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THE VOLUME OF AIR WITHIN THE SWIMBLADDER AND BREATHING CAVITIES OF THE ANABANTOID FISH *COLISA LALIA* (PERCIFORMES, BELONTIIDAE)

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Summary

The swimbladder volume and air volume within the breathing chambers of the anabantoid fish *Colisa lalia* have been measured. These data help in the understanding of some of the functions of these organs and are necessary for an analysis of their role in hearing and sound production. By means of a simple trick (based on new data) it was possible to analyse the time course of air volume changes in the breathing chambers at different temperatures. The results are well described by a simple diffusion model. The temperature-dependence of the time course suggests an interesting increase of the diffusion constant with temperature.

Under constant conditions the chambers were always filled with about the same volume of air. No excess pressure was found. Typical values of a single chamber's air content range from 34 to 58 μl. Air content increases with about the third power of fish length. By using the present data, the time course of air volume changes in the chambers of a given fish can be estimated.

Swimbladder volumes, determined using Boyle's law, ranged from 70 to 220 μl and were also found to increase with about the third power of fish length, in accordance with a simple estimation.

The data are discussed in relation to buoyancy, diffusion processes, blood circulation, hearing and sound production and suggest some interesting new work.

Introduction

The suborder *Anabantoidei* is characterized by the presence of a pair of air-filled cavities which lie above the branchial apparatus and are therefore called suprabranchial chambers. These chambers fulfil a variety of functions. First, they serve as an oxygen reservoir enabling these fishes to breathe atmospheric air – an absolute necessity in their extremely deoxygenated habitats (e.g. see Forselius, 1957). They also seem to serve as aids to buoyancy, as sound radiators (Kratochvil, 1985; Schuster, 1986) and as pressure-displacement transducers necessary for hearing (S. Schuster, in preparation).

Excellent studies concerned with anatomy of the chambers exist (e.g. Henninger, 1907; Bader, 1937; Elsen, 1976; Peters, 1978; Hughes & Munshi, 1973; see

Key words: breathing chamber, swimbladder, air volume, *Colisa*.

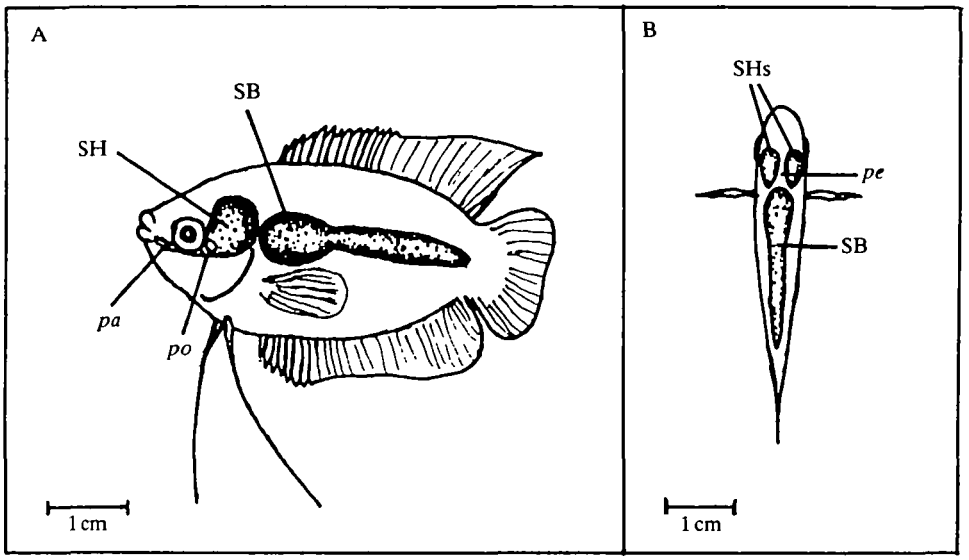

Fig. 1. Diagram showing the position of the swimbladder (SB) and the breathing cavities (SHs) in *Colisa lalia*. (A) Side view. *po*, pharyngeal opening of the breathing cavity; *pa*, pharyngeal apparatus. (B) View from above. *pe*, position of the inner ear.

