

PERCEPTION AND DETERMINANTS OF UNDERWATER VOCALIZATION IN THE CALIFORNIA SEA LION

by
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I. Introduction

The California sea lion (Zalophus californianus) is the best known of all the sea lions, appearing as the trained "seal" in most zoos and circuses all over the world. It is a carnivore and belongs to the Family Otariidae of the Suborder Pinnipedia (55). These marine mammals are characterized by having an external ear or pinna and a hind-flipper which can be turned forward for either standing or for purposes of quadrupedal locomotion (34). The fore-flippers are large and are the primary means of propulsion in swimming (15).

The first systematic account of all the pinnipeds to be published within the past 50 years is the book by Scheffer (55) entitled Seals, Sea Lions and Walruses. The author, who cites some 500 references, shows clearly that we know a good deal about the morphology, ecology and distribution of these animals and something of the physiology of certain selected species. In addition, due primarily to the efforts of Bartholomew and his associates (6,7,8), we know something of the social behavior of the northern fur seal and the northern elephant seal during the breeding season. Yet, in spite of this, our information about the sensory and behavioral capacities of seals and sea lions is extremely meager. Thus pinnipeds in general, and specifically the California sea lion, have been a neglected group of animals in the

area of comparative animal behavior and should be studied more assiduously, both in their own right and especially if we are to place the behavioral capabilities of other marine mammals, such as the whales and porpoises, in proper perspective.

In view of recent research activity and discussion on the sonar or echolocation capabilities of the bottlenose porpoise, Tursiops truncatus, (32,47,48) its vocal and communicative abilities (2,16,38,39), and its visual and auditory perceptual abilities (30,32,56), it behooves the student of animal behavior to run parallel studies on other marine mammals (e.g., seals and sea lions) having grossly different sensory and brain structures from those of porpoises. A start in this direction has been made by the author and forms the substance of this paper.

Since it has been firmly established that the bottlenose porpoise possesses an extremely efficient biological sonar system, it is reasonable to suspect that other marine animals may also be so endowed. As Schevill, Watkins and Ray (57) have pointed out, although little is known about the sea lion's olfaction, audition and vision, what is known about their ecology suggests at least an expert passive use of sonar (listening), if not an active use of sonar (echolocation) for purposes of navigation and finding food.

