

## Temperature and Activities of a White Shark, *Carcharodon carcharias*

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A large (4.6 m) white shark was followed for 3.5 days while its depth, water temperature and muscle temperature were recorded by acoustic telemetry. During this time the shark moved 190 km from an area south of Montauk Point, New York to Hudson Canyon. It made a number of brief excursions to the surface and to the bottom, but usually swam in the thermocline. Muscle temperature of the shark was as much as 5 C warmer than the water, confirming that a system of large retia mirabilia in the circulatory system function as heat exchangers. The shark did not thermoregulate and muscle temperature changed slowly as water temperature changed. The warming of the muscle as the shark swam into warmer water allowed us to estimate its rate of metabolism. The rate obtained is low and despite being warm, it appears that the shark can maintain itself for more than a month on a single large meal. The implications of this for its feeding habits are discussed.

THE circulatory system of the white shark, *Carcharodon carcharias* (Linnaeus), contains the same large retia mirabilia which allow the other lamnid sharks, the porbeagle, *Lamna nasus* (Bonnaterre), and the mako, *Isurus oxyrinchus* Rafinesque, to raise their body temperatures above that of the surrounding water. We report here a telemetry experiment with a free-ranging white shark which demonstrates that it, like the other lamnids, is warm bodied. The acoustic telemetry technique which we used also allowed us to make some observations on the shark's behavior.

The white shark is found throughout the world's tropical and temperate oceans. In the western North Atlantic it has been recorded most frequently north of Cape Hatteras (Bigelow and Schroeder, 1953; Scattergood, 1959; Skud, 1962; Mundus, 1971) and has been found as far north as northern Newfoundland (Templeman, 1963). It occurs in water as cold as 11 C (Squire, 1967; Baldrige, 1974). It is a rarely encountered shark however (Of a total of 4,770 sharks taken by longline between Cape Hatteras and Cape Cod in the years 1961 to 1967, only 36 were *Carcharodon*.), and while it has been suspected for some time that it would prove warm-bodied (Carey et al., 1971), it was only recently that we had an opportunity to measure its temperature.

### METHODS

An acoustic telemetry system was used to continuously monitor muscle temperature, sea-water temperature and depth with three separate acoustic transmitters operating at 50, 40 and 33 kHz. The transmitters were small, had a range of several kilometers and a useful life of about a week. A general description of the system is given in Carey and Robison (1981).

The 50 kHz muscle temperature transmitter had a thermistor mounted on a 40 cm long, 2.3 mm diameter flexible cable. The thermistor was cemented into a hole in a miniature swordfish dart (9 × 3 cm) and the dart was attached to the transmitter by a twisted loop of 1.8 mm diameter monofilament nylon, which took the stress of the thermistor cable as the transmitter was towed through the water. The entire package was arranged to fit on a standard harpoon pole with an adjustable stop on the shaft to limit penetration to 30 cm when it was darted into the shark (Fig. 1).

The depth transmitter used in these experiments was designed for 0 to 350 m, and was not appropriate for the usual 10 to 20 m depth of the shark. Data from the water temperature transmitter were used for a more accurate determination of depth when the shark was in the thermocline. Water temperature variation with

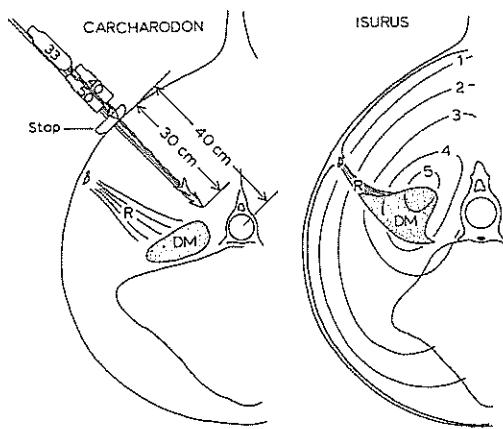


Fig. 1. The diagram on the left shows the approximate location of the thermistor harpoon in the white shark. The shaft was pulled out leaving the transmitters attached to the harpoon head. A stop on the shaft limited penetration to 30 cm. The thermistor was probably in the white muscle a short distance above the dark muscle. In the mako, *Isurus oxyrinchus*, on the right, the temperature relative to that of the water is shown as a concentric pattern of 1 C isotherms. The highest temperatures are in the dark muscle, but the adjacent white muscle is quite warm. The *Carcharodon* weighed 20 times more than the mako illustrated. We expect a similar temperature distribution in the larger shark except that the gradient would probably be more toward the periphery and the center more homogeneous in temperature. R indicates the lateral ratia mirabilia, DM indicates dark muscle. Numerals on the transmitters indicate their frequency: 33 kHz for depth, 40 kHz for water temperature and 50 kHz for muscle temperature.

