Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology

THE VISCERAL TEMPERATURES OF MACKEREL SHARKS (LAMNIDAE)[1]

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The viscera of mako Isurus oxyrinchus and porbeagle Lamna nasus sharks are significantly warmer than the water. The large suprahepatic rete mirabile in these fish is identified as a heat exchanger which retains metabolic heat to warm the visceral organs. An argument is presented that the efficiency of heat exchange in the rete must be greater than 97% to maintain the observed tissue temperatures and that this requirement explains the large size of the rete. A venous passage with a muscular wall which runs through the suprahepatic rete could allow blood to bypass the heat exchanger, and its presence suggests a simple mechanism for controlling temperature. However, measurements of temperature by acoustic telemetry from free-swimming sharks over a 4.5-day period do not give a convincing indication that stomach temperature is altered in a manner independent of the environment.

INTRODUCTION

The mako shark Isurus oxyrinchus Rafinesque 1810, the porbeagle Lamna nasus (Bonnaterre) 1788, and the white shark Carcharodon carcharias (Linnaeus) 1758 have warm bodies (Carey and Teal 1969; Carey et al. 1981). These lamnid sharks have a system of countercurrent heat exchangers (Scholander and Krog 1957) in their circulatory system which serve to retain metabolic heat and allow tissue temperatures to rise (Carey et al.

1971). The heat exchangers are formed by retia mirabilia which occur in the viscera as well as the muscle of these sharks.

An important feature related to heat exchange and blood supply to the viscera of these sharks is the peculiar routing of the arterial blood through the suprahepatic rete mirabile (Eschricht and Müller 1837; Burne 1923). This rete is a conspicuous paired mass of vascular tissue located ahead of the liver and closely applied to the ventral and lateral surfaces of the esophagus. It is a development of a venous space which has been penetrated by a greatly enlarged pericardial artery. This artery divides and redivides, filling the lumen of the sinus with a spongelike mass of small arteries. At the distal end of the rete the small arteries rejoin into a pair of collecting trunks which then send branches to the various visceral organs. While the coelio-mesenteric artery is the major visceral artery in most fish, the pericardial arteries are the largest vessels supplying the viscera of lamnid sharks (Burne 1923). The usual visceral arteries are also present and arise in the normal manner from a small dorsal aorta (in these sharks the major blood supply to the swimming muscles is through the lateral cutaneous vessels, rather than the dorsal aorta). Shortly after arising from the

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aorta, however, the coelio-mesenteric, lieno-gastric, and spermatic arteries receive large connections from the collecting trunks of the rete (Burne 1923). Comparison of vessel size indicates that flow through the suprahepatic rete probably dominates the blood supply to the viscera.

An interesting feature noted by Burne (1923) is a venous passage through the rete which leads directly from the liver to the sinus venosus. In this paper we describe a mechanism for closing this shunt and the effect this would have on temperature. We also report a variety of observations which bear on the question of temperature and temperature control in the viscera of lamnid sharks and on the function of the suprahepatic rete as a heat exchanger.

METHODS

Sharks were taken on longline fishing gear (Bullis and Captiva 1955) using steel leaders and mackerel bait. Since baited hooks were used, all measurements were on sharks which had recently been feeding or about to ingest food.

To measure tissue temperatures, sharks were brought aboard alive and a hose placed in their mouth to irrigate their gills.

Temperatures were measured with thermistors mounted in 16-gauge hypodermic needle tubing and read on a model no. 43 Yellow Springs Instrument Company thermistor bridge. After making a series of muscle temperature measurements, the body wall was cut open and the temperatures of the visceral organs measured. The procedure took from 3 to 15 min. When temperatures were taken in several places in a large organ, such as the liver, only the highest values are given in table 1. Three of the mako sharks in the table were caught along a sharp boundary between Gulf Stream and continental shelf water where there were large variations in water temperature between the surface and fishing depth. Their body temperatures were compared with the temperature of the coldest tissue rather than to the surface water. This procedure used by Ben Franklin's nephew, Johnathan Williams (Williams 1793), assumes that the coldest deep tissues are close to ambient temperature at the depth of the fish, before it was hauled to the boat. No acute temperature measurements were made on sharks used in telemetry experiments.

