

VASCULAR ANATOMY OF THE COUNTER-CURRENT HEAT EXCHANGER OF SKIPJACK TUNA*

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SUMMARY

1. The anatomy of the counter-current heat exchanger of skipjack tuna is described and the pattern of blood flow is analysed.
2. The pattern of blood flow is from the dorsal aorta, through the exchanger to segmental arteries to the tissues, from the tissues to segmental veins and back through the exchanger to the post-cardinal vein.
3. The vessels in the exchanger are about the same size as systemic arterioles and venules and are about 10 mm long. There are about 125 000 of each type in a 2 kg tuna.
4. The velocity of blood flow in the exchanger is about 1/80th of that in the dorsal aorta and post-cardinal vein allowing time for heat transfer.
5. There are many valves in the segmental veins which may be expected because of the resistance offered by the exchanger.
6. The vessels in the tuna heat exchanger are an order of magnitude larger than those in the swim-bladder rete, thus permitting heat transfer but preventing gas transfer.

INTRODUCTION

Tunas are extraordinary fishes. This paper concerns one of the features that makes them extraordinary: the counter-current heat exchanger. The evolution of this device permits tuna to achieve body temperatures much greater than ambient water temperature. For example, the muscle temperature of large bluefin tuna can be as much as 20 °C above ambient water temperature (Carey *et al.* 1971) and the muscle temperature of small skipjack tuna (2 kg) can be as much as 9 °C above ambient (Stevens & Fry, 1971). The body temperature of other fishes is at most 2 °C above ambient (Stevens & Fry, 1970) because metabolic heat is efficiently transferred from the venous blood to surrounding water at the gills (Fig. 1). To maintain a large temperature excess, tuna have had to make a tremendous anatomical investment and construct a thermal barrier between venous blood and the gills. The present paper describes this thermal barrier, the counter-current heat exchanger of skipjack tuna.

MATERIALS AND METHODS

Live skipjack tuna (*Katsuwonis pelamis*) were obtained from the National Marine Fisheries Service in Honolulu. Fresh, frozen, and paraffin-embedded sections were examined. In some cases the vascular system was perfused with formalin, in other

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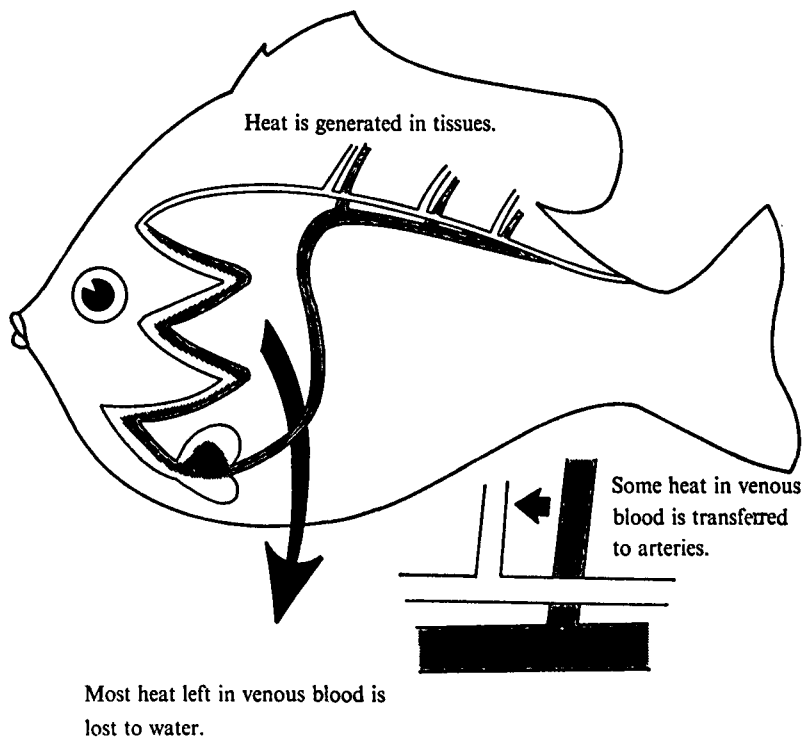


