FUNCTIONAL MORPHOLOGY OF THE TUNA GILL

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ABSTRACT

The tuna gill has a number of structural modifications from that for typical teleosts. A brief summary is given of a series of studies which describe these modifications and attempt to analyse the functioning of the tuna gill. Included is a study of "ram" ventilation - swimming with the mouth agape. The major part of the presentation deals with the unique respiratory blood pathway of the tunas and our hypothesis that it greatly reduces the blood pressure drop across the gill.

Tunas, ranking among the largest (500 kg) and most active of fishes, lack a gas bladder and swim continuously for hydrostatic equilibrium (1). Basal swimming speed is adequate to pass sufficient water over the gills for respiration and the tunas have lost the ability to actively pump respiratory water. The "double pump" of other teleosts has been extensively studied but no attention has been given to the "ram" type of ventilation of the tunas. It is now realized that many other species of fish use ram ventilation when swimming. Our initial study of the morphology of the tuna gill revealed some surprising modifications from the typical teleost structure and we have attempted to deduce their functions in subsequent analyses. This paper briefly summarizes these studies and elaborates on a current one - the effect of blood pathway on blood pressure drop in the secondary lamellae.

Tunas have the largest gill surface area of all species measured (2, 3) and approach the lung surface area of mammals of the same size. The gill area for a 70 kg tuna, for example, is about 60 m². As with some other large pelagic species, the gill filaments of the larger tunas are connected together by "spot fusions" so the gill arch looks a bit like a honey comb. This gives rigidity to the arch and is probably associated with the large gill size and high swimming speeds. In addition, in all of the tunas the "free" border of the secondary lamellae are fused to those of the adjacent filaments (4). This appears to be a support modification but also may contribute to the distribution of water through the interlamellar spaces.

The secondary lamellae are more closely spaced in tunas than in any other species.

Despite the large gill area and the fineness of the interlamellar water channels, the resistance to water flow during ram ventilation is fairly modest. For a 1.67 kg skipjack tuna, swimming at its basal speed of 66 cm/sec, we calculate the gill resistance to be about 1100 dynes and the required energy about 0.009 gm cal/sec (5). This is about 7% of the total swimming resistance and only 1 or 2% of the total metabolism. As oxygen demand goes up, the mouth gape increases to allow more water to flow over the gill and the energy required to overcome the resistance also goes up. If the quantity of water doubles, the cost of swimming increases by 25%.

One of the most striking modifications in the tuna gill is in the respiratory blood pathway. In most teleosts the blood flows along the long axis of the secondary lamellae and water flows counter-currently from the opposite end. In the tunas the blood is distributed so that it flows obliquely across the secondary lamellae at an angle of about 60° as shown in Fig. 1 (6).
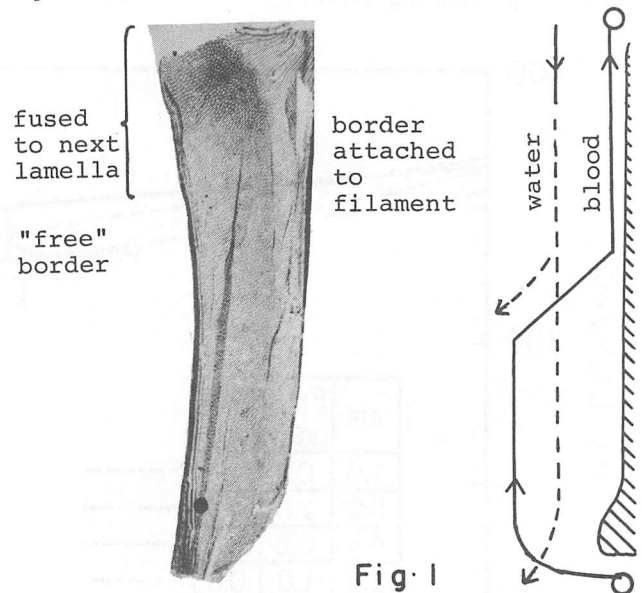

Fig. 1

(Fig. 1 is a photograph of a nearly intact secondary lamella from a skipjack tuna. To the right is sketched the blood pathway, showing one respiratory blood channel, and indicating the two possible water pathways. Cross hatching at

the extreme right is the cartilaginous ray of the filament.) Our examination of the gill of a 1.67 kg skipjack tuna (5, 7) led us to believe that the water could be deflected so that its pathway would be approximately counter-current to that of the blood. However in larger tunas the water must flow mainly with the long axis and "oblique cross-current" must prevail. Analysis of the two types indicates that the cross-current is not greatly less efficient than the counter-current (7). The main effect achieved by the tuna modification is a substantial shortening of the length of the small diameter respiratory blood channels as shown in Fig. 2. (Lamella length increases with fish size).

