LASER LIGHT-SCATTERING INVESTIGATIONS OF THE TELEOST SWIMBLADDER RESPONSE TO ACOUSTIC STIMULI

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ABSTRACT When a laser pencil is directed through the teleost swimbladder fringe patterns can be seen in the far-field that are (*a*) highly sensitive to the orientation and position of the swimbladder with respect to the incident pencil and (*b*) a representation of contributions from each membrane through which the light passes. The fringe pattern fluctuates in intensity, and to some extent in position, in response to driving forces that distort the swimbladder. The spectrum of these very small distortions can be measured by standard light scattering techniques. This method was used to study the response of *in situ* swimbladders to imposed acoustic fields and evidence for a sharp roll-off of the response at frequencies above 1,000 Hz was found. Models for these effects are discussed.

INTRODUCTION

Sound detection and production by a wide variety of teleost fishes involves the participation of the swimbladder as a detecting or "amplifying" device (see reviews by Demski et al., 1973; Popper and Fay, 1973; Tavolga, 1971). The role of swimbladder in sound detection is thought to be that of providing an impedance jump between the surrounding water and the fish body, which otherwise is of the same density and compressibility as water (c.f. Popper and Fay, 1973; Tavolga, 1971). In sound production, the swimbladder acts to "amplify" the sounds produced by other structures and removal of the swimbladder generally reduces the sound level substantially (Schneider, 1967; Tavolga, 1962).

The swimbladder is a gas-filled structure (the nature of the gas may vary in different species) with thin viscoelastic walls that lies in the teleost abdomen just ventral to the vertebral column. The walls consist of two thin layers, a tunica interna and a loosely connected tunica externa (see Alexander, 1966, for a discussion of swimbladder structure). The outer wall is surrounded by tissue (muscle, bone, viscera) while the inner wall is in contact with the gas phase so that the impedance of the structure must be discontinuous. An incident sound wave is thought to stimulate motion in the swimbladder walls and the response is a strain field and time-rate-of-strain field which are

detectable by the inner ear (van Bergeijk, 1967) in at least some species (Fay and Popper, 1974, 1975).

A variety of experiments performed on the swimbladder have demonstrated that it plays a role in the acoustic behavior of fishes although the precise nature of the role is still unclear. If the swimbladder is considered as a single unit, a prime question lies in the degree of damping in the response to small displacements. As a highly damped system (e.g., low Q) the swimbladder would respond rather uniformly to a broad range of sonic frequencies as well as to rapid changes in the signal (pulses, etc.). Both of these points have important behavioral implications in the acoustic behavior of fishes. On the other hand, it is also possible that the swimbladder could act as a slightly damped bubble of air in water (see Alexander, 1966; Weston, 1967) and therefore respond as a high Q system where the resonance frequency is related to the geometry of the structure. In this case, the swimbladder would act as a band pass filter with sharp skirts, thus providing maximum response to a narrow range of frequencies.

Experimental evidence now tends to favor a system that is fairly well damped with a Q of no more than 4 or 5 (as opposed to a Q of 73 for an undamped system) (Batzler and Pickwell, 1970; Popper, 1974; Sand and Hawkins, 1973; Tavolga, 1964). The mechanical properties of fish tissues suggest that a substantial degree of the damping is due to the relatively immobile muscle and other body structures immediately surrounding, and often in contact with, the swimbladder wall (Alexander, 1966; Andreeva, 1964; McCartney and Stubs, 1971; Weston, 1967).

In the relevant frequency range, below 2,000 Hz, the length of the incident sound wave is considerably larger than the swimbladder suggesting that the whole structure may respond coherently to acoustic stimulation. The limited number of experimental observations (Poggendorf, 1952), however, have indicated that different portions of an excised swimbladder, in at least one species of fish, responds with different vibration amplitudes. Further complicating the system in intact animals are the facts that (*a*) the overall shape of the swimbladder is irregular and differs in different species, and (*b*) the amount of contact, and thus potential damping, varies at different parts of the swim bladder. To use an example of the species studied in the experiments reported here, the goldfish (*Carassius auratus*), the swimbladder consists of two chambers which are attached to one another by a narrow duct. The anterior chamber is generally round to ovoid in shape while the posterior chamber is long and narrow, and more elipsoid than the anterior chamber. The anterior chamber is attached to several movable bones (related to audition) and the tunica externa is split in this region and directly attaches to the bones. However, this pattern is not necessarily typical of all or even most species, many species having only a single chamber or more than two chambers. These various structures are probably related to audition in some way although the precise relationship is not predictable with the available data. While studies of the swimbladder response indicate a relatively flat overall frequency response in the auditory range of several species (Popper, 1974; Sand and Hawkins, 1973), it is possible that the observed response is a "sum" of varying responses in different portions of the chamber(s). Although it is possible that every small patch

