Biology of Behaviour, 1977, *2*, 109-128

The role of the swim-bladder in vertical movement of fishes

(Carassius auratus, Salmo gairdneri, and Tilapia mariae)

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Key words: Fishes - Swim-bladder - Muscle activity - Buoyancy - Pressure change.

RESUME

Role de la vessie natatoire dans les mouvements verticaux des poissons

Les théories concernant le rôle de la vessie natatoire (Borelli, 1680 ; Delaroche, 1809) ont été mises à l'épreuve expérimentalement chez trois espèces de poissons : *Carassius auratus, Salmo gairdneri* et *Tilapia mariae.*

1. — Une tendance à un mouvement vertical a été provoquée chez des poissons en leur offrant de la nourriture, tandis que leur déplacement était limité en hauteur à quelques centimètres. Les changements de volume enregistrés semblent une conséquence, et non une cause, des mouvements (*Tableau I*).

2. — Dans une seconde phase expérimentale, les poissons sont laissés libres de se déplacer de haut en bas sur une hauteur d'environ 200 cm. Les changements de volume enregistrés aux altitudes de départ et d'arrivée sont identiques, indépendemment du fait qu'ils aient été mesurés alors que le poisson s'arrêtait, continuait à nager, ou se retournait à l'altitude atteinte (*Figures 3-5*).

3. — Des sujets vivants, anesthésiés ou morts ont été soumis aux mêmes changements de pression. Les changements de volume qui en résultent se correspondent.

Tous les résultats confirment les conceptions de Moreau (1976) selon lesquelles les poissons ne réguleraient pas le volume de leur vessie natatoire par le jeu des muscles — ni à l'origine d'un mouvement vertical (Borelli, 1680), ni à la fin pour annuler les changements passifs (Delaroche, 1809). La revue des études anciennes et plus récentes ne permet d'envisager que deux exceptions, dans les espèces ayant une morphologie très spécialisée de la vessie natatoire et du corps.

Mots clés : Poissons - Vessie natatoire - Activité musculaire - Flottaison - Changements de pression.

Reçu le : 3-5-1976 ; *Accepté le :* 5-7-1976
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INTRODUCTION

There are several theories about the possible functions of swimbladders. It is generally accepted that they variously serve as hydrostatic, respiratory, sound-producing, and sound-intensifying organs as well as apparatuses for measuring oscillations in pressure (summaries see Jaeger, 1903 ; Baglioni, 1908, 1910 ; Eissele, 1922 ; Wunder, 1936 ; Jones and Marshall, 1953 ; Jones, 1957 ; Harder, 1964 ; Alexander, 1966 ; Hawkins, 1973).

However, there remains disagreement on the role played by the bladders in the fishes' vertical movements. It was the aim of this investigation to contribute some further results to this subject—especially to review Borelli's, Delaroche's, and Moreau's results and hypotheses in newer experiments.

Borelli (1680) assumed that the fish causes vertical movements through changes in its specific gravity, resulting from changes in the bladder volume which would be produced by the trunk's mucular system (cited in Eissele, 1922).

On the other hand, in Delaroche's opinion, volume and specific gravity would only change passively when a fish—coming from a state of equilibrium—swims up and down through various intensities of water pressure (1). He claimed that muscles lying in the wall of the bladder should be able to cancel these changes. So, after an upward movement, the muscles should contract to counteract the passive extension of the gas, whereas a downward movement should be followed by a relaxation to cancel the diminution in volume, caused by increasing external pressure.

In this way it should be possible for the fish to keep the same, presumedly most favorable specific gravity in various water-depths (Delaroche, 1809). Moreau (1876) concluded that fishes do not regulate the bladder volume by muscular systems at all, but compensate changes that have occurred passively as a consequence of changes in external pressures by secretion and resorption of bladder-gas in physoclistous species, and mainly by snapping and spitting air in physostomous species (for detailed descriptions see Baglioni, 1908, and compare with Jacobs, 1932 ; Wunder, 1936).

Though Moreau's investigations have often been criticized because of abnormal experimental conditions (e.g. by Jaeger, 1903), even today his results form the basis of arguments against both other hypotheses, which now and then have been directly or indirectly supported in later years (see Jaeger, 1903 ; Hesse, 1935 ; Fänge, 1943 ; Peters, 1951 ; McCutcheon, 1958, 1962 ; Long, 1959 ; Ladiges, 1970).

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(1) In the state of equilibrium or the adapted state the specefic gravity of a fish is nearest to that of water, so that the animal heeds only a minimal frequency of fin-beats to stay within a certain depth.

MATERIAL AND METHODS

The experiments were performed on 5 goldfish (*Carassius auratus*, Cyprinidae), 1 trout (*Salmo gairdneri*, Salmonidae), and 2 cichlids (*Tilapia mariae*, Cichlidae). Goldfish and trout belong to the group of physostomous fishes in which there exists a connection between swim-bladder and gut even in adult animals, whereas in the physoclistous cichlids this 'Ductus pneumaticus' becomes closed and reduced during the first days of life.

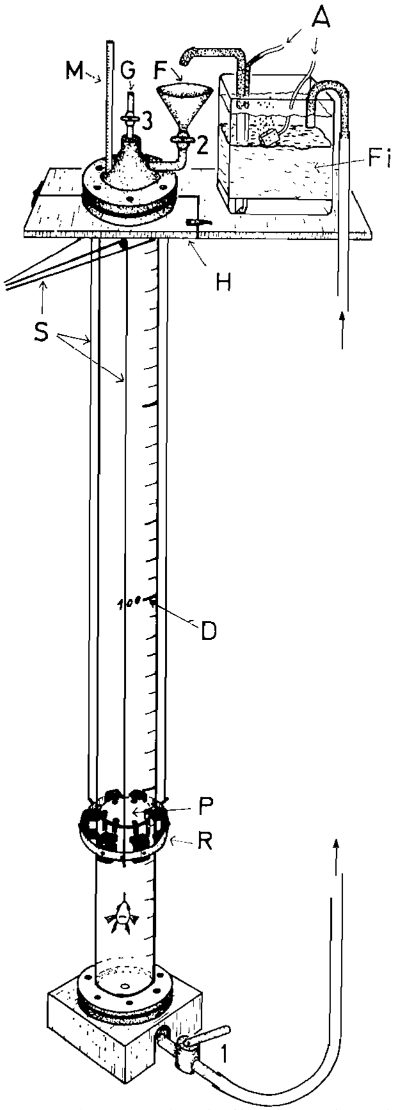

Fig. 1 : *Experimental apparatus. D : marks indicating the altitude ; G : glass tube to remove air bubbles ; H : hold of the apparatus. For further abbreviations and explanations see text.*

Fig. 1 : *Dispositif expérimental. D : indication de l'altitude ; G : tube destiné à l'élimination des bulles d'air ; H : système de maintien de l'appareil. Voir le texte pour les autres abréviations.*

The experimental apparatus (*Fig. 1*) consisted of a 200 cm long plexiglas tube, 14 cm in diameter. At the ends it was closed with covers of PVC. Within the tube there was in experimental series II a single, perforated, horizontal sheet of plexiglas (P) ; in series I and III there was a 7 cm high chamber inside with one sheet each serving as a bottom and a roof and with the walls of the tube as walls of the chamber. Six iron screws and small hoop-irons were attached to the rims, and a ring with six magnets (R), hanging in strings (S), was put around the tube. Thus the sheet and the chamber could be moved up and down within the closed apparatus between 10 and 195 cm magnetically. Before the animals to be tested were shifted from 40 cm deep tanks into the experimental conditions, they were anesthetized in 1:10,000 concentrated solution of MS 222 Sandoz to prevent them from spitting gas out of their bladders during the capture.

