behavior has been observed for white sharks feeding on pinnipeds at the surface (Ainley et al. 1981; personal observations), and for tiger sharks (*Galeocerdo cuvier*) feeding on both surface baits and normal prey (see Moss 1972; Gilbert 1963 for pictures). In addition, it is clear that side-roll behaviors may also occur in natural feeding situations, and are not necessarily responses to obstructions during feeding. Tricas (1979) found that blue sharks approached small, moving anchovy baits from behind and took them in a normal swimming posture, while larger whole mackerel baits were taken from behind by sharks that partially rolled onto their sides. This variation was attributed to the size of the prey and its position relative to the mouth just prior to capture.

Observations of white shark feeding behavior are limited to artificial situations in which sharks were attracted to feed on tethered fish or horsemeat (this study) and the few instances when white sharks were observed feeding on dead cetaceans (e.g., Pratt et al. 1982). Some information has been gained from interviews with shark attack victims, although most of these did not see the shark before or during the attack (cf. Miller and Collier 1981) and may have made biased observations. White sharks have been kept alive for short periods in large aquariums, but none have attempted to feed (McCosker 1981).

On the basis of information discerned from white shark attacks on pinnipeds and humans, and our observations of their feeding on bait, we can best summarize the predatory attack strategy as follows. An adult white shark is not agile enough to capture a fleeing, darting pinniped; hence, it generally attacks its prey by surprise. Bite scars on northern elephant seals (*Mirounga angustirostris*), California sea lions (*Zalophus californianus*), Australian fur seals (*Arctocephalus doriferus*) (Fig. 8), and sea otters (*Enhydra lutris*) (Fig. 9, also see Ames and Morejohn 1980) are usually located on the ventral region of the body (e.g., haunches and flippers). This indicates that attacks were made from behind and beneath the prey. A typical attack scenario might entail a shark swimming a few meters beneath the surface, searching for the silhouette of a pinniped or sea otter at the surface. Once a prey is sighted, the shark ascends and at close range (approximately 1 m) begins a feeding action as described above. After attacking large prey such as an elephant seal, the shark probably routinely retreats a short distance from the injured (and at least partially immobilized) prey and swims cautiously within the area, apparently waiting for the pinniped to bleed to death or lapse into shock. During the attack, white sharks often roll their eyes posteriorly, which reduces the risk of injury to the eye by the teeth or nails of a struggling prey. The retreat behavior is also adaptive since it eliminates the chance of injury via contact after the initial attack is made. This "bite and spit" strategy might explain why seals that have escaped after attack usually have a single massive bite. This might also provide insight into the paradox of why humans are rarely consumed after being attacked. Since humans rarely dive or swim alone, the victim is usually quickly rescued or removed from the attack area by others, precluding a second attack. The white shark-related human fatalities that have occurred in California and Oregon waters since 1926 (5 of 40 attack victims) have all resulted from traumatic blood loss and did not involve massive consumption by the shark. This alternative theory might be more reasonable than the suggestion that humans are "distasteful" to white sharks,

