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REVIEW

Structural Basis for Oxygen Delivery: Muscle Capillaries and Manifolds in Tuna Red Muscle

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ABSTRACT. We summarize our morphometric data on fiber vascularization and aerobic capacity in red muscle of tuna (*Katsuwonus pelamis*), compared to intensely aerobic flight muscles of hummingbird (*Selasphorus rufus*, BW 3–4 g) and bat (*Eptesius fuscus*, BW 15–16 g, *Pipistrellus hesperus*, BW 3–5 g). Three characteristic features of high flux paths for oxygen: (a) small fiber size, (b) dense capillary network and (c) high mitochondrial volume density were found in tuna, but they were not as pronounced as in hummingbird and bat flight muscles. A particular arrangement of capillary manifolds, also seen in flight muscle of birds but not in bats, was found in tuna, forming dense envelopes of capillary branches around portions of muscle fibers. However, all indexes of fiber capillarization were relatively low in tuna red muscle for its mitochondrial volume, compared with other intensely aerobic muscles. Capillary length per unit volume of mitochondria, and capillary surface per mitochondrial inner (and outer) membrane surface area, were about one half of those in hummingbird or bat flight muscles. Consistent differences exist in the size of the capillary network for the size of the mitochondrial compartment in highly aerobic red muscle of tuna compared with bird and mammal. COMP BIOCHEM PHYSIOL 113A;1:25–31, 1996.

KEY WORDS. Oxygen delivery, fiber vascularization, aerobic capacity, red muscle, tuna

INTRODUCTION

Extremely aerobic muscles such as the flight muscles of hummingbird and small bat show distinct structural characteristics for high O_2 fluxes from capillary to fiber mitochondria. All fibers are of one single type, fast-twitch highy oxidative. Their diameter is small, they are highly vascularized and have very high mitochondrial and lipid droplet content. In addition, capillary-to-fiber surface, that is, the size of the capillary-fiber interface is high for the volume of mitochondria in the muscle fibers, suggesting great capacities for O_2 flux in both muscles (31,32,28). Interestingly, the great and remarkably similar capillary/fiber surface per fiber mitochondrial volume in bat and hummingbird flight muscles was achieved via different strategies in terms of fiber size, capillary number and geometry. Also, a similar capillary length per fiber volume and mitochondrial density was found in these muscles, despite their differences in capillary-to-fiber ratio, fiber size and capillary arrangement. Thus, characteristic capillary-fiber morphometrics for high O_2 fluxes can be achieved via different strategies in different muscles or animals.

In this paper, we briefly summarize data from our laboratory on fiber structure and capillarization in tuna red muscle, that is, one of the most aerobic muscles in fish (26). We review the specific structural arrangement for high O_2 fluxes from capillary to fiber mitochondria in the muscle, and how this compares with those in highly aerobic skeletal muscles of bird and mammals.

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MATERIAL AND METHODS

Animals and Tissue Preparation

Details of tissue preparation and analysis have been described elsewhere (26). Briefly, five skipjack tuna (*Katsuwonus pelamis*; body mass 1.5–2 kg; fork length 43–44 cm) were anesthetized and muscles perfusion-fixed with glutaraldehyde solution (four animals) or infused with Batson's casting material (one animal). All muscle samples were taken from transverse sections of the fish at the level of the 8–10th spine of the first dorsal fin. The perfusion-fixed tissues were postfixed with osmium tetroxide and embedded in plastic for light (LM) and transmission electron microscopy (TEM). Those injected with casting material were processed for scanning electron microscopy examination of vascular casts.

Morphometric Analysis

Transverse and longitudinal sections (1 μm-thick) of perfusion-fixed tissues (two samples from the red muscle in each of four tunas) were used for LM morphometry of capillarity and

fiber size, after careful control of the angle of each section. Indexes of muscle capillarization were estimated as follows. Capillary density (i.e., number per fiber sectional area in transverse and longitudinal sections) were collected by point-counting, and the data used to estimate the degree of orientation of capillaries and capillary length per fiber volume in each sample (21). Capillary surface per fiber volume was estimated by intersection-counting on vertical (i.e., longitudinal sections) using a cycloid grid (1). Capillary-to-fiber perimeter ratio in transverse sections was measured by intersection-counting (25), and capillary surface per fiber surface, that is, the size of the capillary-fiber interface, estimated as the product of capillary-to-fiber perimeter ratio and a capillary surface orientation coefficient (29).

