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Mathematical model of echolocation of fish-catching bats

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ABSTRACT

The ability of bats to prey on the insects and catch fish on the wing by means of echolocation is remarkable, since the acoustic power transmission through air–water interface is very small. A mathematical model describing the way in which a bat can detect fish under the water surface is suggested in this article. The problem of scattering of the spherical acoustical wave from the water with the spherical air inclusion under the surface is considered and solved numerically. The frequency dependence on the backscattered pressure shows significant attenuation of the signal at some frequencies. This offers an explanation of the surprising efficiency of the acoustic acuity enjoyed by these animals.

1. Introduction

In 1794, Lazzaro Spallanzani reported experimental results supporting his earlier proposal that bats could "see" with their ears. After repeating many of Spallanzani's experiments, D. Griffin [1,2] detected ultrasonic transmissions from bats by using a high frequency microphone developed by G. Pierce, and coined the term "echolocation" to describe how bats use echoes of the sounds they produce to locate objects in their path.

Much is now known of the natural sonar of bats and their orientational sounds. Several theories have been offered to explain the marvelous ability of bats to use echolocation to navigate in the dark and find food. Today, we know that there is a variation between bat species in the design of echolocation calls, which often coincides with the differences in their behavior and ecology [3–5].

Several studies have attempted to measure the structure and intensity of echolocation signals for bats during flight. The echolocation pulses emitted by a bat can differ markedly in duration and frequency. Some bat species emit compound pulses consisting of constant-frequency (CF) and frequency-modulated (FM) components. Other bats use either only short frequency-modulated (FM) pulses or long constant-frequency (CF) pulses.

The specific echolocation signal structure of horseshoe bat *Rhinolophus ferrumequinum* is discussed in [6]. It has been found that the emitted signals consist of a relatively long component of CF, which is preceded by an initial FM component and followed by a terminal FM component. It has been confirmed that during the flight the bats can compensate the Doppler shift, which is produced by their own movement, and that the terminal FM component is used for ranging.

The behavior of big brown bat *Eptesicus fuscus* during aerial interception maneuvers were videotaped in the dark with a night-vision lens and infrared illumination in [7], and the levels and spectra for a typical echolocation sounds were recorded. The bandwidth of signals emitted remained approximately the same throughout the maneuver, and the levels of emitted sounds were approximately constant until the terminal stage, which ended with capture of the prey.

The adjustment of pulse intensity by bats has been discussed in a number of studies. In [8] has considered the quantitative estimation of the acoustic parameters of the echolocation calls of the fish-catching bat *Noctilio leporinus* during prey capture.

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The results of this study show that during the approach to the target the bat reduces the intensity of emitted pulses, so that the intensity incidence in the process of reaching the target is constant. Similar echolocation behavior of the bats *Pipistrellus abramus* (an FM bat) on the wing was observed in the laboratory by using a custom-made onboard wireless telemetry microphone, Telemike, placed above the bat's head. The basic characteristics of echolocation sounds were recorded, and it was found that as a bat approaches a target the intensity of echoes returning from the target is nearly constant, which suggests that the bat adjusts pulse intensity at an optimal range [9]. The same Telemike system was used for the registration and analysis of the spectrograms and the temporal amplitude patterns of (CF) echolocation pulses and echoes of bats *Rhinolophus ferrumequinum nippon*, and it was suggested that the phase difference in the beat signal provides a useful cue for target localization [10].

Recent studies confirm that bats possess a highly developed sonar system. However, the ability of echolocating long-eared bats of the species *Vespertilionidae* to detect fish under the water surface using its own sonar is especially remarkable. These bats emit FM pulses with the frequency changing linearly over time. The duration of the pulse varies from one to tens of milliseconds, and the change of frequency during the sweep is usually of the order of one octave. This kind of echolocation allows bats *Vespertilionidae* to make their living by catching fish. Bat can do this by flying just above the surface of the water and emitting a rapid series of chirps. Bats dip their hind feet with sharp claws in the water to catch small minnows from still ponds. This they may do on the darkest nights and on a glassy calm coastal waters [11].

