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SOUND AS A TOOL IN MARINE ECOLOGY, FROM DATA ON BIOLOGICAL NOISES AND THE DEEP SCATTERING LAYER

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In studies of specific populations or communities of different animals, the investigator is concerned largely with relative concentrations of individuals and with their feeding and breeding behavior, migratory habits, etc., as individuals or as groups. Information on these aspects is fundamental to an analysis and understanding of the factors that operate as controls within the population.

Direct census of population density based on systematic collecting, and identification or direct visual observations of the population in situ, are time-honored methods in ecological studies, and these will always be an essential part of such investigation whenever possible. Much tedious labor is involved, however, and therefore any physical means that provides a short-cut to useful generalizations or serves as a guide to focus attention on significant aspects, such as relative concentrations and activities in space and time, serves a real need. The application of sound and of underwater photography are two very promising means to this end. Both are still largely in the exploratory stages. The present discussion will be concerned only with sound.

In the past few years a large amount of work has been carried on pertaining to underwater noise phenomena, and a number of reports

1 Most of the studies forming the basis of this report were made while the author was a member of the staff of the University of California Division of War Research at the U. S. Navy Radio and Sound Laboratory (now the U. S. Navy Electronics Laboratory) San Diego, California, under Contracts OEMsr-30 and NOBs-2074, respectively, with the Office of Scientific Research and Development (Section 6.1 NDRC) and the Bureau of Ships, Navy Department. Various members of the Listening and Echo Ranging Sections assisted in the studies, and acknowledgment is made especially to Mr. R. R. Carhart for preparation of Fig. 1, and to Mr. G. Duvall and Mr. R. L. Ely, physicists, who collaborated in study of the deep scattering layer.

2 Contributions from the Scripps Institution of Oceanography, New Series, No. 380.
have been written relative to the behavior of sound in water, spectrum analysis, and identification of ambient noises, but it seems desirable to examine and interpret some of the information from an ecological rather than an acoustical point of view, to present new data and to point out some possible uses that suggest themselves.

There are two principal ways in which sound, depending upon its origin, may serve in biological studies: (1) Underwater sound voluntarily produced by the animals and picked up on appropriate hydrophones and analytical equipment, and (2) sound projected as signals from sonar gear, such as from ships' fathometers or echo-ranging devices, and returned as reflected sounds by organisms.

**UNDERWATER SOUNDS PRODUCED BY ANIMALS**

The significant sound-producing marine animals fall into three general groups: (1) Crustacea, (2) fishes, and (3) mammals. Only the first two will be considered here.

**CRUSTACEAN NOISES**

The crustacean sounds are by far the most widespread and persistent of all known underwater biological noises. This is due to the remarkable claw-snapping habits of two genera of snapping shrimps, *Crangon* and *Synalpheus*, widely distributed in tropical and subtropical waters (Johnson, 1943a).

The characteristic continuous loud crackle caused by populations of such shrimp is readily distinguished instrumentally from other ambient noises because of its continuity and high frequency (up to 50 kc) and great sound pressure spectrum level in the neighborhood of 10 to 15 kc.

The degree to which shrimp crackle dominates the noise in shrimp habitats has been discussed elsewhere (Johnson, Everest, and Young, 1947). It is instructive to consider here mainly the operation of directional hydrophones in seeking out these habitats. Fig. 1 shows results of a survey near San Diego when equipment of the type capable of 360 degrees rotation in a horizontal plane was used. The shrimp habitat at the point where these observations were made is a ledge of shale one mile in width in water of about 10 to 20 fathoms in depth. The shale is heavily pitted by borings and crevices made largely by boring mullusks.

