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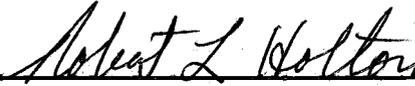
Marilyn P. Guin for the degree of Master of Science

in Oceanography presented on August 25, 1977

Title: THE ROLE OF STRIDULATION IN THE BEHAVIOR OF THE SHORE

CRAB HEMIGRAPSUS OREGONENSIS

Abstract Approved:



Robert Holton

• The claw shuddering display of the shore crab Hemigrapsus oregonensis was explored with acoustic and behavioral observations. Male H. oregonensis stridulate during claw shuddering display. The stridulatory apparatus is present only on the males. The acoustic signal was of brief duration, showed a general pattern of sound bursts, but varied among individual crabs. The larger crabs produced more intense signals. Because H. oregonensis live in a turbid water of a mud-rock habitat or in burrows of the estuary, acoustic communication is well suited to their environment.

Behavioral observations of H. oregonensis, collected from Yaquina Bay, Oregon, were made in habitat replicas of the mud-rock environment. Stridulation by male crabs was elicited equally by male and female crabs but the amount of stridulation increased when all the crabs were males. The stridulating crab was typically maintaining a territory and did not retreat after signaling. The significance of stridulation in the total repertoire has not been resolved but territoriality as exemplified by

burrow defense and communication facilitating ritualization have been indicated, and its importance in sexual behavior has not been demonstrated.

THE ROLE OF STRIDULATION IN THE BEHAVIOR OF THE
SHORE CRAB HEMIGRAPSUS OREGONENSIS

by
Marilyn P. Guin

A THESIS
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degree of

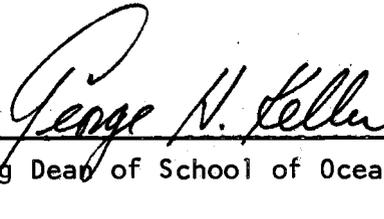
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THE ROLE OF STRIDULATION IN THE BEHAVIOR OF THE
SHORE CRAB HEMIGRAPSPUS OREGONENSIS

INTRODUCTION

The objective of this study was to explore the claw shuddering display of Hemigrapsus oregonensis. In this display the crab extends the chelipeds forward and with claws extended and together moves the chelipeds rapidly apart with a shuddering motion (Symons, 1970). The display is distinct from other displays given by the crab and is confined to males. Specific tasks leading toward this objective were to determine if claw shuddering was a stridulatory behavior, to investigate the qualities of the sounds that might be produced, to describe the behavioral context, and to interpret the ethological significance of the claw shuddering behavior. Two introductory sections provide summaries of: 1) Natural History and Behavior of Hemigrapsus oregonensis and 2) Stridulation in Crustaceans.

Natural History and Behavior of Hemigrapsus oregonensis

Hemigrapsus oregonensis, the yellow shore crab, has a range which extends from Alaska to the Gulf of California along the Pacific Coast of North America (Rathbun, 1918). H. oregonensis occurs intertidally in mud-rock substrate (Hiatt, 1948), and subtidally in estuarine channels and oyster bars (Dimick, Eglund and Long, 1941). Their intertidal abundance is limited by the presence of rocks, vegetation or debris that may be used as cover to escape from predation and by the reducing potential of the substrate (Low, 1970). The reduction potential is the result of an increase in the metabolic activity of sulfur bacteria which produce

hydrogen sulfide. When there is little oxygen in the substrate, the bacteria develop in anoxic conditions.

The reproductive season for H. oregonensis occurs later in the year with increasing latitude. Knudsen (1964) reported egg deposition from mid-February through April with hatching occurring May to July in Puget Sound. A second brood period was observed in late summer with hatching in September. In Yaquina Bay, brooding females have been observed in all seasons of the year (Batie, 1974), and their presence indicates copulation occurs throughout the year. Pearson (1977) observed copulation among captive crabs from January to September. Although similar observations were made during the present study, in the field the greatest number of brooding females were found in early spring. However, brooding females were observed in all months.

According to Hart (1935) the eggs increase in size before hatching since there is a pre-zoeal stage in the egg. This is followed by five zoeal stages and a megalopa stage which lasts four to five weeks. The time between egg deposition and hatching varies from eight to thirteen weeks.

Hemigrapsus oregonensis has been categorized by Knudsen (1964) as primarily a herbivore which scrapes micro-turf (green algae, diatoms and desmids) off rocks. Hiatt (1948), however, concluded H. oregonensis was a scavenger since it will consume dead animal material and other organic material. Low (1970) and Pearson (1977) indicated that the crabs adjust feeding habits in accord with the habitat. The crabs from salt marsh areas ingested plant roots, sand, silt and a small percentage of macroalgae. In the rock-mud habitat of the estuarine intertidal, the

stomach contents included mussels, barnacles, isopods, leaves, sand-silt and a larger percentage of macroalgae (Pearson, 1977). These conclusions are in agreement with Dimick et al. (1941) who reported H. oregonensis was a predator on oyster spat and young oyster in subtidal areas.

The behavior of H. oregonensis is most completely described by Pearson (1977) who constructed an activity budget for the crab based on an extensive behavioral repertoire. Specific aspects of behavior studied in this species include locomotory activity patterns (Batie, 1974), behavioral responses to food, light and temperature (Symons, 1964) and social behavior (Wright, 1966). For the purpose of this study social behavior in the form of displays has been emphasized, but this is not meant to imply that other aspects of the crabs' repertoire - feeding, manipulation of the environment, grooming, etc. - are unimportant or that they do not affect social behavior.

Wright (1966) defined a display as a motor pattern that is: 1) not directly functional in feeding, digging, fighting, insemination or other non-communicatory activities; 2) occurring in a situation in which the pattern of non-communicatory behavior. The latter, however, does not exclude derived activity or behavior. Derived behavior is then defined as a behavior not originally communicatory but which has evolved into a display.

Wright (1966) also described the social repertoire of H. oregonensis as consisting of the following elements: lateral merus display (low, medium and high intensity), Hemigrapsus display, walking leg contacts, piling up, and fighting behavior (pinching and striking). In a lateral merus display the merus of the cheiped is extended laterally

away from the cephalothorax. Wright's (1966) description of the lateral merus details the angle the cheliped makes with the cephalothorax in high, medium and low intensity displays, and includes diagrams. Pearson (1977) concurs with Wright's observations on the repertoire but prefers to consider the posture as well as the angle of the cheliped in determining the relative intensity of a given lateral merus display. Hemigrapsus display appears to be unique to H. oregonensis and is typically, but not exclusively, given by females. One or both of the chelipeds are extended and waved in a circular pattern. The walking leg contacts are usually preludes to other types of social behavior but cannot be dismissed as interactions in themselves. The tactile stimuli, such as walking leg contact, are regarded by Symons (1964) as a primary source of information to H. oregonensis about surroundings since the natural habitats of the crab makes visual cues ineffectual. Piling up refers to a condition which occurs when aggregations of crabs pile up in situations of inadequate cover for the number of crabs. Pearson (1977) observed piling up in both field and laboratory conditions, and described it as a response to environmental stress. Wright (1966) reported fights between crabs as consisting of striking, pushing and pinching; to this Pearson (1977) added lunging, in which the whole body is used in delivering a blow. Crane (1967) described ritualized fighting in the fiddler crab Uca and concluded that it was a deterrent to serious injury. The pattern of the combat appears to be stereotyped and unambiguous communication.

Symons (1970) described a social behavior which he termed claw shuddering. In this display the crab rose on its walking legs and ex-

tended the chelipeds forward. With claws extended and together, and without pause, the crab moved the chelipeds rapidly apart with a shuddering motion. Symons (1970) observed this display coincidentally to another study that commenced during the reproductive season. He saw claw shuddering performed by males who had been captured as potential mates by other male crabs. The signal seldom had to be repeated to gain the signaling crab's release. Symons concluded that this display was used during the reproductive season to obtain escape. He did not observe females performing this display although females unwilling to mate struggled with males until they escaped the grasp of their captor. The crabs blinded for the intended experiment were responsive to vibration because they scurried away from objects dropped into the aquarium. Symons (1970) commented that claw shuddering was potentially well suited for communication in the niche that H. oregonensis occupies, since it could be used at night or in muddy waters when visual displays would be ineffective. Finally, he observed claw shuddering in isolated instances in the laboratory. The crabs claw shuddered to obtain release when they were picked up by the carapace by the experimenter. Pearson (1977) also observed claw shuddering by male crabs only and described the event as dramatic and distinct.

Stridulation in Crustaceans

The invertebrates which have been investigated use a variety of methods to communicate. In addition to visual and tactile cues and olfaction-pheromone detection, many have acoustic receptors. Busnel (1963) described the research on all of the invertebrate types and reviewed invertebrate acoustic communication. Most of the work with in-

vertebrates centers on the arthropods, mainly insects. Sound emissions fall into five general categories: 1) vibration of appendages; 2) shocks to the substrate; 3) expulsion of material (gas or liquid); 4) vibration of membranes; and 5) friction between hard body parts. The latter process is called stridulation and usually denotes sound produced by friction between differentiated hard body parts. These differentiated areas are specialized structures composed of two parts. One part, called the "pars stridens" or strigil, usually consists of a series of protuberances, such as tubercles, granules, ridges, beading, spines or rigid hairs. There is considerable variation between size and type of the protuberances between similar genera which could be of potential taxonomic use in some cases. The other part, the "plectrum" or strigilator, is a raised ridge which may be rubbed against the pars stridens (or vice versa). The plectrum may consist of a series of teeth, or a sharp-edged protrusion. Although the terminology is artificial, the pars stridens is typically located on the body and the plectrum on an extremity.

In the crustaceans the majority of sound production mechanisms are of the pars stridens-plectrum type. The notable exception to this generalization are the snapping shrimp (Alpheidae and Palaemonidae). These acoustic productions and visual displays have been described and reviewed by Hazlett and Winn (1962) and Knowlton and Moulton (1963).

