

ACOUSTIC PROPERTIES OF THE COD SWIMBLADDER

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INTRODUCTION

The teleostean swimbladder has a variety of functions. Though it is best known as a hydrostatic organ, maintaining the fish at neutral buoyancy, it may also serve in respiration, in the detection of static pressure changes, in sound-production and in hearing.

The part played by the swimbladder in hearing is revealed in many fish by the presence of a mechanical connexion to the ear. Thus, in the Ostariophysi, an anterior chamber of the swimbladder is connected to the sacculus of each ear by a chain of small bones – the Weberian ossicles. The functioning of this apparatus has been reviewed by Alexander (1966). An association of diverticula from the swimbladder with the ear has also been reported for the families Anabantidae, Balistidae, Clupeidae, Engraulidae, Holocentridae, Moridae, Mormyridae, Notopteridae, Ophiocephalidae, Sciaenidae and Sparidae (Jones & Marshall, 1953; Alexander, 1966; van Bergeijk, 1967; Tavalga, 1971).

The teleost ear consists of a membranous labyrinth of sacs and canals. Each sac contains a calcareous mass (the otolith) mounted upon an epithelial bed consisting of sensory hair cells and their supporting cells. Though the otolith organs may serve an equilibrium function (Lowenstein, 1971), they are also implicated in hearing. In a sound field the tissues of the fish are effectively transparent to sound and vibrate at approximately the same amplitude as the surrounding water particles. However, the more dense otoliths lag behind these oscillations of the head, thereby stimulating the hair cells (Pumphrey, 1950; Griffin, 1955; de Vries, 1956). The system responds essentially to the kinetic component of any sound – the particle velocity or particle displacement – rather than the sound pressure.

The swimbladder can assist in hearing because it contains gas, which is more compressible than the surrounding tissues and water. The pressure changes accompanying the passage of a sound will cause changes in the volume of the organ, which in turn may be translated into an amplified movement of the otolith. The system responds to sound pressure, though the end organ itself is still sensitive to particle motion.

Poggendorf (1952) and de Vries (1956) examined the displacement amplification provided by a swimbladder. They concluded that if an appropriate mechanism existed for coupling the movements of the swimbladder to the ear, then substantial amplification could occur over a wide range of frequencies. Poggendorf, and more recently van Bergeijk (1967) and Alexander (1966), went further and suggested that the swimbladder might be capable of stimulating the ear even in the absence of a

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mechanical linkage. Pulsations of the swimbladder, induced by a sound, might be communicated to the ear directly, through the intervening body tissues. Indirect evidence that this occurs in the cod has been presented by Enger & Andersen (1967) and Chapman & Hawkins (1973).

Poggendorf (1952) and de Vries (1956), in considering the acoustic properties of the swimbladder, assumed a close correspondence between the behaviour of the organ and that of a free gas bubble in water. The latter can be regarded as a simple mass/spring system, where the spring factor is provided by the low elastic modulus of the contained gas, and the mass results from the high inertia of the surrounding water. Minnaert (1933) has shown that an ideal spherical bubble has a resonance frequency, given by

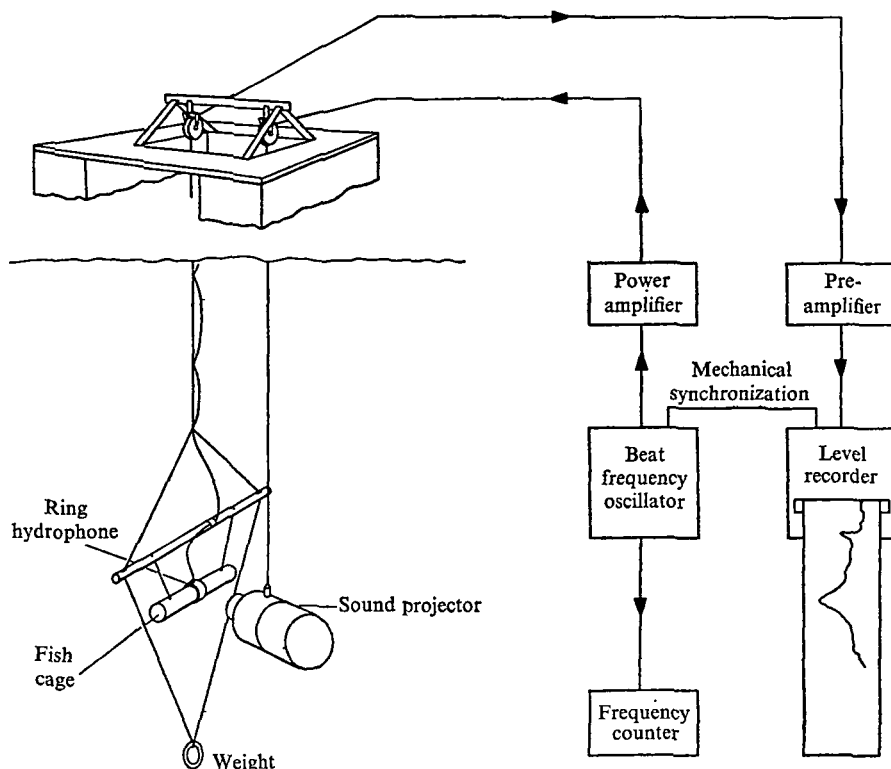
$$f_r = (2\pi a)^{-1} \rho^{-\frac{1}{2}} (3\gamma P)^{\frac{1}{2}}, \quad (1)$$

where a is the radius of the bubble, ρ is the density of the surrounding water, γ is the ratio of specific heats for the gas (which for air equals 1.402), and P is the hydrostatic pressure. If such a bubble is exposed to sound pressures of varying frequency but constant amplitude it pulsates, the response reaching a maximum at the resonance frequency. The magnitude of the response at resonance and the sharpness of the resonance peak are a function of the degree of damping, which is associated with a loss of energy from the system as it pulsates.

It is likely that several additional factors must be taken into account in applying the resonance equation to the fish swimbladder. The organ may not have the spherical shape assumed; the static pressure in the medium and in the contained gases may be different; and in addition the motion of the organ may be restrained by the surrounding tissues. These factors will affect both the resonance frequency and the damping (Weston, 1967). The gas contained within the swimbladder usually has a higher proportion of oxygen than air, but acoustically this makes little difference.

Studies on fish in the deep scattering layers have shown that the swimbladders of these relatively small fish behave acoustically like free bubbles (Hersey & Backus, 1954; Andreeva, 1964; Marshall & Chapman, 1964; Chapman & Marshall, 1966). Andreeva (1964), however, suggested that for fish at shallow depths (< 200 m) the effect of the surrounding tissues on the swimbladder might be much more important. Alexander (1966) later concluded from an examination of the hearing thresholds of several species, and of the sounds emitted by a fish which employed the swimbladder as the sound-producing organ, that the resonance of the swimbladder was indeed heavily damped in shallow water. This has since been confirmed by McCartney & Stubbs (1971) in an experimental study of the low-frequency target strengths of fish.

To elucidate the role of the swimbladder in hearing more fully we have performed a series of experiments to measure the sound field re-radiated by the swimbladders of intact living cod. The technique employed was originally developed by McCartney & Stubbs (1971), and involved measuring the sound pressures generated by a wide-band source, first in the free-field and then in the close vicinity of a fish. Observations were made on cod maintained at different depths to examine the effect of hydrostatic pressure upon the acoustic properties of the organ.



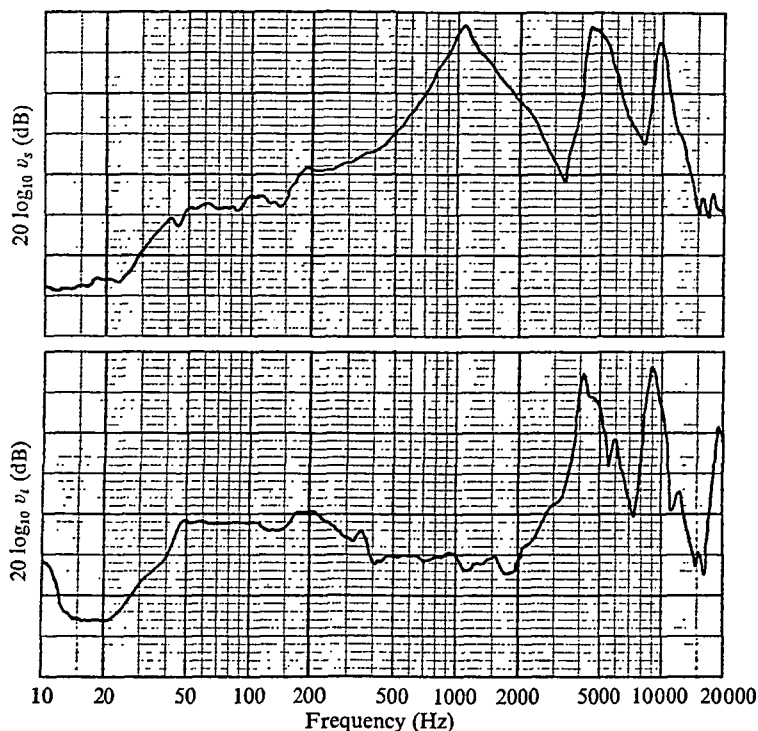
Text-fig. 1. Sketch of the experimental equipment. See text for details.

