J. Exp. Biol. (1971), **55**, 399–408
With 5 text-figures
Printed in Great Britain

OXYGEN TENSION DISTRIBUTION IN WATER AND BLOOD AT THE SECONDARY LAMELLA OF THE DOGFISH GILL

BY G. M. HUGHES AND B. A. HILLS*
Research Unit for Comparative Animal Respiration, University of Bristol, Bristol BS8 1UG

(*Received 22 March* 1971)

INTRODUCTION

One of the major functions of fish gills is the transfer of oxygen from the ventilating water to the perfusing blood. In order to gain a more fundamental and quantitative understanding of this process it is desirable to be able to express the relevant parameters in an analytical form. Since attempts were made to do this by analogy with heat exchangers (Hughes & Shelton, 1962), more detailed studies have been made of the anatomical dimensions of fish gills (Hughes, 1966) and their role in the transfer of oxygen (Hills & Hughes, 1970). More refined experimental techniques have also provided further data on the gas tensions in the two media (Piiper & Baumgarten-Schumann, 1968; Randall, Holeton & Stevens, 1967). After allowing for any gross differences in the ventilation and perfusion flows, both in magnitude and relative direction, a parameter in determining the efficiency in the overall transfer process is the resistance to the diffusion of oxygen across each secondary lamella. Even with a good estimate of the effective gill area for mass transfer, this could only be obtained if we knew the tension differential between blood and water at each point along the flow path.

The blood and water channels are too small for direct measurement of the distribution of oxygen tensions, at least, with present techniques, so indirect methods of estimation are required. The problem is complicated by the interaction between the two fluids with regard to their tensions of oxygen and carbon dioxide, by the non-linearity of the oxygen-dissociation curve of the blood, and by the variations in the area available for gas transfer in the direction of flow. However, the oxygen-tension distribution along the length of a secondary lamella can still be estimated, in both blood and water, if the terminal conditions are known or are assumed to be equal to average values. This approach can be regarded as selecting a channel in which the oxygen tensions for the outlet water and afferent blood are equal to the respective mean values of the expired water and mixed venous blood which have been determined experimentally. Variations in gas-transfer surface along the length of the secondary lamella can be obtained by direct measurements according to the method of Hughes (1970). Here it has been applied to the dogfish gill.

* Usual Address: Department of Surgery, Duke University Medical Center, Durham, North Carolina 27706, U.S.A.

METHODS

As part of the standard procedure for determining the gill area of fish the shape of a number of secondary lamellae from the gill system are sampled and traced out using a projection microscope. To obtain individual profiles a few filaments are taken at regular intervals along a gill arch. Sections are cut transverse to the main axis of the filament using either a freezing microtome or a razor blade. Secondary lamellae are floated off and viewed under a projection microscope, where their outline can be traced. One of these tracings was taken as most representative of the whole gill system (Fig. 1).

RESULTS

The direction of water flow for the particular secondary lamella shown in Fig. 1 is indicated by the thick arrow. This can be taken as the x axis, where x is the distance from the inlet travelled by water in the direction of flow (see Fig. 2).

A line drawn perpendicular to the x axis between 0 and L must make at least two intercepts with the actual lamella profile, the distance between them being proportional to the surface area of the secondary lamella per unit length of water path (α). This assumes no appreciable curvature in the plane perpendicular to the direction of flow.