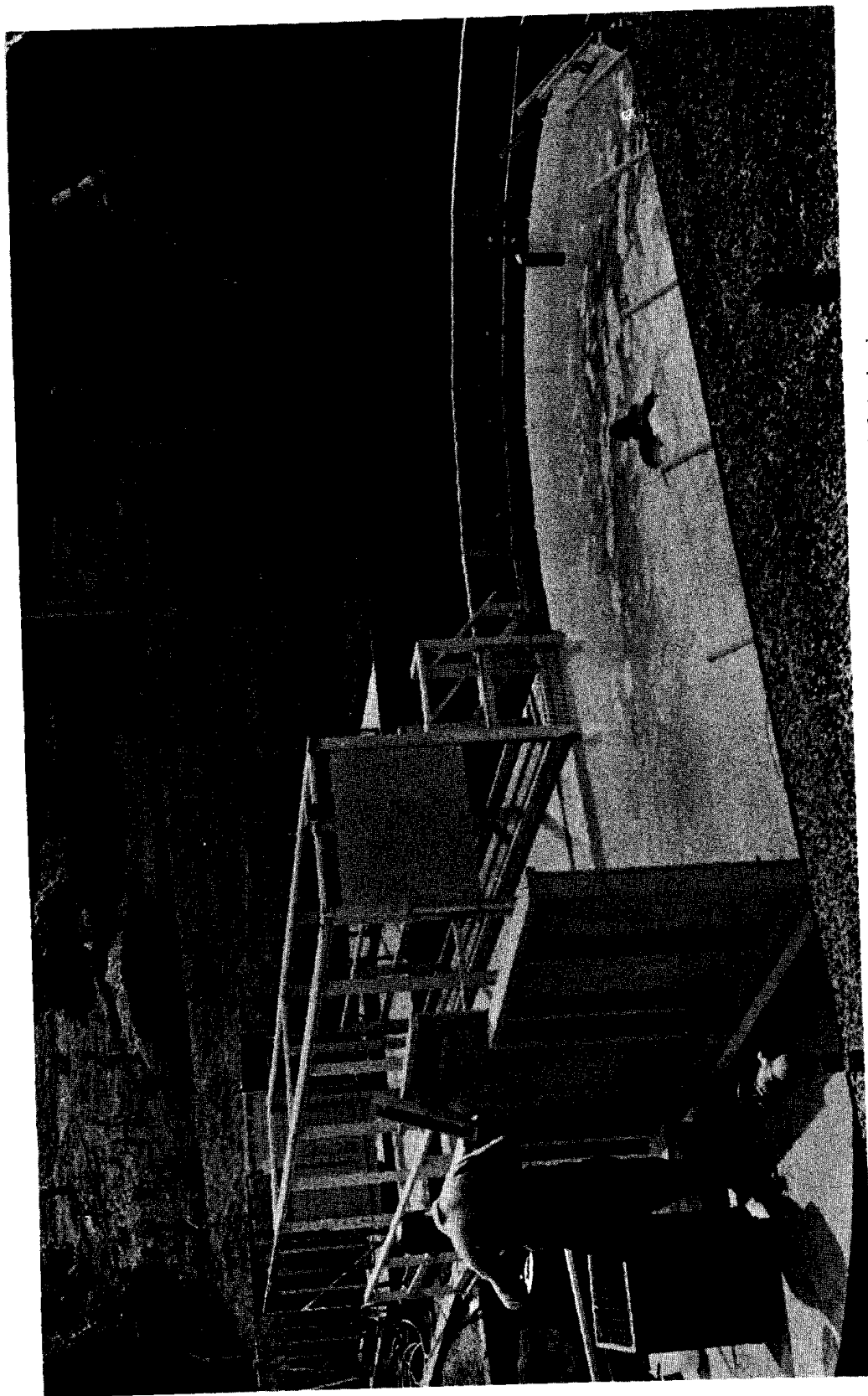
II. The Present Approach

A. The Problem

The initial impetus for these studies was Poulter's report (50,51) that the emission of "sonar" clicks by Zalophus enabled it in total darkness not only to detect pieces of dead fish but also to discriminate between a piece of fish and a piece of horsemeat of approximately the same size. However, as our initial exploratory studies were undertaken,

it was soon apparent that if Zalophus had a sophisticated sonar system, its properties and functioning were much more elusive of demonstration than had originally been suggested by Poulter. Initial observations indicated that the California sea lion was primarily a visual animal. Furthermore, in contrast to the Atlantic bottlenose dolphin (32,48), the "sonar" pulses which were initially elicited from our young captive sea lions were indeed scanty. Thus, it was reasoned that the operation of Zalophus' sonar system, if indeed one exists, ran more along the lines of the oil bird, Steatornis caripusis (25), or possibly the fruit-eating bat, Rousettus (26). These animals orient themselves visually when light is present, but depend on easily audible clicks in the absence of visual cues. The most logical approach, therefore, was to find out something about Zalophus' sensory abilities and to determine under what conditions "sonar" clicks could be elicited.

Since there was virtually no information in the literature regarding the sensory capacities of Zalophus, preliminary studies of their visual and auditory perceptual capabilities were of primary concern. Concurrent with these studies a major effort involved the development or search for a model or concept which would facilitate understanding the causes of Zalophus' production of underwater clicking vocalizations as a general phenomenon, rather than as the first stage of a highly efficient biological sonar system. The most widely applicable approach was to view clicking as part of a single system of vocalization or calling. Furthermore, such vocalizations were considered as one component of the "orientation reflex" or "alerting responses" in general which may be evoked by a complex of stimuli relevant to such states of high muscle tonus and autonomic activity (3,4,5,9,66). This approach was modeled after that of Andrew who has developed the concept of "stimulus



