DIFFUSION LIMITATIONS

FOR OXYGEN TRANSFER IN EXERCISING FISH:

25 YEARS LATER

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EXTENDED ABSTRACT ONLY- DO NOT CITE

Cycles are fundamental to life, whether they involve red blood cells simply circling around the body, or fetal genes being re-expressed during the later years of life. Sometimes, however, you do not realize that you are part of one of these cycles until you have come full almost circle! This talk concerns a circle of investigation, started over 25 years ago when a very generous intellectual, Professor Dave Randall, inspired a Black Country lad.

Dave Randall delighted himself in challenging graduate students with broad questions concerning the physiology of fish. Of course, these questions might come up amid the bridge, darts, soccer and squash games that were so integral to a graduate student's life in the Zoology Department at UBC in the mid to late 1970's. Two of the questions that intrigued me during my graduate days were: Is the rate of gas exchange at the gills diffusion limited or perfusion limited? Why do fish display hypoxic bradycardia?

My Ph.D thesis, under Dave's sagacious guidance and very much buoyed by his considerable investment in state-of-the-art technologies, made a small contribution to these issues by enlightening our understanding of blood flow patterns through gill secondary lamellae. In doing so, I realized that to properly understand gill blood flow, I should first understand the primary pump - the fish heart. Consequently, the path of my research for the next 25 years was set, seemingly to leave behind issues such as rates of gas exchange and hypoxic bradycardia.

In developing an *in situ* working perfused fish heart preparation to examine cardiac control mechanisms, reliable measurements of myocardial oxygen consumption over a physiological range for cardiac work were also possible. This knowledge was used to evaluate myocardial oxygen supply. Most fish lack a coronary circulation, and so the myocardial oxygen supply has to come from venous blood. As it turned out, the venous blood contains about 25-times the amount of oxygen needed by the heart in resting rainbow trout. Similarly, during exercise, when the oxygen content of venous blood declines, roughly the same amount of oxygen is returned to the heart due to increased cardiac output. This brought me full circle to address Dave's questions. Fish are unlikely to encounter many situations where oxygen delivery to the heart is perfusion-limited. In contrast, oxygen delivery to the fish heart may well become diffusion-limited when venous blood oxygen tension decreases during either exercise or environmental hypoxia. Furthermore, if the myocardial oxygen supply were diffusion-limited, then hypoxic bradycardia could be an important compensatory mechanism. Foremost, an increased residence time of venous blood in the lumen of the heart during hypoxic bradycardia would allow a greater amount of oxygen to diffuse from the venous blood per heartbeat, compensating for a low venous blood oxygen tension. Second, the slower heart rate would mean a lower rate of cardiac work, which may improve efficiency. Mammals do not display hypoxic bradycardia; a difference that may be related to the fact that their oxygen supply comes primarily from the oxygenated blood in the coronary circulation. Some fishes have a coronary circulation directly from the gills to the outer portion of the ventricle, but, despite its obvious importance, the coronary circulation in fishes is apparently secondary and supplemental to the venous supply. Even skipjack tuna, with probably the most developed coronary circulation among fishes, develop hypoxic bradycardia.

A new loop in this circle of investigation developed recently, again thanks to Dave Randall, but this time for loaning me a new piece of technology. The new technology is a fibre-optic oxygen electrode (an optode) that has allowed the first on-line measurements of venous blood oxygen tension in exercising rainbow trout. To our surprise, venous blood oxygen tension decreased to a plateau during a critical swimming speed test even though the fish continued to increase its swimming effort and speed after the plateau was reached. Implicit in this observation is that, despite an increased oxygen demand from the locomotory muscle, further oxygen is not extracted from the blood. The finding of a plateau in venous blood oxygen tension during exercise has led to a novel proposal that a threshold level for venous blood oxygen tension exists that serves to "protect" the venous blood oxygen supply to the heart, which then permits maximum cardiac function to be maintained during maximum prolonged exercise. By preventing myocardial hypoxia when the heart is working maximally, a venous blood oxygen threshold suggests the existence of either a novel reflex mechanism (e.g., a venous oxygen receptor) involved in the terminal stages of swimming, or a physical limitation on the rate of oxygen diffusion in tissues. Again, I have come full circle, thanks to some of the seeds that were so well sown by Dave Randall.

Before closing, I will make a prediction, since Dave was never one to shy away from either predictions of a general nature, or a grand-slam for that matter. In my mind, the presence of a venous blood oxygen threshold in exercising fish may represent an orderly transition from aerobic to anaerobic locomotion as fish swim harder that ultimately serves to prevent a catastrophic cardiac hypoxic collapse. How hard a fish exerts itself directly affects its ability to successfully capture prey and avoid predation. But because burst exercise can dramatically decrease venous blood oxygen tension, it may be possible soon to establish a direct experimental linkage between the presence of a coronary circulation in fish and an improved likelihood of either capturing prey and avoiding predators, or exploiting more hostile environments.

Dave, my road continues for a while longer than yours. I will remain forever grateful of the many opportunities you have afforded me along my travels. Wishing you well for the remainder of your travels.

> Who is the happy Warrior? Who is he
> That every man in arms should wish to be?
> It is the generous spirit, who, when brought
> Among the tasks of real life, hath wrought
> Upon the plan that pleased his childish thought:
> Whose high endeavours are an inward light
> That makes the path before him always bright:
> Who, with a natural instinct to discern
> What knowledge can perform, is diligent to learn.

Character of the Happy Warrior
William Wordsworth