FISH BIOACOUSTICS - A PERSONAL HISTORY

by William N. Tavolga

Fish can't make sounds, and they can't hear. Cousteau said so in the title of his book. At least that is what most intelligent, well-educated people thought back in the late 1940's and 1950's. I had assumed so as well, and around 1950, I was observing the mating habits of a tidal zone species of fish: the frilled-fin goby, *Bathygobius soporator*. (1) This was at a small laboratory adjunct to the primogenitor of the dolphin shows: Marine Studios, at Marineland, Florida, near St.Augustine. This popular 50's tourist attraction is now disintegrating and in bankruptcy.

The gobies were so predictable, that I enjoyed showing off their antics to visiting colleagues. Just drop a female into a small tank with a male, and he immediately changes color, approaches the female, and gets her attention with little jerky head butts and head shakes. One bright colleague (Dr. Ted Baylor, of Woods Hole Oceanographic), popped the question:

"Could they be making sounds?"

"But fish don't make sounds, and they can't hear," said I, with assurance.

"Let's see," persisted Ted.

He was a great gadgeteer, and boasted the latest electronic marvels of hi-fi. He had a microphone, amplifier, and speaker. The amplifier was the latest "Williamson" with great big tubes that could double as space heaters. But how to get the microphone close enough to the fish? The size and shape of the microphone was phallic enough to suggest an obvious solution: a condom.

The microphone, suitably waterproofed and protected, was placed near the male goby's home (an empty snail shell), the equipment was plugged in and turned on. What with typical wet laboratory conditions of splatters of sea water around, the dangers of shocks were self-evident. The worst problem was the lack of shielding and the resultant hum coming from the speaker: 60 Hz and all its harmonics. The human auditory system, however, is a great audio filter, and we dropped a nice gravid female into the tank with the male. Sure enough, there came the little grunting sound pulses, synchronized perfectly with the male's head shakes. As the old Greek said, "Eureka!"

Shortly after, I discovered the work of others in the field, notably Dr. Marie Poland Fish (University of Rhode Island). Her pioneering efforts led to the notion that actually a large number of fish species produce sounds. In her early work, she was satisfied to simply "audition" a specimen, and the technique was to isolate a fish in an aquarium tank, and shock it with the equivalent of an aquatic cattle prod. Unfortunately, this evoked a variety of unnatural actions of tooth gnashing, body twisting, tail lashing, death throes and other movements that would generate sonic energy. In actual fact, there are relatively few species known today that generate sounds that have specific functions in social communication. It seemed to me that the proper experimental approach would be to play sounds back to the fish, both in captive and field conditions, and observe the responses.

That little goby turned out to be a valuable experimental animal, and an interesting one on its own terms. The social life of this hardy tidal-zone species involved a complex of communicatory signals using at least three sensory systems: vision, olfaction, audition. Rapid color changes and characteristic movements comprised some of the signals used in territorial defense and courtship. Pheromones secreted by the female served as an indicator of sexual readiness. Sounds emitted by a courting male helped attract and direct a female to his shelter. (2) For successful communication in social life and mating, even in a fish, a complex combination of signals is required. The simplistic notion of "social releasers" is not only inadequate but can be misleading since the notion assumes that some sort of a pent-up behavioral energy is sitting there, waiting to escape.

Once it was apparent that fishes make sounds, the tempting experiment would be: "Let's play these sounds back to the fish and see what happens." This is the naive "let's see what happens" kind of research that exists even among reputable scientists. This approach is rarely, if ever, productive. I have always urged my students to begin with a specific question, and then design the observations and experiments to suit. In the case of sound playback, before the first such experiment could even begin, a major question 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. Common knowledge said they 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. Many eminent scientists had been investigating the ears of fishes, including the Nobel laureate: Karl von Frisch. He used to astound his friends and neighbors by whistling for his fish in his pond to come for dinner. Even back as far as 1820, E.M.Weber theorized that the ear bones, now known as the Weberian Ossicles, in certain fishes, function to enhance underwater hearing. When I first listened to gobies, real 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.

I might add, by way of digression, that about the same time (1950's) the enormous acoustical and vocal properties of the marine mammals - chiefly Odontocete Cetaceans - were beginning to be appreciated. My interest in this was mainly by marriage, since my late wife had been making some of the now classic observations on the social behavior of the bottle-nose dolphin (*Tursiops truncatus*). Because of this relationship, the first international conference on marine bioacoustics (1963 (3)) featured many participants in the area of cetacean study. It was here that the powerful 20 Hz sound pulses common along the Atlantic coast were finally revealed to be emitted by huge baleen whales. For at least a decade, the U.S. military had been aware of these sounds, but had kept their existence a deep secret on the off-chance that they were produced by a flatulent Soviet submarine commander. Too much cabbage in the borshtch?