Fig. 1. Pattern of heat transfer in a typical fish; metabolic heat is lost to the water as blood circulates through the gills.

cases the tissue was placed in Bouin's or formalin fixative. Histological stains used were Mallory's triple stain, Gomori's aldehyde fuchsin, haematoxylin and eosin (Davenport, 1964) and silver stain with or without gold (Winkelmann & Schmit, 1957; Gilbert, 1965). A complete analysis was performed on the heat exchanger of one skipjack tuna (weight 1.93 kg, fork-length 47.2 cm). In this fish the dimensions of the heat exchanger and major vessels were determined at 5 mm intervals throughout the length of the fish. The exact number and size of all small vessels in the exchanger was determined for a segment of the exchanger 6 mm wide and 1 mm long. Cross-sectional areas were determined on photographic enlargements with a planimeter.

RESULTS

The location and size of the heat exchanger in skipjack tuna is indicated in Fig. 5, Plate 1; Fig. 6, Plate 2; and Fig. 2. Most cool oxygenated blood is distributed to the musculature via the centrally located dorsal aorta. Smaller lateral arteries also distribute some blood to muscle. Similarly, most venous blood returns to the heart via a centrally located post-cardinal vein. The arterial blood passes from the dorsal aorta through the heat exchanger and then to segmental arteries. The venous blood from the tissues collects in segmental veins and then passes through the heat exchanger to the post-cardinal vein and back to the heart. In a 2 kg tuna the heat exchanger is about 7 mm wide and the exchanger vessels are 10 mm long.

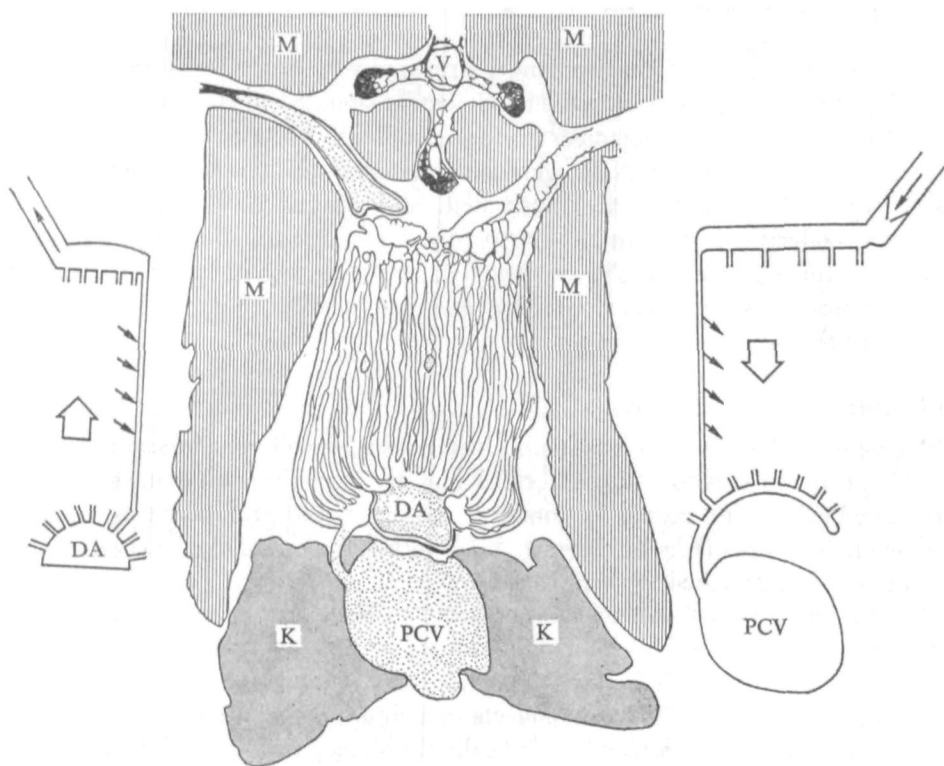


Fig. 2. Schematic drawing that illustrates the major features of the vascular heat exchanger of skipjack tuna – compare with Fig. 6, Plate 2. DA, dorsal aorta, K, kidney, M, muscle, PCV, post-cardinal vein, V, vertebra. Left inset shows pattern of arterial blood flow, that on the right shows pattern of venous blood flow, and small arrows indicate heat transfer from venules to arterioles in the exchanger.