MATERIALS AND METHODS

The experiments were performed on 20 juvenile cod, *Gadus morhua* L., ranging in length from 13 to 50 cm. The fish were captured on baited handlines in shallow water (< 10 m) to avoid damage to the swimbladder, and were subsequently allowed to adjust to captivity in an aquarium tank for one month before transfer to the experimental site. At the site the fish were either kept in a netting enclosure (2 × 1 × 1 m), floating at the surface, or lowered to greater depths in a smaller cage (1 × 1 × ½ m). The fish were allowed at least 48 h to adjust to the appropriate depth, and were subsequently transferred to the experimental apparatus by divers.

Estimates of the swimbladder volumes of cod of different size were required during the experiments to permit comparison of the results with those expected from free gas bubbles of similar volume. These estimates were obtained by measuring the swimbladder volumes of 11 surface-adapted fish using a weighing technique. This gave a mean percentage ratio of swimbladder volume (ml) to the weight of the fish (g) equal to 3.6% (S.D. = 0.46). Alexander (1966) has calculated that percentage volumes of between 3.1 and 5.7 can be expected for marine teleosts at neutral buoyancy.

A sketch of the apparatus used for the acoustic measurements is given in Text-fig. 1. The experiments were conducted from a polystyrene raft, moored in the centre of a flooded quarry at the Island of Seil, Argyll. The quarry diameter and maximum depth



Text-fig. 2. Level recordings with (upper) and without (lower) a 16 cm cod inside the ring hydrophone. The fish was adapted to the surface, and the recordings are from 12 m depth. Note the fish resonance at 1100 Hz.

were 150 and 60 m respectively. The water mass within the quarry over the depth range of interest remained homogeneous throughout the experiments, maintaining a temperature of 7.0 °C and a salinity of 34.2 ‰. The fish was suspended beneath the raft inside a cylindrical cage made from a plastic netting (Netlon) known to be acoustically inert at frequencies below 5 kHz. A ceramic ring hydrophone (10 cm diameter) was fitted around the cage, enclosing the fish at mid-trunk level. Sounds were presented from a moving-coil projector (Dyna-Empire, Type J 11), which was driven by an amplifier (Derriton, Type 25 WT) connected to a beat-frequency oscillator (Brüel & Kjaer, Type 1022), sweeping over the frequency range from 20 Hz to 20 kHz. The projector was suspended separately from the raft, at a horizontal distance of 1 m from the fish.

The fish and sound projector could be raised or lowered from the shore, using an arrangement of ropes and pulleys. By this means the acoustic experiments could be performed at any depth between 4 and 50 m. (Outside this depth range acoustic interference was experienced from either the water surface or the quarry bottom.) For depths shallower than 20 m the sound projector was maintained at the same depth as the fish cage, while for measurements at greater depths the projector remained at 20 m (its maximum depth limit).

The level of the received hydrophone signal was monitored on a logarithmic level recorder (Brüel & Kjaer, Type 2305). This recorder was synchronized mechanically,

With the beat-frequency oscillator to provide a plot of sound pressure (dB) against frequency. As Text-fig. 2 shows, with a fish inside the ring the hydrophone output gave a characteristic peak at the resonance frequency of the swimbladder. A precise measurement of the frequency at which the peak occurred was obtained using a frequency counter (Advance, Type TC-13) combined with manual tuning of the oscillator. Where the distance between the sound projector and the fish was large, the resonance curve was affected by small irregularities arising from standing waves set up between the sound projector, the water surface and the quarry floor. In these cases the resonance frequency was read directly from the smoothed level recordings.

The ratio of the sound pressure re-radiated or scattered from the fish (p_s) to the incident sound pressure (p_i) in the experimental arrangement is given by the expression:

$$p_s/p_i = S_s v_s / S_i v_i, \quad (2)$$

where S_s is the sensitivity of the hydrophone to sound pressures emanating from inside the ring, S_i is its sensitivity to plane waves at 'edge on' incidence, v_s is the voltage generated at the hydrophone output terminals for the sound emanating from inside the ring and v_i is the voltage generated by the plane incident wave.

Though v_i , the voltage generated in the absence of a fish, can easily be measured, v_s cannot be measured directly. The voltage generated with the fish present (v_p) is the sum of both the scattered sound pressure from the fish and the incident sound pressure. However, as McCartney & Stubbs (1971) pointed out, $S_s \gg S_i$, and therefore $v_s \gg v_i$; from which it follows that $v_s \simeq v_p$. Hence, in decibel terms:

$$20 \log_{10}(p_s/p_i) \simeq 20 \log_{10}(S_s/S_i) + 20 \log_{10}(v_p/v_i), \quad (3)$$

where $20 \log_{10}(S_s/S_i)$ is a calibration factor for the hydrophone. McCartney & Stubbs (1971) demonstrated that this calibration factor remained constant for frequencies well below the resonance frequency of the ring hydrophone (nominally 5 kHz). Thus, provided that the swimbladder resonance curve does not extend into the region of hydrophone resonance, it is not necessary to know the calibration factor. Comparison of the voltage/frequency curves obtained in the presence and absence of the fish can be used directly to derive the resonance frequency and damping of the swimbladder.

During the course of our experiments we were able to verify that this technique could be used to derive the resonance frequency of an air-filled balloon of known volume with an acceptable margin of error. Similar observations were made by McCartney & Stubbs (1971), who also reported that variation of the axial and radial position of the balloon inside the ring transducer had little effect upon the measurements.

RESULTS

It was evident for all the fish examined that the swimbladder was resonant, the re-radiated sound pressures reaching a maximum at a particular frequency, the resonance frequency (f_r). However, both f_r and the broadness of the resonance curve (represented by Q , which we define as the ratio of f_r to the bandwidth at the '3 dB down' points) differed considerably from the values predicted for a free air bubble of the same volume. With the fish at a depth to which it was adapted, f_r was higher than predicted, while Q was lower (i.e. the resonance peak was broader).

For a free gas bubble of constant mass the volume is inversely proportional to the pressure. Therefore, f_r varies with pressure, and hence water depth, in a well-defined way. From equation (1) it can be shown that $f_r^{1.2}$ is proportional to P (Weston, 1967). The question of how closely the swimbladder resembles a bubble acoustically can therefore be resolved by comparing the measured f_r values obtained at different depths. However, unlike a bubble, the gas content of the swimbladder can be regulated, the fish tending to maintain constant volume by secreting or absorbing gas. By this means the fish can ensure that the contribution to buoyancy provided by the swimbladder remains the same at different depths. It is therefore necessary to consider two possibilities. If the fish is moved very rapidly up or down through the water column, without allowing time for gas to be added or removed, then the behaviour of a constant mass of gas is being studied. The organ, like a free bubble, will tend to change volume with depth. Alexander (1959) has shown that in these circumstances the swimbladder of many physoclists follows the gas laws closely. That is, within certain limits the volume of the swimbladder is inversely proportional to the pressure. If, on the other hand, the fish is moved only slowly from one depth to another, allowing time for adaptation to each depth, then comparison with the behaviour of a constant volume of gas is more relevant.

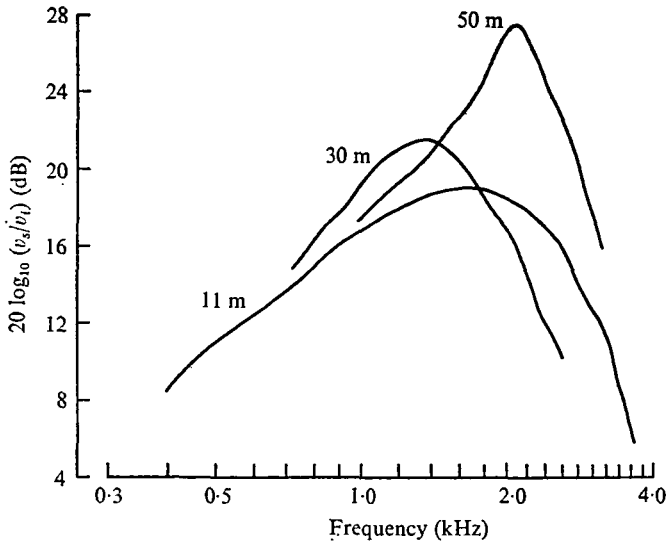
In our experiments, both of these possibilities were considered. In some experiments the fish were moved rapidly from one depth to another, at a speed limited only by the time taken to perform the acoustic measurements and to adjust the suspension ropes (approximately 2 min for each depth examined). However, on other occasions the fish were allowed time to adapt to particular depths.