Hughes *et al.* 1973 for details of the respiratory surfaces in *Anabas testudineus*). The functional studies are those of Peters (1978), who clarified the mechanism of air ventilation in anabantoids, and Hughes & Singh (1970*a*,*b*) on the respiration of *Anabas testudineus* under different environmental conditions. The only description of anabantoid swimbladders is that of Elsen (1976). The position and structure of the swimbladder and the breathing chambers in *Colisa lalia* are shown in Fig. 1.

Present attempts to estimate the sound-radiating and sound-transducing characteristics of the chambers and the swimbladder of *Colisa lalia* make knowledge of their volumes necessary. Volume measurements can also help in understanding other questions concerned with the functions of the chambers, such as the role of the swimbladder and the suprabranchial chambers in buoyancy control, diffusion processes during aerial respiration and the chambers' curious position in the anabantoid blood circulation system. Nevertheless, in these as well as in many other air-breathing fishes (see the excellent review by Johansen, 1970), no volume measurements have yet been carried out, since it is not an easy task to measure the respective air volumes independently.

Materials and methods

All measurements relate to dwarf gouramis *Colisa lalia* (Hamilton-Buchanan) obtained from local dealers.

Air volume within a suprabranchial chamber

From time to time *C. lalia* comes to the water surface to fill its breathing cavities

with fresh air, the inhalation being preceded by exhalation of exhausted air into the atmosphere. By chance, it was observed that dwarf gouramis kept in small flasks on the bottom of the tank release a large air bubble from their mouth as soon as the flask is lifted to the water surface (with its orifice still submerged). If one quickly removes the fish from the flask (the whole action taking place under water, taking care that the exhaled bubble is not sucked in again), one can conveniently measure the volume of the released bubble. But is the emptying of the suprabranchial chambers (SHs) complete?

From the extensive work of Peters (1978) on the filling mechanism of the anabantoid SH, it must be concluded that after exhaustion the chambers are almost completely water-filled before inhalation of fresh air occurs. Unfortunately, it was not possible to make X-ray films of *C. lalia* to visualize the presence of any remaining air within the water-filled chambers. Evidence against a large volume remaining arose from work on oscillation of the swimbladder of *C. lalia* (S. Schuster, in preparation). From these studies it follows that any remaining volume, if present, must be less than about 4 μl. There was no reason to assume different air volumes for the two SHs.

Measurement was as follows. One specimen was caught in a flask (which does not seem to disturb the fishes). It was then allowed to fill its breathing chambers with fresh air and a stopwatch was started. The flask was put on the bottom of the tank where the fish remained for a set time. The flask was then lifted to the water surface and the time at which bubble release occurred was noted. After the fish had been removed from the flask, the bubble was sucked into a 1 ml syringe and the contents of the syringe were weighed with a microgram balance (Bosch S 2000), taking great care that no water remained in the syringe. Before each measurement 5–10 controls were run to test the constancy of the total volume of the syringe. Using this procedure, bubble volume could be measured with an accuracy of about 0·1 μl. Assuming that both SHs have equal volumes, the SH volume (its air content) is half of the measured bubble volume.

To examine the time course of air volume changes within the SH, 131 measurements were made on five animals at four different water temperatures, with the time interval between the inhalation and exhalation as the variable. To compare measurements obtained from different fish, and at different temperatures, a set of up to 14 measurements at different time intervals was obtained for each fish in each condition. From these data, the volume V(t = 120 s) after an interval of 120 s was calculated by logarithmic regression (the values obtained closely match those obtained directly at t = 120s). All data were normalized to this volume [i.e. divided by V(t = 120 s)]. Note that the time course obtained relates to average activity, since in the flask the fish cannot undertake highly energy-consuming actions such as chasing. However, most other typical behaviour (personal observations; Forselius, 1957) was shown in the flask. All the males had foam nests in the tank. To test the effect of flask size (e.g. the effect of CO_2 accumulation), flasks of different size, with or without water exchange with the tank water, were tested, but no difference could be detected.