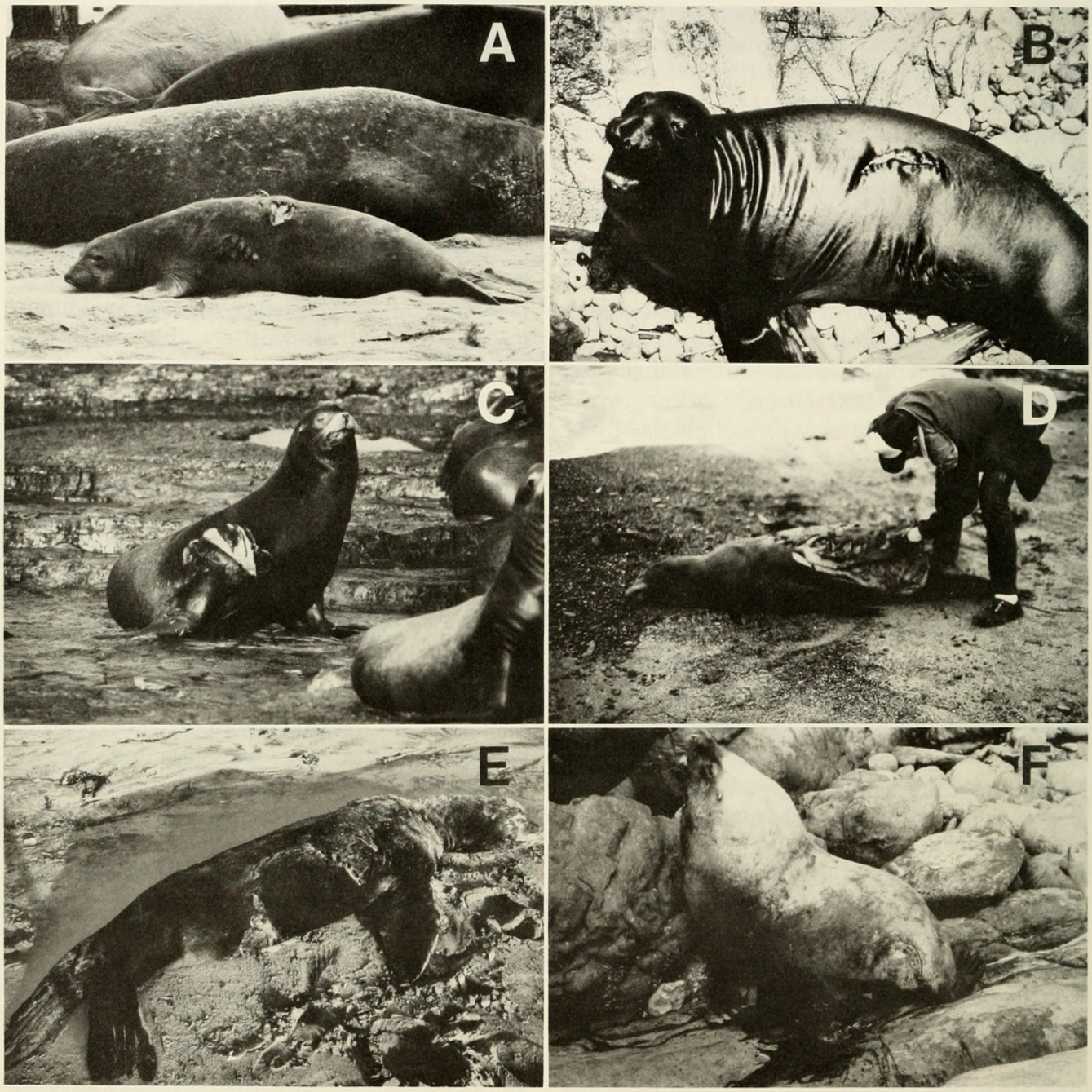


FIGURE 8. Wounds inflicted upon pinnipeds by white sharks. It is possible to hypothesize the posture of prey and the attack behavior of the shark from bite scars. Elephant seals (*Mirounga angustirostris*): (A) Subadult survivor at Año Nuevo Island, California. Note lower jaw puncture wounds and tearing caused by upper jaw teeth. Photo by R. Bandar. (B) Adult female survivor at Southeast Farallon Island, California. Again note lower and upper teeth wounds. Photo by S. H. Morrell. California sea lions (*Zalophus californianus*): (C) Adult survivor at Año Nuevo Island. Photo by R. Bandar. (D) Subadult male carcass (left) and Richard Ellis (right) at Año Nuevo Island. Photo by Pam Wing. (E) Subadult male carcass along the central California coast. Photo by R. Bandar. Southern fur seal (*Arctocephalus doriferus*): (F) Large adult male survivor at South Neptune Island, South Australia. Photo by J. McCosker.

particularly when one considers the euryphagic diet of the fish.

PREDATOR-PREY RELATIONSHIPS.—The stomach contents of nine white sharks (193–511 cm total length) captured in northern and central California waters are presented in Fig. 10. Seventy-eight percent of the sharks had recognizable food items in their stomachs. The most frequent prey was the California bat ray (*Myliobatis californica*), found in four stomachs; other fish prey were less frequent in the diet. Fifty-six percent of the sharks examined contained elasmo-

FIGURE 9. Sea otters (*Enhydra lutris*) from the central California coast. Above, adult in normal feeding or basking posture along the edge of a kelp bed in Monterey Bay. Photo by J. McCosker. Below, lacerated carcass from which several white shark tooth fragments were removed, suggesting that the animal was bitten at the surface while in a belly up, prone position. Pismo Beach. Photo by J. Ames.

branchs, and 44 percent contained teleost prey species. No evidence of predation on marine mammals was found in the nine sharks.