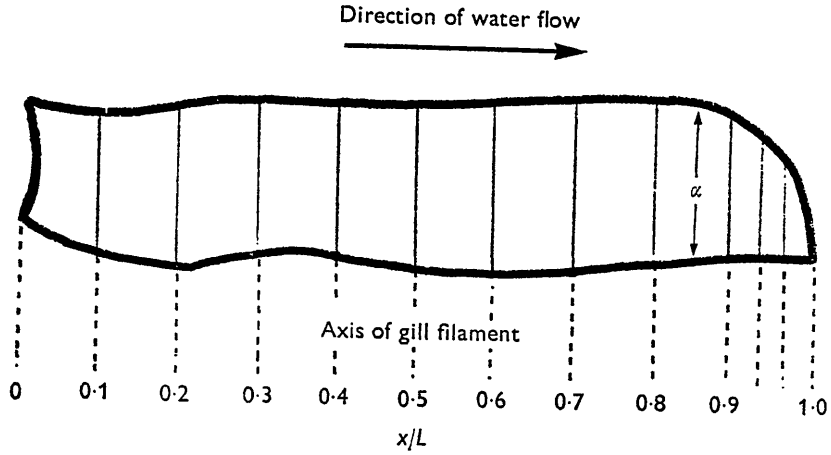

Fig. 1. Profile of a secondary lamella from filament 25 of the 2nd gill arch in a 1 kg dogfish. x is the distance from the water inlet and L is the total path length.

Thus the cumulative area as measured from the water inlet can be expressed as a function (F) of the total area (A) by

$$F = \frac{\int_0^x \alpha\, dx}{\int_0^L \alpha\, dx} = \int_0^x \alpha\, dx/A. \qquad (1)$$

Hence F can be plotted as a function of x simply by dividing the distance between 0 and L into about 10 equal divisions, measuring the areas of the secondary lamella enclosed between each adjacent pair by means of a planimeter, or by weighing the paper, dividing each of these values by the total area, and then adding these fractions

starting from the inlet end ($x = 0$). If A_n is the area enclosed by these divisions ($x = x_{n-1}$ and $x = x_n$) and the outline of the section of the secondary lamella then

$$F = \sum_{1}^{n}(A_n/A).$$

Hence F can be plotted as a function of the fractional distance along the secondary lamella (x/L). This method has been applied to the profile for the dogfish (Fig. 1) to obtain cumulative surface area distribution and plotted in Fig. 3. By using cumulative fractions and fractional path lengths, the plot of F versus x/L can be obtained from a photomicrograph or tracing of the secondary lamella irrespective of the magnification.

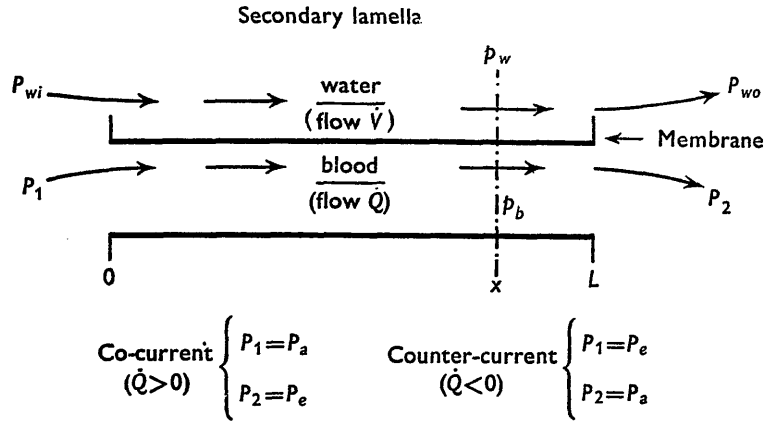

Fig. 2. Schematic diagram depicting symbols used to describe blood and water flows in a typical secondary lamella.