Between the experiments a circulating water flow, driven by air (A), sucked off food remnants and excrement from the bottom, and—after passing through an aerated filter (Fi)—returned clean water into a funnel (F) through which food (*Tubifex* worms and dried commercial food) were also presented. Before beginning the recording, taps 1-3 were closed ; now all volume changes occurring within the tube could be read at the capillary tube (M) with a precision of $\Delta V = 0.001$ ccm (2).

While a camera transmitted the positions and vertical movements of the fish to the picture channel of a video-recorder the occurring alterations in water levels were dictated continuously to the sound-track ; the data were thus synchronized at a monitor for evaluation.

EXPERIMENTS

I. Experimental series I

1) Procedure

The fish were enclosed in the plexiglas chamber so that vertical movements were confined to 2-3 cm. Periodical registration of fin-beats was used to determine when the adapted state was recovered (Jones, 1952). After adaption in experimental series I-1 (fish at a depth of 195 cm) intentions to move upward were elicited by letting food sink slowly from the top of the tube to the bottom. In experimental series I-2 (fish at a depth of 25 cm) some *Tubifex* worms were fastened below the transparent bottom of the chamber. Downward movement intentions could be elicited by switching the light on and off.

In general, " intention to move " could be readily seen in the behaviour of the fish. They abandoned their nearly horizontal bearings and orientated obliquely to either the upper or lower cover. They showed increased fin motion and snapping directed toward the food.

2) Results and Discussion

Fig. 2 shows the course of adaption in a goldfish. Cichlids, possessing a more productive gas gland, needed only 18 hours, whereas the trout, which lacks the gland, could not adapt to greater depths (Jacobs, 1932 ;

(2) Experiments with an empty tube revealed that the temperature remained constant enough to prevent quick volume changes which could have biased the results.

Rauther, 1922 ; Jones, 1952). Therefore the experiments with the trout were only performed on an animal which had its state of equilibrium near the surface (*Fig. 2*).

The average volume changes of maximally 0.003 ccm (*Table I*) occurring during the attempts to reach the food, amount to less than 0.01 % of the body-volume and to less than 0.1 % of the bladder-volume (3). The maximum volume changes correlated with more vigorous tail-beats ; when the tail-beats stopped the water-gauge in the capillary tube immediately returned to its former position.

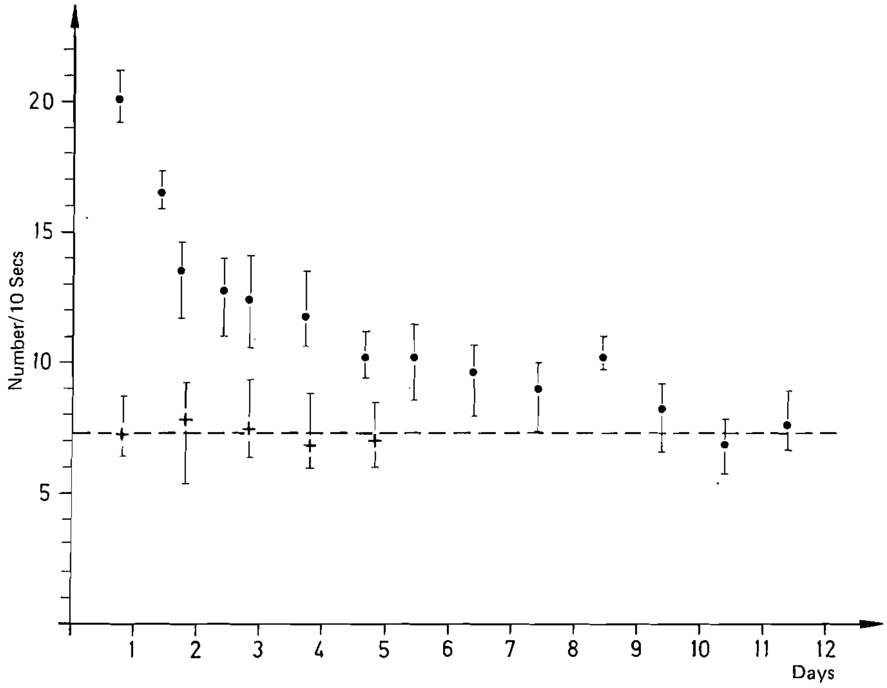

Fig. 2 : *Frequency of fin-beats of the test fish C_3 (●) and of the control animal C_5 (+). At day zero C_3 has been shifted from a 40 cm deep tank into an altitude of 195 cm. When its frequency of fin-beats reached that of C_5 (interrupted line) which had remained in the tank the fish C_3 was considered to be adapted. Dots and crosses represent means of 30 recordin each ; the vertical lines show standard deviations.*

Fig. 2 : *Fréquence des battements de nageoire de l'animal expérimental C_3 (●) et du témoin C_5 (+). Le jour 0, C_6 a été changé d'une profondeur de 40 cm, à une altitude de 195 cm. Lorsque la fréquence de ses battements de nageoire atteint celle de C_5 (ligne pointillée) qui était resté à la position initiale, le poisson C_3 a été considéré comme adapté. Croix et points représentent les moyennes de 30 observations dans chaque cas. Les lignes verticales représentent les déviations standard.*

(3) In fresh-water species the bladder-volume can be computed with 8.3-8.5 % of the body-volume (Jones and Marshall, 1953) which had been measured by water displacement.