of the swimbladder responds differently to sound, it seems more likely that major differences, if any, will be found between different chambers or in major diverticula. In addition, it is likely that there will be differences in response between points that are relatively taut (near connections) and points that have fewer stresses placed upon them.

In the experiments reported here we have used laser light scattering as a tool to investigate the response of specific portions of the in situ swimbladder during sound stimulation. So far as we know, this represents the first attempt to use such techniques for audition studies in fish. While considerable refinement of our methods is possible and desirable, we believe that the technology to be outlined provides a powerful system for exploring the response of biological membranes to perturbing fields.

METHODS AND MATERIALS

Model for the Scattering Effect

The homodyne detection methods for laser light scattering used in our study were discussed by Chu (1970) principally in the context of light scattered from homogeneous solutions. However, the swimbladder wall was shown to be far from homogeneous and when a light beam pencil was transmitted through the walls a striking and complicated diffraction pattern was observed in an arbitrary far-field plane. This pattern results from interferences of the light transmitted by the two membranes in the optical path, and the pattern is very sensitive to the relative displacement of the two illuminated areas. Intensity fluctuations in the far-field can be recorded with great spacial resolution as well as frequency resolution and it was easy to detect the effect of relatively low level sound fields on the swimbladder walls.

Additional measurements showed that the fringe contrast as measured by the maximum intensity to minimum intensity ratio when a fringe pattern was scanned with high spatial resolution was often 10 or larger. Fig. 1 is a lensless photograph of a fringe pattern observed in this work. The pattern changed radically with small changes in the orientation of the fish with respect to the incident pencil.

The following model served to organize the experimental work described in the next section. If we assume that a membrane patch transmits the incident beam according to the transmission function $t_1(x, y, t)$ the transmitted light travels across a small air space and is incident on the second membrane patch of the swimbladder. The second patch then transmits the incident beam according to the transmission function $t_2(x, y, t)$. Assuming that the air space of the swimbladder is transparent ($t_{sb} = 1$) and thin, then the field just outside the membrane is $U_2(+)$ and is given by:

$$U_2^{(+)}(x, y, t) = t_2(x, y, t)t_1(x, y, t)U_1^{(-)}(x, y), \tag{1}$$

where $U^{(-)}$ is the unmodulated incident field and all functions are referenced to a common coordinant system cutting the swimbladder and normal to the optical axis.

The transmission functions are dependent on the local state of strain in the membrane of the swimbladder. This proposition follows from the observation that the membrane is a viscoelastic structure (Alexander, 1966). Membrane response to fluctuations in the local pressure tensor, $\mathbf{P}$, can be thought of as resulting from the projection of the force onto the membrane, $-\hat{n}[\mathbf{P}]\mathbf{I}_{\hat{n}}$, where n is the unit normal to the membrane. $\mathbf{I}_{\hat{n}} = \hat{n}'\hat{n}' + \hat{n}''\hat{n}''$ is the projection operator with the unit vectors satisfying $\hat{n}\cdot\hat{n}' = \hat{n}\cdot\hat{n}'' = \hat{n}'\cdot\hat{n}'' = 0$, and $[\mathbf{P}]$ is the jump of the