Changes in resonance frequency accompanying rapid changes in depth

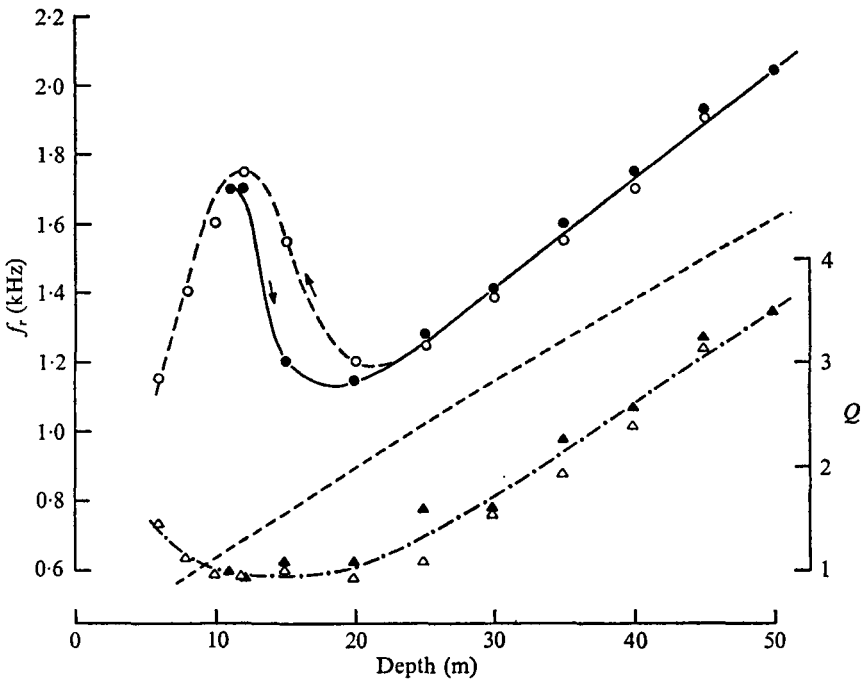
Text-fig. 3 presents the plots of $20 \log_{10} (v_s/v_i)$ obtained from a 16 cm cod transferred rapidly from 11 m (its adaptation depth) to two other depths. These plots illustrate that not only the resonance frequency but also the damping changed with depth, but in a rather irregular manner.

These trends are examined more closely in Text-fig. 4, where f_r and Q are plotted against depth. The f_r values for a bubble of constant mass, having the same volume as the swimbladder at adaptation depth, are included for comparison. In this experiment the fish was first lowered rapidly in steps from 11 to 50 m and subsequently raised to 6 m. Approximately 30 min elapsed before the fish returned to the original depth, so that some adjustment of the swimbladder may have occurred during the experiment, as suggested by the differences between the downward and upward curves.

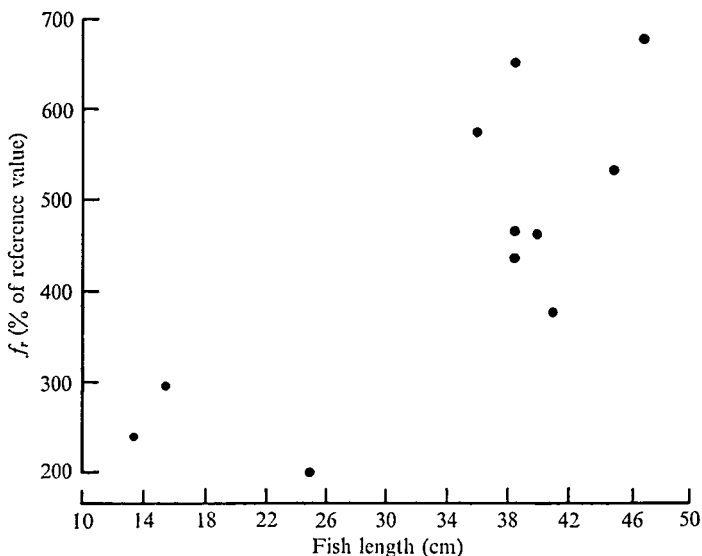
The most striking feature of this figure is that f_r is at a maximum at or near the adaptation depth of the fish, where Q is at a minimum. As the fish is moved deeper, f_r at first decreases until a minimum is reached, followed by a steady increase in f_r with depth. Thus, only at the greatest depths (where the pressure is two or more times greater than the pressure at adaptation depth) does the resonance frequency of the swimbladder increase with depth as does that of a free gas bubble of constant mass. Here, the measured values of f_r are higher than for a bubble of similar volume by a factor of about 1.25. At or near the adaptation depth the deviation is much greater, ranging from two to six times greater for different fish. This is illustrated by Text-fig. 5,



Text-fig. 3. Resonance curves for a 16 cm cod at three different depths. The fish was adapted to 11 m. Note that both f_r and Q change with depth.



Text-fig. 4. Changes in f_r (●, ○) and Q (▲, △) for rapid depth excursions. The fish, a 16 cm cod adapted to 11 m, was lowered to 50 m (filled symbols) and then raised to 6 m (open symbols). The dashed curve shows the expected changes in f_r for a free spherical bubble containing the same mass of gas as the swimbladder.



Text-fig. 5. The relationship between fish length and the maximum value of f_r attained at or near the adaptation depth. f_r is measured relative to the predicted f_r for a free bubble of equal volume at the same depth.

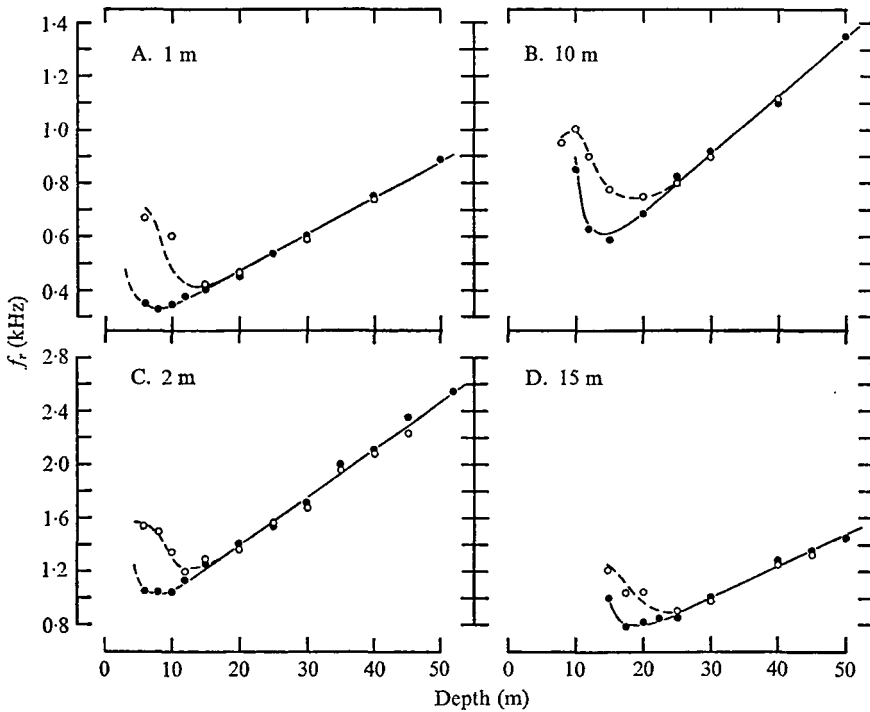
where the ratio between the maximum value of f_r attained at or near the adaptation depth, and the expected value for a free bubble of the same volume at this depth is plotted against fish size. The elevation of f_r is higher for larger fish.

The above observations applied to all the fish subjected to rapid depth changes. This is indicated for four fish by Text-fig. 6. Where surface-adapted fish were examined (Text-fig. 6A, C), the elevated values of f_r at adaptation depth could not be observed directly, but the values obtained at the shallowest depth (6 m) indicated that the same peak in f_r still existed.

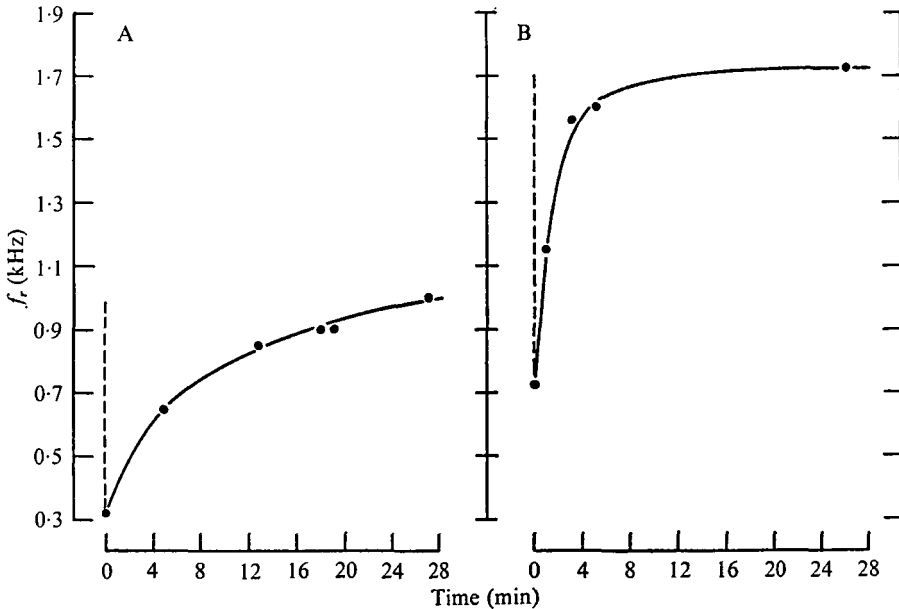
Low values of Q were obtained from all the fish examined. Q is an expression for the degree of damping of the swimbladder resonance, which is dependent upon the energy lost by the organ as it pulsates. A low Q indicates heavy damping. Devin (1959) and Andreeva (1964) considered the various energy losses incurred by a pulsating bubble, and concluded that near the sea surface viscous losses predominated. They predicted, however, that these viscous losses would decline rapidly with increase in depth, and that therefore Q should increase with depth. It was noted for cod (Text-fig. 4) that Q did increase with depth, as predicted, but the values obtained were much lower than those suggested by Andreeva (1964) for free gas bubbles, and for very small fish in midwater scattering layers. For cod, Q at the adaptation depth was approximately 1. The highest value observed was $Q = 4.1$, for a 14 cm cod at 50 m (much deeper than the adaptation depth of 15 m).