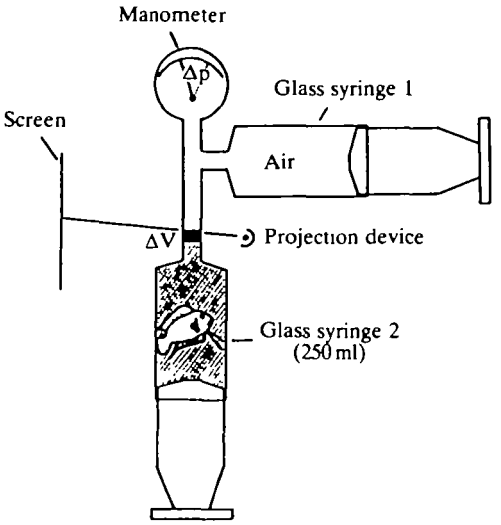

Fig. 2. Apparatus used to determine swimbladder volume. A small volume of water (ΔV) is pressed into glass syringe 2 and the resulting pressure increase Δp is read from the manometer. Volume ΔV is measured by observing the movement of the meniscus. From ΔV and Δp, swimbladder volume can be calculated.

Swimbladder volume

These measurements made use of Boyle's law – an idea successfully applied in the extensive work of Alexander (1959) – as follows. For an ideal gas:

$$pV = \text{constant}. \tag{1}$$

If a pressure alteration Δp is applied, the resulting volume alteration ΔV can be derived from:

$$(p_0 + \Delta p)(V_0 + \Delta V) = \text{constant} = p_0 V_0, \tag{2}$$

where V_0 is the gas volume at pressure p_0. By solving for V_0 one gets:

$$V_0 = -\frac{\Delta V}{\Delta p}(p_0 + \Delta p). \tag{3}$$

If there is no excess internal pressure p_e in the swimbladder, p_0 equals the hydrostatic pressure p_h; otherwise $p_0 = p_h + p_e$. From equation 3 it is possible to calculate V_0 at a swimbladder pressure p_0 by altering ΔV and measuring the necessary Δp.

The apparatus used is shown in Fig. 2. After the test fish had released air from its breathing chambers (as described above) it was put in glass syringe 2 (about 250 ml). This was filled with tank water, which had a reduced content of free air. A known volume of water (10–21 μl, as measured by means of a projection device and a microlitre syringe) was then pressed into syringe 2 and Δp read from the manometer. In these experiments, Δp ranged from 2·7 to 16 kPa – values that seemed not to affect the gouramis. Since other experiments (cited above) have

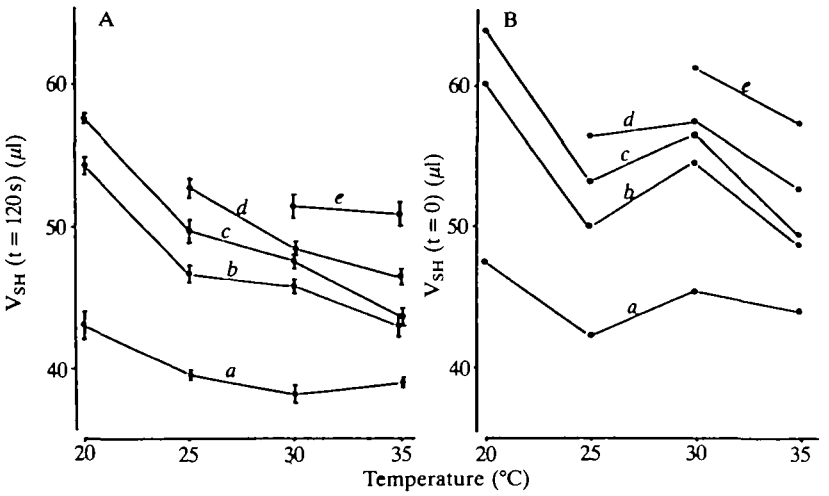

Fig. 3. Air volume within each suprabranchial chamber of five dwarf gouramis *a–e* (both sexes) at different water temperatures. (A) Mean volumes and standard errors of the means measured 120 s after inhalation. (B) Air volumes inhaled (t = 0), as estimated from the time course of changes in the chambers' air content. Data relate to the mean volumes shown in A.

confirmed that the swimbladder is the only gas-filled structure present in the test fish, the water volume pressed into the syringe equals the volume change, ΔV, of the swimbladder (assuming that only the gas can contract under the applied pressures and neglecting the higher solubility of the gas at increased pressures, which has been proved to be negligible).

Up to 15 measurements were made for each test fish, and swimbladder volume was calculated for $p_0 = 102{\cdot}41$ kPa. The standard errors of the means (S.E.M.) were between 0·3 and 1·4 %, tending to increase with decreasing swimbladder volume. 13 males and 11 females ranging from 43 to 59 mm total length were used in these measurements.