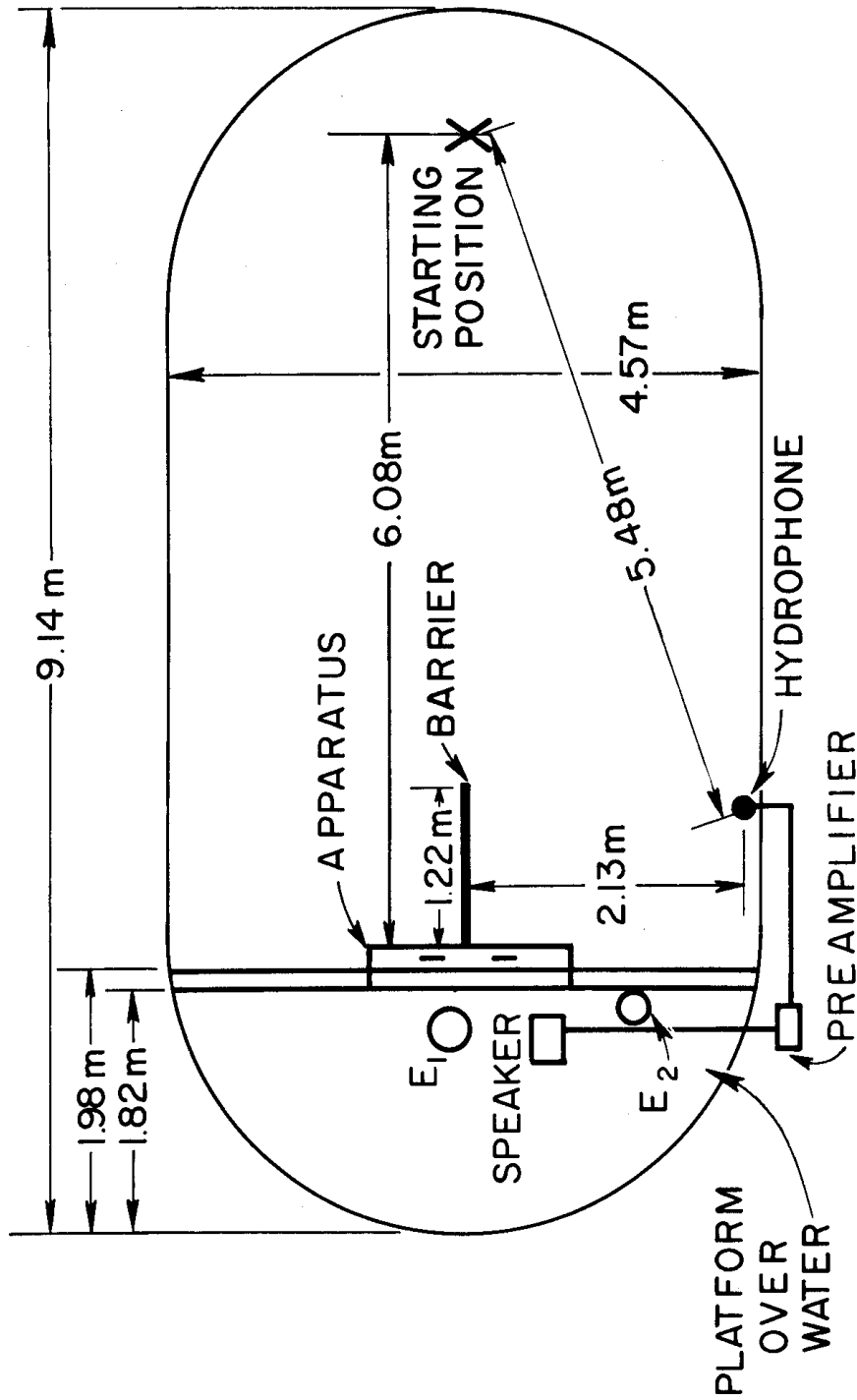
1. A sea lion in the experimental tank waiting for a trial to begin.
The experimenter is in the process of changing targets.

contrast" to account for the vocalizations of chicks and nonhuman primates. According to Andrew, "calls appear to be elicited by any stimulus that by its inherent properties or by valency given by conditioning is capable of arousing intense or prolonged attention. Such stimuli are said to possess 'contrast'. The more intense the contrast, the more intense is the resulting call." (3, p.315).

B. Methodology

All experiments except those dealing with underwater hearing were conducted in an oval tank, constructed of redwood and measuring 4.6 m by 9.1 m and 1.8 m deep. The interior of the tank was painted white; during testing it was filled with 82 kl of fresh water, and animals could be observed and photographed by means of six windows spaced around the perimeter of the tank.

