Reports

Piezoelectric Property of Otoliths

Abstract. *Otoliths of two species of bony fishes have been found to be piezoelectric. Hence, in theory, they constitute a mechanism for depth perception or frequency analysis of sound waves, or both.*

Discrimination of frequencies of sound waves by fishes has been well documented by a number of investigators. As Lowenstein (*1*) summarizes the mechanism for frequency analysis remains undiscovered.

Behavioral responses indicating perception of changes in static pressure, either hydrostatic or atmospheric, can be easily demonstrated in a large number of fishes. Such responses as these could be ascribed to some sort of stretch receptor in a species which has a gas bladder. However, these responses can be observed in a great variety of species in which no compressible gas vesicle can be found. It is known that pressure changes are, at least in part, detected by the ear (*2*), but a transducing mechanism has not been defined.

The ear of the bony fish can be very generally described as a membranous labyrinth consisting of three connecting chambers, the utriculus, sacculus, and lagena. These chambers are continuous with three semicircular canals, and the entire labyrinth is filled with endolymph. Macular areas of sensory receptors of the eighth cranial nerve are found in the chambers. Lowenstein (*1*) gives good descriptions of representative forms, although one finds a high degree of interspecific variation in the configuration and relative size of the various parts of the labyrinth.

An otolith, consisting largely of calcium carbonate, is secreted in one or more chambers of the labyrinth. Otoliths are identified by separate names, the lapillus occurring in the utriculus, sagitta in the sacculus, and asteriscus in the lagena. Inanimately responding to forces of inertia or gravity, an otolith mechanically excites the macular receptors, and their function in equilibrium and position perception is well known (*1*). There is a great variety of morphological types of otoliths, reflecting the anatomy of the labyrinth and the manner in which the stones have been laid down. For example, the lapillus of a catfish, *Ictalurus nebulosus*, appears to be nothing more than a haphazard aggregation of crystals of $CaCO_3$. However, in Fig. 1 we see two sagittas from the nototheneid fish, *Trematomus bernacchii*, and it is immediately apparent that these develop quite symmetrically. Each of the otoliths illustrated is from a right ear, and each shows a different face. The dorsomedial face is sculptured, as is shown by the lower of the two pictured. The upper otolith shows the smoothly convex ventrolateral face. Otoliths of this type grow in concentric increments. A picture of a thin section of a sagitta of *T. bernacchii* appears on the cover, and here we see that the concentric incremental growth results in a crystalline aggregate that is quite orderly and complex.

A thin section about 50 μ thick, cut approximately parallel to the lenticular faces, was prepared from an otolith of *T. bernacchii* (cover, and Fig. 2). There is an eccentric nucleus appearing left of center in Fig. 2, about which the structural features of the otolith are arranged. Two principal kinds of features are visible at the magnification used in the cover picture: (i) annular bands distinguished by fine, dark lines and by variations in the pale brown coloration of the material; and (ii) thin fibrils that are arranged radially about the nucleus, like spokes in a three-dimensional wheel. The annuli consist of narrow bands, about 10 μ wide, which are separated by fine, dark lines; and groups of narrow bands, about 130 μ wide, which are distinguished by variations in coloration. The bands conform to the shape of the otolith and are essentially continuous about it. The radial fibrils appear to be about 1 μ wide, but details of their arrangement are not resolved by the microscope used, partly because of the thickness of the section. Some of the larger bundles of fibrils can be traced continuously from the nucleus to the margin of the otolith. They cross the annular bands and intersect the margin approximately at right angles. Microscopically visible fibrils may not be individual crystallites, for none attain complete optical extinction when polarizers are crossed.

Near the center of the otolith, the fibrils are generally in aggregate extinction when they are parallel to the preferred directions of polarization of the microscope (Fig. 2); however, there are regions near the margins in which fibrils are in aggregate extinction at some angle to the preferred directions of the polarizers, which suggests that, in these regions, the optic axes of the crystalline substance are not parallel to the apparent longitudinal and transverse dimensions of the fibrils.

