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A Field Study of Hearing in the Cod, *Gadus morhua* L.

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Summary. 1. Field measurements of hearing in the cod, *Gadus morhua* L., have shown that these fish are sensitive to pure tones in the frequency range from 30 to 470 Hz with greatest sensitivity in the range 60 to 310 Hz. At the most sensitive frequencies the mean thresholds varied between –18 and –26 dB/μbar (Fig. 4).

2. Variation in the thresholds at most frequencies was related to changes in the level of ambient sea noise (Figs. 5–7). Only in calm sea conditions were unmasked thresholds obtained. The masking effect of noise was confirmed by raising the level artificially. The thresholds increased in proportion to the increase in noise level.

3. The thresholds were largely independent of the distance of the sound source over the range from 1.7 to 50 m, suggesting that cod are sensitive to acoustic pressure. However, a changeover to particle displacement sensitivity was noted at frequencies below 50 Hz when the sound source was moved to within 1 m of the fish (Fig. 9).

4. It is concluded that the swimbladder plays an accessory role in hearing. Differences obtained in the thresholds at different sound source distances may be explained in terms of the displacement sensitivity of the otolith organs. These respond to displacements re-radiated from the swimbladder in the far-field, and to the greater incident displacement in the near-field at very low frequencies.

Introduction

Experiments on the hearing of fish require a very special environment, where sound stimuli can be accurately reproduced and measured. Though laboratory aquarium tanks have often been used for this purpose they are not generally suitable because the fish and measuring instruments are close to reflecting boundaries (Griffin, 1950; Parvulescu, 1964, 1967). At these boundaries a change takes place in the relationship between two fundamental parameters of any sound—the sound pressure and the particle displacement. For a sound travelling progressively through an infinite medium, the particle displacement is a function of the sound pressure, this relationship being described by the acoustic plane wave equation (or close to the sound source by the spherical wave equation). Where the sound meets an interface with a medium of different acoustic properties and is reflected, the ratio between the two parameters changes and these simple equations are no longer valid. Water and air have very different acoustic properties (the acoustic impedance of sea water is 1.54×10^5 g cm^{-2} s^{-1}, compared to 42 g cm^{-2} s^{-1} for air) and sound is therefore readily reflected by any water/air interface. A thin-walled container of water is effectively surrounded by such reflectors and small sound pressures generated inside it will result in relatively large particle displacements at the boundaries. Under these conditions the conventional description of a sound stimulus in terms of the measured sound pressure would be highly misleading.

These fundamental changes in a sound stimulus produced by reflection complicate any tests carried out on the hearing of fish. Particle displacements in water are difficult to measure and any acoustic thresholds must initially be expressed in terms of sound pressure. However, several workers have stressed the potential importance of the associated particle motion, which may stimulate both the lateral-line organ and the ear of fish (Harris and van Bergeijk, 1962; Tavolga, 1965).

We have studied the hearing of the cod, *Gadus morhua* L.[1] in the sea, with the fish and sound transducers positioned in mid-water, away from reflecting boundaries. The response of the fish was examined using a classical conditioning technique, first described by Otis *et al.* (1957), where a change in the animal's cardiac rhythm was established to a sound stimulus by the application of mild electric shock. Hearing thresholds were obtained at several tone frequencies in varying conditions of ambient sea noise and also in the presence of background noise generated artificially. The effect of varying the distance of the fish from the sound source was examined, in order to determine the sensitivity of cod to acoustic pressure and particle displacement.

Methods

1. The Acoustic Range

The experiments were conducted in Upper Loch Torridon on the west coast of Scotland (Admiralty Chart No. 2638, latitude 57° 32.29′ N, longitude 05° 34.33′ W). A temporary laboratory was erected on the south side of the loch. The experiments were monitored from this laboratory, but were performed upon a framework immersed in the sea 100 m offshore. The framework (Fig. 1) was constructed from rigid PVC tubing (Durapipe, type UPVC; 50 and 38 mm diameter) perforated with holes to admit water and to release any enclosed air. The material was chosen for its acoustic similarities to sea water (it has an acoustic impedance of 2.2×10^5 g cm^{-2} s^{-1}). The top of the framework was 15 m below the sea surface (measured from chart datum level) and 6 m above the seabed.

The experimental animal was placed inside a tubular cage, mounted at the top of the framework. Cages were made from plastic netting (Netlon, 12.7 mm mesh), lined with a flexible and opaque PVC sheet. A pair of stainless steel electrodes (30 swg wire, woven into a 6 mm mesh) were built into each cage to permit the application

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[1] The scientific name of the common cod is *G. morhua* L. (s. D. M. Cohen, J. Com. perm. int. Explor. Mer, **25**, 50 1959).

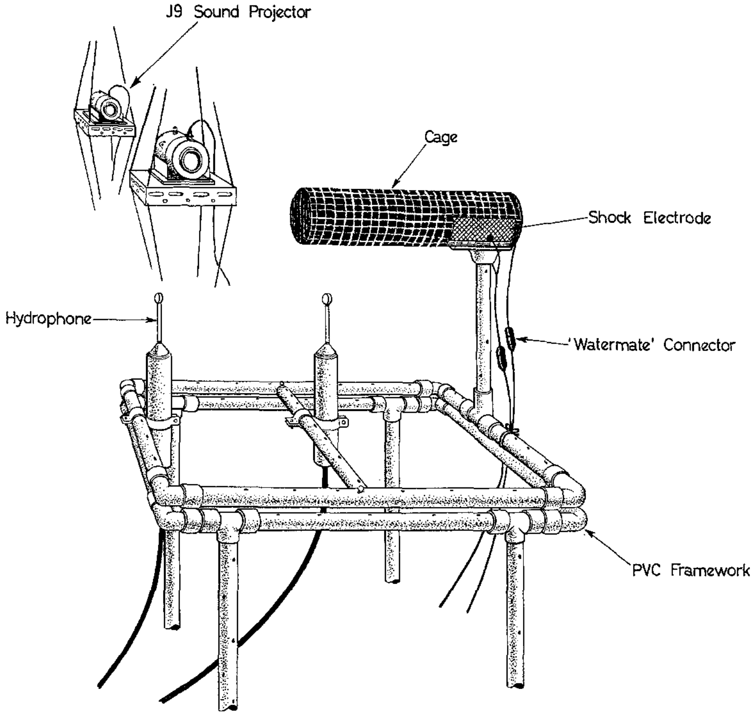

Fig. 1. Diagram showing the top of the underwater framework and the position of the cage containing the fish in relation to the two hydrophones and sound projectors

of an electric shock to the tail of the fish. The electrodes were joined through underwater connectors (Electro-Oceanics) to a cable running along the seabed to the shore laboratory. Another similar plug tied to the underwater framework connected an electrocardiograph electrode implanted in the fish to a further cable running to the shore laboratory.

