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SIGNIFICANCE OF CERTAIN FISH SOUNDS

[Following is a translation of an article by V. R. Protasov and Ye. V. Romanenko in the Russian-language journal Zoologicheskiy Zhurnal (Zoological Journal), Vol XLI, No 10, Moscow, 1962, pp 1516-1528.]

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Underlying biohydroacoustics, a new biophysical trend, are the study of sounds made by water animals, and the elucidation of their significance as signals. The history of biohydroacoustics has been given by us previously (Malyukina and Protasov, 1960).

The first work on biohydroacoustics was done during the Second World War, when, in connection with the mass use of underwater position-finding equipment, the question arose as to interference from living water organisms. Even at that time a large number of different and intense underwater noises of biophysical origin were found. Sometimes, these sounds absolutely muffled the propeller noise of passing ships, and sometimes acoustic "mines" exploded. In order to eliminate the "biological" sound interference special filters began to be put into the position finding apparatus. In connection with this, records and acoustic analysis were made of the sounds of some animals in the Pacific and Atlantic oceans by Japan and the United States. After the War, many countries took up the study of the interpretation of biological underwater sounds and their zoning in the seas (USSR, United States, Japan, France, Norway, and others). During the same period special studies (Fish, 1954; Shishkova, 1958) were made on the acoustic analysis of sounds emitted by fish in connection with the problems of the fishing industry.

Even in these works it was noted that many fish have their own sets of sounds, by which schools of them can be sought and found. After the work of Fish (M. Fish, 1954), abroad and in the USSR studies began to appear by J. M. Moulton (1956), W. Tavolga (1958), V. R. Protasova and M. P. Aronova (1960) clarifying the meaning of the sounds made by fish and other underwater organisms: biohydroacoustics became a new trend in animal ecology and a division of physiological acoustics.

The main task of biohydroacoustics has become the study of acoustic interrelationships of water organisms. Do these water inhabitants give signals of danger, of finding food, and others, as is done, for example, by birds and many mammals? Which organs give off these sounds and how is it done?

Naturally, the only method of answering all these questions is by experimentation. The sounds of water animals usually appear with certain behavior reactions; therefore, for the purpose of interpreting their biological significance it is necessary to create these reactions (feeding, attack, defense) experimentally, with the simultaneous registration of the sounds made. Proof of the signal significance of one sound or another is the possibility of controlling the behavior of the organisms by bringing about the appropriate reaction by sound.

Experiments for learning the significance of sounds made by fish and other water organisms as signals can be performed only with high quality recording and reproduction of the sounds in the water and knowledge of the details of the biological interrelationships of these organisms.

Clarification of the signal significance of sounds made by water organisms and particularly fish can be of great practical importance. Imitation of sounds which are significant as signals can be the basis for working out acoustical attracting and repelling catch methods.

Study of the significance of sounds as signals is associated with the general study of signals made by water organisms. Of particular interest in this connection is the analysis of location types: light, electrical, sonic, infra- and ultrasonic.

The tremendous number of species of underwater fauna living under different conditions have given rise to a great variety in the arrangement and operation of sound-producing and sound-detecting organs among its representatives. Many fish, for example, are capable of orienting themselves to sources of very low sounds with long wavelengths. Their sound detectors (the lateral line and inner ear) make it possible to localize the sources of low- and medium-frequency sounds through a principle different from that used in location technique. No less interesting is the method of production of sounds, distinguished by a high degree of efficiency, by the fish. Biophysical study of living models of perfect sound projectors and receivers may be of interest for hydroacoustical engineering. These, in brief, are the problems confronting biohydroacoustics.

The present report is ~~part of [redacted] work~~ on biohydroacoustics, ~~done under the direction of Academician N. N. Andreyev and B. P. Manteyf[redacted]~~. In it the sounds made by some fish are described; their signal and biological significance are elucidated, and experiments are described for finding out the capabilities of fish in determining the direction of sources of underwater sounds.

