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THE RESPONSE OF THE SWIM BLADDER OF THE GOLDFISH (*CARASSIUS AURATUS*) TO ACOUSTIC STIMULI

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The teleost swim bladder is a gas-filled chamber located in the abdominal cavity just below the vertebral column. It consists of one or more inter-connected chambers which may be partially divided into 'subchambers' by septa that are extensions of the inner lining of the swim-bladder wall (Demski, Gerald & Popper, 1973; Greene, 1924; Tavolga, 1962 and others).

The swim bladder appears to have multiple roles in fish behaviour. One major function is as a hydrostatic organ involved in control of the density of the fish through changes in the amount of gas within the bladder (Steen, 1970). A second role in many species is in the production and detection of sounds (see reviews by Demski *et al.* 1973; Lowenstein, 1971; Popper & Fay, 1973; Tavolga, 1971). During the production of certain types of sound the swim bladder acts as an acoustic transformer between the water and vibrating body structure (e.g. muscles) (Demski *et al.* 1973; Harris, 1964; Tavolga, 1962; Skoglund, 1959, 1961). While the role in sound detection is not as clear as the role in sound production, the gas-filled bladder is of considerably different density from sea water and so it presents an impedance discontinuity that would respond to impinging acoustic energy. It has been suggested that were it not for the swim bladder, sounds would pass directly through fishes without being detected (van Bergeijk, 1964; Griffin, 1955; and others).

Although it has been suggested that the swim bladder plays a role in sound detection there is yet no direct experimental evidence that actually indicates its specific contributions. The bulk of the literature suggests that the swim bladder is a sound detector which vibrates in a sound field thus setting up a secondary displacement field detectable by the inner ear (van Bergeijk, 1967). There are recent suggestions, however, that the swim bladder in at least some species acts as a pressure release system after stimulation of the inner ear via bone conduction (Popper & Fay, 1973; Wever, 1969).

No matter whether the swim bladder performs in a pressure-detection or pressure-release system, its characteristics in a sound field should markedly affect the sound detection capabilities of fish. A number of workers have suggested that the swim bladder is analogous to a free bubble of air in water (Alexander, 1966; Harris, 1964; Weston, 1967) although these authors and others (Tavolga, 1964; Harris, 1967) have argued that the surrounding tissues (muscle, and viscera) significantly dampen the response, resulting in a less sharply tuned response than a free air bubble. However,

the extent of tuning in the swim bladder remains to be shown. The Q factor – a measure of the sharpness of a given tuning curve – of an ideal bubble of air in water is 73, indicating that there is considerable sharpness to the tuning (Weston, 1967) around the resonance frequency. (The resonance frequency is a function, of among other things, the radius of the bubble.) On the other hand, it has been suggested that the Q factor of the swim bladder, as a result of the damping by the surrounding tissue, is probably of the order of 5 to 10. This would make for some preferential passing of signals around the resonance frequency but tuning would be less sharp. By the same token, the swim bladder would respond better to broad-band signals and be capable of following rapid changes in signal phase, frequency and amplitude (Harris, 1967). Poorly damped structures take time to start responding and continue to respond after stimulation has terminated.

Experimental evidence, sparse as it is, points to significant damping of the swim bladder. Direct measurements in a sound field of the response of the excised swim bladder suggest that the tuning (or Q) is fairly sharp and therefore that damping is relatively light (Poggendorf, 1952). However, Tavolga (1964) reported that the excised swim bladder appeared to be less sharply tuned, although some of the apparent damping may have been due to an experimental artifact produced by a microphone placed on the swim bladder and used as a vibration detector. Other studies on the response of the swim bladder in a sound field have measured the echo (or target strength) to different frequencies in fishes with swim bladders intact and deflated. In such studies Batzler & Pickwell (1970) found that the swim bladder does make significant contributions to the strength of the returning echo in a number of species. They also report that there is a slightly (6 dB) greater response at the resonance frequency than at other frequencies, suggesting, on a limited number of animals, that the swim bladder might be well damped with a sharpness of 4 or 5.

While these experiments do suggest that the response of the swim bladder is significantly damped there have been no direct studies on its response in an intact fish in a sound field. In the following series of experiments this was examined by placing a probe microphone directly into the swim bladder to measure the pressure response of the swim bladder. While the appropriate stimulus to measure would have been displacement, techniques for doing this in very small areas are considerably more cumbersome than those for pressure measurements. In addition, pressure could be used since displacement is directly calculable from pressure (Harris, 1964).