Table I: *Results of experimental series I. For further explanation see text.*

Tableau I. *Résultats des séries expérimentales I. Explications complémentaires dans le texte.*

Experimental series	Altitude [cm]	Species	Fish-No.	Max. volume-changes [ccm]	Average volume-changes [ccm]	Quantity of recordings	Volume of the fish [ccm]	Volume of the bladder [ccm]	Density of the fish
I-1	195	*Carassius auratus*	C_1	+ 0.003	+ 0.002	11	44	3.65	—
			C_2	+ 0.004	+ 0.002	38	40	3.32	1.003
			C_3	+ 0.004	+ 0.003	31	31	3.07	1.003
		Tilapia mariae	T_2	+ 0.006	+ 0.003	17	46	3.91	1.002
I-2	25	*Carassius auratus*	C_4	— 0.008	— 0.003	25	38	3.15	1.003
			C_5	— 0.003	— 0.003	25	41	3.40	1.002
		Tilapia mariae	T_1	— 0.004	— 0.002	19	36	3.06	1.002
		Salmo gairdneri	S_1	— 0.006	— 0.003	44	20	1.70	1.003

Since these minimal enlargements or diminutions of volume only affect changes in the normal specific gravities (1.003) of about 0.0001, it is extremely doubtful that they would be able to cause or support vertical movements as suggested by Borelli. The long time which is necessary for adaption (*Fig. 2*) is another argument against muscular regulation. These arguments were strenghthened in experimental series III. Furthermore, experimental series II revealed another possible explanation for the small volume changes.

II. EXPERIMENTAL SERIES II

1) Theoretical basis

A fish which swims up and down freely between defined depths of water is always subjected to the same changes in volume through changes in the external pressure. If there were an additional active influence on the bladder-volume, the total change (which is the recorded one) between the starting point and a certain altitude should depend on whether the animal a) stops at that altitude ("stationary recording"), b) continuously swims in the same direction ("continuous recording"), or c) turns back ("alternating recording"). The constant passive changes should be quite visible only in the case of a). In b) it should be increased by an active change to produce a movement up or down, whereas in c) it should be decreased to slow down and turn back.

2) *Procedure*

Fish C_1-C_3 and T_2 were adapted to a depth of 195 cm, C_4 and C_5 to 10 cm, and S_1 and T_1 to 30 cm. At those depths the fish were restricted to vertical movements of 2-3 cm by a sheet of plexiglas. During the experiments that sheet was lifted (experimental series II-1) or let down (experimental series II-2) in steps of 5-10 cm. Since goldfish, swimming from

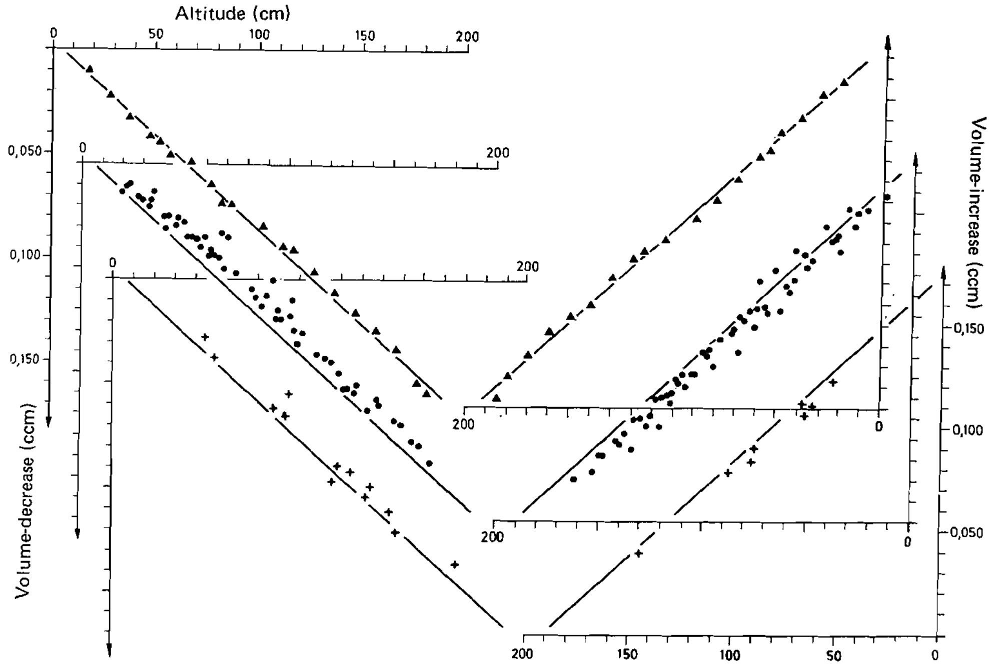

Fig. 3 : *Relations between vertical movements (abscissa) and volume changes (ordinates) for the goldfish C_4 in experimental series II. The descending lines in the left half represent changes in volume of fish swimming downward, the ascending lines in the right half those of upward moving ones.* ▲ *: stationary recording ;* ● *: continuous recording ; + : alternating recording. For clearness the diagrams of the different recordings have been shifted apart. The regression-lines have been computed for the data of stationary recording and then redrawn in the other two diagrams in order to compare them with the results of continuous and alternating recordings.*

Fig. 3 : *Relations entre les mouvements verticaux (abscisse) et les changements de volume (ordonnée)pour le poisson C_4 dans la série expérimentale II. Les lignes descendantes dans la partie gauche représentent les changements de volume chez le poisson nageant vers le bas, les lignes montantes à droite, ceux observés lors des mouvements ascendants ;* ▲ *: enregistrement stationnaire ;* ● *: enregistrement continu ; + : enregistrement alternatif. Pour la clarté du diagramme, les différents enregistrements ont été séparés. Les droites de régression ont été calculées pour les enregistrements stationnaires et reportées sur les deux autres diagrammes pour permettre les comparaisons.*

195 to 90 cm would spit gas from their bladder and loose their state of equilibrium, they were prevented in experimental series II-1 from ascending beyond the 100 cm mark.

The upward and downward movements of the tested fish and the resulting changes in water levels in the capillary tube were recorded on video-tape.

3) *Results*

Results are shown and explained in *Fig. 3-5.*

4) *Discussion*

If Borelli's hypothesis were correct, there should be differences between the results of continuous and alternating recordings. But in contradiction to his hypothesis, *Fig. 3-5* show that fish in a certain altitude possess the same volume—no matter whether they have a tendency to move up or down. The divergence between the values of stationary recordings (straight lines and curves) and continuous recordings in *Fig. 3* and *4* is probably caused by the following influences :

a) In the bladder wall two layers of connective tissue with collagen and elastic fibres in various directions (Eissele, 1922 ; Jones and Marshall, 1953) delay the extension of the gas, when the external pressure decreases.

