THE PHYSICAL PROPERTIES OF THE SWIMBLADDERS OF FISH OTHER THAN CYPRINIFORMES

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INTRODUCTION

The experiments and observations reported in previous papers (Alexander, 1959*a*–*c*) have all been made on Cypriniformes. The swimbladders of these fish are specialized for the operation of the Weberian ossicles. An excess internal pressure is probably essential to the functioning of the ossicles. Outside the Cypriniformes the excess internal pressure has been measured in a 'Vieille de mer' (probably *Labrus bergylta*) by Chabry (1884) who found a pressure of 5–10 cm. of water, and in perch by Evans & Damant (1928) who could detect no excess internal pressure. Chabry does not describe any precautions to ensure that the fish was adapted to the depth at which it was tested. It seemed desirable to make a survey to determine whether the possession of an excess internal pressure is widespread or a peculiarity of the Cypriniformes.

In the work described in a previous paper (Alexander, 1959*a*) the changes in swimbladder volume, which occur as the external pressure changes from the value to which the fish is adapted, were investigated for Cypriniformes. They were found to be smaller, and sometimes very much smaller, than would occur in an unconstrained bubble of gas of the same initial volume. Where there is an excess internal pressure the relative sensitivity must be less than 1; the volume changes will be less than for a free bubble when the pressure is increased as well as when it is decreased. Where there is no excess internal pressure, unless either the swimbladder wall or the body wall is rigid in all its parts, they cannot limit volume changes as the external pressure is increased. They could, if they became taut as the pressure fell, limit the volume changes consequent upon a decrease of pressure. Jones (1951) found not only that the relative sensitivity of the perch swimbladder is 1, but also that when the pressure on a perch adapted to life in a shallow aquarium was reduced by 30 cm. Hg, the volume change was 80% of that to be expected of a free bubble. The swimbladder wall of the perch can thus be of no importance in limiting its change of buoyancy with depth. It seemed important to determine if this condition was the normal one, and that of the Cypriniformes a striking departure from it.

The following experiments were carried out to investigate these problems. The volume of the swimbladder and the sinking factor were also determined for each species examined.

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The marine species were studied at the Plymouth laboratory of the Marine Biological Association. It was not possible to control the depths of the aquaria, and tanks of various depths up to 1 m. were used. Nor was it always possible to allow the desirable 24 hr. for acclimatization. It was usually possible in such cases to determine whether the fish had adjusted its buoyancy to suit the depth of the tank by comparing its behaviour with that of healthy specimens of the same species on permanent exhibition in the aquarium.

EXPERIMENTS

Excess internal pressure

The majority of fish which possess swimbladders but are not Cypriniformes are physoclists. Gas cannot therefore be withdrawn from their swimbladders by reducing the pressure, and the technique described in a previous paper (Alexander, 1959*a*) cannot be applied to them as it stands. The following method was used in an attempt to detect excess internal pressure. A direct manometric method was discarded after trial as unsuccessful.

Part I of the procedure described in Alexander (1959*a*) was carried out. Readings were taken at 0, +6 and +18 cm. Hg. It was not necessary to use water of reduced air content.

Boyle's Law was used to calculate the volume of the swimbladder from the volume change between 0 and +6 cm. Hg, assuming that the pressure of the swimbladder gases was equal to the external pressure throughout. The same was done from the volume change between 0 and +18 cm. Hg. If, as assumed, there was no excess internal pressure, the two results should be identical. If there was an excess internal pressure, the former result should be the smaller.

The sensitivity of this method of detecting excess internal pressure is limited by the accuracy with which the smaller volume changes can be measured. The differences between the volumes calculated from the 6 cm. Hg readings and those calculated from the 18 cm. Hg. ones for thirty-two individual fish outside the Cypriniformes all lay between +6% and −6%, with standard deviation 3·6% and mean −0·31%, which is not significantly different from zero (t test, $P \simeq 0{\cdot}6$). The differences are thus probably due to experimental error, and there is no evidence of widespread excess internal pressure outside the Cypriniformes. It remains possible that a few of the fish may have had an excess internal pressure.

In the case of the pike, a physostome which releases gas readily at reduced pressures, it was possible to carry out the full routine (Alexander, 1959*a*). Three pike which gave differences of −3%, −4% and −6% in the test here described were found to have excess internal pressures of −0·4, +0·3 and +0·3 cm. Hg: that is to say, any excess internal pressure they may have had was too small to be measured by the method. The only fish outside the Cypriniformes which gave a negative difference as large as −6% were the pike mentioned above and an eel. There is therefore no case for ascribing an excess internal pressure to any individual among these fish.