Temperatures of free-swimming sharks

TABLE 1

TEMPERATURES OF FRESHLY CAUGHT MAKO AND PORBEAGLE SHARKS (°C)

| WATER[a] | RETE[b] | | LIVER | STOMACH | SPIRAL VALVE | RED MUSCLE | HEART |
	Proximal	Distal					
			Mako				
21.9	22.3	24.0	25.1	26.8	28.0	28.5	22.3
11–18	15.0	19.0	19.6	19.0	21.9	22.0	...
11–18	16.2	21.0	18.5	21.0	23.8	26.4	15.7
11–18	12.5	15.7	17.9	19.5	20.7	22.5	12.0
20.2	21.4	25.5	22.5	21.6	22.5	26.6	...
Average ΔT			3.76	4.62	6.42	8.24	.1
			Porbeagle				
12.7	...	...	17.6	18.2	21.7	22.6	...
14.0	14.0	14.8	16.7	18.3	20.0	20.8	...
Average ΔT			2.7	4.3	6.0	8.35	...

[a]For mako sharks from water with a surface temperature range of 11–18 C, the ΔT is referred to the temperature of the coldest tissue; the proximal end of the rete at 15 C and the heart at 15.7 C and 12 C.
[b]The terms "proximal" and "distal" refer to the heart end and the liver end of the suprahepatic rete.

were obtained using acoustic telemetry techniques. The transmitters weighed less than 90 g in water, had a useful life of 4–7 days, and a range of 2–5 km under good propagation conditions. A general description of the telemetry system is given in Carey and Robison (1981).

For a telemetry experiment the shark was brought alongside and a large dip net hoop used to maneuver a loop of 2-cm-diam soft braided nylon rope over its tail. It was then quickly lifted onto the deck and a hose placed in its mouth to irrigate the gills with a large volume of low-pressure water. A 50-kHz temperature transmitter was clipped to the end of a 1-m detachable handle and pushed deep into the stomach. In the 1978 experiment, this was followed by five 400-g mackerel (*Scomber scombrus,* Linnaeus, 1758) which were pushed in on top of it. A second, 33-kHz, transmitter for water temperature was attached externally by a small harpoon dart near the base of the dorsal fin. The shark was then returned to the water and the tail loop cut free.

Blood samples were drawn into containers containing a small amount of heparin and were stored on ice for a few hours or overnight. Hematocrit was determined using capillary tubes in a hematocrit centrifuge. Blood oxygen capacity was measured using a method similar to that described by Tucker (1967). The blood sample was equilibrated with air in a small rotating vial.

RESULTS

ANATOMY

We compared the structure and dimensions of the suprahepatic rete from three species of lamnid sharks. The mass of small arteries making up the rete of the porbeagle appears in cross section as figure 4, plate 10 in Burne's 1923 paper. These arteries have an average diameter of 0.079 $\pm$ 0.012 mm and are present at a density of 85/mm^2. Because of the multiple interconnections among the small arteries, many of them are sectioned at branch points and appear as arrays of coalesced rings, rather than circles. Each partial

ring was counted as a separate artery and the diameter was measured along the minor axis when the artery appeared elliptical. A preserved specimen of the suprahepatic rete from a 183-cm-long, 88-kg porbeagle shark measured 8.0 cm long by 18 cm wide and tapered from 3 cm thick at the anterior end to about 1.5 cm at the posterior. It weighed 267 g, had a displacement volume of 240 ml, and an average cross-sectional area of about 30 cm^2 in a plane normal to the direction of blood flow. Weight of the rete was 3.4% of the weight of the visceral organs and 0.3% of the body weight. The density of the arterioles was 41/mm^2 with an average diameter of 0.13 $\pm$ 0.017 mm. This is somewhat coarser than the specimen figured by Burne, but the size of the vessels varies in a complex fashion throughout the rete, and the dimensions given here for various sharks should not be taken as a final description of the tissue.

Rete tissue from the white shark, *Carcharodon,* had somewhat smaller arterioles with a density of 107/mm^2 and an average diameter of 0.066 $\pm$ 0.007 mm. An intact specimen was not available, but examination of the anterior portion of the rete from an eviscerated 2-m shark indicated that in this species the suprahepatic rete is probably comparable in size to that of the porbeagle.

The suprahepatic rete from a 185-cm (snout-fork length), 75-kg mako shark was 15 cm wide by 4.5 cm long with an average thickness of 1.1 cm and weighed 78 g. The retia from three specimens averaged 1.15% $\pm$ 0.14% of the weight of the viscera and 0.101% $\pm$ 0.025% of the body weight. The mako heat exchanger is thus only about one-third as large as that of the porbeagle. The arterioles in the mako rete were 0.086 $\pm$ 0.014 mm diam with a density of 84 $\pm$ 13/mm^2.

In the white shark, porbeagle, and mako which we examined, the connections of the coelio-mesenteric, spermatic, and lieno-gastric arteries with the dorsal aorta were poorly developed. This is in agreement with Burne's description of the porbeagle. The aortic root of

the coelio-mesenteric was smallest in the mako (fig. 1), where it was difficult to tell if there was a patent connection.