Although the white sharks took prey that normally occur in both pelagic and inshore habitats, the two most frequent prey are generally associated with demersal inshore communities. The California bat ray (*M. californica*) is common in bays and inshore sandy habitats 2–50 m deep, where it feeds on benthic sand-dwelling invertebrates. The spiny dogfish (*Squalus acanthias*) is also demersal, being found in both shallows and deeper offshore waters. Other prey species that live on the bottom in inshore areas are the lingcod (*Ophiodon elongatus*) and the cabezon (*Scorpaenichthys marmoratus*). These latter two species are relatively sedentary, have small home ranges, and show cryptic coloration. Limbaugh

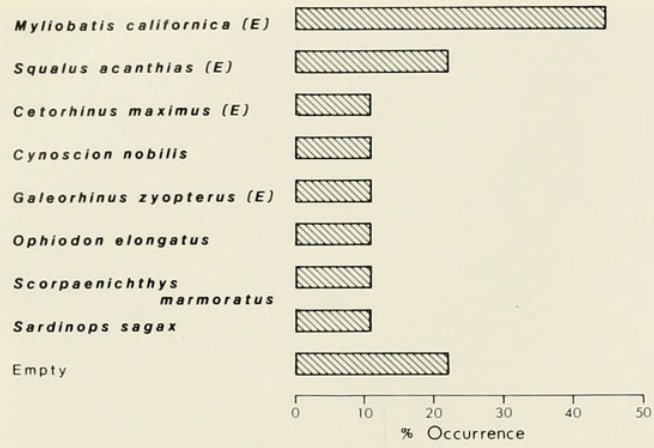


FIGURE 10. Stomach contents of nine sharks captured in northern California waters on record at California Academy of Sciences. % occurrence = percentage of the nine shark stomachs that contained that prey item. E = elasmobranch, all others are teleosts.

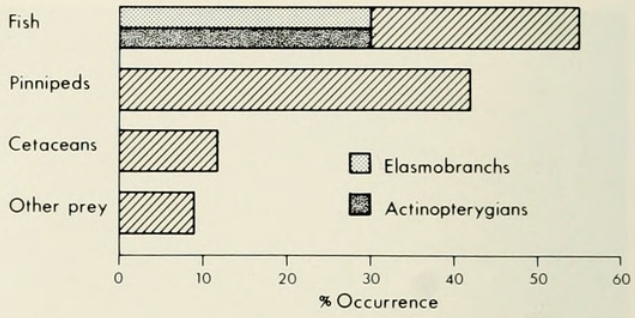


FIGURE 11. Stomach contents of 33 white sharks. Data combined from this study and other published records. % occurrence = percentage of the 33 sharks that contained the prey category. Fish prey subdivided into elasmobranchs and rayed-fin fishes (teleosts and sturgeons). Other prey include birds, crustaceans, and sea turtles.

(1963) reported cabezon from the stomachs of three immature sharks captured at La Jolla, California, and described a number of incidents that indicate *S. marmoratus* is an important prey for young white sharks. Earlier researchers questioned how sharks could detect and capture such inconspicuous and apparently inaccessible prey; our studies suggest that weak electric fields might be involved in prey detection (see Sensory Biology section below).

The white sea bass (*Atractoscion* (=*Cynoscion*) *nobilis*) also occurs in shallow rocky inshore habitats, and is often found among canopies of giant kelp (*Macrocystis pyrifera*). Unlike the majority of the other inshore prey species, however, it occasionally swims in the water column as well as on the bottom.

White sharks have been reported to feed on the carcasses of captured basking sharks (Fast 1955), although we know of no published accounts of predation under natural circumstances. However, potential vulnerability of basking sharks to large predators was suggested by Limbaugh (1963) in an account of a dead basking shark with a large wound probably inflicted by killer whales. Basking sharks, which reach lengths of more than 11 m, are found seasonally in offshore waters of central and northern California. From aerial surveys made over a 2.5-yr period near Monterey, California, Squire (1967) found that basking sharks were most common from September through May, when water temperatures were generally below 14°C. White shark sightings, however, were most common in the warmer-water months of May through August, when water temperatures neared or exceeded 14°C. The cause of the seasonal disappearance of basking sharks from the coastal waters of California remains unknown. Other prey that inhabit pelagic waters include the soupfin shark (*Galeorhinus zyopterus*), the Pacific sardine (*Sardinops sagax*), and occasionally bat rays (*Myliobatis californica*) (Roedel and Ripley 1950; Feder et al. 1974).

Combined data on the food habits of 33 white sharks from this study and other published records are shown in Fig. 11. Here again, fish were the most frequent prey items, occurring in over half of white sharks in the analysis. Elasmobranchs and rayed-fin fishes (teleosts and sturgeons) comprised equal proportions (each occurred in 30 percent of sharks analyzed) of the piscine prey. Pinnipeds were also a major component in the diet of sharks, while cetaceans and other prey groups were less common. Bass et al. (1975) provided the only other gut content data from white sharks useful for comparison. They too found both elasmobranchs (40 percent of sharks examined) and teleost fishes (25 percent) as the most common prey items, although little information was given on specific identification.

