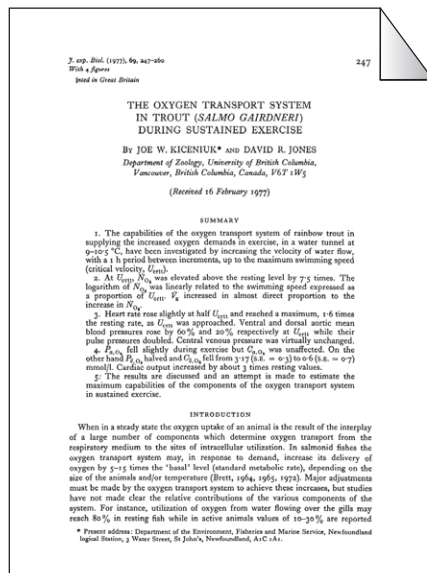


A JEB CLASSIC ON FISH EXERCISE



Tobias Wang and Hans Malte discuss the 1977 paper by Joe W. Kiceniuk and David R. Jones entitled: 'The oxygen transport system in trout (*Salmo gairdneri*) during sustained exercise.'

A copy of the paper can be obtained from <http://jeb.biologists.org/content/69/1/247.abstract>

All animals raise metabolism during exercise, and the increased call for oxygen in muscles must be attended by increased delivery of oxygen from the surroundings to the mitochondria within the working muscles. Because this transport of oxygen, and the opposing transfer of metabolically produced CO₂, depends on a coordinated interplay between all parts of the oxygen cascade, the cardiovascular and respiratory responses to exercise represent an important research area within comparative physiology. In addition to allowing for an understanding of the structural and physiological limitations for oxygen transport, it is also likely that evolution acts particularly on the physiological ability to cope with stressful situations such as exercise; an understanding of how the cardio-respiratory systems respond to exercise is therefore pivotal to understanding why these structures and their underlying control have evolved.

The appreciation of exercise physiology is probably as old as physiological investigations, but because comprehensive physiological studies on live animals performing voluntary exercise are technically extremely challenging, it was not really until the 1970s that such studies were performed on non-mammalian

vertebrates. In terms of exercise studies on fishes, the 1977 JEB paper by Joe Kiceniuk and David Jones really raised the bar and provided the first truly complete quantitative description of oxygen transport in the steady state at various swimming speeds. In this light, it is perhaps not surprising that Kiceniuk and Jones (Kiceniuk and Jones, 1977) is amongst the most cited JEB papers from the 1970s, and their data continue to be used today – simply because no one has been able to surpass the completeness of this *tour de force* in cardiorespiratory physiology!

To describe the changes in gill ventilation and the cardiovascular system, Kiceniuk and Jones placed rainbow trout in a swimming respirometer where the rate of oxygen consumption (\dot{V}_{O_2}) could be measured at various swimming speeds. The trout were equipped with wires to record the electrocardiogram to measure for heart rate (see Fig. 1A), and cannulae inserted in both the dorsal and ventral aorta, as well as in a central vein immediately before the heart (common cardinal vein), allowed for repeated blood sampling and measurements of blood pressures. The blood samples from the dorsal aorta allowed Kiceniuk and Jones to assess whether branchial gas exchange would continue to oxygenate the blood at the various speeds, while the difference in oxygen concentrations between the cardinal vein and the dorsal aorta allowed for calculation of cardiac output, i.e. the rate of blood flow (\dot{Q}) generated by the heart and stroke volume (V_s) of the heart. Finally, the duo measured gill ventilation by placing a skirt – ingeniously constructed from a disposable surgical glove – above the opercula such that sampling of expired water, without contamination from ambient water, could be performed and gill ventilation calculated from the oxygen concentration differences between inspired and expired water (see water sampling cannula in Fig. 1A).

Together, they showed that arterial oxygen levels [i.e. both the partial pressure (P_{O_2}) and concentration of oxygen] remain high even at maximal aerobic exercise, and that the increased call for oxygen was met by increased cardiac output (\dot{Q}) through increased heart rate and stroke volume in combination with increased extraction of oxygen in the blood as revealed by a lowering of the venous oxygen concentration (Kiceniuk and Jones, 1977) (Fig. 1B, Eqn 3). This, we know now, seems to be a uniform pattern during exercise in all vertebrates even across a wide range of temperatures (e.g. Åstrand et al., 1964;