A venous passage leading directly from the liver to the sinus venosus, thus bypassing the suprahepatic rete, was described by Burne (1923) who identified this passage as the true hepatic sinus. This double channel which runs between the lobes of the rete just above the ventral ligament of the liver (fig. 1), was examined for a sphincter or other means of restricting blood flow. A histological section from a small specimen shows that its inner wall is formed into a series of axial folds containing longitudinally oriented bands of
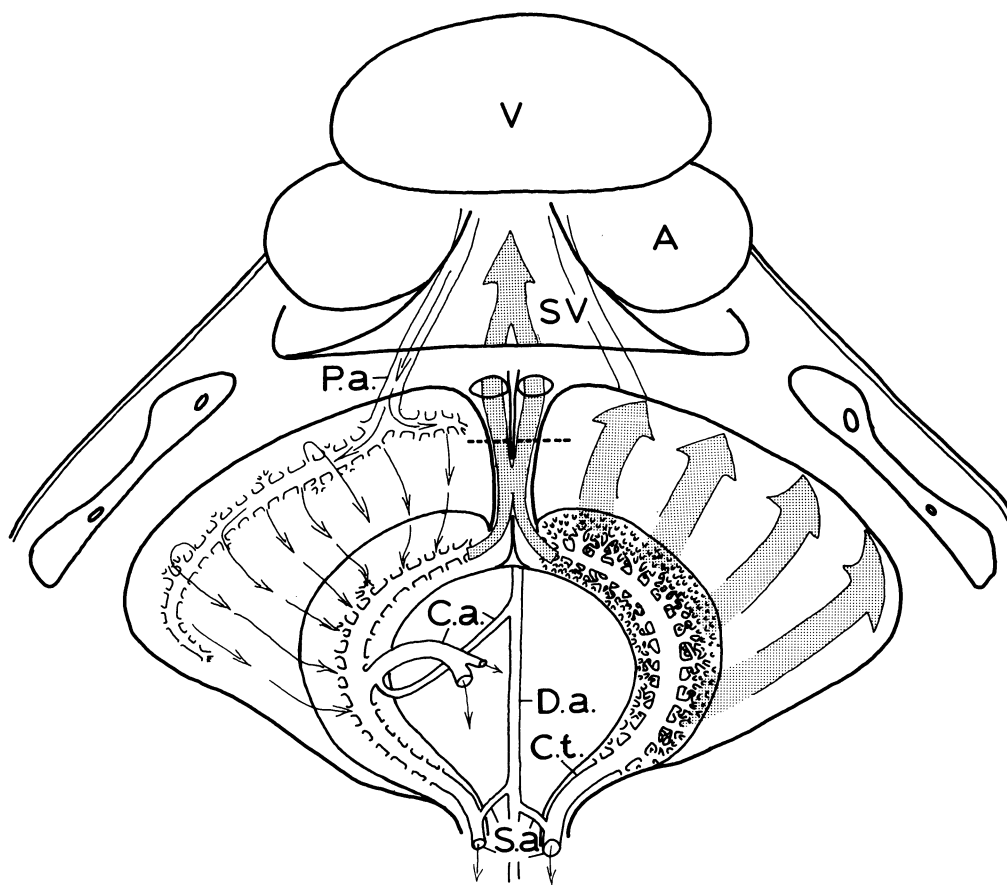
FIG. 1.—Suprahepatic rete of a mako shark exposed by cutting away the ventral body wall and pectoral girdle. A ventral view from the rear. The ventricle of the heart has been lifted up and the auricles pushed aside to show the sinus venousus. The rete fits closely around the esophagus, which is not shown in this diagram. The rete is formed by the arborization of the large pericardial arteries into a mass of small interconnecting arteries which fill a venous sinus. The liver has been removed exposing the arterial collecting trunks which drain the rete. Arterial blood (small arrows) flows from the pericardial arteries through the small vessels of the rete to a pair of collecting trunks and from large branches of these trunks to the visceral organs. Blood from the hepatic veins (large arrows) flows over the mass of fine arteries as a countercurrent to the arterial flow. The hepatic sinus forms a large central channel through the rete which would allow venous blood from the liver to flow directly to the heart (arrow). A cross-section of this passage is shown in fig. 2. The aortic roots of the coelio-mesenteric, spermatic, and lineo-gastric arteries are small and receive large branches from the collecting trunks. Blood flowing to the viscera through the aortic roots of these arteries would also bypass the rete. A, auricle; C.a., coelio-mesenteric artery; C.t., collecting trunk; D.a., dorsal aorta; P.a., pericardial artery; S.a., spermatic and lieno-gastric arteries; S.V, sinus venosus; V, ventricle.

smooth muscle fibers (fig. 2). The folds almost completely constrict the channel in preserved material, but are readily spread out and the channel dilated in fresh specimens. Exterior to the longitudinal muscle is a layer of circularly oriented smooth muscle fibers, which are arranged in numerous bands rather than in a continuous sheet.