Material and Methods

The experiments and observations were made in 1960-1961 on marine and fresh water fish in the Black Sea, Rybinsk Reservoir, at the mouth of the Don River, in the water bodies of Moskovskaya Oblast as well as in the aquaria and pools of the Moscow Zoological Park, Moscow University and the Ichthyology Laboratory of the Institute of Animal Morphology of the Academy of Sciences USSR. More than 40 species of marine and fresh water fish were studied. (A complete description of sounds made by fish will be given in the Atlas Zvukov Ryb /Atlas of Fish Sounds/, being prepared for publication). The volume and nature of the material being analyzed in this article are shown in the Table.

The sounds were recorded within the sound frequency range of 50 to 10,000 cycles a second by means of a specially constructed portable sound recorder, consisting of a hydrophone with a sensitivity of 40 microwatts per bar and a "Reporter 2" tape recorder with an improved amplifier.

For the purpose of throwing light on the general nature of the sound signals the latter were photographed with the aid of an MPO-2 loop oscillograph. The photography was conducted during reproduction of the tape recording. The photographs shown below depict the time and amplitude characteristics of the fish sound signals. For the purpose of clarifying the amplitude-frequency characteristic, the tapes were analyzed with a spectral analyzer (of the ASChKh-1 type).

For the purpose of interpreting the biological significance of the sounds numerous experimental observations were made of the relationship between certain behavioral reactions and the associated sounds. In some experiments the signal significance of the sounds was made clear. For this purpose, the recorded sounds were reproduced in the water by means of a water-proofed projector.

Often, the fish themselves were used as the sources of the sound. After dividing the sound-producing fish in the aquaria and pools into two parts by an opaque, sound-transmitting cheesecloth and making the fish in one compartment emit sounds (feeding, frightening, and others), we observed the behavior of the fish in the other compartment. The fact that the fish were making sounds was checked with the hydrophone.

For the purpose of finding out about the perceptibility of sounds made by fish the fish were trained with respect to the feeding sounds which they made. Food was used as reinforcement. /In other words, tape-recorded fish sounds were projected at the fish when they were offered food/. A similar method was used for finding out about the capacities of fish for determining the direction of sources of sounds. In this case, with the aim of excluding the possibility of elaboration of a conditioned reflex to place, two identical projectors were used /two identical projectors in different places were used in order to be sure that the conditioned reflex formed was not being formed to the place at which the fish were fed/.

The observations of the behavior of the fish during the projection of the sound were made in the sea by means of special underwater equipment and in the aquaria, by means of motion picture photography.