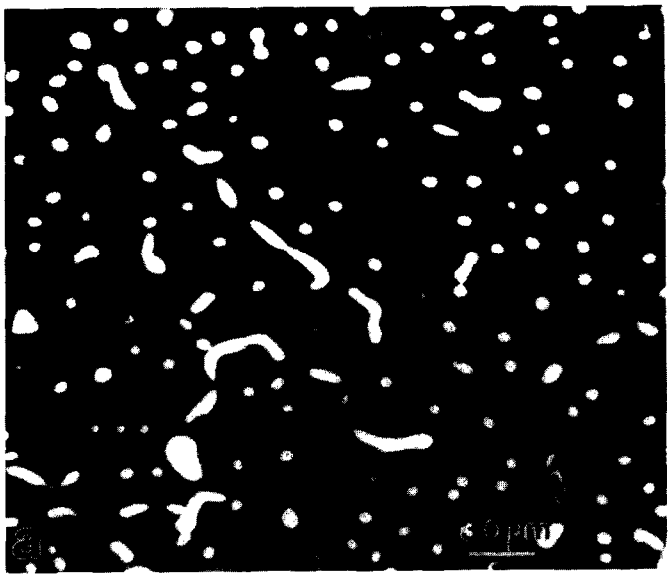
Fiber cross-sectional area, capillary diameter and capillary number around a fiber were measured in transverse sections with an image analyzer. Sarcomere length, measured in longitudinal sections, was used where appropriate to normalize data on capillary density and fiber size. This was necessary to compare morphological data between muscles (or animals), independent of the particular length at which each sample was fixed and therefore examined. We chose a normalizing sarcomere length of 2.1 μm because it is in the mid-range of the sarcomere lengths where maximal tension is developed in skeletal muscle. It is within the range of operating sarcomere lengths in red muscle of fish during swimming at slow speed (1.9–2.2 μm; 36), wing muscles of bird during wing beat cycle (1.7–2.3 μm; 3) and hindlimb muscles of mammal during terrestrial locomotion (range, 1.7–2.7 μm; 4).

Ultrathin transverse sections (50–70 nm) were used for electron microscopy morphometry of the volume of mitochondria and lipid droplets per volume of muscle fiber and the surface of inner and outer mitochondrial membrane per volume of mitochondria (33). Mitochondrial volume per μm fiber length was calculated as the product of mitochondrial volume density and fiber cross-sectional area. Capillary-to-fiber ratio (i.e., capillary number per fiber number) was computed as the product of capillary density and mean fiber cross-sectional area.

Statistical analysis. Data are expressed as means $\pm$ SE. Student's t-test and analysis of variance were used to compare data with those in other species. Differences were taken as significant for $p < 0.05$.

RESULTS

Figure 1a and b illustrates the high capillary density, small fiber size and high mitochondrial volume density in tuna red muscle. Capillary number per fiber cross-sectional area was 3391 $\pm$ 197 mm^{-2} and mean fiber cross-sectional area 475 $\pm$ 25 μm^2 (both values at 2.1 μm sarcomere length). Fiber mitochondrial volume density was 28.5 $\pm$ 1.0%. Longitudinal sections showed capillaries oriented perpendicular to the muscle fibers axis, in addition to those running parallel to the muscle fibers (Fig. 2a). This arrangement suggests the presence of capillary manifolds in tuna red muscle (compare Fig. 2a in this study with Fig. 4 (35)). Figure 2b illustrates the dense envelope of blood formed by capillaries around portions of the muscle fibers in tuna red muscle.