The relative amounts of red and white muscle in various cross-sections are indicated in Fig. 3. The integrated area under the curve for red muscle was used to calculate the total amount of red muscle: 8.2% of body weight. The shape and size of the exchanger generally corresponds to the amount of muscle it supplies (Figs. 3, 4). Fig. 3 also shows six representative cross-sections. Red muscle is located both in the superficial lateral layer and in the larger medial core. Fig. 4 indicates the number of vessels, their cross-sectional areas, and their inside surface areas. The discontinuity in the curve at about 25 cm is real. At this point the exchanger definitely is wider and the vessels are longer. Also at this point there is a marked increase in the size of the lateral red muscle so that it gradually becomes a block of muscle rather than a thin sheet.

(a) Arterial side of exchanger

The dorsal aorta is thick walled and has an internal diameter of about 1.5 mm. The presence of nerves and free nerve endings in the smooth-muscle layer of the dorsal aorta were demonstrated with silver stains. The dorsal aorta gives rise directly to arterial vessels in the exchanger; some of these vessels branch once, shortly after

leaving the dorsal aorta, but they do not branch within the exchanger (Fig. 6, Plate 1 and Fig. 2).

The arterial vessels of the exchanger are approximately the same diameter as arterioles. The vessels are thick walled and contain smooth muscle (Fig. 5(c), Plate 1). However, all attempts to demonstrate nerve endings in the smooth muscle of the arterial vessels within the exchanger were unsuccessful. It is unlikely that the vessels within the exchanger are innervated. The arterial vessels of the exchanger unite into collecting vessels at the top of the exchanger and the collecting vessels become segmental arteries. The oxygenated, and now warm, blood is distributed to the tissues via segmental arteries that look very similar to segmental arteries of non-tuna fish.

(b) *Venous side of the exchanger*

The venous blood, warmed by tissue metabolism, is collected in segmental veins. The blood then passes to collecting veins that are large (internal diameter 0.7 mm), thin walled ($32\ \mu$), and invariably contain regularly spaced protuberances which look like incomplete septa (Fig. 6, Plate 2). The protuberances are elongate with clusters of spherical cells attached to them.

The collecting vein then divides repeatedly to become the venous vessels of the exchanger. The venous vessels in the exchanger are about the same diameter as venules and are thin walled (Fig. 5(c), Plate 1). After passing through the venous vessels of the exchanger the blood collects in a sinus surrounding the dorsal aorta at the bottom of the exchanger, and periodically the sinus passes around the dorsal aorta to empty into the post-cardinal vein. The post-cardinal vein is thin walled, about twice as large as the dorsal aorta, and is immediately below and close to the dorsal aorta.

(c) *The exchanger*

The total number of arterial vessels is very nearly equal to the number of venous vessels in the exchanger, but the venous vessels are much larger (Fig. 4; Fig. 5(c), Plate 1). In addition to the vessels passing through the whole length of the exchanger, there are a small number of them that pass only half-way through the exchanger and then pass to and from white muscle. These vessels do not combine to form an artery or vein but rather pass as a group of five or six small vessels directly into the muscle.

The section of the exchanger examined in detail was 1 mm long and the exchanger was 5.9 mm wide at this point. It contained 706 arterioles, internal diameter $35.7 \pm 1.32\ \mu\text{m}$ (mean \pm S.E.); and 637 venules, internal diameter $83.8 \pm 4.47\ \mu\text{m}$. These data were used in conjunction with measurements of the width of the exchanger and mean lengths of exchanger vessels (determined throughout the length of the fish at 5 mm intervals) to estimate the number of vessels in other parts of the exchanger.