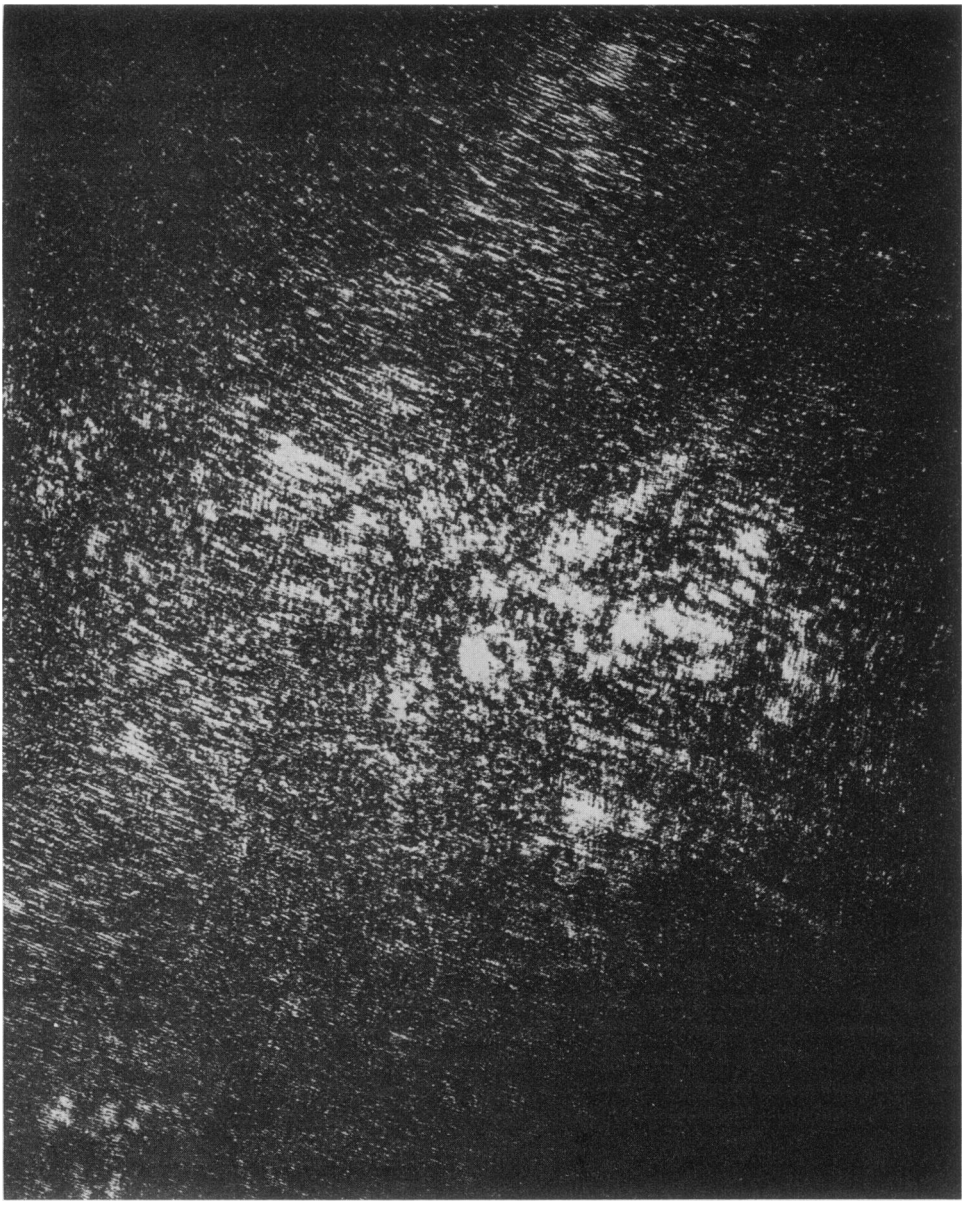

FIGURE 1 Fringe pattern as observed in a plane 10 cm from the swimbladder with the laser pencil focused onto the swimbladder and passed through both walls of the preparation. The photograph was taken without a lens and the Panatomic X film was exposed for approximately 1 s. The enlargement was made so that the optical axis is close to the center of the figure. The maximum angle of scattering shown in the enlargement is approximately 5°. The preparation was optically more dense than was normally used in our experiments. Blurring of some of the fringe patterns is a result of the natural fluctuations of the medium.

pressure tensor calculated across the membrane. Fluctuations in the strain in response to fluctuations in $-\hat{n}\cdot[\mathbf{P}]\cdot\mathbf{I}_{\hat{n}}$ can be further resolved into dilation and shear contributions. Such distortions change the relative locations of optical inhomogeneities in the membranes which are expressed by assuming that the transmission functions, t_i, depend on time and location.

