The vibrational response of single-chambered fish swimbladders to low-frequency sound

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The gas-filled swimbladder of a fish resonates in the ambient noise field, scattering significant amounts of acoustic energy. The Non-invasive Vibration Amplitude Measurement System (NIVAMS) was used to measure the frequency response of the swimbladder of a freshwater species, the oscar (*Astronotus ocellatus* Cuvier), in a range from 200 to 2000 Hz. NIVAMS uses continuous wave ultrasound to measure swimbladder vibrational displacement amplitudes *in vivo*. Advantages of the NIVAMS are that it is non-invasive (no surgery is required to make the measurements) and that it is non-intrusive (the motion is unaltered by the measurement process). The response of the oscar's single-chambered swimbladder followed the general characteristics of the simple theoretical model by Andreeva (1964).

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Introduction

Rogers (1986) proposed the hypothesis that one fish could perceive nearby fish by recognizing the scattering of ambient noise by the swimbladders of other fish. The swimbladder, acting like a gas bubble, resonates in the ambient noise field, scattering significant amounts of acoustic energy. This characteristic scattered noise could allow for the detection and identification of the scattering fish by a receiver.

The first task in testing this hypothesis was to determine the characteristics of the acoustic signal scattered by the swimbladder of a fish. Since the wavelength of sound in the hearing range of a fish (100 to 1000 Hz) is much greater than any characteristic length of the swimbladder, the swimbladder responds to the oscillations of acoustic pressure by scattering sound in all directions. By measuring the radial displacement of the swimbladder, the scattered sound field can be calculated.

Methods

The frequency response of a swimbladder was measured with the Non-invasive Vibration Amplitude Measurement System (NIVAMS) (Lewis, 1994). NIVAMS uses highly focused, low-power continuous wave ultrasound to probe the body of a fish *in vivo*. The gas-filled swimbladder reflects the ultrasound. Since this reflecting

surface moves in response to a low-frequency sound stimulus, the reflected ultrasound is phase-modulated. The frequency spectrum of the reflected ultrasound consists of the original transmitted frequency plus sidebands at the summed frequency and difference frequencies of the ultrasound and the low-frequency stimulus. The radial displacement of the swimbladder is calculated from the relative amplitude of the sidebands to the carrier (Cox and Rogers, 1987).

Two identical focused 10 MHz transducers were used as transmitter and receiver. The transducers were aligned to have both focal regions centered on the same point in space. The minimum detectable displacement was in the order of 2.4 nm.

An anesthetized fish was attached by a flexible suspension to a positioning system inverted over an aquarium. The fish was then positioned so that the focal region of the ultrasound coincided with a surface on the swimbladder. An underwater transducer provided the low-frequency stimulus and a spectrum analyzer measured the amplitude of the carrier and the sidebands. Frequency response curves were constructed from individual measurements made in 50 Hz steps from 200 to 2000 Hz. After data collection, the fish was revived in fresh water.

Advantages to using the NIVAMS were that it was non-invasive (no surgery damaging to the swimbladder

or surrounding tissue was required to make the measurements) and that it was non-intrusive (the motion was unaltered by the measurement process). The small focal volume (0.32 mm in diameter by 0.85 mm deep) also allowed localized measurements to be made on the swimbladder.

Results

Swimbladder response was measured for 30 oscars (*Astronotus ocellatus* Cuvier) ranging in weight from 6.2 to 184.4 g. The oscar is a freshwater fish species whose prolate spheroidal shaped swimbladder has a major to minor axis ratio of about 4. In the following analyses, however, the swimbladder was assumed to be spherical.