The proficiency of a bat on the wing to detect fish in water cannot be simply explained by the extremely high efficiency of acoustic acuity enjoyed by these animals, which has been discovered in many field and lab experiments in the air. The process of detecting fish must be much trickier, because between the bat and the fish there is a gas–liquid interface. Transmission of sound through air–water surface is normally very weak due to a very strong acoustic impedance contrast of these two media. The surface of water is an almost perfect reflector for the incident plane acoustical wave. The acoustic transparency of a plane interface of two homogeneous media does not exceed $\chi = 2m/n$, where m is the ratio of the mass density of air to that in water, and n is the ratio of the sound speed in water to that in air [12]. Under normal conditions in case of air–water interface these values are $m \approx 0.0013$, and $n \approx 4.5$, and thus the acoustic transparency of the air–water interface is equal to $\chi \approx 6 \cdot 10^{-4}$.

The echo signal from the fish would be produced almost certainly by the swimming-bladder, since a fish's body is acoustically similar to water. This sound wave going out into the air would be reduced by a factor $\chi \approx 6 \cdot 10^{-4}$ once again, which means that during two trips through the air–water interface the echo from a fish would be reduced to χ^2, or $3.6 \cdot 10^{-7}$ of the emitted signal. To this large reduction must be added additional losses, because only a small fraction of the sound in water would be reflected by a fish, and only a little part of what did escape into the air would find the listening bat. In this case the bat must detect the echo that is a million times weaker than the echolocation call, and this fact makes it seems almost impracticable for a bat to detect fish through the air–water interface by using their echolocation.

Here we may compare the threshold level of the fish-catching bat with that of the insect-eating bat, providing their echolocation in the air. The intensity of the echolocation call falls off as the square of the distance. Since a small scatterer would be considered as a point source, the intensity of the echo falls off also as the square of the distance. Thus the level of the echo returning back to the bat ears falls off as the fourth power of the distance. Therefore, if we suppose that the fish-catching bat does detect a small fish with 1 cm swimming-bladder at a distance $R_f = 10$ cm, then the insect-eating bat having the same threshold level must detect a flying insect 1 cm in diameter at a distance R_i, which may be found from relation

$$\left(\frac{R_f}{R_i}\right)^4 = \chi^2.$$

This distance $R_i = R_f/\sqrt{\chi}$, or at least 400 cm. At this distance an echo from the insect is equal to the echo from the fish at the distance 10 cm. The distance 400 cm is a very long range for insect-eating bats, and therefore the bats must activate at such distances the highest level of their perception sensitivity, which in fact is the upper bound of its capacity. Here we are not dismissing the ability of a fish-catching bat to detect fish through the water surface by their direct echoes, however, it seems extraordinary, that the main method of getting food rests on the maximum exertion of bat's senses. The purpose of this article is to derive the more reasonable model of the fish-catching bat's echolocation.

2. Problem analysis

First, it seems that the swimming-bladder reflects the incident wave at the resonant frequency rather well, and this fact can help the bat to detect the fish. The usual range of echolocation of bat of the species *Vespertilionidae* lies in range 50–100 kHz. Since the resonance frequency of the swimming-bladder of the radius $a = 1$ cm is equal to approximately 1 kHz, and the swimming-bladder does not radiate significant energy at higher resonance modes, the swimming-bladder oscillations are arguably of "no interest" to bat.

Another plausible explanation of how the echolocating bat detects fish is based on the resonant features of the water layer between the spherical air inclusion and the water surface. In this case one may hope to find a phenomenon similar to that of the wave propagation through the plane layer whose acoustical properties are strongly different from those of the medium in which the wave propagates. It is well known that the acoustical wave reflects back from this layer almost fully, but if the layer's thickness is equal to the integer part of the half of the wavelength, then the layer is completely transparent. It is very interesting to find out whether a similar phenomenon takes place between a plane and spherical surface.