Generally, two types of procedures were used. The first was a discrete-trial procedure in which various kinds of stimulus targets in a fixed position were submerged from the testing platform shown in Fig. 1. The experimenter (E) worked from behind an opaque screen which was set out 15 cm from the dock area and extended down to the water line (see Fig. 1). Unless otherwise indicated, two targets were presented simultaneously so that they projected below the opaque screen and were at least 38 cm below water level. At the beginning of a trial, a stimulus panel located behind the opaque screen was lowered to the water level. Attached to the side of the stimulus panel facing the E were two rods, 1.1 m in length and 0.64 cm in diameter. The targets were attached to the lower portion of each rod by means of set screws. Deflection of either rod activated a microswitch which produced an audible click as well as a light signal behind the stimulus panel. A perpendicular divider of mesh wire projected down to the floor of the tank



2. Schematic diagram of the experimental tank showing the starting position of a sea lion during the discrete-trial procedure. Locations of the recording equipment and test apparatus are also shown.

and 1.2 m outward from the opaque screen, thus lying between the targets and preventing the animals from moving laterally from one target to the other. The distance between the centers of any two targets was 57 cm. A schematic diagram of the testing situation is shown in Fig. 2.

During testing, the sea lion's task was to push one of two targets in order to obtain a small piece of herring (Clupea pallasii) weighing approximately 5 gm. The E immediately reinforced a correct response by dropping a piece of herring through a 16 cm gap situated between the opaque screen and the testing platform. The stimulus display was immediately withdrawn following either a correct or an incorrect response. The position of the target was an irrelevant cue, i.e., it was randomly determined, throughout all the experiments to be described. In addition to errors or correct responses, the principal behavioral measure under this procedure was the presence or absence of a train of clicks on any given trial. A trial began when the stimulus display was submerged and terminated when it was withdrawn from the water.

The second procedure may be called a free-swimming procedure. Typically, an animal was introduced into the tank and two Es made observations from the testing platform by means of a time-sampling technique. This procedure enabled E to obtain a minute-by-minute quantitative record of each sea lion's specific behavior patterns including underwater vocalizations. The details of this technique are outlined in Section VI, E.

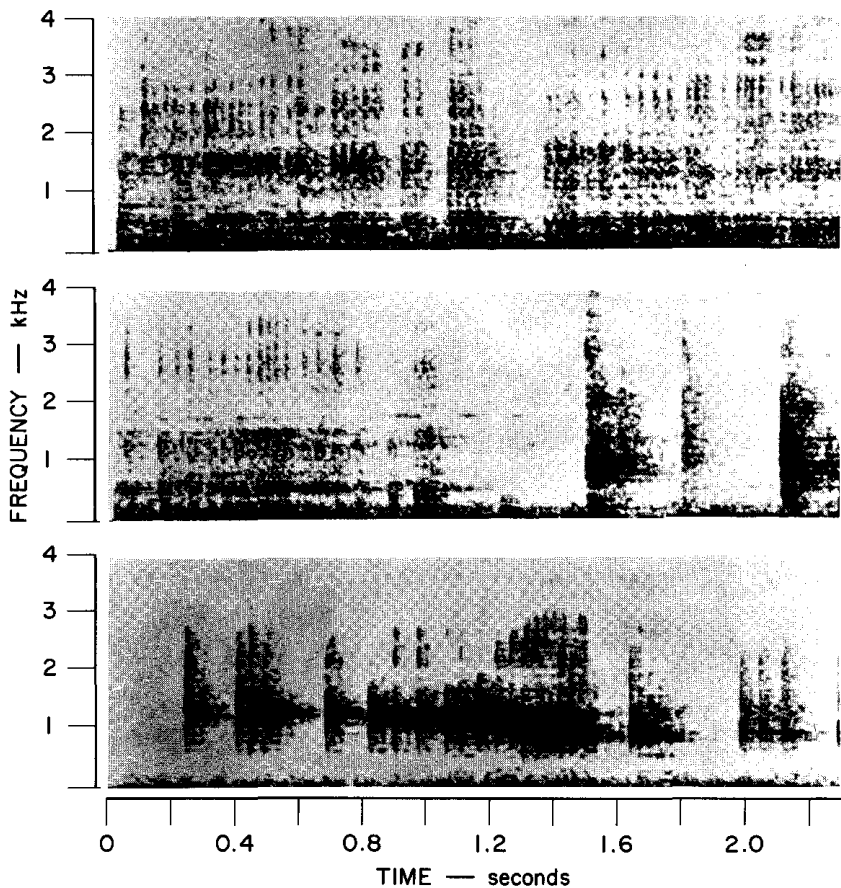
Throughout the entire research effort, underwater vocalizations were continuously monitored by a Channel Industries 275 hydrophone (20 Hz to 150 kHz) and an Ampex 2044 amplifier-speaker system (65 Hz to 13 kHz). Vocal signals were periodically recorded on a Uher 4000-S tape recorder at 20 cm/sec. (40 Hz to 20 kHz) and were analyzed by a Kay 661 audio spectrum analyzer or sonograph.