Changes in resonance frequency accompanying adaptation to a new depth

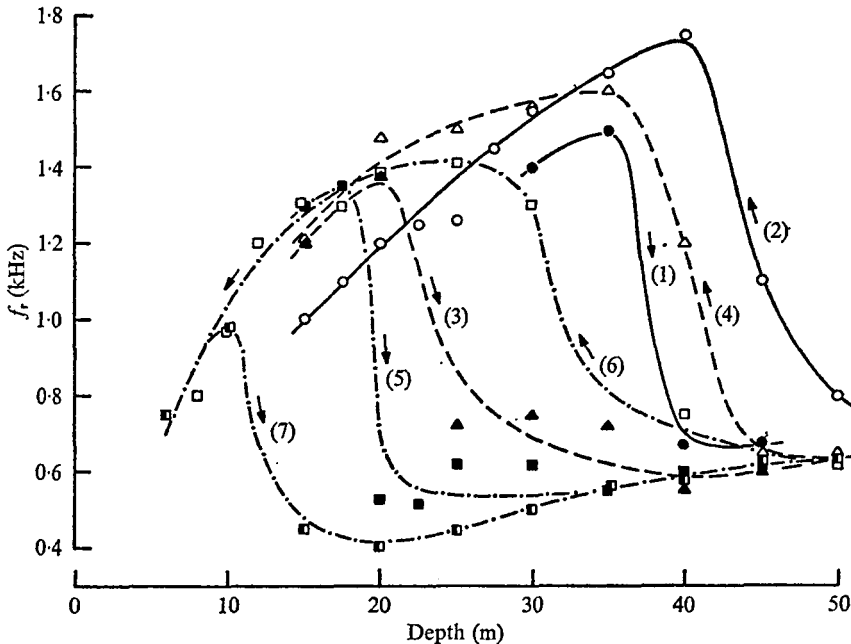
It is unlikely that free-swimming fish normally make such large and rapid depth excursions as those imposed upon our experimental animals. Such changes could only be performed if the animals were willing to accept drastic changes in their buoyancy.



Text-fig. 6. Changes in f_r with rapid changes in depth. Fish A, B, C and D were 44, 25, 14 and 23 cm in length, respectively. The adaptation depths are indicated on each plot. Same symbols as Text-fig. 4.



Text-fig. 7. Changes in f_r with time, following rapid transfer to a new depth. Fish A (47 cm) was lowered from the surface to 6 m; while fish B (14 cm), adapted to 15 m, was raised to 8 m. Note the very rapid increase in f_r , following an initial decrease (dashed line).



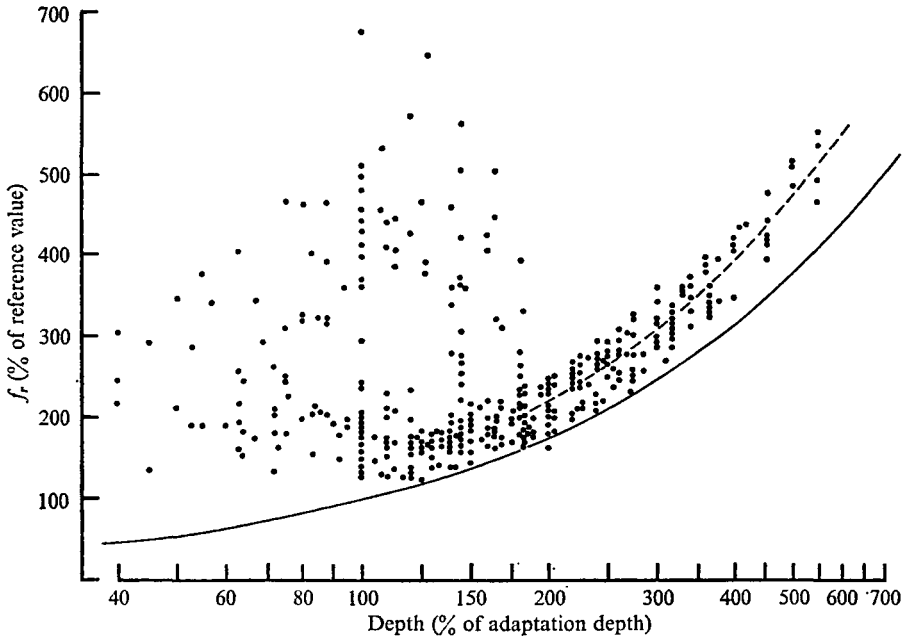
Text-fig. 8. Changes in f_r for rapid depth excursions by a 40 cm cod adapted initially to 30 m (●, ○). Measurements after 4 h at 15 m (▲, △) and after 16 h at 15 m (□, ■) are also included. Filled symbols indicate lowering the fish, journeys (1), (3) and (5); open symbols raising the fish, journeys (2), (4) and (6). After the last series the fish was taken directly down again to 50 m (■), journey (7). Note that the elevated values of f_r are encountered near the adaptation depth; and that the degree of elevation of f_r increases with adaptation depth.

Thus, though the experiments reported so far may prove informative about the general acoustic properties of the swimbladder, they do not fully indicate how the acoustic properties of the organ might vary in nature. To understand this in more detail it is necessary to consider the changes in f_r which attend slower or more permanent changes in depth.

We have already noted that when a fish was rapidly lowered to 50 m and then raised again, the downward and upward plots of f_r were different (Text-figs. 4, 6). This suggests that even during this short time period (approximately 30 min) some form of adjustment to greater depth, not necessarily involving the secretion or absorption of gas, had occurred.

Adjustment of f_r was also observed when a fish was displaced rapidly to a new depth and maintained there. Text-fig. 7 shows two plots of f_r against time for fish taken to deeper and shallower depths. Following the immediate initial decline in f_r caused by the transfer to the new depth, f_r increased, at first rapidly (100% increase in f_r was observed in less than 4 min), and then progressively more slowly until it attained a value rather similar to the value at the original adaptation depth. If the fish was adapting to a greater depth the new adjusted value of f_r was generally higher than the original. For a shallower depth it was generally lower.

Text-fig. 8 depicts the changes in f_r shown by a 40 cm cod, originally adapted to 30 m. This fish was taken rapidly down to 50 m (1) and then brought back to 15 m (2). It was allowed to stay at 15 m for 4 h, and then rapidly taken again to 50 m (3) and



Text-fig. 9. Summary of results from 20 cod, 14–50 cm in length, removed rapidly from their adapted depth. To compare fish of different size, f_r is given relative to f_r for a free bubble at adaptation depth, containing the same volume of gas as the swimbladder. The f_r /depth relationship for this reference bubble is indicated by the fully drawn curve, while the broken curve gives values 25 % above. Note the high variability of f_r around adaptation depth, whereas at greater depths f_r tends to be about 25 % above that of the reference bubble.

back (4). This procedure was repeated after a further 12 h (5 and 6); but this time the fish was brought to 6 m and then taken again to 50 m (7).

On going from 30 to 50 m, journey (1), f_r falls; and this general fall is seen in journeys (3), (5) and (7). On returning from 50 to 15 m, journey (2), f_r rises; and this rise is repeated in journeys (4) and (6). On these upward journeys, which take only a few minutes, f_r is always higher at a given depth than on the corresponding downward journey, confirming that some adjustment to the greater depths had occurred, as also indicated by Text-figs. 4 and 6. Between journeys (2) and (3) the fish was maintained at 15 m for 4 h. During this time with the fish at a constant new depth, f_r increased, showing a similar pattern to that in Text-fig. 7 B. Similarly, between journeys (4) and (5), the fish was maintained at 15 m for a further 12 h. Again f_r increased, though this time by a smaller amount. The fish therefore adjusted to both transient and permanent depth changes by changing f_r in a consistent pattern, always tending to maintain a higher value than that predicted for a free gas bubble of similar volume.

Thus, given sufficient time at a given depth, a fish can be expected to adjust the swimbladder to provide an f_r higher than one would expect from a gas bubble of the same volume. This elevated value of f_r is retained for small excursions from the adaptation depth, but any large or rapid change in depth results in a substantial drop in f_r , necessitating a further period of adjustment before the elevated value is restored. It is possible that these elevated values of f_r at adaptation depth are acoustically advantageous to the fish. Alternatively, they may represent some other advantageous adaptation

of the swimbladder, not associated with an acoustic function. In either case it is possible that the rate at which f_r adjusts to a new depth represents a critical factor, which might limit the vertical excursions that the fish can undertake.

Text-fig. 9 summarizes the results from all the fish examined. It includes all measurements of f_r made on fish whose adaptation depth was known, and presents information on the changes occurring in f_r during rapid excursions from the adaptation depth. The measured values of f_r have been referred to a given percentage change in depth rather than to the absolute depth. In addition, to enable fish of different sizes to be compared each resonance frequency is presented as the percentage of the value predicted for a free bubble of equal volume to the swimbladder at adaptation depth. The changes which occur in the resonance frequency of this bubble of constant mass as it is displaced to different depths are shown for comparison.