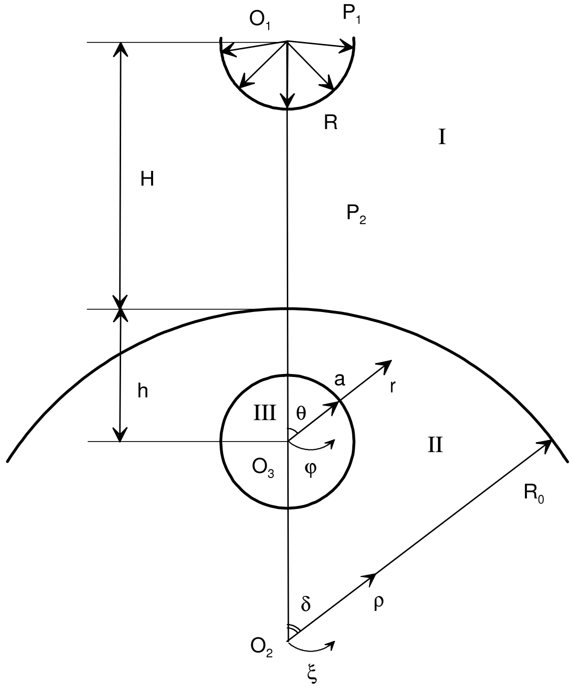

Fig. 1. The spherical coordinate systems and distances involved in calculating the scattering from the water surface with the bubble inclusion.

To verify this supposition the stationary problem of scattering of a spherical acoustical wave by the water surface with the bubble inclusion in the vicinity of the air–water interface was formulated and solved. The graphical statement of the problem is shown in Fig. 1.

The interface between the air region I and water region II is proposed here as a spherical surface with radius R_0. The flat interface can be obtained as $R_0 \to \infty$.

The transmitter (and receiver) is placed at a point O_1, which is a distance H above the water surface. The spherical air bubble of radius a (region III) is submerged at depth h under the water surface, and thus the problem under consideration is axially symmetric.

The pressure of the spherical transmitted wave is

$$P_1 = P_0 R^{-1} \exp(ik_1 R), \tag{1}$$

where P_0 is the constant pressure amplitude, R is the distance from the source point, k_1 is the acoustic wave number for the air, and the time dependent parameter $\exp(-i\omega t)$ is omitted.

The backscattered pressure P_2 in the air, and the pressure of wave P_{II} in the water are presented in the form of a spherical functional series in the spherical coordinate system $O_2\ (\rho, \delta, \xi)$

$$P_2 = \sum_{n=0}^{\infty} \sum_{m=-n}^{n} A_{nm} h_n^{(2)}(k_1\rho) \mathcal{X}_n^m(\delta, \xi), \tag{2}$$

$$P_{\mathrm{II}} = \sum_{n=0}^{\infty} \sum_{m=-n}^{n} [B_{nm} j_n(k_2\rho) + C_{nm} n_n(k_2\rho)] \mathcal{X}_n^m(\delta, \xi). \tag{3}$$

Inside the air inclusion III the pressure of wave P_{III} is presented also in the form of the spherical functional series in the spherical coordinate system $O_3\ (r, \theta, \varphi)$

$$P_{\mathrm{III}} = \sum_{n=0}^{\infty} \sum_{m=-n}^{n} W_{nm} j_n(k_3 r) \mathcal{X}_n^m(\theta, \varphi). \tag{4}$$

Using the series expansion, the spherical transmitted wave P_1 is presented also in the form of a spherical function in the spherical coordinate system $O_2\ (\rho, \delta, \xi)$

$$P_1 = \sum_{n=0}^{\infty} \sum_{m=-n}^{n} g_{nm} h_n^{(1)}(k_1\rho) \mathcal{X}_n^m(\delta, \xi), \tag{5}$$

where

$$g_{nm} = \frac{2ik_1P_0}{N_{nm}} j_n[k_1(R_0+H)]; \qquad N_{nm} = \frac{2}{2n+1}\frac{(n+m)!}{(n-m)!},$$

and

$$\mathcal{X}_n^m(\alpha,\beta) = P_n^m(\cos\alpha)\exp(im\beta).$$

Here j_n, n_n, $h_n^{(1)}$, $h_n^{(2)}$, are the spherical Bessel, Neumann, and Hankel functions; $\mathcal{X}_n^m$ are the spherical harmonics, and P_n^m are the associated Legendre functions. The acoustic wave number k_2 is the wave number for the water, and the wave number for the air $k_3 = k_1$. All series (2)–(5) are satisfied by boundedness condition and the Sommerfeld radiation condition.