Since thermal fluctuations are always present in the surrounding medium (also in each membrane patch) as a result of molecular chaos, t_i is time dependent even without the external perturbation of a sound field. This effect is observable as the zero frequency band that remains when the perturbing field is turned off. In principle, the response function of the membrane system can be determined from measurements of the spectrum of U_2 when thermal fluctuations provide the driving force. Unfortunately, the signal to noise ratios of the measurements we made were not large enough to allow such a determination in the interesting frequency range. Further, our purpose was to measure the frequency dependence of the coupling of sound fields to the membranes.

Membranes are driven in the presence of a sound field. Consequently by a determination of the space and time autocorrelation function of the scattered light intensity in the far-field, the strain response of the swimbladder to the sound field can be determined. The square law detector arrangement is such that the following function is measured:

$$i(t) = c\int_A |U_D|^2\,dA = c\int_A |t_2(x,y,t)t_1(x,y,t)U_1^{(-)}|^2\,dA. \tag{2}$$

The spectrum observed is directly related to:

$$G(\omega) = \int_{-\infty}^{+\infty} < i(t)i(t+\tau) > e^{i\omega\tau}\,d\tau, \tag{3}$$

where U_D is the field at the detector, i is the photocurrent associated with a region A accepted by the detector on the far-field cylinder over which the detector moves. In essence, the spectrum $G(\omega)$ (where $\omega = 2\pi\nu$) was determined as a function of frequency of the sound field. Fig. 2 shows representative spectra. The zero frequency band is observed even when the sound generator is off as was expected. The system is apparently overdamped when excited by very small amplitude thermal fluctuations since the band is not split from the zero frequency. The intrinsic relaxation time for the motion of the membrane system (swimbladder in the fish and both immersed in solution) is close to 20 ms according to a rough line shape analysis.

We have carried the analysis of this model far enough to establish the point that the power spectrum of the scattered light can be quantitatively related to the response of the swimbladder membrane to fluctuating driving forces. Model calculations, however, are outside the scope of this initial report.

Experimental Arrangement

Fig. 3 is a schematic of the experimental arrangement used in the study. A few comments on details of the arrangement are pertinent. The incident laser pencil was focused onto the swimbladder by a lens of focal length ca. 15 cm. A 4-μm pinhole was placed at the focus of a microscope objective in order to give a high spatial discrimination of the diffraction pattern in the far-field. The goniometer on which this detector was placed could be adjusted over a 15 degree range with a micrometer head drive. With this arrangement it was possible to scan a fringe with a resolution of approximately 1/10 of a fringe width. Note that the output of the wave analyzer must be squared in order to represent a spectrum. This was done numerically. A Varian computer of average transients (CAT) (Varian Associates, Palo Alto, Calif.) was used