Two calibrated hydrophones were mounted on the framework, equidistant from the sound projectors. One was placed 10 cm beneath the head of the fish, while the other was placed 30 cm away along the same axis as the cage (Fig. 1). The second hydrophone was used to check the calibration of the first throughout the experiments. The acoustic properties of the materials used in the construction of the cages and supporting framework were examined before the experiments by placing samples of the material between a sound projector and one of the hydrophones. No attenuation of low frequency sounds (below 5 kHz) occurred, confirming that the materials had a negligible effect on the acoustic field at these frequencies.

Two sound projectors (Dyna-Empire, type J 9) were placed on a line running out from the shore, at right angles to the axis of the cage. They were mounted on aluminium platforms, which were anchored to the seabed and buoyed up by sub-surface floats. One projector was positioned relatively close to the fish, the distance varying between 0.5 and 2.0 m on different occasions; the other projector was placed further away at 4, 7, 10 or 50 m.

Temperature and salinity profiles were measured using a temperature/salinity bridge, but no pronounced discontinuities were encountered below 1 m from the surface. Sea temperatures at the top of the framework varied from 11°C (May) to 14°C (September).

2. Instrumentation

Cardiac potentials from the fish were amplified by a low-noise preamplifier incorporating a variable bandpass filter (Tektronix, type 122). The electrocardiogram was monitored on a dual-trace storage oscilloscope (Tektronix, type 564) and displayed on an ultra-violet recording oscillograph (Consolidated Electro Dynamics, type 5-127).

The signals from the hydrophone were amplified by a low-noise amplifier (Brookdeal, type 450) which included a bandpass filter adjusted to pass signals within the frequency range 10 Hz–1 kHz. The amplified output was displayed directly on the oscilloscope and recording oscillograph and also fed to a frequency analyser and level recorder (Brüel and Kjaer, type 2107 and 2305).

Measurements on the sound stimuli were made with the frequency analyser tuned to the appropriate frequency and adjusted to provide a very narrow bandwidth. This filter system was used to obtain spectrum levels of ambient noise by applying a correction for the filter bandwith. The measurements were expressed in dB, referred to a sound pressure of 1 microbar (i.e. dB/μbar)[2].

The pure tone stimuli were derived from a sine wave generator (Brüel and Kjaer, type 1022) which fed a gating circuit to provide a transient-free pulse. The circuit was adjusted to give a pulse of about 8 s duration, with a rise-time of 300 ms. The gated signal passed via a variable attenuator (Advance, type A-64) and a 12 W power amplifier (Leak, type TL-12) to one of the sound projectors. The frequency of the stimulus was monitored on a digital frequency counter (Advance, type TC-6). A relay was operated by the gating circuit at the end of the gate period, feeding a 12 V DC pulse of 0.2 s duration to the shock electrodes.

For some experiments, a high level of random noise was continuously transmitted from the sound projector and the pure tone stimulus superimposed. The noise was derived from a random noise generator (Brüel and Kjaer, type 1024) coupled to an attenuator and adding circuit. The spectrum of the generated noise was approximately uniform in the frequency range from 30 to 500 Hz.

3. Experimental Animals and Conditioning Procedure

Forty-three immature cod were studied, ranging in length from 21 to 47 cm. They were captured on baited fishing lines in the shallower parts of the loch. Only fish caught at depths less than 10 m were used, as the swimbladders of fish from greater depths were often damaged on being raised to the surface.

The fish to be tested was anaesthetised in a 1 part in 15000 solution of MS-222 (Sandoz) in sea water and a small silver or stainless steel wire electrode was then inserted subcutaneously in the ventral aspect, to detect electrical potentials from the heart. The fish was then transferred to the underwater range by divers and the electric shock and electrocardiograph electrodes were connected to the cable terminations at the framework. Each fish was left in position on the framework for at least 24 hours before conditioning commenced.

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[2] 1 microbar $= 10^{-1}$ Newton per square metre in the MKS system of units.

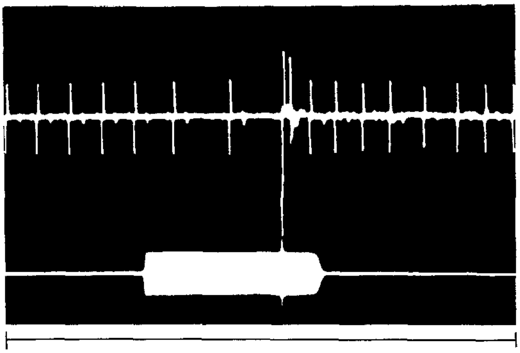

Fig. 2. Oscillographic recording showing a typical cardiac response (upper trace) to the pure tone stimulus (lower trace). The response usually involved an inhibition of the second and/or third heart beat following the onset of the tone. In this example, the electric shock was delivered just before the tone was switched off as indicated by the spurious transient spike on the recording. Lower time scale 30 sec

The tone stimulus was presented to the fish for about 8 seconds followed by the DC electric shock. The coupled sound and shock were presented repeatedly at intervals of 3 to 10 min until the fish eventually showed an alteration in heart rate after the onset of the sound, but before receiving the shock.

The response of the fish consisted of an inhibition of one or more heartbeats (Fig. 2). This was detected by comparing the four heartbeat intervals following the start of the sound with a large number of intervals measured before conditioning commenced and between trials. Only intervals greater than the most extreme measurements obtained before and between trials were accepted as positive responses.