Thus, before any reasonable study on fish sounds could be launched, we needed information on their hearing capacities. There are two fundamentally different ways of asking a fish how well it can hear a particular sound. On the physiological level, one can insert electrodes in the receptor, or in the brain, and detect the animal's responses to a variety of external stimuli. This provides information on the receptor and receptor system, but I was more interested in the behavioral response of the whole animal. This approach might give some insight as to the adaptive value of hearing to a particular species. What I was looking for was a way of getting the fish to tell me unequivocally whether it did or did
not hear the sound signal that I generated in the water.

It was my good fortune to meet my friend and colleague, Dr. Jerome Wodinsky (Brandeis University), when we shared laboratory space at the now extinct Lerner Marine Laboratory on Bimini Island, Bahamas. He was testing an elegant technique called "avoidance conditioning" on a variety of marine animals. On signal, the subject would swim 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. Although published in 1963, these data were almost irretrievably lost, drowned in gin - literally. We kept all the original data (no copy, of course) in standard school-type notebooks, and I was to carry these home in my luggage at the end of our sojourn on Bimini. Jerry stayed behind. He had a gig to play maracas in a Bimini night spot. Back in the sixties, booze was a cheap item on Bimini, and one could import a gallon with no duty. Logically, a couple of imperial quarts of Beefeater gin were ensconced in one our suitcases, neatly padded with dirty laundry and protected by the hardcover notebooks. On return, the baggage manglers did their job, and one of the gin bottles leaked its cargo onto the notebooks. All inked entries were totally erased. However, because of Jerry's old fashioned notions, all the essential data were written in good clear no.2 graphite pencil. Not one record was lost. If this happened today, would a floppy disk survive a gin bath?

The moral of this tale: Follow the nose of your curiosity and write everything down in lead pencil.

At any rate, the survival of the data resulted in the publication of our 1963 paper (4). It was too big to be accepted by any well-known journal, but it was published by the American Museum of Natural History. This privilege was due in large part to the influence of my former professor and mentor, Dr. Charles M. Breder. Not only a major contributor to the science of ichthyology, he was an inventor, engineer and philosopher. He was a seminal influence on my life and career, and I was delighted to find that when

Margaret and I retired to Florida, he was living only a stone's throw away. One of his favorite occupations at his house on the bay was to listen to the catfish go swimming by. This needs some elucidation.

One of the most common estuarine species along the Florida west coast is the marine catfish, Arius felis. They gather in huge schools, especially at night, and emit a constant stream of low-pitched grunting sounds. Underwater, the total effect has been aptly described as the "bubbling of a giant percolator." Dr. Breder deployed a pair of small hydrophones, set apart at a distance about five times the width of the human head. These were placed at the ends of a rotatable boom at the center of which was a pair of stereophonic earphones and matched amplifiers. With this simple arrangement, adjusted for the five-fold difference in sound speed in water as opposed to air, the professor could determine with fair accuracy the position of the bubbling catfish.

About the same time, I too became interested in the sonic capabilities of this catfish species, and I did some acoustic and anatomical work on its sound producing apparatus (5). It was clear that the sounds had some social functions, possibly to help keep the school together in murky water or at night. In captivity, only animals in groups made sounds; isolated individuals were silent. It was my contention that these sounds could function as a crude form of echolocation and that part of the function of the swim bladder structure was to give the sounds some directional properties. Echolocation, since its discovery in bats, has always been associated with very high frequency sounds. In both bats and dolphins, the high frequencies provide the directionality and the precision of the system. Catfish, as is typical of fish, do not have hearing in these ranges. Although the species with Weberian Ossicles (Ostariophysi) appear better than other fish with high limits of perhaps 3 to 5 KHz, as compared to less that 1 KHz for the majority of teleosts tested. True echolocators, however, are up in the 30 to 90 KHz area. Catfish sounds, if used in echo ranging, could only be effective for large masses such as sea bottom or major obstacles. Considering that the sounds are also used as social signals, perhaps this crude method of examining the immediate environment is adequate. Indeed, in the low light conditions of the catfish environment, even such minimal information is better than vision (6).