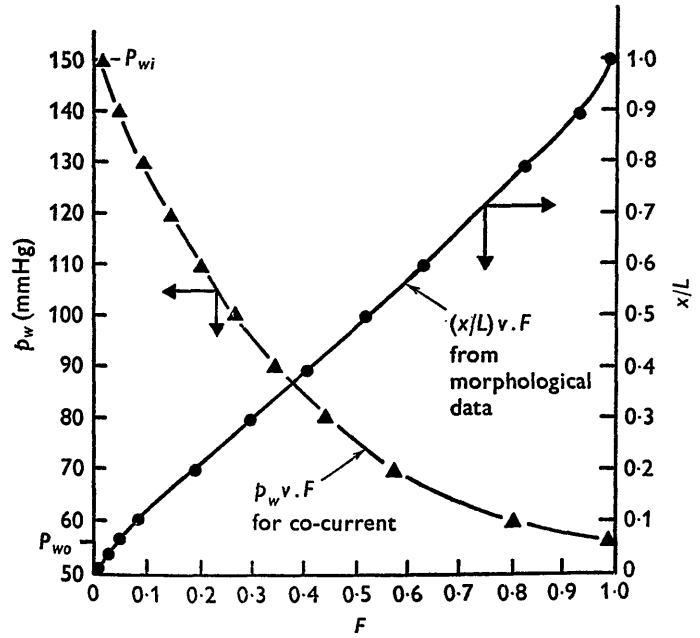

Fig. 3. 'Morphological' plot of F (cumulative area) of the secondary lamella starting from the water inlet against the fractional path length (x/L); and 'functional' plot of F versus oxygen tension of the water. These two plots enable p_w to be matched against x/L.

ANALYSIS

Let us consider the surface area ($a.\delta x$) of a small segment of a secondary lamella of width (δx) located at a distance x from the end for water inlet ($x = 0$ in Fig. 1). The surface area per unit path length of water is a. If δq is the quantity of oxygen transferred across this element per unit time, then

$$\delta q = Ka(p_w - p_b)\delta x, \tag{2}$$

where p_w and p_b are the oxygen tensions in water and blood at x, while K is the overall mass-transfer coefficient for oxygen transport as applied to the gill by Hills & Hughes (1970). For given flow conditions, K is a constant irrespective of the relative contributions of gill membrane and water film to the resistance to oxygen transfer.

Expressing equation (1) in differential form,

$$a = A(dF/dx),$$

which substitution in equation (2) gives

$$\delta q = KA(p_w - p_b)(dF/dx)\delta x. \tag{3}$$

The corresponding rise in the oxygen content of blood (C) at x is given by:

$$\delta q = \dot{Q}(dC/dx)\delta x \quad \text{for co-current flow,} \tag{4}$$

and

$$\delta q = -\dot{Q}(dC/dx)\delta x \quad \text{for counter-current flow,} \tag{5}$$

where $\dot{Q}$ is the blood flow rate irrespective of direction, x having been defined relative to water flow.

The corresponding fall in the oxygen tension of water is given by

$$\delta q = -\dot{V}S_w(dp_w/dx)\delta x, \tag{6}$$

where S_w is the solubility of oxygen in water.

Eliminating δq from equations (4–6) and expressing the result as an integral between a general point (x; p_w) and the point of water inlet ($x = O$; P_{wi}) for co-current

$$(\dot{Q}/\dot{V}S_w)\int_{C_a}^{C} dC = -\int_{P_{wi}}^{p_w} dp_w,$$

giving

$$(\dot{Q}/\dot{V}S_w)(C - C_a) = (P_{wi} - p_w), \tag{7}$$

where C_a is the oxygen content of afferent blood at the corresponding tension P_a. For counter-current flow

$$-(\dot{Q}/\dot{V}S_w)\int_{C_e}^{C} dC = \int_{P_{wi}}^{p_w} dp_w$$

giving

$$(\dot{Q}/\dot{V}S_w)(C_e - C) = (P_{wi} - p_w), \tag{8}$$

where C_e is the oxygen content of efferent flood at the corresponding tension P_e.

The group of unknown constants can be determined by repeating the integration over the whole length of the secondary lamella since terminal oxygen tensions are known in both blood and water. At the water outlet ($x = L$), $C = C_e$ for $p_w = P_{wo}$ in equation (7) (co-current flow) while $C = C_a$ for $p_w = P_{wi}$ in equation (8) (counter-current flow). Both expressions reduce to

$$(\dot{Q}/\dot{V}S_w) = (P_{wi} - P_{wo})/(C_e - C_a) \tag{9}$$

P_{wi}, P_{wo}, P_a and P_e can be determined by direct measurement, where P_a and P_e are the oxygen tensions of afferent and efferent blood respectively. Knowing these values, C_e and C_a can be obtained from the oxygen-dissociation curve of the blood (C versus p_b), which can be measured experimentally. Thus $(\dot{Q}/\dot{V}S_w)$ can be determined for use in equations (7, 8).