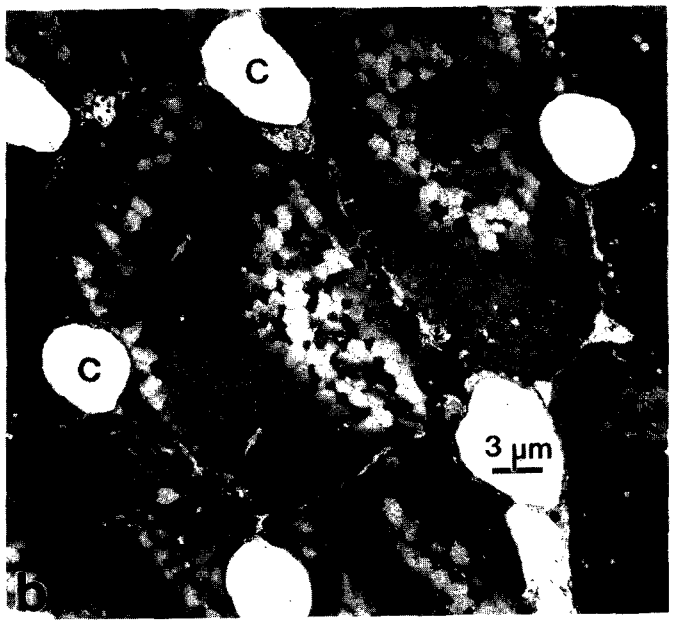


FIG. 1. Micrographs of portions of muscle bundles in transverse sections of tuna red muscle a: light micrograph; b: electron micrograph. Note high capillary density and small fiber size (a, b) and high density of mitochondria, M (b). Capillaries (c) are empty after vascular perfusion fixation. From 26.

If all capillaries were straight tubes strictly parallel to the muscle fiber axis, that is, if they did not show any tortuosity or branching, capillary length per fiber volume would be equal

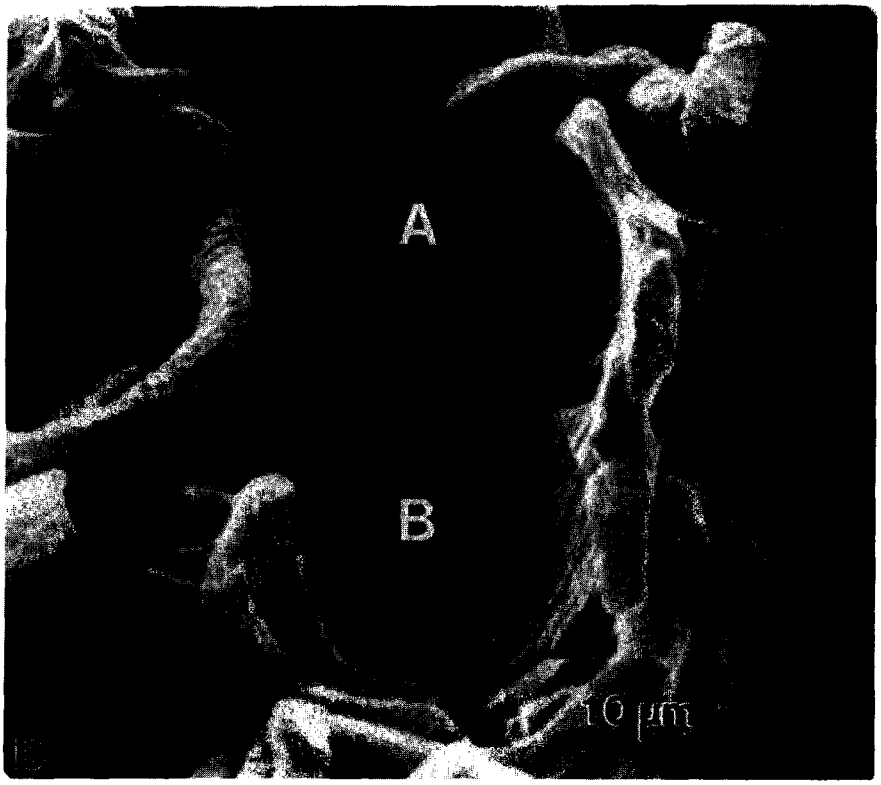


FIG. 2. Micrographs of capillary manifolds in tuna red muscle a: light micrograph of longitudinal section; b: scanning electron micrograph of a cross-sectional view of microvascular corrosion cast. Based on fiber dimensions, two muscle fibers (A and B) could be contained in the empty space in b. From 26.

to capillary density in transverse sections. In contrast, the length density of a network of randomly oriented capillaries is twice as large as capillary density in transverse sections (21). It is known that capillary tortuosity in muscles is a direct function of sarcomere length (22) and that capillary orientation, that is, the relative contribution of tortuosity and branching to capillary length at a given sarcomere length can greatly vary between muscles and animals, depending on the relative number and length of branches in different orientations (23,24,34).

At the sarcomere length range of the samples (1.72–1.87 μm), capillary arrangement in tuna red muscle (Figs. 1 and 2) yielded a capillary length per fiber volume (44 ± 4% greater than would be achieved by straight capillaries running strictly parallel to the muscle fibers. There was 4143 ± 242 mm capillary length per mm^3 fiber volume in the muscles, and capillary surface area per volume of muscle fiber was 51.4 ± 2.9 mm^2/mm^3. Dividing capillary length and surface densities by fiber mitochondrial volume density yields ≈15 km capillary length and 1800 cm^2 of capillary surface area per ml mitochondria. The aggregate surface area of inner and outer mitochondrial membranes was about 400 and 40 times greater than capillary surface area, respectively.