It is seen from Fig. 1 that at a distance of 4,000 yards from the edge of the shrimp habitat the sound spectrum level at 20 kc is low and uniform in all directions, as shown by the solid black area in the center of the circles of pressure levels. Both depth and bottom conditions here were unfavorable to snapping shrimp, and the noise recorded is
Figure 1. Snapping-shrimp noise as detected with a directional hydrophone, with its beam rotated horizontally through 360°, over and at various distances from the shrimp bed.
“water noise.” But upon approaching the ledge, there is a gradual increase of high frequency sound from the direction of the “shrimp ledge.” Because of the directivity of the hydrophone, this increased sound spectrum level shows on the noise pattern as an expanding lobe in the direction of the shrimp bed. The angle of the high noise level increases as the bed is approached, indicating a habitat of great extent. When over the large shrimp bed, the sound spectrum level is again uniform in all directions, but because of intense shrimp crackle it is at a very much higher level than at 4,000 yards from the bed. Upon passing over the bed to the opposite side, where there is a shallow water area (not shown in Fig. 1) with sandy bottom, the sound spectrum level gradually diminishes and the lobe in the noise pattern again points towards the ledge, indicating that the ship now was over a habitat unfavorable to shrimp, apparently because of the sandy bottom.

The sound spectrum level obtained with the nondirectional hydrophone is shown as heavy circles in Fig. 1 for comparison.

In this manner additional information is gained besides that obtained from laborious dredging, which is often extremely difficult or impossible to accomplish. Illustrative of this are the results from dredging in an area of boulders at a depth of 10 fathoms off San Diego, where dredgings failed to yield more than an occasional shrimp, although the shrimp crackle was exceedingly loud over the area, indicating that shrimp are no doubt very abundant there (Fig. 2). Clean boulders have been brought up, but the agile shrimp appear to escape the slow moving dredge, so that their capture is only a matter of chance.

Direct and Indirect Uses of Shrimp Crackle

The crackling of shrimp may be used indirectly to some degree in the study of other benthic animals with which the shrimp are symbiotic or form more or less intimate environmental associations.

The possibility of using shrimp crackle in the study of certain large sponges, including the commercial sponge, should not be overlooked. It is well known that a number of snapping shrimp species, living within the pores and channels of sponges, can be heard when the sponge is removed from the water. A single sponge (Spirastrella) has yielded several hundred shrimp (Hay and Shore, 1915–1916). Though not yet demonstrated directly, there is reason to believe, on the basis of what has been said, that shrimp crackle might serve a commercial purpose in determining the location and extent of sponge concentrations.

The large amount of data showing a sharp drop in shrimp crackle at depths beginning at about 30 fathoms is convincing corroborative evi-
Figure 2. Sound spectrum level of shrimp crackle across a boulder patch in ten fathoms (from Johnson, Everest, and Young, 1947).

dence that this depth marks the maximum at which most species of *Crangon* and *Synalpheus* live in concentrations sufficient to provide instrumental measurements of their crackling. This is in keeping with an analysis of the vertical distribution of these genera as shown in 3,483 dredge hauls from various depths by several major expeditions, but the ease with which the information was obtained through acoustic means is in striking contrast.

The regularity with which shrimp crackle is found in, and is confined to, areas of certain bottom types, such as rock, coral, coarse shell, weed, and litter of harbors, is evidence of the importance that must be attached to the ecological factor which provides easily-maintained shelter for these animals.

If high sound level of crackle is an indication of the general type of
bottom, and since other animals, including some fish, frequent (in some cases confined to) rocky or coral bottoms where snapping shrimp abound, then the noise may serve as a guide to these areas. Examples of such areas are the fishing grounds off North Carolina where isolated coral patches occur (Radcliffe, 1914). Shrimp crackle has been reported from one of these grounds by Dobrin (personal communication), and doubtless it occurs on others as well. On the California Coast, where the agariferous seaweed *Gelidium* is harvested on rocky bottoms, the divers have remarked that they can "hear the *Gelidium* crackle." Though this is an erroneous interpretation of the origin of the sound, the implication is clear.

Ecological Significance of Diurnal and Seasonal Variations in Shrimp Crackle

Certain ecological facts may be gleaned from a study of the diurnal and seasonal variations in shrimp noise.