The stridulatory apparatus has not been found in crustaceans other than Malacostraca, with most examples in decapod genera (Dumortier, 1963). Most of the general studies on stridulation are relatively old and primarily morphological (for example, Ortmann 1901; Alcock, 1902;

Balss, 1956; Scharrer, 1931; and Schmitt, 1931). Guinot-Dumortier and Dumortier (1960) have described stridulation as confined to Brachyurans, which in fact constitute the majority of the stridulating genera. In these crabs sound is produced by friction of the appendages against the cephalothorax or between appendages. The former method is more common, with the *pars stridens* located either in the region beneath the eye or at the anterior-lateral border of the carapace. The plectrum may be located on the merus, carpus, or propodus of the leg.

A quite extensive description of the stridulatory apparatus of the Brachyurans is given by Guinot-Dumortier and Dumortier (1960). They include several interesting observations about the biology of the crabs such as the fact that the majority of crabs with stridulatory apparatus are Brachyrhyncha and that many of these genera are adapted to brackish water, fresh water or have become terrestrial. Many of the stridulatory crabs construct burrows in the substrate and defend these burrows. A number of crabs use bits of animal and vegetable material to "decorate" or camouflage themselves, but this has not been observed in stridulating crabs. The converse to this observation is that the groups known for this decorating characteristic (Dromiacea and Oxyrhyncha) do not include a stridulatory species. Finally, there are numerous species of stridulating crabs which live in close proximity with other individuals in a gregarious or social setting. They cite Balss (1956) who observed Ocypoda and Dotilla in great concentrations on Formosan beaches and concluded that the groups were maintained by stridulatory communication.

The possible functions of stridulation can be separated into

several broad categories. Among conspecific individuals the categories could be listed as: sexual, territorial (burrow defense) and collective behavior (maintaining integrity of the group); and to other species, especially potential predators, the significance could be called intimidation. This statement is not meant to imply that these categories are mutually exclusive, but the arrangement simplifies the discussion.

The majority of the work conducted to investigate sound production in association with sexual behavior involved species of the fiddler crab Uca. Crane (1941, 1947, 1957) recognized that the waving or beckoning movements of the large chela by the male were stereotyped and species specific, and subsequently suggested a phylogeny based on comparative studies of the behavior of Uca as well as ecological and morphological characteristics. This waving initiates courtship. Later Von Hagen (1961), Burkenroad (1947), Salmon and Stout (1962) and Salmon (1965) reported that sound production also plays an important role in courtship of several species of Uca. The sound production, originally thought to be stridulation, replaces the visual cue of waving when the male retreats into a burrow, beckoning for the female to follow. The male continues to lure the female into the burrow by sounds which have been described as rapping or tapping noises. Von Hagen (1967) describes the signaling in Uca and compares it to the tapping by Sesarma, which strikes the cheliped together during similar courtship behavior. The waving previously described for Uca courtship also serves to deter competing males from the burrow area (Burkenroad, 1947).

The arbitrariness of the categories becomes apparent when the behavior is interpreted by different authors. Hughes (1966) reports that

Ocypodidae stridulates only in burrows, and interprets this as burrow defense. If the sand near the Ocypodid burrows was scratched the crab in the nearest burrow responded by stridulating, and this would elicit stridulation from neighboring crabs. Hughes (1966) repudiates Dumortier's (1963) theory that this stridulation in unison unites the colony, and suggests instead that it serves to space the individuals within the colony. Hughes' objection to the theory of unifying a colony seems reasonable since ocypodids are cannibalistic (Williams, 1965).

Guinot-Dumortier and Dumortier (1960) hypothesized that the adaptive significance of stridulation could be to ward off predators and could be analogous to aposematic coloration. Some of the moths and butterflies have large eye-like spots on their wings which serve to "intimidate" predators and these "eyes" blink when the wings are moved. They compared stridulation to aposematic coloration in which a visual cue is present, as a conditioned stimulus, for the predator. The prey is identified as distasteful by the association with the color. In the case of stridulation the disagreeable taste was compared to a severe pinch. If this analogy is valid, stridulation would have adaptive value as a defense. Alexander (1958) is frequently cited to substantiate this possibility. He presented a hedgehog with individuals of a species of scorpion (Opitophthalmus catimanus) which stridulate. The hedgehog immediately devoured a scorpion whose stridulatory apparatus had been removed but hesitated when an intact scorpion stridulated. After the first presentation, the hedgehog did not hesitate to kill either type of scorpion.

Guinot-Dumortier and Dumortier (1960) outlined the research that

had been conducted to determine acoustic reception in the crabs, and concluded that since they produce sound they must be able to receive it, although the receptors responsible had not been found. Included in that review was a prediction by Tweedie (1950) that the "tympana" was associated with the walking legs. Burkenroad (1947), Guinot-Dumortier and Dumortier (1960), Balss (1956), Hughes (1966) and many others commented on the use of the substrate as a conducting media. Several recent investigations on acoustic detection in Ocypodidae have appeared (Salmon and Atasides, 1968 and 1969; Horch and Salmon, 1969; Salmon, 1965; Salmon and Stout, 1962; Horch, 1974 and 1975). These crabs detect substrate borne signals produced from artificial sources and recordings of crab stridulation. The above workers have established the presence of Barth's myochordotonal organ in the meri of the walking legs as the probable receptor of signals. The discovery of the receptors of acoustic stimuli in the legs emphasize the importance of stridulation as a substrate borne or tactile sense.

Salmon and Horch (1976) described three types of interneurons from the fiddler crab (Uca pugilator and U. minax) and ghost crab (Ocypode quadrata) which process acoustic information. The combination of the properties of these cells would permit resolution of sound duration, pulse repetition and the interval between sounds. This resolution would permit species specific discrimination and detection.

MATERIALS AND METHODS

Behavioral Observations

Experimental Apparatus

Hemigrapsus oregonensis is influenced by its surroundings and differing repertoires of behavior can be developed by placing the crabs in various types of surroundings. For example, H. oregonensis feeding patterns are primarily detrital in the natural environment so that placing the animals in a container without substrate would preclude normal feeding behavior, and indeed appears to stress the crabs. The stress is evidenced by increased activity and frequent defecation. Stress is also seen when the crabs are placed in round containers or containers which do not provide cover. In this study, two types of chambers were used. An octagonal vessel was used to increase activity, and therefore elicit more claw shuddering behavior while the acoustical recordings were being made. The behavioral observations were conducted in a series of rectangular vessels designed to model the mud-rock environment at Coquille Point where the animals were collected. These habitat replicas were constructed of glass, fiberglass treated plywood, and silicone sealant. Each replica contained approximately 2 kg of sand, two oyster shells and a plexiglass shelter. The shelters were 3 cm in length and 10 cm square (See Figure 1) and were designed to give thigmotactic shelter to the crabs while permitting observation of the crabs under these plexiglass "rocks". The water in the replicas was supplied by the running seawater system at the Marine Science Center, which draws from Yaquina Bay. Since the collection site was also on Yaquina Bay, the water to which the animals were exposed was similar to the salinities and water tempera-

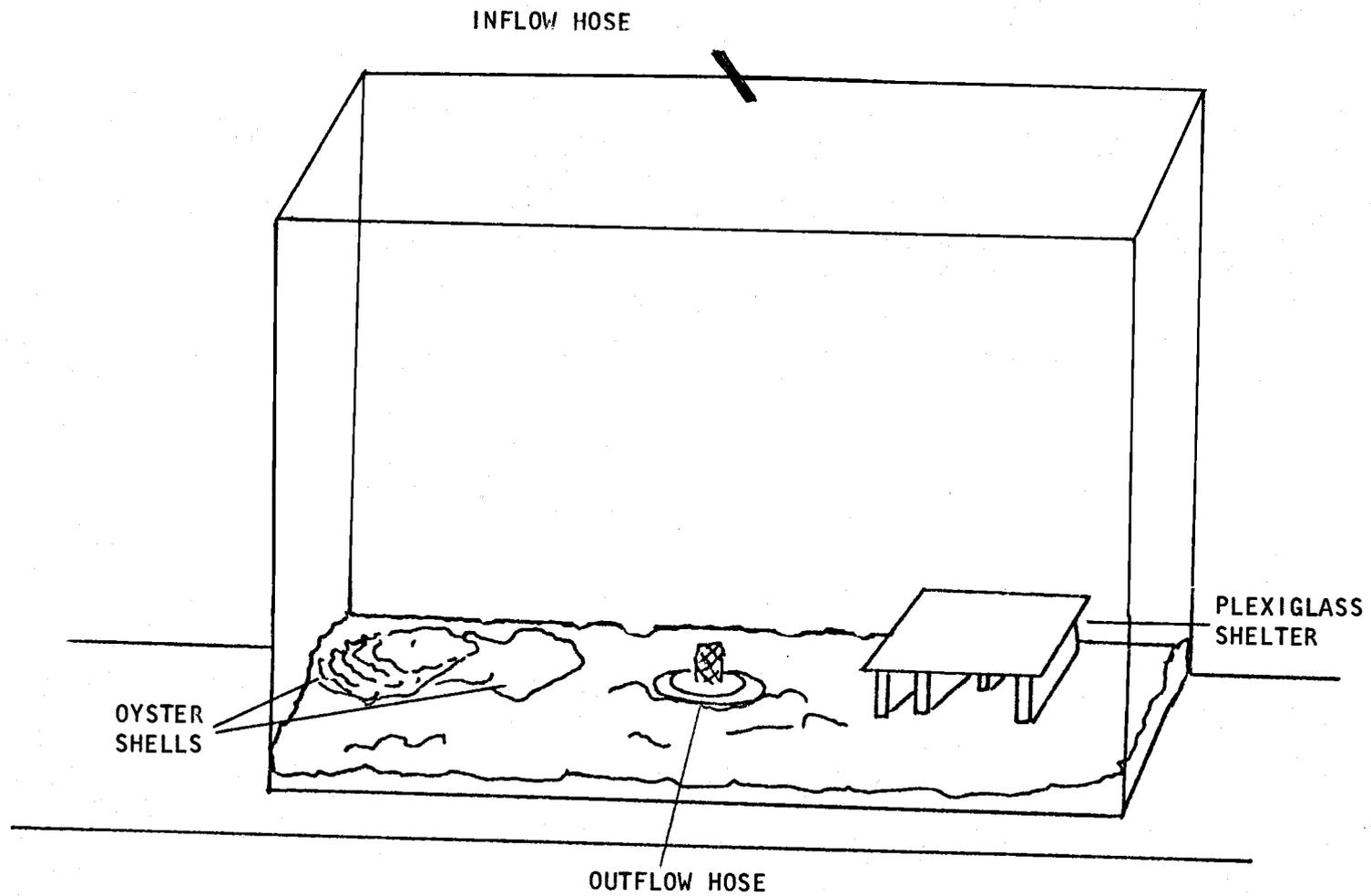


Figure 1. Schematic diagram of habitat replica.

ture of the natural environment. The major difference in the simulated environment was the variation of the temperature of the sea water, since it passes through the pipes in the building and is warmed slightly in the winter. Since this work was done in the spring and summer, this warming effect was minimal.