The experimental animals were goldfish (*Carassius auratus*), a species with a two-chambered swim bladder. The anterior chamber in this species is generally spherical and it is connected by a thin duct on its posterior margin to an elongate posterior chamber. At its posterior end the posterior chamber curves ventrally and terminates near the end of the rectum. A small-diameter pneumatic duct goes from the ventral–anterior margin of the posterior chamber to the gut.

METHODS

The goldfish, 38–42 mm in standard length, were killed in ethanol and immediately placed in a special holder which held them firmly at the head and the caudal peduncle (Fig. 1). After positioning the animal above the water, a 0·5 mm (outer diameter)

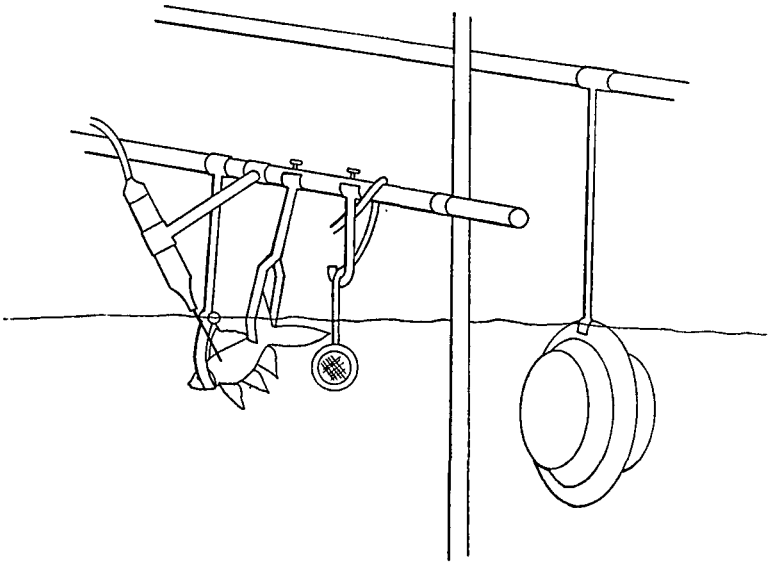

Fig. 1. Schematized drawing of the experimental arrangement. The fish, probe microphone and hydrophone were suspended from one rotatable bar sitting on a foam-rubber insulator. The underwater loudspeaker was on a second series of support bars on an independent foam padding.

probe (no. 25-gauge steel hypodermic needle) held in a Bruel and Kjaer (B & K) probe adapter was inserted into the fish just ventral to the 7th lateral-line scale and perpendicular to the side of the animal – a position lateral to the centre of the anterior chamber of the swim bladder. A stop placed on the probe limited the extent of insertion to a point previously determined to correspond to about the mid-point of the swim bladder. Since the probe tended to fill with tissue during insertion, a small amount of dental impression compound was melted over the tip to block entry of fluids. After insertion, a small diameter wire was passed through the probe to push the brittle impression compound out of the tube leaving a clear passage. A B & K $\frac{1}{2}$ inch condenser microphone (type 4134) and cathode follower (Type 2615) were then attached to the probe adapter.

After the microphone had been clamped in place the support was rotated and the fish was lowered to a depth of about 3·5 cm which completely covered the animal without getting the microphone wet (Fig. 1).

The experiment was conducted in a plastic 40-litre aquarium that rested on 5 cm of foam rubber. The fish and the loudspeaker were supported on separate pieces of foam to minimize acoustic coupling between them. The sounds were presented through a University underwater loudspeaker placed 25 cm from the preparation, and the signals were monitored through a hydrophone (Clevite H-17 t) 5·0 cm to the side of the fish.

