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Sound Perception and Production in the Pink Shrimp, Penaeus duorarum Burkenroad

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PREFACE

The Sea Grant Colleges Program was created in 1966 to stimulate research, instruction, and extension of knowledge of marine resources of the United States. In 1969 the Sea Grant Program was established at the University of Miami.

The outstanding success of the Land Grant Colleges Program, which in 100 years has brought the United States to its current superior position in agricultural production, was the basis for the Sea Grant concept. This concept has three objectives: to promote excellence in education and training, research, and information activities in the University's disciplines that relate to the sea. The successful accomplishment of these objectives will result in material contributions to marine oriented industries and will, in addition, protect and preserve the environment for the enjoyment of all people.

With these objectives, this series of Sea Grant Technical Bulletins is intended to convey useful research information to the marine communities interested in resource development quickly, without the delay involved in formal publication.

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INTRODUCTION

Fishing for the commercially valuable pink shrimp, _Penaeus duorarum_, is economically feasible only at night since it burrows during the day. Daylight fishing became theoretically possible upon the introduction of the electric shrimp trawl. The pulsed D.C. field employed was to bring the shrimp out of their burrows, making them vulnerable to the trawl. Experimentation has shown that in mud bottom the trawl works well, yielding from 96% to 109% of the nighttime catches. In other types of bottom, yields dropped to as low as 50% of the nighttime catches (Pease, 1967).

It has been suggested that the lower catches are a result of the shrimp avoiding the trawl after they are brought out of their burrows. It has been proposed that the introduction of a "confusion factor" may decrease the percentage of shrimp escaping capture, thus increasing the efficiency of the electric trawl.

It is obvious that a confusion factor must be easily detected by the shrimp to be of any use. This requires some knowledge of the sensory physiology of the animal. Unfortunately, little work has been done in this area. Some investigations have been carried out in the area of crustacean vision, but other sensory modalities have largely been ignored. This is particularly true of sound and vibration perception.

Objectives

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The primary purpose of this investigation was to examine sound and vibration perception in the pink shrimp, and on the basis of the findings to decide whether sound would provide a useful confusion factor.

A second purpose was to investigate sound production in the pink shrimp. It was hoped that if the shrimp produced a characteristic sound it might be of some use in detecting large concentrations of the animal.

LITERATURE SURVEY

Sound Production in Crustaceans

Crustaceans are a major sound source in the marine environment, as evidenced by the fact that seventeen families of this class were included on a list of soniferous marine animals compiled by the United States National Museum (Fish, 1954).

The majority of sonant crustaceans produce sound by stridulating, and thus far stridulatory devices have only been reported in the subclass Malacostraca (Barnes, 1963). The order Decapoda alone contains approximately 50 genera with stridulatory organs (Dumortier, 1963); the true crabs, Brachyura, are represented by more than 30 stridulating species (Guinot-Dumortier and Dumortier, 1960). The only sound-producting crustacean that is not in the subclass Malacostraca is <u>Balanus</u> (subclass Cirripedia) (Dumortier, 1963).

Prominent sound-producing crustaceans include true crabs (Brachyura), snapping shrimp (Alpheidae), hermit crabs (Paguridae), spiny lobsters (Scyllaridae), and mantis shrimp (Stomatopoda) (Dumortier, 1963).

The most vociferous of the marine crustaceans is the snapping shrimp. This was first reported in the scientific literature by Kraus (1843), who observed that the large chela is the sound-producing organ. Preceding this early manuscript were numerous reports by mariners of crackling noises which seemed to emanate from the holds of their ships. <u>Teredo</u>, the ship worm, was initially thought

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responsible, but Johnson, Everest, and Young (1947) felt that the probable sources were nearby beds of snapping shrimp whose sound can easily be heard through a ship's hull.

Hulbert (1943) while aboard a small vessel in Beaufort harbor, North Carolina, heard noises which he described as being similar to those produced by "...dragging a blackberry vine". Similar crackling sounds were reported during World War II by submarines operating in coastal waters of low latitude and initially were thought to be a new device developed by the enemy (Johnson, Everest, and Young, 1947). Sounds comparable to the crash of static or coal rolling down a chute were detected off the coast of California by the Coast and Geodetic Survey, but the source of these sounds was not immediately known (Swainson, as reported in Johnson et al, 1947). After considerable investigation in each of the cases cited, the source of the sounds was traced to various species of snapping shrimp (Johnson et al, 1947).

The sounds produced by several genera and species of snapping shrimp have been described. The emission by Alpheus strennus Dana has been compared to the noise made when the rim of a glass dish is struck full force with a wooden ruler (Coutière, 1899). Johnson et al (1947) in a more quantitative study surveyed sound emissions produced by populations of Crangon (now Alpheus Fabr. by a resolution of the commission on Zoological Nomenclature and Synalpheus Bate. They found that sound levels over the shrimp beds were 30 decibels higher than state 1 sea noise. An average pressure peak of 124 decibels above 0.0002 dynes per square centimeter was measured at a distance of one meter from Synalpheus lockingtoni Coutière. Their study

indicated that although the strongest components of the sound were in the 2 to 15 KHz region, similar sounds could be heard by heterodyning ultrasonic bands in the 20 to 50 KHz region down to audible ranges.

Loye and Proudfoot (1946) found that the largest amount of energy in the snap of the shrimp was concentrated in the region between 20 and 25 KHz, whereas Nicol (1960) stated that a broad energy peak existed between 2 and 15 KHz. Everest, Young, and Johnson (1948) reported that the energy was concentrated between 0.5 and 12 KHz, with a peak between 7 and 8 KHz. Hazlett and Winn (1962a) analyzed the sound produced by Alpheus armillatus H. Milne Edwards and determined that it was composed of a large number of frequencies ranging from below 85 Hz to above 12 KHz. A high energy frequency band was located between 85 and 250 Hz. The energy content was found to decrease rapidly above 8 KHz, although there was measurable energy present beyond 12 KHz.

Everest et al (1948) and Albers (1960) found that the duration of the average snap produced by the shrimp was 1.5 msec. Hazlett and Winn (1962a) computed that the mean duration of the snap was 46.2 msec for Alpheus armillatus and 54.2 msec for Synalpheus hemphilli Coutière. Statistically, the means were not found to be significantly different. Hazlett and Winn (1962a) felt that the large discrepancy between their measurements and those of Everest et al (1948) and Albers (1960) was due to the variation in methods employed.

There have been numerous reports on the sound producing mechanism of the snapping shrimp. Kent (1877) believed that the sound was produced by the opening of the large chela, as did Wood-Mason (1878), who advanced the "cork-in-the-bottle" theory. This maintains that the

sound is produced when the plunger on the dactyl (moveable finger) is suddenly removed from its receptacle on the upper face of the fixed finger of the propodus, much in the same manner as the "pop" that is produced when a cork is pulled from a bottle.

Lovett (1886) felt that Alpheus glaber Olivi produces its snapping sound by moving its tail over the spines on its tail segment. Other investigators believed that the tips of the chelae produced the sound when the dactyl struck a glancing blow on the opposing tip of the fixed finger (Johnson et al, 1947; Pope, 1949). Coutière (1899) and Verill (1922) also commented on the snapping mechanism, with the latter presenting a summary of the opinions on the subject to that time.

Volz (1938), on the basis of extensive anatomical investigations, came to the conclusion that a chitinous ridge on the inner margin of the posterior wall of the receptacle, which serves as a breaking device, incidentally produces the sound as the plunger enters the socket.

Nicol (1960) and Hazlett and Winn (1962a) agreed that all parts of the chela that come into contact contribute to the production of sound. Hazlett and Winn (1962a) demonstrated this by recording the sound produced by shrimp which had had various areas of their chelae extirpated. Further evidence that the plunger and socket are not exclusively responsible for sound production is the fact that although Alpheus malleodigitus Bate has no fixed finger, a loud noise is nevertheless produced (Durortier, 1963)

There is not complete agreement as to the significance of sound production in the snapping shrimp. Volz (1938) was not certain that

it served any function. As has already been stated, he thought it might be merely a by-product of the breaking action of the chitinous ridge. It seemed probable to him that the jet of water produced by the plunger entering the socket was the significant factor in that it could be used to frighten away intruders.

MacGintie (1937) and Given (1958) felt that there was a relation between snapping and predation. Given went on to state that the concussion or shock wave produced by the snap could stun a fish. However, the findings of Volz (1938) and Hazlett and Winn (1962a) do not show any association between snapping and predation.

Johnson et al (1947) and Moulton (1957) felt that snapping played a part in defensive or aggressive behavior patterns, while Nicol (1960) suggested that it is interrelated with both food procurement and defensive behavior.

Hazlett and Winn (1962a) disclosed that snapping occurred only when the immediate area inhabited by the shrimp was infringed upon by either another snapping shrimp or a mantis shrimp.

In 1878 Goode reported on sound production by the mantis shrimp, a marine crustacean. He believed that it generated its sound in the same manner as the snapping shrimp. Johnson et al (1947) disagreed with Goode's report, and felt that Gonodactylus oerstedii Hansen, the same species Goode had investigated, produces its sharp clicking sound with its raptorial appendage. The dactyl of this appendage fits into the groove of the propodus in the same manner as the blade of a pocket knife folds into the handle. At the end of the propodus there is an erectile spine which generates the noise upon impact with the dactyl. This mechanism was originally described in Gonodactylus chiragra L.

by Alcock (1902). It has also been reported in Gonodactylus glabrous Brooks and Gonodactylus demani Henderson (Kemp, 1913). Several other genera of mantis shrimp are also known sound producers, including Squilla empusa Say, Squilla mantis L., and Lysosquilla excavatrix Brooks, all of which reportedly stridulate by passing their uropods over the lower surface of their telsons (Brooks, 1886; Giesbrecht, 1910; Balss, 1921). Moulton (1957) stated that the mantis shrimp produces sound with the "...stinging extension of the raptorial appendage".

Hazlett and Winn (1962a) are in sharp disagreement with all previous investigators on the mode of sound production in this species. They found that the sound is produced by the distal portion of the raptorial appendage striking against some object in the environment. They state that the mantis shrimp has no sound-producing organ.