№ п/п	Виды рыб	Характер опытов и наблюдений	Дата наблюдений
1	Белуга (Huso huso L.)	А (д, п, н, о)	1960—1961 V 1961
2	Осетр (Acipenser güldenstädti Br.)	А (д, п, б)	V 1961
3	Севрюга (Acipenser stellatus Pall.)	А (д, п)	V 1961
4	Плотва (Rutilus rutilus L.)	А (д, п, н, б)	V 1961
5	Лещ (Abramis brama L.)	А (д, п, б)	V 1961 1960—1961
6	Сом (Silurus glanis L.)	А (д, п)	IV 1961.
7	Щука (Esox lucius L.)	А (д, н, п)	V 1961, IV 1961
8	Речной налим (Lota lota L.)	А (д, н, п, о)	I 1961
9	Вьюн (Misgurnus fossilis L.)	А (д, п, о)	1960—1961
10	Карп (Cyprinus carpio L.)	А (п, д, о)	1960—1961
11	Орфа (Leuciscus idus var. orphus L.)	А (п, д)	1960—1961
12	Линь (Tinca tinca L.)	А (п, д)	1960
13	Карась (Carassius carassius L.)	А (п, д, н, б)	1960—1961
14	Верховка (Leucaspius delineatus Heckel)	А (п, д, б)	1960—1961
15	Касатка скрипун (Liocassis herzensteini)	А (п, д, у, о)	1960
16	Толстолобик (Hypophthalmichthys molitrix Val.)	А (п, д)	IX 1960 IV 1961
17	Угорь (Anguilla anguilla L.)	А (п, д, о)	1960—1961
18	Амур (Ctenopharyngodon idella Val.)	А (п, д)	IX 1960
19	Змееголов (Ophicephalus argus warpachowskii Berg.)	А (п, д)	XI 1960 IX 1960
20	Судак (Lucioperca lucioperca L.)	А, Б (п, д, о)	II—III 1961
21	Окунь (Perca fluviatilis L.)	А, Б, В (п, д, о)	I—IV 1961
22	Темный горбыль (Corvina nigra L.)	А, В	VII—VIII 1961
23	Рулена (Crenilabrus tinca L.)	А, Б, В (п, д, о)	VII—VIII 1961
24	Зеленушка-оцелята (Crenilabrus ocellatus For.)	А, Б, В (п, д, о)	VII—VIII 1961
25	Рябчик (Crenilabrus griseus L.)	А, Б (п, д, о, у, н)	VII—VIII 1961
26	Морской налим (Gaidropsarus mediterraneus L.)	А (п, д)	VII—VIII 1961
27	Кефаль (Mugil auratus Risso)	А (п, д, о)	VII—VIII 1961
28	Ставрида (Trachurus trachurus L.)	А (п, д, о)	VII—VIII 1961
29	Зубарик (Chara puntazzo L.)	А (п, д, о)	VIII 1961
30	Ласкирь (Sarguss annularis L.)	А (п, д, о)	VIII 1961
31	Барабуля (Mullus barbatus ponticus E.)	А, В (п,д)	VII—VIII 1961
32	Черноморская игла (Syngnathus nigrolineatus Eichw.)	А (д)	VIII 1961
33	Морской окунь (Smaris smaris L.)	А, В (п, д)	VII—VIII 1961
34	Морской язык [Solea lascaris (Risso)]	А, В (п, д)	VII—VIII 1961
35	Морской конек (Hippocampus hippocampus microstephanus Hast.)	А (п, о)	VIII 1961
36	Атерина (Atherina hepsetus L.)	А (п, д)	VII—VIII 1961
37	Бойцовая рыбка (Bettar splendens Regan)	А, Б, В (п,д,у, н)	1960—1961
38	Скалярии (Pterophyllum eimekey E. Aul.)	А, Б (п, н, д, у, о)	IX—XII 1960 IX—XII 1960
39	Нигрофесциаты (Cichlasoma nigrofasciata)	А, Б, В, (п, н, д, у, о)	IV—V 1961 IV—V 1961
40	Макроподы (Macropodus opercularis L.)	А (п, д)	IX 1961
41	Гурами (Trichogaster trichopterus Pall.)	А (п, д)	IX 1961
42	Тиляпия (Tilapia galilaia Artedi.)	А (п)	I—II 1961
43	Данио (Danio rerio)	А (п, д)	I—II 1961

Условные обозначения: А — запись и анализ звуков (п — питания, д — движения, н — нерестовые, у — угрозы, о — ориентировки, б — боли); Б — опыты, выясняющие сигнальное значение звуков; В — опыты, выясняющие способности рыб определять направления источников звуков.