Two lighting systems were used during the behavioral observations. The daylight period was simulated by daylight-type fluorescent lighting controlled by a timer. The timer was adjusted weekly to correspond to the natural photoperiod. The spectrum of the fluorescent tubes approximated a noon sky plus sunlight (General Electric Chroma 50[®] 2 watts). Red safelight (Kodak No. 2 filter over an incandescent bulb) were burned continuously to give illumination for night observation. Generally, crustaceans and specifically crabs have peak spectral sensitivity near 500 nm, and are insensitive to light beyond 600 nm. (Briggs, 1961; Fernandez, 1973; Goldsmith and Fernandez, 1968; Waterman, 1961). The filters used do not pass light below 638 nm. Observation of the crabs was conducted under this artificial night condition and the crabs' behavior indicated that they were oblivious to visual cues.

The tidal regime of the habitat replicas was maintained by a device (Figure 2) which was modified from those described by DeBlok (1964), Evans (1964), Underwood (1972) and Pearson (1977). With this device, the inflow of water is constant and the level of the water is governed by the outflow rate. The rate of water outflow was controlled by raising and lowering the end of the outflow hose so that the water level in the replicas rose and fell with the changing length of the end of the hose. The motion of the end of the outflow hose was generated by an

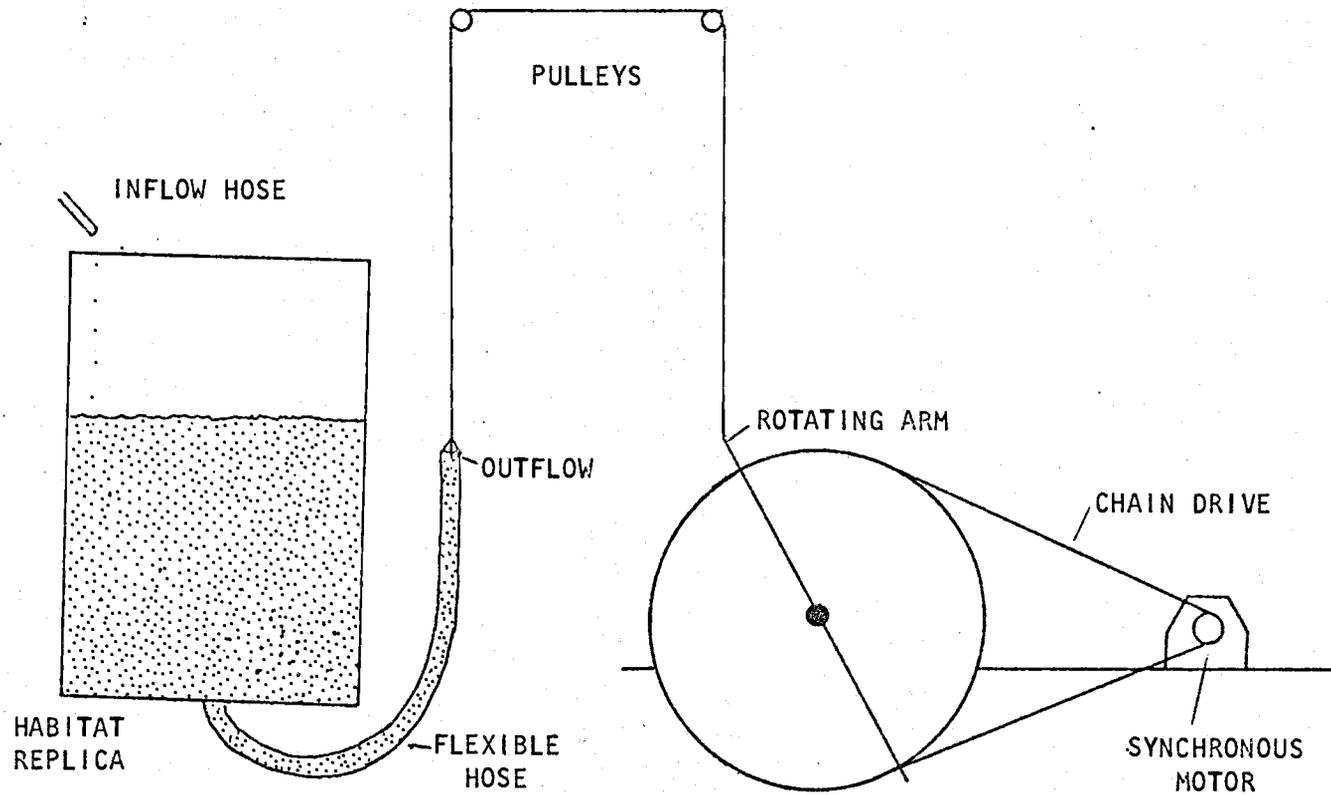


Figure 2. Schematic diagram of tidal apparatus.

arm attached to a wheel which was driven by an electrical synchronous motor (one revolution per hour). A chain served as the gear train between the wheel and motor, and changed the speed of revolution of the wheel by a 12.4:1 ratio. Thus, one revolution of the wheel and arm assembly produced a motion with a period of 12.4 hours. The outflow hoses of four replicas were attached to the arm by a series of lines and pulleys and produced a sinusoidal emptying and filling of the chambers as the arm turned. Two devices were necessary because each device governed four replicas. The times of the tides were set to the Coquille Point location and were adjusted at high tide daily. The water level at high tide was 20 cm above the substrate and the animals were exposed to air for four hours during the low tide. Because the tide generating machine modelled the tides sinusoidally, the mixed character of the semidiurnal tides was eliminated. A complete discussion of the design, construction and calculation of flow requirements appears in Underwood (1972).

The last complement of experimental apparatus that was to be used for behavioral observations was video-tape recording equipment. The physical difficulties encountered in video-recording claw shuddering behavior made it necessary to discard video-tape as an experimental method. Some of the problems encountered were the need for increased lighting, the constraint of too little recording time per video tape, and inability to slow the tape to observe the rapid event. Although the video-tape could not be used for the detailed behavioral analysis, the video tape of claw shuddering was nonetheless valuable because it demonstrated the variability of the event among individuals.

Collection of Animals and Composition of Test Groups

All of the Hemigrapsus oregonensis studied were collected at Coquille Point (Figure 3) in Yaquina Bay at lower low water in the tidal cycle. The crabs were sorted by size and sex, marked and their body measurements recorded. In both sexes, measurements were taken of the carapace width (at the widest point) and the length of the left chela. The crabs were marked by drying the carapace and painting symbols with iridescent fingernail polish on the carapace using a color and geometric code. The polish had no observable toxic effect but the procedure was completed as quickly as possible to minimize dessication. The crabs were then placed in habitat replicas. The grouping of the animals with regard to number and sex ratio varied with the trials.

Three sets of crabs were observed beginning with the first high tide after their collection. Two sets of crabs were acclimatized to the laboratory conditions and observed two weeks later when tidal regime and photoperiod were approximately the same as the day they had been collected. Although these acclimatized crabs were held in habitat replicas they were not placed in a common replica. This was accomplished by dividing the replicas in half, and combining the animals at low tide just prior to the first observation session. The crabs were observed during every high tide to low tide period during a series. At least six observation periods composed the series and in two instances, first and second series, the crabs were observed for eight sessions.

In the first series eight male crabs were observed and in the second series eight male crabs, which had been collected on the same tide, but acclimatized in the laboratory, were observed. The third series was