VISCERAL TEMPERATURES

The liver, stomach, and spiral valve of mako and porbeagle sharks have temperatures which may approach those of the warm muscle (table 1). The heart, which is not served by a heat exchanger, was cold. The rete itself was warm with the proximal end having a lower temperature than the distal end. Incomplete sets of measurements from mako sharks show that other visceral organs may also be warmer than the water: spleen 5.4 C, gonad 3 C. The spiral valve of the intestine was the warmest visceral organ in the specimens we examined.

Temperatures from four other mako sharks were not included in table 1. They appeared in poor condition when boated

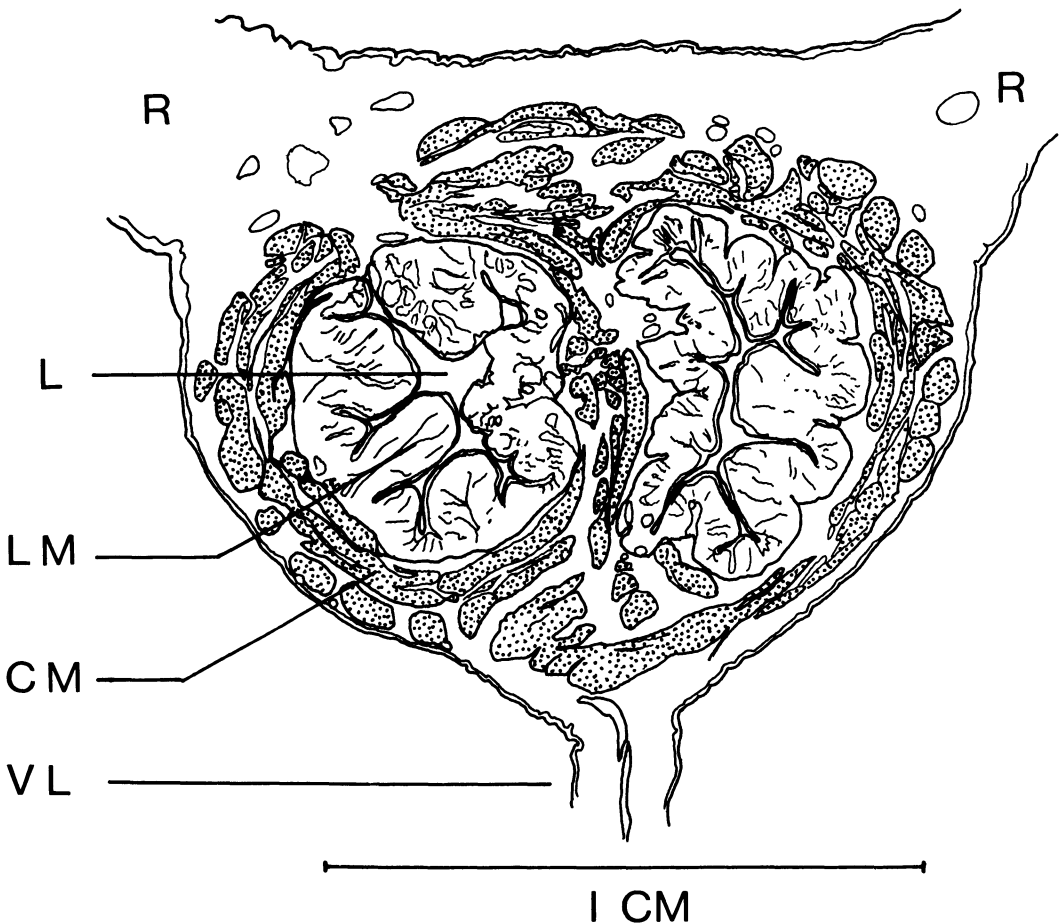FIG. 2.—Cross-section of the hepatic sinus. The position of the section is indicated by the dotted line in fig. 1. In this fixed preparation the muscular walls have contracted, almost closing the lumen. In life this would force blood to pass through the heat exchanger. R, median edge of suprahepatic rete; L, lumen of hepatic sinus; L M, longitudinal muscle fibers; C M, circular muscle fibers; V L, ventral ligament of liver.

and their temperatures were low: 3.5 C above water in the muscle and 1.6 C or less for the warmest visceral organs.

