

THE PHYSICAL PROPERTIES OF THE SWIMBLADDER IN INTACT CYPRINIFORMES

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INTRODUCTION

The functions of the swimbladder make its physical properties important.

In the first place, to be hydrostatically adequate, the volume of the swimbladder must be such that the specific gravity of the fish is equal to that of its medium.

Further, it is desirable for a fish that the rate at which its buoyancy changes with pressure as it moves away from the depth at which it has neutral buoyancy should be as small as possible. The less the rate of change of buoyancy with depth, the less the effort which the fish must exert to maintain its station at a given distance from the equilibrium depth. Since the secretion and resorption of gas are slow processes, and the 'Gasspuckreflex'† of physostomes is irreversible except at the surface, restriction of the rate of change of buoyancy with depth by mechanical means will be useful. Such restriction could be achieved for depths less than the equilibrium depth by the possession of a highly inextensible swimbladder wall. This would confer no advantage at greater depths unless it was also rigid. The ossified swimbladder of the fossil *Coelacanthi* (see Williamson, 1849; Woodward, 1909) was presumably fairly rigid, but no comparable structure is known in modern fish (the swimbladder of *Latimeria*, if it exists at all, is rudimentary and unossified (Millot, 1954)). A swimbladder with a wall of limited extensibility, and with an internal pressure which, at the equilibrium depth, exceeded the external pressure would, however, change its volume with depth less markedly than a bubble of free air, at greater as well as at lesser depths. This point will be demonstrated later in the derivation of equation (5), which is applicable equally to small increases and to small decreases of pressure.

Where a sensory function has to be considered, inextensibility will reduce sensitivity, and a compromise must be reached with the requirements of the hydrostatic function. The operation of the Weberian ossicles will require a certain tautness in the swimbladder wall, such as might be obtained by the maintenance of excess pressure in the swimbladder. In this case sensory and hydrostatic requirements coincide, though an unnecessarily high pressure would reduce sensory sensitivity.

Evans & Damant (1928), using a hypodermic needle attached to a manometer, found that the roach maintains an excess pressure averaging 6 cm. Hg in its swim-

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† This term, literally 'gas-spitting reflex', is used by German authors and by Fänge (1953) to denote the release of gas through the pneumatic duct.

bladder. Franz (1937) claimed to find a slightly larger pressure in the minnow. Apparently the excess pressure discussed hypothetically in the above paragraphs does in fact occur in at least some Cypriniformes.

This paper is concerned with a method whereby the physical properties whose importance has been shown above have been determined for the swimbladders of a variety of Cypriniformes. These properties are volume, excess internal pressure, extensibility and rate of change of swimbladder volume with external pressure; this last property is expressed by a quantity which I call relative sensitivity.

DEFINITIONS

The quantities by which the physical properties of the swimbladder are expressed require a definition. They are listed below.

(1) The *percentage volume* of the swimbladder is the ratio between the volume of the swimbladder gas in millilitres at the depth to which the fish is adapted and the weight of the fish in grammes, expressed as a percentage. For reasons of convenience I follow Evans & Damant (1928) and Black (1948) in using the weight rather than the volume of the fish. My values must be multiplied by the specific gravity of the fish to obtain values exactly comparable with those of Akita (1936), Plattner (1941) and Jones (1951) who compare the volume of the swimbladder to that of the fish. The difference is in any case small.

(2) The *relative sensitivity* of the swimbladder is the ratio of the amount by which its volume changes when the external pressure is increased by a small amount from that to which the fish is adapted, to the amount by which the initially equal volume of a free bubble of air changes when exposed to the same increase of pressure. It has been found convenient to use pressure increases of 2 cm. Hg.

(3) The *excess internal pressure* of a swimbladder is the amount by which the pressure of the gases in the swimbladder exceeds that of the water surrounding the fish, at the depth to which the fish is adapted. The term 'excess pressure' is less rigidly used; it refers to the amount by which the pressure of the gases in the swimbladder exceeds that of the water surrounding the fish under the conditions stated in the context.

(4) The *extensibility* of a swimbladder is its increase in volume per cm. Hg increase in excess pressure, given as a percentage of the volume at 2 cm. Hg excess pressure. As it often varies with excess pressure, the excess pressure or range of excess pressures for which it is determined should be stated. Its value at the excess internal pressure is the *effective extensibility*.

MATERIAL

Experiments on the following species will be reported in this paper:

Cyprinoidei: <i>Leuciscus leuciscus</i> (L.)	Dace
<i>Rutilus rutilus</i> (L.)	Roach
<i>Scardinius erythrophthalmus</i> (L.)	Rudd
<i>Phoxinus phoxinus</i> (L.)	Minnow

Cyprinoidei:	<i>Tinca tinca</i> (L.)	Tench
	<i>Gobio gobio</i> (L.)	Gudgeon
	<i>Abramis brama</i> (L.)	Bream
	<i>Alburnus alburnus</i> (L.)	Bleak
	<i>Cyprinus carpio</i> L.	Carp
	<i>Carassius carassius</i> (L.)	Crucian carp
	<i>C. auratus</i> (L.)	Goldfish
Siluroidei:	<i>Amiurus nebulosus</i> (Lesueur)	

METHOD

Since the effective physical properties of the swimbladder may be affected by muscular tonus and the stiffness of the body wall, it is desirable that they should as far as possible be determined on intact living fish. The measurements were therefore made on intact, unoperated fish in a state of light anaesthesia.