Full conditioning was considered to have occurred when five consecutive trials had yielded positive responses. A threshold for the response was then determined using a staircase technique (von Békésy, 1947; Cornsweet, 1962). Thus, after the fish had been conditioned using a relatively high stimulus level, the level was decreased by 3 dB after each positive response, while conversely, with each negative response the level was increased by 3 dB. The procedure was continued until a plateau was reached with a minimum of 10 alternate positive and negative responses. The threshold level (i.e. the stimulus level to which the fish would be expected to respond on 50% of the presentations) was estimated using a method described by Dixon (1965). Examples of threshold staircases are given in Fig. 5.

During each experiment an estimate was obtained of the number of positive responses occurring in the absence of the sound stimulus. However, these false alarms proved rare and were therefore ignored in calculating the threshold level. A number of blank trials were conducted in which the tone generator and shock voltages were diminished, to confirm that the fish were not responding to cues presented by the experimental apparatus.

At the termination of a series of experiments, the fish was brought to the surface and the condition of the swimbladder was examined.

4. *The Nature of the Sound Stimulus*

The nature of the sound field around simple sound sources in water was considered in detail by Harris and van Bergeijk (1962). These authors distinguished between the region in the immediate vicinity of the source, termed the near-field, and the zone distant from the source known as the far-field. Within the near-field the sound is characterised by a larger amplitude of motion of the component particles of the medium for a given acoustic pressure. Thus, by changing the distance of the fish from the sound source the ratio between the acoustic pressure and particle displacement can be varied. In this way the effective stimulus for the auditory system of the fish may be determined. Harris and van Bergeijk (1962) used this principle to show that the lateral-line organ of *Fundulus heteroclitus* was sensitive to particle displacement.

Harris (1964) later developed a series of equations to describe the sound field around a number of different sound sources. The J 9 projectors used in our experiments were omnidirectional at low frequencies and can be regarded as monopole sources for which the equation relating particle displacement d (cm) to sound pressure p (µbar) was given by Harris as:

$$d = \frac{p}{2\pi f \varrho c}\left[1 + \left(\frac{\lambda}{2\pi r}\right)^2\right]^{\frac{1}{2}}. \tag{1}$$

In this equation r is the sound source distance (cm), f is the frequency (Hz) and λ the wavelength (cm) of the sound. The term ϱc is the specific acoustic impedance of the medium (1.54×10^5 g cm^{-2} s^{-1} for sea water). It can be seen from this equation and Fig. 3 that the particle displacement amplitude[3] associated with a given sound pressure is much larger for low frequencies and small values of r. As the distance from the source increases the second term of the equation approaches unity (when $r > \lambda/2\pi$). The displacement is then proportional to the pressure only and independent of distance, as given by the plane wave (far-field) equation:

$$d = \frac{p}{2\pi f \varrho c}. \tag{2}$$

The particle displacement amplitudes at different frequencies and sound source distances appropriate to our experiments are given in Fig. 3. The displacement amplitude for any threshold was obtained by multiplying the appropriate value from Fig. 3 by the threshold sound pressure.

Results

1. The Conditioning of Cod to Sounds

A relatively high and unvarying heart rate was noted from each experimental fish immediately after transfer to the underwater framework, the interval between heart beats being of the order of 1.2 s. However, the rate gradually declined over the succeeding 24 hours, eventually reaching 1 beat every 1.6 s, or greater, and showing rather more variabili-

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[3] Particle velocity varies with sound source distance but the velocity amplitude is independent of frequency. In this paper we have tried to distinguish between the two fundamental parameters of sound, the acoustic pressure and particle motion (which we represent in terms of particle displacement). Our results do not permit a distinction to be made between displacement and velocity sensitivity but the available evidence suggests that the end organs of the auditory sytem of fish are primarily sensitive to particle displacement (Harris and van Bergeijk, 1962; van Bergeijk, 1967).

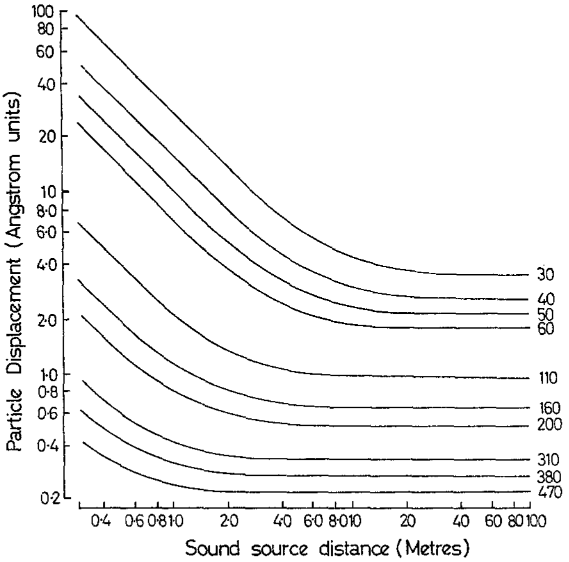

Fig. 3. Variation in particle displacement amplitude with sound source distance for frequencies between 30 and 470 Hz. The values were calculated for a sound pressure of 1 μbar from Eq. (1) (1 Å = 10^{-8} cm)

ty. During the initial period of high heart rate the fish proved difficult to condition.

Once a slow heart rate was obtained the cod readily responded to low frequency sounds. At test frequencies below 520 Hz, positive responses were frequently given when the first stimulus was presented and in most experiments at these low frequencies full conditioning was achieved with less than 10 trials. At frequencies above 520 Hz, on the other hand, the cod could not be conditioned, even to very high stimulus levels (a maximum of +30 dB/μbar at 580 Hz).