The blood vessels were easily counted, but because of size changes during fixation, the diameters had to be determined from fresh material. The data were used to calculate the cross-sectional area of the vascular bed, the blood volume in the exchanger, and the surface area of the exchanger (Table 1; Fig. 4).

Table 1. Total number, cross-sectional area, blood volume and total inside surface area of the counter-current heat exchanger of a 1.9 kg skipjack tuna

	Arterioles	Venules	Total
Number of vessels	133 721	120 652	
Cross-sectional area (cm ²)	1.34	6.65	
Volume (cm ³)	1.21	5.99	7.20
Inside surface area (cm ²)	1350	2858	

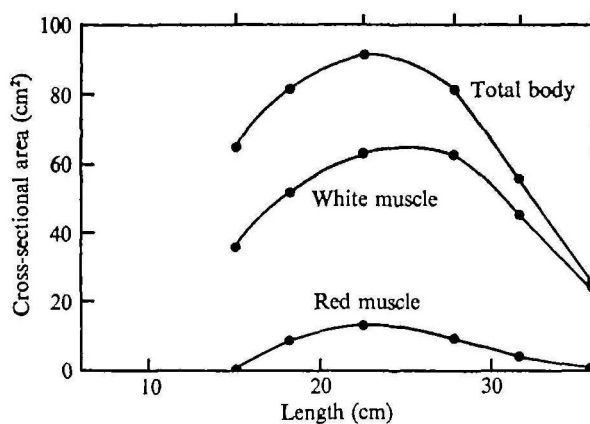
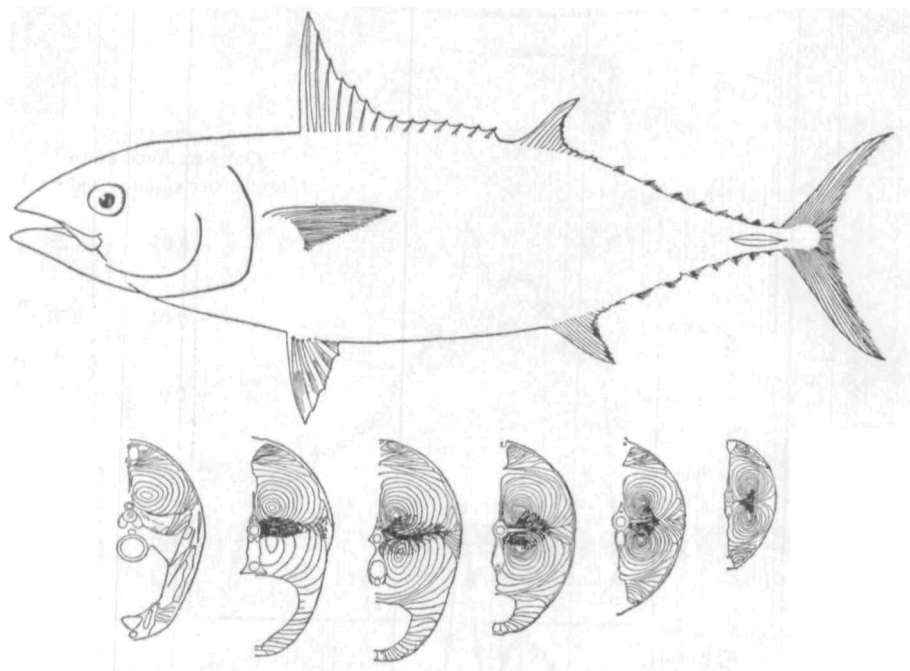


Fig. 3. The relative contribution of red and white muscle to body mass in a 2 kg skipjack tuna. The points on the graph are aligned with the drawing of the tuna. There are also six cross-sections, one for each point on the graph (note that in the figure these are not aligned with either the graph or the drawing of the tuna). Red muscle is stippled. Compare cross-sections with Fig. 5A, Plate 1.