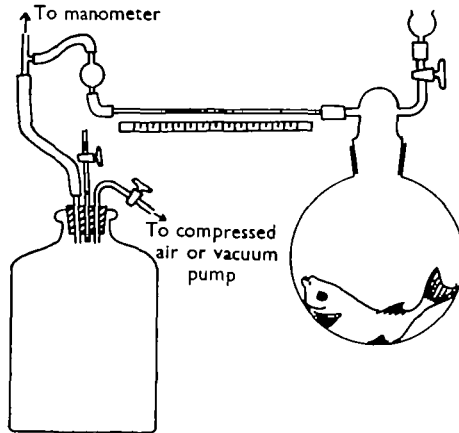


Fig. 1. The apparatus.

Principle

A fish is subjected to changes of pressure. The corresponding changes in the volume of its swimbladder gases are determined: (1) In the swimbladder in the intact fish; (2) when the restraining influence of the swimbladder wall has been eliminated.

From the results it is possible to calculate the volume, relative sensitivity, excess internal pressure and extensibility of the swimbladder.

Apparatus

The apparatus is shown in Fig. 1. All the rubber tubing indicated is pressure tubing, and this was made fast by wiring wherever this seemed advisable. A spring-loaded canvas sling was used to retain the dome on the flask at high pressures, and the joint was only very slightly greased to ensure a firm grip. The bulb between the

capillary and the manometer eliminates the possibility of water being sucked back into the manometer at reduced pressures.

This apparatus was constructed in three sizes, whose dimensions are given in Table 1.

Table 1. *Dimensions of the apparatus*

Reference letter ...	Q	q	qq
Capacity of flask (ml.)*	5000	250	100
Neck size of flask*	B 55	B 34	B 24
Capacity of capillary (ml./cm.)†	0.078	0.0270 and 0.0224	0.00414
Weights of fish suitable (g.)	50-120	15-40	2-15

* Manufacturer's specifications (Quickfit and Quartz Ltd.).

† Determined by weighing the water which fills a measured length of capillary.

The domes of the q and qq apparatus were fitted on their sides with knobs for convenience in handling.

The flask was filled with an aqueous solution containing about 0.3% urethane. The exact concentration used depended on the species of fish under investigation. To avoid bubble formation at low pressures the solution was made up with water of reduced air content: water taken from a geyser at about 55° C. and allowed to cool to room temperature in a brim-full flask covered with a Petri dish was found suitable.

A solution of about 0.7% urethane was used as the initial anaesthetic.

Experimental method

Part I. The fish was kept for at least 24 hr. for adaptation before use in an aquarium containing water to a depth of 28 cm. It was moved directly from this to the stronger anaesthetic solution, in which it was kept for 10-20 min. until spontaneous swimming movements had ceased, but respiratory movements remained normal. This degree of anaesthesia persisted in the more dilute urethane in the apparatus, and was necessary to prevent the fish from swimming up and down in the flask, thus altering the pressure on its swimbladder, and to discourage the 'Gasspuckreflex', which can be released by fright. If the fish released bubbles in the anaesthetic it was returned to the aquarium for at least 24 hr. for re-equilibration.

The anaesthetized fish was put into the urethane solution in the flask. Its mouth was there inspected, and any bubbles of air in it removed. The dome was replaced firmly, and the spring-loaded sling attached. The funnel was used to fill the flask completely with the dilute urethane solution, excluding all bubbles of air. The flask was then attached to the rest of the apparatus and the funnel used to pass solution in until it extended along the capillary to form a meniscus at a convenient position. The rubber tubing connecting the flask to the capillary was wired to prevent leakage. It is very important that the apparatus should include no air bubbles in the flask or behind the meniscus.

The fish usually sank to the bottom of the flask. In this position in the Q, q or qq apparatus it would be 28, 15 or 10 cm., respectively, below the level of the capillary. When the manometer read zero it was thus at a pressure about 0, 1 or 1.5 cm. Hg less than that occurring at the bottom of the aquarium. This information will be used in determining the excess internal pressure of the swimbladder, the bottom of the aquarium being taken, for convenience, as the depth to which the fish was adapted. It was not thought advisable to define the depth to which it was adapted more precisely by using a shallower aquarium or a horizontally divided one, as such conditions would minimize the importance of buoyancy adjustment, which might well fail to occur (see Meesters & Nagel, 1934; Copeland, 1952).

Occasionally, mainly in work at reduced pressures, the fish floated. As the pressure at the top of the flask is lower than at the bottom it was necessary to subtract this difference from the manometer readings for the pressures at which the fish floated.

The pressure was then increased by stages to +24 cm. Hg* (manometer reading), and the position of the meniscus was observed at each pressure. It receded due to compression of the swimbladder and distortion of the apparatus. (The latter was determined in blank experiments, found to be very nearly constant for each apparatus, and corrected for.) The tap to the atmosphere was then opened to release the pressure and the fish was left for 15–20 min. for recovery before repetition of the measurements, or measurements at reduced pressure. In general, measurements were repeatable provided that such an interval was allowed between runs. The interval was apparently made necessary by a small 'slow elastic' effect in the swimbladder wall. Occasionally, marked differences were found between readings. When the displacement of the meniscus on increasing the applied pressure from 0 to 24 cm. Hg differed in two sets of readings by more than 0.5 cm., a significant change was deemed to have occurred and only the first set of readings was used. In other cases means were taken. This phase of the experiment was abandoned immediately if any gas bubbles were released by the fish.