**Diurnal Variations in Activity.** It is well known that many intertidal animals that can be observed during low tide, or at the water's edge, become increasingly active at night. Among these are the crabs, isopods, limpets, and other gastropod mollusks. This increased activity may be explained as an adaptation that is advantageous to the animals in avoiding daytime dessication during low tide and in avoiding the ravages of preying birds.

Is this instinctive nocturnal activity reflected equally in the animals that live in deeper water below the low tide level? A commensurate answer to this question is not readily obtained.

Acoustical measurements of shrimp crackle do, however, give evidence of a marked nighttime increase in noise. These measurements have shown a 2 to 5 db increase in sound pressure spectrum level of crackle during the night, with peak levels just after sunset and shortly before sunrise. The figures are logarithmic expressions, which, interpreted into terms of shrimp activity, reveal a two to threefold increase and perhaps reflect an over-all activity within the shrimp community. Involved in this activity are not only the shrimp but also other animals, who, by their increased wandering about, cause increased irritation to the shrimp and hence more frequent individual snapping.

**Annual Variations.** Studies on seasonal variations have been made only in the San Diego region where the seasonal variation in temperature is about 8° C. However, these studies do not reveal fluctuations in shrimp noise that are greater than those observed diurnally. From this it might be concluded that there is a rather uniform year-round
population of adults capable of snapping, which implies that there may be a production of overlapping generations that do not migrate. In this connection it would be of interest to note what effect a greater range of temperature would have on activity in such an area as Beaufort, North Carolina, where the range is about 20° C, where snapping shrimp are abundant and where sound level due to them is known to be high during early spring and summer. A marked seasonal change in noise level might be inferred as a measure of the effect of temperature on the activity of the shrimp community.

Regarding the application of other crustacean sounds, little can be said. Several species of spiny lobsters produce a strident grating sound when they rub specialized structures on the bases of each of the antennae against opposing structures on the carapace. The sound is readily heard under water over acoustic instruments, but no attempt has been made to use it in locating populations. Indications thus far show that the sound is too rarely produced to be of general ecological use, but seasonal variations and local differences have not been sufficiently investigated.

**Fish Noises**

Many fishes are known to produce noises when removed from the water, but it is uncertain as to how many of these are soniferous in their natural habitat (Burkenroad, 1931). However, there are a number of notable sound-producers with organs well adapted to generation of underwater sound. Among these are especially the Sciaenidae (croakers and drums), the toadfish *Opsanus*, the singing fish *Porichthys*, and the searobin *Prionotus*. Additional underwater sound-producers are listed by Knudsen, Alford and Emling (1948), who also discuss the characteristics of fish sounds as related to "water noise." Other spectral analyses of fish noises are given by Loye and Proudfoot (1946) and Dobrin (1947).

The data available on fish sounds have not been collected or examined as closely with a view to their ecological application as was done for the shrimp studies. The most challenging suggestions come from the acoustical studies of the croaker, *Micropogon undulatus*, in Chesapeake Bay; the toadfish, *Opsanus tau*, at Beaufort, North Carolina; and various croakers at La Jolla, California.

The chorus of sounds produced by *Micropogon* in Chesapeake Bay was reported upon by Loye and Proudfoot (1946). Their findings include several items of ecological interest. (1) The chorus was heard only in the evening and nighttime. The interpretation suggested was that the noise accompanied a period of feeding. (2) The maximum nighttime intensities of the noise were localized to a specific area. (3)
Fish of this type appear to become accustomed to unusual noises, such as underwater explosions of blasting caps when these are detonated during the chorus. (4) Spectrum analyses of croaker noise in May 1942 showed appreciably more energy at frequencies up to 2,000 to 2,500 cps than three months later when there was very little above about 1,000 cps. It was suggested that the fish in the bay had grown during this period and that the correspondingly larger air bladder, which acts as a resonator, resulted in lower frequencies. However, the growth rate of sexually mature *Micropogon undulatus* is only about two to three inches in a year, according to Hildebrand and Cable (1930), so the size increase during three months could not be very great. Actually, the spectrum analysis probably revealed a means of testing a local population shift, which in this case resulted in the younger (smaller) fish being replaced in the area by an older population or by an admixture of older forms sufficient to lower the average sound frequency.