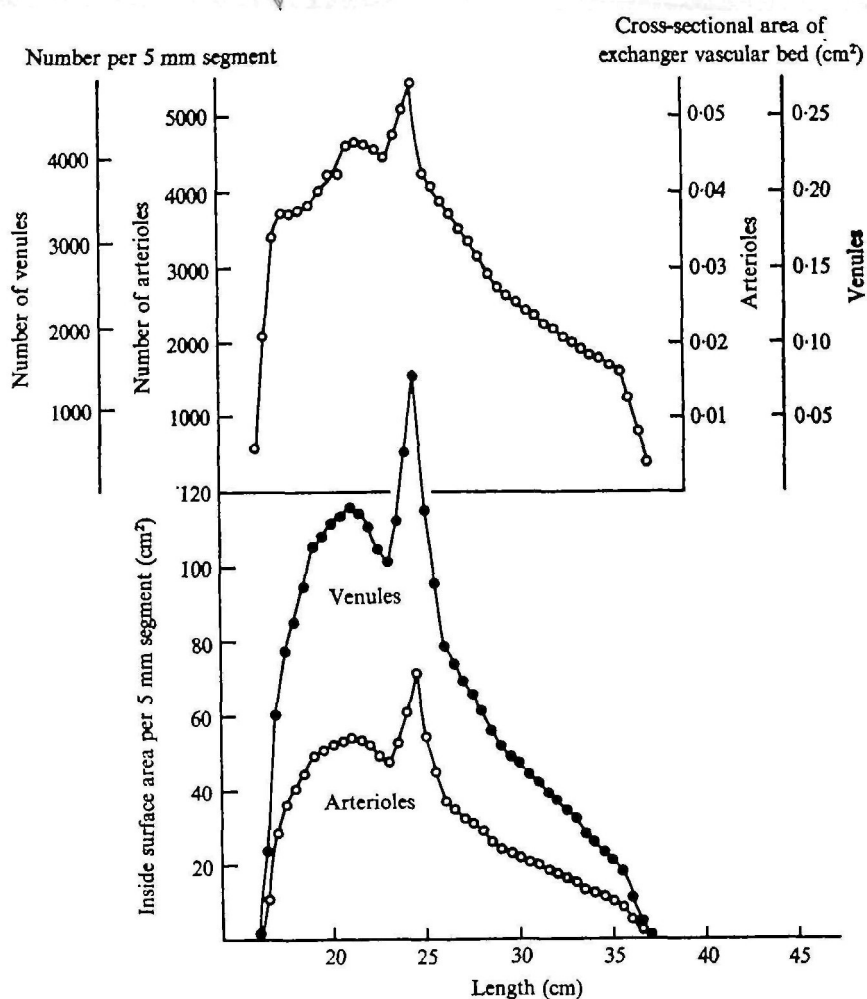
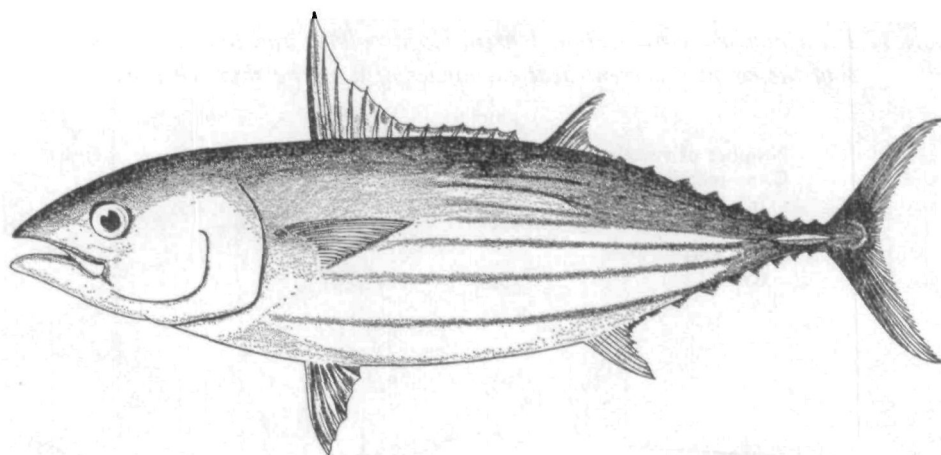