Part II. The pressure was reduced strongly (usually to 36 cm. Hg below atmospheric) to extract a quantity of gas from the swimbladder. This process is of course only effective with physostomes, for which alone this technique is designed. The gas passed to the dome of the flask and atmospheric pressure was restored. Determinations of meniscus position were then made at the same pressures as before. Successive sets of readings could now be made without any interval and were found to agree well with one another. If sufficient gas had been extracted, the wall of the swimbladder would now be slack and the swimbladder gas, whether in the swimbladder or in the dome, would be unconstrained by it. To ensure that this was the case a stronger reduction of pressure (usually to 46 cm. Hg below atmospheric) was applied to extract more gas, and the measurements were repeated. This check was made over a range of pressures including the lowest used for previous readings, since it is at the lowest external pressures that the swimbladder wall is most likely to be taut. If the new measurements agreed with the previous series, the gas had

* +18 cm. Hg in the first few experiments.

clearly been unconstrained in both cases. The volume of the gas would then, by Boyle's Law, be inversely proportional to the external pressure.

The animal was then taken out of the apparatus, killed, dried with a towel and weighed. The experiment was finished.

The bubbles released at decompression are not retained at the same depth as the fish, but rise into the dome. In the largest (Q) apparatus they will there always be subjected to a pressure about 2 cm. Hg less than that on the fish. Hence when the total pressure on the fish changes from 78 to $(78 + \Delta P)$ cm. Hg (i.e. by $100\Delta P/78\%$) the total pressure on these bubbles will change from 76 to $(76 + \Delta P)$ cm. Hg (i.e. by $100\Delta P/76\%$). The latter percentage pressure change is $100(78/76 - 1)$ or about 2.6% larger than the former. The bubbles released on decompression to -36 cm. Hg probably did not exceed one-third of the swimbladder gas. The displacements observed would differ by less than 1% from those to be expected if all the gas had remained at the level of the fish. The error would be correspondingly less in the smaller apparatus.

The meniscus position is necessarily very sensitive to temperature change. A change of 0.1° C. in the temperature of the liquid contents of the largest flask would move the meniscus about 1 cm. Temperature fluctuations were found, however, to be slow. The meniscus might move appreciably in the 20 min. intervals between sets of readings, but the movement was too slow to be significant in the 2 min. period required to take a set of readings. The small thermal capacity of the smallest (qq) flask, containing only about 100 ml. of solution, made it undesirable to leave water to evaporate from its surface, or to handle it more than necessary.

Method of calculation

The differences between the meniscus positions for +18 cm. Hg and +24 cm. Hg in Parts I and II of the experiment were found to be identical or nearly so in most cases (except in the case of the bream). Thus the swimbladder wall was slack over this range of pressures even before decompression and removal of gas. This being so, the +24 cm. Hg readings of Parts I and II represented identical gas volumes, and it was possible to use them as points of reference for superposition of the curves of volume change (shown as meniscus displacement) as is done in Fig. 2. The meniscus positions representing these identical volumes were not in fact often identical, owing to temperature changes, retention of drops of water in the bulb after decompression, and the slight expansion of released bubbles as they rose to the dome.

The information required can be obtained from these curves as described below.

(1) *Percentage volume.* The volumetric capacity of the capillary had been determined. The extent of the volume changes occurring in the course of the experiment was, therefore, known. From those occurring in Part II it was possible to calculate the volume of gas present at, for instance, manometer zero by applying Boyle's Law. The volume of the gas in the swimbladder in Part I was less than this by the volume represented by the difference between the intercepts of the two curves on the displacement axis (see Fig. 2). Since the fish had been weighed, the percentage volume of the swimbladder could be calculated.

(2) *Relative sensitivity.* The displacements of the meniscus on increasing the pressure from manometer zero to +2 cm. Hg in parts I and II are known. As the volume of the gas at manometer zero is slightly greater in Part II than in Part I, the ratio of displacements must be multiplied by this ratio of volumes to obtain the relative sensitivity.

(3) *Excess internal pressure.* The total pressure in the swimbladder when a given pressure is applied to the fish in Part I is equal to the total pressure required in Part II to adjust the volume of the swimbladder gas to the same value. It is thus possible to read off the excess pressure of the swimbladder at any point on the Part I curve as the difference between the abscissae of the two curves at the relevant ordinate. That corresponding to the pressure at the bottom of the aquarium was the excess internal pressure.

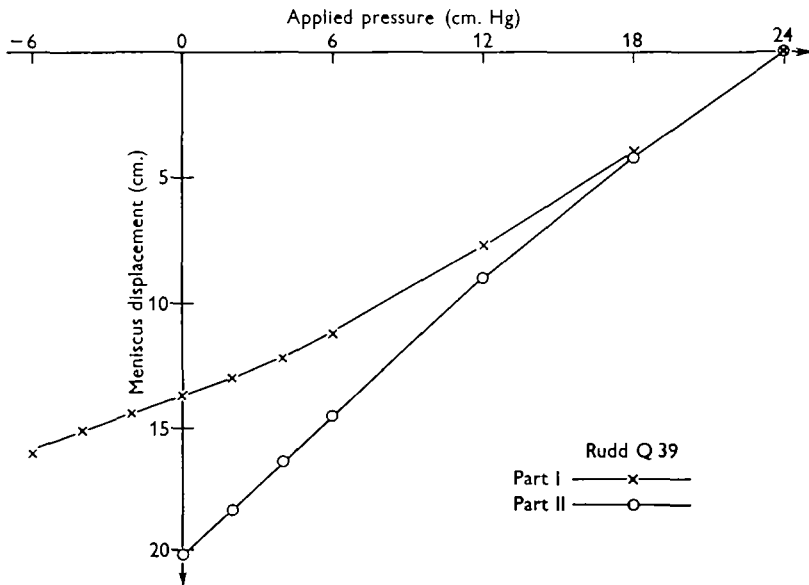


Fig. 2. Graphs of corrected meniscus displacement against applied pressure (in cm. Hg above manometer zero) for parts I and II of the experiment on the rudd Q 39.