III. Underwater Sound Production

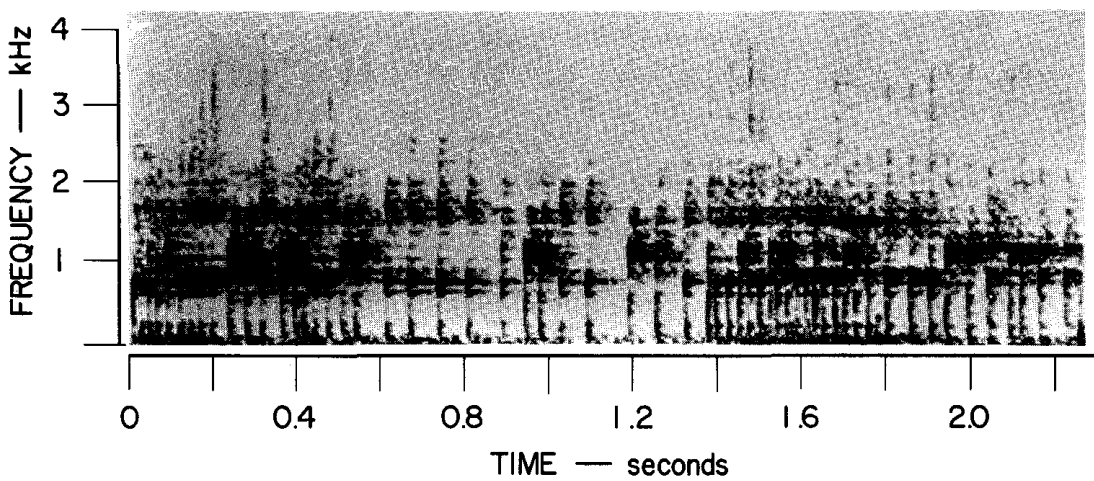
Although it has long been known that cetaceans, especially the porpoises, are capable of producing different kinds of underwater sounds (32), observations of the sea lion's underwater sound production has only recently come to light (50). The California sea lion, thus far, has been especially implicated in the emission of two types of underwater sounds--clicks or short-duration sound pulses and barks (57). In contrast, the bottlenose porpoise has been reported to produce a wide variety of sounds which have been generally categorized as clicks, whistles or squeals, barks (20) and "cracks" (14). Although the clicks have been primarily implicated as the sonar signal of the porpoise, there is good evidence indicating that a variety of whistles have emotional and communicative significance. Some whistle contours and the cracking sounds have been shown to be associated with distress or fright reactions (14,40).

On the other hand, underwater clicks by Zalophus have been reported to occur usually when an animal was in the final stages of searching for food (50,57) or for an object signalling food (19,59). Most of these tests have limited the range of behavior to those involved in feeding activities. In order to determine whether Zalophus is capable of emitting a greater variety of underwater signals and calls than previously reported, several sea lions were monitored while swimming freely under a number of stimulus conditions, including novel or strange objects and social interactions (see Section VI, E for a more detailed account of the stimulus situations).

Sonograms of the evoked signals were made, using the Kay sonograph. This technique provides a graph of frequency against time, with the intensity of each frequency-band shown by the darkness or density of the



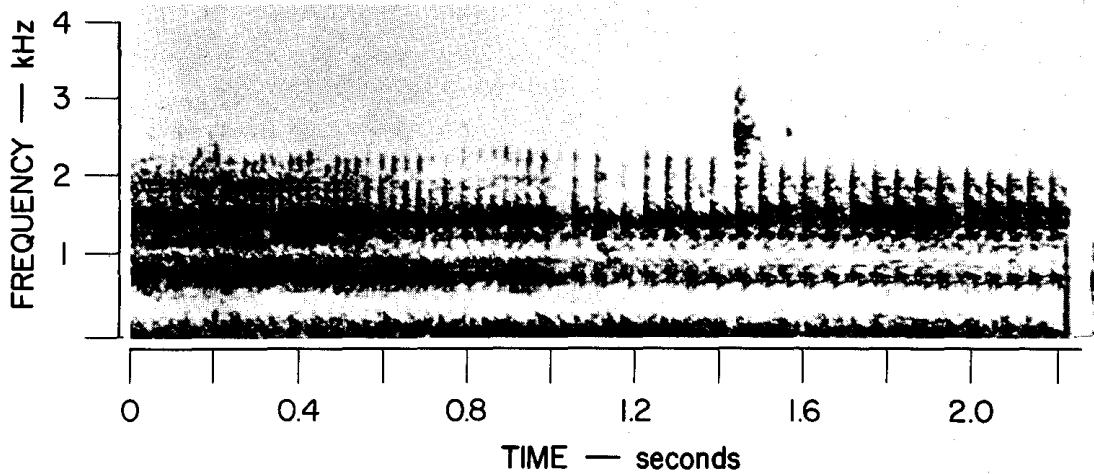
3. Sonograms sampling a continuous series of clicks emitted by a 3-yr-old female California sea lion (Bibi) while apparently searching for live fish in very turbid water (narrow band).