The general pattern in this figure resembles that for individual fish. Though the swimbladder does not behave acoustically as a bubble for moderate changes in depth, it does resemble a bubble very closely at much greater depths. For the latter, f_r is about 1.25 times higher than predicted. At or near the adaptation depth f_r is more variable, and often much higher than expected. The degree of elevation depends, as we have seen, upon the size of the fish, and its previous hydrostatic history.

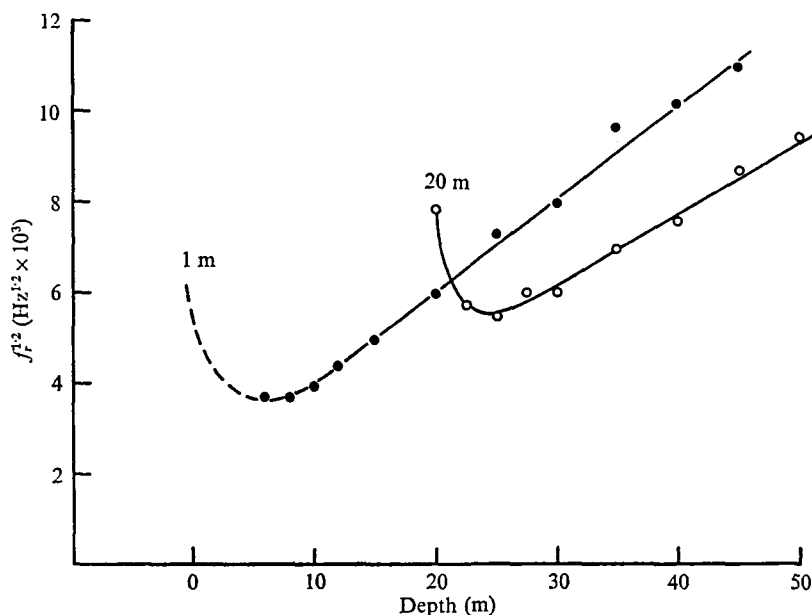
Changes in the mass of gas within the swimbladder, accompanying changes in depth

Fish tend to maintain the volume of the swimbladder constant at different depths to preserve hydrostatic equilibrium. This is done by changing the mass of the contained gas by secretion or absorption. From Text-fig. 7 it was apparent that when a fish was permanently transferred to a new depth, f_r increased rapidly with time, after an initial decrease. However, it cannot be assumed that this change in f_r necessarily reflects gas secretion or resorption.

For a fish adapted to a particular depth the f_r values obtained are not those predicted for a free bubble containing the same volume of gas. It is therefore not possible to follow changes in the volume of contained gas as a fish adapts to a new depth by examining the changes that occur in f_r . If, however, the fish is taken rapidly to depths much greater than the adaptation depth, f_r at these depths is only 1.25 times higher than predicted (Text-fig. 9), and tends to change with depth in the manner expected of a free gas bubble. At these greater depths f_r can therefore be used to calculate the mass of gas contained within the swimbladder, using equation (1). Thus, it is possible to follow changes in the mass of gas in the swimbladder of an adapting fish by periodically lowering it rapidly to greater depths, and raising it again.

On several occasions we were able to compare series of f_r measurements made before and after a permanent transfer from one depth to another. This enabled us to calculate the change in mass of gas that had occurred over a period of time. Our method of doing this is illustrated by Text-fig. 10.

Here, f_r was measured for a surface-adapted 16 cm fish, as the fish was lowered rapidly to 50 m. The fish was subsequently kept at 20 m for 20 h, and then again taken rapidly to 50 m. The f_r measurements obtained at the greatest depths were much lower on the second occasion, indicating that the mass of gas contained within the swimbladder had increased. We have already noted that for a free gas bubble of

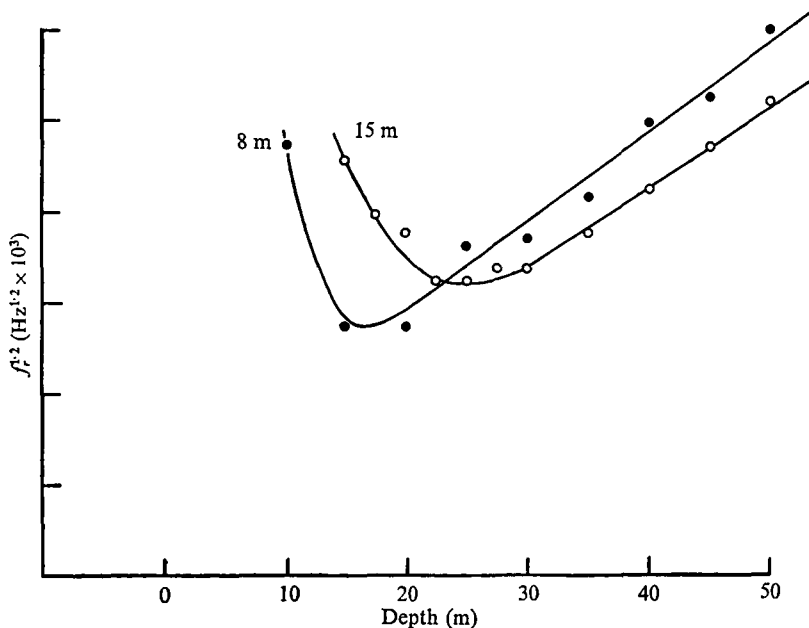


Text-fig. 10. Changes in f_r following a permanent change to a new depth. A surface-adapted cod (16 cm in length) was lowered rapidly to 50 m (●), and then kept at 20 m for 20 h. The procedure was then repeated (○). Note the lower f_r values at the greatest depths for the last series, which indicate that gas secretion has occurred.

constant mass, $f_r^{1.2}$ is proportional to the pressure. Thus, a plot of $f_r^{1.2}$ against P will yield a straight line going through the origin (Weston, 1967). In Text-fig. 10 it is clear that the right-hand side of each curve is close to a straight line, confirming that at greater depths the organ is behaving as a bubble. Assuming (from the data in Text-fig. 9) that the ratio between the values of f_r for the swimbladder and for a bubble is constant at 1.25 for these depths, then the mass of gas has increased to 193 % of the original mass over the 20 h period, calculated from equation (1). In order to maintain the swimbladder at constant volume the new mass would need to be 300% of the original. Therefore this particular animal had not fully adapted to the new depth in the available time.

Text-fig. 11 illustrates the changes which accompany the raising of a fish to a shallower depth. The measurements were made on a 14 cm cod, originally adapted to 15 m, which was raised to 8 m for 13 h. The values of f_r at the greatest depths were higher on the second occasion, indicating that the mass of gas had decreased. From equation (1), it can be calculated that the new mass was 71 % of the original mass. The fish had thus completely adapted to the 28 % decrease in pressure during this period.

Previous and more direct estimates have also indicated that secretion and resorption of gas are rather slow processes. Most fish examined have taken between 4 and 48 h to re-fill their swimbladders after deflation (Wittenberg, Schwend & Wittenberg, 1964). Such slow changes contrast with the very rapid changes in f_r we observed immediately after fish were displaced permanently to a new depth. A fish taken from



Text-fig. 11. Similar experiment to that described by Text-fig. 10, but the cod (14 cm in length) was in this case adapted to 15 m (\circ) and then kept at 8 m for 13 h (\bullet). Note the differences in f_r at the greatest depths, which indicate that gas absorption has occurred between the two series of measurements.

the surface to 6 m subsequently gave a steady value of f_r after only 30 min. Thus, it would seem that the changes in f_r which occur when a fish is displaced to a new level, illustrated in Text-fig. 7, are too rapid to be accounted for by secretion or resorption of gas.

DISCUSSION

Differences in the acoustic properties of the swimbladder and a free gas bubble

Despite many previous suggestions that the swimbladder behaves acoustically rather like a free gas bubble (Pumphrey, 1950; de Vries, 1956; Harris, 1964; van Bergeijk, 1967), we have found that the adapted cod swimbladder has a much higher f_r and lower Q than a free bubble of the same volume. Equation (1) cannot therefore be used directly, and must be modified if it is to be used to predict the acoustical behaviour of the swimbladder.

One factor which will tend to increase f_r for a swimbladder is any difference in shape between the organ and an ideal spherical bubble. Both Strasberg (1953) and Weston (1967) have considered the effect of major differences in bubble shape, and have calculated the resultant increase in f_r for oblate and prolate spheroids of different relative dimensions. In practice, f_r increases with any deformation in shape for a bubble of constant volume.

A further factor was suggested by Andreeva (1964), who stressed that the tissues surrounding the swimbladder might influence its acoustic properties. She assumed

that the swimbladder was completely surrounded by an infinitely thick layer of tissue having a uniform shear modulus, and suggested the following modified expression:

$$f_r = (2\pi a)^{-1} \rho^{-\frac{1}{2}} (3\gamma P + 4\mu_1)^{\frac{1}{2}}, \quad (4)$$

where μ_1 represents the real part of the complex shear modulus [$\mu_0 = \mu_1(1 + j\mu_2)$] for the surrounding tissues.

The shear modulus, and not the bulk modulus, appears in this equation since the deformation produced in the surrounding tissues as the swimbladder pulsates is essentially a change in shape, which involves shearing movements. The change in volume of the tissues is probably negligible in comparison, and can be ignored.