depth was measured with a mechanical bathythermograph which was lowered approximately every two hours and the bathythermograph slides were used to prepare a graph of isotherm depth vs time. Water temperature broadcast from the fish was converted to depth by interpolation on this graph. The accuracy and precision of temperature measurement were good. A transmitter recovered after 13 days on a bluefin tuna was within 0.1 C of its original calibration. When counting 10 pulses over a 30 sec period, a 0.1 sec timing error caused only a 0.1 C error in temperature. Overall accuracy was within 0.2 C, allowing accurate location of the fish in the thermocline where gradients were often more than a degree per meter.

Water depth was determined with the vessel's

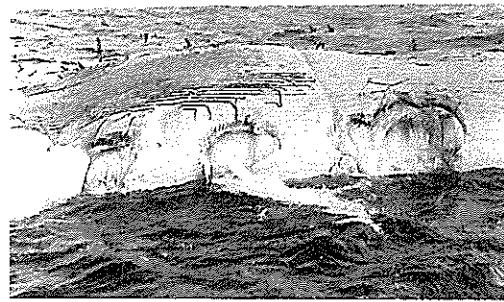


Fig. 2. This decaying 15-meter fin whale clearly shows the bites taken by white sharks. The flesh was gaseous and the whale floated more than a meter out of the water, leaving a slick many kilometers in extent.

fathometer. Navigation was by Loran C. The plot of the ship's course approximated that of the fish.

#### RESULTS

The appearance of a dead fin whale off Montauk Point, New York in the summer of 1979 attracted a group of white sharks and made this experiment possible. The 15 m long whale was in an advanced state of decomposition, and its tissues were very gaseous. It floated 1.3 meters out of the water and produced a slick many kilometers long. There were large holes along the water line of the floating carcass where sharks had bitten out chunks of blubber (Fig. 2). Several thousand petrels fed from the slick of fat droplets, but the common blue shark, *Prionace glauca* (Linnaeus), was conspicuously absent. The white sharks usually appeared one at a time to feed on the whale. Observers thought that during the period from 29 June to 6 July, there were at least five individuals present, based on variations in size and markings. One of these was harpooned by a fisherman and landed in Moriches, New York where we examined it. The shark, which was judged similar in size to the one we later followed, weighed 943 kg, was 4.57 m long, had a girth of 2.6 m, and had 30 kg of blubber in its stomach.

Our experiment began as the shark was feeding on the whale 39 km SSW of Montauk Point, New York on 1 July 1979. Chunks of meat were

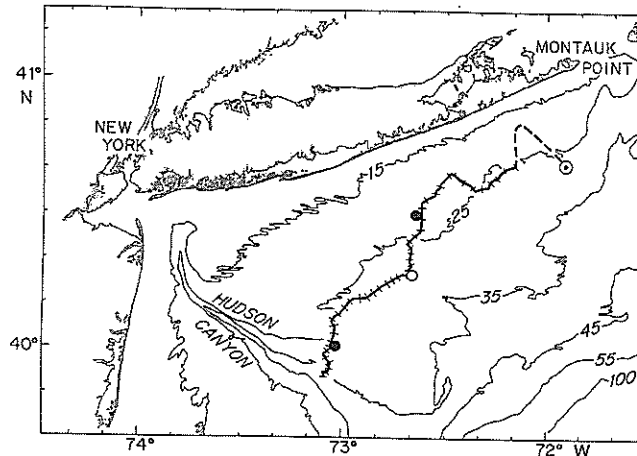


Fig. 3. Course followed by the white shark, 1-5 July 1979. For the first 1.5 days it remained near the whale in the area marked by the circle. It then moved toward the southwest and was finally lost in Hudson Canyon. Dashed line indicates position determined from shore bearings. Ticks at 1 hour intervals. Circles = sunrise; dots = sunset. Bottom contours in fathoms.

hung from the stern of a boat which was tied to the whale. A male white shark estimated to be 4.6 m long seized the meat and was struck with the transmitter harpoon as it turned away. It gave no reaction to being hit, but circled around and took a bite out of the whale. During the next 1.5 days it remained in the area, swimming within a 3-km radius of the whale. It was seen feeding during the morning and evening, and at these times the transmitters indicated that it was on the surface. On the second night it left the whale and moved inshore to within 11 km of the beach, then turned and swam in a southwesterly direction for the remainder of the experiment (Fig. 3). The shark had reached Hudson Canyon on the fourth night and was lost due to a breakdown of the tracking vessel. The shark's average speed after leaving the whale was 3.2 km/h and it moved 190 km during the 83 h long experiment.