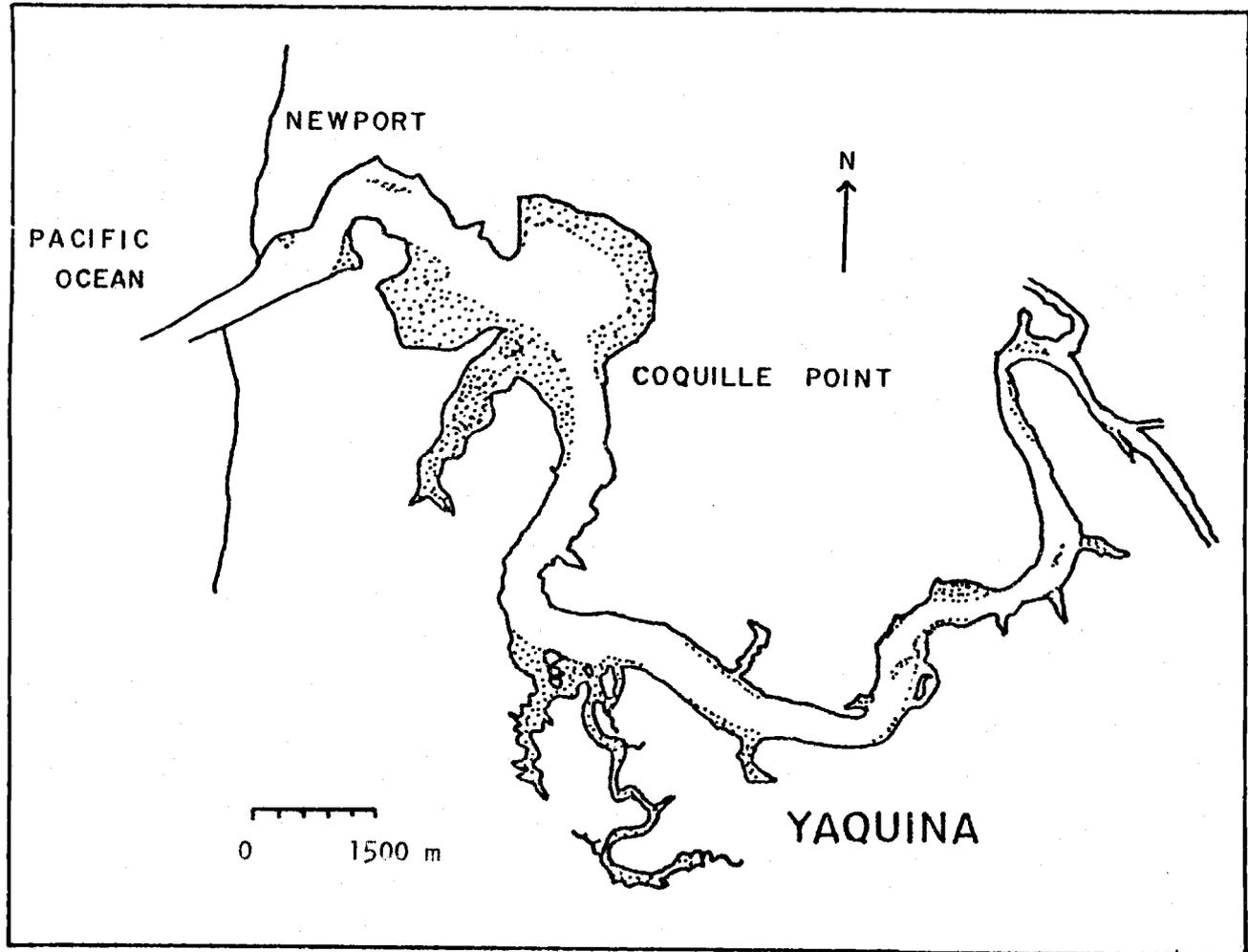


Figure 3. Yaquina Bay and Estuary, Oregon.

composed of four females and four males. The fourth series was composed of four females and four males which had been acclimatized. The original data from the fourth series was discarded because of a power failure which interrupted the tidal regime. A replacement group of four females and four males was collected and acclimatized, but on the third day of observation three of these crabs molted. Therefore, the data from this interrupted fourth series was analyzed only with regard to size, position and retreat information. The second replacement group was collected, acclimated and observed and the data appears as the completed fourth series. To test for a density relationship, sixteen male crabs were observed in the fifth series (Table 1). In all series large 240-270 mm, medium 210-240 mm, and small 170-210 mm crabs were used in an approximate 1:2:1 ratio with an attempt to balance males and females by size since the females are typically smaller.

The decision concerning which information should be recorded during the behavioral studies was made on the basis of several preliminary observation sessions. The crabs were observed in the replicas and when one of the crabs claw shuddered, the following information was recorded: the time of the event; the symbol for crab performing the signal; the symbol for crab receiving the signal; which of the crabs was holding a position or maintaining a personal territory in the replica and which of the crabs retreated after the signal. Narrative notes were also taken during the observation periods.

Before beginning each trial the times of the tides, and of sunrise and sunset, were recorded and later encoded with the information about each claw shudder event and the body size data for both crabs partici-

Table 1. Experimental conditions for observation series.

<u>Series Number</u>	<u>Sex Ratio</u>	<u>Duration of Series</u>	<u>Laboratory Conditions</u>
1	8 males	4 days/8 sessions	not acclimatized
2	8 males	4 days/8 sessions	acclimatized
3	4 males/4 females	3 days/6 sessions	not acclimatized
4	4 males/4 females	3 days/6 sessions	acclimatized
5	16 males	3 days/6 sessions	not acclimatized

pating in the event.

The behavioral observations were made to explain the role of claw shuddering in the repertoire of H. oregonensis. These observations were analyzed with the simplest possible statistical tests: the normal approximation to the binomial, chi-square test and linear regression analysis. Independence among observations was assumed. The binomial test is used where the primary concern is the proportion of individuals or observations falling into one of the two classes. The chi-square test was used when the alternative categories were larger than two (Bliss, 1967). While the first two statistical tests were primarily for enumeration, the regression analysis is used to test a trend.

Acoustic Observation

In order to establish sound production during a claw shuddering display, acoustic recording apparatus was necessary. All of the crab sounds were recorded on a Uher 4400 Report Series[®] audio-tape recorder using Memorex[®] tapes. The response curves for this combination of apparatus shows flat response from 4 Hz to 15 Hz and a useful dynamic range to be from plus 5 db to 55 db (See Appendix 1). The recordings were made using a CL17 hydrophone (Appendix 2) and sounds were amplified (gain = 10) and filtered by a Quan Tech[®] model 206 amplifier (Appendix 3).

Because of the problems with sound reflection and extraneous noise in the glass walled replicas, all of the acoustic data were collected underwater in an octagonal redwood container. The shape of the container was important because the hydrophone must be located equidistant from

the side-walls for better uniformity of signal quality. The redwood itself does not reflect sound waves and aided in removing "echoes" from the data.

During preliminary analysis of the acoustic tapes, the triggering mechanism on the sound analyzer was activated manually. This was necessitated by the speed of the signal. At best, segments of a burst were analyzed but it was not possible to place these segments into a sequence. In order to analyze a recording of the claw shuddering display completely, it was necessary to use a small computer PDP11 with magnetic tape equipment to digitize the signal. The original acoustical tape recordings were re-recorded while the speed had been reduced by a factor of 19 and these new dubbed tapes were digitized. The computer program converted the acoustic signal into numerical values and created a file for each claw shudder. The computer was programmed to scan the numerical information and compute an average amplitude of the sounds included in a file. To locate a burst of sound within the file a threshold volume was selected from the average sound level and the computer listed the sound level and location in the file when the threshold value was exceeded. (The program is listed in Appendix 4 and an example of sampling output in Appendix 5.) The operator could then select sections of the file which contained the signal and plot these segments. Since the number of samples in a file was known from the sampling speed, the plots could be used to analyze the data. Each inch of the strip chart recorder plot equals 2 milliseconds and the sound bursts within the signal could be timed and compared with the signals from other crabs and other signals performed by the same crab. (An

example of the strip chart recording has been included as Figure 4). The acoustic data was compiled in tabular form and included the time of the sound burst, number of peaks in a burst, the mean and standard deviation of the peak amplitude and the duration of the burst.

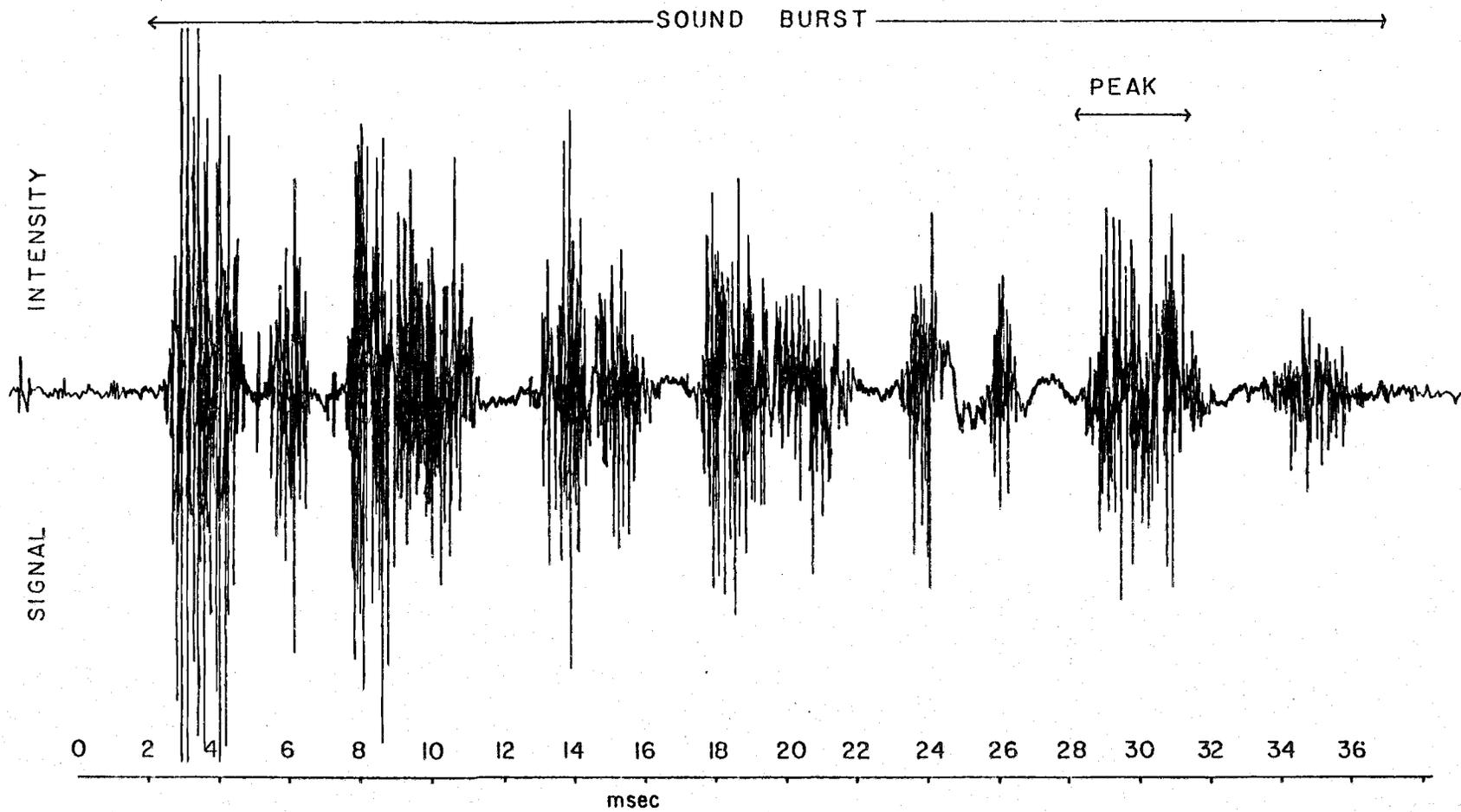


Figure 4. Strip chart recording of sound burst.