TEMPERATURE TELEMETRY EXPERIMENTS

Temperature information was successfully transmitted from free-swimming sharks in four experiments. The first two sharks stayed on the surface and showed little temperature elevation. They seemed moribund, and the results are not presented here. The next two were in better condition.

Mako no. 3.—1115–1620 hours (April 17, 1971). The temperature record for this fish is shown in figure 3. When released, the shark went below the thermocline briefly where it encountered 9 C water. It then returned to 16–17 C surface water and stayed there. During the course of the experiment, stomach temperature rose from 19.5 to 24 C and was 8 C warmer than the water during the final hour. This shark was a small male (28 kg, 136 cm) which swam at an average speed of 2.3 km/h, or 0.47 body lengths per second.

Mako no. 4.—1600 hours (March 27) to 2400 hours (March 31, 1978). This was an 180-kg, 240-cm female which was held on deck for less than 5 min and seemed to be in good condition when released. After the transmitter had been placed in the stomach, five 400-g mackerel were pushed in on top of it to ensure that the stomach contained food. Water and stomach tem-

FIG. 3.—Stomach temperature, upper line; water temperature, lower line. By the end of the experiment the stomach was 8 C warmer than the water.

perature records for this experiment are shown in figure 4. The stomach was commonly 6–8 C warmer than the water. During the period from 0000 hours (March 28) to 0600 hours (March 31), when this shark was away from the influence of the Gulf Stream, it swam at an average speed of 2.5 km/h or 0.3 body lengths per second.

HEMATOCRIT AND BLOOD OXYGEN CAPACITY

Blood from normal, ectothermic sharks had a modest oxygen carrying ability. We recorded hematocrits of 24.3% and 23.5% for two specimens of *Carcharinus longimanus,* the white tip shark, the first having an oxygen capacity of 8.9 vol %. Samples from blue sharks, *Prionace glauca,* had hematocrits of 17.5%, 19%, and 23%; the first of these had an oxygen capacity of 4.8 vol %, another with no hematocrit recorded had an oxygen capacity of 4.3 vol %. The values were higher for warm-bodied sharks. Three porbeagles had hematocrits of 38.7%, 39.5%, and 37.3% with oxygen capacities of 14.8 vol % and 12.3 vol %. Hematocrits of 28.2%, 31.2%, 31.7%, 36.6%, 34.8%, and 38% were measured for five mako sharks, the last two having oxygen capacities of 13.7 vol % and 14.1 vol %.