Fig. 4. The size and number of vessels in the vascular heat exchanger of a 2 kg skipjack tuna. The points on the graphs are aligned with the drawing of the tuna. Each point represents the number of vessels in one segment 5 mm long – the total number of vessels would be the sum of the numbers thus represented. Note that scales are different for arterioles and venules.

DISCUSSION

It has been demonstrated that tuna cool only half as fast as other fishes of the same size when placed in a similar temperature gradient (Neill, 1974). There is little doubt that the elevated body temperatures observed in tunas can be attributed to the thermal barrier generated and maintained by the counter-current heat exchanger.

The numbers of arterioles and venules within the heat exchanger are approximately equal. However, the venules are unquestionably larger than the arterioles, and one consequence of this is that the velocity of blood flow is about five times faster in the arterioles than in the venules. The actual velocity of blood flow can be estimated by the following. In a previous paper it was estimated that cardiac output in skipjack tuna is 80 ml/min.kg (Stevens, 1972). The tuna analysed in the present study weighed 1.93 kg; cardiac output was therefore calculated as being 154.4 ml/min. Assuming that 60% of the blood flows through the exchanger (the balance flows to the head, gut, and small lateral vessels), then blood flow through the exchanger is 92.6 ml/min or 1.54 cm³/sec. The velocity in the arterioles is $1.54 \text{ cm}^3/\text{sec} \div 1.34 \text{ cm}^2 = 1.15 \text{ cm/sec}$. Similarly the velocity in the venules is 0.232 cm/sec. The presence of the exchanger reduces the velocity to approximately 1/80th of that in the dorsal aorta and post-cardinal vein. The blood is in the arterioles of the exchanger for about one second, allowing time for heat transfer from the venules. The velocity of blood flow is approximately the same as that for peripheral arterioles and venules in man, but is 20 times faster than the velocity in capillaries (*ca.* 0.05 cm/sec; Burton, 1965).

The total blood volume is about 7% of body weight (Satchell, 1971) or 135 ml in the 1.93 kg tuna. The blood volume contained in the arterioles and venules of the exchanger is 7.2 ml (Table 1) or 5.3% of the total blood volume (0.9% in the arterioles and 4.4% in the venules). These are substantial amounts and are almost the same as the proportions of the total blood volume contained in the arterioles and venules of the systemic circulation in mammals (1% in arterioles and 5% in venules). Consequently, the blood volume contained in the arterioles and venules of tuna (systemic circulation plus the exchanger) is greater than that of mammals (systemic circulation only). What is more important is that the two vascular beds in tuna are in series, so that tuna must compensate for the additional resistance to blood flow as partial payment for the gain in heat. There are four resistive vascular beds in series: the gills; the arterioles of the exchanger; the arterioles, capillaries, and venules of the tissues; and the venules of the exchanger. Valves in the segmental veins help to overcome the additional resistance to blood flow.

The segmental veins were characterized by the presence of protuberances that give the appearance of being incomplete septa (Fig. 6, Plate 2). The septa have a smooth-muscle core and probably function as valves. There are many of them in series in each vein and they are stronger and thicker than typical venous valves, which may be expected because of the relatively high forward resistance presented by the vascular bed of the exchanger. In most other fish the blood empties directly into a large post-cardinal vein with very little resistance between the segmental vein and the heart.

