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Hearing and acoustic orientation in marine animals*

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Summary—The evidence that underwater sound is important in the behaviour of fishes and cetaceans is reviewed, with emphasis on the possible occurrence of acoustic orientation. Both these groups of marine animals have now been shown to have excellent hearing. At least one fish has a minimum auditory threshold of the same order of magnitude as the typical human threshold at 2000–4000 c.p.s. (about 10^{-16} watt/cm^2 energy flux). Porpoises can hear sounds of moderate intensity at frequencies well above 100 kc. A series of recordings which may have resulted from a deep sea fish engaged in echo-sounding are analyzed and discussed, and the possible role of echolocation in marine animals is compared with the available evidence of its nature and occurrence in bats and other animals relying on airbourne sound. In this connection the possible usefulness of continuous sounds and standing wave patterns is discussed with reference to the observed fact that a low frequency sound in a small tank undergoes marked fluctuations in intensity over distances that are a small fraction of its wave-length in water.

In recent years it has become widely recognized that a variety of sounds are produced by animals living in the ocean. The chief cause of this increased awareness has been the use of improved devices for listening to sounds in water. It had been known since the time of Aristotle that some fish produce sounds (for recent pre-war studies see Tower, 1908; Burkenroad, 1931; Dijkgraaf, 1932; and Hardenberg, 1934). But the unaided human ear is at a great disadvantage in listening to underwater sounds, and hence only those of considerable intensity can be heard without devices to provide us with a sensitivity to sound waves in water that approaches our sensitivity for sounds arriving through the air. Such devices have been developed primarily for military purposes, and it was during the second World War that sounds of fish and other marine animals first aroused serious concern when they interfered with underwater listening operations. Surveys were therefore undertaken to determine the sources and seasonal occurrence of the more intense of these biological noises (Loye and Proudfoot, 1946; Dobrin, 1947; Knudsen, Alford, and Emling, 1948). Since the war such surveys have continued on a broader basis with greater attention to their biological significance (Johnson, Everest, and Young, 1947; Johnson, 1948; Fish, Kelsey, and Mobray, 1952).

As a result of these studies it is now clear that sounds of considerably greater intensity than the ambient background noise level of the ocean are commonly produced by three major groups of animals: (1) many species of fish, (2) several species of marine mammals—certainly some of the smaller whales and porpoises and perhaps some of the larger whales as well, and (3) the snapping shrimps of the genera *Crangon* and *Synalpheus* among the Crustacea. Too little is known about the significance of the " snap " of these shrimps to warrant any discussion of it, and indeed the one serious study to date has led to the conclusion that the noise may well be incidental to some other function of these animals' highly modified claws (Johnson, Everest,

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and Young, 1947). But the sounds of fish and marine mammals are so numerous, so intense, and so diversified, that a review of what is known concerning their biological significance is timely. While only a small minority of the known species of fish emit sounds that are more than mere by-products of other activities (such as the grinding of teeth), many of those that are consistent noisemakers have specialized structures for the generation of sound, such as muscles located in the walls of the swim bladder. It therefore seems likely that these sounds serve some definite purpose in the lives of the fish that make them. Cases are known in which fish are attracted by sound (Westenberg, 1953), but more often they are repelled by artificially generated sounds, while under many circumstances they show no discernible reactions at all. Some species apparently communicate with each other by means of sound, for example the toadfish *Opsanus tau*, in which the male calls principally during the breeding season. There is suggestive evidence to be discussed below that orientation may be maintained with respect to the bottom by a process akin to echo-sounding; and it is not beyond the bounds of possibility that fish or marine mammals may employ a sort of natural sonar—an underwater analog of the process of echolocation so highly developed by bats for use in air. Questions of this type deserve more attention than they have yet received, and the chief purpose of this paper is to review the available evidence of acoustic orientation by marine animals and to suggest promising lines of inquiry for the future. It is particularly appropriate that such a review should be part of a volume dedicated to Professor Bigelow, for he contributed significantly, in 1904, to the basic biological knowledge that has formed an essential groundwork for these recent developments.