Key: A--record and analysis of sounds (П--feeding; Д--movement; H--spawning; Y--threat; O--orientation: б--pain); Б--experiments clarifying the significance of the sounds as signals; B--experiments clarifying the capacity of fish for determining the direction of the sources of the sounds. /the key is continued on the next page/

[key, cont'd]. [The titles of the four columns are: Ordinal Number; Species of Fish; Nature of Experiments and Observations; Date of Observations] 1. beluga; 2. sturgeon; 3. sevriuga; 4. roach; 5. bream; 6. Danube catfish; 7. pike; 8. burbot; 9. loach; 10. carp; 11. ide; 12. tench; 13. crucian carp; 14. "verkhovka"; 15. "banded catfish" [the Russian here is kasatka skripun, a variety of catfish for which the species name is not the one given but rather Pseudobagrus fulvidraco; the species name given is that of a different catfish, called malaya kasatka in Russian]; 16. silver carp; 17. eel; 18. grass carp; 19. snakehead; 20. pike-perch; 21. perch; 22. ombre; 23. sea-parrot; 24. a kind of wrasse; 25. "ryabchik" [another kind of wrasse; all those of the genus Crenilabrus are wrasses]; 26. a rockling; 27. mullet; 28. scad; 29. "zubarik" [a fish with toothed jaws, belonging to the Characinidae]; 30. sargo; 31. Black Sea surmullet; 32; Black Sea pipefish; 33. pickarel; 34. sole; 35. seahorse; 36. atherinid; 37. fighting fish; 38. angelfish; 39. Cichla; 40. paradise fish; 41. gourami; 42. tilapia; 43. danio.

The Experimental Data and A Discussion of Them

Biological Sounds in Water Bodies. For a number of seas it has been determined that the sounds made by water fauna changes in accordance with the season and time of the day (Dobrin, 1947). Thereby, the maximum sound production occurs during periods associated with the reproduction of the water animals and with foraging. Our data confirm this conclusion. Black Sea fish (ombre and sea-parrot) begin to make sounds during the reproduction period (May-August). These fish produce sounds most actively at twilight and at dawn, when they feed. The periodicity of sound production by water animals is manifested in the most clear-cut manner in fresh water bodies (Lake Senezh in Moskovskaya Oblast, Rybinsk Reservoir). In the winter, the biological sounds were not detected under the ice. The silence stops in April-May, and the feeding sounds of the fish begin to be heard. At the end of May-beginning of June the specific fish sounds associated with spawning appear: the chirps of the roach, characteristic sounds of the bream, tapping of the perches, etc. During this period the sound background in the water body changes considerably during the day. At sunset and during the night the sound background is greatest. Various hydrodynamic noises are heard (the chirps of hunting fish), with sounds of unknown organisms resembling chirping of crickets; croaking of frogs, calls of night divers, and others. In the daytime, 80 percent of the sounds of biological origin disappear. In the autumn, the biological sounds in the water bodies become quiescent.

Observations in nature showing the relationship between mass production of sounds by fish during spawning were confirmed by us experimentally on aquarium fish (fighting fish, Pterophyllum, and others). By stimulating or inhibiting spawning and the initiation of the prespawning state in these fish, it is possible at will to increase or reduce their sonic activity.

Feeding Sounds of Fish. Note should be made of the sounds which fish make when they capture and chew the food. Feeding sounds are involuntary; they accompany the act of feeding.

In the nature of their feeding fish can be divided into predatory (cannibalistic) and "peaceful," feeding on other animals and plants. Differences in the mode of feeding are expressed also in the acoustical characteristics of sounds produced by fish. As a rule, the non-predatory fish are omnivorous.

Predatory fish and some large non-predatory fish, namely, the pike, pike-perch, large perches, snakeheads, Danube catfish, beluga, ocean perches, skates, sharks, large ombres, rocklings and others usually swallow their fish whole, without chewing on it. As a rule, the capture is associated with a characteristic clap or impact sound in the snakehead, loach, large perches, rockling, and spiny dogfish; with specific "kick" sounds (Danube catfish) and sometimes with specific shrill sounds (beluga). On Fig. 1, a and b, photographs are shown of the capture sounds made by the pike-perch and snakehead; on Fig. 1, c and d, the spectrum of their frequencies. The capture sounds are different in fish of different species.