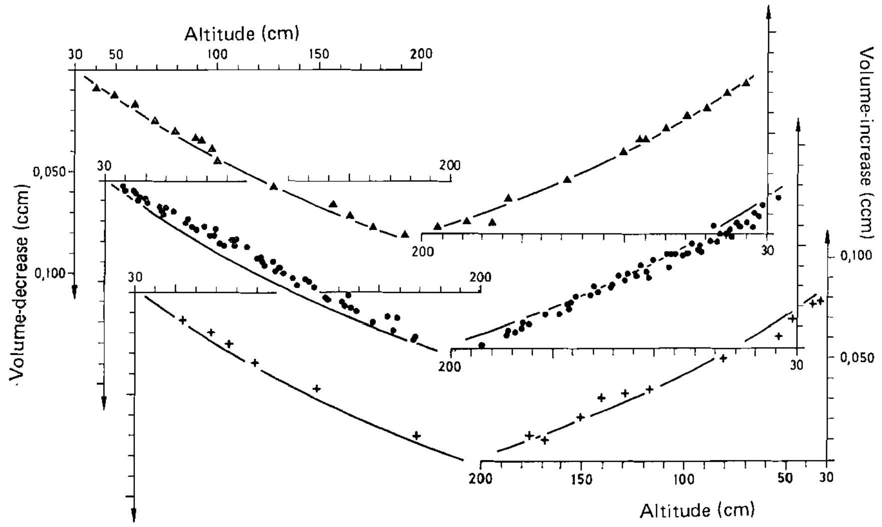

Fig. 4 : *Relations between vertical movements and volume changes for the trout in experimental series II. For explanation see* Fig. 3.

Fig. 4 : *Relations entre les mouvements verticaux et les changements de volume pour une truite dans la série expérimentale II. Explications complémentaire voir* Fig. 3.

b) During cyclical pressure changes (repeated up and down) a hysteresis, as measured in Cyprinids by Alexander (1959a), prevents the starting-volumes from being reached again.

c) There is a little lag between the moment the changes occur and the moment they are predicted. This lag is caused by the transfer of the fish's volume changes to the capillary tube and by the reading. When afterwards the recordings are evaluated from the monitor a certain difference in alitude is coordinated with a change in volume which is too small. The causes a) and b) affect the same.

Factors a) and b) influence the alternating recording, too, factor c) scarcely does since the turning-round requires time enough to make up for the delay. In accordance with this, the crosses of *Fig. 3* and *4* lie closer to the results of stationary recordings than the points do.

Further it would be expected that as a result of the three factors mentioned the differences between stationary and continous recordings should be the greater, the faster the fish swim. That is confirmed if one measures at the monitor the distances and times needed and compares the computed speeds with the corresponding figures (*Table II*) : the values of the quicker descents deviate more from the straight lines and curves than those of the slower ascendings. The correlation coefficient between speed and deviation is 0.9855 ($p < 0.001$).

With speeds less than 6 cm/sec the three factors mentioned above seem to become inconsequential since there are no differences between stationary and continuous recordings in the trout's upward and in the very slow Cichlids' upward and downward movements.

Table II : *Average speeds of descent and ascent. For further explanation see text.*

Tableau II : *Vitesses moyennes de montée et descente. Explications dans le texte.*

Species	Average speed of swimming downward	upward	cm/sec	cf. fig.
C. auratus	14.4	9.8		3
T. mariae	3.7	2.2		5
S. gairdneri	10,2	5.5		4

Another support is given by the results of experimental series III.

Following Borelli's hypothesis that the change in volume is the cause of the movement one further would expect a change in volume *before* a change in altitude has occurred (Baglioni, 1908). Such alterations in water levels are missing. Of course, the relatively high range of values belonging to a definite change in altitude (e.g. ± 0.015 ccm in *Fig. 3*, continuous recording) might conceal alterations within that size-range. Firstly, however, the deviations are sufficiently explained by the different speeds of swimming. Secondly, at the beginning and the end of the curves where the active changes should be expected the values deviate no more than they do in the intermediate range. Thidly, volume changes of such sizes (e.g. ± 0.015 ccm) would have only produced an alteration in the specific gravity of 0.0004. As mentioned in section I-2 such values are too small to support a vertical movement efficiently (see section III-3). Further, they are too small to stop or even turn round a descending (ascending) which becomes more and more accelerated as a result of increasing (decreasing) specific gravity with increasing (decreasing) external pressure.

These experiments show that in all likelyhood, the volume changes are passive ones which originate from the increases and decreases in water pressure while the fish swim up and down. From the *Fig. 3-5* it becomes evident that fish moving 2-3 cm in the vertical line experience volume changes between 0.001-0.010 ccm. Thus, the average oscillations of 0.003 ccm in experimental series I, in which vertical movements of such a range have been possiblee, can be explained as passive volume changes (*cf. Table I*).

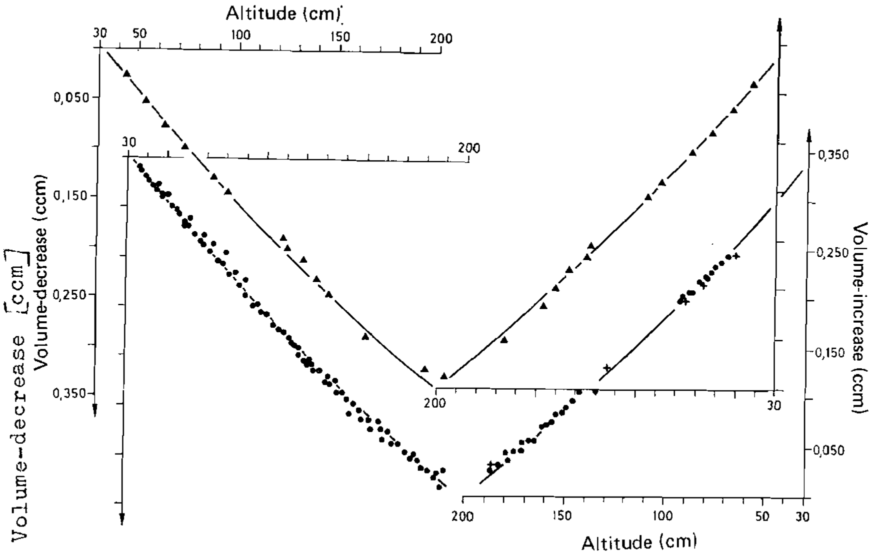

Fig. 5 : *Relations between vertical movements and volume changes for the cichlid T_1 in experimental series II. For explanation see* Fig. 3.

Fig. 5 : *Relations entre les mouvements verticaux et les changements de volume pour le poisson T_1 dans la série expérimentale II. Explications complémentaire voir* Fig. 3.

The results of experimental series II are in contradiction to Borelli's hypothesis but not to that of Delaroche since the recorded changes in volume are smaller than one computes for the bladder-volumes (*Table I*) after Boyle's law (*Fig. 6*) :

$$\Delta V = V_2 - V_1 = \frac{p_1 V_1}{p_2} - V_1$$

when: p_1 = water-pressure at the starting point of the movement;
p_2 = water-pressure at the end of the movement;
V_1 = bladder-volume at the starting-point (*see Table I*);
V_2 = bladder-volume at the end of the movement.