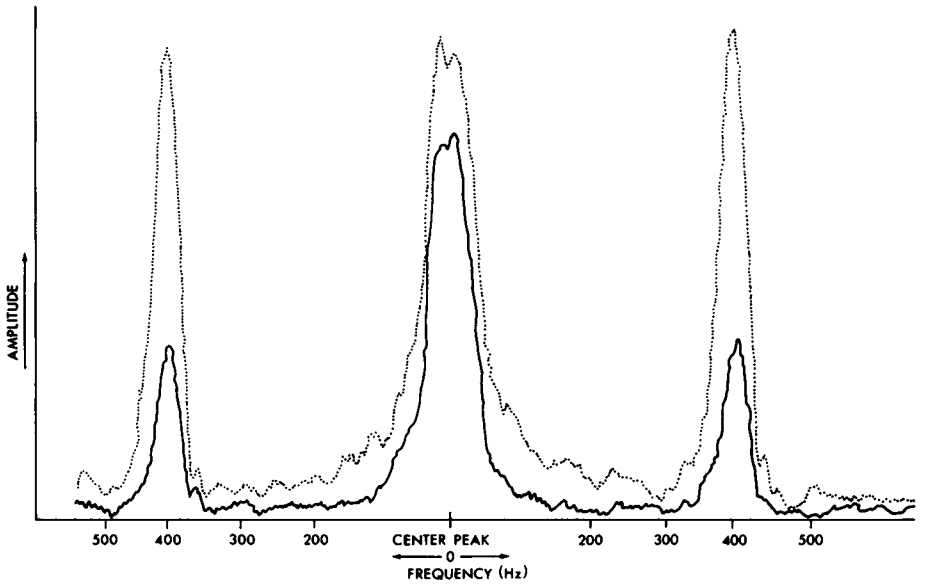

FIGURE 2 Examples of spectra collected at a scattering angle of approximately 1° with the detector positioned to admit a part of a bright fringe. The spectra were taken 15 min apart on the same preparation. The driving frequency was 400 Hz. The attenuation of the peaks was interpreted as an aging effect in the biological materials (see Discussion). See Fig. 3 for a schematic of the instrumentation.

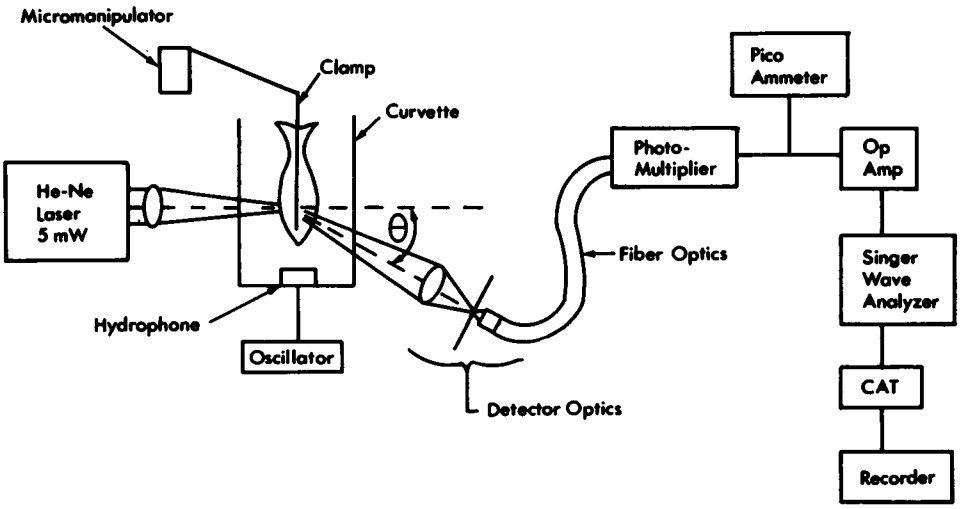

FIGURE 3 Schematic of the spectrometer. The scattering angle is θ_s and is actually in the plane of incidence perpendicular to the plane of the figure. The detector optics were arranged for high spatial resolution.

to enhance the signal to noise ratio of the output from the wave analyzer. The polarized output of the laser was in the range of 1–5 mW for this study.

The sound source was a Gould CH-17T hydrophone (Gould, Inc., Cleveland, Ohio) in a silastic seat on the floor of the cuvette with the head facing up. The sound field was propagated perpendicular to the optical axis and parallel with the long axis of the fish. The hydrophone (driven by a Hewlett-Packard audio-oscillator; Hewlett-Packard Co., Palo Alto, Calif.) had been calibrated so that the input voltages necessary to give a constant field independent of frequency over the range studied was known. The experiments were done in runs of 100 Hz steps from 200 to 1,600 Hz, with the field held constant at all frequencies. At this state of the research the chamber holding the fish as well as the hydrophone was not optimized acoustically and so it is unlikely that a uniform sonic field was set up in the cell. Even with this limitation, however, we were able to demonstrate certain response properties of the swimbladder as to be described below.

The experimental animals were goldfish (*Carassius auratus*) approximately 3.0 cm in standard length obtained from commercial sources. In preparation for these experiments the animals were quickly killed and small openings slightly larger than required to pass the light beam were made on opposite sides of the animal in order to expose the swim bladder. The opening was made at the level of the center of the anterior chamber and between two ribs.

The fish was then clamped securely at the head and tail, and was submerged in fish Ringer's solution, head down, in the glass cuvette which measured 5 cm by 5 cm by 7.5 cm. Initially, a metal holder was used but was found to corrode in the saline solution, changing the scattering properties of the solution significantly. The holder was then replaced with one made of Plexiglas.