On average, there was 4.97 ± 0.13 capillaries around each fiber, and capillary per fiber number (i.e., capillary-to-fiber ratio) was 1.59 ± 0.06. Capillary-to-fiber surface ratio was 0.30 ± 0.01, and mitochondrial volume per μm length of fiber (i.e., the product of mitochondrial volume density and fiber cross-sectional area) 159 ± 10 μm^3. Thus, capillary-to-fiber surface per unit mitochondrial volume was 0.0019 ± 0.001 μm^{-3}.

DISCUSSION

Whereas the tuna red muscle shows several structural features characteristic of a design for high flux paths for O_2, comparison with the most aerobic muscles of birds and mammals reveals both similarities and consistent differences in the degree of fiber capillarization for the size of the mitochondrial compartment.

Comparison with Other Fish

High capillary density, small fiber size and high mitochondrial volume density are well known characteristics of tuna red muscle (2,6,13). However, none of these variables show extreme values in tuna compared to other fishes. Mitochondrial densities in the 20–30% range have been reported in red muscle of shark, eel, trout and carp (19,14,18) and the highest mitochondrial volume density for fish (45.5%) was found in anchovy red muscle (15). Comparisons with fiber size and capillary densities in other studies of fish muscles is difficult because the sarcomere length at which the tissues were examined is often not reported. However, fiber size does not appear smallest in tuna red muscle compared to other fish (17), and a small fiber size is not necessarily a characteristic of highly aerobic fibers in fish. Cross-sectional area of highly aerobic fibers in anchovy (mitochondrial volume density, 45.5; see above) was 1115 μm^2 (15), that is, about twice that in tuna red muscle. Capillary-to-fiber number ratio in tuna red muscle (range 1.29–1.74; 26) was also not the highest for fish. It was 2.2 ± 1 in 28°C acclimated carp and increased to 4.8 ± 0.2 as fiber size increased with acclimation to 2°C (16). It was 12.9 ± 0.5 in highly aerobic muscle of anchovy (15).

Capillary Geometry

Capillary manifolds were first described in pectoralis muscle of pigeon. Potter *et al.* (35) showed that they are venular capillaries, forming dense clusters oriented perpendicular to the muscle fiber axis and converging into venules. The functional implications of this arrangement are not fully understood. It increases capillary surface and therefore could facilitate vascular supply to and from the muscle fibers at the venular end of the network where O_2 and substrate content are lowest and metabolite concentration highest. In bird pectoralis muscle, it could also be related to other aspects of the microcirculation, such as heat dissipation or the blood pumping action of the muscle during flight (7). However, capillary manifolds were also found in flight muscle of hummingbird (31) but not in bats (32,28). Also, the fact that manifolds are found in tuna red muscle (Fig. 2) suggests possible rheological implications, since both fish and bird blood red cells are nucleated and less deformable than mammalian red cells. Another possibility in tuna is heat recovery from the muscle at the venular end of the network, as it possibly favors heat removal in bird flight muscle (31,27). It is not known whether this capillary arrangement is unique to tuna red muscle or whether it is also found in other highly aerobic muscles of fish.

Interestingly, the percentage added to capillary length by the particular geometry (compared to straight capillaries running strictly parallel to the muscle fiber axis) was much greater in tuna red muscle (44 ± 4%) than in bird flight muscle (6–26%; 24,31). In fact, the contribution of tortuosity and branching to capillary length was as large in tuna as in rat muscles with no evidence of capillary manifolds (30). The different contribution to capillary length in tuna and bird muscle may be related to differences in length or number of branches in manifolds. As a result, the added capillary length in tuna red muscle was large (1300 mm per mm^3 of fiber), and very close to that in hummingbird flight muscle with considerably greater capillary density in transverse sections (7522 ± 749 mm^{-2}) and an arrangement of capillary manifolds, but only 19 ± 2% added to capillary length (31). This underscores the importance of considering capillary length rather than density in transverse sections alone to compare capillarity between muscles, even if capillary arrangement is similar (e.g., presence of manifolds or not) or all samples are fixed at the same sarcomere length.