The sensitivity of hearing in fish

Fundamental to any consideration of the role of underwater sound in orientation, or in other types of behaviour, is the question of sensory capacities of the animals concerned. No animal can react to a sound it cannot hear, and even the author of an authoritative textbook recently wrote, in introducing the auditory system, "Through the long and complex evolution of the fishes no progress was made, since no auditory receptors exist. . . . Fish do not hear, and there would be little to hear under water . . . Hearing is developed on the assumption of terrestrial life, hence, is first encountered in the amphibia" (Krieg, 1942). Even when a particular species has been shown, qualitatively, to be able to react to underwater sound, any careful analysis of its behaviour is likely to require quantitative measurement of the range of frequencies and intensities that it can hear. It was to this basic question that Bigelow addressed himself more than fifty years ago.

There was already observational and anecdotal evidence that certain fish reacted to sound, usually to sounds generated in air. On the other hand several attempts to demonstrate hearing in fish under controlled conditions had produced negative results, or at best ambiguous evidence. Among the more recent of these investigations had been those of Kreidl (1895, 1896), who had a few years previously carried out in Sigmund Exner's laboratory in Vienna one of the classic experiments of comparative physiology (the substitution of iron filings for sand grains in the equilibrium organs of certain shrimps, so that the action of the statoliths could be demonstrated unequivocally by the use of a magnet). Kreidl had observed the responses of goldfish (*Carassius auritus*) to sounds of moderately low frequency, but the fish responded just as well after the inner ear had been exposed and the semi-circular canals plucked out with forceps—a procedure which seemed likely to damage the organs of hearing. Hence KREIDL concluded that goldfish detect underwater sound not by means of the inner ear but through mechanical receptors of the lateral line or skin.

BIGELOW repeated KREIDL'S experiments, working under the guidance of the late G. H. PARKER, who had just demonstrated the auditory sensitivity of *Fundulus*, and he extended them with a simple elegance of experimental design which merits the respectful consideration of current investigators. Having found that his goldfish responded more than 80% of the time when stimulated by a 100 c.p.s. tuning fork, he cut virtually the entire sensory nerve supply to the skin and lateral line, and still observed almost the same percentage of responses. Yet when both eighth cranial nerves were cut there were no responses in 73 trials with seven different goldfish. As a control against side effects of exposing and cutting the auditory nerve, both eighth nerves were exposed but only one was cut; this fish still responded to sound, but ceased to do so when the remaining auditory nerve was severed. In another control the spinal cord, lateral line nerves, and the cutaneous branches of cranial nerves V and VII were cut without effect on the response to sound. BIGELOW went on to repeat KREIDL'S operation, and he obtained the same result. But he also found from histological sections that plucking out the semi-circular canals left much of the sacculus and lagena intact, these being the portions of the ear that would be expected to play the major role in responses to sound. Q.E.D.: goldfish could hear.

Like many biological problems the question of hearing in fish underwent a long subsequent history of complications and controversies, and a generation later an active debate still centred around the simple question, " can fish hear, and if so, what ? " (For complete reviews see VON FRISCH, 1936, and KLEEREKOPER and CHAGNON, 1954). In many of the earlier experiments spontaneous responses were obtained from fish when vibrations of various frequencies and intensities were imparted to the water by a wide variety of methods. In other cases fish were conditioned or trained to give responses when the water around them was set into oscillation, and considerable evidence pointed to the importance of the lateral line and the skin, especially for low frequencies (PARKER and VAN HEUSEN, 1917). The methods used to generate underwater sound in these earlier experiments were (1) to generate the sound in air near the tank containing the fish, (2) to place a vibrating object such as a tuning fork in contact with the tank, or (3) to immerse a buzzer or telephone receiver in the water itself. In all cases the stimulus undoubtedly set the water into vibrations with a complex frequency spectrum, but the component most obvious to the experimenter may not have been the one which was most effective in stimulating the fish. This situation was greatly clarified by the careful work of VON FRISCH and his associates from 1929 to 1941; and although most of the experiments employed freshwater fish, important general conclusions were reached which can be applied directly to marine species, as has recently been demonstrated by DIJKGRAAF (1952).

STETTER reported in 1929 that two common freshwater fish, (the European minnow, *Phoxinus laevis*, and the common catfish, *Ameiurus nebulosus*) could be trained to come for food to a particular part of the tank (or to give other characteristic feeding movements) when a sound was produced in the air at some distance from the aquarium. The fish were blinded to prevent them from responding to visual rather than auditory stimuli associated with feeding. Clear responses were obtained from sounds generated by tuning forks, whistles, and pipes, even when the frequency was as high as 6,960 c.p.s. with the minnows, and 13,139 c.p.s. with the catfish.