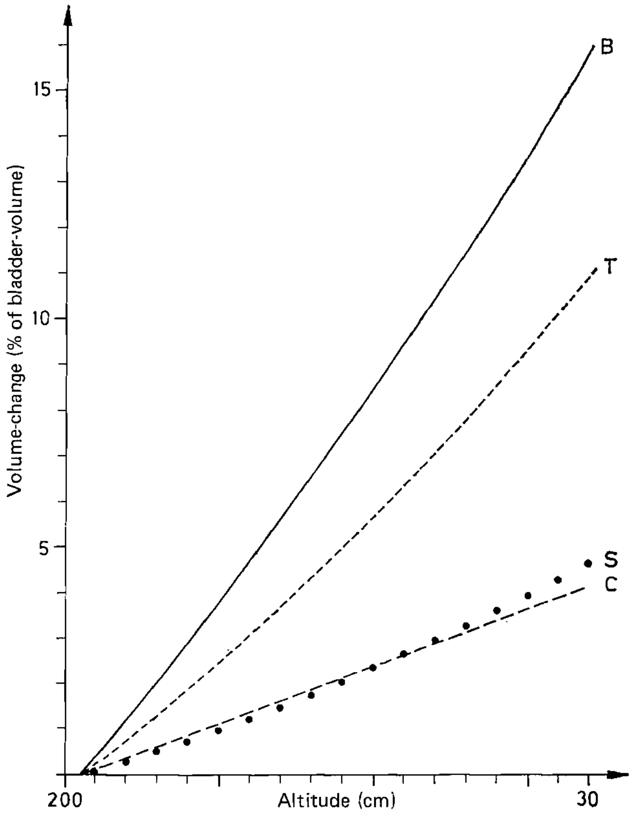

Fig. 6 : *Observed extension of bladder volume in % for* Carassius (C), Salmo (S), *and* Tilapia (T) *for an ascent from 195 to 30 cm and the expected values* (B) *according to Boyle-Mariotte. Because of the symmetry which can be seen in* Fig. 3-5 *the curves—if they are read from above to below—also show the diminutions of descending fish.*

Fig. 6 : *Extension observée de la vessie natatoire en % pour le* Carassius (C), *le Salmo* (S) *et le* Tilapia (T) *pour une montée de* 195 *à* 30 *cm et valeurs attendues* (B) *selon Boyle-Mariotte. En raison de la symétrie qui apparaît dans les figures 3-5, les courbes, lues de haut en bas, présentent également la diminution pour le poisson qui descendrait.*

« Whether or not the gas obeys Boyle's law will depend on the passive resistance that the bladder wall and surrounding tissues offer to its expansion and on the degree to which the fish can actively conrol the volume of its swimbladder by muscles lying in or about the bladder wall » (Jones, 1951). In order to decide whether the deviations from Boyle's law depend on muscular activity as Delaroche proposed or on a passive restriction by elastic properties of the tissues, a third experimental series was performed.

III. EXPERIMENTAL SERIES III

1. *Theoretical basis*

If one follows Delaroche's hypothesis and compares the volume changes of active, narcotized and dead fish which occur with identical changes in external pressure, one should get greater extensions and shrinkings in dead fish, at least, since they are no longer able to counteract the passives changes. If the trunk's striated muscles were responsible for the control of volumes, the same should hold for narcotized fish. On the other hand the ability for control should persist if the regulation were brought about with the smooth muscle fibres of the bladder wall which do not become paralyzed by the applied narcotic MS 222 Sandoz (Peters, 1951).

2) *Procedure*

Experimental series IIIa :

When a fish had adapted to a depth of 195 (IIIa-1) or 30 cm (IIIa-2) the anesthesia was gradually added to the tube until a concentration of 1:12.000 was reached. 30-40 minutes later the fish—now lying on its side —was subjected to several external pressures by moving the plexiglaschamber magnetically up and down over various distances.

The readings of the volume changes were made after stopping the chamber. Furthermore in experimental series III-1 it was observed at what altitude the narcotized fish rose from the bottom of the chamber (indicating that neutral buoyancy was reached) when passively moved upward. When these experiments had been finished the anesthesia was slowly drained from the tube while at the same time fresh water was filled in from above. The experiments were repeated two hours later with the fish active again ; and they were carried through for a third time with the dead fish four hours after a greater quantity of MS 222 Sandoz had been added. To be sure that the concentration of 1:3.000 had been sufficient for killing the animal, once more the solution was replaced with fresh water, but the fish never recovered.

Experimental series IIIb :

In the case of the golfish C_4 finally the swim-bladder was ectomized and subjected to external pressure changes in the same way and with that speed, which is characteristic for goldfish (*see Table II*). The occurring volume changes were recorded stationarily as well as continuously.

3) *Results*

Experimental series IIIa :

For comparable changes in altitude the volume changes of active, anesthetized and dead fish are all the same. In *Tilapia* they also correspond exactly to the results obtained in experimental series II (*Fig. 5*). But in the trout and in goldfish they lay between 11.5 and 14.5 % higher than in experimental series II. *Fig. 8* shows the results for a living, active and for a dead trout ; *Fig. 7a* gives the corresponding data for a goldfish. The identical data from the narcosis experiment have been omitted for clearness in *Fig. 8* ; but for the goldfish they have been entered into a second *Fig. 7b* ; so have the volume changes gained with the isolated swim-bladder. The regression lines in *Fig. 7a* and *7b* are identical. They have been computed from all the data in *7a* and *7b* together.

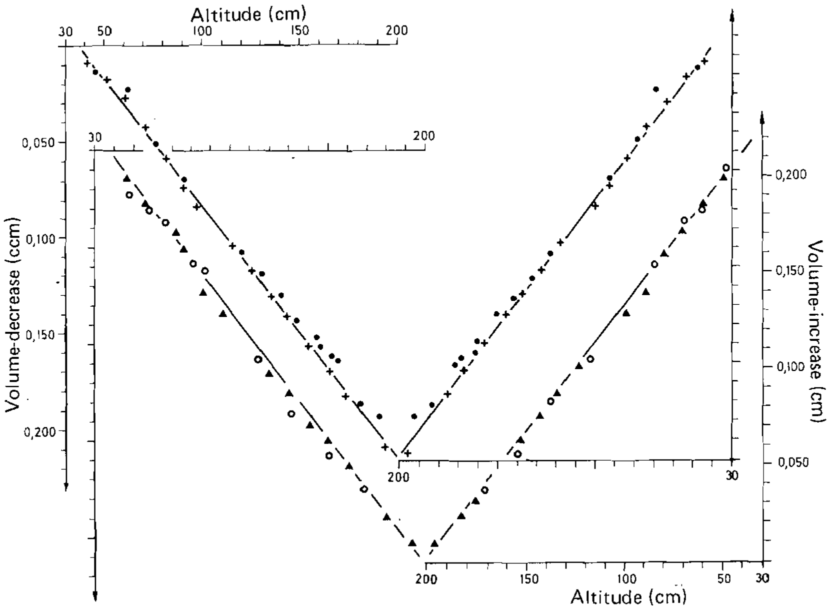

Fig. 7 : *Relations between vertical movements (abscissa) and volume changes (ordinates) for the goldfish C_4 in experimental series III. The volume changes of the active* (●), *the dead* (+) *and the paralysed fish* (▲) *and of the isolated swim-bladder* (O) *are drawn. For further explanation see text.*