Results

Air volume within a breathing chamber

Determinations of SH volume at different times after filling, at different temperatures (from 20 to 35 °C) and for different animals gave values ranging from 34 to 58 µl. The mean values at time t = 120 s for five test fish are plotted against temperature in Fig. 3A. The data show that SH volume decreases with increasing temperature.

To understand this result one should first consider the time course of changes of air volume within each chamber. Fig. 4 shows the results of all 131 measurements at 20, 25, 30 and 35 °C for five fish of both sexes. As described in Materials and methods, values were divided by the volume at t = 120 s in order to pool the

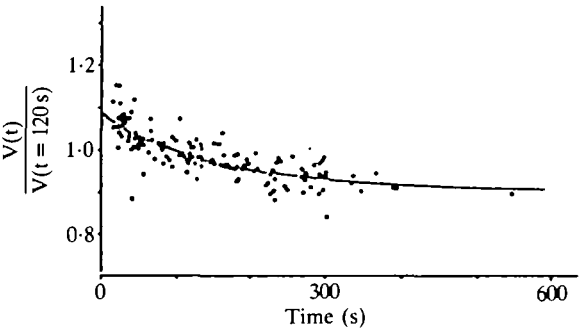

Fig. 4. Time course of air volume changes within the suprabranchial chamber. Data are pooled from 131 measurements made on five fish at four different water temperatures. A set of measurements was obtained for each fish in each condition and a mean volume after t = 120 s was determined. All the volumes in the set were divided by this value to allow comparison of data obtained at different conditions. Also shown is the graph of the function $V_n(t) = a + ke^{-\lambda t}$ with parameters a, k, λ obtained from the data by means of a least-squares method.

different sets of data. The results are plotted against the time for which the air had been present in the SH. A decrease of volume is evident, its time course being best described by a function:

$$V_n(t) = a + ke^{-\lambda t}, \tag{4}$$

where a, k, λ are constants and $V_n(t) = V(t)/V(t = 120\,s)$. The values obtained from the pooled data by means of a least-squares method were: $a = 0{\cdot}906$, $k = 0{\cdot}179$ and $\lambda = 0{\cdot}0064$.

The pooled data fitted the exponential function well, showing that the volume changes followed a similar time course in all five fish. However, measurements made at each of the four water temperatures fitted the exponential function better when taken individually. The values of the parameters are shown in Table 1. The most striking feature of these data is the enormous increase in λ between 25 °C and 30 °C, by more than a factor of 3. Parameter a seems to increase with temperature, but k did not appear to be temperature-dependent (see Table 1). From these data it is not obvious why, in Fig. 3, the SH volume decreases with increasing temperature. Fig. 3B shows the volumes of air inhaled (at t = 0) calculated from the known time course of air volume changes at the four temperatures. Gas volumes taken up at 25–35 °C did not differ significantly from each other, but were significantly smaller than those taken up at 20 °C.

With the available data it is possible to describe the time course of changes in air volume within an SH for a given fish when one precise measurement is available. The volume at any instant t is:

$$V(t) = \frac{V(t_1)}{V_n(t_1)} V_n(t). \tag{5}$$

Table 1. *Parameters of the function* $V_n(t)$

Temperature	Number of measurements	a ($\pm s_a$)*	k ($\pm s_k$)*	λ (s^{-1})
20°C	21	0·868 (±0·014)	0·236 (±0·038)	0·0050
25°C	41	0·897 (±0·020)	0·166 (±0·035)	0·0046
30°C	42	0·943 (±0·006)	0·221 (±0·020)	0·0156
35°C	27	0·963 (±0·010)	0·145 (±0·024)	0·0179

*The standard deviations of values a, k are estimated by analysing the linear problem obtained for fixed λ.