VON FRISCH and STETTER (1932) later experimented with the effects of sensory impairments on the ability of minnows to respond to various frequencies. Damage to the utriculus and semicircular canals caused little reduction in sensitivity to sounds, although equilibrium was severely impaired. But when the sacculus and lagena were put out of action the sensitivity to frequencies above 150 c.p.s. was almost totally destroyed. Even frequencies as low as 32 c.p.s. were less effective in arousing responses than when the sacculus and lagena were intact. Very low frequencies such as 16 c.p.s., however, were almost as easily perceived as they had been before the operation. Nor did impairment of the lateral line receptors reduce the fishes' sensitivity to low frequencies. These investigators therefore concluded that low frequencies must be detected through very sensitive tactile receptors in the skin (see also REINHARDT, 1935).

Absolute thresholds could not be determined in these experiments, because no calibrated underwater transducers were available for the purpose. In an attempt to obtain approximate thresholds, the source of the stimulating sound was moved to greater and greater distances from the aquarium, and the threshold of response of the fish was compared with the threshold of hearing of men standing beside the aquarium. The fish ceased to respond at levels somewhat above the human threshold; but when a man was held entirely underwater in a large aquarium, he was unable to hear the sound at intensities to which the minnows would still react.

In later experiments at the same laboratory by BOUTTEVILLE (1935) and DIESSELHORST (1938) the sound was generated by a loudspeaker close to the aquarium, and its intensity *in the air* was measured by means of a calibrated microphone. The threshold of response of a fish could thus be expressed in terms of sound pressure in the air just outside of the glass-walled aquarium. The most sensitive of the minnows gave consistent responses to 652 c.p.s. when the sound level in the air was 20 decibels above the customary reference level of 0·0002 dynes/cm^2, or ten times the threshold sound pressure for a typical human listener. This is a remarkable sensitivity when one considers that the energy loss was unquestionably great as the sound waves passed from air to water. I once duplicated approximately the acoustic conditions of this type of experiment and measured sound pressures inside the aquarium with a calibrated hydrophone while those in the air were measured with a calibrated condenser microphone. The sound pressures in air and water were roughly the same (within 5 to 10 decibels). But the greater acoustic impedance of water causes a given sound pressure to correspond in water to a 35 db lower energy flux (watts/cm^2) than in air. This means that the minnows studied by VON FRISCH and his associates had auditory thresholds of the same order of magnitude, in terms of energy flux, as the human auditory threshold in air.

When a number of species were compared with the minnow *Phoxinus* with respect to their sensitivity and frequency range of hearing, it became clear that fish can be divided into two distinct groups. The minnow *Phoxinus*, the catfish *Ameiurus*, and certain other fish, display low thresholds and a wide frequency range, while the other fishes studied were less sensitive and responded only to frequences below 1000–2000 c.p.s. This difference is correlated with the anatomy of the fish: for the more sensitive species have an air-filled chamber directly coupled to the inner ear labyrinth. In the order *Ostariophysi* (families *Cyprinidae, Characinidae, Siluridae* and *Gymnotidae*) this involves the Weberian apparatus, an intricate structure consisting of bones, cartilages and air ducts which serve to effect a mechanical coupling between the swim bladder and the inner ear. VON FRISCH and STETTER (1932) demonstrated experimentally that the minnow suffered a considerable hearing loss when this mechanism was damaged surgically. Air chambers can improve the sensitivity of fish's hearing because sound travels almost without disturbance from one aqueous medium to another, and the soft tissues of any animal are so much like water in their acoustical properties that a " pure " fish is relatively " transparent " to underwater sound. An air bubble or an air-filled chamber, on the other hand, represents a marked acoustical discontinuity much as does a solid object in the air. For a detailed consideration of the acoustical properties of the catfish swim bladder see POGGENDORF (1952). Other fishes with keen hearing also have some type of air chamber coupled to the inner ear. These structures have different morphological origins, but seem to serve the same auditory function as the swim-bladder and its ramifications in the *Ostariophysi.*