The identity of the excess internal pressures in the two sacs of cyprinoid swimbladders is assumed. The following evidence supports this assumption:

(i) Evans & Damant (1928) found a pressure difference greater than 1 cm. Hg between the two sacs of only four roach out of seventeen. Their measurements appear, for the most part, to have been made to the nearest cm. Hg.

(ii) In another series of experiments, involving a variety of cyprinoid species, the sphincter between the two sacs of dead fish was never found to be closed except after removal of the tunica externa. In this operation the tunica externa was pulled round the sphincter and may have constricted it.

On the other hand, Wittenberg (1958) states, without giving evidence, that the ductus communicans of the goldfish is open only during secretion.

(4) *Extensibility.* From the various volumes of the swimbladder in Part I and from the corresponding excess pressures in it a curve of swimbladder extension against excess pressure can be constructed, as is done in Fig. 3 for the four rudd examined. As the volume of a swimbladder at zero excess pressure is indeterminate, and the volume at which its wall just becomes taut is not accurately determinable on account of the high extensibility found at low pressures (see later), the extension is calculated as the percentage difference from the volume with 2 cm. Hg excess pressure.

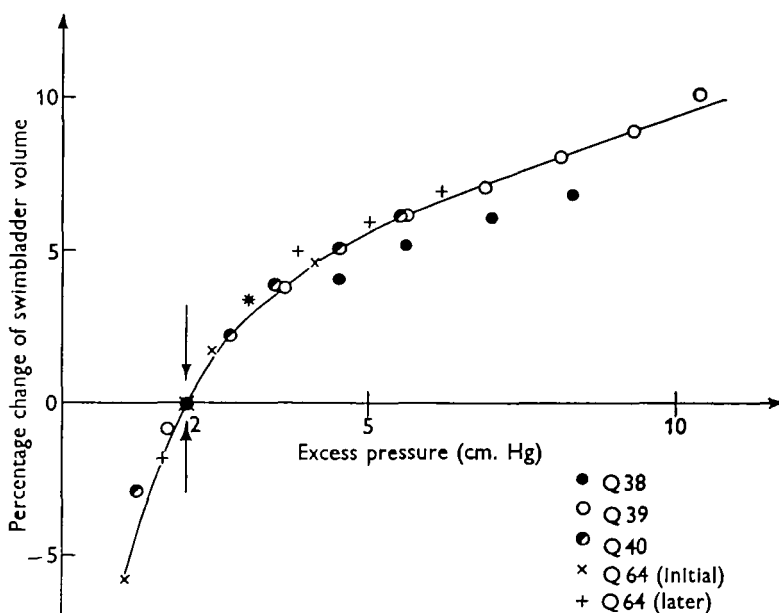


Fig. 3. Extension plotted against excess pressure for the swimbladders of the four rudd examined.

The bream swimbladder normally has a higher excess internal pressure than is found in other species. The differences between the meniscus positions at +18 cm. Hg and +24 cm. Hg in Parts I and II were not for it identical. This means that the swimbladder wall is not slack at +18 cm. Hg applied pressure. As it is in general slack at this pressure in all other species examined, it seems reasonable to assume that it will be slack by +24 cm. Hg in the bream, and as the apparatus was not suitable for work at higher pressures the values for +24 cm. Hg were superimposed as in other species. It remains possible that the values for excess pressure in the bream may be slightly too low.

RESULTS

The results of these experiments are given for individual fish in Appendix 2. They are summarized and compared with the data of previous workers below.

(1) *Percentage volume.* There is considerable variation of swimbladder volume within each species, but the variation between species is larger. There is a clear

Physical properties of the swimbladder in intact Cypriniformes 323

distinction, for instance, between the small swimbladders of carp (5.0–6.5%), the medium ones of bream (7.0–8.2%) and the large ones of roach (8.8–10.4%).

Mean values for each species, with those of previous authors, are given in Table 2.

Table 2. *Percentage volumes of the swimbladders of Cypriniformes*

Species	Mean % volume	Previous values
Roach	9.9	9.74* (Plattner, 1941) 9.1 (Evans & Damant, 1928)
Rudd	8.9	10.61 (Plattner, 1941)
Dace	8.0	—
Minnow	6.1	6.6† (calculated from data in Franz, 1937)
Tench	7.0	7.74 (Plattner, 1941)
Bream	7.6	—
Bleak	6.7	—
Carp	5.8	—
Goldfish	7.9	8.25 (Plattner, 1941)
Crucian carp	8.0	—
Gudgeon	6.2	—
<i>Amiurus</i>	5.8	—

* Plattner calculated his mean incorrectly. The correct value is given here.

† A highly aberrant value of 9.2% is neglected.

Table 3. *Relative sensitivities of the swimbladders of Cypriniformes*

Species	Mean relative sensitivity	Species	Mean relative sensitivity
Roach	0.41	Bleak	0.64
Rudd	0.44	Carp	0.72
Dace	0.65	Goldfish	0.66
Minnow	0.79	Crucian carp	0.57
Tench	0.50	Gudgeon	0.73
Bream	0.23	<i>Amiurus</i>	0.87

The results agree reasonably well with those of previous authors, except in the case of the rudd. It should be noted that, whereas my values are for the swimbladder gas only, Plattner's values for cyprinoids include the swimbladder wall.

(2) *Relative sensitivity*. Considerable variation within each species is again exceeded by variation between species. The values of 0.18–0.26 for the bream contrast strongly with those of 0.63–0.93 for the carp.

The mean values found for each species are given in Table 3.

(3) *Excess internal pressure*. A much lower pressure is found in *Amiurus* than in any of the Cyprinidae examined. Within the Cyprinidae themselves there is a wide range of variation between the extremes of the gudgeon (1.6–2.9 cm. Hg) and the bream (8.9–14.6). Most of them have mean excess internal pressures between 2.0 and 3.1 cm. Hg; only the roach, rudd and bream lie outside this range, all with much higher pressures.