Fig. 7 : *Relations entre les mouvements verticaux (abscisse) et les changements de volume (ordonnée) pour le poisson C_4 dans la série expérimentale III. Les changements de volume concernent le poisson actif (point), mort (croix), paralysé (triangle) et la vessie natatoire isolée (cercle). Explications complémentaires dans le texte.*

Narcotized and dead *Tilapia* did not rise from the bottom of the chamber until the pressure had been reduced by about 30 cm H_2O (which corresponds to an increase in volume of 0.075 ccm) ; narcotized and dead goldfish rose only after a reduction of 90-100 cm H_2O, which corresponds to an extension of 0.110 ccm. So, in *Tilapia* the 25-fold, in goldfish the 37-to 55 fold of the average volume changes measured in experimental series I-1 would have been necessary to cause a neutral buoyancy (*see Table I*).

Experimental series IIIb :

As far as size and direction is concerned, the continuously recorded volume-changes in the isolated swim-bladder deviated from the stationarily recorded ones in the same way as in the freely swimming fish. That is another support for the opinion that the differences between stationary and continuous recording are not due to muscular activity (*cf.* above).

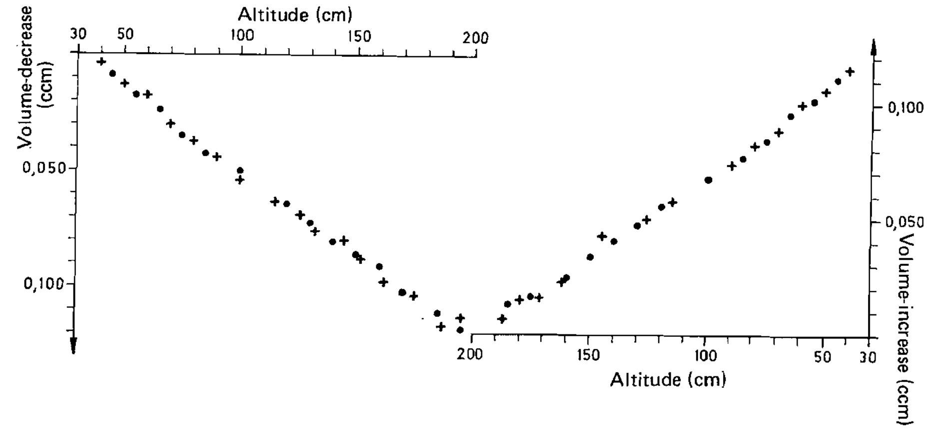

Fig. 8 : *Relations between vertical movements and volume changes for the active* (●) *and the dead* (+) *trout. For further explanation see text.*

Fig. 8 : *Relations entre les mouvements verticaux et les changements de volume pour une truite active* (*point*) *et morte* (*croix*). *Explications complémentaires dans le texte.*

4) *Discussion*

Since differences between active, anesthetized and dead fish—expected according to Delaroche—could not be found, I consider his theory disproved for the three species investigated. Restrictions in the free extension of the gas I presume to be due to the resistance of the surrounding tissues. In goldfish in which an isolated swim-bladder yielded the same changes in volume as an intact fish, I suggest that the bladder wall itself is responsible for the resistance.

That is in accordance with the results which Alexander (1959c) describes for various Cyprinids.

The same should be true for the two other species investigated, since *Tilapia* was found to have a bladder with a thin wall, whereas the bladder wall of the trout resembles that of goldfish in strength. These results square with the corresponding extensions (*cf. Fig. 5, 7 and 8*). Furthermore they are in conformity with detailed morphological investigations of bladder walls (Rauther, 1922 ; Eissele, 1922 ; Jaeger, 1903 ; Gegenbaur, 1901 ; Saupe, 1939 ; Fänge, 1943 ; Jones and Marshall, 1953).

Whereas the curves of the trout and cichlids at least have a similar shape as the computed ones (*cf. Fig. 6*), the volume changes of goldfish increase linearly. (For volume changes in other species see Alexander, 1959a, c ; Jones 1951). The following explanation of this difference is a hypothetical one and should be verified by further experiments :

The coefficient of elasticity of elastic, collagen and contractile fibres, which form most of the material in the bladder wall, do not obey Hook's law, i.e. they are not constants (4).

At the beginning the extensions of such " biologic elastomers " are large, but then with increasing loads such extensions decrease (Lullies,

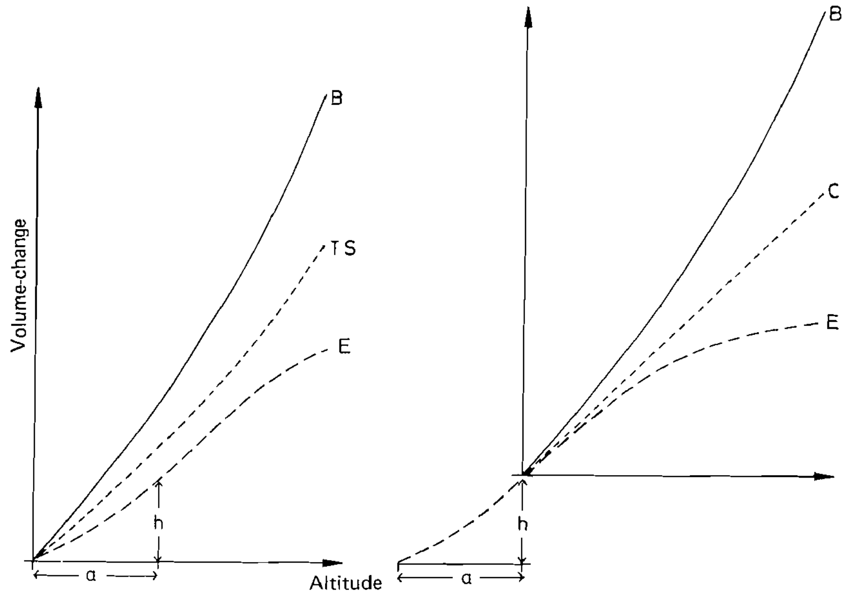

Fig. 9 : *Schematic graph for explaining the differences in the curve-shapes of* Fig. 3-6. *B : curve-chape as it has been computed after Boyle's law. E : assumed curve-shape of the expansion of tissues. a : distance of vertical movement. h : assumed expansion of the tissues. Left : T, S : curve-shape as it has been recorded for* Tilapia *and* Salmo. *Right : C : curve-shape as recorded for* Carassius. *For further explanation see text.*

Fig. 9 : *Représentation schématique expliquant les différences dans les formes des courbes des fig. 3-6. B : forme de courbe calculée d'après la loi de Boyle. E : Courbe supposée de l'extension des tissus : a : distance de mouvement vertical. h : expansion supposée des tissus. A gauche : T, S : courbe enregistrée sur* Tilapia *et* Salmo. *A droite : C : courbe enregistrée pour* Carassius. *Explications complémentaires dans le texte.*

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(4) Hook's law says : within certain limits the extension ε of an abject is proportional to the affecting strain. $\varepsilon = 1/\rho \, . \sigma$ (ρ = coefficient of elasticity).