This anatomical correlation is an important one; for it permits one to predict with some confidence that fish possessing structures that connect some air-filled chamber with the inner ear labyrinth will have keen hearing. Among marine fish there are very few groups which have such accessory organs of hearing. The sea catfishes are anatomically similar to the freshwater catfish *Ameiurus*, and they might be expected to have keen hearing on that account. In this connection it is interesting to note that sea catfishes are listed among the species reported by BURKENROAD (1931) and DOBRIN (1947) as significant producers of underwater noise. The herrings (family Clupeidae) are another group which one would expect to have keen hearing because of their auditory structures, which have been described by RIDGEWOOD (1891), WOHLFAHRT (1936), and EVANS (1940). There is an elaborate set of air passages extending from the air bladder into close apposition with the membraneous labyrinth of the inner ear. There are also reports that herrings are easily frightened by noises made in fishing boats. Since the herring family is an abundant marine group having great commercial importance, their ability to hear various frequencies of underwater sound merits quantitative investigation.

Two recent investigations have included quantitative measurements of auditory thresholds in fish, and the results have amply confirmed the earlier conclusions of VON FRISCH and others regarding the approximate equality of auditory thresholds in fish and men, when expressed in terms of energy flux (watts/cm^2). AUTRUM and POGGENDORF (1951) and POGGENDORF (1952) used a calibrated Rochelle salt crystal to measure the sound pressure in a small aquarium containing single catfish (*Ameuirus nebulosus*), and they determined auditory thresholds at frequencies from 60 to 10,000 c.p.s. The threshold values varied considerably, but the average of the measurements at a given frequency is probably valid within ± 10 db. KLEEREKOPER and CHAGNON (1954) have estimated auditory thresholds of a small cyprinid fish, the creek chub *Semotilus atromaculatus*, and they report a rather narrow range of maximum sensitivity, the thresholds being lowest at about 300 c.p.s. and rising by tenfold at 100 and at 2000 c.p.s. In view of the absolute, though approximate, calibration of the measuring instruments used by AUTRUM and POGGENDORF, their data for the catfish provide the best available evidence concerning the sensitivity of hearing in fish to underwater sound. They found the auditory threshold to be approximately constant from 60 to 1600 c.p.s. at slightly above 0·01 dyne/cm^2 or approximately 10^{-16} watt/cm^2. This threshold energy flux corresponds closely to the minimum human threshold in air (between 2000 and 4000 c.p.s.), but the catfish is considerably more sensitive at lower frequencies. Above about 2000 c.p.s., on the other hand, this fish's threshold rises much more steeply than the human threshold.

AUTRUM and POGGENDORF also demonstrated that the catfish's responses depended upon sound pressure rather than amplitude or particle velocity. They confirmed the earlier qualitative findings of VON FRISCH *et al.* that fish without air bladders have thresholds roughly 30 db higher than the catfish. Other experimenters have reported that the Ostariophysii at least can discriminate between sounds differing in frequency by as little as 1/4 octave (WOHLFAHRT, 1939; DIJKGRAAT and VERHEIJEB, 1949; and KLEEREKOPER and CHAGNON, 1954). Directional sensitivity, or the ability to localize the source of an underwater sound, has not yet been adequately demonstrated, and indeed both REINHARDT (1935) and VON FRISCH and DIJKGRAAF (1935) obtained negative results in attempts to demonstrate localization of sound sources by stationary fish. On the other hand, KLEEREKOPER and CHAGNON concluded, on the basis of extensive observations and photography of the movements of *Semotilus* in a tank approximately one metre square, that these small members of the order *Ostariophysii* could immediately turn towards the louder of two equidistant sources of 50 c.p.s. sound.

A possible case of echo-sounding in fish

Having thus reviewed the overwhelming evidence for a high degree of auditory sensitivity in fish, it must be admitted that very little critical evidence is available to indicate what significance sound may have in fish behaviour. Rather than summarizing unsatisfactory anecdotal evidence I shall merely describe one observation that suggests the occurrence of echo-sounding by a deep sea fish, with the hope that the need for substantial and imaginative investigation of auditory behaviour in fish will thus be emphasized. I am indebted to Dr. J. B. HERSEY of the Woods Hole Oceanographic Institution for permission to make a detailed study of a series of underwater sound recordings made north of Puerto Rico in water approximately 5100 metres deep. Among many hours of recordings made far from land, that include noises of biological origin, those made about 3 p.m. on March 7, 1949 contain several loud calls, each followed after a short interval by a fainter repetition of itself. In listening to these sounds, it is difficult to avoid the impression that they are the calls of some marine animal followed by echoes of these calls. While no similar calls and apparent echoes have been noted subsequently, as far as I can ascertain, a brief analysis of this recording is of interest.