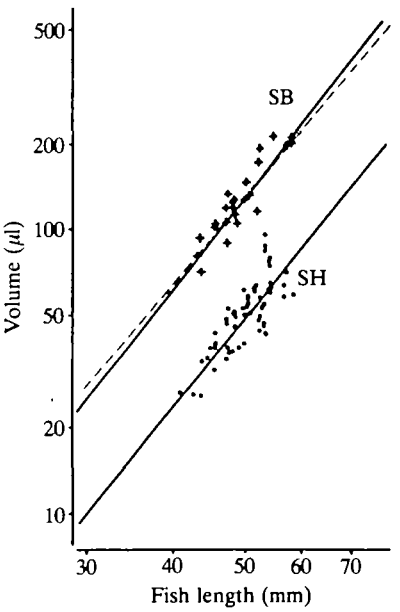

Fig. 5. Double-logarithmic plot of air volume within the swimbladder (SB) and a single suprabranchial chamber (SH) as a function of fish length. The slopes of the regression lines are both about 3 (the slope of the dashed line).

$V_n(t)$ is known for any of the four temperatures and $V(t_1)$ is the SH volume measured at a given time, t_1, for which the air has been present in the chamber.

To obtain a quick estimate of the SH volume, V_{SH}, its dependence on the total length l of the test fish was measured (Fig. 5). First, the measurements cited above were used to analyse this dependency. For both sexes, and at all temperatures, $V_{SH}(l)$ is well described by a power function $V_{SH}(l) = bl^m$. The value of m seems to

be independent of temperature and sex. Parameter b tends to be smaller at higher temperatures, but no significant trend was observed. The values of b and m, as determined with the apparatus used from measurement of swimbladder volume at 25°C, did not differ from directly measured values and could therefore be pooled with the above measurements. The pooled data ($N = 58$) yielded: $b = 2{\cdot}65 \times 10^{-4}$ and $m = 3{\cdot}10$, with a confidence interval ($\alpha = 0{\cdot}05$) of 0·55 for m.

It should be noted, that this function $V_{SH}(l) = 2{\cdot}65 \times 10^{-4} \times l^{3{\cdot}1}$ (with l in mm and V in μl) is only a rough estimate of the single SH volume at $t \approx 120$ s and at about 26°C. The exponent $m = 3{\cdot}1$ is not statistically different from $m = 3{\cdot}0$.

Swimbladder volume

Swimbladder volumes, V_{SB}, ranged from 70 to 220 μl. All volume determinations are plotted in Fig. 5 in which a double-logarithmic scale is used. The measurements of V_{SB} made with fish of different length l are well described by a power function $V_{SB}(l) = Bl^M$. Parameters, as estimated from the linear regression of log$l$ and logV, were first determined separately for males and females. Since no sexual difference was present (using a Fisher-transformation), data were pooled and the corresponding regression line is shown in Fig. 5. The values determined were: $B = 4{\cdot}4 \times 10^{-4}$ and $M = 3{\cdot}2$. The value of M is not statistically different from 3·0 and a fit of the data to $V(l) = Bl^3$ yielded (using the method of least squares) $B = 0{\cdot}0010$. The corresponding line (dashed) is also shown in Fig. 5.

In only one case were the volumes of a male's SB measured at temperatures of 20, 24 and 26°C and they were 145, 170 and 194 μl, respectively. Whether these data indicate a real tendency of SB volume to increase with temperature cannot be determined at the moment, but they are mentioned here to avoid uncritical generalization of the results.

To test the apparatus, after each measurement of SB volume, the test fish was allowed to fill its breathing cavities and then the volume measurement was immediately (within 1–2 min) repeated. These experiments yielded values which agreed well with those expected from the known air volume of both SHs.

Internal excess pressure of SB and SH

By chance it was possible, in the test just described, to determine the total volume of gas (SB + both SHs) first with the air inside the chambers, and then after the air had been exhaled (as a free gas bubble in the water). There was no difference ($P < 0{\cdot}05$, t-test) between these cases, indicating that (under the present conditions, e.g. just after refilling) there was no excess pressure inside the SHs.

Is there any excess pressure in the SB? This was investigated using the following experiment. The SB volume of a test fish was determined. The fish was then killed in the apparatus, using the anaesthetic MS 222, and the swimbladder opened. Great care was taken to prevent exchange of gas between the apparatus and the atmosphere. The only two tests made yielded equal volumes of gas whether it was inside or outside the SB. There is, therefore, no evidence for excess pressure in the SB.

Discussion

The data allow estimation of the volume of the swimbladder (SB) and breathing chamber (SH) of *Colisa lalia*, if fish length is known. The time course of changes in air volume within a SH can be predicted if the water temperature is known and one measurement of gas volume at an arbitrary time t is available. This provides the necessary background for studies of the physics of hearing in the dwarf gourami. However, it is also interesting to discuss the data in another context.