Figure 12 shows the distribution of fish and mammal prey in relation to shark size. Fish prey predominated in the diet of sharks approximately 3 m or less (TL), while pinnipeds and cetaceans predominated in those of larger sharks. This shift in diet may occur for a number of reasons. For example, larger sharks are less agile and would be less successful in chasing and cap-

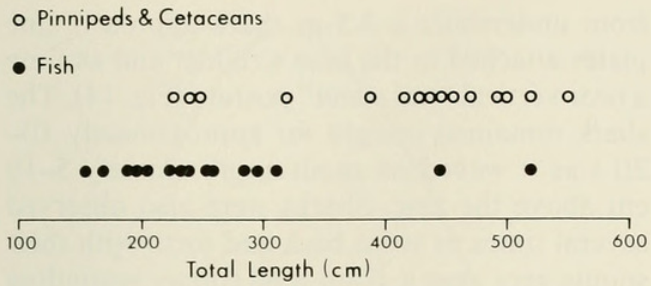


FIGURE 12. The relationship between white shark length and prey type. Data taken from stomach contents of the 33 specimens in Fig. 11.

turing smaller fish prey that dart about when pursued. Larger sharks may thus switch to different prey types and associated new hunting modes. In addition, the energetic requirements of large, warm-bodied sharks may be better met by prey high in fat content (i.e., high-energy–density prey). Carey et al. (1982) estimated the metabolic rate for a 4.6-m white shark, and concluded that the animal could survive for approximately 1.5 months on 30 kg of whale blubber (a conservative meal size). They suggest this to be adaptive during long intervals between encounters with prey. Although little is known of the movements of white sharks, they do show seasonal peaks in abundance in California waters (Squire 1967; Ainley et al. 1981), which might indicate some sort of regional or long-distance movement.

Morphological differences between large and small sharks may also account for different predatory tactics. Fig. 13 shows the relationship between tooth shape and shark total length. Smaller sharks have a relatively long, narrow tooth shape that is better adapted for grasping prey like small fishes. This feature is so well developed in small white sharks that they are often incorrectly identified as mako sharks (*Isurus* spp.) (Smith 1951, 1957). At about 3 m TL, the teeth broaden at the base and take on the diagnostic triangular serrated form. Unlike the long narrow teeth, this shape is well-suited for gouging and cutting pieces from prey too large to swallow whole. Le Boeuf et al. (1982) found evidence that marine mammals were the only prey of large white sharks they examined from California. Of seven specimens examined, all but one were approximately 4 m or longer and had evidence of marine mammals in their stomachs. The only exception was the smallest shark (2.4 m TL), which had only a 10-cm patch of pinniped pelage in its stomach.

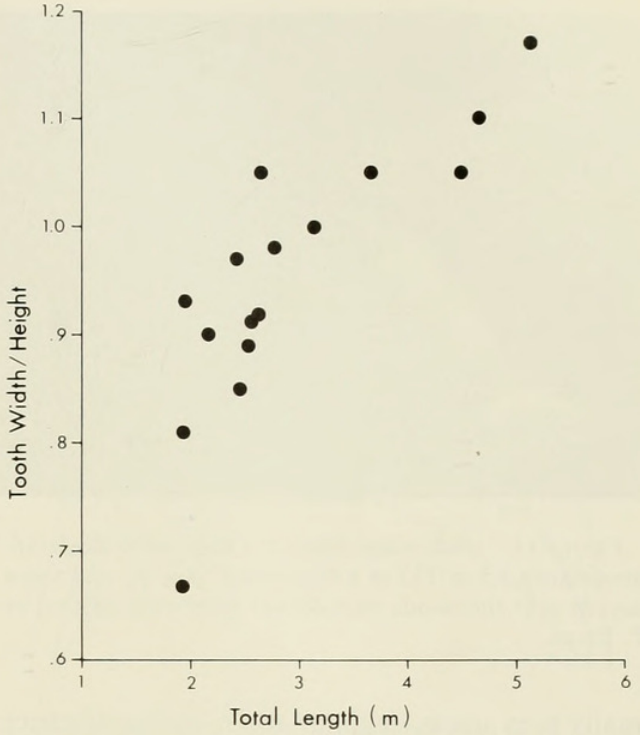


FIGURE 13. The relationship between shark total length and tooth shape. Tooth shape expressed as the ratio of width of enamel base to medial height of enamel for the first tooth, right side, upper jaw of 16 sharks. Low ratio indicates a long narrow tooth shape; higher ratio indicates relatively broad triangular shape.