DISCUSSION

The following considerations indicate why these warm sharks are unusual and why most fish are within a fraction of a degree of water temperature. Under normal conditions metabolic heat is generated aerobically. To obtain the oxygen required, blood is pumped through the gills where it approaches equilibrium with oxygen dissolved in the water. Since thermal diffusion is more than 10 times as rapid as molecular diffusion (Hensel and Bock 1955; Altman and Dittmer 1971)[2] most of the heat contained in the blood is lost during passage through the gill (Stevens and Sutterlin 1976) and the oxygenated arterial blood is close to water tem-
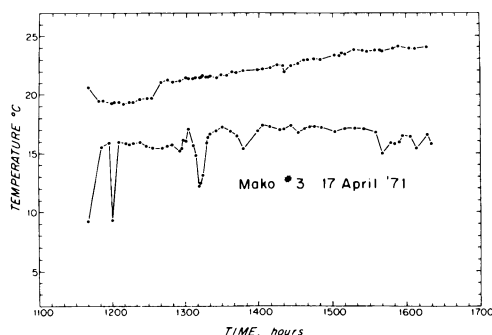
[2]The ratio of the thermal conductivity of human tissue to the diffusion coefficient for oxygen in water is 55.
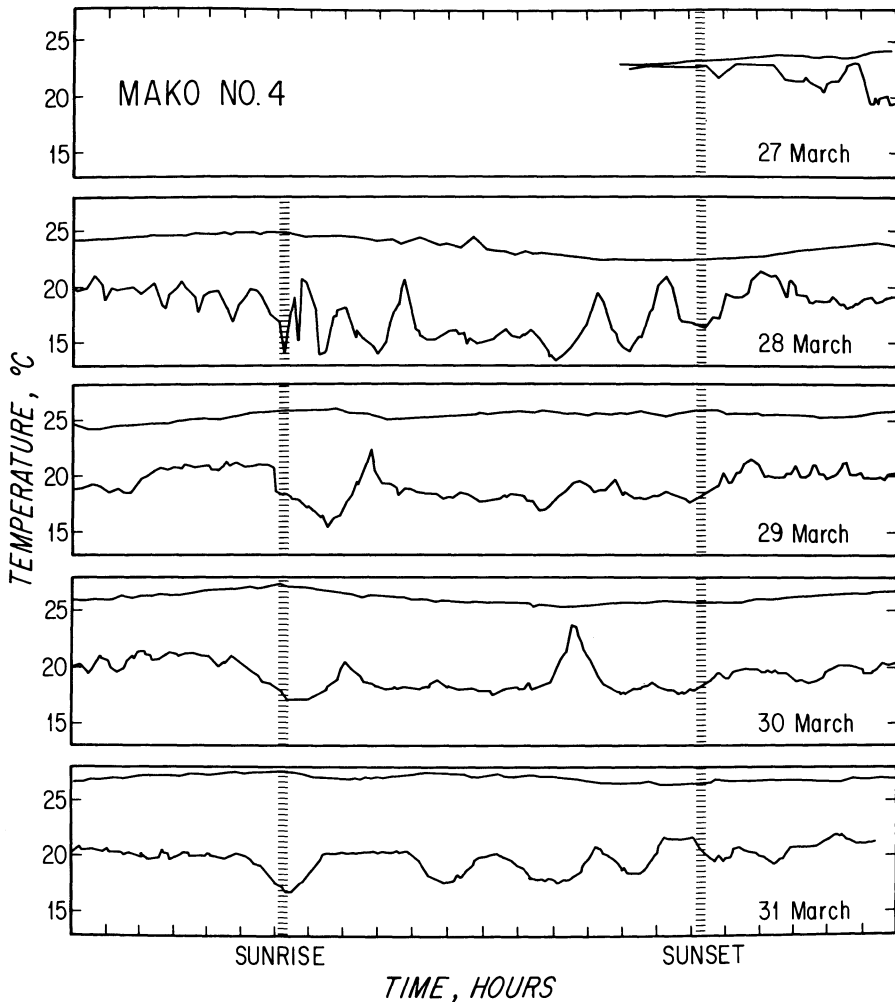
FIG. 4.—Temperature data for mako no. 4 plotted from midnight to midnight over a 4 day period. Upper smooth line, stomach temperature; lower varying line, water temperature.

perature. When blood enters the tissues, metabolic heat is generated in proportion to the amount of oxygen released. Mako blood may carry some 0.14 volumes oxygen per volume of blood. If half of the oxygen carried by the blood is extracted in the tissues, 1 ml of blood flowing through the tissue will allow the generation of 0.35 cal of heat. This will warm the blood 0.35 C (Mendlowitz 1948).[3] In a normal

[3]The specific heat capacity of blood which is about 0.9 is taken as 1.0, and the caloric yield of oxygen as 5.0 cal/ml.

fish this amount of heat would be carried away by the venous blood to be lost in the gills, and the tissues will remain within 0.35 C of water temperature. The stomach of the lamnid sharks in our experiments were much warmer than this with temperature elevations of 6–8 C. This is possible because these fish have heat exchangers in the circulation which transfer heat from the warm venous blood to the cold arterial stream and return it to the viscera to produce a rise in temperature.

The suprahepatic rete has the following properties which identify it as the site of heat exchange in the visceral circulations.

1. The blood flow in the small arteries of the rete is countercurrent to the flow through the venous spaces as required for efficient heat exchange.

2. The dimensions of the small arteries in the suprahepatic rete, 60–130 μ, are appropriate for a heat exchanger. Smaller, capillary-size vessels are found in oxygen-exchange retia: 10 μ for the eel swim bladder (Krogh 1922), and 10.5 μ for the arterial, and 23.2 μ for the venous capillaries of the choroid gland of tuna (Wittenberg and Wittenberg 1974). Retia serving as heat exchangers have larger vessels: 500–1,000 μ in the sloth (Scholander and Krogh 1957), 100 μ in bluefin and yellowfin tuna (Carey and Teal 1966; Graham 1974), 36 μ arterial and 84 μ venous in the skipjack *Katsuwonnus pelamis* (Stevens, Larry, and Kendall 1974).

3. A clear temperature gradient occurs within the rete with the cold proximal end at the temperature of the heart and gills and the distal end approaching the temperature of the viscera. The temperature gradient is in the proper direction and of the appropriate magnitude to identify the rete as the site of heat exchange.

