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MAKO AND PORBEAGLE: WARM-BODIED SHARKS*

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Abstract—1. Mako and porbeagle sharks are able to conserve metabolic heat and maintain their bodies 7–10°C above ambient temperatures.

2. Highly developed countercurrent heat exchangers located in the vascular system of these fish form a thermal barrier which prevents heat from being carried off by the circulating blood and lost in the gills.

INTRODUCTION

LAMNID sharks are swift, active fish. The mako (*Isurus oxyrhynchus* Rafinesque, 1810) in particular is noted for its spectacular leaps when taken by hook and line. Reports by reliable witnesses and photographs indicate that mako can jump 15–20 ft into the air. To rise 16 ft requires a starting velocity of 22 mph in the water, indicating that the fish are capable of at least this speed. The power requirement for swimming increases rapidly with speed. With each 10°C rise in temperature, the power available from vertebrate muscle increases about threefold (Hartree & Hill, 1921). We have measured temperatures of mako and porbeagle sharks and found them to be considerably warmer than water. We believe that these fish obtain the extra power needed for high-speed swimming by operating their muscles at an elevated temperature.

MATERIALS AND METHODS

Temperatures were measured with thermistors mounted in the tips of 30-cm lengths of 16-gauge (1·65 mm) stainless steel tubing and read on a Yellow Springs Instrument Co. thermistor bridge. Holes were cut in the skin at various positions and the probes pushed measured distances into the muscle to obtain a grid of temperature measurements in both cross-section and frontal section.

Twelve mako sharks were caught with long-line fishing gear during cruises 66-13 and 67-2 of the Bureau of Commercial Fisheries Research Vessel *Delaware* in the Atlantic and on cruise 14 of the Research Vessel *Anton Bruun* during the Southeastern Pacific Biological Oceanographic Program. Two porbeagles (*Lamna nassus* (Bonnaterre, 1788)) were caught on cruise 155 of the Research Vessel *Gosnold*. Some of these sharks were quieted by curarae and kept alive on a rack on deck by inserting a 5-cm diameter hose in their mouth and flushing the gills with a stream of water at low pressure. Temperature measurements were begun as soon as it seemed safe, usually less than 5 min after the fish was brought aboard.

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Injection masses of colored latex or gelatin were used as an aid in dissection and study of the circulatory system of the mako, porbeagle and white shark, *Carcharodon carcharias* (Linnaeus).

RESULTS AND DISCUSSION

The distribution of temperature in the muscle is shown in Fig. 1. The pattern of isotherms is similar to that in a tuna with the warmest temperatures in the red muscle at the heaviest region of the body (Carey & Teal, 1966).

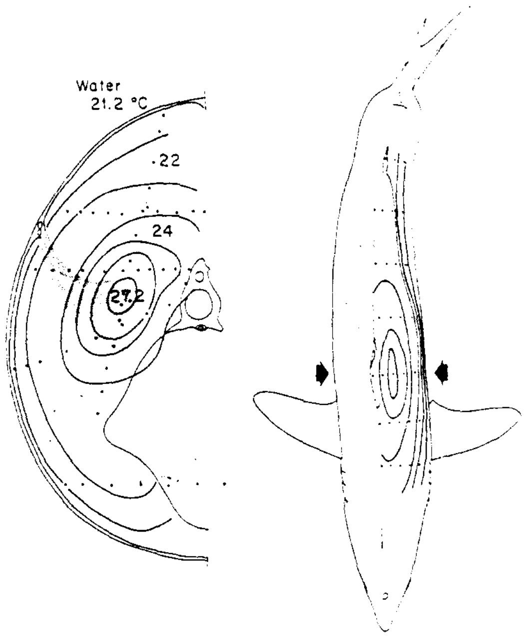

FIG. 1. Distribution of temperatures in cross-section and frontal section of a mako shark. Temperatures were measured with a thermistor probe at positions indicated by dots. Heavy lines are 1°C isotherms. The stippled area and hatching indicate the location of the dark muscle and rete. The highest temperatures are in the dark muscle at the inner end of the rete.