Eliminating δq from equations (3) and (6),

$$\frac{KA}{\dot{V}S_w}\int_0^F dF = \int_{P_{wi}}^{p_w} \frac{dp_w}{p_w - p_b},$$

when

$$\frac{KA}{\dot{V}S_w}F = \int_{P_{wi}}^{p_w} \frac{dp_w}{p_w - p_b}. \tag{10}$$

At $x = L$, $F = 1$ by definition (equation 1) and $p_w = P_{wo}$; then the above expression gives the group of unknown constants $(KA/\dot{V}S_w)$ as

$$\frac{KA}{\dot{V}S_w} = \int_{P_{wo}}^{P_{wi}} \frac{dp_w}{p_w - p_b}. \tag{11}$$

When substituted in equation (10) this gives

$$F = \frac{\int_{p_w}^{P_{wi}} \frac{dp_w}{p_w - p_b}}{\int_{P_{wo}}^{P_{wi}} \frac{dp_w}{p_w - p_b}}. \tag{12}$$

Hence F can be plotted against either p_w or p_b. Since F has already been determined from equation (1) as a function of position (x/L) along the secondary lamella by direct measurement of area, p_w and p_b can now be plotted against (x/L). Thus the change in oxygen tension in both blood and water can be determined along the length of a secondary lamella with the following data:

(1) The profile of the secondary lamella.

(2) The oxygen-dissociation curve for the blood of that fish (C versus p_b) – given for dogfish blood by Piiper & Baumgarten-Schumann (1968).

(3) The oxygen tensions of the inlet and outlet water and of the afferent and efferent blood – given for dogfish as $P_{wi} = 149$ mmHg, $P_{wo} = 56$ mmHg, $P_a = 10$ mmHg, and $P_e = 49$ mmHg (Baumgarten-Schumann & Piiper, 1968).

Computation

The determination of p_w and p_b versus (x/L) can be demonstrated for the particular secondary lamella of a dogfish shown in Fig. 1. The computation can be affected in accordance with the above analysis in the following steps:

(1) The range of oxygen tension between afferent and efferent blood is divided into 5–10 roughly equal increments, the actual number depending upon the number of points required on the final curves. In the example of the dogfish, for which $P_a = 10$ mmHg and $P_e = 49$ mmHg, nine points are selected in column A for computation in Table 1.

(2) The corresponding values of oxygen content of blood (C) can be read off from the experimentally determined curve of C versus p_b. These are shown in column B as the percentage saturation given in the plot of Piiper & Baumgarten-Schumann (1968).

(3) The group of constants $(\dot{Q}/\dot{V}S_w)$ can be determined by substituting actual values for P_{wi}, P_{wo}, C_a and C_e (149, 56 mmHg, 32·0 and 90·4% sat. respectively for the dogfish) in equation (9). Thus $(\dot{Q}/\dot{V}S_w) = 1{\cdot}59$ for the dogfish.

(4) The above constant can then be used in equations (7) and (8) to give values of p_w according to whether the flows are co-current (column G) or counter-current (column N) respectively, since C_a, C_e and P_{wi} are also known.