Non-predatory and some predatory fish, namely, the carp, ide, tench, crucian carp, "verkhovka", roach, ombre, mullet, small scad, and others feed on varied food (plants, relatively sessile bottom organisms and moving plankton). It should be noted that the sounds which they make during feeding depend on the nature of the food. When they feed on relatively immobile organisms (Chironomus, mussels, and others) the capture sounds made by the majority of fish are inaudible. Sometimes, only the hungriest fish capture the food with smacking and sucking noises (loach, bream and others) or with a very much muffled cracking (sea-parrot). When feeding on mobile organisms (Gammarus, insects and others), they usually make sounds during the capture: cracking (sea-parrot, small ombres and others), impact sounds (small perches, small pike-perches, angel fish and others), loud champing (crucian carps, carps). It should be noted that many non-predatory fish eat noiselessly.

In contrast to predatory fish, all non-predatory fish usually grind up captured food, thereby making characteristic sounds which resemble rubbing or grating sounds or the sound of fat being fried ("verkhovka") with various tone shadings in various fish; the amplitude-frequency characteristics of the grinding and food-forcing sounds are similar and represent a continuous spectrum with the irregularity in the frequency range not exceeding 5-6 decibels. On Fig. 2, a and b, photographs are shown of the sounds made by forcing food in by fishes of the perch family (Cichlasoma nigrofasciata) and by grinding with the pharyngeal teeth in members of the carp family; on Fig 2, c and d, the spectrum of the frequencies of these sounds is shown.

When excited by sensing food, fish make characteristic sounds; Chara puntazzo makes a sound resembling the putt-putt of a motorcycle (Fig. 3, a and b); the beluga makes loud rattling.

Among the sounds made by fish when feeding are also the hydrodynamic noises arising from the lunges of the fish for the food. In the present article these sounds are not being analyzed, because their fundamental frequencies are lower than 50 cycles a second.

Perception of Feeding Sounds by Fish. The spectrum of frequencies of the fish feeding sounds extends, as a rule, from 50 to 10,000 cycles a second; the pressure amplitude reaches several bars. The auditory properties of the fish are the following: in the majority of fish the spectrum of sonic frequencies perceived (Malyukina and Protasov, 1960) lies between 25 and 13,139 cycles a second, while the threshold sensitivity amounts to 0.002 bar. Comparison of these data permits drawing the conclusion that the sounds made by fish during feeding can be perceived by other individuals of the same species. With the aim of confirming this conclusion, we performed an experiment on river perch with the elaboration of a conditioned reflex to sounds of capture and grinding of food. The experiment was performed in a pool measuring 2x0.7x0.5 meter with 17 specimens of perch. The feeding sounds were reproduced through an electrodynamic sound projector. Food (chironomid larvae) served as reinforcement. The hungry perch reacted to the first reproduction of the sounds with a unanimous positive reaction: an investigative food-securing reaction appeared in the majority of them; part came up to the source of the sound. The reflex was consolidated after 18 combinations. After this, the reflex to the sounds was manifested even under conditions of considerable sonic interference and not only to the actual feeding sounds but also to rough imitations of them. Therefore, the fact that fish perceive their feeding sounds was shown experimentally.

In parallel with the experiments for the elucidation of the ability of fish to perceive feeding sounds, experiments were performed in aquaria, in pools and in the sea for the purpose of finding out whether fish can determine the direction of the source of underwater sounds. The material of these experiments confirm data in the literature (Malyukina and Protasov, 1960) concerning the capacity of fish for determining the direction of a source of sound. In the pool (19x13x2 meters) the surmullets and scads turned toward the source of sound of a frequency of 500 cycles a second from a distance of 5-6 meters, which exceeded the wavelength of the sound; in the sea the sea-parrot and sole reacted in a clear-cut manner from a distance of four meters.

The Significance of Feeding Sounds as Signals. The answer to the question of the significance of fish feeding sounds as signals was given in a number of experiments and observations.