Perhaps this shark's teeth were too narrow to excise a portion of flesh.

In California waters, elephant seal populations at offshore rookeries peak in both the spring and winter months (Le Boeuf et al. 1974), but almost no predation occurs during the spring peak. Hypothetical explanations advanced to explain this seasonal discrepancy in predation include either: 1) sharks fasting while breeding; 2) water too cold for sharks to feed; or 3) emigrations of sharks from the area. Even though sharks occur in California waters during the spring (Miller and Collier 1981), the decrease in shark attacks is probably due to emigrations of large sharks from coastal areas (see Squire 1967). Adult male seals are more susceptible to shark predation because they spend more time in the water near the rookery during the breeding season than do females (Le Boeuf et al. 1982). It is possible that the loss of peripheral males to sharks may not adversely affect the population because of the polygynous mating system of the elephant seal, where relatively few dominant males do the majority of the breeding.

Although it is clear that white sharks do nor-

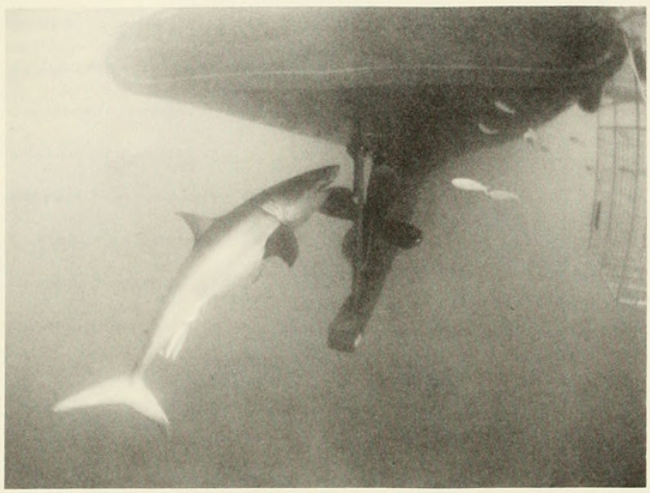

FIGURE 14. Underwater photo of a male white shark (approximately 3.5 m TL) in a "tail stand" posture with snout directly over zinc anode on rudder of study vessel. Photo by T. Tricas.

mally prey upon elephant seals, the significance of the interaction is not evident. Ainley et al. (1981) reported an increase in the number of attacks on elephant seals at the Farallon Islands between 1970 and 1979, but their data indicate a density-dependent relationship between number of attacks and numbers of elephant seals. More data are needed on the mortality rates of attacked seals and on numbers in the shark population before any effects of shark predation on elephant seal populations can be quantitatively assessed.

SENSORY BIOLOGY.—Our cursory field experiments and observations qualitatively indicate white sharks are sensitive to electric fields. In the pulsed electric field tests, sharks took the experimental bait 8 times (73 percent) and the control 3 times (27 percent). In the constant current (DC) tests the experimental was taken 4 times (44 percent) and the control 5 times (56 percent). Although our sample size was too small to show any statistically significant preference for baits with either type of electric field, sharks did take baits with the pulsed electric field almost three times more often than the control. The sharks also appeared to be more responsive to pulsed fields than to continuous fields. Kalmijn (1971, 1974) reported that sharks were most responsive to weak electrical fields at frequencies from 0 (DC) to 8 Hz.

We also observed the behavior of sharks to metallic objects attached to the bottom of the boat. On three occasions one of us (TCT) watched from underwater a 3.5-m shark approach zinc plates attached to the boat's rudder and assume a near vertical "tail stand" posture (Fig. 14). The shark remained upright for approximately 10–20 s as it waved its snout approximately 5–10 cm above the zinc. Sharks were also observed several times to swim back and forth with their snouts very near a 10-m-long copper grounding strip on the bottom of the boat's hull.

We interpret these observations as a response by sharks to the galvanic currents produced by the electrochemical interaction between the metallic plates and seawater. White sharks have a well-developed system of ampullae of Lorenzini (Fig. 15), and although the role of electric detection of prey by sharks is well demonstrated (see Kalmijn 1978, 1982), the degree of importance for such a sensory modality in white sharks remains unknown. It is noteworthy, however, that electric fields produced by large mammals (e.g., humans and presumably pinnipeds) in seawater are well within the sensory range of elasmobranchs (Kalmijn 1971). Perhaps young white sharks are able to detect electrically sedentary camouflaged fish prey like the cabezon (*Scorpaenichthys marmoratus*). It also seems reasonable that the ampullae would be particularly useful to detect: 1) the location of a marine mammal at the moment just prior to attack; 2) any change in position or escape attempts by the prey; and 3) any change in the prey's condition, such as bleeding, which might alter the strength or signature of the electric field.