RESULTS

Preliminary Observation

The claw shuddering display appeared distinct and perhaps ritualized when it was compared with other H. oregonensis displays. This lack of resemblance suggested another, different aspect of communicating behavior, was being used and acoustic signaling was not an unreasonable hypothesis. The method described in Guinot-Dumortier and Dumortier (1960) of manipulating the crabs was used on dead specimens of both sexes of H. oregonensis and H. nudus without prior knowledge of stridulation in crustaceans. There were no audible results from either sexes of H. nudus or from females of H. oregonensis, but the males of H. oregonensis could be made to produce a sound consisting of a series of four or five clicks. The number of clicks appeared to correspond to the number of tubercles on the pars stridens of the male. Although this sound production was indicated it was not strong evidence for acoustic communication in live animals. The description of the plectrum and pars stridens of H. oregonensis given by Guinot-Dumortier and Dumortier (1960) was then verified (Figure 5).

Acoustic Characteristics of the Signal

To test the hypothesis that H. oregonensis stridulates, acoustic tape recordings were made, and the claw shudder signals were timed relative to the tape. These recordings (Figure 4) established that sounds were being produced by claw shudders but the signals were much too brief to discern individual clicks that might comprise the sound. Pre-

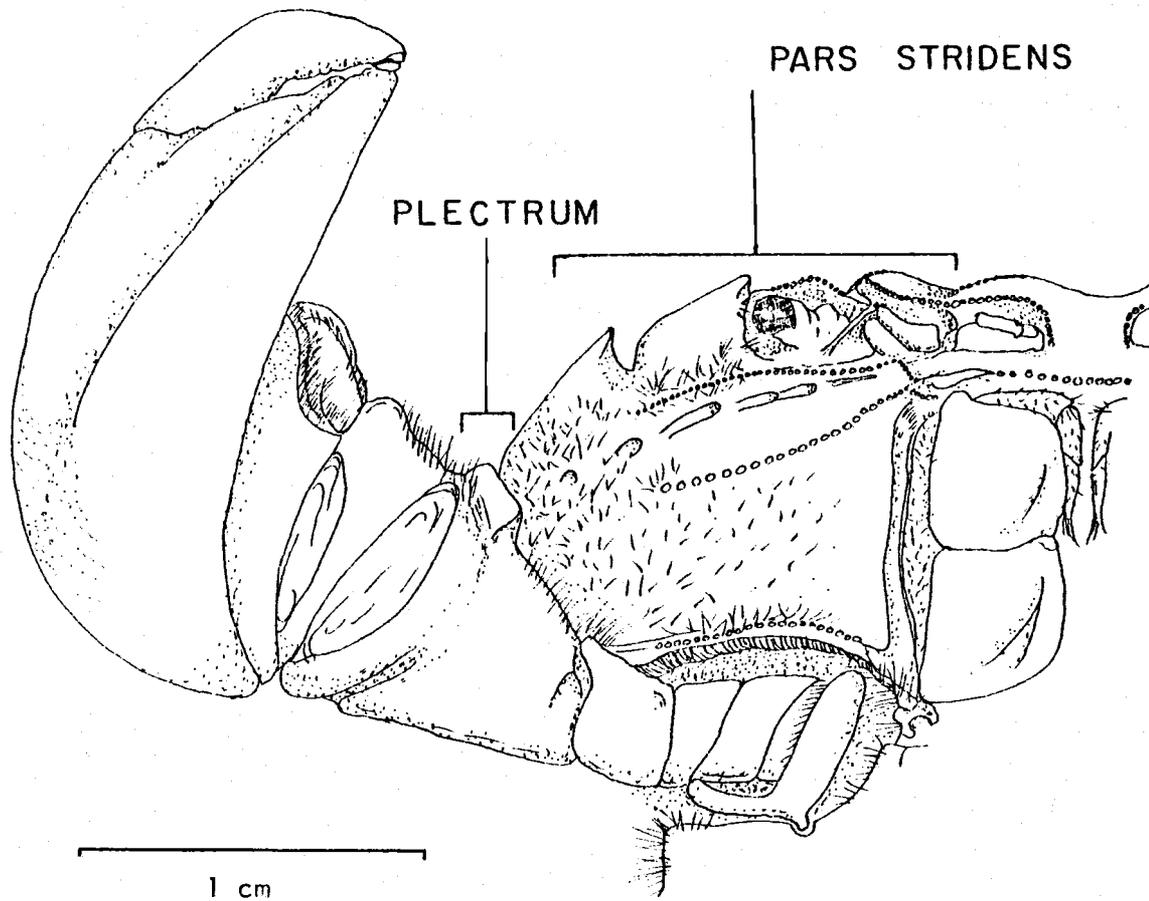


Figure 5. Stridulatory apparatus of Hemigrapsus oregonensis.

liminary analysis of the tapes showed the sound to be less than one second in duration. The videotape showing claw shuddering was timed with a stopwatch and the event lasted an average of .6 to .8 seconds. The more sophisticated recordings using the apparatus described in the materials and methods section were made to resolve the signal. The stridulation process is basically frictional in nature and therefore the signal produced could be hypothesized as composed of broad bands of frequencies and occurring sporadically. Indeed, it can be seen from the strip chart recording (Figure 4) of one of the signals that the clicks were divided into bursts of sound as the plectrum was scraped against the pars stridens. The spacing of the clicks relative to each other and the number of sound bursts in a click appeared to be characteristic for each crab (Table 2). The technical problems associated with making this type of recording of a rare behavior did not permit the analysis of large numbers of signals. The signals that have been analyzed were typically those free of background noise, internal electronic noise, interference from other crabs and of sufficient amplitude to permit re-recording and digitizing. Although great care was taken to record the entire signal, the data table seems to indicate that portions of some signals were lost. Analysis of the sound into the frequency components was not conducted. Within these constraints it was possible to make the following generalizations about the recordings.

First, the largest crab (crab A, carapace 270 mm) produced the highest energy signals (i.e. magnitude of peaks), which was seen in the mean of the peak height. The standard deviations for this data were high which showed that the peak height was not uniform within a sound burst

and that some of the individual peaks were of very high amplitude (Figure 4). This tendency was not present in the smaller crabs' signals, which were typically characterized by mean peak size of small magnitude and relatively smaller standard deviations (Table 2). The data indicated that there was a difference in intensity (frequency and amplitude) of signal between signals from large and small crabs.

Secondly, when all of the acoustic data was considered, there appeared to be a relationship between average duration of a peak and the height of the peak. The duration of the signal was divided by the number of peaks in the signal to yield the average duration of a peak (indicated in column six, Table 2). Linear regression analysis was used to test the significance of apparent relationship between peak duration and height. The results of this analysis are presented as a scatter diagram (Figure 6). The calculated value for t in this regression was -1.49 which indicated significance at the 80% but not at the 90% level in a two-tailed test. These results were not statistically significant but they do indicate that with more data, collected with better equipment, a definite trend might emerge.

The total claw shudder signal would be composed of a number of sound bursts like the burst shown in Figure 4 which has nine peaks. The form of the peaks in the burst indicated frictional sound and probably corresponded to the plectrum rubbing against the flattened portions of the *pars stridens*. The projections of the *pars stridens* interrupted the sound and divided the signal into a pattern of bursts. The amplitude of the peaks would then be proportional to the force exerted on the *pars stridens* by the plectrum.

Table 2. Data from acoustic recordings.

		1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6						
Crab A carapace 270 mm.	File 1	0	9	1.3	.8	46	5.1	55	11	4.1	3.3	72	6.6	179	9	4.6	2.3	33	3.7	246	1	2.5	0	4	4	392	3	3.3	3.6	8	27
	File 2	0	9	6.6	2.3	42	4.7	106	7	4.1	2.5	32	4.6	265	3	2.3	5.1	27	8.8												
	File 3	0	9	2.5	.8	45	5.0	54	9	5.1	3.6	52	5.8	179	10	4.8	5.1	10	3.3	246	1	1.0	0	4	4	352	3	3.3	2.3	3	27
	File 4	0	8	11.7	5.8	40	5.0	118	9	15.2	5.6	24	2.7	166	3	4.3	2.3	18	6	282	9	6.4	4.3	42	4.7						
Crab B carapace 240 mm.	File 5	0	12	3.3	2.3	52	4.3																								
Crab C carapace 231 mm.	File 6	0	4	3.8	2.5	12	3.0	116	3	2.0	1.8	18	6.0	279	2	.6	0	11	5.5												
Crab D carapace 221 mm.	File 7	0	8	1.8	1.0	33	3.7	132	6	2.0	1.3	27	4.5																		
Crab E carapace 196 mm.	File 8	0	8	1.8	1.0	61	7.6	219	5	2.0	1.3	53	10.6																		
Crab F carapace 196 mm.	File 9	0	15	2.3	1.0	78	5.2	53	14	1.5	1.0	77	5.5																		

- 1: Time of burst (msec)
- 2: Number of peaks in burst
- 3: Mean height of peaks (cm)
- 4: Standard deviation of peak heights
- 5: Duration of burst (msec)
- 6: Average peak duration (msec)