It is remarkable that the SHs are almost entirely filled with water during exhalation. Perhaps there are simply no 'dead spaces' in the SH when the fish is filling it.

The air volume inside the chamber is not under significant additional pressure – its pressure varies only about 100 Pa around the hydrostatic pressure during breathing (G. M. Hughes & H. M. Peters, unpublished results).

Another point should be considered: all SH volumes of individual fish were (of course) measured after they had inhaled fresh air. If fish did not to inhale constant air volumes, volume determinations could hardly be expected to lie on the same line when plotted against time. But this was the case in most experiments. Thus, the present data suggest that, at every breath, similar gas volumes are inhaled.

Buoyancy

A swimbladderless fish with mass m_f and density ρ_f in water of density ρ ($\rho_f > \rho$) can adjust its mean density to that of water by 'adding' an appropriate gas volume V_{gas} (mass of gas neglected):

$$V_{gas} = m_f \left(\frac{1}{\rho} - \frac{1}{\rho_f}\right) . \tag{6}$$

This shows, that a constant ratio of V_{gas}/V_{fish} is necessary for a fish to be neutrally buoyant. The ratio is $(\rho_f - \rho)/\rho$. A ratio between 0·057 and 0·083 is to be expected for freshwater fishes (Alexander, 1966).

Accordingly, the increase of $V_{SB}(l)$ and $V_{SH}(l)$ with about the third power of l is not surprising, since this is the condition for:

$$C = \frac{V_{SB}(l) + V_{2SH}(l)}{V_{fish}(l)}, \tag{7}$$

where C is the above constant (independent of fish length l). Let $V_{fish} = fl^3$, $V_{SB}(l) = b_1 l^3$ and $V_{2SH}(l) = b_2 l^3$, then C becomes $C = (b_1 + b_2)/f$. Parameter b_1 seems to be constant (apart from a moderate effect of temperature), whereas parameter b_2 depends strongly on time and temperature. The gas volume within the SHs becomes smaller with time, and decreases more rapidly at higher temperatures. Does buoyancy set the limits for refilling the chambers to readjust the value of b_2 appropriately?

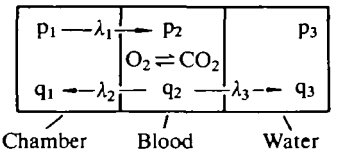

Fig. 6. Diagram used to analyse the time course of air within a breathing chamber. p denotes the P_{O_2} values in the compartments, q denotes the P_{CO_2} values. λ_1, λ_2, diffusion coefficients.

Decreasing air volume within the breathing chambers has another consequence. Any decrease in SH volume (with SB volume being constant) will displace the centre of air volume caudally, whereas the centre of mass of the fish's body does not change. Thus, a torque is acting on the fish until buoyancy and gravitational force lie on the same vertical line. In this equilibrium position the fish's length axis is inclined by an angle ϕ relative to its normal position (the head always being in an upward position). If one assumes that the centre of SH volume and the centre of SB volume are constant and denotes their distance apart as c, one obtains:

$$\phi(t) = \arctan\left[\frac{V_2}{(V_2 + V_1)^2}\frac{c}{d}\Delta V(t)\right], \tag{8}$$

where d is the vertical distance between the centre of the fish mass and the line through the centres of volume of the swimbladder and breathing chambers, V_1 is the volume of both SHs at $t = 0$, V_2 is SB volume (assumed to be constant) and $\Delta V(t)$ is $V_1 - V(t)$ with $V(t)$ equal to the volume of both SHs at t. The angle ϕ of resting fish with water-filled breathing chambers ($\Delta V = V_1$) was observed to be about 50–60°, and thus parameter d could be estimated. Since c is known from anatomy and the volumes involved are known from the present work, it is possible to calculate $\phi(t)$ for a given fish. Such calculations show that, just before refilling of the chambers, angles of about 4° would be expected, if there were no compensation. To keep their normal position, gouramis may either move swimbladder gas rostrally or periodically have to do work $W = k\rho g\Delta V\,\phi$ (where k is the horizontal distance between the centre of volume of the SHs and centre of mass of the fish).