The displacement data were related to the scattering cross-section by

$$\sigma_{s} = \frac{4\pi a_{0}^{2} (\omega \xi_{sb})^{2}}{\left(\frac{p_{inc}}{\rho_{w} c_{w}}\right)^{2} \left[1 + \frac{1}{(ka_{0})^{2}}\right]}$$
(1)

where a_0 is the radius of the scattering swimbladder, ω and k are the stimulus frequency and wave number, ξ_{sb} is the measured displacement, p_{inc} is the incident acoustic pressure, and $\rho_w c_w$ is the characteristic impedance of water (Lewis, 1994). The data were then fitted to the generalized scattering cross-section function for a resonant scatterer:

$$\sigma_{s} = \frac{4\pi a_{0}^{2}}{\left[\left(\frac{\omega_{0}}{\omega} \right)^{2} - 1 \right]^{2} + \left[\frac{1}{Q} \frac{\omega_{0}}{\omega} \right]^{2}}$$
 (2)

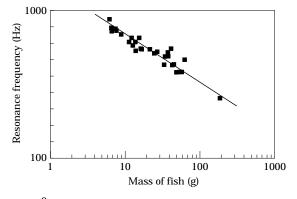
where ω_0 is the resonance frequency and Q is the quality factor. Figure 1 shows the resultant curve fit parameters ω_0 and Q for the 30 subjects.

Discussion

A simple model for swimbladder resonance was proposed by Andreeva (1964). The swimbladder was assumed to be a spherical gas bubble with the fish's body a visco-elastic matrix characterized by a complex shear modulus $\mu\!=\!\mu_1(1\!+\!i\mu_2),$ where μ_1 is the real part of the shear modulus and μ_2 is the loss factor in shear. This physical model leads to the following equation for the resonance frequency (Andreeva, 1964)

$$\omega_0 = \frac{1}{a_0} \sqrt{\frac{3\gamma p_0 + 4\mu_1}{\rho_w}} \tag{3}$$

where c is the specific heat ratio for the gas in the bubble, p_0 is the ambient pressure, and $o_{\rm w}$ is the density of water.



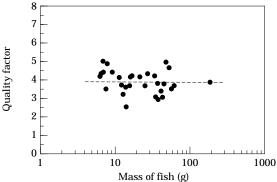


Figure 1. Resonance frequency versus mass (top) and quality factor versus mass (bottom) for the oscar. In the top graph, the solid line represents the best fit to a cubic function (Equation (5)). In the bottom graph, the dashed line represents the average value of 3.9.

The quality factor for this model has three factors: radiation damping, thermal damping inside the bubble, and viscous damping in the surrounding tissue. Since radiation and thermal losses were much smaller than viscous losses for these near-surface measurements (Lewis, 1994), the quality factor reduced to

$$\frac{1}{Q} = \frac{4\mu_1\mu_2}{3\gamma p_0 + 4\mu_1} \tag{4}$$

The difficulty in using this model for comparison was in the accurate determination of the shear modulus. Andreeva (1964) presented tentative measurements of $\mu_1 \! = \! 10^5$ to 10^6 Pa and $\mu_2 \! = \! 0.2$ to 0.3. Lebedeva (1965) directly measured the complex shear modulus of fish muscle tissue specimens and demonstrated that, although it was similar for different species, the shear modulus was a strong function of specimen fiber orientation and frequency.

By inverting Equations 3 and 4 and using the measured values for ω_0 and Q, estimates for the shear modulus and the loss factor in shear were calculated. There was no apparent correlation between the shear modulus and frequency, with an average and standard deviation of μ_1 =61 900 \pm 33 900 Pa.

Using Equation 3, the average value for μ_1 , and assuming the volume fraction of the swimbladder to be 8% of the total fish volume (Alexander, 1959), the relationship between resonance frequency and fish mass, m_f , was:

$$\omega_0 = \frac{975.7}{\sqrt[3]{m_f}}$$
 (5)

This equation best fits the cubic function to the swimbladder data and is shown in Figure 1.

The loss factor was also not well correlated with frequency. The average and standard deviations were $\mu_2 = 0.72 \pm 0.18$. These values were two to three times higher than those of the tissue data in Lebedeva (1965).

Andreeva's model adequately predicts the general characteristics of these data (inverse cubic function for resonance frequency and constant Q). However, independent measurement of the relevant tissue parameters must be made before this, or any other physical model, is accepted.

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