Although there is a diversity of opinion as to how the mantis shrimp generates its characteristic sound, there is general agreement that the physical qualities of the sound are the same as those of the snapping shrimp (Johnson et al., 1947; Moulton, 1957; Hazlett and Winn, 1962a).

The function of the sound produced by the mantis shrimp is unknown. It may be merely a by-product of the raptorial appendage inadvertently striking some nearby object (Hazlett and Winn, 1962a), or it may have some defensive significance (Alcock, 1902).

Stridulatory apparatus has been found in a number of marine crabs. The hermit crab, Coenobita rugosus H. Milne Edwards, produces a chirping sound (Borradaile, 1901). Its stridulatory apparatus has been described in detail by Hilgendorf (1869) and Ortman (1901). A

similar apparatus was also found in Coenobita perlatus H. Milne Edwards

(Dumortier, 1963). Balss (1921), who also described the sound produced

by Coenobita as a chirp, stated that he had found sexual dimorphism in

regard to the stridulatory apparatus amongst several species. Other

pagurid crabs, including seven species of Trizopagurus Forest, are

also equipped with stridulatory structures (Forest, 1952; Henderson,

1888).

Brachyuran crabs have been found to stridulate in two ways: by

friction of appendages against the cephalothorax, or mutual friction

of the appendages (Dumortier, 1963).

The first group includes Ovalipes ocellatus Herbst, Ommato-

carcinus macgillivrayi White, Pseudozius bouvieri A. Milne Edwards,

Helice tridens De Haan, Potamon africanum A. Milne Edwards, and the

genera Acmaeopleura Stimpson, Macrophthalmus Desmarest, Metaplax

H. Milne Edwards, Matuta Weber, Acanthocarpus Stimpson, Menippe

De Haan, Hexapus De Haan, Lambdophallus Alcock, Hexaplax Doflein, and

Dotilla Stimpson (Aurvillus, 1893; Ortman, 1901; Alcock, 1902;

Rathbun, 1914; Crane, 1947; Guinot-Dumortier and Dumortier, 1960;

Dumortier, 1963).

The group of brachyuran crabs that produce sound by mutual

friction of appendages includes Ovalipes punctatus De Haan, Uca

musica Rathbun, Uca terpsichores Crane, and the genera Ocypode Weber

and Globopilumnus Balss (Alcock, 1892, 1902; Anderson, 1894; Barass,

1963; Crane, 1941a, 1947; Cott, 1930; Guinot-Dumortier and Dumortier,

1960; Dumortier, 1963; Ortman, 1901; Rathbun, 1914; Schmitt, 1931;

Hughes, 1966).

A number of workers have found a correlation between sound

production and sexual behavior in the fiddler crab, Uca (Dembowski, 1925; Crane, 1941a, 1943; Burkenroad, 1947; Salmon and Stout, 1962). Dembowski (1925) claimed that one fiddler crab can lure another from its burrow by rapidly waving its large cheliped. Crane (1941a) found that in the Pacific American species of Uca, and in Uca pugilator Bosc (Crane, 1943), the motion of the cheliped is modified so that it beats on the ground, producing sound. Burkenroad (1947), however, was unable to observe any disturbance of the sand grains beneath the cheliped and felt that Crane's findings were incorrect. He believed that the sound must be produced by some unknown method since he could detect neither rattling of the dactyl nor vibration of the body.

Burkenroad (1947) and Salmon and Stout (1962) agree that sound production substitutes for visual stimuli under certain circumstances, such as when the male and female are out of the line of sight or at night.

The sound produced by the fiddler crab lasts from 0.2 to 0.3 seconds, with the major part of the energy concentrated between 85 and 2,000 Hz (Salmon and Stout, 1962).

Gerstaecker (1901) reported on another sound producing crustacean, the ghost crab, Ocypode Weber. He compared the sound it produced to the low buzz of a double bass. Harms (1929, 1932) described it as a fine filing noise, while Crane (1941b) characterized it as a series of twittering creaks, which become louder and higher pitched when the animal enters its burrow. Peters (1955) stated that it was a croaking sound, and Hughes (1966) reported three distinct sounds: short rasping sounds, burbling gargles, and sharp knocking sounds.

Schmitt (1931), Crane (1941b), and Cohen and Disjkgraaf (1961)

have described the stridulatory apparatus found in Ocypode. Guinot-Dumortier and Dumortier (1960) pointed out that stridulation in Ocypode, which consists of rubbing a row of tubercles on the inner face of the propodus of the larger of the two chelipeds against a smooth ridge on the ischium when the cheliped is folded against the body, is unique among arthropods in that the apparatus is not a modification of already existing structures.

Several functions have been associated with sound production in Ocypode. Cott (1930) felt that its purpose was to warn others of the species of danger. Barass (1963) thought it was used to entice females, while Dumortier (1960) theorized that it might help keep the colony together. Hughes (1966) could find no evidence for these conjectures, and was inclined to agree with Alcock (1892, 1902) and Crane (1941b), who felt that it was a warning to territorial intruders.

The spiny lobster, commented upon by Athenaeus in the third century, is probably the first crustacean known to stridulate. Leach (1815) offered the first scientific description of stridulation in Palinurus vulgaris Latr. Numerous investigators have subsequently published information on stridulation in the spiny lobster (Yonge, 1854; Mobius, 1867; Kent, 1877; Goode, 1878; Heldt, 1929; Parker and Haswell, 1940; MacGintie and MacGintie, 1949; Dijkgraaf, 1955; Moulton, 1957; Hazlett and Winn, 1962a,b). Detailed descriptions of the stridulatory mechanism in Palinurus vulgaris Latr. were given by Parker (1878) and Dijkgraaf (1955); Moulton has done the same for Panulirus argus Latr.

The stridulatory sounds of the spiny lobster can be divided into two categories: rasps and slow rattles (Moulton, 1957). The slow rattle consists of five or six pulses containing frequencies of 0.5 to 3.3 KHz. The mean number of pulses per second is 27, and the greatest energy peak appears to be at 0.6 KHz. Moulton (1957) found that the rasp has a duration of 0.1 second and contains frequencies from less than 40 Hz to about 9 KHz.

Hazlett and Winn (1962a) also analyzed the sounds produced by Panulirus argus Latr. They reported that it contained many frequencies, measurement of which was limited by their equipment. The sonogram showed a fairly even energy distribution from 85 Hz to 4.8 KHz, but there was measurable energy up to 12 KHz. The duration of the sound was 63 to 111 msec. Panulirus guttatus, reported on in the same paper, emitted sound that had measurable energy from 85 to 12,000 Hz, with an energy dip between 300 and 600 Hz. The mean duration was 53.3 msec.

Hazlett and Winn (1962b) performed a similar analysis on the sound produced by Justitia longimanus. The sonogram indicated that there was measurable energy from below 85 Hz to above 12 KHz. The greatest amount of energy was between 0.1 and 4 KHz, with a distinct peak between 1.2 and 2.4 KHz. The duration of the sound was 55.1 msec. They pointed out that the duration of the sound produced by Justitia longimanus was close to that of Panulirus guttatus, but differed considerably from the larger Panulirus argus. On the other hand, the frequency spectrum of Justitia longimanus resembled that of Panulirus argus, but not that of Panulirus guttatus.

Hazlett and Winn detected a diel variation in the sound production of _Panulirus argus_. Although calls occurred throughout the 24 hour period, the number sharply increased at night. Moulton (1957) reported the exact opposite, i.e., a far greater number of sounds produced during the day. Hazlett and Winn made their measurements over a reef, whereas Moulton's were made in a live car tied to the dock.

Lindberg (1955), working with _Panulirus interruptus_, and Dijkgraaf (1955) with _Palinurus vulgaris_, came to the conclusion that stridulation by the spiny lobster has a threatening significance. Moulton (1957) stated that in _Panulirus argus_ the slow rattle is characteristic of lobsters gathered in groups, whereas the rasp is a component of defensive behavior.

There are only scattered reports in the literature of sound-producing organs in shrimp of the family Penaeidae, the group to which the subject of this paper belongs. The few species that have been studied have a unique apparatus. It consists of a row of small crests on the sides of the cephalothorax in the branchial region. When the animal stridulates these crests rub against the antero-lateral edge of the first segment of the abdomen (Dumortier, 1963).

The number of stridulatory crests varies among the species in which they have been found. _Metapenaeopsis barbatus_ De Haan has approximately 20; _Metapenaeopsis acclivis_ Rathbun has from 13 to 18; _Metapenaeopsis durus_ Kubo has 28 to 35; and _Penaeopsis stridulans_ Wood-Mason has between 5 and 12 (Balss, 1921; Kubo, 1949).

Other than those in the subclass Malacostraca, the only crustaceans known to produce sound are species of the genus _Balanus_ Da Costa which belong to the subclass Cirripedia; they do not possess

stridulatory organs. These barnacles produce a crackling noise which consists of one millisecond clicks produced at the rate of approximately ten per minute (Busnel and Dziedzic, 1962). Large populations of Balanus produce a continuous sound which composes an important component of marine biological noise in some areas.

Sound and Vibration Perception in Crustaceans

The question whether true hearing was possible in Crustacea was discussed by Minasi in 1775. After observing the hermit crab, Pagurus, he came to the conclusion that the auditory sense is better developed in the hermit crab than it is in man. He claimed that the crabs he observed perceived the tolling of a distant church bell before he did.

Aelianus (1784) made even wider claims than Minasi. He reported that the fishermen in his area used music to collect Pagurus.

Farre (1843), who was the first to describe the statocyst accurately, felt that it was an organ of hearing; hence, the name otocyst was initially applied to this organ. This belief was seemingly confirmed by the experiments performed by Hensen (1863). Upon examining the statocysts of the spiny lobster, he found 468 projections which he referred to as auditory hairs. These varied in a nearly continuous spectrum from 0.14 to 0.72 mm in length. He computed that the ratio of the volume of the largest to the smallest hair was 140 to 1. Drawing an analogy between these hairs and organ pipes, he estimated that if they responded to different sound vibrations, the statocyst would have an auditory range of three octaves.