Fig. 2
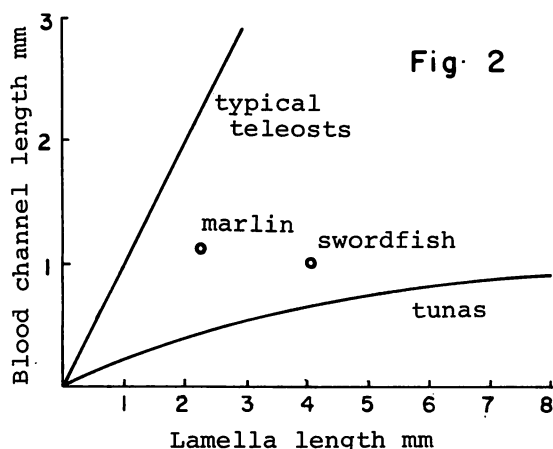
Obviously the channels are long enough for sufficient gas exchange, but that they need not be any longer is an inadequate explanation for the development of the modification. An increased blood velocity could make equally efficient use of longer channels and a fully counter-current system.

Seeking a greater advantage for the modification, we examined the effect of the pathway on blood pressure drop and concluded that a very substantial saving of cardiac work could be obtained with the tuna pathway. We derived the following equation for blood pressure drop across all the respiratory channels for the whole gill (8):

$$\Delta p = \frac{8K\mu \dot{V}_b \ell^2}{\pi A_g d^3} \quad dynes/cm^2$$

We assumed that the channels were cylindrical tubes so $K = 30$, and that blood viscosity $\mu = 0.024$ poise. $\dot{V}_b$ is cardiac output, A_g the effective gill surface area, ℓ the blood channel length and d the diameter.

For the 1.67 kg skipjack tuna, the representative lamella length was 0.142 cm. Blood channels were 0.034 cm in length and 3.4×10^{-4} cm in diameter. The above equation yields 3.5 mm Hg pressure drop but it would have been 48 mm Hg had the channels run the long axis

as in other teleosts. Similarly, for a 270 Kg bluefin tuna the lamella length was 0.8 cm and the channels were 0.09 cm in length and 6×10^{-4} in diameter. For the observed pathway the pressure drop calculates to 4.4 mm Hg. It would have been an incredible 348 mm Hg had the channels been the usual way.

Testing the equation on Atlantic cod, which has a typical teleost pathway, we calculated a 20 mm Hg pressure drop for a 1 Kg fish and 29 mm for a 19 Kg one. The channel diameter increased more rapidly with fish size for the cod (from 4.5×10^{-4} to 6.2×10^{-4}) and this appears to be the main way it keeps the pressure drop from becoming excessive. Had the large bluefin tuna followed the same strategy, its channels would have been of the order of 13×10^{-4} (13μ) to keep the pressure drop down to about 30 mm Hg. For channels of this diameter, the supporting tissues would have to be increased and the diffusion efficiency would undoubtedly suffer.

The pillar cells, which form the blood channels are evidently modified smooth muscle cells (9) and may function to alter the diameter of the blood channels. From the above equation, pressure drop varies as the cube of the diameter so the fish may have some control over the blood pressure drop.

REFERENCES

1. Magnuson, J.J. 1970. Hydrostatic equilibrium of a pelagic fish without a gas bladder the scombroid *Euthynnus affinis*. Copeia 1970(1): 56-85.
2. Muir, B.S. and G.M. Hughes, 1969. Gill dimensions for three species of tunny. J. Exp. Biol. 51(2): 271-285.
3. Muir, B.S. 1969. Gill dimensions as a function of fish size. J. Fish. Res. Bd. Can. 26: 165-170.
4. Muir, B.S. and J.I. Kendall, 1968. Structural modifications in the gills of tunas and some other oceanic fishes. Copeia 1968 (2): 388-398.
5. Brown, C.E. and B.S. Muir, 1970. Analysis of ram ventilation in fish gills with application to skipjack tuna. J. Fish. Res. Bd. Can. 27(9).
6. Muir, B.S. 1970. Contribution to the study of blood pathways in teleost gills. Copeia 1970(1): 19-28.
7. Brown, C.E. and B.S. Muir. Analysis of respiratory gas exchange in tuna gills. In preparation.
8. Muir, B.S. and C.E. Brown. The effect of blood pathway on blood pressure drop in fish gills with special reference to tunas. In preparation.
9. Munshi, J.S.D. and B.N. Singh, 1968. On the microcirculatory system of certain freshwater teleostean fishes. J. Zool. (London): 154: 365-376.