TELEMETRY.—Two sharks were tagged with temperature-sensing transmitters during this study. The first shark (a 4.5-m male) carried a unit that monitored ambient water temperature only. After tagging, the shark remained around the boat even after all baits were removed from the water. The boat was then moved away from the area and the shark began to move westward; parallel to the north shore of Dangerous Reef. Once past the island the shark moved offshore in a northwesterly direction. Contact was lost with the animal approximately 4 h after initial tagging, due to its rapid speed and bad seas that created poor tracking conditions. During this time the shark swam in waters 20–21°C as indicated by the temperature sensor on the transmitter.

The second shark was tagged on 22 January 1980. The body temperature probe was placed 31 cm deep into the lateral musculature, ap-

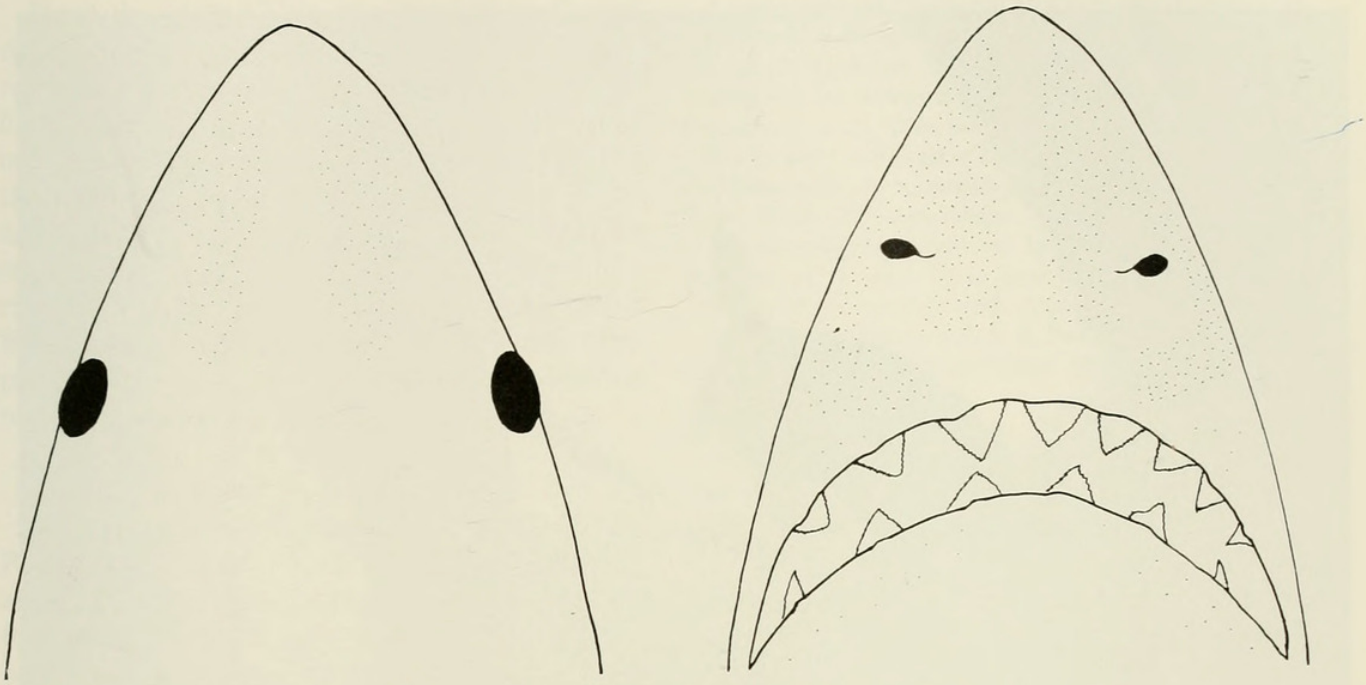

FIGURE 15. Distribution of the ampullae of Lorenzini on the head of a young female white shark (CAS 37917). Figure by C. J. Slager.

proximately 25 cm below the first dorsal fin. This shark was monitored continuously near the boat for approximately 2 hr, until it swam out of range. It returned to the anchored boat near midnight, and then again departed. Results of the thermal data are presented in Table 1 and Fig. 16. The shark swam in water ranging from 20.9° to 21.5°C. Mean difference between ambient and body temperature was 3.7°C, and ranged from 3.2° to 4.3°C.