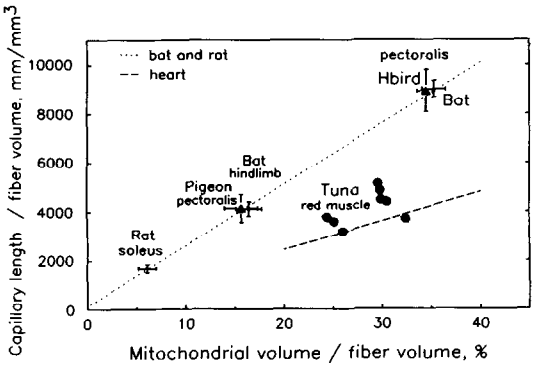


FIG. 3. Plot of capillary length per fiber volume against fiber mitochondrial volume density in tuna red muscle (solid circle) compared with group mean values (±SE) in highly aerobic muscles of bird (solid triangle) and mammal. From 24 (pigeon), 26 (tuna), 31 (hummingbird) and 32 (rat and bat). Linear relationships in bat pectoralis, bat hindlimb and rat soleus (dotted line; r = 0.993) is from 32. Linear relationship in mammalian heart (dashed line; r = 0.85) is from 11.

Fiber O_2 Supply Compared to Other Muscles

Figure 3 shows that the plot of capillary length density against fiber mitochondrial volume density in tuna red muscle compared to other aerobic muscles. It illustrates the strong linear relationship between capillary length and fiber mitochondrial volume density in mammalian and bird skeletal muscles over a wide range of aerobic capacities, from rat soleus to bat and hummingbird flight muscle. In tuna red muscle, capillary length per ml mitochondria was about 56% of that in skeletal muscles of birds and mammals. Whether this represents an excess of mitochondrial volume for the size of the capillary network in tuna, or a shorter capillary length for the volume of mitochondria in the muscle is poorly understood. Interestingly, the value in tuna is close to that in mammalian heart (Fig. 3 and ref. 11), another muscle which contracts continuously throughout an animal lifespan. It is not known whether the entire mitochondrial compartment functions synchronously in muscles during maximal work, and whether different fractions are alternately recruited in continuously contracting muscles such as myocardium and tuna red muscle. If a smaller fraction of the mitochondrial machinery is functioning at any given time in continuously contracting muscles, then fiber mitochondrial volume would be in excess for their capillary supply compared with other muscles. Another possibility in tuna is that constraints of function at different temperatures necessitate capillary length per unit volume of mitochondria to be substantially shorter than in skeletal muscles of bird and mammals.

In tuna red muscle, capillary surface per mitochondrial inner and outer membrane surface area (26) was also about half that in hummingbird flight muscle (31), indicating no appreciable difference in mitochondrial size or density of cristae between the muscles. Mitochondrial volume per μm fiber length ranged from 130 to 200 μm^3 in tuna red muscle. These values are within the range of those in rat soleus muscle (Fig. 4), a tissue with substantially less mitochondrial volume density (Fig. 3) but greater fiber size (tuna 475 ± 25 μm^2; rat soleus, 2028 ± 125 μm^2; both fiber cross-sectional areas as 2.1 μm sarcomere length). Figure 4 shows that capillary surface per fiber surface at a given mitochondrial volume per unit fiber length was similar in tuna red muscle and rat M. soleus, and about half that in bat and hummingbird flight muscles. The ratio between capillary-to-fiber surface and mitochondrial volume (μm^3) per μm fiber length was 0.0019 ± 0.001 in tuna red muscle, 0.0021 ± 0.0004 in rat soleus, 0.0041 ± 0.0002 and 0.0046 ± 0.0004 in bat and hummingbird flight muscles, respectively (31).

The twofold greater capillary-to-fiber surface per fiber mitochondrial volume in the flight muscles suggests an increased capacity for O_2 flux, consistent with an important role of the capillary-fiber interface in determining flux rates in working red muscles (9). It is also consistent with the twofold greater mitochondrial respiratory rates in flying hummingbird (7–10 ml O_2 per ml mitochondria per min; 37) compared to locomotory muscles of mammals running at $\dot{V}_{O_2max}$ (5 ml O_2/ml mitochondria/min; 12). It is interesting that in tuna red muscle, capillary-to-fiber surface per fiber mitochondrial volume was similar to that in rat soleus (Fig. 4), in spite of the lower capillary length per unit volume of mitochondria (Fig. 3), lower capillary surface per mitochondrial volume and lower capillary-to-fiber ratio in tuna (26). The smaller fiber size in tuna red muscle yielded a similar capillary-to-fiber surface as in rat soleus muscle at the same volume of mitochondria per unit fiber length in the muscles (Fig. 4).