On three occasions when live whales were seen within a few km of our boat there was no noticeable change in behavior of the shark. On the afternoon of 3 July the shark swam through a conspicuous chum slick set out by fishermen trying to attract bluefish to their small boat. We could detect no alteration in course or speed of the shark as it passed through the slick.

The muscle of *Carcharodon* is warm. As shown in Fig. 4 it was commonly 3 to 5 C warmer than the water; about as warm as the muscle of the mako shark but somewhat cooler than maximum temperatures in the porbeagle (Carey

and Teal, 1969). In mako and porbeagle the highest temperature is found in the dark muscle. In *Carcharodon* the dark muscle lies in a strip above the body cavity and close to the vertebral column (Fig. 1). The thermistor harpoon was placed near the dark muscle and while it is doubtful that we were recording the maximum muscle temperature, the measurement was certainly made in one of the warmer regions.

The muscle temperature was not constant, but responded to changes in water temperature. During the first 12 hours the average water temperature decreased gradually, then sharply as the shark made a series of dives into cold water (Fig. 4). The decrease in mean water temperature resulted in a cooling of the muscle. The changes in muscle temperature were slow and lagged behind changes in water temperature by several hours.

The shark located itself in the well-developed thermocline which exists in the New York Bight area in the summer. Depth telemetry placed it in the steepest part of the thermal gradient while a more accurate depth derived from water temperature placed it 1 or 2 m higher near the upper surface of the thermocline, but still in water colder than the mixed layer. The shark came to the surface to feed on the whale and went to the bottom a number of times (Fig. 5). The dives to the bottom caused sharp cold pulses in the water-temperature record (Fig. 4), and seemed quite different in nature from the

small-scale vertical movements that the shark made while in the thermocline.

#### DISCUSSION

This experiment demonstrates that the white shark is warmer than the surrounding water. The retia mirabilia act as countercurrent heat exchangers (Scholander and Krog, 1957) which retain metabolic heat within the tissues and prevent heat from being carried away by the circulation and lost through the gills during respiration (Carey and Teal, 1966). Although warmer than the water, the shark did not appear to thermoregulate. Its muscle temperature changed slowly with water temperature and showed considerable thermal inertia (Neill et al., 1976). Since heat transfer by the circulation is greatly reduced by the countercurrent heat exchangers and since heat transfer by conduction is slow in such a large bulk of muscle, it is to be expected that muscle temperature would respond slowly to changes in water temperature.

The shark swam in the thermocline where it could pass through an ambient temperature change of several degrees by moving only a few meters in the vertical direction. While this might seem convenient for behavioral thermoregulation, neither water temperature nor muscle temperature were held constant (Fig. 4). It seems that the position in the temperature gradient and not the absolute temperature itself was important to the shark. The temperature gradient may provide a convenient feature for orientation. On this interface small vertical movements would allow the shark to sample two water masses; the mixed layer above and the cold water below. The larger excursions to the surface and to the bottom which can be seen in Fig. 5 may indicate that the shark was exploring the limits of its environment.

Aside from a clear preference for the thermocline, we saw no other obvious patterns in the activities of the shark. There were none of the cyclical inshore-offshore movements described for blue sharks, *P. glauca* (Sciarrotta and Nelson, 1977), nor did we see any diel vertical movements in response to light as reported for other pelagic fish (Blaxter and Parrish, 1965; Yuen, 1970; Tesch, 1978; Carey and Robison, 1981).