The mean values are given in Table 4 with those of previous authors.

(4) *Extensibility*. Extension is plotted against excess pressure for the four rudd which were examined in Fig. 3. It will be seen that there is good agreement between the individuals of the species. This is also true of the other species examined.

Table 4. *Excess internal pressures of the swimbladders of Cypriniformes*

Species	Mean excess internal pressure (cm. Hg)	Previous values		
		Anterior sac	Posterior sac	Authors
Roach	7.0	5.9	6.2	Evans & Damant (1928)
Rudd	6.1	—	—	—
Dace	2.7	—	—	—
Minnow	2.6	7.8*	6.8*	Franz (1937)
Tench	2.9	—	—	—
Bream	10.8	—	—	—
Bleak	3.1	—	—	—
Carp	2.6	—	—	—
Goldfish	2.4	—	—	—
Crucian carp	3.0	—	—	—
Gudgeon	2.1	—	—	—
<i>Amiurus</i>	0.6	—	—	—

* The serious discrepancy between Franz's values and mine is discussed in Appendix 1.

The effective extensibilities of these species, being the gradients of these curves at the relevant mean excess internal pressures, are given in Table 5. There are no comparable data in the literature. No value was obtained for *Amiurus*, whose excess pressure was less than 2.0 cm. Hg at the lowest pressures at which readings were taken.

Table 5. *The effective extensibilities of the swimbladders of Cypriniformes*

Species	Effective extensibility (%/cm. Hg)	Species	Effective extensibility (%/cm. Hg)
Roach	1.0	Bleak	2.7
Rudd	0.9	Carp	3.5
Dace	3.9	Goldfish	3.3
Minnow	4.1	Crucian carp	1.2
Tench	1.1	Gudgeon	4.7
Bream	0.4		

In Figs. 4-6 extensibility—the gradient of the extension curve—is plotted against excess pressure. The extensibilities of the swimbladders of roach, rudd, tench, goldfish, crucian carp and possibly minnow and gudgeon agree in falling from a high level to a steady one of about 1%/cm. Hg as the pressure rises. This fall is completed at 3-6 cm. Hg excess pressure. The bream swimbladder is less extensible than the others throughout, while the extensibilities of dace and carp are asymptotic to values of about 2.5%/cm. Hg, and of bleak to just under 2%/cm. Hg.

The excess internal pressure is extremely important in determining the effective extensibility. Thus the goldfish and the rudd have closely similar curves of extensibility against excess pressure, but while the former has an excess internal pressure of 2.4 cm. Hg and an effective extensibility of 3.3%/cm. Hg, the latter has 6.1 and 0.9.

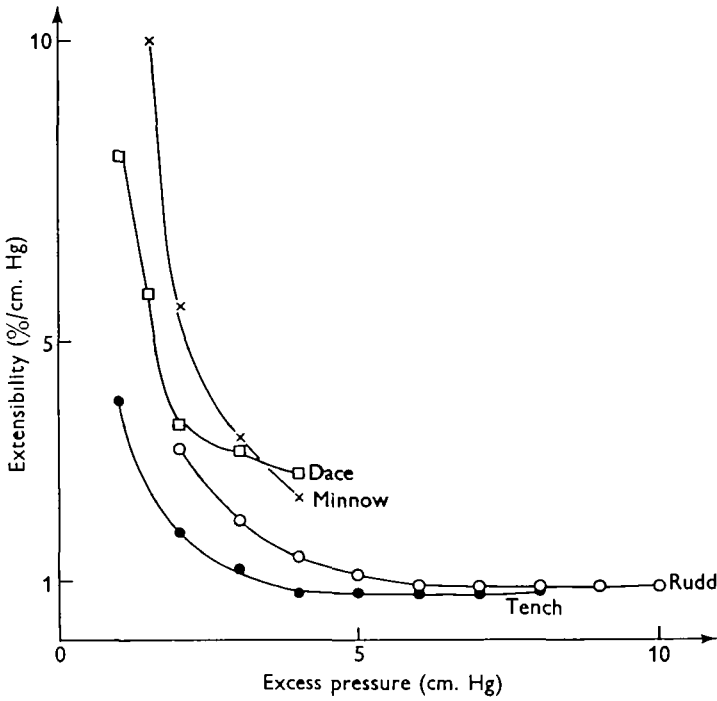


Fig. 4. The relation between extensibility and excess pressure for the swimbladders of dace, minnow, tench and rudd.

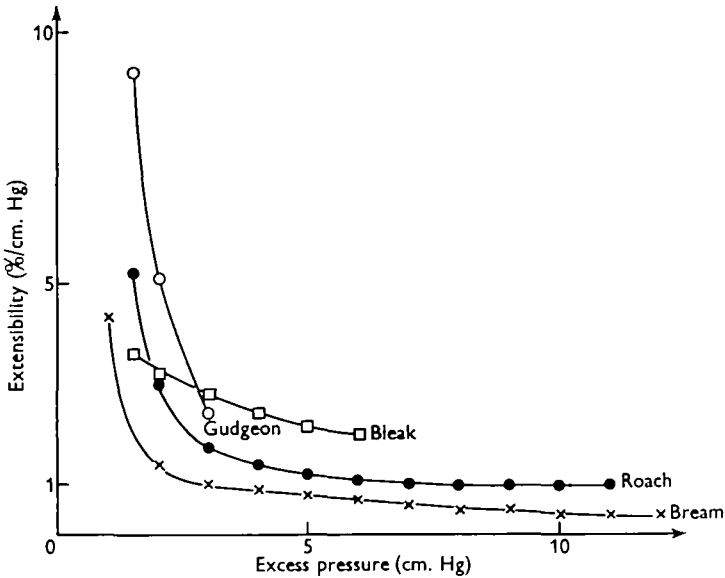


Fig. 5. The relation between extensibility and excess pressure for the swimbladders of bleak, gudgeon, roach and bream.