The sound signals used in the experiments were sine waves from 50 to 1600 Hz in one-third octave steps produced by an oscillator, passed through an attenuator, and then amplified (Fig. 2). The sound-pressure level (SPL) at the hydrophone was kept constant at 36 dB (re: 1 μbar). Sounds from the hydrophone and probe went to an audio frequency spectrometer (B & K Type 2112) which consisted of a one-third

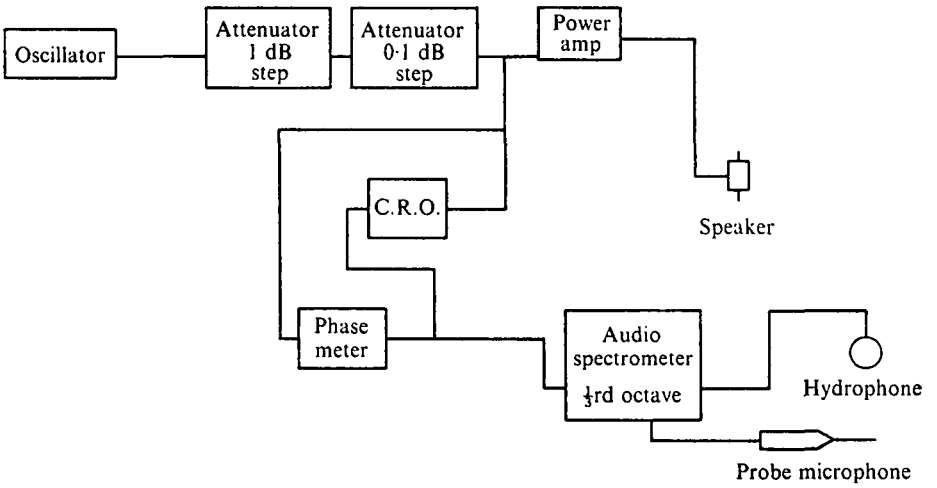

Fig. 2. Scheme of the electronic apparatus used in the experiments.

octave filter and pre-amplifier. The phase of the hydrophone and microphone were separately compared to the phase of the signal going to the power amplifier to assess phase shifts inside of the fish.

Each signal was presented at least twice to each preparation at 20 min intervals. The sound-pressure level (SPL) and phase (both measured relative to the signal at the hydrophone) generally varied by no more than ½ dB or 5° respectively, indicating no significant changes in the swim bladder and surrounding tissue during time of the experiment. After all of the data had been obtained from a given animal, the fish and probe were rotated out of the water without disturbing the relationship between them. A midventral incision was made in the fish, and the position of the probe noted to ensure that it was properly located in the centre of the swim bladder.

Calibration

All measurements of pressure and phase are reported relative to measurements of the sound made at a hydrophone 5 cm from the fish. To make sure that the SPL and phase at this point represented the signals at the fish, measurements were made in the normal hydrophone position and then with the hydrophone at the position of the fish. There were no significant differences in either SPL or phase angle at any of the test frequencies. However, since the hydrophone itself imparted phase shifts on the signal, the phase and amplitude responses of the hydrophone were calibrated against a B & K microphone placed in a rubber sac underwater. While the hydrophone SPL response was 'flat' over the range of test signals, the phase shift at the hydrophone was taken into consideration in calculation of data. Phase shifts and amplitude attenuation due to the low-pass characteristics of the probe tube were measured in a B & K calibrator, and these corrections were also added to the final data.