Hensen then carried out an experiment which he felt proved this hypothesis. He conducted sound into a container of water through a

mechanical analog of the mammalian middle ear. In the container were mysids, whose auditory hairs were observed through a microscope throughout the course of the experiment. Hensen observed that certain hairs would disappear when a certain note was sounded on a musical instrument. Other hairs would respond in the same way to different notes.

Hensen, having satisfied himself that various hairs responded to specific frequencies, went on to demonstrate the response of crustaceans to vibrational stimulation. He accomplished this by placing a resonant wooden bar in a vessel containing both Mysis and Palaemon. He reported that when the wooden bar was struck, both organisms responded by jumping away from the source. In addition, he discovered that gradual strychnine poisoning amplified the response of Palaemonetes.

The auditory capabilities of Crustacea were widely accepted as fact after Hensen's experiments (Milne Edwards, 1876; Jourdain, 1880; Garbini, 1880; and Delage, 1877). But Kreidel (1893), after a series of what have since become classic experiments, stated that the otocyst is used exclusively as an organ of orientation and not audition. He proposed changing the name from otocyst to statocyst.

The first mention of the possibility that hearing in Crustacea is not dependent solely upon the statocyst is made by Bethe (1897). He stated that removal of the statocyst in mysids impairs their auditory ability but does not destroy it. He went on to state that mysids are more sensitive to low tones than to high ones.

Beer (1898) felt that the response of decapods to different sounds does not prove that they can hear. Their actions, he states, might be attributable to their sensing vibrations transmitted to the water from

the walls of the vessel in which the animal is confined. In his own experiments he found that carideans and mysids exhibited pronounced reactions when partially submerged jars, bells, and other objects were struck. They reacted, however, only if they were at no greater distance than that at which the sound could be felt by the experimenter's hand. He noticed that the animals responded more strongly when they were nearer the walls of the vessel, thus confirming his hypothesis that a vibration sense rather than hearing is involved.

Beer (1898) felt that for an animal well supplied with tactile organs, pure audition would be unlikely. He reasoned that vibrations could be felt as soon as sounds could be heard, thus making audition useless. Beer (1899) followed up these experiments with work on the blind shrimp, Penaeus membranaceus. He felt that if an auditory sense existed in Crustacea, it would be most acutely developed in this species. His conclusions remained unchanged.

Prentiss (1901) repeated the experiments on which Beer had reported in 1898. Using Palaemonetes, Prentiss came to the conclusion that reactions formerly attributed to sound stimuli were nothing more than tactile reflexes. He pointed out that decapods respond vigorously to low frequencies, but not at all to high ones. He considered this fact to be good evidence that vibrations perceived by decapods are analagous to those which produce tactile rather than auditory sensations in vertebrates.

Vibration perception, meaning sensitivity to sounds or vibrations reaching the animal through the substrate, was found to exist in mysids by Bauer (1908). This work partially confirmed Hensen's findings. Vibration perception has also been demonstrated in Brachyura

and Paguridea (Harms, 1929, 1932).

Our knowledge of the role that the statocyst plays in vibration perception was greatly enhanced by the work of Cohen, Katsuki, and Bullock (1953). In monitoring the electrical activity of the statocyst nerve in the spiny lobster, Panulirus argus, they discovered that lightly tapping the table supporting the preparation elicited discrete bursts of neural activity. A similar experiment on the spider crab, Loxorhynchus grandis Stimpson, failed to show any increase in activity when the table was tapped. Hand claps, speech, and tuning forks with frequencies ranging from 128 to 320 Hz failed to elicit a response in either animal. Similarly, no response was evoked by vibrations conducted through the water in which the statocyst preparation was submerged. Tapping metal rods placed within 5 mm of the statocyst aperature and placing tuning forks (128 to 320 Hz) against the wall of the glass container were ineffective. A paddle held close to the statocyst and driven by a phonograph recording head at frequencies ranging from 7 to 1,000 Hz had no effect except at very high intensities between 70 and 120 Hz. The authors came to the conclusion that the statocysts of Panulirus argus and Loxorhynchus grandis are "...apparently not usefully sensitive to sound".

Cohen (1955) monitored the statocyst nerve of the American lobster, Homarus americanus, while tuning forks with a frequency range of 178 to 320 Hz were struck and placed 5 mm from the statocyst aperature. Although he was unable to record any change in neuronal activity in this manner, he was able to elicit a bursting response by tapping on the table supporting the preparation. He concluded: "It appears only high intensity, low frequency vibration such as that carried through

a solid substrate provides an effective stimulation".

Dijkgraaf (1955) carried out an instructive behavioral study on the spiny lobster, Palinurus vulgaris. He described how the stridulatory sound produced by the lobster could be imitated by scraping a fingernail on glass. If this is done in the presence of a lobster, he discovered, a defense reaction is evoked on the first one or two trials. On the third trial the lobster responded with stridulation. Dijkgraaf then removed the statocysts and repeated the experiment. The same results were achieved. This led him to the conclusion that sound perception must be associated with organs other than the statocyst. While Dijkgraaf does not believe that this is exclusively vibration perception, i.e., sensitivity to vibrations reaching the animal through the substrate, he is unable to say whether the phenomenon observed is sound perception, which is defined as the perception of air- or water-borne sounds, or true hearing, which implies organs or sensory endings especially developed for the purpose of sound perception are present.

In 1960 Cohen published a paper describing experiments which were essentially refinements of his earlier work. Instead of monitoring the entire statocyst nerve as he had done previously, he was able to monitor the electrical output of single receptors in the statocyst. He was able to attribute vibrational sensitivity to certain thread hairs.

Laverack (1962) showed in an electrophysiological study that the hair fan organs of the lobster Homarus vulgaris may be considered as receptors of low frequency pressure waves and vibrations in water. The threshold was calculated by dropping a known mass of water from a known height while monitoring the neural activity of the organ. On

this basis the threshold was found to be 0.40 dynes per square centimeter.

Taylor (1967) pointed out another crustacean system that was capable of perceiving vibrations. In his study of the functional properties of the chordotonal organ in the antennal flagellum of the hermit crab, Petrochirus californiensis, he attached a cover slip to the end of a stylus and placed the apparatus 10 mm away from the antenna. A hydraulic system was employed to generate low frequencies, while higher frequencies were supplied by a voice coil and cone from a loud speaker attached to the stylus. The nervous activity was monitored throughout the experiment. He found that in this experiment and in a similar one where the stylus was attached directly to the antenna, there was a response up to 1,000 Hz. This then is a clear case of sound perception and not merely vibration perception.

In a more recent study Taylor (1968) demonstrated another case of sound perception. He monitored spike activity in the circum-esophageal connectives of unrestrained crayfish (Procambarus spiculifer and Oronectes virilis), and demonstrated that an interneuron in each connective and a collateral branch or second interneuron in each contra-lateral connective excited by the homolateral statocyst, antenullar and antennal flagella, were sensitive to water-borne vibrations. Furthermore, the interneurons coded the stimulus, frequency, amplitude, and direction. He also showed that movement of the walking legs in-hibited the response.

Although vibration perception and sound perception have been demonstrated in the aforementioned experiments, true hearing, as previously defined, has not been shown to exist. The reason that true hearing can not be ascribed to any of the crustaceans discussed

is the failure to discover organs or sensory endings especially

developed for the purpose of sound perception. However, the existence

of such organs or sensory endings can not be ruled out on the basis of

the incomplete studies thus far conducted in this area.

METHODS AND EQUIPMENT

Experimental Animal

The animal used in both parts of this study (the examination of sound and vibration perception and the production of sound) was the pink shrimp, Penaeus duorarum Burkenroad. The shrimp varied in size from 14 mm to 20 mm (carapace length), and were obtained from local bait fishermen. The animals were held in two 30 gallon aquaria supplied with running sea water and fed finely chopped mullet and squid. They can be kept for several weeks in this manner with a low mortality rate.

The shrimp populations from which the experimental animals were obtained contain both Penaeus duorarum and Penaeus brasiliensis. Occasional strays of Penaeus aztecus have been reported, but this species is so uncommon in Biscayne Bay that it is of no concern. Penaeus duorarum is always the numerically dominant species, but Penaeus brasiliensis can comprise up to 41% of the population in mid summer (Saloman, et al, 1968). Fortunately, from November to May the percentage of Penaeus brasiliensis falls to about 2%. For this reason the majority of the experiments were conducted with shrimp collected during those months when Penaeus brasiliensis is virtually absent.

After each experiment the shrimp were sacrificed and the species composition determined. If contamination by Penaeus brasiliensis exceeded 5%, the results were discarded and the experiment was repeated. This occurred only once, after a trial of the preliminary experiment.

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It is doubtful whether the results of this study would have been appreciably changed even if there had been considerable contamination by _Penaeus brasiliensis_ because of the great similarity of the two species from the standpoint of morphology, behavior, and physiology.

Experiment 1: Preliminary Study

Objective

The purpose of the preliminary study was to determine whether the pink shrimp displays any overt deviations in its behavioral pattern upon the introduction of sound waves at various frequencies and amplitudes. In order to detect any behavioral anomalies, it was first necessary for the author to observe the normal regimen of the shrimp for several weeks prior to the onset of this experiment.

Equipment

The experimental tank used in the initial phase of this study was a 20 gallon aquarium 35 cm wide, 75 cm long, and 35 cm deep, and was constructed of glass with a stainless steel frame. It had a 5 cm calcareous sand substrate and was supplied with running sea water. A 25 watt red lamp was mounted one meter above the tank for nighttime observations. A red bulb was chosen because shrimp are relatively insensitive to this color.

The sound-producing apparatus was mounted 20 cm above the water surface. It consisted of an 8 inch Olson high fidelity loudspeaker (model S-783) with a frequency response of 40 Hz to 18,000 Hz. The signal was produced by a Heathkit sine wave generator (model IG-82),

and amplified by a 2 watt linear amplifier (Saxton Products, model
MA-106).