1966 ; King and Lawton, 1950). So, if one considers the volume changes ΔV measured in the experimental series II and III as the results of the gases' free extension (B), which are superimposed by the restricted expansions of the tissues (E), then a curve like T and S (*Fig. 9, left*) would result in fishes whose internal bladder pressure is equal to the external water pressure.

It seems probable to me that the increase in tonus and the swelling of the somatic muscular systems occurring during those swimming movements are responsible for the differences. That opinion is confirmed by the results with *Tilapia.* Even in series II they did not wriggle their bodies but moved by fanning only their pectoral fins ; and in this species no differences between the results of series II and III had been recorded.

Such an influence of the wriggling cannot be interpreted as a compensation in the sense of Delaroche because it always leads to a reduction of volume.

Cyprinids, however, in the adapted state have an over-pressure of 2-3 cm Hg (= 27-40 cm H_2O) in their bladders (Alexander, 1959a). Therefore it might be, that the tissues have already expanded by an amount of h before the upward movement has been started ; whereas in other species a similar expansion does not occur before the fish has moved vertically over a distance a. That is why in the Cyprinids the decreasing extensibility of the bladder wall might make itself conspicuous earlier than in other fishes. Superimposed by the free extension of the gas the linear ascent C (*Fig. 9, right*) would result.

GENERAL DISCUSSION

I. Regulation of the bladder-volume through the trunk's muscles

Though the results of series III indicate that the resistance against the free extension of the gas comes first of all from the bladder wall itself, a comparison with the results of series II shows that the trunk's muscles might be involved, too. The differences in volume changes of 11.5-14.5 % might have been caused by the different behaviours of the fish in both series. During experimental series III the animals seemed to be very frightened by the compelled vertical movements ; after transporting them upward or downward they always lay motionless on the lower sheet of plexiglas. On the other hand in series II, when swimming freely, the goldfish and the trout even then wriggled their bodies incessantly when they stayed at a certain altitude.

The question whether regulation of volumes though muscles only takes place in more critical situations, e.g. during vertical movements which cause extensions that might tear the fish up to the surface, this question is answered in the negative by the literature. Generally physoclistous fishes can only move without difficulties within a range of 1/6 of the original pressure (Jones, 1952). That range had been covered by the cm high experimental apparatus used in these experiments. Physostomous fishes spit gas from their bladers if the pressure is reduced by 3-10 % (Alexander, 1966) ; that is also in accordance with my results in goldfish. They spit gas nearly on the same level (h = 105 cm) on which they would experience a lift when anesthetized or dead.

Furthermore an efficient regulation of volume can only be brought about if nearly equal pressures act upon the bladder from all sides ; otherwise the wall would give way in some places. But, as Harder (1964), Eissele (1922) and McCutcheon (1958, 1962) point out, such a pressure would also affect blood-vessels, the gut, the kidney, and other organs. They could be pressed to such a degree that their functions would be blocked.

It is true that experiments with ether (Jaeger, 1903) and electrical stimulation (Long, 1959) have shown an influence of the trunk's muscles on bladder-volume and bladder-pressure of 15-20 cm H_2O ; but they do not show whether or not a fish uses that possibility on normal terms. That is the point which Jaeger overlooked when he pretended that his experiments with the paralysing ether had supported Borelli's hypothesis.

In comparison with this McCutcheon's investigations on *Lagodon rhomboides* (Sparidae) are more revealing. Fish of this species react to an increase of bladder-volume with a ' yawn '. In doing so the bladder-pressure increases within 1-2 min by 1-5 cm H_2O and can be maintained for 5-10 min. Thus the releasing volume changes become compensated. " Though intrinsic muscles may be involved ", McCutcheon (1958, 1962) holds the trunk's muscles responsible for these results. The muscles wrap in two long dorso-lateral lobes of the bladder which run along the spinal column on both sides.

II. The role of the swim-bladder's muscles

Rauther (1922) and Eissele (1922) state that there exist only smooth muscles in the wall of the swim-bladder. Where striated fibres have been found in connection with the bladder they serve in all known cases as sound-producing organs and derive from the trunk's hypaxoneus muscular systems (Jones and Marshall, 1953 ; Schaller, 1971).

Fänge (1943) has proven that strips of muscles which had been extirpated from the swim-bladders of various species of Cyprinidae contract when they are stimulted electrically or chemically (with epinephrine). Long (1959) quotes some older studies of other investigators which revealed changes in the tension of the smooth bladder-muscles after having stimulated the innervating nerves in the carp (*Cyprinus carpio*).

Peter's (1951) studies on the seahorse (*Hippocampus brevirostris*, Sygnathidae) are more revealing. Animals which Peters had narcotized with MS 222 Sandoz sometimes rose from the bottom and ascended to the surface without any detectable movement of the trunk or the fins. The reverse happened, too. According to Borelli, Peters explains this behaviour by sudden volume changes of the bladder ; but unlike Borelli he holds contractions and relaxations of the smooth bladder muscles responsible for the vertical movements since the trunk's muscular system had been paralysed by MS 222. But this second explanation exclude a possibility which is included in Borelli's hypothesis : the intended regulation of the volume in order to cause vertical movements. The smooth muscles of the bladder are innervated by branches of the Nervus vagus (Jones and Marshall, 1953). Thus they are under the control of the autonomous nervous system and cannot be influenced on purpose. There could only exerts a reflexive control as supposed by Delaroche.

This conception is confirmed by other results of Peters of which he says that they need further verification : in contrast to Baglioni (1908) he found that sea-horse are not lifted to the surface when the external pressure is reduced by 0.12-0.13 atm (= 120-130 cm H_2O). They seem to compensate the lowered pressure successfully by diminishing the bladder volume.

The studies of McCutcheon and Peters are the only I know in which regulation of volume by muscles has been proven possible. Both species are highly specialized in their morphology : *Lagodon* in that of its swim-bladder, *Hippocampus* in that of its trunk.

Aknowledgement : The subject has been suggested and supported by Dr. W. Wickler who also carefully read the manuscript. I am grateful to him and Dr. J. Lamprecht for useful suggestion. I am indebted to Dr. R. Fernald for correction of the English translation. Further thanks are due to Mr. H. Jakobs for helping with the experimental apparatus, to Mrs. S. Baur for assistance in evaluating the recorded data, and to Miss B. Knauer for help with the figures.