Observers in aircraft have seen large *Carcharodon* swimming in the surface waters south of New England. These observations raise the question of what the sharks might be feeding

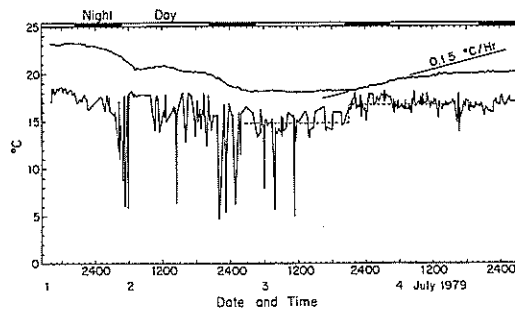


Fig. 4. Muscle temperature of the white shark, upper line, and water temperature, lower line. The muscle is 3 to 5 °C warmer than the water and responds to changing water temperature with a time lag of several hours. Sharp decreases in water temperature occurred when the shark swam to the bottom. The dashed line indicates average water temperature before and after a 2 °C increase in water temperature at 2100, 3 July. The initial rate of increase in muscle temperature which followed (0.15 °C/h, indicated by diagonal line) was used to calculate metabolic rate.

on in this area. The seals, sea lions and elephant seals which are common items in the diet of white sharks in other regions (Five white sharks ranging in size from 139 to 1,882 kg, taken in Californian waters in 1975 and 1976, had the remains of harbor seals, elephant seals and unidentified marine mammals in their stomachs. [John Rupp, Curator of Fishes, Sea World, Orlando, Florida, pers. comm.]) are not available. Fishes are abundant here and among 26 small (1 to 2.3 m) white sharks taken by longline, 92% had been feeding on fishes. It seems likely however that the 3 to 5 m sharks are feeding on something larger. Whales are common off our coast. The sharks in this experiment were feeding on a dead whale and white sharks have been reported to feed on dead whales in other areas (Randall, 1973).

The University of Rhode Island Cetacean and Turtle Assessment Program (CETAP) conducted an aerial survey which located three dead whales floating between New York and Cape Cod during the summer of 1979. On a later CETAP flight another dead whale was seen with five large (up to 5 m) sharks feeding on it (H. Winn, G. Carter, CETAP, pers. comm.). Only floating whales will be seen from aircraft and presumably most of the common balaenopterid whales will sink to the bottom when dead (Slijper, 1979). Dead whales may be more common than the number of sightings

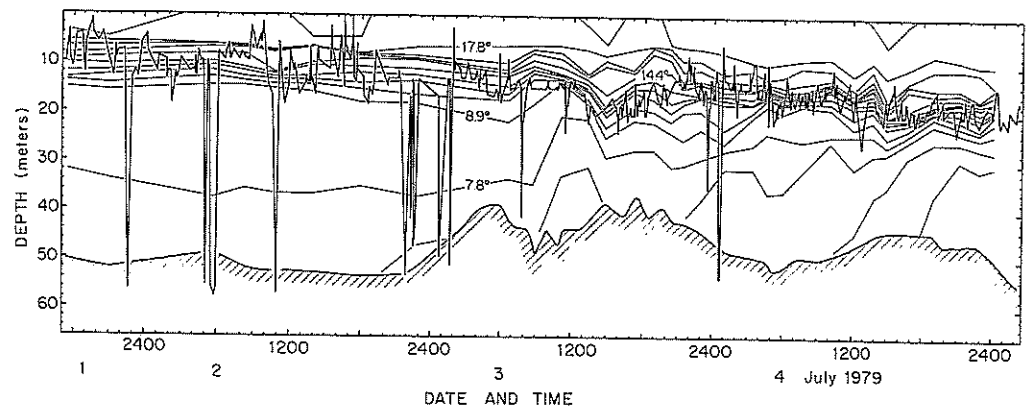


Fig. 5. Depth record for the shark superimposed on a pattern of 2 F (1.1 C) isotherms. The position of the thermocline is indicated by a crowding together of the isotherms. The shark located itself in the thermocline and made a number of brief dives to the bottom. Because our data acquisition rate was slow, brief dives which appeared in the depth record sometimes did not appear as a drop in the water-temperature record and vice versa, accounting for the difference in the pattern of diving shown in Figs. 4 and 5. A systematic 10% error in depth telemetry resulted in a record which exceeds bottom depth on a number of occasions.

would indicate and might represent an important source of food for white sharks.

It is interesting to estimate how long a single meal might last a white shark. The shark which had been killed a week before our experiment had 30 kg of blubber in its stomach. This shark was harpooned while still feeding and its stomach was not full. Presumably the shark we worked with, which apparently had fed to saturation, would have ingested more than 30 kg of blubber. Nevertheless, 30 kg would yield 200,000 Kcal of metabolic heat (Clowes, 1929; Kleiber, 1961). Knowledge of the white shark's metabolic rate would allow us to calculate how long this would last.