The instruments used were a crystal hydrophone, amplifiers, filters, and recording equipment sensitive to 50–1200 c.p.s. The hydrophone was within 70 feet of the surface, and the background noise level was 75–80 db above 0·0002 dyne/cm^2. The calls of what was dubbed the " echo fish " consisted of short notes lasting 1/3 to 1·5 seconds, and having a rather constant frequency of about 500 c.p.s. The apparatus was not precisely calibrated, but the calls were typically two to three times the background noise level, and occasionally the signal-to-noise ratio was as high as seven. The interval between the loud call and its faint repetition was quite constant, and when the recording was played through a 500 c.p.s. tuned filter both the call and the apparent echo could be seen clearly in oscillographic records. When the intervals between peaks of original call and apparent echo were measured in 11 oscillographic records showing the highest signal-to-noise ratio, the average interval was 1·58 seconds, the extremes being 1·47 and 1·77 seconds ($\sigma = 0{\cdot}08$ second). The ratio of amplitudes of the apparent echo and original call averaged 0·405, the extreme values of this ratio being 0·27 and 0·56.

If these recordings do indeed consist of calls and echoes, the time interval between them, together with the amplitude ratio and the known depth of 5100 metres, establishes certain geometrical requirements for the location of the " echo fish ". The difference in length of the direct path from source to hydrophone and the path followed by sound waves reflected from the bottom was approximately 2400 metres (the distance travelled by underwater sound in 1·58 seconds). In the simplest case we might assume that the source was directly below the hydrophone, so that its distance above the bottom would be 1200 metres or 3900 metres below the surface. If we make the further assumption that in these cases, when the bottom reflection was maximal, the angles of incidence and reflection were equal, the possible locations of the source are limited to a locus having the form of a shallow dish-like surface with its deepest point 3900 metres below the hydrophone and gradually rising towards the surface as the source is assumed to be displaced laterally. Unless one assumes the source to have been some miles away it must have been at a considerable depth, probably well below the levels to which light can penetrate, and below the depths reached by whales or other marine mammals. These geometrical relationships are thus consistent with the hypothesis that this recording reveals a deep sea fish emitting calls loud enough for them and their echoes from the bottom to be audible at the surface three to four thousand metres away.

This explanation of the " echo fish " recordings can be considered only as a speculative possibility, however, until means are devised to explore the depths of the ocean in greater detail, both acoustically and biologically. Alternate explanations for the sounds recorded in this instance are: (1) that a single fish emitted a double call, (2) that the second call came from a different fish, or (3) that the sounds had a non-biological origin. The third alternative seems quite unlikely because this type of sound was heard on several occasions during the day the recording was made, because it became louder and fainter from minute to minute, and because it was recorded when the ship was many miles from land or other ships under conditions when all possible precautions had been taken to avoid sound production by the ship herself. Reflections from other surfaces than the bottom are rendered most unlikely by the relatively high amplitude ratio and the difference of 2400 metres in path length for the direct and reflected sound. Finally it must be pointed out that even though this recording does reveal a fish call plus its echo from the bottom, we have no direct evidence that the unknown fish could hear such an echo, and still less that it would pay any attention if it did. Yet the " echo fish " could easily have heard these bottom echoes if it had an auditory sensitivity equal to that of any fish adequately studied to date, and in the unlighted depths of the ocean echolocation could be as advantageous to a fish as it is to a bat flying in darkness through the air. We are dealing here with one of many phenomena pertaining to the deeper layers of the ocean concerning which we can only speculate, and dream of future investigations by methods yet to be devised.

Sounds and hearing of marine mammals

A variety of complex sounds are produced by several species of the smaller toothed whales, porpoises, and dolphins. As in the case of fish, a few observations of noises from cetaceans had been reported many years ago, but only during and after the war was it realised how vociferous some of them actually were. The white whale or beluga *Delphinapterus leucas* had long been known to make noises, for these could be heard in the air or through the hull of a ship; and SCHEVILL and LAWRENCE (1949) have described and analyzed in some detail their large vocabulary that includes whistles, squeals, chirps, clicks, and rasping noises. Several other species of porpoises and dolphins have also been studied in captivity or under natural conditions, and all appear capable of producing sounds (SCHEVILL and LAWRENCE, 1949; KRITZLER, 1952). The baleen whales, on the other hand, have not yet been definitely shown to emit sound, although there have been reports from several observers of loud, low pitched notes heard when humpback whales (*Megaptera nodosa*) were in the vicinity.