Time course of changes in SH volume

Let us first consider the time course of changes in the volume of inhaled air within the SH. The situation is described by the model shown in Fig. 6, with the partial pressures $p_i = P_{O_2}$, $q_i = P_{CO_2}$ and the diffusion constants λ_j for different gases and membranes. To get the time course of changes in p_1 one simply has to solve a set of coupled differential equations. The solution is easy if one assumes p_3 to be about zero, p_2 and q_3 to be constant and describes the equilibrium between O_2 and CO_2 by constants γ_1 and γ_2. This treatment is not given here, since the

results of Hughes & Singh (1970*a*), showing that nearly all the CO_2 in the blood diffuses into the water *via* the gills, justify the simple statement:

$$\frac{dp_1}{dt} = -\lambda_1 (p_1 - p_2), \tag{9}$$

and with $p_0 = p_1$ ($t = 0$) one gets:

$$p_1 - p_2 = (p_0 - p_2)e^{-\lambda_1 t}, \tag{10}$$

and thus the time course of changes in P_{O_2} in the chamber is:

$$p_1(t) = (p_0 - p_2)e^{-\lambda_1 t} + p_2, \tag{11}$$

where p_2 (P_{O_2} in the blood) is assumed to be constant, i.e. all oxygen diffusing into the blood is immediately bound to haemoglobin. Since it is volumes that are to be calculated, all partial pressures used are treated as dimensionless values (divided by their unit). Thus, in a volume V_0 at $p_0 = 1$ atmosphere ($\approx$101 kPa), the volume of each kind of gas is obtained by multiplication of its dimensionless partial pressure by V_0. Using this convention, the volume of gas within the breathing chamber is simply derived. With V_0 = volume of air within the chamber at $t = 0$, V_{N_2} = volume of N_2, $V_1(t)$ = volume of O_2, p_N = dimensionless P_{N_2} (0·79), $p_1(t)$ = dimensionless P_{O_2}, it follows that:

$$\begin{aligned} V(t) &= V_{N_2} + V_1(t) \\ &= V_0 p_N + V_0 p_1(t) \\ &= V_0 (p_N + p_2) + V_0 (p_0 - p_2)e^{-\lambda_1 t}. \end{aligned} \tag{12}$$

$V(t)$ thus has the form $V(t) = a + ke^{-\lambda t}$, with the following properties:

$$V_0 = a + k, \tag{13}$$

$$p_2 = (0{\cdot}21a - 0{\cdot}79k)/(a + k). \tag{14}$$

Estimates of the mean values of P_{O_2} in the blood which passes the first two gills and runs to the respiratory epithelia yield values of about 0–8000 Pa at different temperatures. These values appear to increase with temperature. From the 131 pooled data pairs in this study, mean P_{O_2} was estimated to be about 5000 Pa. No attempt was made to analyse directly the accuracy of this value.

Blood supply of the breathing chambers

In the light of the present data, it is interesting to look at blood circulation in anabantoids as described by Henninger (1907) and Bader (1937) (Fig. 7). No attempts have yet been made to understand this curious circulatory system from a functional point of view. Especially interesting is the function of the first two gills (the larger ones). Perhaps their main function is to keep the level of CO_2 in the breathing chambers low. Indeed, Hughes & Singh (1970*a*) showed, for *Anabas*, that CO_2 is effectively released through the gills. If there were no such protection, P_{CO_2} in the chambers would rise until no more CO_2 could be released from the blood running through the respiratory epithelia and thus O_2 uptake would decline

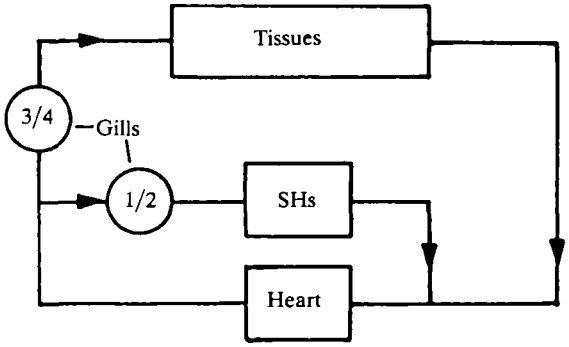

Fig. 7. The blood circulation of anabantoids. SHs are the suprabranchial chambers and 1/2, 3/4 denotes the first two and the third and fourth gills, respectively. The direction of blood flow is also indicated.

to the value of physically soluble oxygen. Release of CO_2 through the gills could also be achieved if the first two gills lay in series with the third and fourth ones before the branch to the SH. Is there any advantage to the first two gills being *in series* with the SH? Future studies should be designed to clarify any 'co-operation' between these organs. A careful observation of any differences between the gill pairs is important.