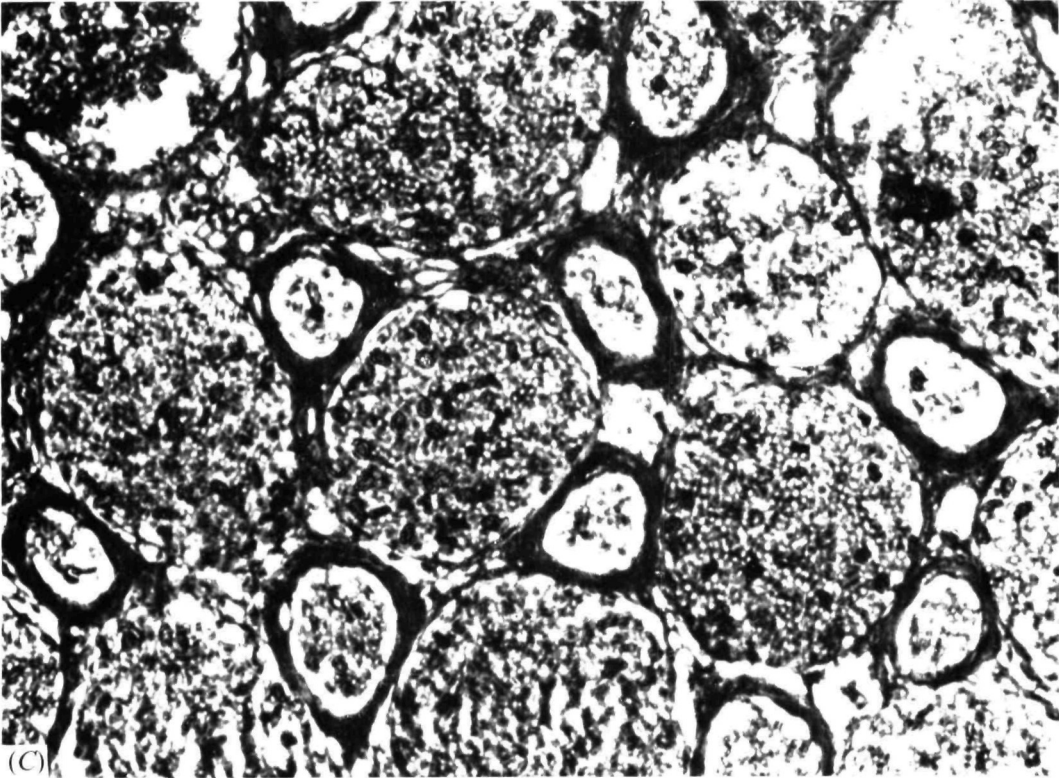
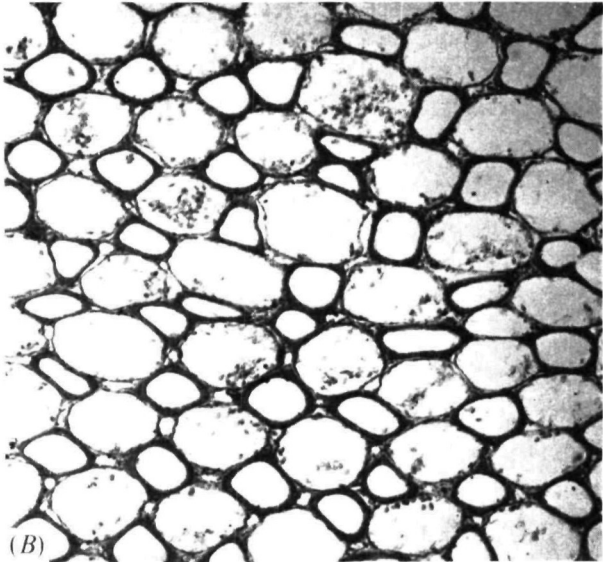
The general features of the heat exchanger of skipjack tuna have been compared with those of other tunas by Carey (1973); and the gross vascular anatomy of the cir-

culatory system of tunas has been beautifully described by Kishinouye (1923). In almost all other tunas the exchanger is located laterally, near the surface of the animal, and the main blood supply to the musculature is through lateral arteries rather than the dorsal aorta. The only apparent advantage of placing the exchanger centrally, as in the skipjack, is that it ensures that the spinal cord is kept warm and that the exchanger is insulated from fluctuations in ambient water temperature by the surrounding tissues. This is especially important in small tuna like skipjack. In this regard it is interesting to note that the exchanger in skipjack is always surrounded with a very thin layer of fat that probably thermally insulates the exchanger from the surrounding tissue.