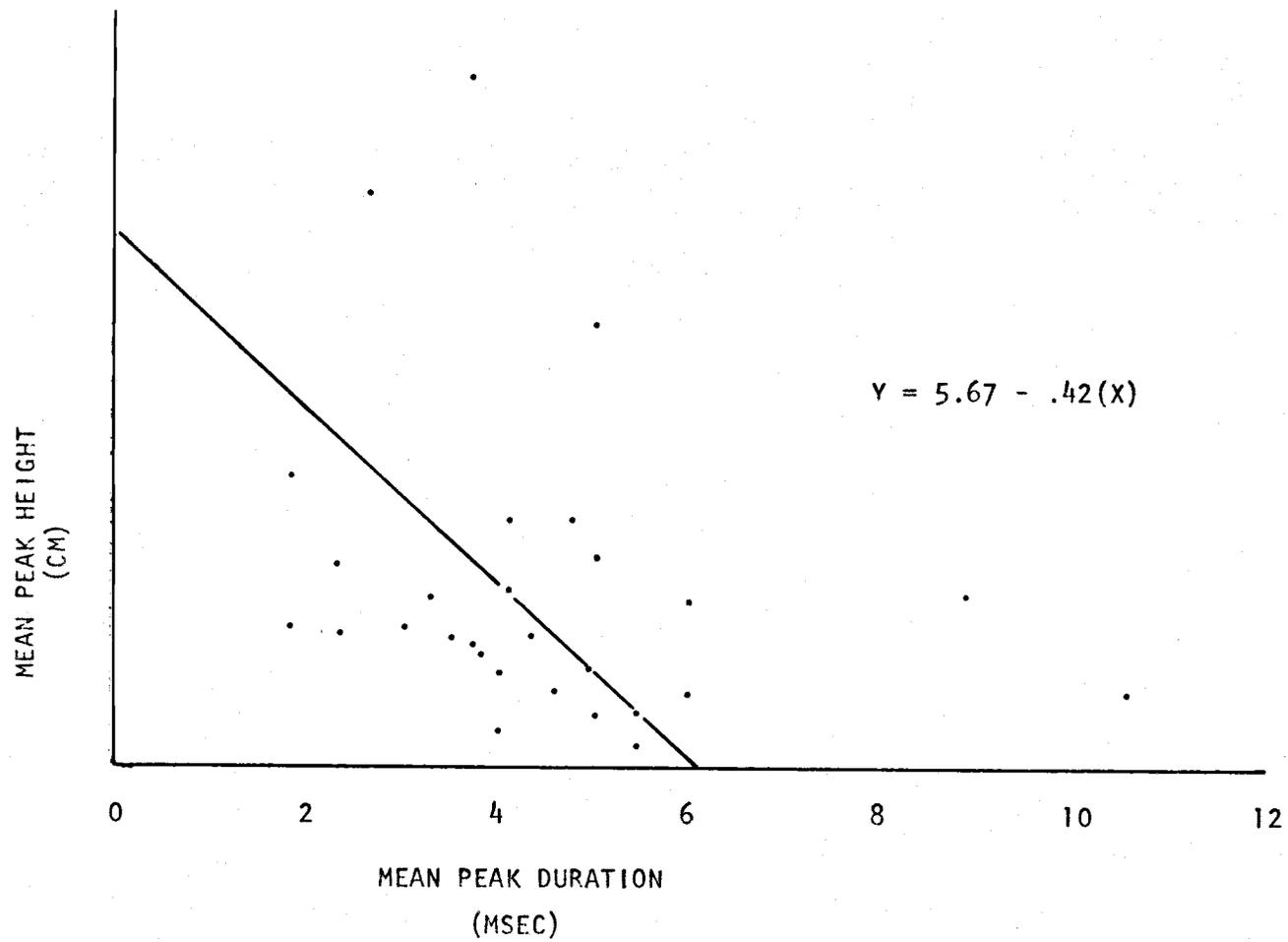


Figure 6. Scatter diagram of peak height vs. peak duration.

Behavioral Observations

During each of the series the number of claw shudders decreased in subsequent sessions (Table 3). For example in the first series the number of events dropped from 52 in the first observations period to 17 in the last. The tendency was present in all series and the statistical significance of the trend was tested using regression analysis. The null hypothesis was that there was no difference among observation sessions and independence among the events was assumed. The regression analysis showed that for all series the decrease in signaling was significant at the 95% level (Table 4). The negative values for the slope indicated that the amount of signaling diminished as the trials progressed.

This result contrasts with the series of equal numbers of female and male crabs in the total amount of claw shudders performed (Table 3). It would seem that the amount of signaling in a group of eight male crabs would be twice as great as a group of four female and four male crabs, because only the male's claw shudder. The null hypothesis to test this was that there would be half the total amount of signaling in the female-male series (series 3 and 4) as in the series with all males (series 1 and 2). There was a significantly greater total amount of signaling in the all male series and the difference was greater than would be expected from the sex ratio alone.

In the fifth series, sixteen male crabs were observed in the replica to determine if the amount of claw shuddering increased as the density of crabs increased. As a result of technical problems, the fifth trial was not continued for four days and cannot be statistically com-

Table 3. Number of claw shuddering events during observations sessions.

<u>Series Number</u>	<u>Observation Sessions</u>								<u>Total</u>
	<u>1*</u>	<u>2</u>	<u>3*</u>	<u>4</u>	<u>5*</u>	<u>6</u>	<u>7*</u>	<u>8</u>	
1 (8 males - no acc)	52	37	51	23	21	14	24	17	239
2 (8 males - acc)	63	31	16	21	22	21	17	6	197
3 (4 males - 4 females - no acc)	5	7	5	2	1	1			21
4 (4 males - females - acc)	15	6	9	2	4	1			37
5 (16 males - no acc)	34	24	16	16	15	10			115

*Majority of observation session was at night.

Table 4. Linear regression analysis of the number of claw shuddering events during observation sessions.

<u>Series Number</u>	\hat{B}_0	\hat{B}_1	<u>R</u>	<u>df</u>	<u>t Observed</u>	<u>t (95%) Critical Value</u>
1	52.5	-5.04	-.82	7	-3.58	2.36
2	48.9	-5.39	-.77	7	-3.02	2.36
3	7.6	-1.17	-.87	5	-3.58	2.57
4	14.5	-2.37	-.85	5	-3.29	2.57
5	33.9	-4.20	-.92	5	-4.69	2.57

pared with series one and two. Although numerical comparisons are impossible, it can be demonstrated that the amount of claw shuddering was substantially less and the decrease in the signaling during this series was steady (Table 3).

Territorial defense is another possible role of claw shuddering in the behavior of H. oregonensis. Data were therefore taken to establish which of the crabs involved in an exchange might be holding a position or maintaining a territory. If neither signaling nor eliciting is related to a territorial behavior, the role of the crab holding the territory would be random. On numerous occasions the crab eliciting the claw shudder would himself perform a claw shudder in return or the signaling crab might repeat the claw shudder. This return of the signal might bias the test of territoriality but the data were taken assuming that if the eliciting crab returned the signal, he had established a position. Therefore, a second test was performed with these multiple signal interactions eliminated.

Generally in a series of observation periods, the first trials occurred in the evening since the crabs had been collected on the low tide during the morning. Locomotory activity in H. oregonensis were strongly influenced by the photoperiod and stage of the tide (Batie, 1974). The crabs were typically inactive at low tide and extreme high tide, and less active during the day than at night. The null hypothesis that there was no difference in the amount of claw shuddering due to photoperiod was tested statistically by the normal approximation to the binomial. At the 95% level the amount of signaling at night was significantly greater than the amount during daytime (acceptance region 287.52

<x<335.48 with an observed value of 353). A different test of the crabs' rhythmicity was conducted with respect to the stage of the tide. Using the time of the claw shuddering event, the number of signals during each hour of the observation session was compiled (Table 5). The session began at high tide and there were approximately six hourly divisions. This variation occurred because the time between high and low tide is not equal and therefore in some observation sessions more than six hours of observation were necessary to complete the high tide to low tide time schedule. A few claw shudders were observed during the beginning of this sixth hour after high tide. Because observations made beyond six hours never lasted more than a quarter of the subsequent hour, those claw shudders were incorporated into the data from the preceding hour. The null hypothesis was that there would be no difference in the amount of claw shuddering among the hour divisions of the observation session, than from an expected distribution in which each of the six possible divisions would have equal amounts of signaling (total number of claw shudders divided by six observation periods). However, the chi-square values exceeded critical values indicating that the amount of signaling in some of the hour periods was significantly different. The amount of signaling in each of the six time division were examined with regard to Batie's (1974) work with activity patterns. His data showed peak locomotion and interaction shortly before high tide and again as the tide was ebbing. The six observation periods were re-grouped into three categories; high, medium and low locomotor activity (total number of claw shudders divided by three observation periods). The high locomotor activity at these projected times was hypothesized

Table 5. Amount of signaling during each hour of the observation.

	Hours of Observation						Total
	0	1	2	3	4	5	
Observed Number of Claw Shudders	133	89	107	160	108	27	624
Expected Number of Claw Shudders	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	624
	3	3	3	3	3	3	

$$\sum_{i=0}^5 \frac{(O_i - E_i)^2}{E_i} = \chi^2_{(5df)} = 97.6 \chi^2_{(5df)}$$

two-tailed test at $p=.01$: critical value of χ^2 at 5df =15.1

	High Stress (hours 0 & 3)		Medium Stress (hours 2 & 4)		Low Stress (hours 1 & 5)		Total
Observed Number of Claw Shudders	133	160	107	108	89	27	624
Expected Number of Claw Shudders	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	$\frac{624}{3}$	624

$$\sum_{i=0}^3 \frac{(O_i - E_i)^2}{E_i} = \chi^2_{(2df)} = 75.67$$

two-tailed test at $p=.01$; critical value of χ^2 at 2df =9.21

to be a result of predatory pressure while the crabs found shelter. The null hypothesis was that there would be no difference in the amount of claw shuddering in the categories than from an expected distribution in which the amount of signaling in each of the three categories was equal. The chi-square values for this test exceeded the critical values. This indicated that claw shuddering behavior coincided with peak locomotor periods and times of peak interaction.