Using the addition formula [13,14] for the spherical wave functions, the pressure of wave P_{II} in water can be rewritten in the spherical coordinate system O_3 (r,θ,φ) in the form

$$P_{\mathrm{II}} = \sum_{n=0}^{\infty}\sum_{m=-n}^{n}[U_{nm}j_n(k_2r) + V_{nm}n_n(k_2r)]\mathcal{X}_n^m(\theta,\varphi). \tag{6}$$

The relationship between the coefficients is given by

$$B_{nm} = \sum_{p=0}^{\infty}\sum_{s=-p}^{p} U_{ps}Q_{nmps}^{(0)}(k_2R_0); \qquad C_{nm} = \sum_{p=0}^{\infty}\sum_{s=-p}^{p} V_{ps}Q_{nmps}^{(1)}(k_2R_0), \tag{7}$$

where

$$Q_{nmps}^{(0)}(k_2R_0) = \frac{2}{N_{ps}}\, i^{p-n}\sum_{\sigma=|p-n|}^{p+n} i^{\sigma}b_{\sigma}^{(nmps)}j_{\sigma}(k_2R_0)\mathcal{X}_{\sigma}^{m-s}(0,\varphi),$$

$$Q_{nmps}^{(1)}(k_2R_0) = \frac{2}{N_{ps}}\, i^{p-n}\sum_{\sigma=|p-n|}^{p+n} i^{\sigma}b_{\sigma}^{(nmps)}n_{\sigma}(k_2R_0)\mathcal{X}_{\sigma}^{m-s}(0,\varphi),$$

and

$$b_{\sigma}^{(nmps)} = (-1)^s\left\{\frac{(n+m)!(p+s)!(\sigma-m+s)!}{(n-m)!(p-s)!(\sigma+m-s)!}\right\}^{1/2}(np00|\sigma 0)(npm,-s|\sigma,m-s).$$

The symbol $(n_1n_2m_1m_2|n, m_1+m_2)$ denotes the Clebsch–Gordan coefficients, the sets of numbers that arise in angular momentum coupling under the laws of quantum mechanics. The explicit form of these coefficients and coefficients $b_{\sigma}^{(nmps)}$ is given in [13].

Using the asymptotic formulas for the spherical functions at $x \longrightarrow \infty$

$$h_n^{(1),(2)}(x) \simeq (\mp i)^{n+1}e^{\pm ix}/x,$$
$$j_n(x) \simeq \frac{1}{x}\cos\left(x - \frac{n+1}{2}\pi\right),$$
$$n_n(x) \simeq \frac{1}{x}\sin\left(x - \frac{n+1}{2}\pi\right),$$

and the characteristics of the associated Legendre functions,

$$P_n^{-m}(z) = (-1)^m\frac{(n-m)!}{(n+m)!}P_n^m(z), \quad z\in(-1,+1),$$
$$P_n^m(z) \equiv 0 \quad \text{if } m>n,$$
$$P_n^m(1) = 0 \quad \text{if } m\neq 0, \qquad P_n(1) = 1,$$

the expressions for $Q_{spmn}^{(0,1)}$ at $\varphi = 0$ are determined by

$$Q_{nmps}^{(0)} = (-1)^{n-m}i^{p-n}\frac{(2n+1)}{k_2R_0}\frac{(n-m)!}{(n+m)!}\sum_{\sigma=|p-n|}^{p+n} i^{\sigma}b_{\sigma}^{nmps}\cos\left(k_2R_0 - \frac{\sigma+1}{2}\pi\right),$$

$$Q_{nmps}^{(1)} = (-1)^{n-m}i^{p-n}\frac{(2n+1)}{k_2R_0}\frac{(n-m)!}{(n+m)!}\sum_{\sigma=|p-n|}^{p+n} i^{\sigma}b_{\sigma}^{nmps}\sin\left(k_2R_0 - \frac{\sigma+1}{2}\pi\right).$$

The acoustic pressure waves must satisfy the boundary conditions

$$P_1 + P_2 = P_{\mathrm{II}}, \quad \text{at } \rho = R_0, \tag{8}$$

$$\frac{1}{\mu_1}\frac{\partial}{\partial\rho}(P_1 + P_2) = \frac{1}{\mu_2}\frac{\partial}{\partial\rho}P_{\mathrm{II}}, \quad \text{at } \rho = R_0, \tag{9}$$

$$P_{\mathrm{II}} = P_{\mathrm{III}}, \quad \text{at } r = a, \tag{10}$$

$$\frac{1}{\mu_2}\frac{\partial}{\partial r}P_{\mathrm{II}} = \frac{1}{\mu_3}\frac{\partial}{\partial r}P_{\mathrm{III}}, \quad \text{at } r = a. \tag{11}$$

Here μ_1 is the density of the air ($\mu_3 = \mu_1$), and μ_2 is the density of the water. The wave number $k_3 = k_1$ also.