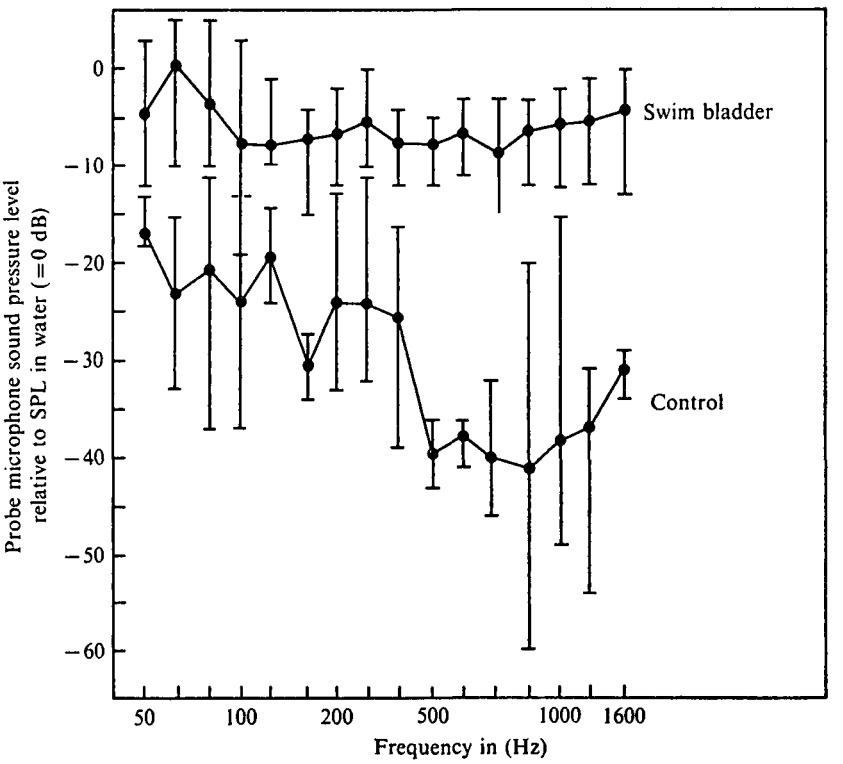

Fig. 3. Responses of the sound levels recorded with the probe microphone in the swim bladder and in controls where the tip of the probe was inserted into muscle, viscera, a deflated swim bladder or filled with water. The sound levels are presented relative to the sound levels at the hydrophone (0 dB) to the side of the fish. The mean sound levels are shown along with the ranges for all the animals.

RESULTS

Measurements of the phase and sound-pressure levels were made in the swim bladders of 10 animals, and control measurements were taken in six animals. The mean sound-pressure levels are shown in Fig. 3, along with measurements made in the viscera or body musculature as controls. The phase measurements are shown in Fig. 4 where the mean phase angles are shown in the swim bladder and at the control positions.

The sound-pressure level in the swim bladder was generally 5–10 dB below the SPL measured close by the fish, with the standard deviation at all frequencies being less than 2·5 dB. The sound levels at the different frequencies did not differ significantly, and the slightly lower loss at 63 Hz was possibly due to electrical noise in the system. Higher and lower frequencies could not be tested due to overloading of the speaker. The sound pressure levels in the viscera were considerably below the level in the water or in the swim bladder, and the range and standard deviations were considerably greater than those in the swim bladder.

Phases were more variable than sound pressure levels. However, except for the readings at 50 Hz, the phases within the swim bladder were generally close to those outside of the fish, and the standard deviations was no greater than 10°. The phases

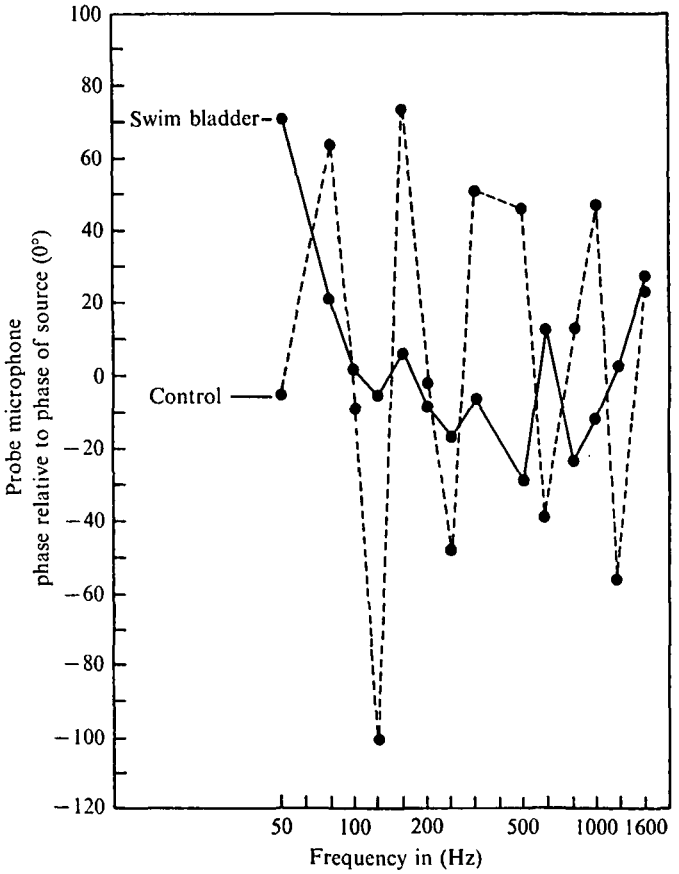

Fig. 4. Responses of the probe microphone in the swim bladder and controls (see legend of Fig. 3) relative to the phase angle at the hydrophone (0°). The phase angles were all measured against the phase of the signal to the power amplifier. Since the output of the hydrophone and probe microphone went to the same filtering and measuring system any phase shift caused by electronic apparatus was eliminated from consideration.

obtained in the tissues were considerably more divergent than those in the swim bladder with standard deviations as high as 75°.