The experiments on the reactions of river perches and sea-parrots were performed in a pool and in aquaria. Reproduction of the feeding sounds (sounds of capture and grinding of food) made by domesticated hungry river perch in a pool measuring 2x0.7x0.5 meter caused a positive reaction in them: investigative food reactions and a purposeful movement toward the source of the sound. When the feeding sounds were repeated many times without food reinforcement the reaction to these sounds by the perches died out. This speaks for the naturally elaborated conditioned-reflex character of this reaction.

During feeding, different species of wrasses make loud sounds: "cracking" and sounds of food grinding. The first observations (Protasov and Aronov, 1960) were made on a group of hungry sea-parrots [Crenilabrus ocellatus] and "rulen" [Crenilabrus tinca], separated from several feeding fish by an opaque, sound-transmitting partition. The isolated fish became excited when they heard the sounds coming from the other side of the partition and began to swim about actively over the whole aquarium. However, there were no purposive reactions in the direction of the source of the sound. Only in individual cases, when the experimental fish were at a distance of less than 15 cm from the partition, was a purposeful movement observed toward the source of the sound.

Subsequently, an experiment was performed on the reactions of sea-parrots to reproduction of feeding sounds. The majority of sea-parrots became excited and swam directly toward the source. This reaction occurred most vigorously in the aquarium if, at the same time, one of the sea-parrots near the projector made investigative movements (visual signal).

The significance of the sounds of feeding as signals is also confirmed by numerous observations of the behavior of hungry fish under experimental conditions. The Cichlasoma aquarium fish make loud noises when grinding food (Fig. 2). Unfed Cichlasoma fish were separated from feeding specimens by an opaque soundproof [sound transmitting intended] partition. When the Cichlasoma behind the partition heard the feeding sounds, first an orientating and then an investigative food reaction appeared. The larger individuals at a distance of less than one meter from the "source" of the sound reacted with a persistent motor reaction to the source of the sound, trying to get through the cheesecloth.

In our observations a positive reaction of some specimens to the feeding sounds of others was noted repeatedly. When in turbid water, the sea parrots swam up to the other sea parrots, making the food capture sounds, from a distance of 10-30 centimeters. Very often, by the feeding sounds the male fighting fish seeks out a hiding female from a distance of 50-60 cm. The fish feeding sounds are of signal significance not only for the individuals of the same species; they often acquire the nature of interspecies signals.

In one of the observations the aquarium with several species (loach, "banded catfish", river and blue perch, mullets and grass carps) was incompletely separated into two parts. The fish were able to go freely from one compartment to the other, although when they were in different compartments they could not see one another. When fish of the same species were in one of the compartments they were given food. If the feeding fish were loaches or perches the other fish, which were at a distance of 50-70 cm from them, were excited and swam to the other compartment as soon as the feeding sounds began. It should be noted that the rate of the reaction of fish to feeding sounds is practically instantaneous, whereas the reaction time (in a control observation) of the same fish to squeezed juice occurs after several minutes and is manifested differently. This excludes the possible idea of chemical attraction of the fish to the feeding place.

Predatory fish react in a particularly clear-cut manner to the feeding sounds of non-predatory and predatory fish. Unfed perches are very excited by reproduction of feeding sounds of perch, "banded catfish" and loaches, and go directly toward the sound projector from distances of 10-80 cm.

Both in the experiments and in the observations a clear-cut purposeful reaction by some fish to the feeding sounds of others occurs at short distances, of the order of a few score centimeters. In the majority of cases the feeding sounds are orientative signals, which are interpreted by the fish as "attention!" The combination of this signal with others, namely, the sight of investigative movement by other fish (visual signal) or juice squeezed out of food (olfactory and gustatory signal) immediately causes a purposeful reaction of going toward the source of the sound. In the literature facts are well known which also speak for the signal significance of sounds of feeding. R. Busnell (1958) and J. Westenberg (1953) describe means of catching some predatory fish of Africa and Indonesia by making the feeding sounds of some non-predatory fish. The catching of the Danube catfish by the "klok" sound (Sabaneyev, 1911) has also been known a long time; it apparently imitates the sound made by this fish in catching food.