Excellent hearing has been demonstrated in porpoises and other cetaceans ranging in size up to the pilot whale or " blackfish " *Globicephala macrorhyncha* (KELLOGG and KOHLER, 1952; SCHEVILL and LAWRENCE, 1953; KRITZLER, 1954). While auditory thresholds have not yet been measured, the observational evidence is adequate at least for the bottlenosed porpoise *Tursiops truncatus* to demonstrate that sensitivity of hearing is high. In the most carefully controlled of these studies, SCHEVILL and LAWRENCE trained a *Tursiops* to come for food when it heard pure tones of short duration generated without switching transients or clicks. The intensity level was of the order of 10^{-12} watt/cm^2 or 1 dyne/cm^2, and this porpoise learned to respond almost every time the tone was sounded in the frequency range from 150 c.p.s. to 120 kc, i.e. the animal's auditory threshold was below this level over a very wide range of frequencies. Above 120 kc. the percentage of positive responses fell rather rapidly to less than 20% at 150 kc.

Since marine mammals are often active at night or in turbid waters, it is natural to suggest, as KELLOGG, KOHLER, and MORRIS (1953) have done, that some of their complex and impulsive sounds may be used for echolocation, either to maintain orientation with respect to the bottom, surface, or large obstacles, or possibly to locate fish or other prey in the water as bats appear to do in the air (GRIFFIN, 1953 A). KELLOGG *et al.* have shown that certain of the noises emitted by these porpoises have components of considerable amplitude as high in frequency as 120 kc, and some energy as high as 170 kc; and when intense sounds of short duration are generated in the water there will of course be echoes from any solid objects in the vicinity. Since porpoises have a high degree of adaptability and intelligence as well as keen hearing (MCBRIDE and HEBB, 1948; WOOD, 1953; and LAWRENCE and SCHEVILL, 1954) it is plausible to infer that they might take advantage of the possibilities of echo ranging. No direct evidence has yet been forthcoming, however, to support this inference; and indeed SCHEVILL and LAWRENCE report that porpoises remained silent, as far as could be discerned, even during long periods of swimming about through turbid water where it would seem that echolocation would have been most helpful. It may well be that porpoise sounds are used solely or primarily for communication, especially since solitary porpoises seem ordinarily to be silent. Yet the observation of MCBRIDE (in press) that porpoises can avoid small mesh but not large mesh nets in turbid waters points towards some type of acoustic orientation.

It is pertinent to recall in this connection that the critical evidence that bats (and at least one species of bird) employ echolocation is not alone their production of sound but, more important, their ability to fly without seeing and the disorientation caused by impairment of hearing or sound production (GRIFFIN and GALAMBOS, 1941; GRIFFIN, 1953 B). Comparable experiments are obviously more difficult with cetaceans, but observations of blinded porpoises, or even the use of intense interfering noises, should permit a resolution of this question. It is even possible that porpoises use fainter sounds for echolocation than those studied to date, and that more sensitive apparatus, or improved signal-to-noise ratios, would disclose a more continuous emission under conditions where vision is restricted. The most intense high-frequency sounds of bats are not the pulses used for echolocation, but the noisy cries of much longer duration (which are audible owing to minor low frequency components even though most of their energy is at frequencies above 20 kc). Prolonged listening to bats with relatively insensitive equipment in the presence of moderately high noise levels at ultrasonic frequencies might well have led to a picture of their sounds not unlike our present information that porpoise sounds are numerous, loud, and varied, but often not detectible when needed for acoustic orientation. This comparison is especially relevant for those species of neotropical bats that feed on fruit and orient themselves adequately by means of faint pulses which can easily be overlooked even with reasonably adequate apparatus (GRIFFIN and NOVICK, 1955). All of these considerations warrant an open mind regarding the role of acoustic orientation in marine mammals, and further careful investigation of the matter is clearly called for.