The temperature of the warmest region of muscle is plotted against water temperature in Fig. 2. When the sea temperature is below about 22°C the fish maintain a relatively fixed temperature differential above the water, but in warmer water they may be able to thermoregulate and maintain a more constant body temperature. The bluefin tuna shows a similar ability to thermoregulate, but over a much wider range of water temperature.

Porbeagle sharks may show an even greater temperature elevation over that of the water. We have three records for this shark showing maximum temperatures of 20·2° in 11·0°C water, 17·9° in 6·6°C water and 13·5° in 6·5°C water, the last measurement being made for us by Mr. Frank Mundus. The temperature distribution in the porbeagle was similar to that in the mako and in tuna, with the highest temperatures centered around the dark muscle and the steepest thermal gradients along the rete supplying this tissue. We expect that the third member of this family, *Carcharodon*, will also be found to be warm-bodied when we have an opportunity to measure its temperature.

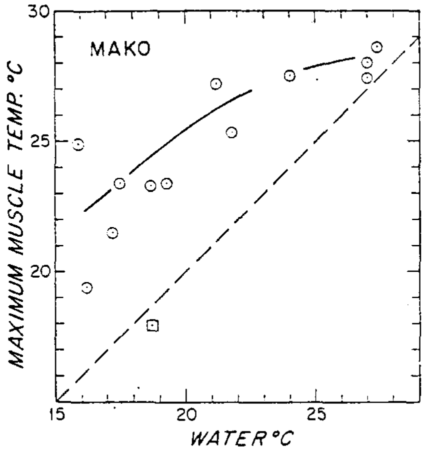

FIG. 2. Temperatures of mako caught at various water temperatures. The anomalously low temperature indicated by ⊡ is for a shark caught in a region with a strong thermocline near the surface. The fish was probably below the thermocline in water several degrees colder than the surface temperature. The light broken line represents a limit of body temperature = water temperature.

In most fish the circulation of the blood serves as an efficient cooling system, carrying the heat produced by the tissue to the gills where it is lost to the water. To raise its body temperature, a fish must be able to conserve metabolic heat. The lamid sharks, like the tuna, accomplish this through use of a set of countercurrent heat exchangers located in the circulation between the gills and the tissues. The heat exchangers form a thermal barrier which permits the flow of blood but blocks the flow of heat.

The structures which serve as countercurrent heat exchangers are the rete mirabile, masses of vascular tissue which are prominent features in the circulatory systems of the three species which make up the family Lamnidae. The circulatory system of the porbeagle, which was described by Burne (1923), is quite similar in its main features to that of the mako and to that of the white shark. In these three sharks the dorsal aorta is much reduced and the main blood supply to the muscle is through a set of greatly enlarged cutaneous vessels which run the length of the body. The cutaneous artery arises from the efferent artery of the fourth gill arch, near its dorsal root, and the vein empties into the duct of Cuvier. A multitude of small vessels arise along the entire length of the cutaneous artery and vein. These intermingle and form a rete of parallel arteries and veins which runs deep into the body. In the mako this rete lies on the upper margin of the dark muscle (Fig. 3) and forms a continuous slab of vascular tissue about 5 mm thick and running the length of the fish from the level of the front of the pectoral fin to near the level of