The sensitivity of the test can be gauged by applying it to Cypriniformes of known excess internal pressure. This was done, using the data previously collected (Alexander, 1959*a*) for those specimens which had excess internal pressures less than 3 cm. Hg. The results suggested that a fish having an excess internal pressure greater than 2·0 cm. Hg. would be most unlikely to show a difference within the range, +6% to −6%, found for fish outside the Cypriniformes. Only one minnow with an excess internal pressure of 2·2 cm. Hg and a difference of −5% breaks this rule.

It must be emphasized that no attempt is being made to establish an exact relationship between excess internal pressure and the result of the test. Extensibility would have to be considered in such an attempt. But it seems possible to conclude that the mean excess internal pressure of the thirty-two fish examined from orders other than the Cypriniformes was very close to zero, and that it is unlikely that any one of these fish had an excess internal pressure greater than 2·0 cm. Hg. The results of the test are given in detail in the Appendix.

None of the fish examined had rigid swimbladder or body walls. Zero excess internal pressure would therefore imply a relative sensitivity of 1.

Percentage volume and sinking factor

As these fish had no detectable excess internal pressure, the volumes calculated for the swimbladder gas from the volume change as the external pressure was increased by 18 cm. Hg should be the true volumes of the swimbladders. Since the fish were weighed, the percentage volumes of their swimbladders could be calculated. They are given in the Appendix and summarized in Table 1.

The available specimens of *Gobius flavescens* were too small for satisfactory determination of the swimbladder volume by this means. The following method was adopted, as it seemed interesting to know the size of the swimbladder in this, the only pelagic species among the British gobies; the other gobies have reduced swimbladders. The flotation pressures of three specimens were determined and the specimens were weighed. They were then placed in a wide-mouthed density bottle which was filled with distilled water and weighed. They were cut in half transversely at the level of the swimbladder, whose gases were allowed to escape, and the weighing in the density bottle was repeated. Care was taken to avoid introducing bubbles of air, e.g. in their mouths, into the density bottle. The difference in grammes between the two weighings equalled the total volume of the swimbladder gases in millilitres. It was not possible to test this species for excess internal pressure.

The sinking factors of the species discussed here were determined in the manner described elsewhere (Alexander, 1959*b*). The flotation pressures of marine species were, of course, determined in sea water. The relative sensitivity was in all cases taken to be 1. Where 'dense' is given for the sinking factor, the fish failed to float at −24 cm. Hg and the sinking factor could not be determined by this method. The specimens of *Esox*, *Anguilla* and *Conger* were too long for it to be possible to determine their flotation pressures in my apparatus.

Table 1. *Mean percentage volume of the swimbladder, and mean sinking factor, for fish other than Cypriniformes*

Species	Mean % vol.	Previous values	Mean S.F.	Previous values
		Freshwater species		
Salmo trutta	5·1	—	1008	—
Esox lucius	4·9	—	—	—
Anguilla anguilla	3·7	—	—	—
Anguilla anguilla (silver eel stage)	1·3	—	—	—
Perca fluviatilis	—	7·94 (Plattner, 1941)	1001	1010* (Plattner, 1941)
	—	7·5† (Jones, 1951)	—	1005 (Jones, 1951)
Acerina cernua	8·7	—	1000	—
		Marine species		
Conger conger	3·5	4·7 (Plattner, 1941)	—	993 (Plattner, 1941); 1000 (Lowndes, 1942)
Gadus luscus	4·9	5·0 (Plattner, 1941)	998	1001 (Plattner, 1941)
G. merlangus	3·6	—	999	—
Onos mustelus	1·5	0·7 (Plattner, 1941); 1·1 (Jones, 1951)	Dense	1060 (Plattner, 1941); 1024 (Jones, 1951)
Spinachia spinachia	5·5	—	1004	—
Trachurus trachurus	4·2	—	1004	—
Labrus bergylta	5·5	—	1001	—
Crenilabrus melops	5·5	4·9 (Plattner, 1941); 4·9 (Jones, 1951)	1002	1004 (Plattner, 1941); 1005 (Lowndes, 1942); 1007 (Jones, 1951)
Gobius niger	2·2	—	Dense	—
G. paganellus	1·2	0·3 (Plattner, 1941)	Dense	1080 (Plattner, 1941)
G. minutus	2·0	—	Dense	—
G. flavescens	5·0	—	1002	—
Trigla gurnardus	5·3	—	1010	—

* Plattner's wrongly calculated mean is here corrected.