2. *Sensitivity to Different Frequencies*

The mean thresholds obtained from 43 cod against a background of sea noise are plotted in terms of the measured sound pressure in Fig. 4. The data are based on 194 separate threshold determinations at frequencies between 30 and 470 Hz. The lowest thresholds to pure tones were obtained in the frequency range from 60 to 380 Hz, where the mean varied between –18 and –26 dB/μbar. The fish showed a sharp rise in threshold at frequencies above 380 Hz and a more gradual rise below 60 Hz. The highest frequency for which reliable thresholds were obtained

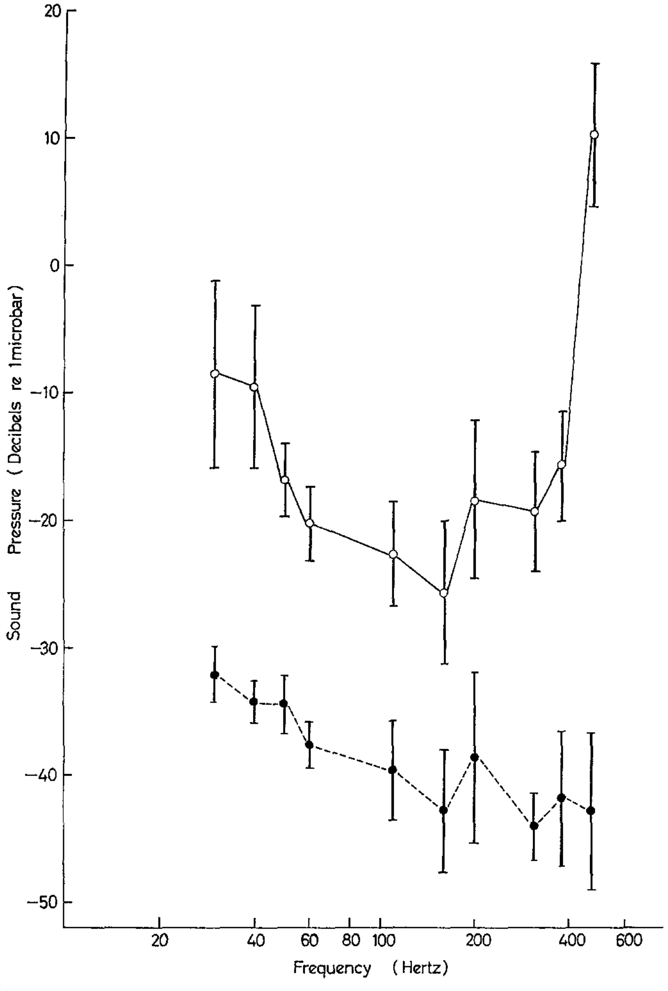

Fig. 4. Summary of hearing data for 43 specimens of cod; mean and standard deviation of thresholds (○) and spectrum level of sea noise (●) at frequencies between 30 and 470 Hz

was 470 Hz where the mean threshold was +10.5 db/μbar. The steep rise of the thresholds above 400 Hz, together with the lack of success in conditioning to frequencies higher than 520 Hz, suggests that cod are insensitive to high frequency sounds.

Variability was apparent in the data at all frequencies. While this could partly be attributed to individual differences between fish, it was clear that variation in the thresholds at low frequencies resulted from changing the distance between the fish and the sound projector. It was also evident that the thresholds at the most sensitive frequencies were influenced by changes in the level of ambient sea noise. For example, dependence upon the sea noise level is suggested in Fig. 4 by the similarity in the shape of the threshold and noise spectrum curves at frequencies between 30 and 380 Hz.

3. *Effect of Sea Noise*

At most frequencies it was apparent that any increase or decrease in the prevailing level of sea noise was accompanied by a corresponding upward or downward shift in threshold. This is illustrated in Fig. 5A where a threshold determined against a high background noise level (accompanying high winds in the area) was redetermined after the weather had moderated. As the noise level declined there was a corresponding drop in the threshold. However, the threshold remained about 16 dB above the spectrum level of the noise at the frequency of the tone. This separation between the threshold and the noise spectrum level is subsequently referred to as the threshold/noise ratio (expressed in dB).

The level of sea noise at the underwater site could be directly related to weather conditions. Any increase in wind speed, and hence surface motion, was accompanied by a proportional increase in the noise level particularly at frequencies above 100 Hz. Heavy rain also resulted in a pronounced rise in noise level at the higher frequencies. Gusts of very strong wind (squalls) were experienced occasionally resulting in short term fluctuations in noise level which caused corresponding changes in the threshold plateau (see threshold 1, Fig. 5B). In a number of experiments (50 threshold determinations), noisier conditions were simulated by transmitting broad band random noise through the sound projector. The thresholds increased in proportion to the noise level though the threshold/noise ratio remained relatively constant (Fig. 5 B and C).

The relationship between the thresholds obtained and the prevailing spectrum level of noise is shown graphically for several frequencies above 50 Hz in Figs. 6 and 7. Thresholds obtained in a background of sea noise and artificial noise are plotted separately but in some cases the two groups of data have been combined in calculating the regression and correlation coefficients (Fig. 7A and B). The data show that there is a significant correlation between the thresholds and the spectrum level of the background noise at most frequencies. At 470 Hz there is no correlation and it is clear that the thresholds were not masked by sea noise. At 50 and 60 Hz the variation in the level of sea noise was small and no correlation between the thresholds and noise level was apparent until the background noise level was increased artifically. The same was also apparent at 30 and 40 Hz where, as discussed below, most of the variations