The circuit was activated by closing a micro-switch, which in
turn closed a photo-switch. The photo-switch consisted of an incan-
descent lamp and a photosensitive resistor sealed in an aluminum
housing. The sound-producing circuit is shown in figure 1.

Methods

A total of 40 shrimp were tested during the preliminary study--
20 during the day and 20 at night. Ten frequencies (40 Hz, 100 Hz,
500 Hz, 1 KHz, 3 KHz, 5 KHz, 7KHz, 10 KHz, 14KHz, and 18 KHz) were
arbitrarily selected. Two shrimp were exposed, one at a time, to
each frequency. The amplitude was the maximum capable of being
delivered by the system without audible distortion. Since the in-
vestigator was unable to hear sound produced at 18 KHz, the amplitude
control was left at the same setting that had been used at 14 KHz.
The duration of the tones, which were not closely controlled in this
preliminary study, varied from approximately 0.5 to 5 seconds.

It should be noted that the sound was initially monitored with
a hydrophone, and it was established that at all frequencies and
amplitudes employed, the sound level was well above the ambient noise
levels.

Each shrimp was exposed to approximately 15 bursts of sound
randomly spaced over 10 minutes. Any behavioral anomalies were noted.
After a shrimp had been tested it was removed to one of the holding
tanks and a new shrimp was placed in the experimental tank. The second
shrimp underwent the same treatment at the same frequency as the first
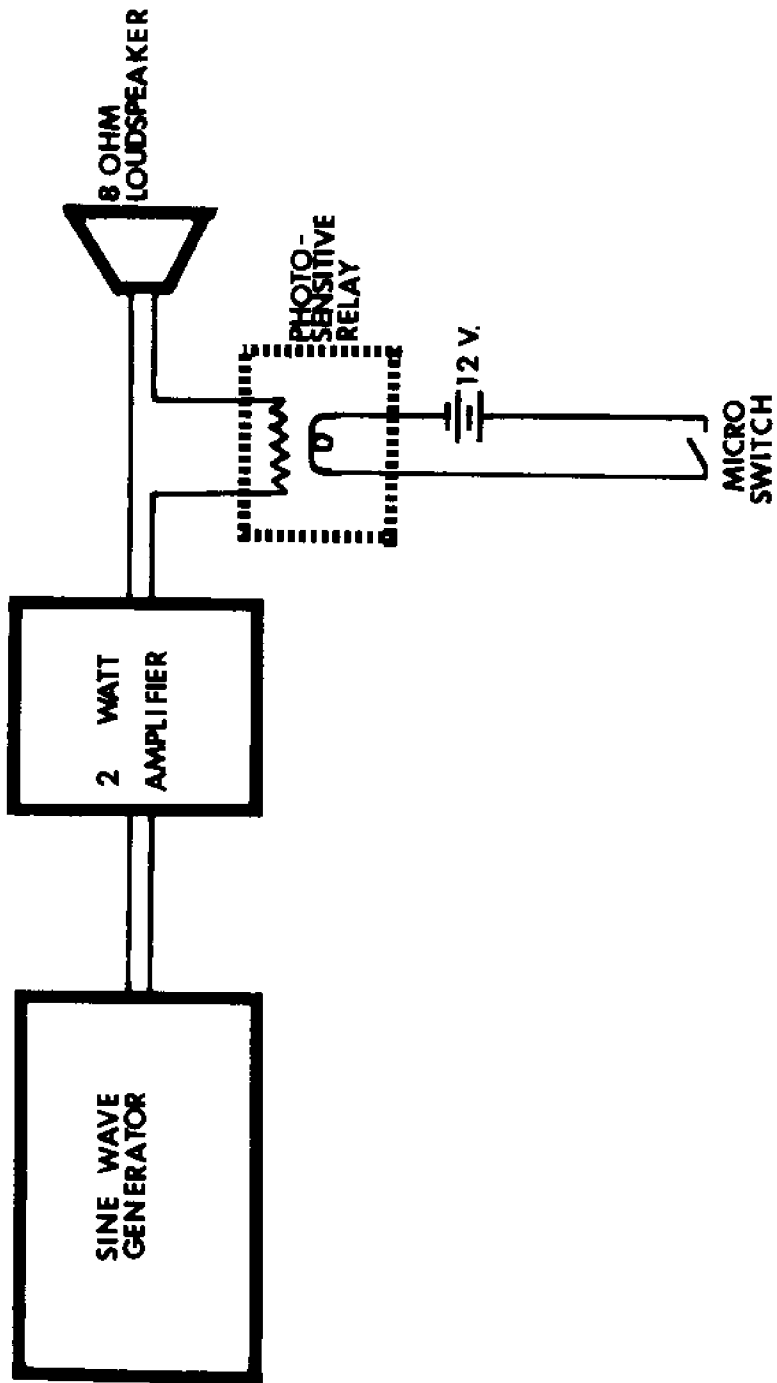
Figure 1. Circuit diagram of the apparatus used in the preliminary study.

one. After 2 shrimp had been tested at a specific frequency, the frequency was changed and 2 more shrimp were observed until 2 shrimp had been observed at each of the frequencies. This experiment was performed once during the day and once at night. The test schedule appears in table 1.

Experiment 2: Conditioning with the Shrimp in Contact with the Substrate

Objective

Successful conditioning at a particular frequency would indicate that perception is occurring. The purpose of this experiment was to determine at which sound frequencies it is possible to condition the shrimp. However, this experiment was not able to distinguish between perception of water-borne sounds and substrate vibrations.

Equipment

The conditioning apparatus consisted of a micro-switch which activated a double pole-double throw 24 volt relay. This relay, in turn, closed 2 loops. One was to a time delay relay adjusted to close 0.5 second after being activated; the other was to a photo-conductive switch. When the double pole-double throw relay closed, the photoconductive switch was activated. This completed the sound-producing circuit, which was identical to that used in the preliminary study, i.e., an 8 inch loudspeaker, a sine wave generator, and a 2 watt linear amplifier. The time delay relay was simultaneously activated with the sound-producing loop; 0.5 second later the time

Table 1. The test schedule for Experiment I (The Prelim-
inary Study). Each box represents one test
animal. The number within the box indicates
the number of times the animal was exposed to
the indicated frequency over a 15 minute interval.

	A.M.		P.M.	
40 Hz	14	15	15	15
100 Hz	15	15	13	15
500 Hz	15	12	15	15
1,000 Hz	13	15	15	12
3,000 Hz	15	15	15	15
5,000 Hz	14	13	15	14
7,000 Hz	15	14	15	15
10,000 Hz	15	15	14	15
14,000 Hz	12	15	15	13
18,000 Hz	15	14	15	15

delay relay closed the shocking circuit, which consisted of 2
stainless steel electrodes measuring 15 cm by 20 cm, a 110 volt to
12 volt step-down transformer, and a variac. The conditioning
circuit is illustrated in figure 2.

The electrodes were placed 25 cm apart in a 20 gallon aquarium.
The shrimp were confined to the area between the electrodes by a
series of plastic lattices. The experimental tank is illustrated in
figure 3.

Methods

A shrimp was placed in the enclosed area of the experimental
tank, after which the desired amplitude and frequency were set on the
sine wave generator. The microswitch was then closed. This in
turn closed the double pole-double throw relay which completes both
loops. The sound-producing loop is activated immediately, but the
time delay relay in the shocking circuit prevents the animal from
receiving the shock until 0.5 second after the initiation of the sound.
As soon as the shocking circuit was activated, the microswitch was
released. This constituted one pairing of the unconditioned stimulus
(the electric shock) and the conditioned stimulus (the sound). The
series of events experienced by the shrimp is illustrated in figure 4.
Forty such pairings were randomly spaced over approximately 15 minutes,
after which the shocking circuit was turned off. The conditioned
stimulus (sound) was then presented and the shrimp's reaction noted.
Ten additional pairings of the unconditioned stimulus and the con-
ditioned stimulus were then presented over the next 5 minutes, after
which the sound was again presented alone, and the shrimp's behavior
noted.

