

This Week's Citation Classic®

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Holeton G F & Randall D J. The effect of hypoxia upon the partial pressure of gases in the blood and water afferent and efferent to the gills of rainbow trout. *J. Exp. Biol.* 46:317-27, 1967.

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Aquatic hypoxia resulted in a large increase in gill water flow and a reduction in oxygen extraction from the water, but little change in oxygen uptake by the trout. Heart rate was reduced, but there was an increase in stroke volume such that cardiac output was unchanged. Oxygen, carbon dioxide, and pH changes in blood were described. Blood lactate levels increased, indicating an increase in anaerobic metabolism during hypoxia. [The SCJ® indicates that this paper has been cited in over 180 publications.]

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As we stated in the introduction: "Van Dam (1938), Itazawa (1957) and Saunders (1962) have recorded some of the effects of hypoxia on the gas tensions in blood and water afferent and efferent to the gills of fishes, but there has been no integrated study in which several of these parameters have been measured simultaneously in a single species of fish." This we then set out to do, and our study, along with many others, has led to a much better understanding of oxygen and carbon dioxide transfer in aquatic animals. The study did not lead to any new theory but rather was a more complete description than any previous study of oxygen transfer across fish gills. The data have stood the test of time and are a credit to the careful measurements made by George Holeton, who did most of the bench work.

George died in a car crash some years ago. I miss his wise counsel and steady hand. I had come to the University of British Columbia from England as a green, young faculty member. George was one of my first

MS students. I had little research money, so I made contact with Roly Brett at the Biological Station in Nanaimo to see if I could beg, borrow, or steal space and equipment. I have always had a high opinion of Brett's work, and he, along with Gordon Bell and Lynwood Smith, had been working on surgical and anesthetic techniques for fish, including methods of blood vessel cannulation. The development of these techniques allowed us to investigate gas transfer in fish in more detail.

George was a great improviser and a collector of junk. He would arrive at the laboratory by bicycle, often carrying some new prized acquisition—an old stove top or a broken motor. I throw away such things, but not George, and of course we always found a use for his junk. For example, during the above study, we mixed gases and stored them in the car tire inner tubes collected by George on one of his forays. The inner tubes were suspended in large number from the ceiling in the small laboratory, much like some modern art exhibit.

In our study, having once overcome the technical problems, experimental design and what to measure were fairly straightforward. We had a Beckman Physiological Gas Analyser that had a pH module in addition to an oxygen and carbon dioxide system. Because we had the pH electrode, we measured blood and water pH and reported the data. At the time we did not know what to say about these results, so we avoided the problem and did not mention them in the discussion. In retrospect, I am pleased to find that the pH measurements of blood were accurate and agree with subsequent theory.

I was surprised to find that this paper is a *Citation Classic*. I suppose one reason it may be quoted often is that it was one of the first studies to take a more integrated approach to oxygen and carbon dioxide transfer across the gills of fish. It was published in a readily available journal of good quality. In addition, most of our conclusions have been substantiated by subsequent studies.¹

1. Randall D & Daxboeck C. Oxygen and carbon dioxide transfer of fish gills. *Fish Physiology* 10A:263-341, 1984.

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