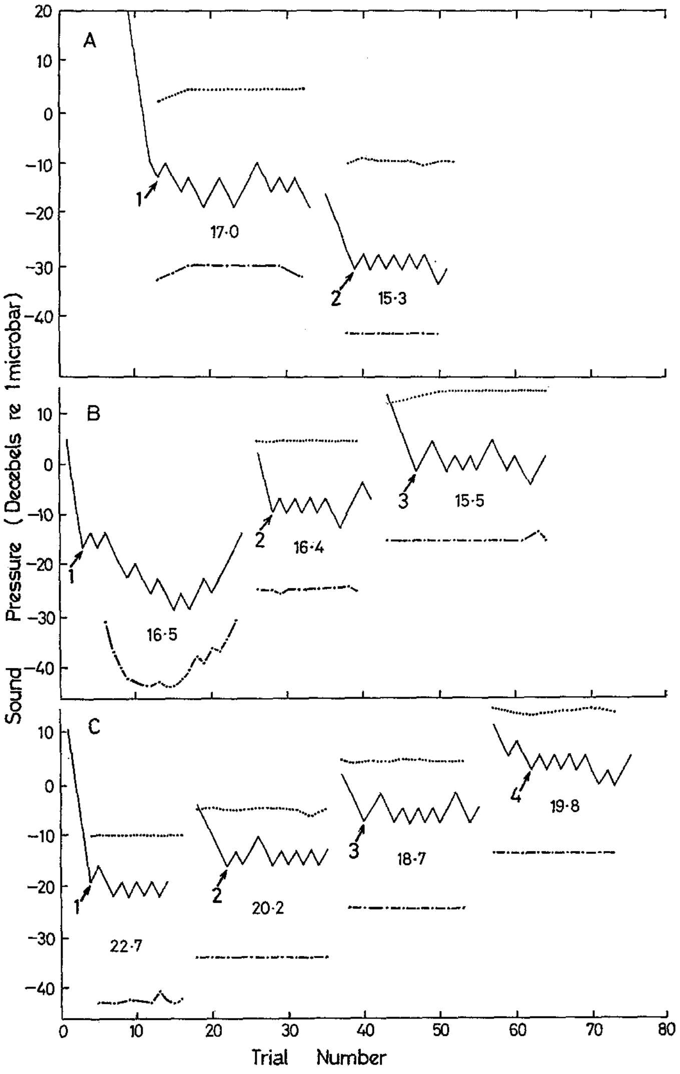

Fig. 5. Threshold determination curves (solid lines) obtained in different levels of ambient noise. *A* 160 Hz-thresholds determined in sea noise during and after the passage of a 'squall' in Loch Torridon. *B* 160 Hz-threshold 1 was obtained in sea noise fluctuating in amplitude and thresholds, 2 3, were obtained after raising the background noise level artifically. *C* 380 Hz-threshold determination in sea noise (1) and then in increasing levels of transmitted random noise (2–4). The figure below each threshold plot is the threshold/noise ratio (dB). —·—·—· spectrum level of noise; ············ total noise level in 20–1000 Hz band

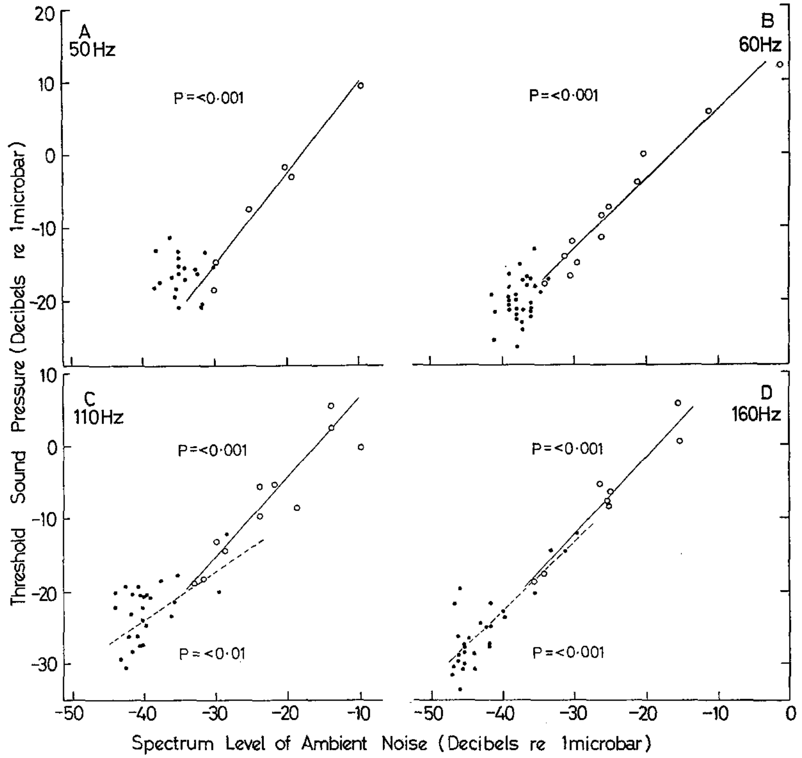

Fig. 6. Relationship between the thresholds and noise spectrum level at frequencies 50–160 Hz. •, – – – – – thresholds obtained in sea noise. ○, ———— thresholds obtained in transmitted random noise. In *A*, *B* there is little variation in sea noise level and therefore no correlation with the thresholds. The level of significance (*P*) of the correlations are given on each graph

in the thresholds could be attributed to changes in the distance of the sound source.

In Figs. 6 and 7 it can be seen that the slope of the regression lines is approximately unity in most cases suggesting that the thresholds were directly proportional to the noise level over the entire noise range. Departure from unity, for example the regressions of the thresholds obtained under sea noise conditions at 110 and 380 Hz, suggests that a proportion of the thresholds obtained at the lowest noise levels were not masked. This possibility was further tested by subtracting the spectrum level of noise from each threshold to give the threshold/noise ratio, and then comparing the ratios obtained at different noise levels using a multiple

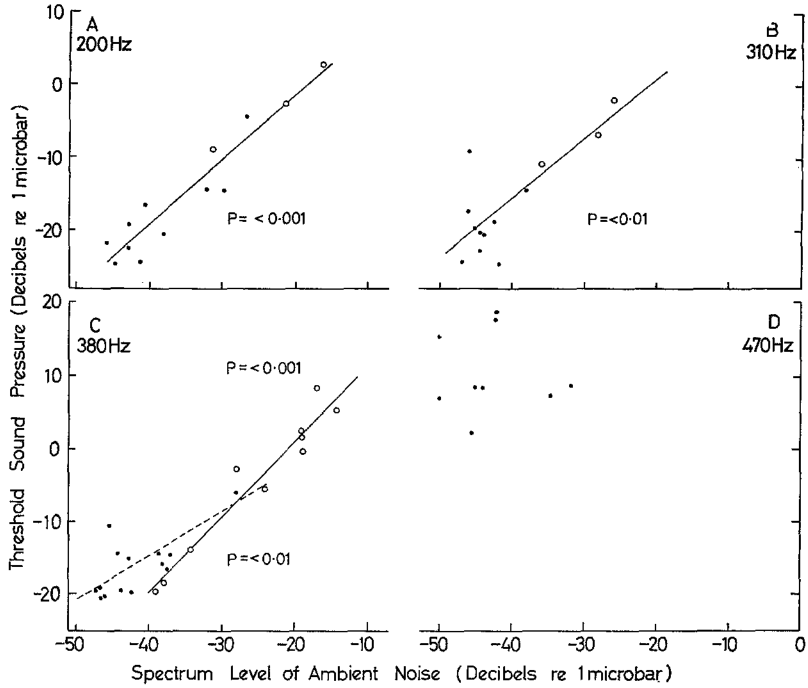

Fig. 7. Relationship between the thresholds and noise spectrum level at frequencies 200–470 Hz. • – – – – – thresholds obtained in sea noise. ○———— thresholds obtained in transmitted random noise. In *A*, *B* the two sets of data have been combined in calculating the regression. In *D*, there is no correlation between the thresholds and the noise level. The level of significance (*P*) of the correlations are given on each graph

range test (Duncan, 1955). Significant differences were apparent in the ratios at different noise levels for all frequencies between 50 and 380 Hz (Table 1). The data for four of these frequencies, plotted in Fig. 8, show that the threshold/noise ratios are greater at the lowest noise levels (the first point on each curve corresponds to sea state 0 at that frequency), confirming that the thesholds obtained in calm sea conditions were not masked by the background noise.