Table 1. *Typical computation for the dogfish secondary lamella*

	p_b (A)	C (B)	$C-C_a$ (D)	$P_{wi}-p_w$ (E)	p_w (G)	p_w-p_b (H)	$1/(p_w-p_b)$ (I)	F (J)	x/L (K)
Source	—	Blood	$B-32{\cdot}0$	$1{\cdot}59D$	$149-E$	$G-A$	$1/H$	Fig. 4	Fig. 3
	—	Curve	$C_a = 32{\cdot}0$	eqn. (7)	$P_{wi} = 149$	—	—	—	—
Units...	mmHg	% sat.	% sat.	mmHg	mmHg	mmHg	$(\text{mmHg})^{-1}$	0	0
Flow...			Co-current						
	10	32·0	0	0	149	139·0	0·0072	0	0
	15	48·0	16·0	25·4	123·6	108·6	0·0092	0·118	0·135
	20	61·1	29·1	46·3	102·7	82·7	0·0121	0·245	0·253
	25	70·6	38·6	61·4	87·6	62·6	0·0160	0·361	0·357
	30	77·8	45·8	72·8	76·4	46·4	0·0216	0·483	0·478
	35	82·6	50·6	80·5	68·5	33·5	0·0299	0·610	0·582
	40	86·2	54·2	86·2	62·8	22·8	0·0439	0·725	0·698
	45	88·8	56·8	90·3	58·7	13·7	0·0730	0·894	0·858
	49	90·4	58·4	92·9	56·0	7·0	0·1429	1·000	1·000
	p_b (A)	C (B)	C_e-C (L)	$P_{wi}-p_w$ (M)	p_w (N)	p_w-p_b (Q)	$1/(p_w-p_b)$ (R)	F (S)	x/L (T)
Source	—	Blood	$90{\cdot}4-B$	$1{\cdot}59L$	$149-M$	$N-A$	$1/Q$	Fig. 4	Fig. 3
	—	Curve	$C_e = 90{\cdot}4$	eqn. (8)	$P_{wi} = 149$	—	—	—	—
Units...	mmHg	% sat.	% sat.	mmHg	mmHg	mmHg	$(\text{mmHg})^{-1}$	0	0
Flow...			Counter-current						
	10	32·0	58·4	92·9	56·0	46·0	0·0217	0	0
	15	48·0	42·4	67·4	81·6	66·6	0·0150	0·204	0·215
	20	61·1	29·3	46·6	102·4	82·4	0·0121	0·395	0·389
	25	70·6	19·8	31·5	117·5	72·5	0·0108	0·553	0·531
	30	77·8	12·6	20·0	129·0	99·0	0·0101	0·677	0·653
	35	82·6	7·8	12·4	136·6	101·6	0·0098	0·802	0·775
	40	86·2	4·2	6·7	142·3	102·3	0·0098	0·890	0·853
	45	88·8	0·6	1·0	148·0	103·0	0·0097	0·959	0·931
	49	90·4	0	0	149	100·0	0·0100	1·000	1·000

(5) Since p_w is now known for each value of p_b initially selected, $1/(p_w-p_b)$ can be determined (columns I and R) and plotted against p_w (Fig. 4).

(6) The total area under each curve (Fig. 4), between P_{wo} and P_{wi}, can now be measured to give a value proportional to $(KA/\dot{V}S_w)$ for each flow regime according to equation (11).

(7) The areas under the curve bounded by the limits of p_w for each of the original intervals can be similarly measured and divided by the total area $(KA/\dot{V}S_w)$ for that particular flow regime, i.e. 172 for co-current and 121 for counter-current in Fig. 4. By adding successive fractions starting from the water inlet ($p_w = P_{wi}$), the cumulative value of F can be determined for successive steps in p_w in accordance with equation (12).

These values have been determined from Fig. 4 by use of a planimeter and are given in columns J and S for the co-current and counter-current curves respectively.

(8) The morphological data from Fig. 1 can be plotted as F versus (x/L). This is plotted in Fig. 3 for the secondary lamella of the dogfish shown in Fig. 1.

(9) Values of (x/L) can be read from this 'morphological' curve, the values of F being determined by 'functional' considerations for each value of p_w (and hence of p_b) originally selected. Thus p_w and p_b can be plotted against (x/L) for both co-current and counter-current flow regimes. Values for the dogfish are shown in columns K and T of Table 1 and plotted in Fig. 5.