As happens with most people engaged in basic research, someone always asks: "What is the practical value of your work?," meaning, usually, can it be used to make money? My reply has been to point to a particular study that resulted in a improving the success and income of a certain fishing guide. Fishing for bonefish requires both patience and skill, and this was especially true of the bone fishing guides on the island of Bimini (Bahamas - 50 miles east of Miami). I became friendly with one of these as we shared rum drinks in Brown's Bar (Alice Town, Bimini). Bersoll Cox was bright and curious, and visited the laboratory often. Eventually, we worked out a deal where he would take me fishing, and I would simultaneously gather data on the acoustic life of the bonefish. During the course of the summer, we observed and recorded those sounds that frightened the fish most, and those that they ignored. Dropping bait from a high trajectory, for example, generated a "plop" with a fundamental frequency of about 300 Hz. This chased the fish quickly. On the other hand, skipping the bait along the surface produced high pitched "plink" noises that they ignored. Running the boat engine at high speed evoked a minimal response, but as the engine slowed down to a stop, the fish would flee. The critical range of frequencies, including boat sounds, that the bonefish responded to were in the 300-500 Hz area. The audiogram of this species, as determined in the laboratory with avoidance conditioning, showed the highest auditory sensitivity was in the 300-500 Hz range. (7) This was more than coincidental, and demonstrates the close relation of the sensory system and the normal environment of a species. I should add that in the clear waters around Bimini it was obvious that there were many species other than bonefish, and they did not display the same responses to sounds as did the bonefish. Several of these other species had been tested for hearing acuity by Dr. Wodinsky and myself (see above), and their best hearing range was about the same as that of the bonefish. I guess that all the fish in the area were hearing the same things, but it is just that the bonefish "listened" better. In the end, Bersoll discovered that wooden boats were quieter that fiberglass and aluminum; that even loud conversation on the boat did not penetrate the water surface; that empty beer cans must not be dropped on board, but laid down softly; that bait must be "skipped", not just dropped; that it is more effective to stalk the fish with oars in muffled oarlocks than to chug the motor slowly. Armed with all this information, Bersoll became one of the most successful bonefishing guides on Bimini. If that isn't a practical result of basic science, then the discovery of penicillin was a waste of time.

On a biographical note, I was born in New York City, and grew up in range of the magnificent dinosaurs at the American Museum of Natural History. I was a member of the next to the last class of the Townsend Harris High School; closed by LaGuardia to save money. Undergraduate study was at City College of New York, later to be come part of the City University of NY. Master's and PhD were received from New York University (Washington Square), with most of my doctoral and subsequent research done at the American Museum. Eventually, I returned to City College as a teacher, and, after 30-odd years, retired to Sarasota, Florida. For several years, I continued research at the Mote Marine Laboratory, but then I decided that writing computer programs gave faster gratification than scientific research, so I went through a late career change. I think my timing was good, because there is little interest or encouragement for science today. Fortunately, there has been enough of a body of knowledge built up by scientific research to keep technology riding on its back for years to come.

(1) 1954 Reproductive behavior in the gobiid fish, *Bathygobius soporator*. *Bull. Amer. Mus. Nat. Hist.*, **104**, pp. 431-459.

(2) 1956 Visual, chemical and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish, *Bathygobius soporator*. *Zoologica*, **41**, pp. 49-64.

(3) 1964 "Marine Bio-Acoustics." Pergamon Press, Oxford, pp. I-xii, 1-413. (editor)

(4) 1963 Auditory capacities in fishes. Pure tone thresholds in nine species of marine teleosts. *Bull. Amer. Mus. Nat. Hist.*, **126**, pp. 179-239. (with J. Wodinsky)

(5) 1962 Mechanisms of sound production in the ariid catfishes, *Galeichthys* and *Bagre*. *Bull. Amer, Mus. Nat. Hist.*, **124**, pp. 5-30.

(6) 1971 Acoustic orientation in the sea catfish, *Galeichthys felis*. *Ann. New York Acad. Sci.*, **188**, pp. 80-97.

1976 Acoustic obstacle detection in the sea catfish (*Arius felis*). *In*: "Sound Reception in Fish," A. Schuijf and A.D. Hawkins, eds., Elsevier, Amsterdam, pp. 185-204.

(7) 1974 Sensory parameters in communication among coral reef fishes. *Mt. Sinai Jour. Med.*, **41**, pp. 324-340.

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