4. The major blood supply to the viscera is through the rete. The arteries supplying the viscera from the suprahepatic rete are much larger than the aortic roots of the coelio-mesenteric, lieno-gastric, and spermatic arteries, and the connections of the latter with the aorta are tenuous. These aortic roots are the only arterial blood supply to the viscera which bypass the rete, and blood flow through these vessels must be minimized for the viscera to attain the observed temperatures. While, in general, it is not safe to use the size of vessels to infer blood flow, the differences here are so great that it seems to us (as it did to Burne) that most, if not all, of the blood supplying the viscera passes through this rete.

Temperature elevations of 8 C as observed in the telemetry experiments are only possible if the heat exchangers work with high efficiency. The venous blood can be assumed to have been at tissue temperature, $\Delta T = 8$ C, before entering the rete. We assumed earlier that oxygen removed from the blood will only generate 0.35 cal/ml blood. Therefore, if temperature is to remain constant, only 0.35 of the 8 excess cal/ml in the venous blood can be permitted to pass through the rete to be lost in the gill. The remaining heat must be transferred to the arterial stream, warming it 7.65 C before it enters the tissue. The fraction of heat lost is thus limited to 0.35/8.00, and the exchanger must work with an efficiency of 95.6%. As other routes of heat loss, such as conduction to the surface of the fish, become important, higher efficiencies will be required to maintain the observed temperatures. If half of the heat is lost through the skin (Brill, Guernsey, and Stevens 1978), only 0.175 cal/ml can be lost in the circulation, and an efficiency of 97.8% is required in the exchanger.

The high efficiency required for heat exchange may explain the large size of the suprahepatic rete. From measurements of the dimensions of the rete of an 88-kg porbeagle and of the number of arterioles per unit area and their average diameter, it can be calculated that the interface area between arterial and venous blood in this organ is greater than 4 m^2. This large area of contact makes possible the efficient exchange of heat needed to maintain the observed tissue temperatures.

The large size of the suprahepatic rete may also be associated with a requirement for low resistance to the flow of venous blood from the liver to the heart. Venous pressure is low in fish and may actually reach negative values in elasmobranchs (Johansen 1965; Satchell 1971). The large cross-sectional area of the porbeagle rete (30 cm^2 in a section normal to the blood flow for the 88-kg specimen) would help reduce flow resistance in this low-pressure system.

The amount of metabolic heat produced is proportional to the oxygen which can be

removed from the blood, while the convective cooling by the circulation is proportional to the mass of blood flowing through the tissues. It is apparent that the highest tissue temperatures can be achieved when the maximum amount of oxygen is obtained from the minimum flow of blood. The hematocrit and oxygen capacity of mako and porbeagle blood are significantly higher than found in cold-bodied sharks. A high oxygen capacity is a feature expected and found in the blood of all warm-bodied fish where values may approach those of mammals: bluefin tuna 18.5 vol %, human 21 vol %. To increase the oxidative metabolic heat available per unit blood flow, a greater fraction of the oxygen might be removed from the blood. If 80% of the oxygen were utilized instead of 50%, in the previous example, 0.56 cal/ml blood would be generated, and the heat exchanger could operate with an efficiency of 96.5%. Thus, even if more oxygen were extracted from the blood, a high efficiency of heat exchange would still be essential to maintaining the observed temperatures.

The hepatic sinus appears to form a shunt which would allow venous blood to pass directly from the liver to the sinus venosus, bypassing the suprahepatic rete (fig. 1). The control of flow through this channel would have a marked effect on visceral temperature and suggests a mechanism for temperature control in the viscera. Burne (1923) described the protuberant valvular lips at the opening of the hepatic sinus into the sinus venosus, but if these serve a valving function it appears to be that of check valves rather than a means of restricting flow. Johansen and Hanson (1967) discuss the function of discrete sphincters found in hepatic veins of elasmobranchs. They find that these structures are able to control blood flow from the liver in the dogfish, *Squalus binoculata*. In fresh material, the sphincter opened when perfused with acetylcholine solution and closed in the presence of adrenalin. There are no discrete sphincters in the material we examined,

but the muscular wall of the sinus is capable of closing this passage. Contraction of the longitudinal muscle thickens the folds, and the circular muscle fibers press them into the lumen (fig. 2). In fixed material the channels are constricted, but they can readily be expanded while fresh, and it seems certain that they can be opened and closed in the living animal. In addition to the regulation of blood flow through the liver proposed by Johansen and Hanson, this valving action would provide a ready means of controlling blood flow through the rete and, thus, visceral temperatures. If 0% of the venous return from the viscera passed through the shunt when it was closed and 20% when open, the efficiency of the heat exchanger would drop from the 95.6% calculated previously to 76.5%. The temperature of the blood and tissues distal to the rete is very sensitive to the efficiency of heat exchange and in this case would decrease from 8 C to 1.5 C above ambient when the shunt opened. Thus, there should be a marked effect on visceral temperature if only one-fifth of the blood bypassed the rete. This shunt provides the only clear anatomical basis for controlling temperature in any of the warm fishes that we have investigated.