Although the experiments were not conducted in a soundproof room, the noise measured in one-third octave bands was considerably below the level of the test signals and the signals recorded in the swim bladder or even in the viscera. The noise in all one-third octave bands was below 40 dB (re 0·0002 μbar), the limits of the measuring equipment.

DISCUSSION

The present experiments on the swim bladder of the goldfish indicate that the pressure response of the structure is essentially flat (therefore highly damped) from 50 to 1600 Hz. In addition, preliminary results at 2000 Hz were very similar to those at lower frequencies both in terms of intensity and phase response. Calculations based upon a monopole source (Harris, 1964) showed that the velocity response was also flat and displacement attenuated at 6 dB per octave.

There are several implications to these results and clear reasons why they could be expected in terms of the acoustic function of the swim bladder.

The first implication comes from the finding that there is little if any loss in sound pressure from the outside of the fish to the swim bladder as opposed to the 40 dB loss normally found at an interface between air and water (Albers, 1965). In fact, the 5 or 6 dB losses found in these experiments may be artifacts due to slight positioning differences in the tank from animal to animal. As a result, the animals would be at slightly different points relative to the standing waves in the tank and this would have a significant effect on phase relationships in the swim bladder. In addition, surface-wave resonances in the tank set up by ripples on the water surface as well as flexures in the tank walls could have caused variation in the sound level and phase readings (E. A. G. Shaw, personal communication, 1972; Parvulescu, 1964).

The small (or no) loss between the outside and inside of the swim bladder suggests that there is close acoustic coupling between the water and swim bladder. This situation was predicted in an analogous situation by Parvulescu (1964) who demonstrated that there is close coupling between the sound produced by a loudspeaker in air and the sound in a small tank of water. The relevant factor was that the tank had to be smaller than the wavelength of the sound. In the case of the swim bladder the size of the structure is considerably smaller than the wavelength even at 2000 Hz (the speed of sound in water is about 4·8 times faster than in air). The close coupling between the water and the swim bladder has significant implications for both sound production and detection. In sound productio the coupling is needed to get the sound into the water (Harris, 1964; Salmon *et al.* 1968; Tavolga, 1964). The sound is produced by contraction of muscles or the rubbing of bones attached to or in close proximity to the swim bladder. The swim bladder couples energy to the water, and experiments have shown that while deflation of the swim bladder does not cause a change in the spectral characteristics of the sounds, there is a significant decrease in sound amplitude as the swim bladder is deflated (Skoglund, 1959, 1961; Tavolga, 1962). The coupling also plays a role in sound detection in both of the models of audition proposed for teleosts. In the model proposed by van Bergeijk (1967) the swim bladder acts as a signal detector and a 40 dB loss would have significant effects on auditory sensitivity. Similarly, in the model proposed by Wever (1969) the swim bladder acts as a pressure release (or 'round window') for sounds detected through bone conduction.

A second implication of these findings is for the range of response of teleost hearing. It is possible that the swim bladder could act to selectively pass different frequencies thereby acting as a sort of peripheral filter to signals. However, the evidence so far available suggests that at least for the region of maximum auditory sensitivity for the goldfish (300–1000 Hz) the swim bladder does not selectively affect different frequencies. In fact, while the response in auditory sensitivity in goldfish drops off above 1000 Hz at almost 40 dB per octave (Jacobs & Tavolga, 1967; Popper, 1971; Fay, 1969; and others) the pressure response of the swim bladder does not change. Similarly, the velocity response of the swim bladder is also constant and the drop in displacement is only 6 dB from 1000–2000 Hz. This suggests that the limiting factor in auditory sensitivity at least up to 2000 Hz in this species is not the swim bladder but instead, some other structure(s) associated with hearing. However, before the swim

bladder can be eliminated as being involved in the high-frequency cutoff of the goldfish (between 2000 and 3000 Hz) further experiments will be needed at these frequencies. It should be further noted that the calculated resonance frequency for a bubble of the approximate size of the swim bladder for the goldfish used here would be between 1500 and 1600 Hz (Alexander, 1966; Weston, 1967; Popper, 1971), and the data do not indicate any significant change in the response of the swim bladder in this frequency region. These data then suggest that the tuning sharpness may be less than the Q of 4 to 5 suggested by others (Alexander, 1966; Batzler & Pickwell, 1970; Weston, 1967). In fact, it is possible that the swim bladder is a totally untuned system passing all impinging signals.