Substitution of (2)–(5) into (8)–(11) results

$$g_{nm}h_n^{(1)}(k_1R_0) + A_{nm}h_n^{(2)}(k_1R_0) = B_{nm}j_n(k_2R_0) + C_{nm}n_n(k_2R_0), \tag{12}$$

$$l\left[g_{nm}h_n^{(1)'}(k_1R_0) + A_{nm}h_n^{(2)'}(k_1R_0)\right] = B_{nm}j_n'(k_2R_0) + C_{nm}n_n'(k_2R_0), \tag{13}$$

$$U_{nm}j_n(k_2a) + V_{nm}n_n(k_2a) = W_{nm}j_n(k_1a), \tag{14}$$

$$l\left[U_{nm}j_n'(k_2a) + V_{nm}n_n'(k_2a)\right] = W_{nm}j_n'(k_1a). \tag{15}$$

Here $l = (k_1\mu_2)/(k_2\mu_1)$, and the primes represent the derivatives of the respective Bessel functions with respect to their arguments.

Using (7), the infinite system of equations for deriving the coefficients U_{ps} and V_{ps} is employed

$$\sum_{p=0}^{\infty}\sum_{s=-p}^{p} V_{ps}Z_{nmps}^{(1)} = G_{nm}^{(1)}; \qquad \sum_{p=0}^{\infty}\sum_{s=-p}^{p} U_{ps}Z_{nmps}^{(2)} = G_{nm}^{(2)}, \tag{16}$$

$$m = n, n+1, \ldots, \quad \text{for } n \geq 1, \quad \text{and} \quad m = 1, 2, \ldots, \quad \text{if } n = 0.$$

Here

$$G_{nm}^{(1)} = \frac{F_{nm}}{d_n}; \qquad G_{nm}^{(2)} = \frac{F_{nm}}{c_n}; \qquad \Omega_{np} = \frac{c_nf_p}{d_nb_p}.$$

$$F_{nm} = -\frac{2il}{(k_1R_0)^2}q_{nm},$$

$$b_n = lj_n'(k_2a)j_n(k_1a) - j_n'(k_1a)j_n(k_2a),$$

$$f_n = ln_n'(k_2a)j_n(k_1a) - j_n'(k_1a)n_n(k_2a),$$

$$c_n = lh_n^{(2)'}(k_1R_0)j_n(k_2R_0) - j_n'(k_2R_0)h_n^{(2)}(k_1R_0),$$

$$d_n = lh_n^{(2)'}(k_1R_0)n_n(k_2R_0) - n_n'(k_2R_0)h_n^{(2)}(k_1R_0),$$

$$Z_{nmps}^{(1)} = Q_{nmps}^{(1)} - \Omega_{np}Q_{nmps}^{(0)}; \qquad Z_{nmps}^{(2)} = Q_{nmps}^{(0)} - \Omega_{np}^{-1}Q_{nmps}^{(1)}.$$

The analysis of the infinite systems of the algebraic equations similar to the system (16) is presented in [15], where it is also shown that such systems can be solved by a truncation method.

3. Numerical analysis

In the present study we are particularly interested in obtaining the backscattered pressure P_2 only at the source point O_1. The calculation procedure is the following. At the first step we can find the constant coefficients V_{ps} and U_{ps} from the infinite systems of Eqs. (16). The next step is the calculation of coefficients B_{nm} and C_{nm} using the relationships (7). Then the relationship (12) allows one to obtain the constant coefficients A_{nm}, and thus to determine the backscattered wave P_2 according to Eq. (2).

The solution of the infinite systems of Eqs. (16) can be obtained by truncating the systems to an order of $p = N$, where N is the maximum number of terms required in the summation series. To avoid complex calculations, we will consider here the low frequency range. The order of N can be determined by using a stepwise approach until the numerical results converge. If we choose the maximum non dimensional frequency $k_1a \simeq 15$, then we have $k_2a \simeq 3$, and the suitable accuracy can be achieved by truncating the systems (16) to an order of $N > k_2a = 3$.

The approximate solution for the backscattered pressure in the frequency range $0.05 < k_1a < 18$ was obtained for the source point O_1 ($H = 6$ cm above the water surface), and the spherical inclusion O_3 (radius $a = 1$ cm), submerged at the depth $h = 5$ cm. Here k_1a is the non dimensional wave number for the air. This non dimensional frequency range corresponds to the approximate acoustical range 250–90 kHz.