Since calm sea conditions were relatively infrequent in Upper Loch Torridon, it follows that the majority of the thresholds were masked by ambient noise and that the audiogram in Fig. 4 does not represent an absolute sensitivity curve for the cod. If thresholds obtained in sea state 0 conditions only are considered the mean unmasked audiogram for the species is about 2 dB less than that indicated by the mean values in Fig. 4.

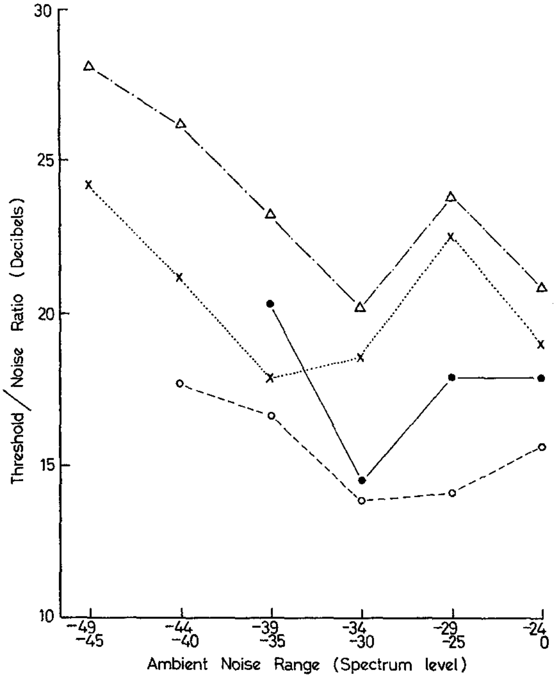

Fig. 8. Graphs showing the variation in threshold/noise ratio at different levels of ambient noise. ○ 110 Hz; ● 50 Hz; × 200 Hz; △ 380 Hz

Table 1. Variation in mean threshold/noise ratio with different levels of background noise (sea noise and random noise data combined) at frequencies 50–380 Hz

Frequency (Hz)	Range in noise spectrum level (dB/μbar)						Overall Mean
	-49/-45	-44/-40	-39/-35	-34/-30	-29/-25	-24/0	-49/0
50	—	—	20.26	14.52	17.90	17.93	18.58
60	—	18.83	17.38	15.64	16.38	16.58	17.33
110	—	17.68	16.63	13.85	14.10	15.62	16.55
160	17.83	16.29	16.23	17.50	18.05	18.27	16.52
200	24.20	21.20	17.90	18.63	22.50	18.95	20.69
310	28.25	21.98	24.50	—	22.80	—	23.38
380	28.06	26.22	23.20	20.20	23.75	20.80	23.70

4. *Effect of Sound Source Distance*

The threshold measurements obtained at different sound source distances are summarised in Fig. 9. Data, based on over 140 threshold determinations, are given for frequencies between 30 and 160 Hz. Two

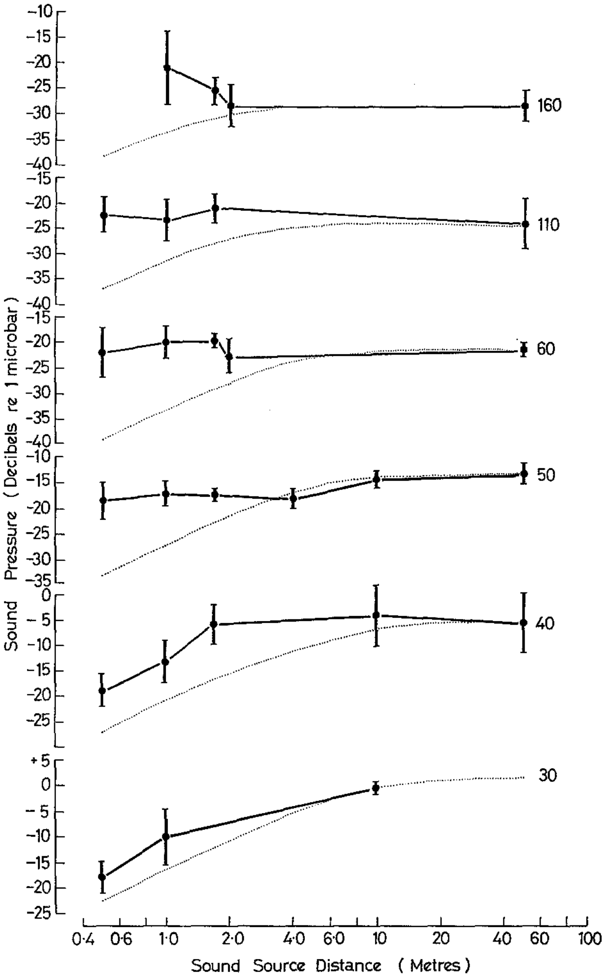

Fig. 9. Mean and standard deviation of thresholds for frequencies between 30 and 160 Hz obtained at different sound source distances (• ———). The fine dotted line on each graph is theoretical and shows the way in which the thresholds would be expected to vary if the cod were sensitive to particle motion (see text for further details)

curves are shown for each frequency; the plotted means and standard deviations of the threshold sound pressure measurements, and a theoretical curve (shown by the dotted lines) which shows the decrease in sound pressure corresponding to a constant displacement amplitude as the sound source distance is varied. The latter curve essentially shows how the thresholds would vary with distance if the cod were sensitive to particle displacement. At frequencies between 60 and 160 Hz the thresholds are largely independent of sound source distance whereas at lower frequencies a decrease in the thresholds was obtained when the source was very close to the fish. The difference is slight at 50 Hz but very obvious at 30 and 40 Hz. The thresholds at these low frequencies tend to follow the theoretical curve, though the correspondence is not precise. At 40 Hz, for example, the thresholds do not begin to decrease until the sound source is less than 2 m from the fish, and between 2 and 50 m there was little variation in the thresholds. These observations suggest that the auditory system of cod is effectively sensitive to sound pressure at all frequencies between 60 and 160 Hz[4]. However, at frequencies below 60 Hz there is a decrease in the sound pressure thresholds close to the source, suggesting a changeover to displacement sensitivity.