STAINLESS STEEL ELECTRODES

8 OHM LOUDSPEAKER

VARIABLE POWER SUPPLY

TIME DELAY RELAY

2 WATT AMPLIFIER

PHOTO-SENSITIVE RELAY

SINE WAVE GENERATOR

12 V.
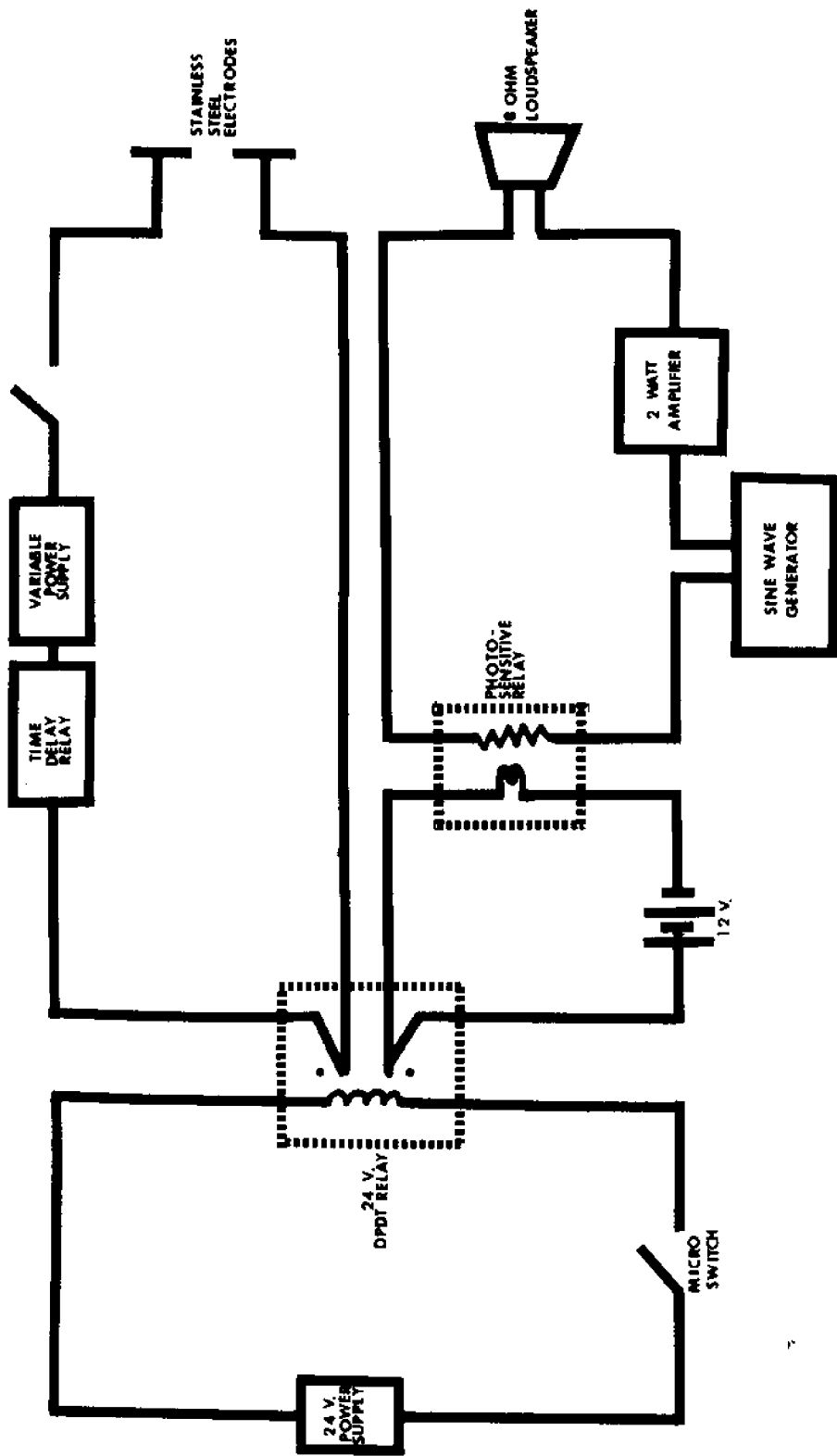
DPDT 24 V. RELAY

MICRO SWITCH

24 V. POWER SUPPLY

Figure 2. Circuit diagram of the conditioning apparatus.

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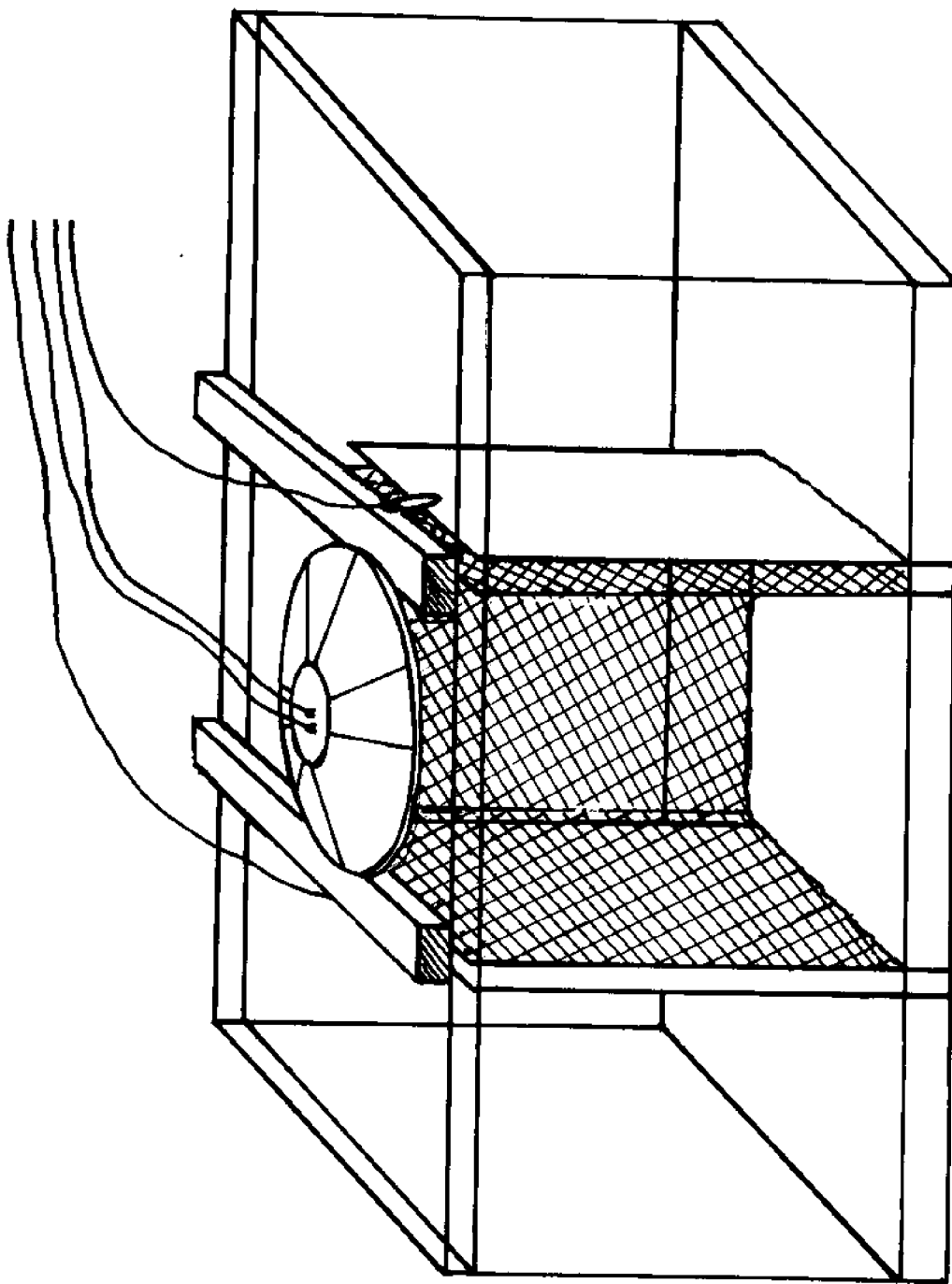
Figure 3. Experimental tank for the conditioning experiments.
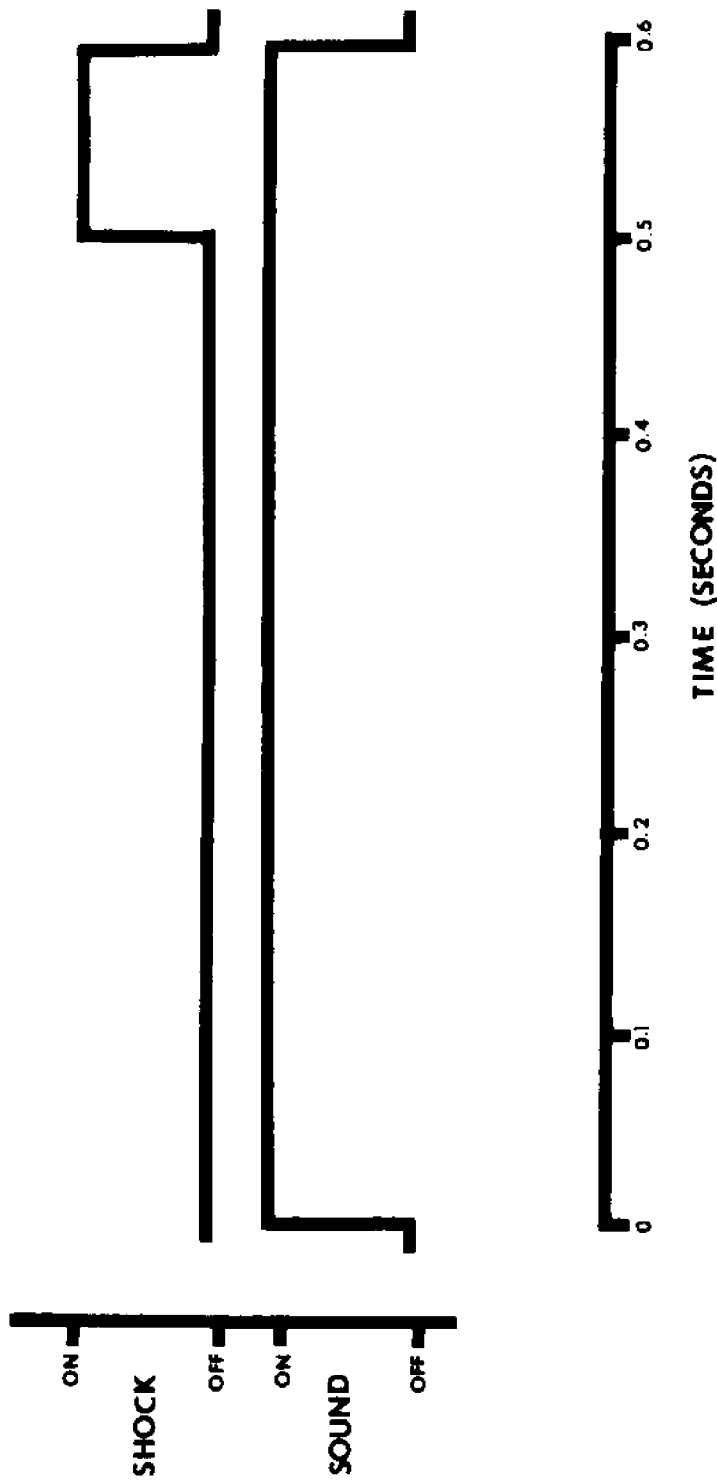
Figure 4. The sequence of events experienced by each shrimp during the conditioning experiments.

The shocking voltage had to be constantly varied during the experiment. The minimum voltage necessary to elicit the unconditioned response, an abdominal flexure, varied from 0.5 volts to 2.0 volts and was dependent on two factors: the size of the shrimp and the orientation of the shrimp in reference to the electrodes. Large shrimp oriented perpendicular to the electrodes required the minimum voltage, while small shrimp oriented parallel to the electrodes required the maximum voltage. The variac setting had to be adjusted each time a shrimp changed its position.

