Sound and Fish

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A.D. Hawkins

Marine Laboratory, Aberdeen, Scotland

1. Introduction

The sea is often described as silent. In fact, however, it is continually noisy, perhaps the most interesting sound sources being the living inhabitants of the underwater world. The various biological sources of sound, and especially the marine fishes, are the subject of this 1978 A.B. Wood Memorial lecture.

2. The Underwater Sounds of Fish

Many of the sounds made by marine organisms are purely incidental to other activities - like a crab scraping its limbs against a stone, or a fish digging up the seabed - but some animals produce characteristic calls of their own, which serve a definite adaptive function in their lives. The cod family or Gadidae contains several vocalists including the cod, haddock, pollack, and ling (Hawkins & Rasmussen, 1978). The sounds produced by the various species are all quite different to the human ear, but have in common the feature that they are made up of serially repeated low frequency pulses of sound. The timing or grouping of the pulses varies from one species to another. Thus, the cod produces short grunts, up to 0.2 seconds long, made up of between 4 and 15 rapidly repeated pulses, separated by about 12 ms. In the same behavioural context the haddock produces a long string of knocking sounds, lasting several seconds, the individual knocks or pulses being separated by about 200 ms. Even within any species the calls produced in different situations may vary in terms of their temporal characteristics. The repetitive knocking sounds of haddock are emitted during brief bouts of aggressive activity between fish, but in the middle of courtship of the female by the male the latter produces a different call like a motor cycle revving up, consisting of the same low frequency pulses, repeated at a much faster rate, with intervals as short as 25 ms.

Within the various gadoid calls the individual sound pulses appear much the same in oscillograms, though they sometimes seem to have a double structure. Frequency spectra of the individual pulses indicate that they are each produced by the 'ringing' of a heavily damped simple resonator with a Q of between 1 and 4. Repetition of the pulses to form the composite full call results in spectra consisting of a whole series of evenly spaced harmonics, the frequency spacing depending on the repetition rate of the pulses.

The resonator responsible for the sounds is the gas-filled swimbladder of the fish. Contraction of a pair of well-developed muscles attached to the organ results in a low frequency pulse of sound, a repeated and regular contraction resulting in the train of pulses that makes up each characteristic call.

Sounds are not produced indiscriminately by the fish, but recur in the same behavioural contexts, usually accompanying relatively stereotyped postures and movements by the animal. Thus, when the haddock produces long calls at a fairly fast pulse repetition rate (with an interval of about 22.5 ms) the fish is performing a dance, twisting its body with exaggerated curves, and flaunting its fins from side to side. In this species there appears to be a continuum of calls, and the closer the behaviour to a spawning climax the more elaborate the behaviour of the fish. In general, fish sounds appear to be almost entirely social in function, mediating aggressive or sexual encounters between individuals.

3. The Hearing Abilities of Fish

One of the main problems in furthering our knowledge of the hearing of fish has been the development of suitable techniques for finding out whether a fish has detected a particular sound or not. On the one hand, various training techniques have been developed, where the fish is forced to show an unequivocal response to every sound which it detects. On the other hand very sophisticated electrophysiological recording techniques have been applied to detecting the nervous response of the various sound receptors.

An example of a successful training technique is the method of cardiac conditioning described by Chapman & Hawkins (1973). The response of the fish is observed by monitoring changes in the electrocardiogram, (or heart rate). Thus, the fish is trained to show a change in the ECG on hearing a sound, in anticipation of a mild electric shock which is administered several seconds later. Once a response has been clearly established to high level sounds the amplitude can be progressively reduced until an auditory threshold is obtained. A plot of several thresholds for pure tone stimuli presented at different frequencies is termed an Audiogram.

In experiments performed on an acoustic range where the fish is mounted on a tower in midwater in the sea (to achieve good acoustic conditions), my colleagues and I have determined audiograms for a range of marine fish. The cod, for example, is sensitive to pure tones in the frequency range from 30 to 470 Hz, with greatest sensitivity in the range 60 to 310 Hz. Though the range of the fish is restricted to low frequencies the animal is nevertheless acutely sensitive to some tones with thresholds as low as -26 dB/μbar. Indeed, at its most sensitive frequency the fish is limited only by the level of ambient noise in the sea. Thus, in the natural environment there is considerable variation in the thresholds obtained which can be related to changes in the prevailing level of ambient sea noise. In addition, it has been shown that the cod has an auditory filter, which can be tuned to the frequency of a sound to aid discrimination against ambient noise (Hawkins & Chapman 1975). The width of this auditory filter has been investigated by experiments where pure tone thresholds were determined in the presence of narrow bands of noise centred at different frequencies. Thresholds declined (ie the fish detected the tones more readily) with increasing frequency separation between the stimulus and noise band. The masking function obtained has been described in terms of an equivalent rectangular filter of finite width, the bandwidth for cod varying from 59 Hz at 40 Hz to 165 Hz at 380 Hz.

Other experiments have shown that a species like the cod can readily distinguish between two different frequencies, presented in sequence, and that the fish can also distinguish between sound pulses of differing amplitude. Perhaps most important of all, the fish can distinguish between identical sounds emitted by sources in different positions, both in the horizontal and vertical planes. Thus fish not only detect underwater sounds, they can also classify the sounds, and determine the direction from which they are coming.

4. Hearing Mechanisms in Fish

Perhaps the most interesting recent work on fish hearing has been directed at investigating the mechanisms by which fish detect and analyse sounds. The fish auditory apparatus is very different to the more familiar mammalian ear. There is no connection between the fish ear and the outside medium, the hearing organ consisting of a heavy mass - the otolith - mounted on a membrane of sensory hair cells and completely sealed inside the acoustically transparent head. Recent experiments have shown that the otolith organ is not sensitive to sound pressure, but to particle displacement (Hawkins & MacLennan, 1976). In some fish, however increased sensitivity is achieved by coupling the otolith organ to the gas-filled swimbladder, which transforms sound pressure into an amplified particle motion at the otolith. In a few species, like the cod, this pressure to displacement transformation is transmitted to the ear without any special conducting mechanism but simply by virtue of the front end of the swimbladder being positioned close to the otolith organ.

The otolith organ is inherently directional, since particle displacement is a vector. In many fish, directional sensitivity to sounds is achieved by a process of vector weighing - with the two bilateral otolith organs with their axis of orientation at a different angle. Such a system incorporates a 180° ambiguity. In those fish with the swimbladder connected to the otolith organ the ambiguity is believed to be resolved by comparison of the phase of the displacement signals received directly by the otolith organs, and the sound pressure signal reradiated from the swimbladder.

The mechanism of frequency analysis within the fish auditory system is only poorly understood and will be the subject of future research.

5. References

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