Measurement of Scattering from Swimbladders

Initial experiments were performed to obtain the responses of the swimbladder to a broad range of frequencies played concurrently by using a white noise generator as the sound source. However, this experiment produced an array of inconsistent and dissimilar curves and blanks which could not be explained or well reproduced. Part of the difficulty with this particular experiment was the nonlinear response of the hydrophone with driving frequency. There is no doubt that a redesign of the entire cell system using a much more efficient driver in the frequency range of interest would result in an instrument that could utilize the white noise method of measuring the swimbladder response to sound fields. It is relatively easy to design driving electronics that would take into account the spectral response of the speaker and produce a white noise sonic field over the frequency range of interest in this investigation. Since we found that the response of the swimbladder changed somewhat with time it would be an advantage to collect data throughout the whole frequency range of stimulation simultaneously.

As a result of the difficulties with using concurrent frequencies the considerably slower protocol of pumping the system at constant frequency and level was used for the bulk of the experiments. The runs reported here were taken at three scattering angles that corresponded to fringe maxima. When the fish was properly oriented with respect to the incident pencil a fringe maximum was found in the angular region between 0 and 1°, a second one was found in the angular region around 5°, and a third suitable fringe maximum was found in the angular region around 12° measured with respect to the transmitted beam.

Since it required roughly 2 h to collect data at one angle it was found that the fringe pattern shifted slightly during that period so that a small correction in the location of the receiver was necessary (less than 0.1°). The total current produced by the photomultiplier system was continually monitored. Small angular adjustments were then made to keep that level constant over the run.

To check whether or not there was undesired mechanical coupling in the system several controls were run. The response of the system was checked with the sound stimulus present, but without the fish in the cuvette, and also with the fish in the cuvette but with no sound. A glass scattering plate was placed in the laser field using the clamping arrangement for the fish. The experiments indicated that such inappropriate coupling was down by at least a factor of 10 and most likely was down by a factor of 100 or better from the response of the fish. Occasionally some 60 Hz pickup and its harmonics were noted. However, this problem was not severe and could always be handled appropriately. The result of these control experiments was to establish that the spectra to be reported involved the response of the swimbladder and fish to the stimulus.

The entire fish should respond to the sound field as well as the swimbladder. An experiment was run that established the motion of the lower jaw of the fish near the opercle. There was a slight response of this region at frequencies less than 500 Hz. It was convenient in discussing certain features of the data on the response of the swimbladder to reference the response to that of the jaw.

RESULTS

Several data sets are shown in Figs. 4 and 5. There was a larger variation in replications of the response at a given angle than one might expect. One reason for this

