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FISH BIOACOUSTICS: A PERSONAL HISTORY

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and to design appropriate experimental approaches benefit from broad interactions between scientists from the diverse, basic and applied sub-disciplines of sensory biology and behaviour, acoustic oceanography and bioacoustic engineering?

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FISH BIOACOUSTICS: A PERSONAL HISTORY

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My first fish talked to me almost 60 years ago, in the early fifties. It was at Marineland, Florida, where they had the first trained dolphins. It was called “Marine Studios” at the time, since its original function was a movie studio.

My research there was on reproductive behaviour of the frill-fin goby, *Bathygobius soporator*, and I was observing the behaviour, with colour changes of the approach of the male to a gravid female during courtship (Tavolga 1954). A colleague of mine asked if it were possible that these fish made sounds during courtship. Common knowledge at that time was that fishes do not make sounds nor could they hear much of anything. Actually, information on fish sounds was available, but only to those with military clearance. Fish sounds were “classified”.

My colleague, Dr. Ted Baylor (of the Woods Hole Oceanographic Institution) had audio electronics with him, and we put his question to the test. He boasted of having the latest electronic marvels of hi-fi – a microphone, amplifier, and speaker. The amplifier was the latest “Williamson” with huge tubes.

The microphone, waterproofed by a condom, was placed near the male goby’s home (an empty snail shell). The worst problem was the lack of shielding and poor grounding, with a resultant hum from the speaker: 60 Hz and all its harmonics. The human auditory system, however, is a fine audio filter, and when we dropped a gravid female into the tank with a male, we could hear little grunting sound pulses, synchronised perfectly with the male’s head shakes. I had heard my first fish (Tavolga 1956).

Shortly after, I found out about the work of others in the field, notably Dr. Marie Poland Fish (University of Rhode Island). Her pioneering efforts revealed the fact that a large number of fish species produce sounds (Fish 1954). In her early work, she simply “auditioned” each animal in an aquarium, by shocking it with a sort of an aquatic cattle prod. In actual fact, a well-established correlation between sound production and specific functions in social communication is known in only a small number of fish species. Unfortunately, the availability of Dr. Fish’s data to the scientific community was severely delayed because the recordings were stamped: “classified”.

Once it was apparent that fishes make sounds, playback experiments would be designed to test the possible social functions of the sounds. But before the first such experiment could even begin, major questions appeared. What kinds of sounds to use? How loud should they be? In other words, a more fundamental study had to be first undertaken in the area of fish hearing. Most information, at the time, suggested that fish were deaf, but by 1950 we were beginning to appreciate the importance of sound in the ocean. This was mainly because of the release (declassification) of huge amounts of submarine warfare data accumulated during WW II. When I first listened to gobies, quantitative data on fish hearing were not available. We knew that many fish could hear sounds, but beyond that, very little. What was the range of fish hearing? In frequency (pitch)? In intensity (loudness)? Especially little was known of hearing in marine teleosts.

It was my good fortune to meet Dr. Jerome Wodinsky (Brandeis

University), when we shared laboratory space at the now extinct Lerner Marine Laboratory on Bimini Island, Bahamas. He was testing a technique called "avoidance conditioning" on a variety of marine animals. On signal, the subject swam from one side of a tank to the other to avoid getting a mild electric shock. As I watched this experimental psychologist work with fish, shrimp, crabs, worms, and all available varieties from the rich coral island communities, it occurred to me that here was my way of getting the fish to tell me: "Yes, I heard it" or "No." For the next several years, Jerry and I worked together to obtain quantitative data on the hearing abilities of several species of marine teleosts. Our major paper on nine species was based on experiments done over a period of three months in the summer of 1961 (Tavolga and Wodinsky 1963).

The Bimini work was done with the most basic of electronics, i.e., something to produce and measure the sound, and some way to observe and regulate the sound and shock. Controlling all this was the first generation of a piece of equipment which we later called the Audioichthyotron. The first model consisted of two telegraph keys, borrowed from a ham radio. One key started the sound (the conditioned stimulus), and the other was tapped to provide the shock (the unconditioned stimulus), should the subject not cross the barrier in time. A mirror, suspended from the ceiling, enabled the observer to see what the subject was doing.

Over a period of several years, the mirror became a photocell, the sound level was controlled by an automatic attenuator, and timing was electronically set and recorded. The evolution of the "Audioichthyotron" tracked the advances in electronic science, moving through vacuum tubes and Schmitt trigger devices through solid state transistors, then to integrated circuits and decade counters, and eventually to complete computer control. Data, originally taken down by hand, were later entered into electronic calculators, then tape and punch cards, and finally came to reside on computer disks (Tavolga 1966).

Avoidance conditioning was a useful tool because the subjects provided unequivocal responses much more rapidly than with positive reward (Skinnerian) techniques. Classical conditioning, measured by "involuntary" responses such as breathing or heart rates, was not considered as a reliable indicator of behaviour.

Unconditioned responses are now more widely used with lower vertebrates, and the detection of UR's has improved with more sensitive equipment and computers to control the presentation of stimuli. One used to rely on well-trained, rugged subjects, and I remember that Jerry and I used the same fish daily, for weeks at a stretch. With today's techniques, we stab the animal with a couple of electrodes, and within a minute or less, we have a complete audiogram. We can now test species that are delicate and difficult to keep alive in experimental conditions. My colleague, David Mann will describe our latest studies on the

detection of ultrasound in certain fishes. Among the species that we tested was the anchovy, in which we obtained hearing thresholds within a few minutes, before it succumbed.

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ULTRASOUND PERCEPTION—AN OLD QUESTION

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My interest in fish hearing began in the early 50s when, as a masters degree student in Oslo, I was given the task of finding an answer to the question of whether fish perceive ultrasound. This question was raised because the catch of Arctic cod in the traditional winter fisheries in North Norway had gone down considerably. The fishermen claimed that the use of echo-sounders was the cause of the decline. Was there an easy way to find out whether cod could perceive ultrasound? The method of recording the electro-encephalogram (EEG) seemed worth while trying inasmuch as in mammals the EEG changed pattern upon visual and acoustic stimulation.

The recording of the EEG was performed by implanting electrodes in the codfish brain while the fish was kept in a small tank. There were clear responses to light and sound, but since no response was obtained even to frequencies far below 1000 Hz, perception of ultrasound was considered more than unlikely (Enger 1957). Seen in retrospect, it is more surprising that responses were obtained at all, in view of the severe stress under which the animals must have suffered – a factor which at least for fish was not considered at all at that time.

In his invitation to this conference, Arthur Popper asked me to tell a little about how I had seen the field of fish bioacoustics change during the close to 50 years I have participated, which I will do in a very subjective manner.