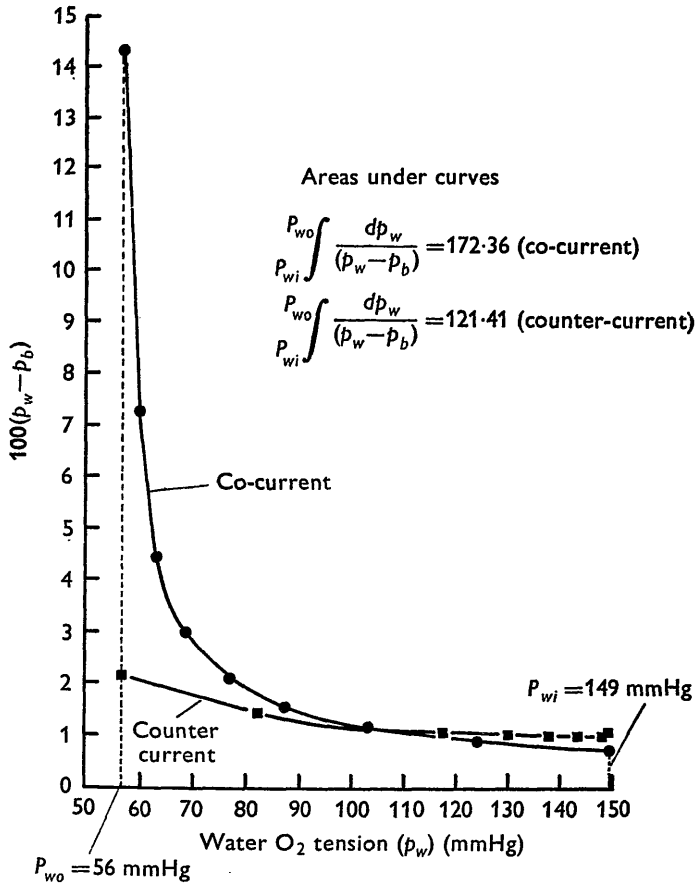

Fig. 4. Plot of $1/(p_w-p_b)$ against p_w which permits graphical integration of equation (10) (column I versus G, and R versus N in Table 1).

The effect of carbon dioxide

In the above analysis no allowance has been made for the effect of the simultaneous diffusion of carbon dioxide upon the oxygen tensions. While this is quite acceptable for the above example in view of the negligible Bohr effect in dogfish blood, it introduces a small error when the method is applied to other species.

This may be largely avoided if the carbon dioxide tensions of the blood are known at both ends of the lamella and if, for the blood of that fish, a plot of the type depicted by Rahn & Fenn (1955) is available. If such information is replotted as carbon dioxide content versus oxygen content, showing contours of equal oxygen tension and equal

carbon dioxide tension, then a straight line drawn between the two points depicting afferent and efferent conditions represents a uniform respiratory exchange ratio at all points, i.e. an R line. This assumption is also made in the Bohr integration for the alveolar capillary.

The oxygen contents used in column B of Table 1 are then those corresponding to the intercepts of the oxygen isobars with this R line rather than those determined for a single carbon dioxide tension.

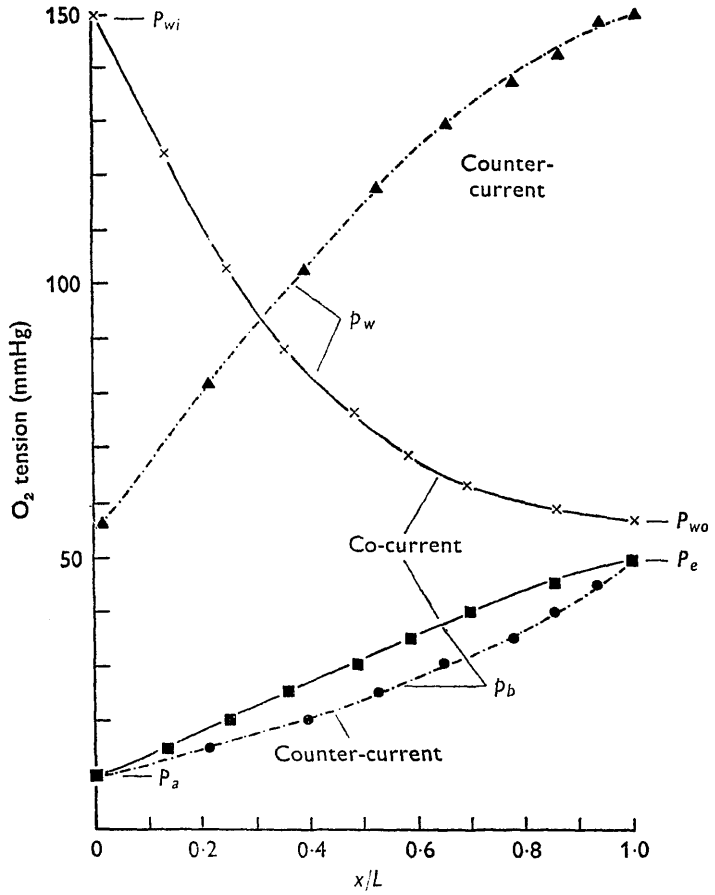

Fig. 5. Distribution of oxygen tensions in blood and water along the secondary lamella For co-current (column G versus K for water, A versus K for blood), and for counter-current, (column N versus T for water, A versus T for blood).

