from J.D. Jones. 1972. Comparative Physiology of Respiration.

In fishes ~~the arrangements are even more sophisticated. Here~~ the passage of water through the fine sieve-like arrangement of the gill filaments and lamellae (see below) is effected by two pumps working in series, one either side of the gill resistance. This ensures that the flow of water over the respiratory epithelium is virtually continuous, an important advance over the pulsating flow of the cephalopods. A model of this double pumping mechanism is illustrated in Fig. 7.2. The continuity of flow has been deduced by observations of the pressures in the buccal and opercular chambers which lie on either side of the gills. An early, simple observation by van Dam[36] of continuity of flow in an external tube connecting the two chambers was interpreted as an indication that the pressure is always higher in the buccal than in the opercular chamber. Hughes and Shelton,[92] using sensitive recorders inside the chambers, were able to measure the changing pressures within each chamber with some precision and confirmed the superiority of the buccal pressure during at least 90% of each pumping cycle (Fig. 7.3). The morphological arrangements and functional details will not be elaborated here as they are well summarized in the excellent account of vertebrate respiratory physiology by Hughes.[89]

The dual pump arrangement is found in essentially the same form in elasmobranchs. There are a few detailed differences including entry via the spiracle in addition to the mouth and exit by five paired parabranchial cavities instead of by a single pair of opercular cavities. The predominantly higher buccal pressure again ensures a virtually continuous flow over the gill epithelium. Some fishes which swim strongly and almost continuously, do not make active respiratory movements while in motion but, swimming with the mouth permanently open, rely on the ram effect. This is well seen in some sharks but the mackerel has gone so far as to lose the power of active irrigation and must swim continuously to maintain the oxygenation of its blood.

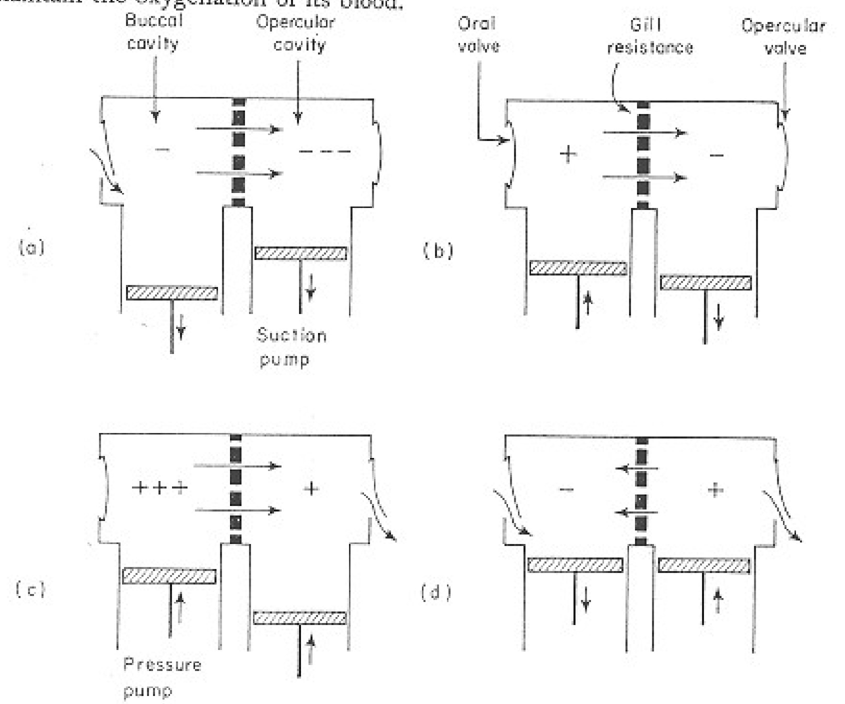


Fig. 7.2 Model of the double pumping mechanism for irrigation of the gills in teleosts and elasmobranchs. The pressures in the buccal and opercular cavities (indicated by + or −) are relative to the water outside. The principal phases are (a) and (c), when water is forced through the gill resistance by suction pumping and pressure pumping respectively. The transition phases (b) and (d) each occupy only about 10% of the duration of the whole cycle. There is a potential reversal of flow during phase (d), due to the momentary reversal of pressure difference but the inertia of the water probably prevents any actual back flow during this very short phase (*c.* 0.1 sec). (Hughes[89])