TABLE 1. EPAXIAL MUSCLE TEMPERATURES OF A 3.5 M (TL) MALE WHITE SHARK MONITORED AT DANGEROUS REEF, SOUTH AUSTRALIA ON 22 JANUARY 1980. Mean ($\Delta T$) = 3.7°C. SD = 0.37.

| Measurement | Temp (°C) | | |
|---|---|---|---|
| | Water | Body | Difference ($\Delta T$) |
| 1 | 21.2 | 25.2 | 4.0 |
| 2 | 21.5 | 24.7 | 3.2 |
| 3 | 21.2 | 24.7 | 3.5 |
| 4 | 21.2 | 25.2 | 4.0 |
| 5 | 21.2 | 25.2 | 4.0 |
| 6 | 21.2 | 25.2 | 4.0 |
| 7 | 21.2 | 24.7 | 3.5 |
| 8 | 20.9 | 25.2 | 4.3 |
| 9 | 20.9 | 24.7 | 3.8 |
| 10 | 20.9 | 24.2 | 3.3 |
| 11 | 20.9 | 24.2 | 3.3 |
| 12 | 20.9 | 24.2 | 3.3 |

Largest and smallest differences were recorded when the shark entered water of a different temperature, before internal temperatures could conform. This time lag to thermal equilibrium and variation in muscle temperature indicate that the shark did not thermoregulate. Carey et al. (1982) found that a 4.6-m white shark had a body temperature 3–5°C higher than the surrounding water. Their shark swam over deeper waters, and for the most part remained in the thermocline. Temperatures were lower in their study, ranging approximately from 5° to 19°C ambient, and 18°

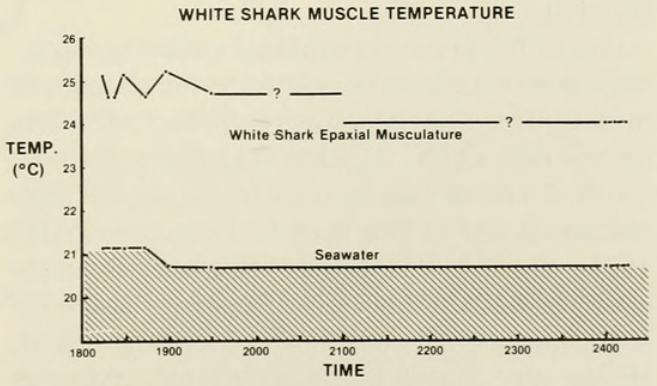


FIGURE 16. Temperature difference between ambient seawater and epaxial musculature of a 3.5 m TL white shark, monitored on 22 January 1980 at Dangerous Reef, South Australia. Question marks (?) indicate time interval when shark swam away from anchored study vessel and out of telemetry range. Figure by K. O'Farrell.