Sounds occurring during feeding cause more than just a positive reaction; the hydrodynamic sounds created by predatory fish in capturing fish cause a defense reaction in small fish. On hearingthe hydrodynamic sounds of the lunging of ombres, small atherinids scatter from their schools, fading away on the surface of the water (the experiment was performed with poor illumination).

Aggressive Sounds and Their Biological Significance. Defense and attack are the main elements in the inter- and intraspecies relations of fish. Aggressive behavior of fish is often expressed in: food relations, in defense of territory, in relations between males during the spawning period. Previously, threat signals in the form of a drum beat by Crenilabrus griseus have been described (Protasov and Aronov, 1960). Sound signals of threat during excitation by food are made by unfed river perches (clapping noise), thereby raising the dorsal fin. The strongest fish make the loudest claps. Often, after these claps, the strong perch begin to race after the weak ones which have captured food. A distinct reaction of the perch (swimming away) is seen in response to these sounds when made at short distances, less than 10 cm. Some marine fish, namely, sea parrots, sargoes, and others, makes the same sounds (clapping) during excitement from sensing food. In aquarium fish—angel fish, Cichlasoma, banded catfish—as well as in marine fish—sea parrots and sargoes—the warning sounds often appear in connection with the defense of territory captured in the aquarium. In this connection the behavior of the Cichlasoma is most significant. In the aquarium they usually divide off in pairs (male and female), occupying a certain territory. The "capture" of the territory leads to fights. At a distance of 15–30 cm the males assume threatening poses and make loud claps. The small specimens near the sites of the fights, drop to the bottom, assuming defensive poses. The observations showed that during the fights these sounds do not occur from mechanical impacts of colliding fish but are made as signals of threat.

These clapping threatening signals are made by male Cichlasoma, fighting fish and angel fish during fights for the female as well as when the male chases the female. Experiments with the separation of fish by opaque sound-transmitting partitions showed that the occurrence of these sounds in the aquarium excites the fish. A clear-cut defense reaction (swimming away, flight) is manifested when the source of sound is at a distance of several centimeters (less than 10). In the majority of fish the defense reaction is expressed in the most clear-cut manner when the sound and "visual" signals act simultaneously.

Threatening signals occur among fish not only in the form of clapping. The banded catfish make threatening signals similar to a shrill squeak. They usually make these sounds when chasing after fleeing fish.

In Fig. 4, a and b, the menacing signals of angel fish and Cichlasoma are shown. On Fig. 4, c and d, the spectrum of the frequencies of these sounds is shown.

Sounds of Fright and Pain in Fish. When frightened some fish also utter sounds. The roach, caught in a casting net during its reproductive period, makes a loud chirping sound. This sound is evidently of defensive significance, apparently causing the nearby roaches to run away.

Characteristic hydrodynamic sounds are made by the following schools of fish when frightened: perches, roaches, young atherinids, carp, sea parrots and others.

The acoustic fright signals of schools of fish are apparently of definite importance as signals, making it possible for individuals in the schools to carry out rapid maneuvers. This is also indicated by some data in the literature (Moulton, 1960). On Fig. 5 the fright sounds of schools of young carp are shown. The spectrum of these sounds is mainly of low frequencies.

In the literature (Haas, 1959) there are statements to the effect that wounded fish must utter cries of pain. With the aim of clarifying this problem experiments were performed with wounded fish. Small specimens of various species (roach, crucian carp, perch, sea parrot, bream, ocean perch, scad and others) fail to make characteristic sounds when wounded. Large fish (sturgeon, loach, roach and bream) frequently make loud sounds when wounded: the roach and bream—loud chirping; the sturgeon and loach—loud cries. On Fig. 6, a and b, the sounds made by the loach when wounded are shown. These sounds apparently occur from vigerous contraction of the swim bladder and intestine, squeezing out a portion of the air. The significance of these sounds as signals has not been clarified.