Considering the third and fourth gills, it is interesting to note that, with diffusion properties comparable to the first two gills, the P_{O_2} of blood running to the tissues would be about 5000 Pa (≈38 mmHg). At such values fish blood would be nearly saturated with oxygen (e.g. see Randall, 1970). Thus the gills effectively release CO_2 into the water without losing too much O_2. How this is done is unclear. Perhaps the data of Hughes & Munshi (1973), who showed that the blood–water distance in the gills of *Anabas testudineus* is up to a factor of 3 larger than values commonly found in other fishes, are connected with such a balance between the necessity for release of CO_2 and the avoidance of O_2 wastage. However, this system is far from being understood.

Temperature-dependence

The diffusion properties of the SH surface vary with temperature. The constant λ, which is proportional to diffusional area and mean thickness of the membranes, increases maximally between 25 and 30°C. The sigmoid shape of the curve relating λ to temperature (Fig. 8) seems to reflect the properties of the membranes involved. This interesting property should be analysed in detail.

With the known temperature-dependence of $V_{SH}(t)$ it should be possible to interpret measurements on surfacing frequency of the dwarf gouramis as a function of temperature. This interpretation could also shed light on the factor(s) involved in refilling the chambers. Consider the normalized $V_n(t)$ (as shown in Fig. 4) at different temperatures. If one assumes that a decrease of V_n to a certain threshold value $V(t_1)/V(0)$ is the releasing 'factor' (P_{O_2} or problems with

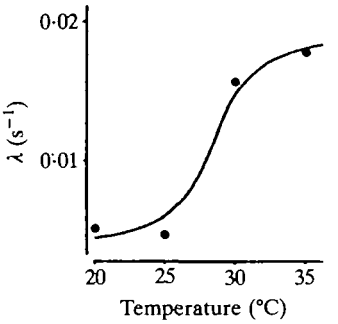

Fig. 8. Temperature-dependency of the diffusion parameter λ. This parameter may be interpreted as a transfer factor relating O_2 flow from chamber to blood to the P_{O_2} gradient across the respiratory epithelium.

buoyancy may be correlated with this decrease) for refilling the chambers, then it should be possible to calculate, for controlled conditions (e.g. P_{O_2} in water near saturation), the time after which refilling should occur. Using the functions already obtained, the condition $V(t_1)/V(0) = c'$ is expressed by the condition $V(t_1)/V(120\,s) = c$ where c is the factor by which the volume at t_1 is different from the volume at $t = 120\,s$. The time would then lie near:

$$t_1 = -\frac{1}{\lambda} \ln \left(\frac{c - a}{k} \right) , \tag{15}$$

where a, k and λ are the constants describing $V_n(t)$.

Implications for hearing and sound production

Since hearing and sound production will be discussed in further accounts concerned with oscillation of the sound-driven swimbladder and the air within the chambers, only a few comments are made here.

Assuming that these structures behave like free gas bubbles in water, one would expect the swimbladder's natural frequency (given in Hz as a function of fish length, l, in mm) to be:

$$f_0 = \mu b^{-1/3} l^{-1} , \tag{16}$$

with the theoretical value of $\mu = 5295{\cdot}4$ and $b = 0{\cdot}0010$ (see Results). Then:

$$f_0 \text{ (in Hz)} = 5{\cdot}2 \times 10^4 / l \text{ (in mm)} . \tag{17}$$

For an adult 60 mm male f_0 would be about 900 Hz. The value of f_0 for one filling of the SH can be derived from a similar calculation. It would be about 1200 Hz for such a male with a freshly filled chamber, but would increase with time. This increase can be calculated and a factor $1{\cdot}06 f_0$ ($t = 0$) for a maximal diving time of 600 s can be obtained.

Since the SHs are the resonators implied in sound production (Kratochvil, 1985) and are also necessary as pressure-displacement transducers in hearing, different

volumes of air in the chambers of communicating fish, and variation of these volumes with time, could be a problem. The implications of these variations for the acoustic communication of dwarf gouramis will be treated in a separate account.

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