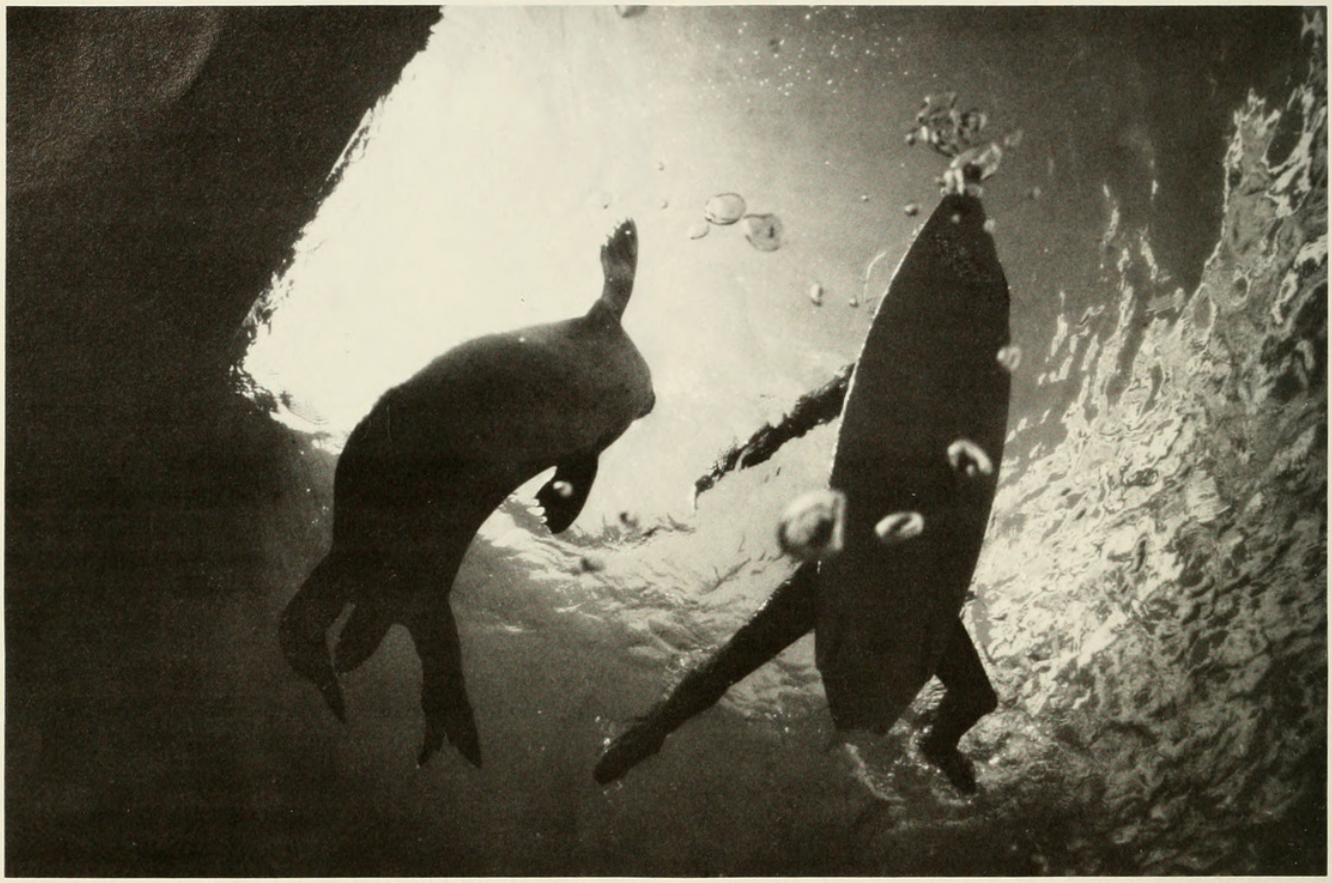

FIGURE 17. (Right) Silhouette of a surfer on a contemporary surfboard. (Left) Silhouette of an adult female (TL = 1.7 m) harbor seal (*Phoca vitulina*). Photo by Al Giddings.

to 23°C muscle temperature. Our study took place in relatively shallow waters around Dangerous Reef (<30 m), and we found no sign of a marked thermocline. The water and shark-muscle temperatures we recorded were generally higher (20.9°–21.2° and 24.2°–25.2° C, respectively), but they are consistent with the values for body temperature elevation over ambient recorded by Carey et al.

One of the primary advantages of being warm-bodied is thought to be related to the changes in muscle physiology as temperature increases. It is known that a 10°C increase in temperature may result in a three-fold increase in the contraction-relaxation rate of frog muscle (Hartree and Hill 1921). For fish, this may be translated to an increase in potential tail-beat frequency and a related increase in sustained swimming speed. Higher speeds may be selectively advantageous when chasing prey or fleeing from predators. In addition, conservation of heat theoretically allows for more total energy conversion to work, thus enabling an animal to swim longer distances on a given meal. Being warm-bodied might also allow for temporary excursions into colder or deeper waters. This thermal inertia (see Neill et al. 1976) would not only expand the range of environments which the animal could exploit, but would also permit increased swimming efficiency for predation at otherwise limiting environmental temperatures.

ON WHITE SHARKS AND SURFBOARDS.—In conclusion, we comment on the increasing attacks by white sharks upon humans who surf in the north Pacific. Since 1972, there have been 11 recorded white shark attacks upon surfers in California and Oregon (Miller and Collier 1981) and one such attack in Hawaii in 1959 (Balazs and Kam 1981). The similarity in appearance of the silhouette of a prone human on a surfboard or "belly board" to a large surface-basking pinniped is clear (Fig. 17), and observations of attacks by sharks upon surfers fit well with our assessment of the feeding strategy of white sharks. Attacks have occurred in the vicinity of pinniped rookeries, such as the much-publicized death of Lewis Boren on 19 December 1981 at Spanish Bay, Monterey, California.

Since the early 1970s, the trend in surfboard design has been toward an increase in flotation, reduction in board length, multiple posterior-fixed rudders ("skegs"), and bifurcated or "V" tails. All of these modifications have enhanced the similarity between the silhouette of a surfer and that of a pinniped, and we suggest that this may increase the probability of attack of surfers encountered by white sharks. We feel it advisable that those who surf be aware of and consider the potential risks of surfing in coastal waters known to be frequented by white sharks.

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Senior authorship of this paper was determined by the outcome of a pinball match played at Port Lincoln, South Australia, in January 1980.

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