McCartney & Stubbs (1971) modified Andreeva's equation to take the thickness of the tissues into account. They also considered that an excess pressure might exist inside the swimbladder, and derived the following equation:

$$f_r = (2\pi a)^{-1} \rho^{-\frac{1}{2}} [3\gamma(P + \Delta P) + 4\mu_1(3t/a)]^{\frac{1}{2}}, \quad (5)$$

where ΔP is the difference between the gas pressure inside the swimbladder and the hydrostatic pressure in the surrounding water (P), and t is the thickness of the tissues. The equation indicates that f_r will be raised by the presence of an excess pressure inside the swimbladder, and by any increase in the shear modulus of the surrounding tissues.

For pressures two or more times greater than the adaptation pressure our results showed a ratio of approximately 1.25 between f_r for the swimbladder and that for a gas bubble of equal mass. If an excess static pressure exists in the swimbladder at adaptation depth, this will most certainly have diminished at these greater depths, and it is therefore unlikely that the departure from the predicted values can be attributed to this cause. Two factors are therefore left to explain the observed deviation at depths greater than the adaptation depths, namely effects due to differences in shape compared to a sphere, and effects arising from the surrounding tissues.

Radiographs of living cod show that the swimbladder is relatively elongate (Pl. 1, fig. 1), with a length/diameter ratio of between 5 and 6. This can be expected to provide an increase in f_r of approximately 13% (Weston, 1967). The remaining difference in f_r may arise from tissue effects. Assuming a value of $t/a = 0.2$, as suggested by McCartney & Stubbs (1971), our observed values of f_r would imply that μ_1 has an approximate value of 1.7×10^6 dyne/cm² at these depths. In fact, Lebedeva (quoted by Andreeva, 1964) obtained μ_1 values of between 1×10^6 and 1×10^7 dyne/cm² by direct measurement, while McCartney & Stubbs (1971), from measured f_r values, estimated values ranging from 3.5×10^5 to 2.6×10^6 dyne/cm². Our value is therefore in good accordance with those previously reported. A slight discrepancy might be expected, since the effects of the tissues on resonance will tend to decrease with depth, whereas our observations show that the ratio between f_r for the swimbladder and a free bubble remains constant below a certain depth. However, such small differences can easily be accounted for. For example, the attachment of the swimbladder to the vertebral column in the cod is such that the length of the organ will tend to remain the same, despite any decrease in volume. The length/diameter ratio will thus increase with depth, and so the resultant increase in f_r will tend to compensate for any decrease in the tissue effect.

The most striking deviation of f_r from the expected values occurred at or near the

adaptation depth of the fish. From equation (5) it can be seen that the observed elevation of f_r can be explained by an increase in the gas pressure inside the swimbladder or by an increase in μ_1 , the term representing the real part of the complex shear modulus of the surrounding tissues.

Alexander (1959) has determined the relationship between swimbladder volume and hydrostatic pressure for several physoclists (species with closed swimbladders, like the cod), and has shown that the organ behaves very similarly to an unrestrained gas bubble when it is subjected to rapid changes in pressure. This suggests that there is little or no excess pressure inside the swimbladder. Furthermore, McCutcheon (1958) has made precise pressure measurements on the swimbladder of the pinfish, *Lagodon rhomboides*, and has shown that the poised and rested fish, in a state of neutral buoyancy, maintains only a very small excess pressure (of the order of $+3 \text{ cmH}_2\text{O}$). The direct effect such a slight excess pressure will have upon f_r is negligible. To account for the elevated f_r values around adaptation depth, internal excess pressures of up to several atmospheres would be required.

Thus, the high values of f_r we obtained from fish near adaptation depth cannot be attributed solely to the existence of an excess pressure inside the organ. They must therefore be associated with an increase in the shear modulus of the surrounding tissues. An increase from $1.7 \times 10^6 \text{ dyne/cm}^2$ to between 1×10^7 and $2 \times 10^8 \text{ dyne/cm}^2$ would account for our observed values (assuming a negligible excess pressure). Such an increase in shear modulus might result indirectly from the existence of an excess pressure inside the swimbladder, since this would tend to stretch the walls of the organ, increasing its stiffness. In this event, an additional term would be required in equation (5), relating μ_1 to ΔP . Indeed, McCartney & Stubbs (1971) considered this possibility. From their analysis, however, it is clear that for a ΔP -dependent increase in μ_1 to account for the observed f_r values we would have to postulate rather high values of ΔP (of the order of 1 atmosphere). Such values are considerably greater than those recorded from physoclistous fish (Alexander, 1959).

Our measurements showed that the damping of the cod swimbladder was very high (i.e. the Q was very low) throughout the depth range examined. Energy losses causing damping can arise from several causes. These include the re-radiation of sound by the organ, thermal effects, and viscous effects. At shallow depths Andreeva (1964) suggested that viscous losses would predominate, and that Q could therefore be represented by

$$Q = (3\gamma P + 4\mu_1)/4\mu_1\mu_2. \quad (6)$$

From this it is evident that in shallow water Q will tend to increase with depth. (At depths greater than 150–200 m re-radiation losses will tend to predominate, and Q will decrease with depth.) We observed that below adaptation depth the value of Q did in fact increase with depth. However, the average value of μ_2 indicated by our experiments was about 2. This is nearly 10 times the value quoted by Alexander (1966). A similar discrepancy was noted by McCartney & Stubbs (1971). These low Q values are in good accordance with Weston's prediction (1967) that heavy damping can be expected from fish at shallow depths.

The maintenance of an elevated resonance frequency near the adaptation depth

The possibility that fish might maintain an elevated swimbladder resonance frequency has not previously been considered. Though other workers have correctly suggested that the damping of the organ might be high, they have generally assumed values of f_r corresponding approximately to those of a free bubble (Harris, 1964; Alexander, 1966).

McCartney & Stubbs (1971) reported higher f_r values, corresponding approximately to our own measurements, for some individual cod. However, they interpreted these high values in terms of a small swimbladder volume. Thus, in one case they transferred a cod from a shallow depth to 30 m, and then subsequently observed a 50 % increase in f_r within 6 h. By applying equation (1) directly to the swimbladder they concluded that this change must have represented a loss of gas from the swimbladder, either through the organ being ruptured at capture, or because oxygen was absorbed as a result of deficiencies in the animal's respiration. We found similar results from fish transferred to a new depth (Text-fig. 7). After an initial drop in f_r as the depth was changed, f_r subsequently increased rapidly. We concluded, however, that these changes in f_r could not be interpreted directly in terms of a volume change of the organ. They merely represented a restoration of the elevated f_r value found at adaptation depth, which may or may not have been accompanied by changes in the mass of gas.

We have pointed out that the very high f_r values maintained at or near the adaptation depth could be explained by a large increase in the shear modulus (μ_1) of the tissues surrounding the swimbladder. We suggest that this higher μ_1 at adaptation depth may be associated with a maintained stress or tonus in the tissues surrounding the swimbladder, created by an active muscular mechanism. We can only speculate on the identity of the muscle fibres which might create such a tonus, however. There is a layer of smooth muscle in the loose tunica interna of the swimbladder, but this is concerned with the mobility of this inner lining, and with controlling the secretion and absorption of gas. The muscle fibres do not appear to occupy an appropriate position for imposing stress upon the swimbladder wall. There are paired striated muscles running from the anterior ribs to insert upon the tunica externa in the cod, but these are associated with a sound-producing function (Brawn, 1961). There remains the axial body musculature of the fish, which completely surrounds the viscera and hence the swimbladder.

We can find no evidence in the literature that the body musculature of fish is normally in a state of tonus. However, McCutcheon (1958) has provided some evidence that fish are able to compress the gas within the swimbladder to a slight degree, by a muscular response. Indeed, McCutcheon has suggested that fish normally maintain a muscular tonus sufficient to create a very slight positive pressure level ($\simeq +3$ cmH₂O) in the swimbladder at resting depth. Such a tonus might also increase the stiffness, and hence shear modulus, of the surrounding tissues.

The elevated f_r values noted from cod at adaptation depth were at first lost, but then restored relatively quickly when the fish were displaced to new depths (Text-fig. 7). This rapid adjustment of f_r cannot be explained in terms of a rapid restoration of the bladder to its original volume by the secretion or absorption of gas. However,

having suggested that a high f_r is normally maintained by muscular action, it is possible that rapid adjustment of f_r at a new depth can be explained in terms of a restoration of muscle tone.

Our observations therefore suggest that the acoustic characteristics of the swimbladder may be controlled by the stiffness of the tissues surrounding the organ. The resonance frequency is normally maintained at an elevated value, which may be reduced, by this stiffness relaxing as the depth of the fish is changed, but which can rapidly be restored. This does not necessarily imply that only the acoustics of the organ are particularly important to the animal. The maintenance of a tonus in the surrounding tissues could conceivably be connected with the control of buoyancy (as suggested by McCutcheon, 1958), or with the use of tension receptors to detect changes in hydrostatic pressure. In any event, the changes which occur in the mechanical properties of the swimbladder and contained gases as the fish moves up and down in the water deserve further investigation.

The role of the swimbladder in hearing

Von Frisch (1938) first pointed out that the swimbladder could function as an accessory hearing organ. He demonstrated that the ostariophysan fish had particularly acute hearing, and suggested that large local movements occurring at the surface of the swimbladder in response to applied sound pressures were transmitted to the ear by a chain of small ossicles described by Weber (1820). Similar conclusions were later drawn for many other teleosts where the swimbladder is closely associated with the ear. These studies have been listed and reviewed by Jones & Marshall (1953), Alexander (1966), van Bergeijk (1967) and Tavalga (1971).