SUMMARY

The theories of Borelli (1680) and Delaroche (1809) on the functions of swim-bladders have been experimentally investigated in two physostomous species (*Carassius auratus* and *Salmo gairdneri*) and one physoclistous one (*Tilapia mariae*).

1. A tendency to make vertical movements was elicited in the fishes by offering food, with only few centimeters of movement allowed. The recorded volume-changes (*Table I*) are considered not a cause but a consequence of the movements.

2. The fish were allowed to move freely up and down over a range of almost 200 cm. The volume changes which they showed between the beginning and end altitude are identical—no matter if they have been measured when the swimming fish stopped, continued, or turned round at that altitude (*Fig. 3-5*).

3. Living, anesthetized, and dead fish were subjected to the same pressure changes. The resulting volume changes corresponded with each other.

All results confirm Moreau's (1876) conception that fish do not regulate the volume of their swim-bladders by muscles—neither to start a vertical movement (Borelli, 1680), nor at its end to cancel the passive changes (Delaroche, 1809). The final review of some elder and more recent studies reveals only two possible exeptions from these findings and interpretations ; that is in species with a very specialized morphology of the swim-bladder and the body.

REFERENCES

Alexander, R.McN., 1959a. The physical properties of the swim-bladder in intact Cypriniformes. *J. Exptl. Biol., 36,* 315.

Alexander, R.McN., 1959b. The densities of Cyprinidae. *J. Exptl. Biol., 36,* 333.

Alexander, R.McN., 1959c. The physical properties of the isolated swim-bladder in Cyprinidae. *J. Exptl. Biol., 36,* 341.

Alexander, R.McN., 1966. Physical aspects of swim-bladder function. *Biol. Rev. 41,* 141-176.

Baglioni, S., 1908. Zur Physiologie der Schwimmblase der Fische. *Z. allgem. Physiol. 8,* 1.

Baglioni, S., 1910. Zur Physiologie der Schwimmblase der Fische. *Z. allgem. Physiol. 11,* 145.

Borelli, A., 1680. De motu animalium, Bd. 1 ; Rom.

Bové, F.J. MS 222 Sandoz, Das Anaestheticum und Sedativum für Fische, Frösche und andere Kaltblüter. *Sandoz Ag,* Basel.

Delaroche, F., 1809. Observations sur la vessie aérienne des Poissons. *Ann. Mus. Hist. nat.,* Marseille, *14,* 184.

Eissele, L., 1922. Histologische Studien an der Schwimmblase einiger Süsswasserfische. *Biol. Zbl., 42,* 125.

Evans, H.M., 1925. A contribution to the anatomy and physiology of the air bladder and the Weberian ossicles in Cyprinidae. *Proc. Roy. Soc. B, 97,* 545.

Fänge, R., 1943. Preliminary notes on the reactions to electrical and chemical stimulation of smooth muscles in the swim-bladder of Cyprinids. *Kungl. Fysiogr. Sällskapets i Lund Förhandlingar, 13.*

Gegenbaur, 1901. Vergleichende Anatomie der Wirbeltiere, Bd. II, Leipzig.

Gerthsen, C., 1966. Physik ; 9. Aufl., *Springer-Verl.,* Berlin.

Harder, W., 1964. Anatomie der Fische ; in : Demoll-Maier-Wundsch : Handbuch der Binnenfischerei Mitteleuropas II A. *E. Schweizerbartsche Verlagsbuchh.,* Stuttgart.

Hawkins, A.D., 1973. The sensitivity of fish to sounds. *Oceanogr. Mar. Annu. Rev., 11,* 291-340.

Hesse, 1935. Tierbau und Tierleben, Bd. 1, 2. Aufl., Jena.

Jaeger, A., 1903. Die Physiologie und Morphologie der Schwimmblase der Fische. *Arch. Physiol.* 1903, 77.

Jacobs, W., 1932. Untersuchungen zur Physiologie der Schwimmblase. II. Volumenregulation in der Schwimmblase des Flussbarsches. *Z. vergl. Physiol. 18,* 125.

Jones, F.R.H., 1951. The swim-bladder and the vertical movement of teleostean fishes, I. Physical factors. *J. Exptl. Biol. 28,* 553.

Jones, F.R.H., 1952. The swim-bladder and the vertical movements of teleostean fisches. II. The restriction to rapid and slow movements. *J. Exptl. Biol., 29,* 94.

Jones, F.R.H., 1957. The swim-bladder ; in : Brown, M.E. : The physiology of fishes II. *Acad. Press Inc. Publ.,* New York.

Jones, F.R.H., and Marshall, N.B., 1953. The structure and functions of the teleostean swim-bladder. *Biol. Rev., 28,* 16.

King, A.L.,and Lawton, R.W., 1950. Elasticity of body tissues.*Medical Physics* (O. Glasser, Hrsg.), *2,* 303.

Ladiges, W., 1970. Die Knochenfische ; in : Grzimek's Tierleben, Bd. IV, 134. *Kindler,* München.

Long, L., 1959. Central control over functions of the air-bladder in fish. *Fizziol. Z. SSSR., 45,* 880.

Lullies, H., 1966. Animalische Physiologie ;in : Medizin von heute. *Troponwerke,* Köln-Mühlheim.

McCutcheon, F.H., 1958. Swim-bladder volume, buoyancy and behavior in the pinfish, Lagodon rhomboides (Linn.). *J. Cell. Comp. Physiol. 52,* 453.

McCutcheon, F.H., 1962. Swim-bladder volume control in the pinfish, Lagodon rhomboides. *J. Cell. Comp. Physiol. 59,* 203.

Moreau, F., 1876. Recherches experimentales sur les fonctions de la vessie natatoire. *Ann. Sci. nat. Zool.* ser. 6, *4,* 1.

Peters, H.M., 1951. Beiträge zur ökologischen Physiologie des Seepferdes (Hippocampus brevirostris). *Z. vergl. Physiol. 33,* 207.

Rauther, M., 1922. Zur vergleichenden Anatomie der Schwimmblase der Fische. *Ergebn. Zool. 5,* 1,

Saupe, M., 1939. Anatomie und Histologie der Schwimmblase des Flussbarsches (Perca fluviatilis) mit besonderer Berücksichtigung des Ovals. *Z. Zellforsch. A. 30,* 1.

Schaller, F., 1971. Uber den Lautapparat von Amazonasfischen. *Naturwissensch. 58,* 11, 573.

Wunder, W., 1936. Physiologie der Süsswasserfische ; in : Demoll-Maier : Handbuch der Binnenfischerei Mitteleuropas II B. *E. Schweizerbartsche Verlagsbuchh.,* Stuttgart.