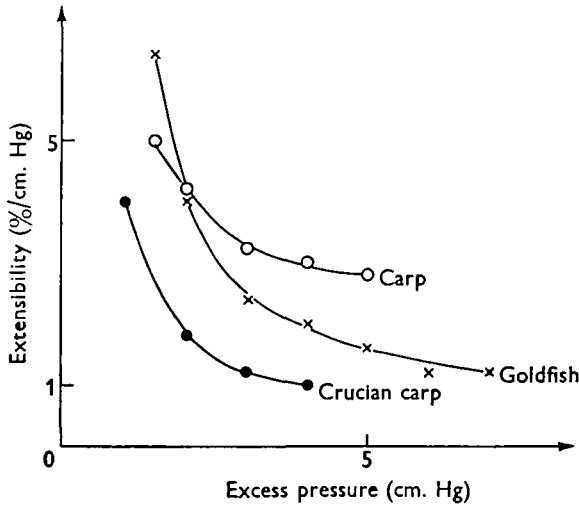


Fig. 6. The relation between extensibility and excess pressure for the swimbladders of carp, goldfish and crucian carp.

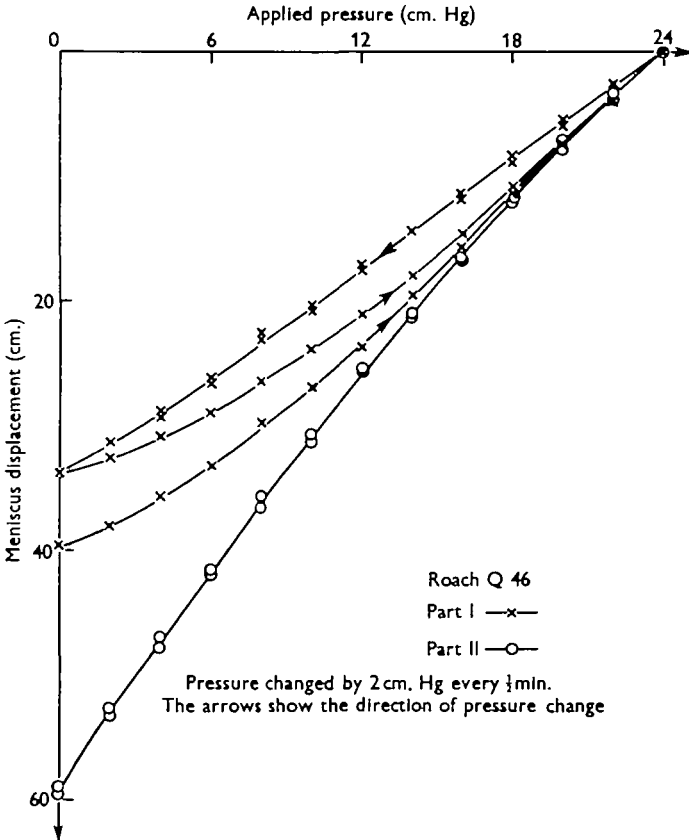


Fig. 7. Meniscus displacements for a roach undergoing cyclical pressure changes, showing a hysteresis effect due to the slow elastic behaviour of the swimbladder.

The variability of extensibility with pressure, even over small ranges of extension, requires explanation in terms compatible with Hooke's Law. It seems probable that as the swimbladder extends, its elastic elements do not all become taut at once. The final value of the extensibility is reached when all these elements are taut: the higher values at lower pressures are due to the slack condition of some of the elements.

There is no evidence to identify these elements which are supposed to tauten successively. They may be molecular chains (see King & Lawton, 1950) or they may be fibres.

The slow elastic effect

The slow elastic behaviour of the swimbladder has already been mentioned. On account of it, when a cyprinoid is exposed to cyclical changes of pressure its volume changes show a hysteresis effect. This is illustrated in Fig. 7, which is a graph of the same type as Fig. 2. A roach in the Q apparatus underwent cyclical changes of pressure between manometer zero and +24 cm. Hg. The pressure was changed by 2 cm. Hg every 30 sec. The first two cycles are shown. The meniscus movements showed a marked hysteresis. In Part II of the experiment the readings were obtained on a similar pressure cycle. There is no observable hysteresis. The hysteresis found in Part I is thus a property of the fish, not of the apparatus.

Franz (1937) and Moehres (1940) have shown that the 'Gasspuckreflex' in the minnow and the gudgeon, respectively, has a lower threshold for a slow than for a fast pressure drop. Moehres found mean thresholds for the gudgeon of 6.22 cm. Hg when the pressure was reduced at 50 cm. Hg/min. and 2.17 cm. Hg for 2.4 cm. Hg/min. Three explanations of this are possible.

(1) The threshold was at 2 cm. Hg but there was a delay of 5 sec. between the passing of the threshold and the response.

(2) Owing to a slow elastic effect the expansion of the swimbladder during a given reduction in pressure is greater if the reduction is slow than if it is fast. This assumes, as seems probable, that the necessary stimulus for the 'Gasspuckreflex' is the expansion of the swimbladder to a definite size.

(3) There is both a delay and a slow elastic effect.

As a slow elastic effect has been demonstrated and the assumption involved in (2) appears to be justified, explanation (2) or (3) must be accepted. As the passage of air from the swimbladder to and out of the mouth cannot be instantaneous, we are driven to explanation (3).