An analysis of the part played by the swimbladder in the Ostariophysi was performed by Poggendorf (1952), who examined the hearing abilities of the catfish, *Ictalurus* (= *Ameiurus*) *nebulosus*. Poggendorf showed that this fish was essentially sensitive to sound pressure, rather than particle displacement. In addition, he demonstrated that extirpation of one of the Weberian ossicles – removing the link between the swimbladder and the ear – reduced the sensitivity of the fish by 30–40 dB at some frequencies. These results were later confirmed by Kleerekoper & Roggenkamp (1959), who deflated the swimbladder, and thereby decreased the animal's sensitivity by 20 dB.

Poggendorf (1952) suggested that the swimbladder could be compared to a gas bubble, and that it would therefore give a maximal response at a particular frequency, the resonance frequency. He went on to measure this frequency for isolated swimbladders from several minnows, *Phoxinus laevis*, using an optical technique, and obtained values ranging from 1.4 to 1.78 kHz. His experiments suggested that in the intact fish the damping of the organ was heavy.

Poggendorf calculated the relative amplitudes of motion of the swimbladder at different frequencies, and showed that these closely followed the sound-pressure thresholds of *Ictalurus*. In particular, the resonance frequency of the swimbladder matched the frequency of greatest sensitivity of the fish. Poggendorf concluded that the swimbladder played an important part in the hearing of the Ostariophysi. In addition, since *Ictalurus* remained sensitive to sound pressure even with the chain of Weberian ossicles disrupted, he also suggested that the swimbladder could be of

importance in the hearing of other fish, despite the lack of a conducting link to the ear. This point was later taken up by Alexander (1966) and van Bergeijk (1967).

Van Bergeijk (1967) referred to the swimbladder as a *secondary* source of sound, radiating its own pressure and displacement fields when subjected to sound pressures. He suggested that in many fish the otolith organs of the labyrinth were close enough to the swimbladder to be stimulated by the radiated displacement field, provided that the axes of sensitivity of the hair cells coincided reasonably well with the direction of these displacements. The fleshy structures of the fish, lying between the swimbladder and labyrinth, would transmit these displacements directly, because they have nearly the same density (and thus acoustic impedance) as water. Both Alexander (1966) and van Bergeijk (1967) stressed that the swimbladder would need to be quite close to the skull if it were to provide any advantage, since the displacement field would decline with distance from the centre of the swimbladder, probably according to an inverse square law.

If this analysis is correct, then fish with swimbladders should have better hearing than those without. In addition, they should be sensitive to sound pressure, rather than to particle displacement. Certainly studies of several fish with swimbladders have yielded very low acoustic thresholds (Poggendorf (1952), Kleerekoper & Roggenkamp (1959) and Jacobs & Tavalga (1967) for Ostariophysi; Tavalga & Wodinsky (1963) for *Holocentrus ascensionis* – which also has a connexion between the swimbladder and the skull; Iversen (1967) for *Thunnus albacares*; and Chapman & Hawkins (1973) for the cod). Unfortunately, however, there are few comparable data for species without swimbladders. Dijkgraaf (1949) demonstrated that *Gobius* was able to hear frequencies up to 800 Hz. In addition, Kritzler & Wood (1961), Wisby *et al.* (1964) and Nelson (1967) have obtained responses from elasmobranchs to sounds, and Banner (1967) has provided evidence that the lemon shark, *Negaprion brevirostris*, is sensitive to particle displacement rather than to sound pressure. Though in general such fish appear to be less sensitive to sounds than fish with swimbladders, more detailed and satisfactory experimental study of this question is necessary.

Enger & Andersen (1967) compared the hearing of the cod and the bullhead, *Cottus scorpius* (which does not have a swimbladder), using an electrophysiological technique. By changing the sound-source distance the ratio of sound pressure and particle displacement presented to the fish could be varied. It appeared that the bullhead was sensitive to particle motion, since saccular microphonics could only be obtained when the fish was extremely close to the sound source (where the particle motion is high). For the cod, on the other hand, microphonics could be obtained at all sound source distances, and at the higher frequencies tested (400, 600 Hz) their amplitude followed the sound-pressure amplitude. Enger & Andersen therefore concluded that the cod was sensitive to sound pressure. The results of their experiments did not entirely justify this conclusion (for reasons discussed in detail by Chapman & Hawkins (1973)). Indeed, at a lower frequency (200 Hz) their results suggested that the fish was sensitive to particle motion.

The hearing of the cod appears to differ markedly from that of many other teleosts (Buerkle, 1967; Chapman & Hawkins, 1973). The cod is most sensitive over the relatively low-frequency range from 60 to 380 Hz, and shows a very steep decline in sensitivity above 400 Hz. Most other teleosts have shown a more extended frequency

range (Tavolga, 1971). However, at its most sensitive frequencies the hearing of the cod is very acute, and under most circumstances is limited only by the level of ambient sea noise.

Chapman & Hawkins (1973) followed Enger & Andersen in examining the relevant stimulus parameter for the cod by varying the distance of the fish from the sound source. At frequencies below 50 Hz, significant differences in acoustic thresholds (expressed in terms of sound pressure) were obtained at different distances. The thresholds were lower close to the sound source, strongly suggesting that the fish were sensitive to particle displacement at these frequencies. At 50, 60, 110 and 160 Hz the mean thresholds at different source distances were not significantly different, though the particle displacements accompanying a given sound pressure differed widely. Chapman & Hawkins were unable to extend the experiments to frequencies above 160 Hz (for technical reasons), but concluded that over the frequency range from 50 Hz to the upper frequency limit (approximately 400 Hz) cod were sensitive to sound pressure.

Thus, there is indirect evidence that the swimbladder is used as an accessory hearing organ by the cod. It would appear, however, that the functioning of the swimbladder/ear system in this fish is rather different from that in the Ostariophysi. Poggendorf (1952), Alexander (1966) and van Bergeijk (1967) suggested that for the Ostariophysi the greatest hearing advantage was conveyed by the swimbladder at its resonance frequency. This cannot be the case for the cod, since we have shown that the resonance frequency of the swimbladder is maintained at a value well above the hearing range. We must therefore consider the acoustics of the organ in more detail to ascertain whether it can still convey a significant advantage. This is best done using a simplified model.

From the theory of forced vibrations, it is possible to calculate the radial displacement amplitude, A , at the surface of a spherical elastic gas-filled shell of given natural frequency and damping when it is exposed to a sound-pressure field. The equation describing the motion of the shell is given by Poggendorf (1952) as

$$A = ap/3\gamma P [(1 - f^2/f_o^2)^2 + f^2/f_o^2 Q^2]^{-\frac{1}{2}}, \quad (7)$$

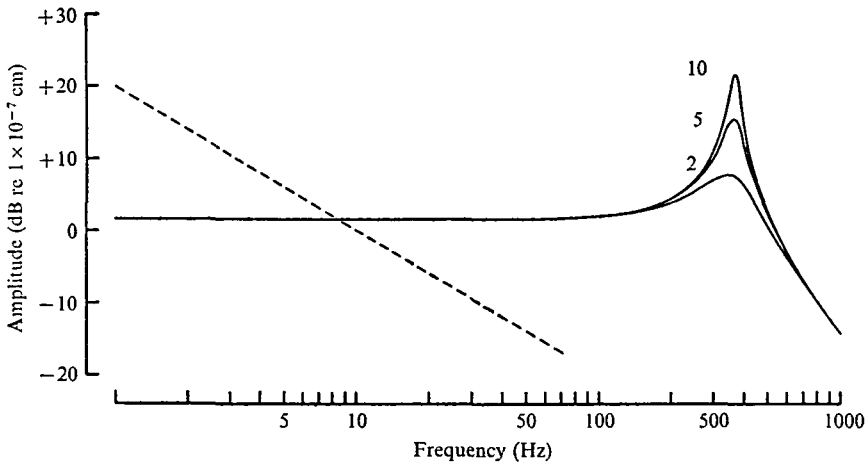
where p is the incident sound pressure, f the forcing frequency, and f_o the natural frequency of the shell ($f_o = f_r$ for an undamped system). It should be noted that this equation is only strictly valid for a lightly damped system, where $Q \gg 1$.

We have used this equation to compare the amplitude of displacement generated at the surface of an ideal gas-filled sphere with that generated in the free field for the same sound pressure. In Text-fig. 12 these values are plotted for a sphere of radius 1.5 cm, at a depth of 20 m in the presence of a sound pressure of 1 dyne/cm². The displacements which accompany the same incident sound pressure in the absence of the sphere are provided for comparison, and were derived using the acoustic plane wave equation

$$d = p/2\pi f \rho c, \quad (8)$$

where c is the velocity of sound in the medium.

From Text-fig. 12 it can be seen that the greatest amplitude of movement at the surface of the sphere occurs at the resonance frequency, though this amplitude declines as the Q of the system is reduced (damping increased). However, the displacement amplitude at the surface of the sphere is substantially greater than for a plane wave at



Text-fig. 12. Curves illustrating the radial pulsation of a damped bubble (Q values of 10, 5 and 2, are indicated) in a sound field. Bubble radius is 1.5 cm and the depth 20 m. The sound pressure is kept constant at 1 dyne/cm². The water displacements accompanying this sound pressure for a propagated plane wave in the free field are shown by the broken line.

frequencies extending well below resonance. In the examples given, the sphere can serve effectively as a displacement amplifier for all frequencies above 10 Hz.