Conditioning was attempted at 40 Hz, 100 Hz, 125 Hz, 150 Hz, 200 Hz, 500 Hz, 1 KHz, 3 KHz, 7 KHz, 10 KHz, 13 KHz, and 18 KHz. Initially 3 shrimp were used at each of these frequencies, but subsequently, 2 additional shrimp were tested at 40 Hz, 100 Hz, 125 Hz, and 150 Hz. The amplitude at each frequency was again set at the maximum the system was capable of delivering without noticeable distortion.

Experiment 3: Conditioning with the Shrimp Suspended Above the Substrate

Objective

The purpose of this experiment was to determine whether the shrimp could be successfully conditioned while suspended above the substrate. This would clarify whether perception of water-borne sounds was occurring or whether only substrate vibrations were being detected.

Equipment

The apparatus used in this experiment was the same as that for the previous one, with a single modification: a small net of the type used by tropical fish hobbyists was suspended above the substrate. A piece of wire screening was fastened over the mouth of the net in such a way that the investigator could easily open and close it.

Methods

The procedure was the same as that described in the previous conditioning experiment, with the exception that each shrimp was suspended in the net within the test area rather than being allowed to rest on the substrate.

Conditioning was attempted on 5 shrimp at each of the following frequencies: 40 Hz, 100 Hz, 125 Hz. Again the amplitude was maximal.

Experiment 4: Conditioning to Establish Thresholds

Objective

The objective of this experiment was to determine the thresholds of the pink shrimp to substrate vibrations.

Equipment

The apparatus used was the same as the initial conditioning experiment, with the addition of a device capable of measuring the substrate velocity. It consisted of a seismic detector (Geo Space Corporation, type HS-J) buried in the substrate in the test area. This was connected to a Tektronix low level preamplifier (type 122). The remainder of the circuit was comprised of a Krohn-Hite variable

band pass filter (model 330M), and a Tektronix type 502 dual beam oscilloscope. The preamplifier was powered by a type 125 Tektronix power supply. The detection apparatus is illustrated in figure 5.

Methods

Conditioning was attempted at 40 Hz, 100 Hz, and 125 Hz in the same manner described in the previous sections. It should be noted that the shrimp were permitted to come into contact with the substrate in this experiment.

There were 10 unit settings on the fine control of the amplitude adjustment control. The amplitude was set one half unit lower than the setting used in the previous conditioning experiments, i.e., one half unit below the maximum distortion free amplitude. Conditioning was attempted on 3 shrimp at each of the indicated frequencies. If conditioning was successful at a particular frequency and amplitude on any of the 3 shrimp, the amplitude was lowered another one half unit, and conditioning was attempted on 3 additional shrimp. The experiment was terminated at each frequency when none of the 3 shrimp could be successfully conditioned. The unit readings on the amplitude adjustment were converted into more meaningful substrate velocities with the seismic detector and its associated instrumentation.

Experiment 5: The Effect of Sound on an Aspect of Behavior

Objective

The purpose of this experiment was to determine whether the apparent increase in the antennule flicking rate of the shrimp at

Figure 5. Block diagram of the apparatus used to measure substrate velocity.

POWER SUPPLY

LOW LEVEL
PREAMPLIFIER

SEISMIC
DETECTOR

VARIABLE
BAND PASS
FILTER

OSCILLOSCOPE
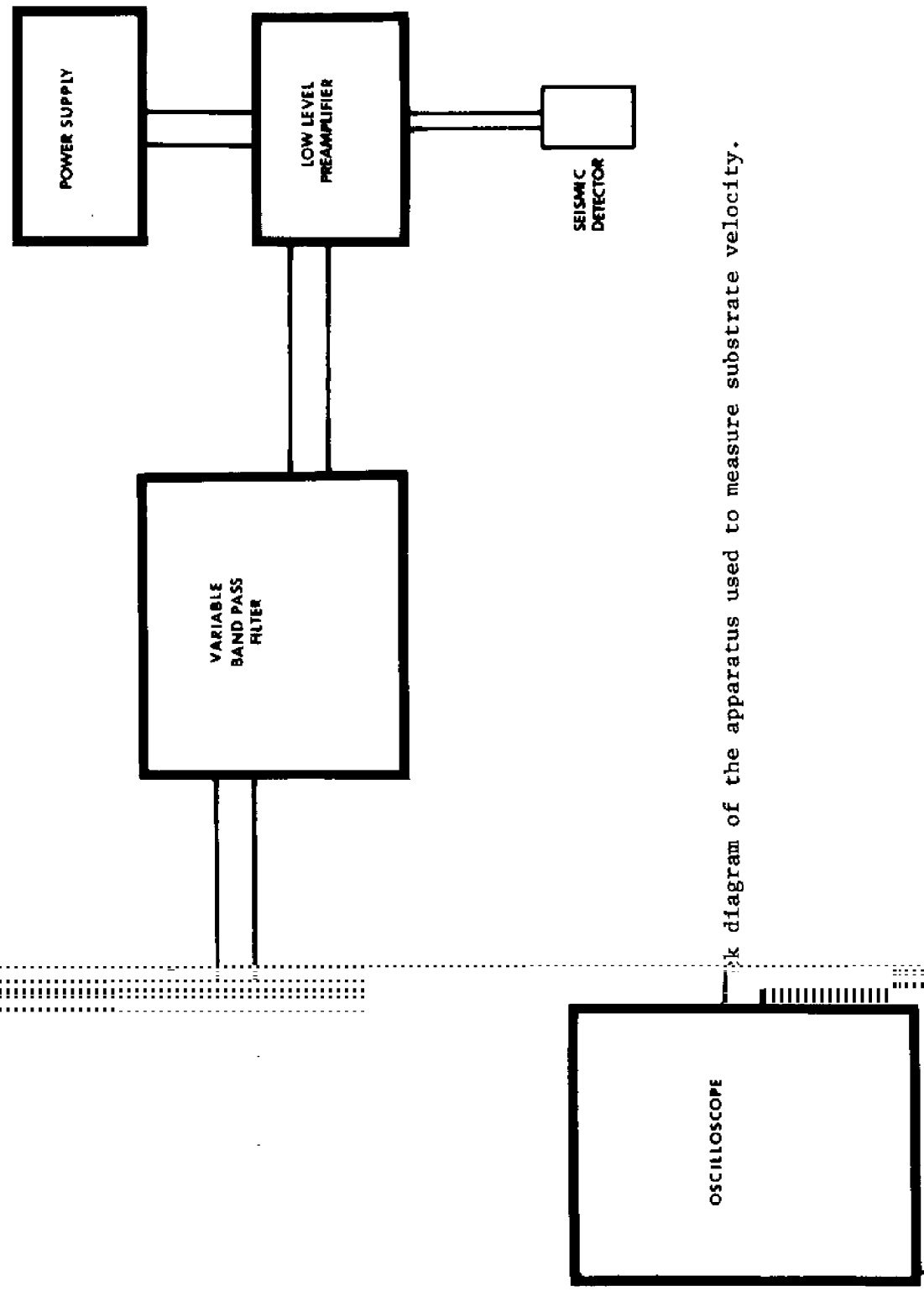
certain frequencies (see "Results of Preliminary Study") was statistically significant.

Equipment

In this experiment the experiment tank consisted of a 4-liter beaker with a 5 cm calcareous sand substrate. At the start of each session, 2.5 liters of sea water were added to the beaker. A screen was kept over the beaker during the experiment to prevent the shrimp from escaping.

The sound-producing apparatus was the same one used in the preliminary study.

Methods

A shrimp was placed in the beaker, and after it was quietly resting on the substrate (this usually occurred after approximately 10 minutes), a tone was played for 10 seconds. During this 10 second period the number of times the shrimp flicked its antennules was recorded. The shrimp was then removed and another one introduced into the beaker. Ten shrimp were observed at each of the following frequencies: 40 Hz, 100 Hz, 150 Hz, 500 Hz, 1 KHz, 2 KHz, 4 KHz, 8 KHz, and 16 KHz. The volume in this experiment was again maximal.

In addition to the 10 shrimp at each of the frequencies mentioned above, a control group of 10 shrimp was used. The control group was handled in the same manner as the experimental groups, with the exception that after the controls were resting on the substrate they were observed for 10 seconds, and the number of times they flicked their antennules with no sound being played was recorded.

Experiment 6:   Sound Monitoring

Objectives

The purpose of this experiment was to determine whether the pink shrimp produced any sounds other than those caused by its disturbing the environment as it moved about.

Equipment

The sound monitoring experiment was carried out in a 20 gallon aquarium with a 5 cm calcareous sand substrate. An egg-type hydrophone was suspended approximately 1 cm above the substrate. A small solid state, battery-powered amplifier provided sufficient gain for the signal to be monitored with headphones. The entire monitoring apparatus was manufactured by Oceanetics, Inc.

Methods

Ten shrimp were placed in the experimental tank and monitored on 3 consecutive days for a period of 1 hour each day. During these periods food was introduced in the vicinity of the hydrophone. The shrimp were also stimulated to move rapidly about by gently prodding them with a net handle. This procedure was repeated on 3 consecutive nights.

A second experiment consisted of keeping a single shrimp in the experimental tank for several days and then introducing a second shrimp while monitoring.

RESULTS

As a result of this study it appears that pink shrimp do not react to water-borne sounds at the frequencies and amplitudes tested. There was a slight detectable reaction to vibrations through the substrate at low frequencies. This was manifested by slight antennule flicking. To determine if the shrimp were detecting these stimuli without exhibiting this by body movements, conditioning experiments were conducted. One of these confirmed that perception was occurring at low frequencies. The second series of conditioning experiments revealed that the stimuli were apparently borne through the substrate and not through the water.

The shrimp made no sounds in the range monitored. The only sounds which were detected were those from the animal disturbing its environment as it moved about.

Results of the Preliminary Study

During the preliminary study only one unique behavioral pattern was observed, and this occurred at only two frequencies. It consisted of an increased rate of antennule flicking upon introduction of sound at 40 Hz and 100 Hz. This phenomenon was observed both during the day and at night.