A third factor that must be considered in evaluating these data is the communicative significance of sounds to fishes and the implications of a widely tuned or totally untuned system such as reported here. In a sharply tuned system the response of the structure tends to lag behind the start of an impinging signal and, at the same time, only ends slowly after the signal stops. However, this type of system is unsuitable for at least some species of fish where the communicatively significant portion of the sounds appear to be in the form of pulsations (Winn, 1964). Instead, fishes need a system that will be suitable for wide-band and time-locked reception such as indicated by the functioning of the swim bladder described in these experiments. An additional point, as suggested by Harris (1967) and Popper (1971), is that if the swim bladder were sharply tuned, species would be found where sounds produced by large animals with large swim bladders would not be readily detectable by small animals of the same species. Behavioural studies of fish hearing have clearly shown a similarity in acoustic sensitivity between large and small goldfish (Popper, 1971), and so it is likely that different-sized animals can successfully communicate with the same bandwidth signals.

The findings for the goldfish are of considerable interest, but further experiments must now be carried out using both a wider range of frequencies and animals with swim bladders of different sizes and shapes. In addition, while the goldfish, as all ostariophysines, has a slightly higher than ambient internal pressure in the swim bladder (Alexander, 1959) the insertion of the probe may have resulted in a loss of excess pressure. Thus it is possible that the results reported here are more like those one would get with non-ostariophysines which have the same internal as external pressure. Consequently, experiments should be carried out on fishes with a mechanism to prevent loss of internal pressure and also on non-ostariophysines.

The architecture of the swim bladder also poses interesting questions. There is considerable variability in the size, shape and number of compartments and chambers in different species. While there have been suggestions that these structures may have something to do with sound production (Greene, 1924) there is no substantiating data; and, in fact, the little data available suggests that intraspecific architectural differences have little bearing on sound production (Demski *et al.* 1973). The implications of structural differences, while apparent in a few cases, are almost as unclear as for sound production. In some species of fishes, most notably the holocentrids (squirrelfishes) and clupeids (herring-like fishes), there are anterior projections from the swim bladder that come close or attach to the inner ear (Nelson, 1955; O'Connell, 1956). The suggestion for these and other species is that the projections result in greater auditory

sensitivity than in species where there are greater distances between swim bladder and inner ear. However, there is still no indication whether the different chambers of the swim bladder or the compartmentalization affect the response patterns or sensitivity of the structure. It is possible that the goldfish data are only typical for species with relatively simple bi-chambered swim bladders, and that animals with more complicated structures have a more complex contribution to sound detection or production.

SUMMARY

1. Sound-pressure levels were measured in the swim bladder of the goldfish using a probe microphone. Measurements of pressure and phase were made relative to the sounds immediately outside of the fish.

2. Results showed that the response of the swim bladder is flat from 50 to 2000 Hz with sound-pressure levels within the swim bladder about 4 or 5 dB below the sound pressure outside of the fish.

3. Phase measurements in the swim bladder were not significantly different from those made outside of the fish.

4. The data indicate that there is little loss between the water and the inside of the fish, indicating that the swim bladder acts to closely couple the fish to the water. This has significant implications since a poorly coupled system would severely limit detection capabilities for sounds and greatly increase the energy needed to get sound into the water during sound production.

5. The fact that there is a flat response over the major portion of the range of auditory sensitivity in goldfish indicates that the swim bladder is most probably not a limiting factor in acoustic sensitivity, at least below 2000 Hz. In addition, the swim bladder, as a poorly tuned or untuned system, does not selectively affect signals around what would be the resonance frequency in a more sharply tuned system.

6. The poor tuning of the swim bladder is important for communication since a portion of the communicatively significant sounds for fishes are broad-band, rapidly repeating pulses. A sharply tuned system cannot respond to these signals while a poorly tuned system is suitable for wide-band and time-locked reception.

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