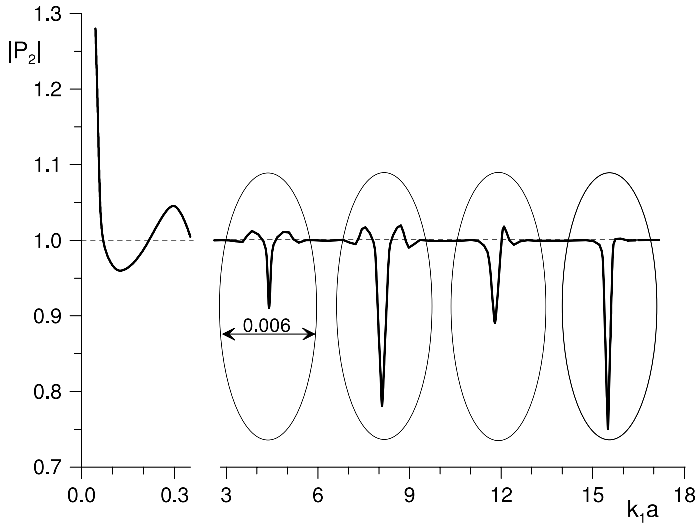

Fig. 2. Frequency dependence on the backscattered pressure.

The frequency dependence of backscattered pressure is shown in Fig. 2. For the low frequencies ($k_1a < 0.3$) the backscattered pressure is mainly determined by a resonant frequency of the swimming-bladder.

If the bat detected the echo from the swimming-bladder directly, in a high frequency range we could expect to see an almost constant value of the pressure amplitude with a very small (10^{-6}) modulation due to the scattering from the swimming-bladder, and nothing else. But, in fact, the amplitude of the backscattered wave reflected from the water surface depends on the frequency of the incident wave significantly. At some frequencies we may find the narrow dips (marked by magnifying glasses), where the amplitude falls by up to 75% of the mean level. The width of these dips is equal to 0.006 in k_1a units, or 30 Hz approximately.

We will now attempt to provide a qualitative estimation of application of stationary case to the problem of the bat echolocation. Experimental measurements show that bats can detect a shift in echo frequency with a high degree of accuracy, as small as 50 Hz [16,17]. Also, if the bat emits the frequency-modulated pulses such that frequency changes as a linear function of time, with the velocity of alteration 5 kHz/ms, then the dip of the width of 30 Hz is scanned through the time interval 6 μs. It is a rather long interval, because the bat can resolve as little as 2 μs in the time separation of echoes [18,19]. In addition, the duration of emitted pulse is equal to about several milliseconds. During this period, in the water layer of thickness 4 cm, the wave can take over a hundred re-reflections. Thus, the process of the frequency change is quite slow, and one may consider the process of the echolocation as a stationary problem.

In spite of the dip narrowness, it is evident that if the frequency of the emitted signal is equal to the corresponding frequency of the dip, the echo from the water surface drops out significantly, indicating the presence of fish under the water surface. Conceivably, the impact of the fish tissue surrounding the swimming-bladder expands the dip width, and this phenomenon helps the bat detect the air inclusion in water by using frequency-modulated pulses more easily.

4. Conclusions

Although the analysis in this article considers an ideal model of the fish and its swimming-bladder, a plausible method of the bat's echolocation was derived. The important evidence of the theory, which is presented here is the fact that only the echolocating bats of the species *Vespertilionidae* that emit the frequency-modulated pulses (FM) can detect the fish under the water surface. The bats of the other species *Rhinolophidae* who emit the long constant-frequency (CF) pulses followed by short FM component are not fish-eaters [3].

The method of the bat echolocation is explained here in terms of the interaction of the frequency-modulated acoustical pulse with the water layer between the swimming-bladder and the water surface. It was shown that in the presence of the swimming-bladder the amplitude of the echo reflected by the water surface depends on the signal frequency. In the usual range of 50–100 kHz of the echolocation there are at least three regions of frequency for which the amplitude of the echo reflected back to the bat varies by up to 25%. Thus, the bat can locate the fish in water not through the detection of echo directly reflected by the fish, but using information about the reflection features of the water surface, which may indicate the presence or absence of the fish.

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