One possible interpretation of claw shuddering is sexual behavior, for example courtship, because the stridulatory apparatus is present only on male crabs. Four female and four male crabs were observed in series three and four. Because claw shuddering is performed by male crabs exclusively, in these series the crab eliciting the signal has a three in seven chance of being male and a four in seven chance of being female. Therefore, the null hypothesis for this test was that the number of signals elicited by male crabs would be three sevenths of the total. The number of claw shudder signals elicited by males was not significantly different (at the 95% level) from the number of claw shudders elicited by females (acceptance region $16.75 < x < 31.25$, with observed value of 30 signals). The null hypothesis for both of the above tests could be stated as follows: There was an equal probability that the crab signaling would be holding a position as the crab eliciting the signal. The acceptance region for all data was $287.52 < x < 335.48$ and for the data minus the multiple interactions the region was $224.26 < x < 267.74$. The observed values of 501 and 389 signals were outside these respective regions that were calculated by the normal approximation to the binomial at the 95% level.

When claw shuddering interactions occurred, one or both of the crabs might have retreated from the other, or neither crab might have retreated. The movement of both crabs subsequent to claw shuddering was noted. Although territoriality is a complex behavioral concept, it was assumed that retreat or failure to retreat could be used as an indicator of territoriality. From this assumption, the working hypothesis was formulated that after a claw shuddering signal the tendency to retreat would have been as probable as failure to retreat. Therefore, the number of retreats by the signaling crab would equal the number of occasions when he did not retreat. The null hypothesis was as follows: the number of retreats equaled the number of times the signaling crab failed to retreat. The multiple signal interactions, previously described were eliminated as a second part of the test, because in these cases failure to retreat was implied. The acceptance region for all data was $287.52 < x < 335.48$ and for the data minus the multiple signal interactions the region was $224.26 < x < 267.74$. These regions were calculated by the normal approximation to the binomial at the 95% level. The observed values of 60 and 51 retreats fell outside these acceptance regions. In the majority of events, the signaling crab did not retreat and maintained a position.

From the narrative notes taken during all series, it was observed that when the claw shuddering interaction took the following form - crab A signaled, crab B returned the signal and crab A signaled again - a fight ensued in every instance. Seven of these interchanges followed by a fight occurred and three of them happened in the fifth series which contained the highest density of male crabs.

Because preliminary observations had indicated that the body size of the crab might be an important variable, both carapace width and cheliped length were recorded for each of the crabs in the study. The crab with the wider carapace usually also had a longer cheliped in a given interaction although this was not always true. The normal approximation to the binomial was not an appropriate test of whether either of these measurements were directly correlated with the retreat of a crab, because more than two variables were concerned. Statistical analysis therefore was not done with this data but Table 6 lists the data involved. Considering either carapace width or cheliped length, the larger crab typically did not retreat. Whether a crab used carapace or cheliped size as the discriminant in perceiving if he was larger was certainly not indicated in these results.

Table 6. Body size and retreating.

	<u>Wider Carapace</u>	<u>Longer Cheliped</u>
<u>All Data:</u>		
Crab Retreats	122	122
Crab Does Not Retreat	503	502
<u>Multiple Signal Interactions Removed:</u>		
Crab Retreats	9	8
Crab Does Not Retreat	117	118

DISCUSSION

The results of this study clearly demonstrated that H. oregonensis has the apparatus required to stridulate and that the stridulatory act was the claw shuddering display. Only males have the stridulatory apparatus and females have not been seen executing a claw shudder. The sound was composed of bursts or clicks and these bursts were probably created when the plectrum scraping against the pars stridens encountered the tubercles of the pars stridens. The signal was of brief duration and showed a general pattern of sound bursts but indicated variation among individual crabs. The larger crabs produced more intense signals and the behavioral data indicated that the larger crab seldom retreated after having given a claw shudder. The results also indicated that the signaling crab generally was holding a position or territory and seldom retreated after signaling. The claw shuddering display communicates information to the crab eliciting the signal about the presence of a crab defending a territory, the size of that crab and that the crab is male.

Symons (1970) interpreted claw shuddering as an aspect of sexual behavior because he observed the display during the reproductive period. His conclusion was correct concerning the efficacy of vibration as a means to communicate but he misunderstood the role of the display. The low incidence of claw shuddering in series conducted with both male and female crabs seems to lend more evidence to the argument that claw shuddering is not an aspect of courtship behavior. The Hemigrapsus oregonensis used in this study were all collected from under rocks in a mud-rock habitat. This species also lives in burrows in the nearby

salt marshes and therefore the use of an acoustic form of communication in burrow or territory defense is not unreasonable.

During the preliminary observations for this study in the reproductive season, male crabs stridulated during copulation with females. This usually happened when the pair was approached by another male. Symons' (1970) observation of claw shuddering to gain release was corroborated, but the claw shuddering occurs throughout the year and these situations are special cases of defensive behavior. The concept of stridulation as a ritualized form of social interaction cannot be dismissed. After three signals were exchanged - crab A signaled to crab B, crab B signaled in return, crab A repeated the signal to crab B - a fight always ensued and these fights were not the ritualized fight observed by Crane (1967) but approached what Schone (1968) called a "wild fight." These fights lasted longer than the fights described by Pearson (1977) which lasted only a few seconds. During a ritualized fight the crabs grasp each other, strike, lunge and push while the surrounding crabs continue to behave as though they were oblivious to the encounter. Wild fighting, however, was more violent and the combatants scuffled over a wider area while surrounding crabs retreated from the fight. In some cases injury was noted. Most of these wild fights occurred during the fifth series conducted with sixteen male crabs.

It is interesting to compare the series in which the crab density was very high relative to natural conditions, with those series in which eight crabs were observed. As stated in the results, the high density series actually produced fewer signals than the other all male series. The increased density may have inhibited "normal" social in-

teraction, as it would be reasonable to expect that the high kinetic level of this series would increase signaling. In all the series, the number of claw shudders given from trial to trial decreased. Since the second and fourth series were conducted with acclimatized crabs it seems unlikely that this diminished signaling is the result of becoming adjusted to laboratory conditions. It appears, however, that the claw shuddering display was used less frequently as the crabs became "adjusted" to each other. It is possible that during the first trials initial encounters were the basis for forming a type of hierarchy. After this hierarchy was established the need for claw shuddering to demonstrate relative size was reduced, since smaller crabs deferred to the larger. This may also have implications for the series conducted with both male and female crabs. Females are usually smaller than male crabs, and because females equal in size to males were difficult to collect the proposed hierarchy may have become established more rapidly. Thus the number of claw shuddering events in these series would be significantly less than half of the number of claw shudders seen in the all male series.

The trials within each series demonstrated a close correlation between the amount of claw shuddering and the condition of the environment, specifically tidal and photoperiod influences. For the purpose of analyzing the data the increased number of claw shudders were considered to be part of the general increase in activity just after high tide and during the maximum ebb of the tide. This idea presupposes that increased activity and increased locomotion would increase the number of possible interactions and hence increase the frequency of

claw shuddering behavior. As has been discussed previously for the fifth series (high male density), increased contacts do not necessarily increase claw shuddering displays. The increased contacts do not necessarily increase claw shuddering displays. The increased locomotion could be the search for shelter from predation. Fish and diving birds are predators during peak high tide and birds devour shore crabs at low tide (Pearson, 1977). The search for shelter would produce displays to defend a territory and therefore claw shuddering would increase during the period when crabs were establishing themselves in refuges. This study did not directly address this question and the environmental results demonstrate when high numbers of claw shuddering might be expected, but does not attempt to explain why.

Guinot-Dumortier and Dumortier (1960) hypothesized that stridulation could be directed toward a potential predator in the manner of a conditioned stimulus. Symons (1970) reported that claw shuddering was released by the experimenter, but did not report the pinching that would form the logical completion of the analogy with aposematic coloration. Since in this study, claw shuddering was not released by a non-crab, it is not possible to verify this idea as being an ethological significance of stridulation.

Balss (1956) suggested that stridulation might unite a number of crabs as a colony. This notion appears to have been repudiated by Hughes (1966) who also studied Ocypodidae. The results of this study with respect to crab density and total signaling would not tend to support the social unit or colony theory (Guinot-Dumortier and Dumortier, 1960).

In conclusion, the results of this study show claw shuddering display to involve stridulation. The significance of stridulation in the total repertoire has not been resolved but territoriality as exemplified by burrow defense and communication facilitating ritualization have been indicated, and its importance in sexual behavior has not been demonstrated.

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Appendix 1. Specifications for Uher 440 tape recorder.