During a preliminary survey (Johnson, 1943b) of underwater noise at Beaufort, North Carolina in April 1943, the most conspicuous noise encountered in Beaufort Harbor, other than shrimp crackle, was a soft cooing sound that was produced as isolated notes both day and night. This sound, later studied in detail by Dobrin (1947), was believed by him to be produced by the toadfish. The outbursts, as heard over the nondirectional hydrophone, always appeared to come from fixed locations on the bottom where they persisted for days at a time. They were found to be associated with the nest building habit of *Opsanus*. This is interesting evidence of persistent guarding of the nest or area as well as maintenance of a system of territorial rights, an instinctive habit known to be common also for some other fish.

In the summer of 1942 a chorus of fish noises was discovered at the outer end of Scripps Institution pier, which extends 1,000 feet outward from shore. Since that time, except for the spring and summer of 1946, and the summer of 1947, listening observations have been carried on at irregular intervals throughout the year. From these it was found that the chorus began in the spring about May 3, 1943; April 11, 1944; April 25, 1945; May 14, 1947. It continues throughout the summer and disappears about the middle or latter part of September. There are only occasional individual outbursts of sound at other seasons.

The chorus begins about sunset and increases gradually to a steady uproar of harsh froggy croaks, with a background of soft drumming.

* Thanks are due to Dr. H. F. Prytherch, Director of the U. S. Fish and Wildlife Service Laboratory, for facilities at Beaufort.
Figure 3. Fathograms of Deep Scattering Layer, 18 kc, E. W. Scripps, 1945, off San Diego: A, Layer during afternoon of June 26; B, Layer ascending August 18; C, Layer descending August 19.
This continues unabated for two to three hours and finally tapers off to individual outbursts at rare intervals. From tests and recordings of isolated fish in aquaria, it seems clear that the chorus consists of one or more of the following species of Sciaenidae: black croaker, *Sciaena saturna*; spotfin croaker, *Roncadro stearnsi*; yellowfin croaker, *Umbrina roncador*. Each of these fish produced vigorous froggy croaks which were nearly identical to those heard in the “chorus.” In addition to croaking, *Sciaena saturna* produced a series of rapid clicking sounds. In the tests, none produced sounds similar to the soft background drumming.

Although tests of the black croaker demonstrated that individual fish are capable of producing more than one kind of sound, the soft drumming in the chorus may be produced by a species not tested, for it was never a part of the chorus during the first weeks in spring.

Further evidence which strengthens this view was obtained in July 1945 when listening alternately over stationary hydrophones, one placed at the pier and one at a distance of 2,000 feet from the pier. The sounds picked up on the distant hydrophone were dominated by the soft drumming, whereas on the nearer hydrophone the harsh croaks were dominant, with only a rare outburst of drumming. Thus it appears that two separate schools of different fish were involved.

The above is the only locality where a “croaker chorus” has been observed along the west coast, though individual outbursts are often heard elsewhere. Evening listening tests have been made at a few other locations with negative results, but it is highly probable that many other such choruses do hold forth at other localities south of Point Conception. The significance of this croaking in unison is not known, but it is difficult to believe that so marked and regular a phenomenon does not have some ecological significance.

**REFLECTED SOUNDS**

**THE DEEP SCATTERING LAYER**

The “deep scattering layer” refers to a sound scattering layer within the sea. This layer, which was first observed in 1942 (C. F. Eyring, R. J. Christensen, and R. W. Raitt, 1948), may have a thickness of about 50 fathoms and be spread horizontally over vast areas at depths of 150 to 450 fathoms during the daytime. Outgoing signals of 18 kc frequencies are more or less scattered by reflections from bodies of scatterers that make up the layer. This results in more or less pronounced “false bottoms” being indicated on the recording fathometer tapes.
Biological Hypothesis

Precisely what these sound-reflecting bodies are is not known, but while working from the author's hypothesis that the deep scattering layer may be caused by stratification of either planktonic life or nektonic forms associated with the plankton, it was possible, in a 24-hour series of observations on June 26 and 27, 1945 aboard the E. W. Scripps, to show for the first time that the layer is not stationary at any depth but that it behaves biologically in performing vertical diurnal migrations in a manner paralleling the well known behavior of many planktonic animals (Anonymous, 1946).