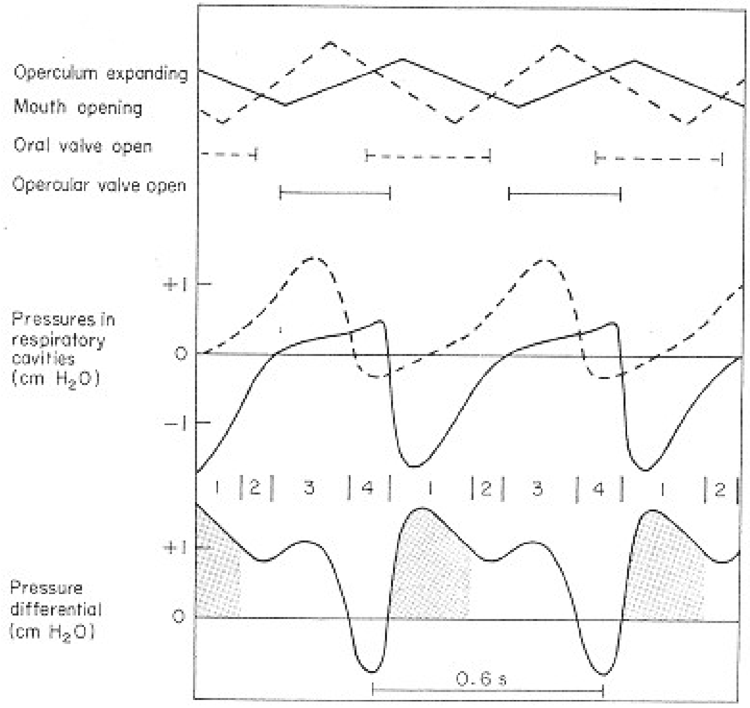
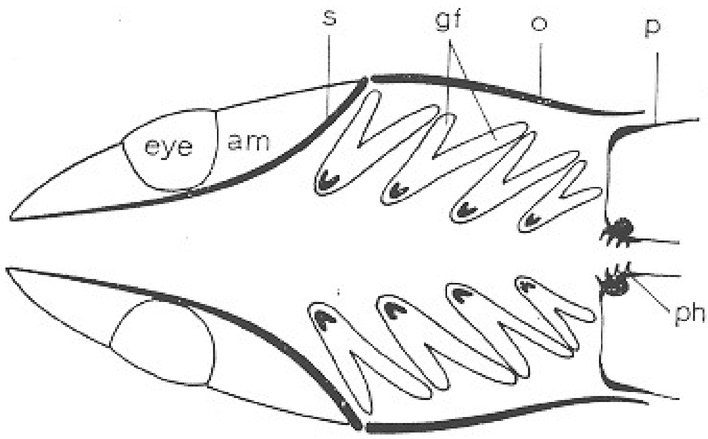
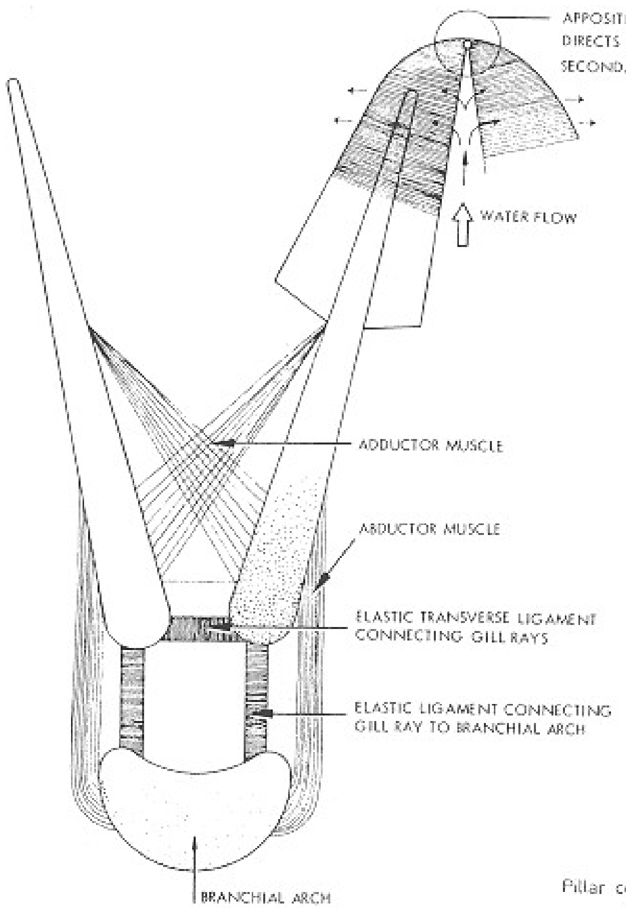