Antennule flicking occurs periodically whether or not sound is introduced. The rate of change of antennule flicking caused the author to incorporate the section of this study entitled "The Effect of Sound on an Aspect of Behavior". The data in that section lends

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itself to statistical analysis and is, in effect, a quantitative

extension of this preliminary study.

Certain movements of the shrimp, both during the day and at night,

occasionally seemed to correspond to the onset of sounds at various

frequencies, but these were not consistent and are regarded as random

movements of the animal that happen to coincide with the onset of the

tonal burst. The increase in the antennule flicking rate at 40 Hz and

100 Hz was the only consistent response observed.

Results of Conditioning: Shrimp in Contact With the Substrate

After 40 and 50 pairings of the unconditioned stimulus (the electric

shock) and the conditioned stimulus, the responses of sound were tested.

The shrimp's response was rated as "positive" if conditioning had

clearly occurred, "negative" if it clearly had not occurred, "ques-

tionable (positive)" if conditioning appeared to have occurred but

the response was weak or aberrant in some way, or "questionable

(negative)" if the response was so weak that it was possibly a

coincidental motion of the animal and not a conditioned response.

The last two categories are clearly subjective judgments of the

observer. Fortunately, it was necessary to categorize only 5 of 47

shrimps' responses as either "questionable (positive)" or "ques-

tionable (negative)".

No shrimp were successfully conditioned at 150 Hz, 200 Hz, 500 Hz,

1 KHz, 3 KHz, 5 KHz, 7 KHz, 10 KHz, 12 KHz, or 18 KHz. At 125 Hz, 2 of the

5 shrimp were rated as "questionable (negative)", 1 as "questionable

(positive)", and 2 as "positive". The results at 100 Hz were the

same as those at 40 Hz: one "negative", one "questionable (positive)",

and three "positive". A summary of these results appears in figure
6.

Results of Conditioning: Shrimp Suspended Above the Substrate

No successful conditioning was achieved in this phase of the
experiment. All 15 of the shrimp were rated as "negative" after
testing.

Results of Conditioning to Establish Thresholds

The thresholds at 40 Hz (in terms of substrate velocity) were
found to lie between 0.041 inches per second and 0.035 inches per
second. At 100 Hz the thresholds were between 0.041 inches per second
and 0.032 inches per second, and at 125 Hz they were found to lie
between 0.039 inches per second and 0.036 inches per second. The
results appear in table 2.

Effect of Sound on an Aspect of Behavior

The antennule flicking rates observed appear in table 3. These
data were subjected to an analysis of variance and a calculated F
value of 16.11 was found. Since this calculated value exceeds the
tabular value of 2.62 interpolated from table A.6 in Steel and Torrie
(1960), it can be stated that there is a real difference among
treatment means.

To compare the treatment means with the control, Dunnett's pro-
cedure was followed (Steel and Torrie, 1960). The significant
difference, d' at an error rate of 0.01 was calculated to be 1.34.
The only means that can be declared significantly different from the
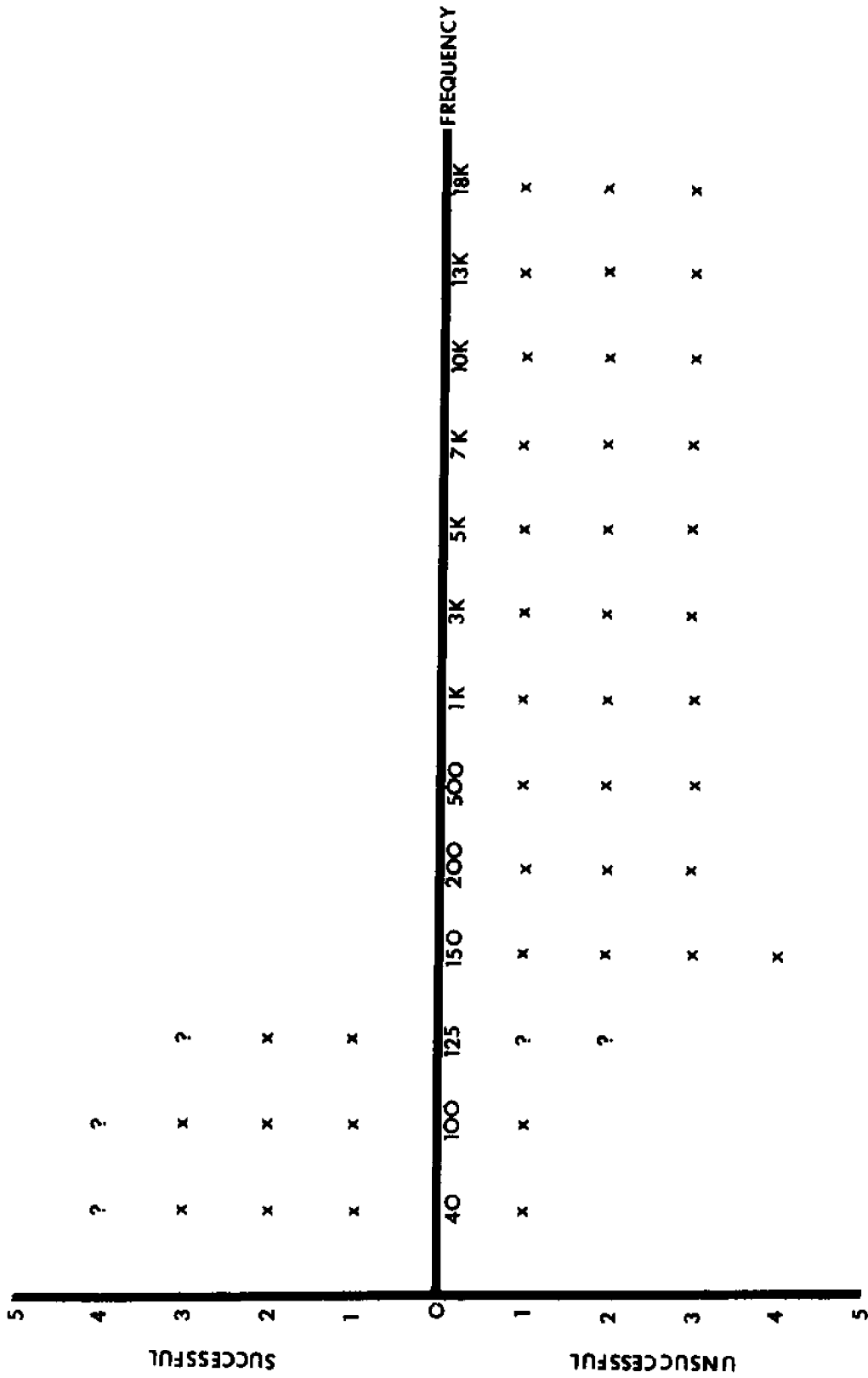
Figure 6. Results of the conditioning experiment with the shrimp in contact with the substrate (Experiment 2).

Table 2. The results of Experiment 4 (Conditioning to Establish
Thresholds). The number of shrimp (out of 3 attempts)
successfully conditioned at the indicated frequency
and substrate velocity.

Frequency	Substrate Velocity (inches/second)	No. of Shrimp (out of 3) Successfully Conditioned
40 Hz	0.049	2
	0.045	3
	0.041	2
	0.035	0
	0.032	0
100 Hz	0.048	3
	0.044	2
	0.041	1
	0.032	0
	0.029	0
125 Hz	0.048	2
	0.045	1
	0.041	1
	0.039	1
	0.036	0
	0.034	0

Table 3. The statistical analysis (ANOV and Dunnett's Test) of the data from Experiment 5 (The Effect of Sound on an Aspect of Behavior). Each box represents the number of times each shrimp flicked its antennule during a 10 second esposure to sound of the indicated frequency.

	FREQUENCY								
0	40	100	150	500	1K	2K	4K	8K	16K
0	4	2	1	0	1	0	0	1	0
0	2	3	0	0	0	0	1	0	0
1	3	4	0	0	0	0	0	0	0
0	2	2	1	1	0	1	1	0	1
0	1	1	0	0	0	1	0	0	0
0	4	3	0	0	0	0	0	0	1
0	4	3	0	0	1	0	0	1	0
1	3	0	2	1	0	0	0	0	0
0	3	0	0	0	0	0	1	1	0
0	2	1	1	1	0	0	0	0	0
2	25	22	5	3	2	2	2	3	1
2	79	62	7	3	2	2	2	3	1
C	0.4	62.5	48.4	2.5	0.9	0.4	0.4	0.4	0.9	0.1
SS	1.6	16.5	13.6	4.5	2.1	1.6	1.6	1.6	2.1	0.9
$\bar{x}$	0.2	2.5	2.2	0.5	0.3	0.2	0.2	0.2	0.3	0.1

C = 43.56

Source	SS	DF	MS	F
Column	73.09	9	8.12	16.11
Error	45.40	90	0.504	
Total	118.5	99		

Dunnett's Test:
t (Dunnett, one tail) = 3.09
d' = 3.09 2(.504)/9 = 1.34

control are 40 Hz and 100 Hz.

Results of Monitoring for Sound

The only sounds produced by the shrimp that could be detected were those caused by the disturbance of sand grains as the shrimp moved about on the substrate. No feeding noises were detected upon introduction of food.

In the second experiment, where a second shrimp was introduced to the experimental area after the first shrimp had been living there for several days, no detectable sound production was elicited other than the moving about of sand grains.

DISCUSSION

The results of the preliminary study indicated that perception of
sound or substrate vibrations by the shrimp was probably occurring at
low frequencies (40 Hz to 125 Hz) and high amplitudes. The fact that
there were no responses to high frequencies, or to lower amplitudes at
the lower frequencies, does not eliminate the possibility that per-
ception was occurring since failure to respond can not be construed
as evidence for a lack of perception. Even the positive results had
to be carefully weighed because they were based solely on subjective
observations, and the possibility of bias had to be considered.

It was hoped that the conditioning experiments would eliminate
any purely subjective judgments, but as the results indicate, while
there was a significant reduction in the number of these judgments
required, they were not eliminated. The results of the preliminary
study, taken in conjunction with those of the initial conditioning
experiments, permit it to be stated with a fairly high degree of
certainty that some form of perception occurs below 125 Hz and down
to at least 40 Hz.