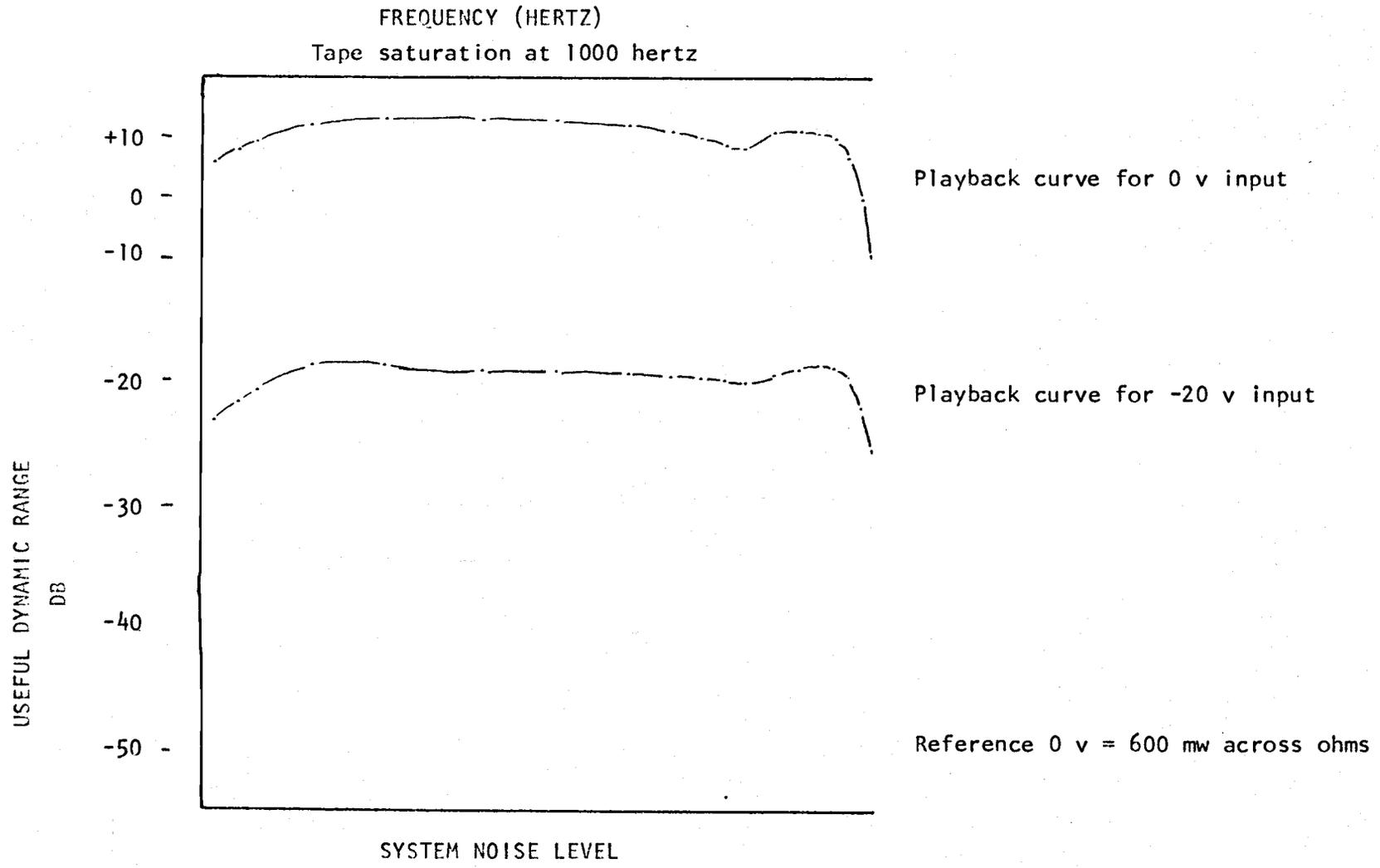


Figure 1. Play and record response curves for Uher 440 tape recorder for Memorex tape sample.

Appendix 2. Specifications for the CH-17 transducer.

CH-17 Transducer is a low level acoustical source with omnidirectional, uniform response over the entire sonic frequency range.

Useful frequency range: 10kHz to 150kHz

Maximum drive voltage: 100 volts rms

Figure 1
Input parameters

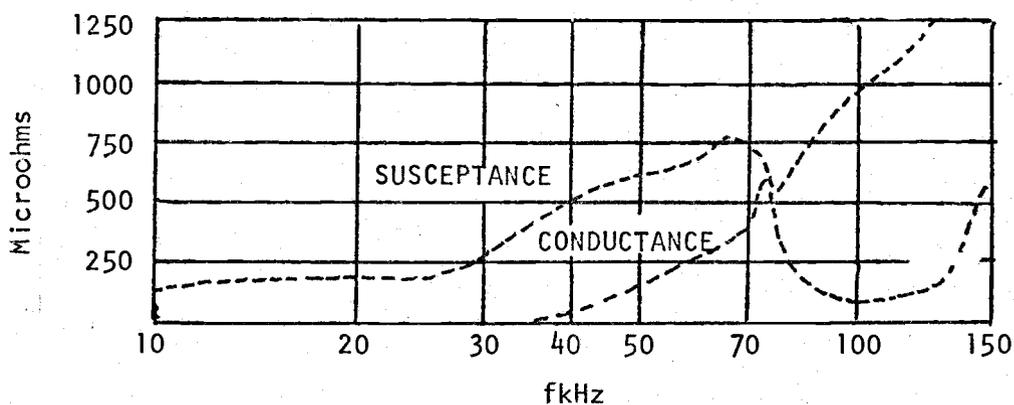
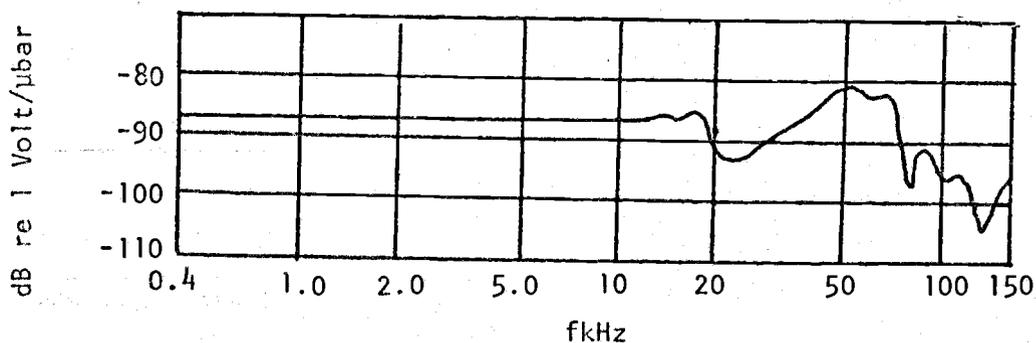


Figure 2
Receiving voltage
response



Appendix 3. Specifications for the Quan Tech Model 206C general purpose low noise amplifier.

Output:

frequency response: 1 Hz to 100 Hz \pm 1 db
maximum voltage: 1 volt RMS at 1 ma
distortion: less than 50 ohms

Input:

maximum overload: 30 volts
impedance: 1 megohm, 30 pF

Noise:

voltage: less than 10 volts
spectral density: 5×10^{-9} volts per root Hz and 3×10^{-12} amperes
per root Hz measured from 1kHz to 100kHz

Power:

battery: two 5.4 volt mercury batteries

Appendix 4. PDP 11 Program used to manipulate and plot digitized acoustic data.

FOCAL-11, V3.9

```

1.01 O READ MARILYNS TAPES, THRESHOLD, & PLOT
1.10 X FB(L,4096);A!!," BLOCKS/FILE = ",NB,!
1.20 X FMT(7);A" FILE ",NF,!
1.30 I (NF)1.2,1.5,1.4
1.40 X FMT(4,100);S NF=NF-1;G 1.3
1.50 D 5;T " AVERAGE = ",AV;A " THRESHOLD = ",TH,!
1.60 F 1B=1,NB;X FMT(1,0);D 2;C SEARCH FOR THRESHOLDS
1.70 X FMT(5,NB) ;A " DO AGAIN? ",A,!;T (FABS(A-OYES)-1)1.5
1.80 S BN=0;6 3.1

```

```

2.01 C SEARCH FOR PEAKS THAT CROSS THRESHOLD
2.10 S I=0
2.20 S I=I+4;I (I=4096)2.3;R
2.30 I (FABS(FF(0,I))-TH)2.2
2.40 T %6.00," BLOCK* ",IB," SAMPLE* ",I," AMPL= ",FF(0,I),!
2.50 S I=I+96;6 2.2

```

```

3.01 C SELECT BLOCK T PLOT
3.10 A " PLOT/ ",A,!;I (FABS(A-OYES)-1)3.2;6 1.2
3.20 A " X SCALE FACTOR= ",SX," Y SCALE FACTOR= ",SY,!
3.25 A " BLOCK* ",B,!
3.30 I (B) 1.2;I (B-BN)3.4,3.6,3.5
3.40 X FMT(5,2);X FMT(1,0)S BN=BN-1;6 3.3
3.50 X FMT(1,0);S BN=BN+1;6 3.3
3.60 S BN=B;D 4;6 3.25

```

```

4.01 C PLOT ROUTINE
4.10 A " FIRST SAMPLE* ",S1," LAST SAMPLE* ",SL,!
4.20 A " NEW ORIGIN SET? ",A,!;XFP(0);S P=2
4.30 F X=S1,SX,SL;X FP(P,(X-S1)/SX,FF(0,X)/SY);S P=1
4.40 X FP(2,SL-S1,0);R

```

```

5.10 X FMT(1,0)S AV=0
5.20 F 1A=1,8,4096;S AV=AV+FABS(FF(0,1A))
5.30 S AV=AV/512;X FMT(5,1);R

```

Appendix 5

File 11

AVERAGE	10	THRESHOLD	60		
BLOCK	1	SAMPLE	2068	AMPL	60
BLOCK	2	SAMPLE	3268	AMPL	64
BLOCK	2	SAMPLE	3468	AMPL	73
BLOCK	2	SAMPLE	3592	AMPL	64
BLOCK	3	SAMPLE	80	AMPL	82
BLOCK	3	SAMPLE	632	AMPL	63
BLOCK	3	SAMPLE	732	AMPL	162
BLOCK	3	SAMPLE	1684	AMPL	63
BLOCK	6	SAMPLE	280	AMPL	73
BLOCK	6	SAMPLE	576	AMPL	223
BLOCK	6	SAMPLE	1252	AMPL	87
BLOCK	6	SAMPLE	1352	AMPL	64
BLOCK	6	SAMPLE	1476	AMPL	102
BLOCK	6	SAMPLE	1616	AMPL	60
BLOCK	6	SAMPLE	1796	AMPL	63
BLOCK	6	SAMPLE	1896	AMPL	458
BLOCK	6	SAMPLE	1996	AMPL	509
BLOCK	6	SAMPLE	2100	AMPL	90
BLOCK	6	SAMPLE	2440	AMPL	75
BLOCK	6	SAMPLE	2548	AMPL	65
BLOCK	11	SAMPLE	2976	AMPL	80

DO AGAIN? NO

PLOT? YES

X SCALE FACTOR 1

Y SCALE FACTOR 33

BLOCK 2

FIRST SAMPLE 3100

LAST SAMPLE 4095

NEW ORIGIN SET?

BLOCK 3

FIRST SAMPLE 1

LAST SAMPLE 2000

NEW ORIGIN SET?

BLOCK 6

FIRST SAMPLE 200

LAST SAMPLE 3000

NEW ORIGIN SET?

BLOCK 11

FIRST SAMPLE 2800

LAST SAMPLE 3100

NEW ORIGIN SET?

BLOCK