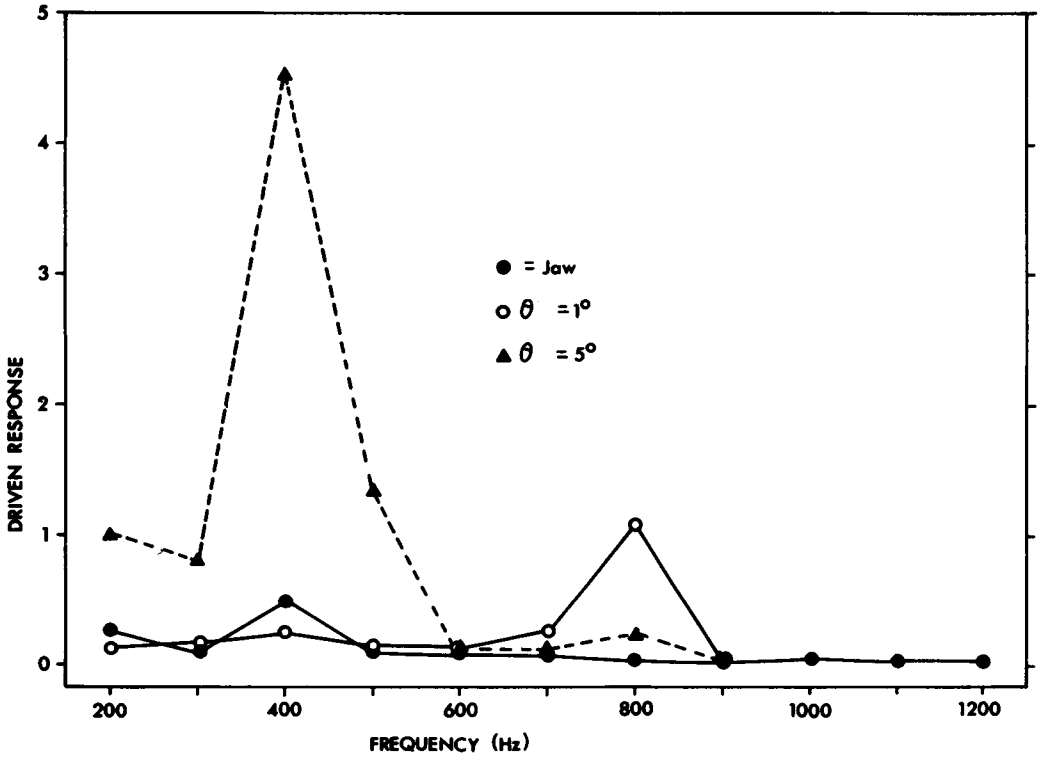

FIGURE 4 The driven response of two *in situ* swimbladder preparations and the jaw as a function of driving frequency as well as scattering angle. The square of the time averaged output of the wave analyzer (e.g. Fig. 2) that obtained at each driving frequency was plotted.

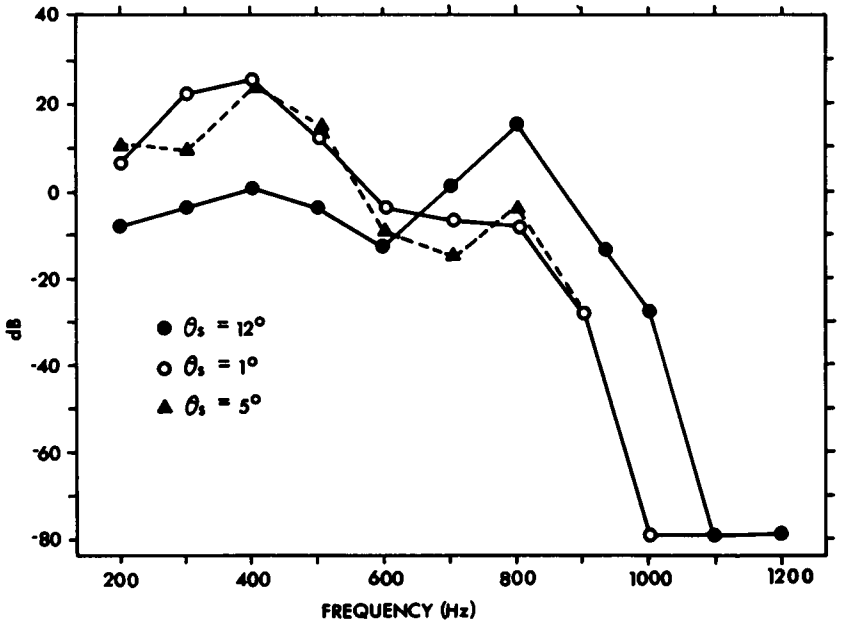

FIGURE 5 The logarithmic response of the *in situ* swimbladder preparations as a function of frequency and scattering angle. The response level shown beyond the roll-off frequency is a conservative estimate of the actual response at higher frequencies. These plots were constructed from data tables of the square of the time averaged output of the wave analyzer that obtained at various driving frequencies.

behavior certainly was the slow drift in the overall location of the fringe pattern with time. The exact origin of the drift was obscure. However, the tissue properties certainly show aging effects after death. Even when care was taken to keep the detector on the center of the fringe during the entire run, variations were observed in the spectra that appeared to suggest a change in the response of the swimbladder membrane with time. It was surprising and interesting to find that our method was quite sensitive to such effects. Controls were run frequently to be sure that the effects were not due to some intrinsic instrumental behavior. The results plotted were averages of several spectra taken under similar conditions of aging.