Bone has been reported to show a piezoelectric effect, not by virtue of its particular mineral composition but because of the fact that it is a multicrystalline structure (*3*). The cover picture indicates that the manner in which otoliths are built up could easily result in a similar multicrystalline structure, although bone itself is never found in the composition of an otolith. Shamos and Lavine (*4*) have recently reported that soft biological tissues can also be expected to show a piezoelectric effect.

It occurred to us that the detection of pressure and sound could be admirably served by an otolith if it were a piezoelectric body. We examined an otolith sample of *Sebastodes* sp. by x-ray diffraction but we found no crystalline material other than aragonite (orthorhombic $CaCO_3$) (*5*), which is centrosymmetric and thus nonpiezoelectric.

Trapping of benthic fishes in McMurdo Sound, Antarctica, during the past two austral summers clearly demonstrated that there was a depth stratification of species, and intraspecifically there exists a well-defined stratification of sizes. None of the species under study has a gas bladder. Hence, one could not hope to find pressure receptors that might be associated with such an organ. Secondary cues that might indicate depth to these fishes would appear to be minimal or nonexistent. During much of the year there is no temperature gradient, the water being about −1.9°C from surface to bottom in the area in question (*6*). It would seem that light would be of little significance during much of the year at 78° south latitude. Otoliths of one of the study species, *Trematomus bernacchii,* were examined. This species has two otoliths in each ear. The sagitta is of reasonable size, weighing about 10 mg in a fish having a wet weight of 100 g. There is a very tiny lapillus which shows up on x-ray pictures but which is difficult to find in dissection. Sagittas were collected from about 40 specimens. Weights of the stones ranged from approximately 10 to 45 mg.

Analysis of the otoliths of *T. bernacchii* by x-ray diffraction indicates that the principal constituent is aragonite. The x-ray determination of the material as aragonite is not verified by measurement, by the immersion method, of principal refractive indices of otolith fragments. The lowest index measured in the crystalline *aggregates* is about 1.515, which is less than the lowest principal index of pure aragonite (N_x = 1.530) (*7*). The fast (lowest-index) direction of the aggregate is approximately normal to the longitudinal dimension of the fibrils.

Six of the otoliths were individually dissolved in HNO_3 and examined with a Beckman DU flame photometer. We found calcium to be present at a constant value, 0.369 mg Ca^{++}/mg of otolith (standard error of the mean, 0.002). Hence, calcium is deficient by about 7.5 percent of the amount (0.40 mg/mg of otolith) that one would expect of pure $CaCO_3$. Potassium analyses were all negative. However, sodium is consistently present at 2.31 percent ($S.E._{mean}$, 0.042) of the amount of calcium, calculated on a mole basis.

Another collection of saccular otoliths was made from 25 specimens of a north Pacific flatfish, *Parophrys vetulus*. These stones were taken from fish heads obtained from a market in Charleston, Oregon. Species identification was verified by checking the heads against specimens in the collection at the Department of Fisheries and Wildlife, Oregon State University. The otoliths ranged from about 25 to 75 mg in weight. X-ray diffraction analysis of a sample of them indicated aragonite; however, there are four low-intensity (I/I_0, 2 to 8) peaks at spacings of 3.07, 3.03, 2.29, and 2.23 Å, which are not accounted for by the pattern of aragonite (*6*). Five specimens were analyzed by flame photometry. No potassium was found. Calcium is present in the amount of 0.372 mg Ca^{++}/mg of otolith ($S.E._{mean}$, 0.002); and, again, sodium is in constant proportion to calcium. On a mole basis, sodium amounts to 1.43 percent ($S.E._{mean}$, 0.031) of the calcium.

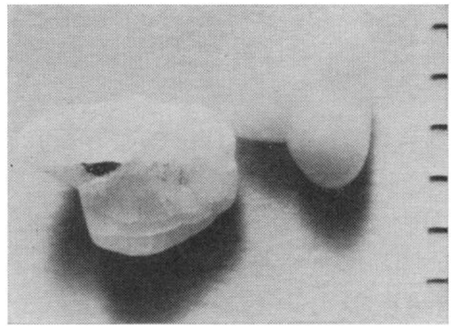

Fig. 1. Two views of right sagittas of *T. bernacchii.* Upper right, ventrolateral face; lower left, dorsomedial face, which has been smeared with paint to show concavities. The scale at the right is in millimeters.