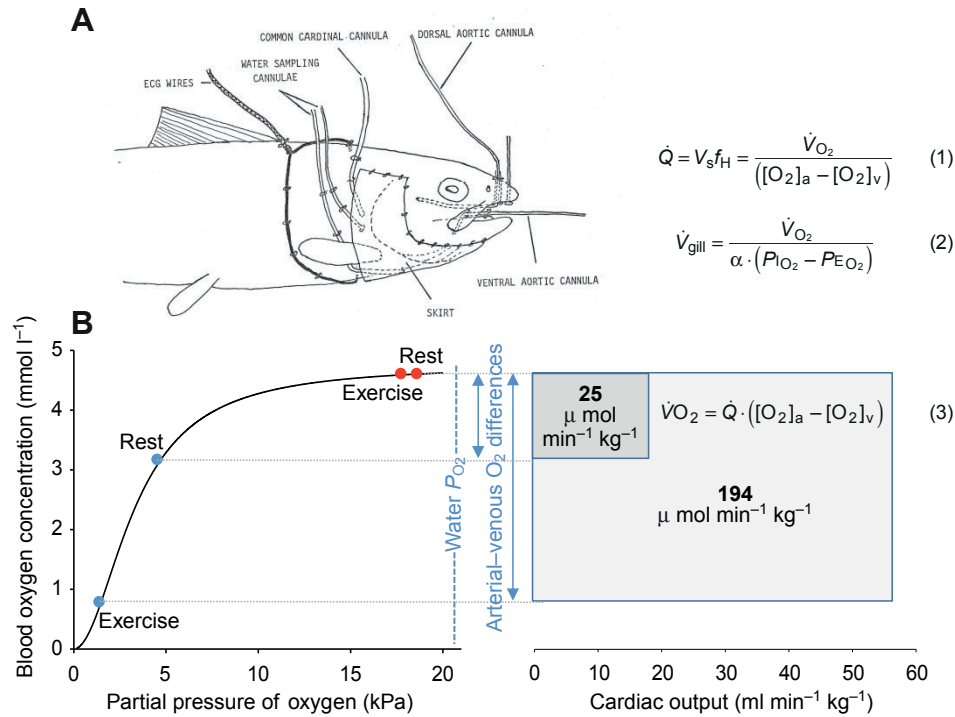


Fig. 1. (A) An illustration from Joe Kiceniuk’s PhD dissertation demonstrating the placement of the cannulae for withdrawal of arterial and venous blood samples from the dorsal aorta and the common cardinal vein, respectively. These cannulae were used to determine blood gases and, in combination with the simultaneous measurements of oxygen consumption (\dot{V}_{O_2}), allowed for a calculation of cardiac output (Q) using Eqn 1 (where f_H is heart rate). The skirt placed above the opercula allowed for measurements of expired water, such that the rate of gill ventilation (\dot{V}_{gill}) could be calculated using Eqn 2 (where P_{IO_2} and P_{EO_2} are the partial pressures of inspired and expired O_2 , respectively). (B) As shown in the lower panel, Kiceniuk and Jones (Kiceniuk and Jones, 1977) demonstrated that arterial oxygen levels are maintained during exercise and that the increase in oxygen consumption is governed by a rise in cardiac output – primarily by increased stroke volume (V_s) – in combination with a widening of the O_2 concentration difference between arterial and venous blood ($[O_2]_a - [O_2]_v$), i.e. increased extraction (Eqn 3). This response is shown as a graphical solution to the Fick principle on the right-hand side of the figure.

Kiceniuk and Jones, 1977; Butler et al., 1977; Andersen and Wang, 2003; Clark et al., 2005).

Two additional observations emerge from the observation that arterial \dot{P}_{O_2} remains high during exercise in fish and other vertebrates. Firstly, the high arterial \dot{P}_{O_2} shows that ventilation of the gas exchange surfaces (i.e. gills in fish and lungs in air-breathers) increases proportionally to the rise in aerobic metabolism during exercise. Secondly, the high arterial \dot{P}_{O_2} demonstrates that the gill has sufficient capacity to allow for the tenfold rise in oxygen diffusion across the branchial epithelium, even though the oxygen partial pressure difference between the blood and the water only increases to a rather limited extent because \dot{P}_{O_2} of the venous blood only decreases by a few kPa. Thus, the increased flux of oxygen implies that the diffusion conductance or ‘transfer factor’, i.e. the flux of oxygen for a unit partial pressure difference, increases considerably during exercise. The mechanisms for the increased conductance probably stems from a combination of increased perfusion recruiting more area for diffusion and a

shortening of the diffusion distance as blood pressures increases (Jones and Randall, 1979; Farrell et al., 1980). Similar responses are characteristic of vertebrate lungs (Turino et al., 1963; Hsia et al., 2008), but in the fish gill the actual mechanism and structural changes remain difficult to quantify.

What makes Kiceniuk and Jones’ 1977 JEB paper a classic? Earlier studies on fish had shown that the increase in oxygen uptake is almost exponential as swimming speed increases and reaches maximal values that are up to tenfold higher than resting values (e.g. Brett, 1964; Brett, 1965; Brett, 1972). Several other studies reported on parts of the oxygen transport cascade (Stevens and Randall, 1967a; Stevens and Randall, 1967b). However, the relevant changes in ventilation, the cardiovascular system and the blood gases had not been measured simultaneously until Kiceniuk and Jones published this classic paper. Thus, Kiceniuk and Jones’ tenacity and perseverance allowed the first calculations of transfer factors in the gills and the systemic circulation of exercising fish. In fact, the original data from Kiceniuk and Jones’

1977 publication provided the most complete set of input parameters (including gill ventilation, cardiac output and gill diffusion conductance) available when we recently devised an integrative mathematical model to describe maximal oxygen uptake and transport from water to tissues (Wang and Malte, 2011). Using this model we were able to clarify to what extent the oxygen affinity of the blood is important for maximal oxygen uptake and transport in the steady state.

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Tobias Wang
Aarhus University
tobias.wang@biology.au.dk

Hans Malte
Aarhus University
hans.malte@biology.au.dk

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