The fortuitous movement of the shark from cold to warm water on 3 July allowed us to estimate its rate of metabolism from the rate of change in its body temperature. At 2100 water temperature increased abruptly from 14.7 to 16.7 C in a short time (Fig. 4). Muscle temperature responded to this change by increasing from 18 to 20 C over a 17 hour period after entering the warmer water. These temperature changes can be related to metabolic rate as follows: If the animal were perfectly insulated, the production of metabolic heat would cause its temperature to rise and the rate of temperature increase would be directly related to the rate of metabolism. The shark, of course, was not perfectly insulated and its body temperature was the result of an equilibrium between heat pro-

duction and heat loss. When it swam into warm water, this equilibrium was upset but with time the gradient was re-established at a new and higher temperature. The warming was caused by metabolic heat production. It was not due to heat gain from the water, since the latter was at all times colder than the muscle. The initial rate of warming can be converted to metabolic rate by correcting for heat loss.

The shark's metabolic heat flows outward to the water through two parallel thermal barriers. One barrier is the resistance to conductive heat transfer which is presented by the large mass of muscle tissue. The other barrier is the retia mirabilia system which greatly reduces convective heat transfer by the circulation. At the point of measurement, 30 cm deep in the muscle, heat flow to the surface by conduction was slow and became insignificant for a time when the temperature difference between peripheral tissues and the water disappeared after entering warm water. Heat loss through the circulation decreased in proportion to the temperature gradient between deep muscle and water, which at 2100 dropped from 3.7 to 1.5 C, or to 40% of the original gradient. The initial rate of temperature rise after 2100 was estimated to be 0.15 C/h. This would require a heat production of 0.123 Kcal/kg/h. Correcting this by adding the 40% of metabolic heat lost through the circulation and not appearing as a temperature rise, brings the total heat production to 0.20

Kcal/kg/h, which is equivalent to an oxygen consumption of 60 mg/kg/h (Assuming a specific heat of 0.82 for muscle and caloric yield of 3.36 Kcal/g O<sub>2</sub> (Schmidt-Nielsen, 1979). We have ignored the fraction of metabolism used to do work on the environment and thus not appearing as a rise in muscle temperature. This might amount to as much as 20% of the total.). This value would be for the warm muscle and is a high estimate since the average over the whole fish, including colder and less active tissue, should be considerably lower.

Only a few measurements of elasmobranch metabolic rates are available for comparison and all of these are from small fish. A 2 kg lemon shark, *Negaprion brevirostris* (Poey), had a metabolic rate of 210 mg O<sub>2</sub>/kg/h at 26 C (pers. comm., S. Gruber, Univ. Of Miami). Brett and Blackburn (1978) reported that *Squalus acanthias* Linnaeus had a routine metabolic rate of 49 mg O<sub>2</sub>/kg/h when swimming slowly in 10 C water. They summarized three previous measurements of routine metabolic rate in *Squalus* and *Scyllium* and give an average value of 106 mg O<sub>2</sub>/kg/h at 13 C. They also suggested that metabolic rate for the warm lamnids might be quite different from other sharks. Our metabolic rate for the white shark is about three times larger than would be expected for a one ton dogfish at 20 C after the latter had been adjusted for temperature and scaled for size (Schmidt-Nielsen, 1979). We do not pretend to great accuracy in our calculation of metabolic rate, but consider it better than extrapolating from smaller specimens of other species.

With a metabolic rate of 0.20 Kcal/kg/h, the 943 kg shark was producing heat at a rate of 189 Kcal/h and 30 kg of blubber would have provided enough energy to last it for 1.5 months. Since our procedure would overestimate the shark's metabolic rate, it is likely that this amount of energy would actually have lasted considerably longer. It seems clear that *Carcharodon* requires only a small expenditure of energy for swimming. It is interesting that a hundred-fold extrapolation for size on Schmidt-Nielsen's (1972) curve for efficiency of swimming indicates that a 943 kg shark would use 0.05 Kcal/kg/km. At the observed speed of 3.2 km/hr this is 150 Kcal/h, close to our estimate of 189 Kcal/kg.

The large amount of blubber that it can ingest and the low metabolic rate and energy efficient mode of swimming indicated by our cal-

culations make it seem possible that these great sharks can search for food over a long time and distance. Dead whales may not occur frequently, but when available, they represent a very large amount of food. The slick which extends for many kilometers should make it easy for a shark to locate a dead whale. The diving behavior which we observed shows that on the continental shelf the sharks will pass through the thermocline into the cold bottom water and might locate and feed on a sunken whale. The large size of these white sharks and their ability to take huge bites (Fig. 2) make dead whales seem a more reasonable diet than one of small fishes captured individually.

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