† This value given by Jones (1951) appears to be that reported by him in a thesis (Jones, 1950) as the mean for twenty-nine male perch. The thesis gives a mean of 6·2 for twenty-one female perch. All Jones's perch were mature fish caught in the spawning season.

The sinking factors found are shown with the swimbladder volumes in Table 1 and in more detail in the Appendix.

In many cases the values are based on one or two specimens only. The main object of these experiments was the search for excess internal pressure, and the accumulation of values for percentage volume and sinking factor was not thought sufficiently important to justify a more prolonged study.

Two of the values of percentage volume differ markedly from those of previous authors: those for *Conger* and *Gobius paganellus*. In the latter species the swimbladder is reduced, there is no question of buoyancy adjustment, and no great constancy of volume can be expected (cf. the differences between Plattner's, Jones's and my mean values for *Onos*, and the wide scatter, 0·3–2·6, of my individual values for *Onos*). Plattner had only one and I had only two specimens of *G. paganellus*. In *Conger* the swimbladder is well developed, and my specimens appeared to be very close in density to sea water. But Plattner's specimen was much less dense than sea water, and his experiments on others whose swimbladder gases had been partly removed showed (see his graph, figure 5) that a density equal to sea water could be expected when the percentage volume was about 3·5.

The silver eel was denser than fresh water but considerably less dense than sea water. Its swimbladder was small, as were those of the bottom-living species (*Onos mustelus*, and the gobies other than *Gobius flavescens*). Many marine bottom-living teleosts have no swimbladder (e.g. *Blennius*, *Callionymus* and the flatfish). The remaining marine species (including *G. flavescens*) are pelagic in habit and were found to have sinking factors close to 1000 (the one specimen of *Trigla* was in poor condition) and mean percentage volumes between 3·5 and 5·5. The buoyant fresh-water species require rather larger swimbladders on account of the lower density of their medium; mean percentage volumes for them vary from 4·9 to 8·7. The corresponding range for the Cypriniformes (Alexander, 1959*a*) is 5·8–9·9.

Experiments at reduced pressures

The experiments described above demonstrate that the species examined have no excess internal pressure, and hence that their swimbladder walls can be of no importance in controlling swimbladder volumes at depths greater than that to which they are adapted. It remains possible that they might become important as the gases expand at reduced depths. A number of determinations were therefore made of swimbladder volume changes at reduced pressures. These were compared with the changes predicted by Boyle's Law from the volume changes occurring between 0 and + 18 cm. Hg external pressure. When the pressure was restored and a reduction repeated a slightly larger volume change usually occurred, but close constancy was achieved in successive cycles. Apparently the elastic behaviour of the swimbladder wall is, as in Cypriniformes, slow. The steady volume change achieved in pressure cycles between − 24 cm. Hg and manometer zero was recorded.

Negative buoyancy at reduced depths can normally only be a problem to fish whose sinking factors are near 1000. Five such fish were examined. The results for the pressure change 0 to − 24 cm. Hg are shown in Table 2.

Table 2. *Volume changes between* 0 *and* − 24 *cm. Hg*

Specimen	Observed meniscus displacement (cm.)	Predicted meniscus displacement (cm.)	Difference (%)
q 78. *Gadus merlangus*	21·9	21·0	+ 4
qq 23. *Spinachia spinachia*	33·6	36·3	− 7
q 86. *Acerina cernua*	52·0	54·4	− 5
qq 29. *Trachurus trachurus*	44·2	43·2	+ 2
qq 24. *Crenilabrus melops*	37·1	41·9	− 11

The positive differences are clearly due to experimental error, but the volume changes of *Spinachia* and *Crenilabrus* were significantly less than the Boyle's Law prediction. The differences are, however, small—smaller even than Jones's (1951) mean difference of − 14% for the perch (reduction of 25 cm. Hg).

Jones (1952) found that perch adapted to a given pressure could not maintain their stations without discomfort when the pressure was reduced by more than one-sixth, and not at all when the reduction was more than one-third. For perch adapted to 80 cm. Hg the critical reductions are 10–15 cm. Hg and about 25 cm. Hg. Marine fish, with rather smaller swimbladders, would require less energy to counteract negative buoyancy at a given pressure reduction, and may be expected to be able to withstand rather larger reductions.