One of the many large and small nerve-trunks running directly through the exchanger is visible in Fig. 6, Plate 2 (arrowed). Two aspects of this observation are interesting. On the one hand we have observed muscle temperatures 9°C above ambient in small skipjack and thus these neurones in the exchanger must possess compensatory mechanisms in order to operate in the very sharp temperature gradient, a 9°C temperature change in 1 cm. On the other hand, the sharp temperature gradient in the exchanger may be used in perception of changes in ambient temperature; for it is here that the spatial gradient between ambient and muscle temperature is sharpest, and the presence of specialized nerve endings could allow detection of this gradient. The temperature at the arterial end of the exchanger is almost the same as ambient because arterial blood equilibrates with ambient water temperature at the gills. The temperature at the venous end of the exchanger is almost the same as warm muscle because venous blood equilibrates with muscle temperature in the tissues. Thus the temperature change per unit distance is probably greatest in the exchanger and therefore may be easiest to perceive there.

Any examination of an extensive exchanger like this immediately leads to the important question 'is this exchanger limited to exchanging *only* heat and nothing else?'. This question can only be answered empirically, but it may be useful to compare the heat exchanger to the swim-bladder rete that is known to transfer gases.

Krogh (1922) analysed the capillary bed of the rete of the eel swim bladder. He counted 116000 arterial and 88000 venous capillaries; only about 20% fewer than the number in the heat exchanger of the tuna. However, the vessels of the rete are much smaller than those of the heat exchanger: the cross-sectional area of one rete vessel is $72\ \mu\text{m}^2$ as compared to $1002\ \mu\text{m}^2$ for the arterial and $5518\ \mu\text{m}^2$ for the venous vessels of the skipjack heat exchanger. The ratio of total diffusion area to the rete volume is $1700\ \text{cm}^2/\text{cm}^3$; but is an order of magnitude less in the heat exchanger, $187\ \text{cm}^2/\text{cm}^3$. The capillaries of the rete are about ten times longer than those of typical muscle capillaries; but the vessels of the heat exchanger are ten times longer than those of the rete. The diffusion distance from arterial to venous capillary in the swim-bladder rete is $1\ \mu\text{m}$, whereas in the tuna heat exchanger the minimum diffusion distance is 10 times larger, $10\ \mu\text{m}$, about the diameter of one red blood cell (Fig. 6, Plate 2). On the basis of this analysis it seems likely that in order to permit gas exchange, an exchanger must contain vessels an order of magnitude smaller than those present in the heat exchanger of tuna. Mass transfer (e.g. of gases or ions) rather than heat transfer might also be precluded by special permeability properties of the vascular endothelium of the exchanger, but we have not looked for these.





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EXPLANATION OF PLATES

PLATE 1

Fig. 5. (A) Cross-section of a 2 kg skipjack tuna. The vascular heat exchanger is below the vertebral canal. Red muscle appears dark.

(B) Tangential section of the vascular heat exchanger of a formalin perfused skipjack tuna (that is, a cross-section of the vessels of the exchanger). The number of thick-walled arterioles is about the same as the number of thin-walled veins.

(C) Same section as Fig. 5 (B) except that the tissue was fixed rather than perfused. Red blood cells (10 μ m diameter) are evident and reveal the size of the vessels. It can be seen that the arterioles have thick, muscular walls whereas the venules are thin walled.

PLATE 2

Fig. 6. Cross-section of skipjack tuna showing the vascular heat exchanger - compare with Fig. 2. Small vessels in the exchanger are about 1 cm long. A nerve trunk is indicated by the arrow.