DISCUSSION

In order to make this more quantitative analysis it has been necessary to adopt a particular model of the secondary lamella system for the dogfish, and the model involves certain assumptions. This is particularly true with respect to the direction of water flow and blood flow, for though the general direction of the bulk flows is fairly certain, there are probably variations in the microflow of water and certainly of blood across the gills. In the dogfish the direction of water flow is less definitely known than in the teleosts. The presence of the well-developed interbranchial septum in elasmobranchs is a complicating factor, but recent studies by Kempton (1969),

and in this laboratory, certainly indicate an important component of water flow along the secondary lamella as assumed in the present model. Further evidence in favour of this direction of water flow has been obtained by pressure measurements on the shark gill septum (Grigg, 1970). The approach adopted here should be ultimately realizable for application to teleost gill systems, and in those systems where carbon dioxide markedly affects the oxygen-carrying properties of the blood it will need to be modified as indicated above.

There are also difficulties in deciding which particular values of gas tensions in water and blood are applicable to the secondary lamella profile which has been chosen. As indicated, the reasonable assumption is made that the mean values are those appropriate to certain secondary lamellae but of course we cannot be certain that it includes the one chosen as typical. Obtaining samples for the determination of mean values for the oxygen tensions in both water and blood is fraught with difficulties as there are certainly variations across the gill sieve, as has been indicated by a number of recent observations in this laboratory and elsewhere (e.g. Garey, 1967).

As indicated above, there is an element of choice in the particular profile taken, and this also ignores any curvature of the secondary lamellae, which is certainly present in some cases, e.g. tunas (Muir & Hughes, 1969). Furthermore, it may be argued that not all of the morphological area is equally effective in gas exchange. However, provided that the fraction of the area which is not effective remains uniform along the path length there would be no effect on the tension distributions (Fig. 5) because the analysis is based upon area ratios, i.e. any factor representing a decrease in effective area would cancel in equation (1).

Nevertheless, the assumptions that have been made in the model seem reasonable in the present state of our knowledge and enable some idea to be obtained of the quantitative changes in oxygen tensions of blood and water oxygen during passage of these fluids through the secondary lamella system. Only in gills such as those of the crab (*Carcinus maenas*) has it been possible to determine actual profiles of water oxygen tensions (Hughes, Knights & Scammell, 1969). The relative efficiencies of the co-current and counter-current flow systems are indicated as areas under their respective curves in Fig. 4. Thus if the outlet conditions are not defined, the surfaces required to effect the same total oxygen transfer would be proportional to the areas under these curves, which show that co-current flow is particularly inefficient at the outlet end ($x = L$) where the oxygen tensions of blood and water are close together and there is only a small diffusion gradient.

Although integrals have been employed to facilitate the exact definition of terms, the analysis used in this paper requires little mathematical operation beyond simple algebra and uses only empirical data, all of which can be obtained by experiment and measurement of the gill system. It is hoped that by the extension of this type of analysis a greater insight will be gained into the significance of differences in morphological patterns of the gills in a variety of teleost fish.

SUMMARY

1. An analysis is given which makes it possible to trace out the changes in oxygen tensions in the blood and water during their passage along a secondary lamella of the dogfish gill.

2. The analysis depends on a knowledge of the oxygen-dissociation curve of the blood, the shape of the secondary lamella and the oxygen tensions of the two media, before and after their passage through the gills. It indicates the differences to be expected according to whether the flows are co-current or counter-current.

3. The method, with modifications, could be applied to the gills of all fishes.

We wish to thank the Nuffield Foundation for their financial support.

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