My investigations, down to −24 cm. Hg, may be taken as covering at least the range of comfortable swimming of the species examined. Within this range any influence the swimbladder wall has on swimbladder volume is very slight. It is concluded that in *Gadus*, *Spinachia*, *Acerina* (a fresh water species), *Trachurus* and *Crenilabrus* the swimbladder wall has no importance in restricting buoyancy changes. Jones has found the same to be true of the perch. It seems probable that this condition is general outside the Cypriniformes. It is very markedly in contrast with the situation within the Cypriniformes. In Fig. 1 the volume change with pressure of a roach swimbladder is compared with that of *Spinachia*.

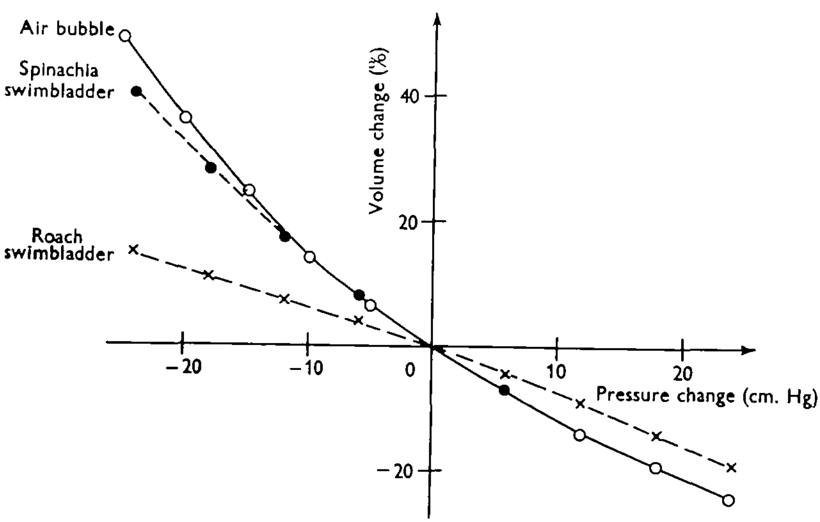

Fig. 1. Comparison of the changes of volume with external pressure of an air-bubble and of the swimbladders of *Spinachia* and roach adapted to life in shallow aquaria.

In a previous paper (Alexander, 1959*b*) the significance of the product of percentage volume and relative sensitivity was discussed. Outside the Cypriniformes the relative sensitivity is 1 and the product is equal to the percentage volume. The product is an index of the rate of change of buoyancy with pressure. Its importance is confined to species which have sinking factors close to 1000. In buoyant marine species it lies between 3·5 and 5·5—limits very similar to those found in Cypriniformes. In buoyant freshwater fish outside the Cypriniformes it lies between about

5 and 9. The lower value in marine fish is due to the adequacy of smaller swimbladders in the sea than in fresh water; that of the Cypriniformes, to a reduction in relative sensitivity.

Experiments on isolated swimbladders

It has been shown that the swimbladder wall has no importance in controlling swimbladder volume outside the Cypriniformes, at least in the species investigated. It is usually much more delicate than is normal in the Cypriniformes. It was felt that it would be interesting to investigate its elastic properties.

The method described (Alexander, 1959*a*) for determining extensibility in Cypriniformes cannot readily be adapted to other fish, in whose swimbladders only a slight excess pressure develops even at much reduced external pressures. It is, however, possible to calculate from Jones's (1951) results with the perch that its extensibility is uniformly 7·6%/cm. Hg over the range 1–3 cm. Hg. There is no sign of the change of extensibility with pressure reported for Cypriniformes.

The method previously described (Alexander, 1959*c*) was used to study the volumetric extension of trout and pike swimbladders. A ball-ended hypodermic needle was used to avoid unnecessary risk of puncture. The tunica externa of the pike is so firmly fixed to the vertebrae that it cannot be separated from them without damage. The vertebral column and a little of the muscle on either side of it was therefore left attached to the excised pike swimbladders.

The swimbladders of both species usually burst when the excess pressure in them exceeded 3 cm. Hg, whereas those of tench will stand pressures of 20 cm. Hg and perhaps much more. The very few readings which could be taken on the two trout in which the experiment was successful indicate an extensibility of 8–10%/cm. Hg between 1 and 3 cm. Hg, and do not suggest any change of extensibility with pressure. In pike, on the other hand, very marked plastic stretching occurs; in each of the two specimens examined the capacity of the swimbladder was about doubled when they were stretched by an excess pressure of 2 cm. Hg.