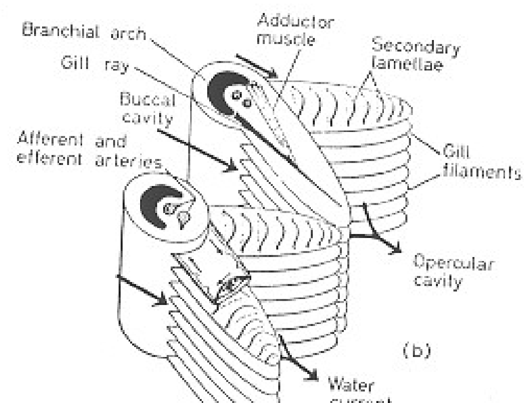
Fig. 7.3 Movements of the mouth and operculum with associated pressure changes in the buccal and opercular cavities in the trout. Broken lines represent the buccal side and continuous lines the opercular side of the system The upper record shows the operculum expansion and mouth opening cycles which are out of phase; the second pair of lines indicate the relations of oral and opercular valve opening. The pressure changes are shown as separate records of actual observed pressures on either side of the gill resistance and below as the difference between the two sides; shaded areas show the period when water flow is mainly due to the opercular suction pump. The figures above the pressure difference line refer to the phases illustrated by Fig. 7.2. The possibility of independent variation of the two pressures depends on the resistance to water flow afforded by the gill structure (see Fig. 7.4) and is essential to the elimination of intermittent flow. The short negative differential period may be further reduced and the opercular suction pump assume even greater importance in bottom-living forms such as the plaice. (After Hughes[89])

Counter-current flow in fish gills

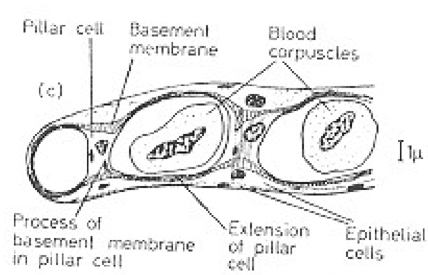
The most effective uptake of oxygen from the irrigation stream results from a well-ordered flow of water over one side of the gill epithelium and an appropriately adjusted flow of blood in the *opposite direction* on the other. The principle of such a counter-current system, which is illustrated in Fig. 7.4, finds employment in a variety of other physiological fields in addition to gas exchange in the mammalian placenta (see Scholander[200]) and is well-known to engineers. Potentially, the recipient stream can come to equilibrium with the highest value in the donor stream instead of the two streams equilibrating at a mean value. Counter-current involvement in the gas exchange of fishes was first appreciated by van Dam[36] and it undoubtedly contributes to the very high levels of utilization which characterize teleost gas exchange (p. 15). A proper adjustment of the two flow rates is also important and as Hughes has pointed out,[89] even with parallel flow a large volume of water moving rapidly past a small slowly moving stream of blood will yield a high degree of oxygenation of the blood but a low utilization; such an arrangement will supply the needed oxygen but at a high cost in irrigation metabolism.







Filaments and associated structures attached to two neighbouring branchial arches.



Section through a secondary lamella, based upon electron micrographs.

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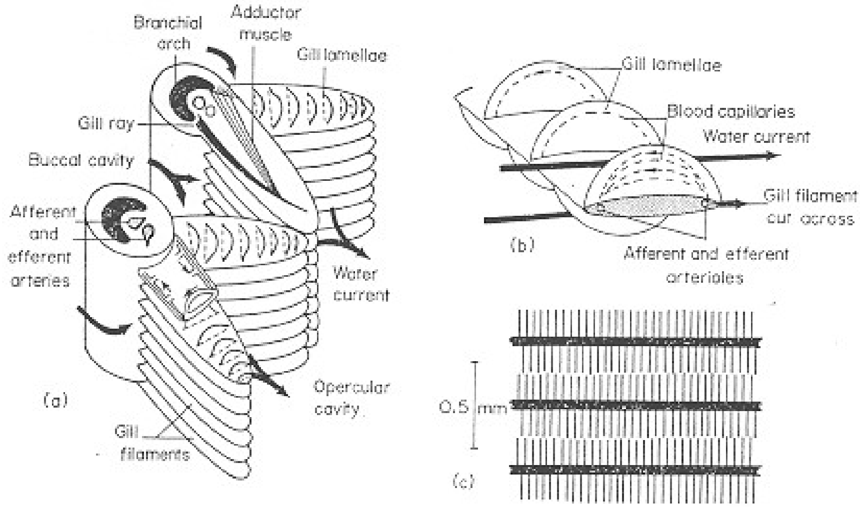

Fig. 7.4 The structure of the teleost gill and counter-current flow of blood and water. (a) Portions of two adjacent gill arches bearing double rows of filaments, which interlock at the tips—a passive posture due to the elasticity of the gill rays. Each filament bears rows of alternating lamellae on upper and lower faces in which the capillary blood flow runs counter to the flow of the water stream between the lamellae. (b) At higher magnification, part of a single filament with three lamellae above and below. (c) Diagrammatic representation of part of the seive-like arrangement provided by the filaments (3) and lamellae in the trench; the water flow is at right-angles to the page. (Hughes[38])

Fig. 1. The circulation in ~~the~~ one gill filament of a typical teleost. (From Randall, Perry & Heming, 1981*b*.)