In considering the swimbladder, rather than our simplified model, it is clear that the degree of advantage gained at the resonance frequency will be much reduced because the organ is very heavily damped. Since the resonance frequency of the swimbladder is well above the hearing range of the animal, however, this decline in amplitude at resonance is of less interest than the degree of advantage gained at lower frequencies. We have seen that a simple resonant system acts as a displacement amplifier at frequencies well below the resonance frequency and that this tendency is not affected by changes in the Q of the system, provided that the damping is not too heavy. We can expect that the swimbladder will also serve as a displacement amplifier over this extended range of frequencies, but the amplification provided will depend in addition on several factors which cannot readily be estimated. For our model system we have taken a simple spherical shape, and have assumed that the surrounding medium has uniform acoustic properties. Anatomical observations on the cod swimbladder show that this is not so (see Pl. 1, fig. 1). Not only is the organ non-spherical, but a pair of anterior cornua are present, extending cranially. Though these are small in juvenile fish, in the adult they are well developed, and may be reflected back to lie alongside the main portion of the organ. In addition, the swimbladder wall is formed into pronounced diverticula along its length, closely attached to strong wing-like lateral parapophyses from the vertebrae. The equations describing the motion of a bubble assume that the structure forms a monopole sound source, radiating equal amplitude displacements in all directions. However, the movements of the swimbladder are undoubtedly restrained in some directions and the organ may perhaps be more properly described as a dipole, or n -pole. While well away from the organ the radiated field will still be spherical, since the scatterer is smaller than one wavelength; closer to the swimbladder the field may be more complex. Indeed, Poggendorf (1952)

examined the amplitude of oscillation of an ostariophysan swimbladder at different points around the periphery and reported larger amplitude movements at the cranial end, and at the lateral edges (where the radius of curvature was smaller). Quite apart from the effect such differences in the acoustic properties of the swimbladder will have upon the degree of advantage gained, we can also expect differences to arise from the physical separation of the swimbladder and otolith organs, and from the orientation of the hair cells.

Despite the relatively high resonance frequency of the swimbladder, and its high degree of damping, we conclude that it may still convey a distinct advantage in hearing, transforming incident sound pressures into re-radiated particle displacements which can stimulate the otolith organs over a wide frequency range. At low frequencies the advantage conveyed by the organ can be expected to lessen and disappear, as the free field displacements become comparable in amplitude to the re-radiated displacements. At high frequencies, the response of the swimbladder will show a slight peak at the resonance frequency, with a steep cut-off above this frequency. However, the hearing abilities of cod do not appear to extend up to the resonance frequency, showing a sharp decline in sensitivity at about 480 Hz (Chapman & Hawkins, 1973).

It is useful to speculate whether the cod gains any special acoustic advantage from maintaining the resonance frequency of the swimbladder at a high value, well above the hearing range. If the bladder behaved like a free gas bubble, the resonance frequency of the organ would only be above the upper frequency limit of hearing for small fish, or for large fish at great depths. At shallow depths f_r for most fish could be expected to fall within the frequency range of the ear. The fish would be most sensitive at this resonance frequency, which would vary with depth. The hearing ability of the fish would thus be expected to alter with depth, as well as with the size of the fish. However, by maintaining an elevated f_r , higher than that of a comparable bubble and well above the upper frequency range of hearing, and by showing heavy damping of the resonance, these changes with size and depth are minimized. There may, as we have already discussed, be other less direct reasons for the resonance frequency of the swimbladder being high. Nevertheless, we believe that the maintenance of a reasonably stable hearing capability regardless of size and depth is in itself a distinct advantage, particularly for a species like the cod, which undertakes extensive vertical movements.

SUMMARY

1. The resonance frequency and damping of the swimbladder were measured for intact living cod at different depths.
2. At adaptation depth, the resonance frequency (f_r) of the organ was much higher than that predicted for an unrestrained gas bubble of similar volume. However, at much greater depths (where the hydrostatic pressure was 2 or more times greater than the adaptation pressure) f_r was only higher than expected by a factor of 1.25, and changed with depth in the manner of a free gas bubble.
3. The elevated values at greater depths can be explained in terms of the difference in shape between the swimbladder and an ideal spherical bubble, together with a

light effect from the surrounding tissues. We have calculated that the shear modulus of these tissues (μ_1) has a value of approximately 1.7×10^6 dyne/cm². However, we have suggested that the much higher elevation of f_r found at the adaptation depth results from a large increase in μ_1 (by a factor of between 6 and 120). This increase may be the result of a maintained muscle tonus.

4. There is an immediate drop in f_r as a fish is moved to a new depth, but the elevated values are rapidly restored with time. This process of adjustment is too rapid to be accounted for by the restoration of the swimbladder to its former volume by the secretion or absorption of gas. It is possible that it is achieved by a muscular mechanism which restores μ_1 to the former high value.

5. Though the maintenance of f_r at a high value may reflect mechanical processes concerned with the hydrostatic function of the swimbladder, or with the detection of static pressure changes, we suggest that it may also be of some value if the swimbladder is used as an accessory hearing organ. The maintenance of an f_r well above the hearing range of the fish ensures that the relative sensitivity of the animal to different frequencies does not alter with changes in depth.

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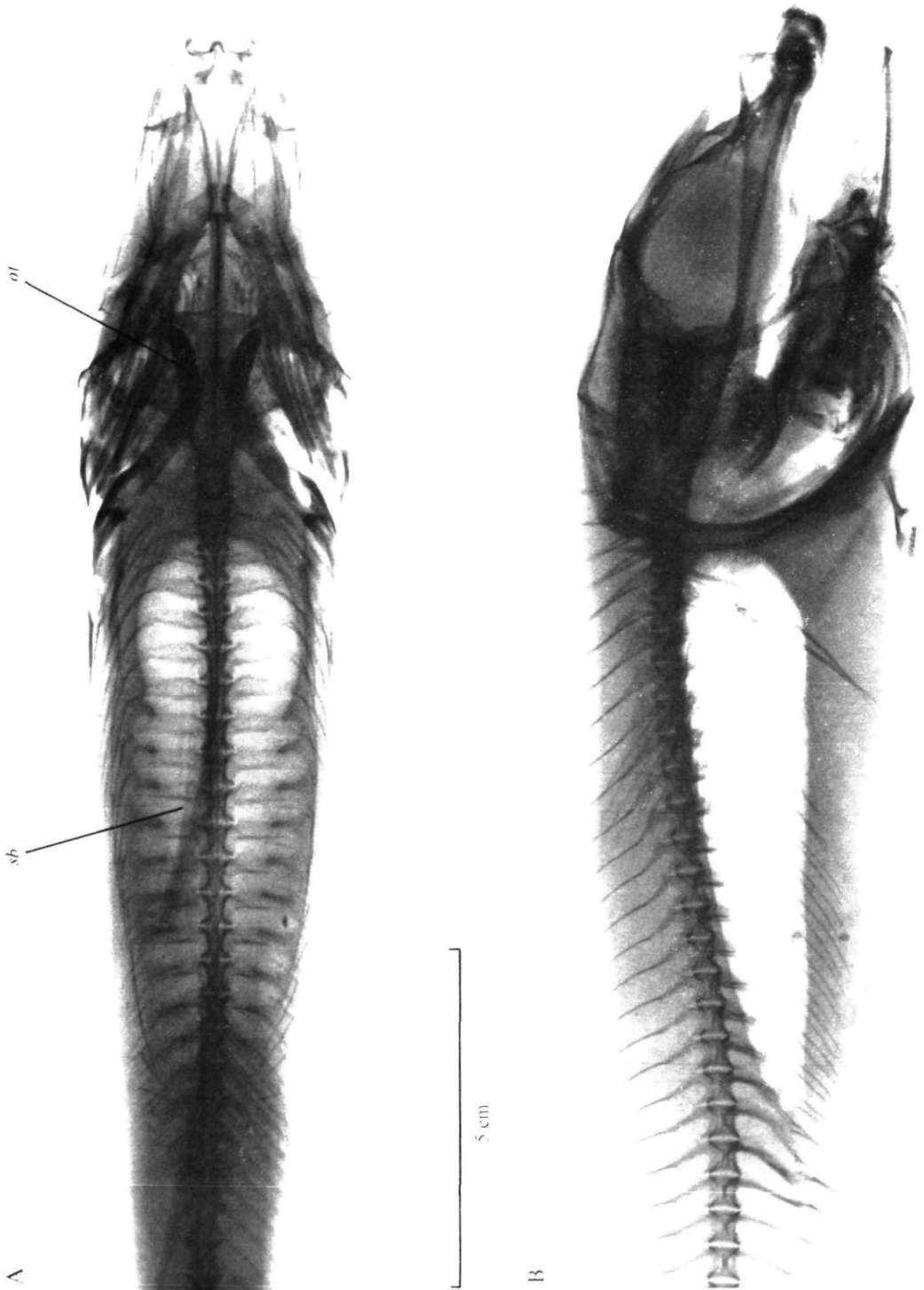
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EXPLANATION OF PLATE

Fig. 1. Radiographs of a 35 cm cod, dorsal (A) and lateral (B) view. Note the elongate shape of the swimbladder (sb), the prominent lateral diverticula, and the position of the large saccular otoliths (ot).



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