Measurements of maximal respiratory rates of tuna red muscle mitochondria *in vitro* yielded estimates of mitochondrial respiratory rates *in vivo* at least 3–5 times lower than that estimated in locomotory muscles of mammals running at $\dot{V}_{O_2max}$ (33). The reason for this difference is not fully under-

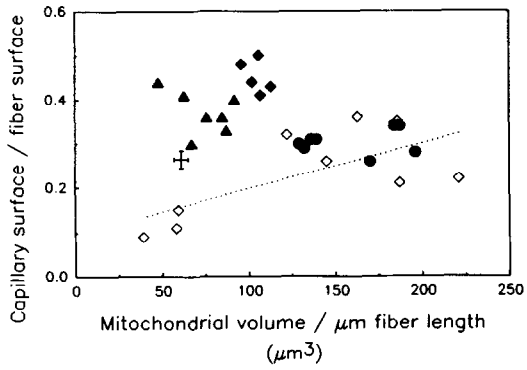


FIG. 4. Plot of capillary/fiber surface ratio against mitochondrial volume per μm length of fiber (i.e., mitochondrial volume density multiplied by fiber cross-sectional area) in tuna red muscle (solid circle) compared with flight muscle of hummingbird (solid triangle) and bat (solid diamond), rat soleus (open diamond) and group mean value (±SE) in bat hindlimb. From 26 (tuna), 31 (hummingbird) and 32 (rat and bat).

stood. As mentioned earlier, the actual fraction of the mitochondrial compartment recruited at any given time in a continuously contracting muscle such as the red muscle of tuna is not known. Also, differences in operating temperatures may play a role. Accounting for a O_{10} value of about 2.5–3 for mitochondrial respiratory rates (8) yields maximal respiratory rates in tuna close to those in mammals. Another possibility is that portions of the mitochondrial compartment may be designed for functions other than simply oxidative phosphorylation. Protein and amino acid metabolism is up-regulated in fish muscle compared to other vertebrates (8), which may require greater mitochondrial density for the enzymes of amino and protein turnover. Also, substrate and heat transfer may require additional capillary-fiber surface in tuna independently of O_2 flux per se (26).

Intrafiber Lipid Deposition

Increased volume fraction of intrafiber lipid droplets is a well known adaptation of skeletal muscles to endurance training (10). Muscles with sustained activity such as flight muscles also show a greater volume fraction of lipid droplets than other muscles. Group mean values for the volume density of lipid droplets per volume of fiber were about 2% in pectoralis muscle of pigeon (27), 4% in hummingbird flight muscles (31), and 4–14% in pectoralis muscle of bat (32,28), compared to only 0.1 and 0.7% in bat hindlimb and rat soleus muscle, respectively (32). In fish red muscle, the volume fraction of intracellular lipid droplets increases with adaptation to cold, yielding increased O_2 flux and intracellular O_2 stores (5).

In tuna red muscle, the volume density of lipid droplets per volume of muscle fiber ranged from 0–2% and varied greatly between samples (26). This range is comparable to that seen in other aerobic muscle of fish (20). It is modest compared to the 8% of fiber volume in cold-acclimated bass (5), or values in hummingbird or bat flight muscles (see above). Thus, similarly to other structural parameters, the volume fraction of intrafiber lipid droplets is not particularly high in red muscle of tuna.

In conclusion, examination of fiber capillarization and ultrastructure in red muscle of tuna reveals both similarities and differences with features found in the most aerobic skeletal muscles of birds and mammals. Three characteristic features of high flux paths for oxygen: (a) small fiber size, (b) high capillary density and (c) high mitochondrial volume density are found in tuna, but these are not as pronounced as in bird and bat flight muscle, nor are the values in tuna extreme compared with other fish. A particular arrangement of capillary manifolds, that is, venular branches running perpendicular to the muscle fiber axis, seem to be required in highly aerobic muscles of birds and tuna, but not in mammals. All indexes of fiber capillarization in tuna red muscle are low for its mitochondrial volume. This could be related to differences in mitochondrial or capillary function, or both, in tuna compared to highly aerobic skeletal muscles of birds and mammals.

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