Samples of approximately 400 mg of otoliths of each species were broken up in a mortar into particles of various sizes and were qualitatively tested for piezoelectricity in a circuit adapted from that described by Giebe and Scheibe (*8*). The circuit is illustrated by Buerger (*9*). In our work we picked up the feedback signal with an oscilloscope instead of with a speaker. The circuit was tested with quartz, Rochelle salt ($KNaC_4H_4O_6 \cdot 4H_2O$), and $CuSO_4 \cdot 5H_2O$, the last mentioned serving as a nonpiezoelectric control. Otolith samples of both species gave strong positive results. Since, in such a test as this, particle size is not controlled and crystals are randomly oriented in the electric field, it is not possible to quantitate results with any degree of precision (*8*). However, it seems important to point out that when comparable amounts of material were used, the magnitude of output of the flatfish otoliths was similar to that of Rochelle salt, a substance having an extremely high piezoelectric effect (*10*).

Individually, otoliths representing each species were mounted between spring-loaded plates of a crystal holder and the plates were connected to an audio frequency oscillator. A microphone was taped against the top plate and connected to one circuit of a dual beam oscilloscope. The crystal holder and microphone were enclosed in an insulated box to exclude ambient noise. Output of the audio oscillator was monitored with the second beam of the oscilloscope. The otolith of *Trematomus* oscillates over a range of 300 to 8000 cycle/sec. The *Parophrys* otolith oscillates from as low as 1 up to 15,000 cycle/sec.

Twenty of the 32 known classes of crystals are piezoelectric and ten of

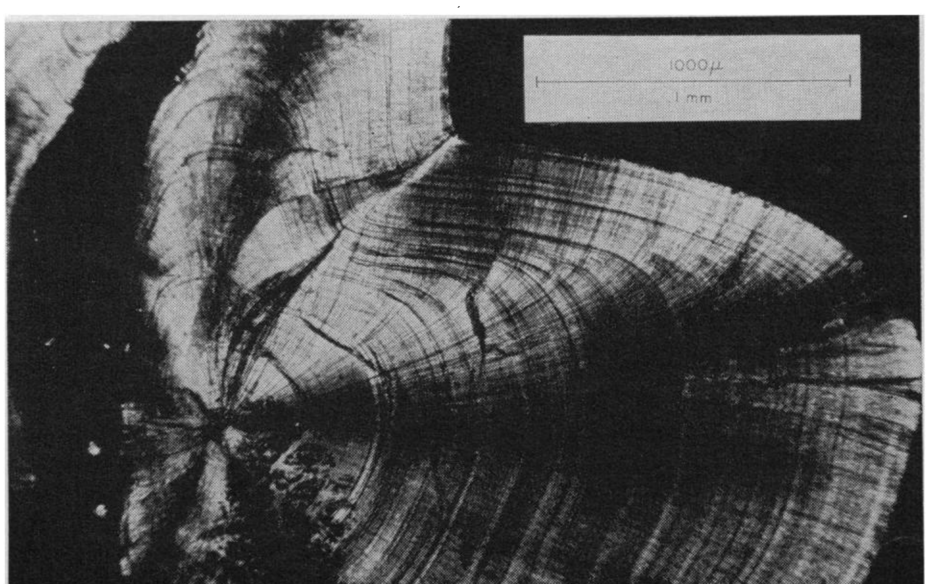

Fig. 2. Thin section (about 50 μ thick) of sagitta from *T. bernacchii* in cross-polarized light. Preferred directions of polarizers are parallel to edges of the picture.

the piezoelectric classes respond to hydrostatic pressure as well as to compression and torsion (*8*). Among these ten classes are some interesting mineral representatives such as shortite [$Na_2Ca_2(CO_3)_3$] and pirssonite [$Na_2Ca(CO_3)_2 \cdot 2H_2O$] which could easily fall within the exploratory analyses we have made so far. It would seem that there might be many possibilities that an organic constituent is responsible for the piezoelectric property.

We believe we have presented sufficient evidence to warrant exhaustive analytical studies of otoliths and physiological experiments designed to test whether or not piezoelectricity has any significance in the function of the fish ear. It appears that such a piezoreceptor is unknown in biological systems.