Figure 4. Vertical distribution of zooplankton. I. Animals greater than 2 mm. II. Animals 2 mm or less.
The observations were made about 20 miles off Point Loma where the depth is 660 fathoms. Fathograms were made of the layer from about noon June 26 to noon June 27 (Fig. 3). During this time it moved towards the surface in the evening and descended again the following morning, apparently under the stimulus of changing light intensity. It reached its maximum depth in early forenoon, suggesting that while light was the stimulus initiating the downward movement, some other factor (which might be temperature or pressure) became dominant in limiting the depth of descent. The partial or complete disappearance of the layer at night may result from a tendency of the scatterers to become dispersed as a result of the absence of the stimulus (light) which in the daytime causes them to accumulate in a relatively narrow zone.

Using the fathometer as a guide to the position of the scattering layer, a series of 14 vertical plankton hauls were made below, through and above the main layer (a faint secondary layer was indicated above the main layer). Nansen closing-type nets with No. OX and No. 8 bolting silk and a 40-cm mouth were used. In Fig. 4 is given the number of animals caught, adjusted to 100 meters of haul and shown as two size groups, i.e., those greater than 2 mm in length and those 2 mm or less.

The daytime vertical distribution of the zooplankton was similar in general for the two days. The preponderance of smaller forms (mainly copepods 1 to 2 mm in length) in the 0 to 110 yard stratum was very striking. Below 110 yards the number of this size fell off markedly but increased again to a secondary maximum which in the early afternoon of June 26 was at about 360 to 475 yards, partly within and partly below the scattering layer. In late afternoon the maximum was somewhat higher and within the layer. On June 27, the secondary maximum of smaller forms was within and somewhat above the layer.

Animals of size greater than 2 mm in length showed a small increase within the scattering layer on both days. Most abundant of these were copepods ranging from 2 to 8 mm and including mainly Calanus and Metridia, but also Heterorhabdus, Euchaeta, Eucalanus, and Rhincalanus. The largest organisms caught were sagittae (total 35) ranging from 6 to 27 mm. Included also were a few euphausiids, ctenophores, medusae, polychaetes, and amphipods. Previous work

4 It is obvious that in order to obtain larger samples and to minimize the effect of patchiness, horizontal tows should be resorted to in sampling the various strata. But samples collected in this manner at the deeper levels have thus far appeared unreliable because of the difficulty of maintaining the net within the narrow horizontal limits required.
in this area has often shown daytime swarms of euphausiids at depths below 200 yards. They are relatively strong swimmers and are capable of avoiding small nets during the daytime.

The largest body cross section for animals other than the medusae was only 5 mm, and none of the animals was found to have air bubbles which would make them strong scatterers (cf. Raitt, 1948). Yet from these preliminary observations there appears to be some direct correlation of the planktonic animals with the scattering layer. If the size and acoustic properties of these forms are not suitable to scatter sound, the alternate explanation must then be that larger forms not sampled by the small, slowly moving net are responsible and that they occur more or less concurrently with the small planktonic forms upon which many of them presumably subsist. The larger fast swimming forms must include euphausiids, prawns, deep-sea fish, and squids, for it is well known that all these do frequent the waters within the range of the scattering layer.

The fact that correlation appears to be best with the larger planktonic forms may be of special significance. It suggests that many of the larger scatterers are not strictly filter-feeders (that is, do not filter out the small forms less than 2 mm in length with fine gill rakers, etc.) but probably select more or less individually the larger planktonic forms. The feeding habits of these deep-sea forms have received little attention, but the manner of feeding can be inferred largely from study of feeding structures. Fish such as the cyclothones, myctophids, and the hatchet fish (Argyropelecus) are not strictly of the filter-feeding types, nor are the squids. Hersey and Moore (1948) have recently shown the deep scattering layer to be widespread in the Atlantic Ocean, and present evidence that the euphausiids are perhaps among the planktonic forms involved as scatterers.