Discussion

1. Comparison with Previous Hearing Studies on Cod and Other Species

Hearing measurements on cod have been reported by a number of workers, who have used a variety of techniques under widely different acoustic conditions. The upper frequency limit to hearing established in our experiments is essentially similar to that reported by Buerkle (1967) and Olsen (1969). However, at lower frequencies the thresholds obtained by these authors were much higher than our results (by 20 dB or more). This was almost certainly due to masking of the tones by aquarium background noise.

Enger and Andersen (1967) recorded microphonic potentials from the sacculus of the cod, and obtained a measurable response at frequencies as high as 1000 Hz. However, the microphonic potential decreased steeply with increasing frequency above 200 Hz. Thus, the results of electrophysiological experiments confirm the suggestion made from conditioning experiments that cod are relatively insensitive to high frequency sounds.

The frequency range and sensitivity of a number of fish, representative of different families and habitats, have been comprehensively reviewed by several authors (Kleerekoper and Chagnon, 1954; Lowenstein, 1957; Tavolga and Wodinsky, 1963; Tavolga, 1965, 1971). Compared with cod, the upper frequency limit of hearing is higher in the majority of fish examined. Sensitivity to sounds in marine teleosts generally ex-

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[4] The same conclusion is likely to be true at higher frequencies but this was not confirmed since it was impractical to test sound sources sufficiently close to the fish. Consequently, the ratio of the sound pressure to the particle displacement component of the stimulus did not vary.

tends to at least 1000 Hz, and in the Ostariophysi (a largely freshwater group) the hearing range may extend to about 5000 Hz.

The rather restricted frequency range of the cod is paralleled in other gadoid species, including the ling *Molva molva*, haddock *Melanogrammus aeglefinus* and lythe *Pollachius pollachius* (Chapman, 1973). However, there are marine fish which show an even more limited frequency range. Recent cardiac conditioning studies on the plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, have indicated that the auditory thresholds for these species rise steeply above 200 Hz (Chapman and Sand, 1973).

Close comparison of the thresholds obtained from cod with those obtained from other fish under rather different acoustic conditions is difficult. We have already pointed out that the acoustic conditions prevailing when hearing measurements are made are of major importance, and have stressed the serious deficiencies of small aquarium tanks in this respect. One other major factor which may influence the thresholds obtained from fish is the level of ambient noise. Little attention has been paid to this potential source of disturbance by many workers. The ambient noise spectra for Loch Torridon were similar to the typical shallow water spectra described by Wenz (1962). The relationship demonstrated between the hearing ability of cod and the level of sea noise in Loch Torridon is therefore likely to apply to cod in other sea areas. Similar conclusions have been drawn from data on the haddock, ling, and lythe by Chapman (1973). We suggest that in fact the hearing of the majority of marine teleosts will prove to be limited by sea noise, particularly under adverse sea conditions.

2. *The Mechanism of Hearing in the Cod*

At frequencies above 50 Hz, no significant differences were noted between the thresholds obtained at different sound source distances. We can therefore conclude that the U-shaped audiogram (Fig. 4) showing a gradual decline in sensitivity at low frequencies is based on sensitivity to sound pressure. However, the decrease in low frequency thresholds at distances closer than 1 m indicates a changeover to particle displacement sensitivity.

Sensitivity to sound pressure indicates that the gas-filled swimbladder may be involved in the hearing of cod as suggested by Enger and Andersen (1967). These authors compared the hearing of cod and the bullhead [*Myoxocephalus* (=*Cottus*) *scorpius*] by recording saccular microphonic potentials with the fish at different distances from a sound source. Potentials could only be recorded from the bullhead when the fish were close to the source whereas responses from cod were obtained at greater distances. Since the bullhead lacks a swimbladder, these differences were attributed to the accessory role of the swimbladder in the hearing of cod, even though there is no direct coupling with the labyrinth. However, Enger and Andersen did not establish clearly that cod were sensitive to sound pressure. At the higher frequencies tested (400, 600 Hz) the microphonic amplitude was certainly proportional to sound pressure, but the fish were always within the far-field where the particle displacement does not vary with distance. Thus, the microphonic amplitude could also have been said to be proportional to particle displacement. Indeed at a lower frequency (200 Hz) higher microphonic amplitudes were obtained close to the source, suggesting that the fish were sensitive to particle displacement.

The acoustic properties of the swimbladder of cod and other gadoids have been studied recently by McCartney and Stubbs (1971) and by Sand and Hawkins (1973). These authors have observed resonance of the equilibrated swimbladder in the frequency range from about 600–2000 Hz, depending upon the depth and size of the fish. The resonance of the bladder was heavily damped with values of Q (the damping factor) ranging from <1 to 3. Although the hearing range of the cod appears to be confined to frequencies below resonance, Sand and Hawkins (1973) have suggested that the swimbladder could still convey a significant advantage in hearing.

The radial displacement amplitude, A, at the otoliths due to radiation from the swimbladder may be estimated from the theory of forced vibrations, as given by Poggendorf (1952):

$$A = \frac{p\,a^3}{3\,\varkappa\,P_0\,R^2}\left[\left(1-\frac{f^2}{f_0^2}\right)^2+\frac{f^2}{f_0^2 Q^2}\right]^{-\frac{1}{2}}. \qquad (3)$$

At frequencies below resonance ($f \ll f_0$) equation (3) reduces to:

$$A = \frac{p\,a^3}{3\varkappa\,P_0\,R^2} \qquad (4)$$

where p is the incident sound pressure, a is the effective radius of the swimbladder, P_0 is the ambient pressure and R is the distance from the swimbladder. For these calculations, R was measured from the centre of the most strongly curved portion of the swimbladder, at the anterior end, by means of an x-ray photograph (given by Sand and Hawkins, 1973). The effective radius of the swimbladder was assumed to be the radius of a sphere having the same volume.