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Geological Exploration in an East Coast Submarine Canyon from a Research Submersible

Abstract. *Large talus blocks litter the flat floor of Oceanographer Canyon at a depth of 1460 meters; they indicate down-axis mass transport of floor sediment at an unknown time and rate. From 1460 to 1310 meters the sidewall is covered by unconsolidated sediment lying at 35° to 40° from the horizontal. An outcrop of Pleistocene or younger sediment at 1460 meters is probably a remnant of a former fill.*

The first descent into an East Coast submarine canyon was made on 15 October 1966 in the research submersible *Alvin*, which carries two men (three by redesign in 1967), and can go to a depth of 1830 m. It has four viewing ports, a six-motion mechanical arm, an exterior tool rack and sample basket, four exterior incandescent lamps, closed-circuit television, an exterior 500-shot strobe-illustrated 35-mm camera, and varied depth-indicating, navigation, and communication systems.

Sedimentary strata ranging in age from Late Cretaceous to Recent have previously been dredged from the walls of submarine canyons off the East Coast (*1*), but dredging techniques have not revealed the depth of individual samples. Currents have been measured (*2*) and photographs have been taken at the bottom of the canyons, but little information about geologic processes or dynamic events has resulted. Numerous traverses made near and across the canyons with continuous seismic profilers (*3*) indicate that large-scale slumping is a common process on the continental slope in the area.

The dive was made in Oceanographer Canyon at 40°14.9′N, 68°06.1′W (Fig. 1). The submersible, piloted by McCamis, landed on the canyon floor at depth 1460 m, traversed west approximately 100 m to the sidewall, ascended the sidewall to a depth of 1310 m, and returned to the surface. The dive was terminated after 2⅓ hours because the anchored navigation reference buoy went adrift; the submersible could have spent more than twice as much time on the bottom.

The canyon floor where first seen, about 100 m from the western sidewall, was planar and appeared level; an inclination of much more than 1° would probably have been detectable. The unconsolidated bottom sediment (not sampled) appeared to be the dark olive-brown clay-silt-sand that blankets that general area. Virtually all the surface was disturbed by the action of burrowing organisms. Circular pits as deep as 10 cm were surrounded or flanked on one side by mounds of the removed material. The only numerous bottom-dwelling organisms seen were off-white stalks or tubes roughly 8 mm in diameter, projecting 6 to 8 cm above the sediment surface. They were not associated with the pits.

Within about 75 m of the sidewall, the canyon floor is inclined about 5° toward the wall. The inclined part of the floor appears the same as the flat part, except for the presence in the inclined area of a small area of old-appearing inactive ripple marks about 10 m from the sidewall. The profile of the ripple marks indicated a down-canyon current. No ripple marks were seen on the flat part of the floor.

Small strands of organic matter attached to the canyon floor streamed in the 10 cm/sec down-canyon water current, but no sediment was seen in motion. In both the flat and the inclined floor areas, ridges and depressions in the sediment near to and concentric with projecting talus blocks indicated a down-canyon current; they were similar in appearance and presumably in origin to wind sculpturing of a snow surface near an obstruction.

The junction of floor and sidewall was smooth and covered by sediment; the radius of curvature at the junction was 1 to 2 m. No evidence of relative motion between the floor sediment and the sidewall was seen.

Large talus blocks protruded above the sediment in both the flat and the inclined area. One block about 2 by 6 m appeared to be tabular and to be resting on the sediment surface. It had an open, sinuous, parallel-sided break that indicates fracture after emplacement on its bed of sediment. Another block of talus projected monolithically 3 m at a high angle from the floor sediment (see Fig. 2). The talus blocks were not in contact with one another at or above sediment level, and did not appear to be in contact below that level. Shapes of the tabular rocks suggested that they are sedimentary. Talus blocks as small as 15 cm also rested on the sediment. The smaller blocks were highly angular; the large ones, subrounded.

An outcrop of semiconsolidated, well-bedded, clayey and silty sandstone was found at the base of the sidewall. Its base was hidden by overlapping floor sediment. The part seen was about 5 m high and 20 m long; one end was out of sight in the darkness. The