Practical Utilization of Fish Sounds. Previously, it has been mentioned (Malyukina and Protasov, 1960; Shishkova, 1958) that sounds made by fish are characteristic of different species and can be used in the practice of exploratory fishing for localization and detection Specifically, we believe that it is possible, with the aid of sounds made by schools of fish, to observe the migration of commercial schools with the use of a special cybernetic automat. A detailed description of the method will be given in the future.

Another aspect of practical application of fish sounds is the possibility of using them for attracting and repelling fish. Along this line, the problem has not yet been finally solved (no critical experiments have been made in the sea; no study has been made of the ultra- and infrasonic ranges of the majority of the sounds). The data obtained on the sound range make it possible to express certain tentative considerations. From experiments and observations on the significance of feeding and danger signals in various fish it follows that the motor reaction of fish to these sounds is manifested at short distances; in some fish, only with the participation of other signals. This characteristic is apparently related to the dominant role of one analyzer [sense organ in entirety] or another of the fish in the existing ecological relationships. For fish (Danube catfish and some others) in which acoustic signals are basic, the sounds which are of importance as signals can be used for attracting and repelling fish in fishing practice. For the majority of fish, in which, aside from hearing, vision and olfaction are of significance, the food and defense reactions (signal, direction and control) are manifested in response to the action of the total signals (sound, light, chemical agents).

The behavior of these fish can be controlled through the action of a combination of signals, which bring about the expression of investigative or defense reactions.

Conclusions

1. The sounds made by various fish species are characteristic, which can be shown easily by listening and by acoustic analysis. This characteristic feature can be used practically.

2. Fish are capable of perceiving the sounds made and, at short distances (less than one meter), of determining the direction from which they come.

3. Feeding and threatening sounds in some fish are of significance as signals for attracting and repelling other fish, but they exert their effects at short distances. In the majority of fish the food and defense reactions can be controlled only through the comprehensive action of several signals (sound, light and others).

4. Sounds of fright and pain are characteristic of wounded fish and probably are of importance as signals.

5. There is reason to believe that the majority of the sounds studied are part of the acoustic signals covering larger areas of the sound spectrum. Therein lies one of the possible reasons for the low reactivity of the majority of fish to biological signals in the sonic range.

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[Photographs available in text not suitable for reproduction]

Captions of Photographs

Fig. 1. Sounds Made by the Pike-Perch (a,c) and Snakehead (b,d) in Capturing Fish (Verkhovka). a,b—general nature of the signals; c,d—amplitude-frequency characteristics of sounds (the frequency in kilocycles a second is plotted on the abscissa; on the ordinate, the amplitudes of the spectral components in relative units). (Linear scale). 1. frequency, kilocycles a second.

Fig. 2. Sounds Made by Percidae (Cichlasoma nigrofasciata) when Forcing Food in (a,c) and by Carp when Grinding with the Pharyngeal Teeth (b,d). a,b—general nature of the signals; c,d—amplitude-frequency characteristics of the sounds.

Fig. 3. Sound Made by Black Sea "Zubarik" [Chara puntazzo] during the Period of Food Excitation. a—general nature of signal; b—amplitude-frequency characteristic of sound.

Fig. 4. Menacing Sounds Made by Angel Fish (a,c) and Cichlasoma (b,d). a,b—general nature of the signals; c,d—amplitude-frequency characteristics of the sounds.

Fig. 5. Sounds of Fright Made by Schools of Young Carp.

Fig. 6. Sounds Made by the Loach when Wounded. a—general nature of the signal; b—amplitude-frequency characteristics of the sound.

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