The rate at which the layer ascends or descends may be a measure of swimming speed and therefore may be an aid in deducing what animal groups might be involved in its formation. This rate apparently varies somewhat. In the June 26–27 observations the maximum rate of ascent appeared to be around six feet per minute. The record for August 18–19, 1945 aboard the E. W. Scripps in the same area (Fig. 4 B and C) gives approximately the same rate of movement. According to the clearest records obtained by Dietz (1948) in an extensive survey of the geographic range of the layer, the rate of movement is 10 to 18 feet per minute. This rate of movement would exclude many slow swimming planktonic forms. However, the adult stages of such planktonic animals as euphausiids, chaetognaths, and amphipods can easily swim at this speed, and when under a directive stimulus, such as decreasing or increasing light, they might be expected to mi-
grate vertically at a speed paralleling that observed in movements of the layer. Preliminary tests show that, for short distances at least, euphausiids are capable of swimming at rates ranging upward to 39 feet per minute, and the copepod *Eucalanus* as high as 30 feet per minute. The deep-sea fishes, such as the myctophids, sometimes caught in deep plankton hauls in this area, do not possess air bladders which would limit the speed of their vertical movements because of change in the hydrostatic pressure. At night they are also commonly caught at the immediate surface.

The vast extent of the layer (sometimes present for a whole day's run of the ship) presupposes an abundant and rather uniformly scattered community that shows up on the fathogram as being more widespread than schools of fish or squid commonly observed near the surface. Squid have been suggested as the probable cause of scattering (Lyman, 1948), but while they may be expected to be a part of the scattering layer along with other animals, the type of squid known to be abundant, i.e., *Loligo*, has been observed to school at the surface. If this habit is not abandoned when they are present at great depths, then it might be expected that they would appear as limited patches on the fathograms. For example, Tester (1943), in a study of reflected sounds applied to fisheries, has shown how schools of herring in shallow water can be detected as patches on the fathograms.

The acoustical evidence does not readily lead to the assumption that only one kind of animal is involved. On the other hand, Russell (1928) has reported a different migratory response for different age groups and sexes of copepods.

The daytime formation of two scattering layers, or the splitting of the layer, with one part migrating upward with increased darkness while the other remains stationary, as shown by Dietz (1948), presents complicated and intriguing problems for the ecologist. Do the layers represent segregations of different species, stages of development, or sexes?

These are questions that remain to be answered, but with the aid of acoustic gear as a guide to collecting the solution should be greatly simplified.

**SUMMARY**

Underwater sounds produced by animals or reflected by them can be used in studying concentrations and behavior of certain marine populations.

*Biological Sounds.* Crustacea and fishes are the main sound producers. Crustacean sounds consist mainly of high frequency crackle produced by snapping shrimp. With directional sound equipment,
their habitats can be detected to distances of 2,000 yards or more.

Studies of the continuity and sound spectrum level of shrimp may
give evidence pertaining to stability of populations, their diurnal
activities, geographical distribution, and type of bottom and depth
of water preferred.

Observations on fish noises have given less useful ecological data.
They do, however, demonstrate a regular and pronounced seasonal and
diurnal habit of certain Sciaenidae to form localized choruses, as con-
trasted with isolated solos by the toadfish (Opsanus tau).

Reflected Sounds. The “deep scattering layer” has been shown by
its diurnal vertical migrations to be biological in nature. The partial
reflection of fathometer signals in this layer promises to be a useful
ecological tool in studying the organisms involved.

While using sound as a guide, a preliminary study in 1945 showed a
positive correlation with plankton stratification and the depth of the
scattering layer. This relationship may be partly secondary, since
the more effective scatterers may be larger forms that subsist upon and
migrate more or less concurrently with the plankton.

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