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Hughes G M. The dimensions of fish gills in relation to their function. *J. Exp. Biol.* 45:177-95, 1966.
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Gill dimensions were measured and calculations using a modified Poiseuille relationship showed that water flow rates measured experimentally are consistent with the small differential pressure because of the very large number of pores. Active species have larger gill areas. Diffusion resistance in interlamellar water is significant. [The *SCI*® indicates that this paper has been cited in over 125 publications since 1966.]

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As a result of recording the time course of pressure changes on the two sides of fish gills, we came to the conclusion that these structures provide an important resistance to water flow whose detailed nature and properties must be taken into account in any analysis of fish ventilatory mechanisms as well as in relation to gas exchange. For this purpose, gill dimensions were measured, particularly the surface area but also dimensions of the pores through which the water flows. The relationship between applied pressure differences and water flow was also studied. Recordings had shown pressure differences of less than 1 cm H_2O for most of the ventilatory cycle. Before giving my first seminar in the US, at the University of California, Los Angeles, I remember my alarm when thinking that this pressure might be insufficient to produce the known volume flows of water. As a result, I consulted engineers at the California Institute of Technology when I was working on crayfish neurophysiology, and we made a rapid estimate using the Poiseuille relationship. This confirmed that the flows measured were compatible with my measurements of differential pressure and dimensions of the gill sieve.

The hydrodynamicists later asked me to accompany them to Marineland of the Pacific with members of the US Office of Naval Research who had become interested in the dolphin problem (Gray's Paradox). I remember very well the sight of an underwater cameraman in the centre of a training tank ready to photograph a dolphin swimming through a cloud of dye injected into its path. This was quite an exciting moment, especially when the first dolphin came up to the cloud and did a neat "sidestep" to avoid the dye! This was probably the first attempt to visualise water flow past a swimming dolphin, and spontaneously we applauded the dolphin!

While at Marineland, I also made some interesting observations of swimming sharks that ram ventilate but when at rest show active ventilatory movements. Although there had been brief reports of this phenomenon, I believe that my film was one of the first definitely showing this, and it was very useful in teaching at Cambridge and Bristol. A still from this film was used on the cover of my book *Comparative Physiology of Vertebrate Respiration.*[1]

The measurements in the gill dimension paper were made in 1958 and were probably the first made specifically in relation to calculations regarding the dimensions and resistance of the water flow pathways. It is for this reason that the paper is often cited. Other authors had measured the gas exchange surface but had paid little attention to other dimensions.

The suggestion that there may be different paths of water flow was an early indication of the heterogeneity of fish gills that is now generally accepted.[2] This led to analogies with the physiological and anatomical dead spaces of the mammalian lung and the first suggestion that a large proportion of the resistance to gas transfer resides in the water. Since 1966, there has been a very marked increase in the comparative study of vertebrate respiration, much of which has centred on fish. Important applied aspects have arisen, notably in relation to the effects of water-borne pollutants. These aspects have also emphasised the need for a more complete analysis of the gill sieve.

1. **Hughes G M.** *Comparative physiology of vertebrate respiration.* London: Heinemann, 1963. 145 p.
2. ----------------. General anatomy of the gills. (Hoar W S & Randall D J, eds.) *Fish physiology.* London: Academic Press, 1984. Vol. 10, pt. A. p. 1-72.

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