Discussion

In most considerations of the possibility that marine animals orient themselves by echolocation it has been assumed that they would use an analogue of pulse sonar, emitting sounds of very short duration and hearing echoes arriving in the silent intervals between the pulses. Pulsed sounds are employed in the echolocation of all the bats studied to date, although in bats of the family *Rhinolophidae* the pulses may last about 100 msec, so that there must be considerable overlap between outgoing sound and returning echo (MÖHRES, 1953). While some of the sounds emitted by fish and cetaceans consist of rapidly repeated clicks, others are continuous tones or noises; and since sound travels faster in water than in air most of the known fish and porpoise sounds seem poorly suited for echolocation owing to the inevitable mixing of echoes with the outgoing sound. In this regard " echo fish " discussed above, and certain ticking sounds of uncertain origin recorded during Woods Hole Oceanographic Institution cruises, seem to be exceptions to the general rule. It is quite possible, however, for echolocation to be based upon continuous sound, but since the echoes will almost always be fainter than the outgoing sound some special means must be employed to discriminate between the two—frequency as in the case of frequency modulated radar, or the high degree of isolation of the ear from the source of the emitted sound that MÖHRES postulates for the bats of the family *Rhinolophidae*, which use 100 msec pulses to detect objects at such close range that echoes begin to return in 5–10 msec.

There is another aspect of underwater sounds which might be related to echolocation, and which has not been thoroughly considered. The wave lengths of the sounds emitted by most fish, and those to which they are most sensitive, range from about one to ten metres. Most of these sounds last for at least one second, so that in the immediate vicinity of the fish there is ample time for interference and reinforcement between successive waves to be set up, especially if it is close to the bottom or to other solid objects, as is very often the case. At first thought one would expect the principal nodes of such standing waves to be separated by distances equal to the wavelength in water of the particular frequency involved; for 500 c.p.s. this would mean nodes roughly three metres apart. Yet when I have arranged apparatus to generate sounds of a few hundred c.p.s. in small tanks, and measured the resulting sound levels with a hydrophone, there have always been wide fluctuations in the sound pressure over distances that were only a very small fraction of the wavelength. (See also Poggendorf, 1952, and Kleerekoper and Chagnon, 1954, for similar observations.) The physical basis for these variations in sound level is no doubt somewhat complex, perhaps involving interactions between sound waves in the water and in the materials of which the tank is constructed. Comparable conditions would not ordinarily prevail in the open ocean, but they must often occur near the bottom, rocks, or other hard objects.

Since fish have keen hearing, they must experience fluctuations in the loudness of whatever sounds are present as they swim about in the proximity of any major acoustic discontinuity, and indeed their own movements would alter the standing wave patterns. Since such changes in sound level bear some relation to the geometry of the fish's environment, it is possible that they could learn to use them for orientation (for evidence that fish can easily learn to react to sounds see Bull, 1928, and Haralson and Bitterman, 1950). Presumably such standing wave patterns would be simpler, and hence more readily interpreted by fish, if they were caused by relatively pure tones. Dijkgraaf (1933, 1947) and Kramer (1933) have described in fish and amphibians respectively a type of orientation based on very low frequency sounds or vibrations (or even perhaps static pressure). The sense organs involved are those in the skin or lateral line, rather than the ear. This type of orientation which Dijkgraaf calls "*Ferntastsinn*" seems limited to distances of much less than one metre. At higher frequencies the specialized inner ear and accessory structures provide a much greater sensitivity, and hence a potentially greater range of acoustic orientation. It therefore seems desirable to devote some future research to testing the possibility that fish or cetaceans orient themselves by reacting to the complex standing wave patterns set up in water near solid objects.

Whether such a type of acoustic orientation would be based on variations in sound fields generated by the fish itself or those from other sources, if it occurs at all, can only be learned by further investigation. As stimuli for such investigations the attention of interested readers is called to the papers of Supa, Cotzin, and Dallenbach (1944), Cotzin and Dallenbach (1950), and Twersky (1951) for convincing evidence that blind men detect obstacles by acoustic orientation based on a variety of continuous sounds, including pure tones. Furthermore Lissmann has reported that certain fish orient themselves by means of *electrical* fields of their own making, apparently sensing in some manner yet to be explained the changes in electrical field due to the proximity of objects differing from water in dielectric properties. (See Lissmann, 1951, and Gray, 1953, for preliminary accounts of these remarkable findings concerning which no complete report has yet been published). In view of the existence of such modes of orientation we should be prepared to find cases of acoustic orientation in fish or marine mammals based either upon pulsed or continuous sounds.

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