An arterial shunt around the rete may also be present. The aortic roots of the coelio-mesenteric, spermatic, and lieno-gastric arteries offer a route by which arterial blood might reach the viscera without passing through the heat exchanger. While these roots are quite small in the mako and were not filled with injection mass in the specimens we examined, they can be injected in the porbeagle. If these passages can be opened and closed in life, it would provide another means of varying heat exchange and temperature in the viscera.

Food may be an important factor in stomach temperature. Telemetry experiments with bluefin tuna (*Thunnus thynnus*) show a regular pattern of temperature changes with feeding (Stevens, Carey, and Kanwisher 1978). In these fish there is an abrupt decrease in temperature after in-

gesting a 10–20 kg meal of cold food. During the next 18 h or so the stomach warms, reaching a temperature of 8–16 C above ambient. If the fish is not fed the following day, the temperature decreases again reaching an equilibrium at 5–6 C above ambient about 36 h after the meal.

Because food has such a strong influence on stomach temperature in the bluefin tuna, it seemed likely that stomach temperature of the mako might also respond to feeding. Since 40% of the mako sharks taken by longline had empty stomachs when boated (personal communication, Charles Stillwell, National Marine Fisheries Service [NMFS], Narragansett, R.I.), in mako no. 4 we added mackerel along with the transmitter to assure that food was present. The stomach temperatures were close to ambient at the beginning of the telemetry experiments, but a temperature differential soon developed (figs. 2–3). Mako no. 3 (with a 60% chance of having food in its stomach) warmed from 3 C to 8 C above water temperature in 4.5 h. The stomach of no. 4, which contained 2 kg of mackerel, was initially at water temperature, 23 C. During the first 12 h it warmed to 25 C while water temperature dropped to 18.5 C, a net increase of 6.5 C above ambient. While the first few hours of the telemetry experiments suggest a certain independence from ambient temperature, we were disappointed in not seeing a clear pattern of temperature changes which would demonstrate that the shark could control its stomach temperature. The added food appeared to have little effect, and the dramatic rise in temperature seen in bluefin tuna did not occur. Two kg of mackerel is a small meal for a 180-kg shark, but 400-kg bluefin tuna do show a stomach temperature response after ingesting several kilograms of fish.

Lamnid sharks often die when caught on longline fishing gear, and those that are brought up alive are probably adversely affected by the experience. The low temperatures at the beginning of the telemetry experiments were probably associated with the trauma of capture. Recovery from its struggles may have masked a normal response to food in mako no. 4. The experiment should be repeated in a less stressful situation where the shark is allowed to ingest a transmitter during its normal feeding activity. Because of the effects of the struggle during capture, it is likely that normal temperatures are usually higher than the values in table 1 would indicate. The temperatures given there should not be taken as typical normal values, but only as evidence that the viscera are warm.

The temperature of the stomach was quite stable during rapid variations in water temperature, with a time scale of several hours, but it did follow slower, 8–12 h, changes in mean water temperature (fig. 3). The rete provides an effective thermal barrier which greatly reduces convective heat transport by the circulation. Heat transfer by conduction is necessarily slow in an animal this size, and the reduction in convective heat transfer greatly increased the thermal inertia of the fish (Neill, Chang, and Dizon 1976).

Size and activity were probably not important in determining the observed stomach temperatures. Mako no. 3 weighed only 28 kg, while mako no. 4 was six times heavier, but both achieved stomach temperatures 8 C above ambient. They swam at slow speeds, 2.3 and 2.5 kn/h or 0.47 and 0.3 body lengths per second, a low level of activity for a fish which can be very active. In any case, heat produced in the muscle should not have a strong effect on visceral temperatures, since the two heat exchange systems are completely separate and heat transfer from muscle to viscera would be by conduction only.

The warm gut of these sharks could enable them to process food rapidly. A Q_{10} of 2 or more is common for digestive processes in fish (Brett and Higgs 1970; Fabian, Molnar, and Tolg 1973; Schrable, Tiemeier, and Deyoe 1969) and the tem-

perature elevations we observed might halve the time required for maceration, digestion, and absorption of food. There is little information on the feeding patterns of sharks, but it is probably irregular.

Rapid processing of a meal may allow the shark to eat more during those times when food is available and to make better use of sporadically abundant prey.

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