A striking feature of the results was that the intensity of the shifted peak observed at the driving frequency of the sound field went to the noise level above roughly 900–1,000 Hz. Several experiments were attempted in order to establish the levels at these higher frequencies. With the apparatus available it was our conclusion that the shifted signal was down by at least a factor of 50–100 below the signal observed in the low frequency domain. An estimate of the high frequency level was assumed in constructing the logarithmic plots of Fig. 5 and represents an upper bound of the actual signal level so far as we could determine it.

DISCUSSION AND CONCLUSIONS

The principle feature of the spectra collected from the swimbladder is the very rapid roll-off of the response to the sound field at frequencies above 900 Hz. For comparison with other data in the hearing literature it was convenient to construct a decible function. These data are plotted in Fig. 5. Since the high frequency data could not be resolved with our particular spectrometer a measure of the upper bound of the response in that frequency range was estimated by observing the sonic field needed to show a minimal spectrum response. The data implied that the power spectrum of the scattered light was down by at least a factor of 50^2 to 100^2 in that range. A linear plot of the data, Fig. 4, shows those numbers to be zero. Therefore, in order to derive a logarithm representation, the upper bound of the high frequency response was assumed. It should also be observed that the data show a possible resonance at 400 Hz. However, the swimbladder and the jaw respond in the same pattern at that frequency and are likely to correspond to a global motion of the tissue of the fish to the sound field. On the other hand it was obvious that the response of the jaw fell to a very low level beyond about 500 Hz. The spectrum of the swimbladder on the other hand, tends to approach a maximum at around 800 Hz consistently at each scattering angle and for each fish examined in this study. That could well be a feature of some interest in understanding the hearing mechanism of fish. Since a variation of the spectrum was noted with aging of the fish after death the existence of such resonances must be qualified. Nevertheless there was no doubt that the response of the swimbladder to the sound field rolled-off strongly above about 900–1,000 Hz.

Before discussing the biological implications of these results we wish to make a few comments concerning the extention of this technique to measuring the global as well as local vibration characteristics of biological structures such as the swimbladder. It would be interesting to establish any global extent of the vibrational modes excited by a sound field in the in vivo or at least the in situ swimbladder. The methods explicitly used in this paper give a measure of the response of one segment of the swimbladder with respect to a second. It may be possible to use such a configuration in deciding which modes of vibration are present in the global response of the swimbladder to the sound field but the analysis a priori is difficult if not impossible. It is easier to visualize a swimbladder as either a very thin spherical shell or ellipsoid of revolution. It can be imagined as being surrounded by a viscous fluid but with air internally. The vibrational motion of such bodies has been discussed in the literature previously (Alexander, 1966; Harris, 1967; Weston, 1967, and others). However one modification of this to suit our purposes would be to imagine that the shells are covered by a net of lines of differing optical densities. The transmission functions can then be modeled as simple gratings so that the electric field can be computed at the plane of detection. The results of various modes of vibration would be to distort the transmission function according to the mode of vibration of the shell. The calculation of the spatially resolved autocorrelation function for the electric field far from the scattering region could then be used to investigate the discrimination one might obtain in separating out the various

modes of motion by simply observing the scattering phenomena in a far plane. It is possible that a number of the lower modes can be separated out by the geometry that we have adopted in this study. However we do not have either experimental evidence or detailed calculations to confirm that conjecture.

Several points can be made from these data about the biological role of the swimbladder. The most significant point is that, contrary to experiments on the whole swimbladder, these data suggest that at least one isolated region of the membrane does have a slight intrinsic resonance response and that there is a sharp drop in response above 900 Hz. The former conclusion is subject to some uncertainty as a result of our inability to control aging effects observed in the preparation. The latter conclusion is secure for our preparation. Earlier data have indicated a relatively flat response to the system and so it is clear that further experiments, involving different regions of the swimbladder are necessary before its function in audition can be understood. The body tissue of certain fish species is transparent so that light-scattering experiments are possible with the tissue surrounding the swimbladder intact. A second point is that various morphological variations found in the swimbladders of different species may have significant, albeit subtle, effects on the acoustic response of the swimbladder. Again, further experimentation is necessary to resolve these effects. A third, and highly significant point that must be considered in future experiments on the swimbladder is the change in response noted over time after death of the animal. These effects could markedly alter the apparent response of the swimbladder and so attempts must be made to use living (but immobilized) preparations.

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