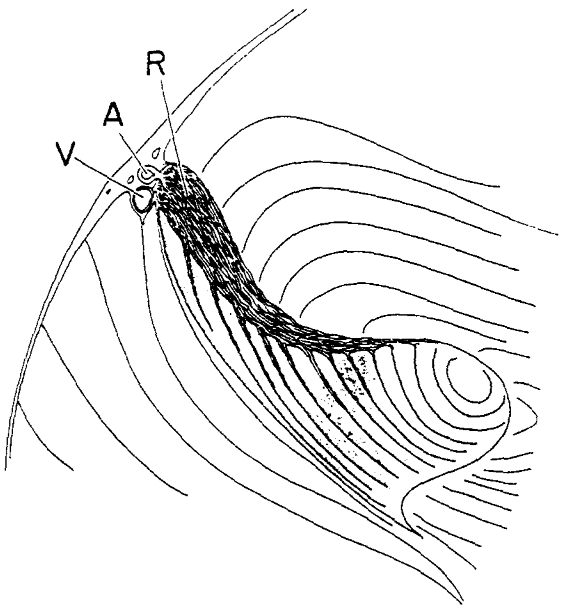

FIG. 3. Cross-section diagram showing the location of the muscle rete in a mako shark. Small vessels arising from the cutaneous artery (A) and cutaneous vein (V) intermingle and branch to form a mass of parallel arteries and veins running medially along the upper margin of the dark muscle. The rete (R) sends wide branches of many vessels into the dark muscle.

the second dorsal fin. As it passes inward from the cutaneous vessels the rete sends off wide branches of many parallel vessels into the dark muscle. The highest temperatures are at the inner end of this rete and the steepest thermal gradients are along it, in accord with its function as a heat exchanger. The white muscle is supplied with blood through segmental arteries and veins which arise from the cutaneous vessels and run dorsally and ventrally along the surface of the muscle mass under the skin. Branches from the segmental vessels have the form of vascular bands, single layers of alternately arranged arteries and veins which penetrate into the white muscle. The vascular bands also act as heat exchangers, retaining heat in the white muscle. The highest temperatures in the white muscle are found near the origin of the segmental vessels where these vascular bands are most numerous.

The arrangement of retia in the porbeagle and in *Carcharodon* is somewhat different from that in the mako. The small arteries and veins arising from the lateral vessels are dispersed through the muscle fibers rather than being concentrated into a solid mass of vascular tissue (Fig. 4). The rete serves a considerable region of light muscle as well as the deeply seated dark muscle and the vascular bands are numerous. From the elevated temperatures found in the porbeagle, this more diffuse rete appears to be as efficient as that of the mako.

The circulatory system serving the muscle of lamnid sharks is thus similar to that found in bluefin and bigeye tuna (Kishinouye, 1923) in that the dorsal aorta is much reduced and the main blood supply to the muscle is by way of large laterally located vessels through retia located on the margins of the dark muscle. The tuna, however, has a double system with two sets of cutaneous vessels and two retia closely applied to the dorsal and ventral surfaces of the dark muscle. There are other differences in the heat exchangers such as the arrangement of the vessels in the vascular bands. In tuna these are a ribbon of alternating arteries and veins with the arteries being most lateral, the simplest arrangement being a triad of artery–vein–artery. The lamnid vascular bands are arranged vein–artery–vein and are not as many vessels in width as the tuna.

We are impressed with the similarities between tuna and the lamnids and with the number of features which can be related to the requirements of high-speed swimming. Both groups of fish have heavy, streamlined bodies, shapes which give room for a large bulk of muscle, yet offer low drag. Their caudal fins are thin, hard and of lunate shape and they beat with short rapid strokes, making an effective high-speed propulsion system.

A number of internal anatomical features can be related to swimming speed through their role in the heat conservation system which allows the muscles to produce the great power needed for high speeds. Thus the dark muscle which fish use for continuous swimming at cruising speeds (Bone, 1966) is usually a lateral surface layer. These warm-bodied fish which must swim constantly in order to respire have a heavy band of very dark muscle which is remarkable for being set deep in the body rather than located superficially. This location places it in the warmest region where its power factor will be increased by the higher temperatures.

The arterial blood supply to the muscle is centripetal, from the skin through retia and vascular bands towards the vertebral column. The thermal gradients along these heat exchangers result in the surface being cool, thus reducing surface heat losses to the water while the deep muscle, including the dark muscle, is warm and able to produce more power. To achieve this centripetal arterial flow, the importance of the aorta has been greatly decreased and the flow through superficial vessels increased. The main blood flow to the muscles is thus through vessels which are of minor importance in other fish.

The ability to swim swiftly, achieved through the extra power available from warm muscles, must have been a powerful selective advantage in the evolution of tuna and lamid sharks. Starting with the basic features of a fish vascular system the stringent requirements of speed have resulted in the remarkable parallel evolution of almost identical systems in two completely unrelated groups of fish.

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