For an incident sound pressure of 1 μbar and using appropriate values of a and R for a 30 cm cod ($a = 1.5$ cm, $R = 2$ cm) at 15 m depth, the radial displacement amplitude from the swimbladder, is 8 Ångström units for frequencies below resonance. This figure can be compared to the displacement amplitude of the incident sound wave [d, Eq. (1)],

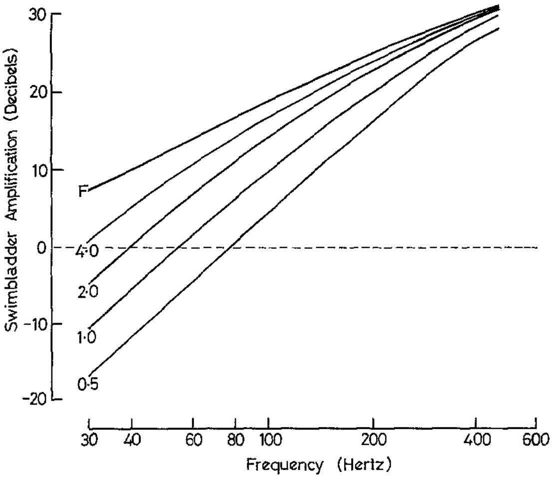

Fig. 10. The estimated displacement amplification of the cod swimbladder at different sound source distances from 0.5 m to far-field (*F*)

values for which are given in Fig. 3. The re-radiated displacements are larger than the incident displacements except at very low frequencies and with the source close to the fish.

An estimate of the displacement amplification provided by the swimbladder can be found from the ratio between *A* and *d*. Values for this ratio, expressed in dB, are given in Fig. 10. These curves show clearly the advantage gained from the swimbladder particularly at large distances from the sound source. The swimbladder gain is about 30 dB at 500 Hz but is reduced at lower frequencies as the incident displacement amplitude increases. Some of the curves intersect the zero dB line at a particular frequency which varies with the sound source distance. The 2 m curve, for example, intersects at 40 Hz. At distances less than 2 m, therefore, the displacement amplitude of the incident sound exceeds that of the swimbladder and the sound pressure thresholds would be expected to decrease as shown by the extrapolation of the curves below the zero line in Fig. 10. Table 2 shows that there is reasonable agreement between the measured threshold differences, at frequencies of 30–50 Hz, and the threshold differences predicted by the extrapolated curves in Fig. 10.

It would therefore seem that the hearing thresholds obtained from the cod can be readily explained in terms of the sensitivity of the otolith organs to particle displacements re-radiated from the swimbladder. However, at low frequencies, close to the sound source, the displacements associated with the incident sound wave are even larger than those

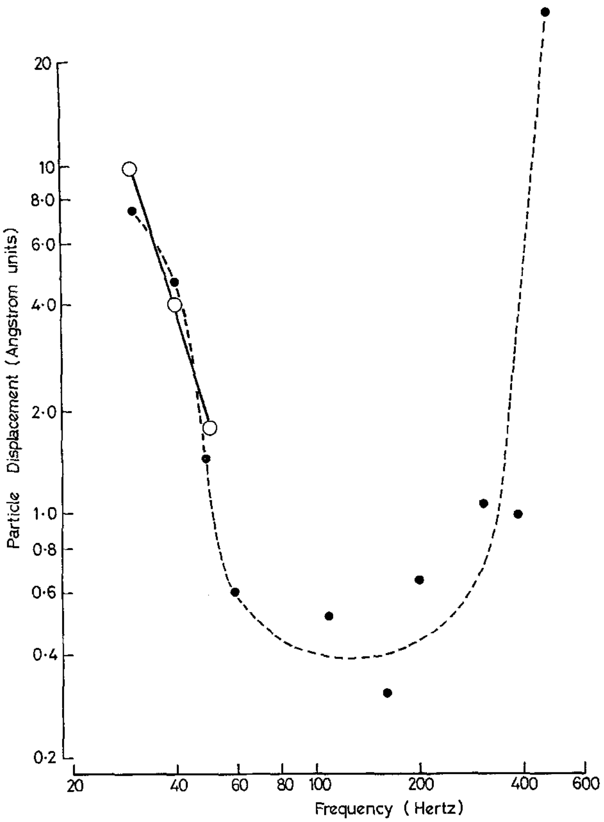

Fig. 11. Estimated displacement sensitivity of the otolith organs in the labyrinth. • – – – – curve obtained by inserting into Eq. (4) values of p corresponding to the mean thresholds given in Fig. 4. ∘ ——— low frequency displacement thresholds calculated from the measured sound pressure thresholds obtained at source distances below 2 m using Eq. (1)

Table 2. Threshold differences at frequencies between 30 and 50 Hz obtained at different sound sources distances, compared to values predicted by the theoretical curve in Fig. 10

Frequency (Hz)	Sound source distance (m)	Threshold difference relative to far field (dB)	
		Theoretical (Fig. 10)	Measured (Fig. 9)
30	0.5	−16.7	−19.3
	1.0	−10.7	− 9.3
	2.0	− 4.9	− 7.5
40	0.5	−11.7	−13.1
	1.0	− 5.8	− 7.3
50	0.5	− 7.8	− 5.7
	1.0	− 7.9	− 3.9

re-radiated and therefore stimulate the otolith organs directly. The displacement sensitivity of the otolith can be calculated from Eq. (4) by inserting values for p corresponding to the mean pressure thresholds for different frequencies (given in Fig. 4). The displacement sensitivity of the otoliths at low frequencies (30–50 Hz) can also be calculated directly from the thresholds obtained at sound source distances below 2 m (Fig. 9) using Eq. (1). The resulting sensitivity curve is shown in Fig. 11. The otolith organs appear to be most sensitive over the range 100–200Hz, where the threshold values were about 0.4 Å. Above and below this frequency range the thresholds increase sharply.

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