It is concluded, then, that the dependence of the apparent 'Gasspuckreflex' threshold on the rate of reduction of pressure must be explained in terms of a delayed response and the slow elastic effect. Insufficient work has been done for it to be possible to estimate the relative importance of these two factors.

DISCUSSION

(1) *Factors controlling relative sensitivity*

The following discussion concerns the relationship of relative sensitivity to extensibility and excess internal pressure.

Consider a closed elastic gas-filled bladder and let its volume be v and the excess pressure in it p at external pressure P .

Now let the external pressure increase by a small amount δP . The excess pressure is now, say $(p + \delta p)$ and the total internal pressure $(P + \delta P + p + \delta p)$. The volume is now $v(1 + \delta p e)$, where e is the extensibility of the bladder at excess pressure p .

The change in volume $\delta v = v \delta p e$. (1)

By Boyle's Law, since the mass of gas in the bladder is unchanged

$$\left. \begin{aligned} (P+p)v &= (P+\delta P+p+\delta p)v(1+\delta p e), \\ P+p &= P+\delta P+p+\delta p e(1/e+P+\delta P+p+\delta p), \\ \delta P &= -\delta p e((1/e)+P+\delta P+p+\delta p), \end{aligned} \right\} \quad (2)$$

From (1) and (2)

$$\delta v = \frac{-\delta P v}{(1/e)+P+\delta P+p+\delta p}. \quad (3)$$

Now consider an unconstrained mass of gas also having volume v at pressure P . When the pressure rises to $(P+\delta P)$ the volume becomes $Pv/(P+\delta P)$.

Whence the change in volume

$$\delta v' = \frac{\delta P v}{P+\delta P}. \quad (4)$$

From (3) and (4)

$$\frac{\delta v}{\delta v'} = \frac{P+\delta P}{(1/e)+P+\delta P+p+\delta p}. \quad (5)$$

Now consider the bladder as the swimbladder of a fish adapted to an external pressure P . $\delta v/\delta v'$ is the relative sensitivity, p is the excess internal pressure and e is $\frac{1}{100}$ of the effective extensibility.

If we apply equation (5) to the fish of my experiments we may write, taking cm. Hg as the unit of pressure, $P \simeq 78$, $\delta P = 2$, $e < 0.05$. δp cannot exceed 2 and can be ignored as it is small compared to $((1/e)+P)$.

We may thus re-write equation (5):

$$\text{relative sensitivity} \simeq \frac{80}{80+(1/e)+p}. \quad (6)$$

This expression gives values for relative sensitivity which agree well with those calculated by the normal method.

In equation (6) $1/e$ varies from 21 (gudgeon) to 250 (bream) and is extremely important in determining relative sensitivity. p varies among Cyprinidae from 2.1 (gudgeon) to 10.8 (bream) and is of relatively little importance. But e varies markedly with p , being higher at low values of p . Excess internal pressure thus influences relative sensitivity almost entirely through its effect on extensibility.

Although its relationship to the other properties which have been measured makes the inclusion of relative sensitivity tautologous, it is convenient to retain it as it summarizes the effect on the swimbladder of small pressure changes.

(2) *The rate of change of buoyancy with depth*

It has been shown that all the species examined have an excess pressure in the swimbladder. It was suggested in the introduction that such a pressure would be necessary to the proper functioning of the Weberian ossicles. The mean excess internal pressure is found to be 0.6 cm. Hg for *Amiurus*, and between 2 and 3 cm. Hg for most of the Cyprinidae examined. The roach, rudd and bream have much higher excess internal pressures (7.0, 6.1 and 10.8 cm. Hg, respectively). The effect of these is to reduce the effective extensibility and so the relative sensitivity of the swimbladder: their mean values for this last quantity are 0.41, 0.44 and 0.23, respectively. Such extreme increases in pressure and decreases in relative sensitivity can hardly be advantageous to the sensory functioning of the swimbladder, and we must assume that there is a tendency in the Cypriniformes to evolve for its own sake a low rate of change of buoyancy with depth, such as was discussed in the introduction. Such a property will only lead to a net saving of energy, and our assumption will only be valid, if the density of the fish is so close to that of its medium that the fish's plane of neutral buoyancy lies within its normal vertical range. A subsequent paper (Alexander, 1959) will present evidence that this is in fact the case.

SUMMARY

1. A method is described whereby certain physical properties of the swimbladder have been determined in intact, unoperated Cypriniformes. These properties are volume, excess internal pressure, extensibility, and relative sensitivity (an index of the rate of change of volume with depth).

2. The mean volume of the swimbladder varies in the twelve species examined from 5.8 to 9.9 ml./100 g. body weight.

3. In most Cyprinidae the swimbladder gases are maintained at a mean pressure 2-3 cm. Hg above that of the surrounding water at the depth to which the fish is adapted. Higher pressures occur in a few species, most notably the bream (10.8 cm. Hg). A much lower pressure is found in *Amiurus*. An excess internal pressure is probably necessary to provide a taut swimbladder wall to operate Weberian ossicles.

4. The swimbladder wall has non-linear elastic properties such that as the excess pressure in the swimbladder rises the extensibility of its wall falls. The swimbladder also shows slow-elastic properties. The significance of these properties is discussed.

5. Excess internal pressure and low extensibility combine to limit the rate at which the volume of the swimbladder, and so the buoyancy of the fish, changes with depth. For small depth changes the swimbladder of the bream (an extreme case) changes its volume only one-quarter as much as would a free air-bubble.

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APPENDIX 1

Criticism of Franz's determination of the excess internal pressure of the minnow

Franz (1937) used the direct manometric method of Evans & Damant (1928) to determine the excess internal pressure of minnows. He found values of about 1 cm. Hg, with a maximum of 1.5 cm. Hg.