The swimbladders of pike and trout clearly have very different properties from those of the Cypriniformes.

SUMMARY

1. No excess internal pressure, such as has been found in the Cypriniformes, could be detected in the swimbladders of seventeen species from other orders. The swimbladder wall in these fish exercises no appreciable constraint on changes of buoyancy with depth.

2. Determinations of sinking factor and swimbladder volume are reported.

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REFERENCES

ALEXANDER, R. McN. (1959*a*). The physical properties of the swimbladder in intact Cypriniformes. *J. Exp. Biol.* **36**, 315–32.

ALEXANDER, R. McN. (1959*b*). The densities of Cyprinidae. *J. Exp. Biol.* **36**, 333–40.

ALEXANDER, R. McN. (1959*c*). The physical properties of the isolated swimbladder in Cyprinidae. *J. Exp. Biol.* **36**, 341–46.

CHABRY, L. (1884). Sur l'équilibre des poissons. *J. Anat., Paris*, pp. 139–48.

EVANS, H. M. & DAMANT, G. C. C. (1928). Observations on the physiology of the swimbladder in cyprinoid fishes. *Brit. J. Exp. Biol.* **6**, 42–55.

JONES, F. R. H. (1950). The role of the swimbladder in regulating the vertical movements of teleostean fishes. A thesis presented for the degree of Ph.D. in the University of London.

JONES, F. R. H. (1951). The swimbladder and the vertical movements of teleostean fishes. I. Physical factors. *J. Exp. Biol.* **28**, 553–66.

JONES, F. R. H. (1952). The swimbladder and the vertical movements of teleostean fishes. II. The restriction to rapid and slow movements. *J. Exp. Biol.* **29**, 94–109.

LOWNDES, A. G. (1942). The displacement method of weighing living aquatic organisms. *J. Mar. Biol. Ass. U.K.* **25**, 555–74.

PLATTNER, W.-A. (1941). Études sur la fonction hydrostatique de la vessie natatoire des poissons. *Rev. suisse Zool.* **48**, 201–338.

APPENDIX

Details of results

Species	Specimen	Weight (g.)	% vol.	Sinking factor	Pressure test (%)
Salmo trutta	Q 21	65	4·6	1008	−1
	Q 23	60	5·5	—	−5
	Mean		5·1	1008	
Esox lucius	Q 35	140	4·7	—	−3
	Q 36	250	4·5	—	−4
	Q 37	160	5·6	—	−6
	Mean		4·9	—	
Anguilla anguilla	q 87	22	3·7	—	−6
Anguilla anguilla (silver eel stage)	q 74	95	1·3	—	+1
Conger conger	Q 101	165	3·8	—	−1
	Q 102	210	3·2	—	+2
	Mean		3·5		
Gadus luscus	Q 99	69	4·9	998	+3
G. merlangus	q 77	62	2·8	1006	+1
	q 78	23·5	4·4	992	+5
	Mean		3·6	999	
Onos mustelus	qq 26	1·8	2·6	Dense	+4
	qq 34	8·0	1·7	Dense	−5
	qq 79	30·5	0·3	Dense	—
	Mean		1·5		
Spinachia spinachia	qq 23	4·5	5·7	1006	−1
	qq 35	10·0	5·2	1001	+3
	Mean		5·5	1004	
Perca fluviatilus	Q 45	—	—	1001	−4
Acerina cernua	q 86	31	8·7	1000	0
Trachurus trachurus	qq 29	9·3	4·2	1005	+4
	q 76	45	4·2	1003	+4
	Mean		4·2	1004	
Labrus bergylta	qq 37	16·0	5·5	1001	−3
Crenilabrus melops	qq 22	3·6	6·0	997	+6
	qq 24	7·8	5·3	1001	+2
	qq 25	2·9	6·2	1005	0
	qq 36	6·6	5·3	1003	−1
	Q 103	66	4·5	1006	+3
	Mean		5·5	1002	
Gobius niger	qq 31	2·4	2·4	Dense	−5
	qq 38	14·2	2·1	Dense	+2
	qq 39	7·9	2·0	Dense	−1
	Mean		2·2		
G. paganellus	qq 30	14·3	0·8	Dense	−5
	qq 33	8·8	1·6	Dense	+4
	Mean		1·2		
G. minutus	qq 32	2·6	2·0	Dense	0
G. flavescens	3 fish	Total 2·03	5·0	1002	—
Trigla gurnardus	q 71	17·8	4·6	1010	−3