It then became necessary to determine, if possible, what type
of perception was occurring. The definitions offered by Cohen and
Dijkgraaf (1961) of the various types of perception that may have
been occurring were followed. They attributed hearing to animals
which are: 1) sensitive to air- or water-borne sounds, and 2) capable
of detecting sounds with receptors or sensory endings developed

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primarily for this purpose. If the second requirement is not fulfilled, the phenomenon is referred to as sound perception. If the animal is sensitive only to vibrations reaching it through the solid substrate, the term vibration perception is then employed.

The purpose of the conditioning experiment, in which the shrimp were suspended above the substrate, was to determine whether the animals were detecting the low frequency waves through the water or through the substrate. The failure to condition any of the suspended shrimp at the same frequencies which had been successful when the shrimp were allowed to come into contact with the substrate provided an indication that vibration perception rather than sound perception or hearing was occurring.

These results lead one to speculate as to which organ or organs are responsible for this vibrational sensitivity. Undoubtedly the best studied decapod organ has been the statocyst. Although none of the studies has dealt with the statocyst in _Penaeus duorarum_, the similarity of this organ throughout most of the order permits one to extend the results of these studies on other species to the pink shrimp with a fair degree of certainty. On the basis of the electro-physiological work carried out by Cohen (1960) on the statocyst of _Homarus americanus_, it seems likely that this organ plays at least some role in the reception of vibrations. The apparent necessity of _Penaeus duorarum_ to be in contact with the substrate in order to perceive sounds indicates that the vibrations are probably conducted through the exoskeleton, moving the animal relative to the statolith. This movement would then be detected by the thread hairs causing an initiation of impulses in the afferent neurons.

It would seem that while the pink shrimp is above the substrate,
vibrations of sufficient magnitude and of the proper frequencies might
cause movement of the statolith relative to the statocyst, thereby
stimulating the thread hairs and bringing about the same results as
when vibrations reach the animal through the substrate. But such
behavior was not observed. Perhaps they physical composition of the
statolith, sand grains held together by glandular secretions from the
cyst wall, is such that it does not couple well with water-borne
vibrations. It is possible, of course, that such a phenomenon might
occur outside of the range of frequencies employed in this study, i.e.,
below 40 Hz or above 16,000 Hz.

If it is assumed that the statocyst is at least partially responsible
for vibrational sensitivity, an interesting observation can be made that
while the animal is in the water column the statocyst is apparently
incapable of vibration perception. While this may be due to poor
coupling of water-borne vibrations with the statolith, it may also be
due to the reverse--poor coupling with the exoskeleton. A third
possibility is that both the exoskeleton and the statolith are coupling
with the water-borne vibrations but are in phase, and therefore there
would be no relative motion. Whichever is the case, the result is
~~physiologically advantageous to the animal, while the interpretation online the~~
~~primary function of the statocyst is to supply information regarding~~
spatial orientation and angular acceleration. Cohen (1960) has shown
that it is the thread hairs that play the key role in the detection
of angular acceleration. If water-borne vibrations were capable of
causing relative movement between the statolith and the statocyst,
the animal would not be able to differentiate between sound perception

and angular acceleration of its body. The neural output from the thread hairs would in some instances be indistinguishable, thus rendering the statocyst useless as an accelerometer.

It would seem, however, that the capability of perceiving vibration played no role in the evolution of the statocyst. Its sensitivity to vibration is apparently not adequate to supply any selective advantage. It appears more likely that substrate vibrations of high amplitude simply are a form of "static" which can occur only when the animal is in contact with the substrate.

It is doubtful that the statocyst is the sole receptive organ of substrate vibrations. This is pointed out in the studies conducted by Prentiss (1901) and Dijkgraaf (1955). These experiments involved studying vibrational sensitivity before and after statocysts had been extirpated. Although sensitivity seemed to decrease, it was not eliminated. It is obvious that other receptors are involved.

Vibrational sensitivity has been reported for a number of crustacean organs other than the statocyst. These include chordotonal organs, hair fan organs, and several proprioceptive organs (Burke, 1954; Laverack, 1962; Taylor, 1967). Young (1959) conducted a comprehensive anatomical study of the white shrimp, Penaeus setiferus. However, the lack of any complimentary physiological investigations makes it difficult in many instances to associate structure with function. There is an even greater scarcity of information with regard to Penaeus duorarum where even a detailed anatomical study is lacking. But it seems improbable that any organ will be discovered which is used exclusively for vibration perception. The high thresholds found in this study seem to indicate that vibration perception

is occurring through sensory modalities which have evolved for purposes other than this. The statement made earlier that the relative insensitivity of the statocyst to vibration would supply no selective advantage holds true of other organs.

Although the conditioning experiments greatly reduced the number of subjective judgments required of the observer, it was felt that an experiment which required no such judgments and which lent itself to statistical analysis would be advantageous in increasing the confidence in the preliminary study and conditioning experiments. It was also of interest from the methodological point of view. For these reasons the experiment involving the antennule flicking·rate was undertaken. The observer was required only to count the number of times a shrimp flicked its antennule in a given time period. The results confirmed those of the earlier experiments. It is possible to state on the basis of the statistical analysis of the data and with an error rate of 0.01, that perception is occurring between 40 Hz and 100 Hz. In view of the results of these experiments, which indicate a complete lack of sensitivity to water-borne sounds and only limited sensitivity to substrate vibrations, it is not entirely surprising that sound production in the same range of frequencies (40 Hz to 16,000 Hz) was not detected. Although it is obvious that if sound receptors are not present in a species, sound production would be of no value in such functions as intra-specific territorial warnings or reproductive behavior, this fact has largely been ignored by investigators working with sonant crustaceans. This author is not aware of a single study in which considerable biological significance has been attached to sound production in crustaceans that·has even briefly

mentioned the animal's capabilities of perceiving these sounds. Generally, the unwarranted assumption is made that receptive capabilities exist. A small number of authors have stated that sound production in certain species may not have any biological significance and is merely coincidental to other functions. This may prove to be the case with a number of the species in which considerable significance has been attached to sound production.

It is conceivable that a species lacking appropriate receptors may still have evolved a sound producing mechanism if it provided a selective advantage. This advantage would be supplied if the sound could be successfully employed in a territorial warning directed towards species that have sound-sensing capabilities. It is also possible that a separate function may have evolved which coincidentally produces sound when it operates. This may be the case with the snapping shrimp, although there is considerable controversy regarding it. It is unlikely, however, that either of these two situations is applicable to the pink shrimp. It does not exhibit a strong territorial behavior; this is due in part to the significant percentage of its life spent moving about. Most of the sound-producing crustaceans tend to occupy permanent or semi-permanent dwellings whereas the pink shrimp merely buries itself in the substrate and builds no structure that is used more than once.

Although it seems safe to rule out sound production by the pink shrimp between 40 Hz and 16,000 Hz, the same can not be said of frequencies beyond 16,000 Hz. Equipment was not available for monitoring these higher frequencies, but in light of the findings of Johnson et al. (1947) who showed considerable production of sound in

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these regions by the snapping shrimp, such an investigation should be undertaken. It is possible that sound may be caused by friction between various parts of the exoskeleton.

A basic aim of this study was to investigate the possibility of applying the results to the valuable pink shrimp fishery. It was hoped that sound might be used as a confusion factor to reduce avoidance of the electric trawl by the shrimp. The complete lack of sensitivity to sound and the relative insensitivity to vibrations make this idea untenable. However, the basic concept of a confusion factor should not be abandoned. Other sensory systems, especially vision, may prove to be susceptible to such a factor.

On the basis of this research, it would appear that the concept of locating populations of the pink shrimp by their characteristic sounds must be deemed unfeasible. This application should not be ruled out, however, until the suggested study of sound production in the ultrasonic range is completed.

SUMMARY

This investigation attempted to determine the sensitivity of the pink shrimp, Penaeus durorarum Burkenroad, to sound and vibration. Experiments were also undertaken to determine if this species produces sound in the audio range (40 Hz to 18,000 Hz).

A preliminary study indicated that perception of high amplitude sounds or vibrations may occur at low frequencies. A subsequent experiment, in which 47 shrimp were conditioned using sound as the conditioned stimulus and an electric shock as the unconditioned stimulus, indicated that sound or vibration perception was occurring between 40 Hz and 125 Hz. Perception below 40 Hz and above 18 KHz was not tested due to instrumental limitations.

In the initial conditioning experiments the shrimp rested on the substrate. A second conditioning experiment was conducted with the shrimp suspended above the substrate. Frequencies between 40 Hz and 150 Hz were used. Lack of successful conditioning indicated that perception occurs through the substrate rather than the water. This is indicative of vibration perception rather than sound perception.

A third conditioning experiment employing decreasing amplitudes at 40 Hz, 100 Hz, and 125 Hz was carried out to determine thresholds in terms of substrate velocities. At 40 Hz the threshold was found to lie between 0.035 inches per second an 0.041 inches per second, while at 100 Hz it lies between 0.032 inches per second and 0.041 inches per second. At 125 Hz the threshold was found to lie between 0.036 inches per second and 0.039 inches per second. The thresholds

appeared to be essentially flat in terms of velocity versus frequency.

A statistical analysis of the antennule flicking rate confirmed the results of the conditioning experiments at 40 Hz and 100 Hz. There was a discrepancy between the two approaches at 125 Hz. The conditioning experiment seemed to indicate that perception was occurring at 125 Hz, but the statistical analysis of the antennule flicking rate did not confirm this. The error rate in the statistical analysis was 0.01.

The pink shrimp apparently does not produce sound of a significant amplitude in the audio range. It is possible that sound production is occurring below 40 Hz and above 16,000 Hz. These frequency ranges were not examined.

The author recommended that other sensory modalities be investigated for use as a confusion factor in the fishery. Energy requirements to produce suitable substrate vibrational levels would be prohibitive. It was also recommended that sound production in the ultrasonic range be investigated.

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