He was dissatisfied with this method, and did some further experiments in which he measured the volume of the swimbladder gases in the isolated swimbladder and after release from it. These measurements, which were very rough, showed that the isolated swimbladders had a mean excess internal pressure of about 1.2 cm. Hg. Franz believed, however, that the excess internal pressure in the intact fish was considerably higher. He found that the flotation pressure for a minnow whose body cavity had been opened and swimbladder exposed averaged about 6 cm. Hg above the value for the intact animal and supposed this to be due to pressure exerted by the body wall. He added this difference to the values obtained for the isolated swimbladder, and so obtained his mean values of 7.8 cm. Hg for the anterior sac and 6.8 for the posterior.

Physical properties of the swimbladder in intact Cypriniformes 331

As the values obtained for the excess internal pressure of the minnow by the method described in this paper were very much lower than those reported by Franz, his work on the change of flotation pressure when the swimbladder is exposed was repeated. It was found necessary to take great care to avoid catching air bubbles in the opened body cavity. Of six minnows tested, three showed no change of flotation pressure and three showed decreases (perhaps due to stray bubbles of gas in the body cavities of intact fish). In no case was an increase in flotation pressure found. It seems probable that Franz's result was due to capture of air-bubbles in the opened body cavity. He describes no precautions against this hazard.

For this reason I reject Franz's high values for the excess internal pressure of the minnow. His direct measurements are probably more reliable, though he himself rightly criticizes the direct method as likely to give low values.

APPENDIX 2

Details of results

Species	Specimen	Weight (g.)	Excess internal pressure (cm. Hg)	Relative sensitivity	% vol.
Roach	Q 13	135	5.0	0.48	10.3
	Q 14	—	9.5	0.34	—
	Q 15	100	6.9	0.40	10.2
	Q 16	165	8.8	0.31	10.4
	Q 17	100	4.6	0.53	8.8
	Mean			7.0	0.41
Rudd	Q 38	130	8.3	0.42	8.5
	Q 39	70	6.9	0.40	8.9
	Q 40	40	5.2	0.44	9.3
	Q 64	—	4.1	0.48	—
	Mean	—	6.1	0.44	8.9
Dace	Q 10	—	3.4	0.55	—
	Q 18	100	3.1	0.61	8.5
	Q 19	90	1.8	0.73	8.2
	Q 22	105	3.4	0.60	8.4
	Q 48	55	3.2	0.54	8.5
	qq 7	5.56	2.0	0.89	7.7
	qq 8	4.62	1.7	0.60	6.5
	Mean		2.7	0.65	8.0
Minnow	q 47-70	41 (24 fish)	2.2	0.77	5.1
	qq 12	2.35	2.3	0.62	6.6
	qq 14	3.00	2.5	—	5.9
	qq 15	2.91	1.9	0.88	7.7
	qq 16	2.11	3.5	0.65	5.9
	qq 17	2.49	3.3	0.89	5.7
	qq 18	3.21	2.2	0.92	5.9
	Mean		2.6	0.79	6.1
Tench	Q 4	—	1.8	—	—
	Q 7	—	1.5	0.65	—
	Q 8	—	2.7	0.47	—
	Q 9	—	3.4	0.39	—
	Q 96	73	5.9	0.28	6.4
	Q 97	102	2.9	0.50	7.4
	qq 21	20.8	2.4	0.73	7.3
	Mean		2.9	0.50	7.0

APPENDIX 2 (*continued*)

Species	Specimen	Weight (g.)	Excess internal pressure (cm. Hg)	Relative sensitivity	% vol.
Bream	Q 65	105	10.6	0.26	8.0
	Q 66	100	8.9	0.21	8.2
	Q 67	95	14.6	0.18	7.7
	Q 68	60	10.6	0.22	7.0
	Q 94 (P 24)	65	9.4	0.26	7.1
	Mean	—	10.8	0.23	7.6
Bleak	q 83	16.3	1.9	0.65	6.3
	q 84	20.8	5.6	0.58	6.9
	q 85	15.8	1.7	0.68	7.0
	Mean	—	3.1	0.64	6.7
Carp	Q 41	65	1.3	0.93	5.0
	Q 42*	75	1.0	0.86	5.1
	Q 43	60	1.9	0.71	6.0
	Q 44*	40	1.1	0.83	5.0
	Q 49*	50	3.4	0.71	6.4
	q 80	38	3.5	0.63	6.1
	q 81	37	5.0	0.48	6.4
	q 82	45	3.5	0.64	6.5
	Mean	—	2.6	0.72	5.8
Crucian carp	Q 90	90	1.5	0.75	5.6
	Q 91	120	3.8	0.49	7.8
	Q 92	75	2.0	0.62	8.0
	Q 93 (P 21)	75	4.8	0.42	10.7
	Mean	—	3.0	0.57	8.0
Goldfish	Q 24	35	1.8	0.82	8.9
	Q 25	35	3.7	0.51	8.9
	q 43	40	2.8	0.48	6.3
	q 45	26	1.6	0.85	7.3
	q 46	—	2.0	0.65	—
	Mean	—	2.4	0.66	7.9
Gudgeon	Q 74-89	180 (17 fish)	2.9	0.73	5.9
	qq 1	11.3	1.8	0.84	6.5
	qq 2	9.3	1.6	0.61	6.2
	Mean	—	2.1	0.73	6.2
<i>Amiurus</i>	qq 3	3.74	0.8	1.00	6.6
	qq 4	4.67	0.4	0.61	5.2
	qq 5	2.48	0.5	1.00	5.7
	Mean	—	0.6	0.87	5.8

* Mirror carp.