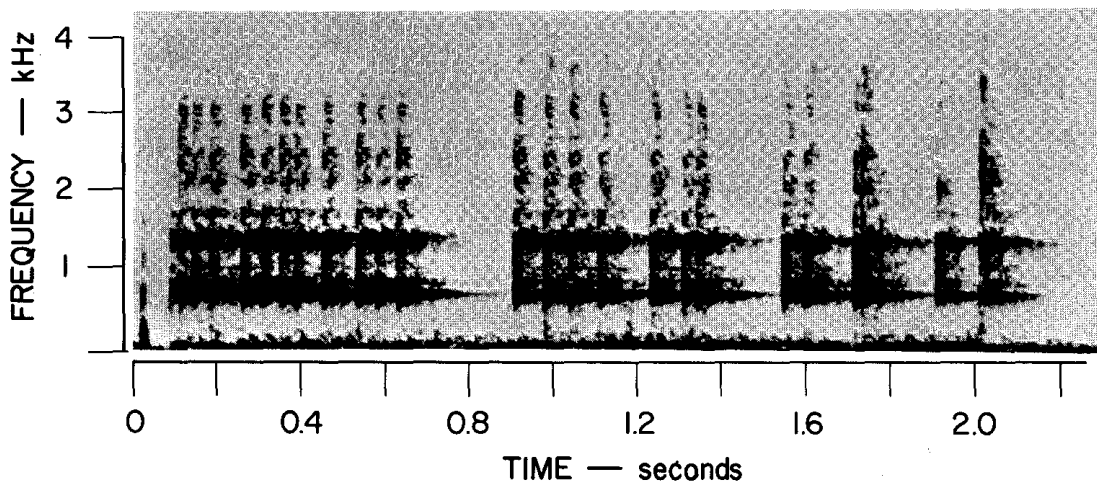
4. Sonograms of clicks emitted by a 3-yr-old female California sea lion (Cathy) while play-fighting with another sea lion (narrow band).

paper markings. Either of two analyzing bandpass filters (narrow or wide) may be used with the Kay sonograph. The wide-band filter has an effective bandwidth of 300 cycles, and the narrow-band filter has an effective bandwidth of 45 cycles. The analysis used is indicated on each of the sonograms presented. The use of this method for the analysis of biological sounds has been described by Borror (12).

Clicks. From our analysis, and as is apparent from a careful inspection of the sonograms illustrated in this section, Zalophus produces almost an infinite variety of click patterns. Although most of the click trains have a duration of 2 sec. or less, many trains last as long as 23 sec. with pauses of less than 0.5 sec. A few clicks are merely very narrow columns of "noise", i.e., without harmonic structure (e.g., sonograms b and c shown in Fig. 3). Most, however (e.g., Fig. 4), are composed of a fundamental and at least one harmonic. In the sonograms shown the dominant frequencies range from below 500 Hz to as high as 1200 Hz with components only slightly above 4 kHz. The click repetition rate may vary from less than 5/sec. to 70 or 80/sec., all within a given click train (separation between clicks of 0.5 sec. or less). Figure 3 presents a particularly interesting series of clicks. The sonograms show a sample of 7.2 sec. of a continuous series of clicks lasting approximately 22 sec. The sea lion (Bibi) produced this series while apparently searching for live mudsuckers (Gillichthys mirabilis) under extremely poor visibility conditions (see Section VII, B). The figure shows the beginning of the click series (a) which had some very low frequency components with a repetition rate of about 50 clicks/sec. During the middle of the series, there was a short pause (b) followed by two high energy "cracks" or "bangs".



5. Sonogram of clicks emitted by a 4-yr-old male California sea lion (Growler) while swimming freely in clear water (narrow band).



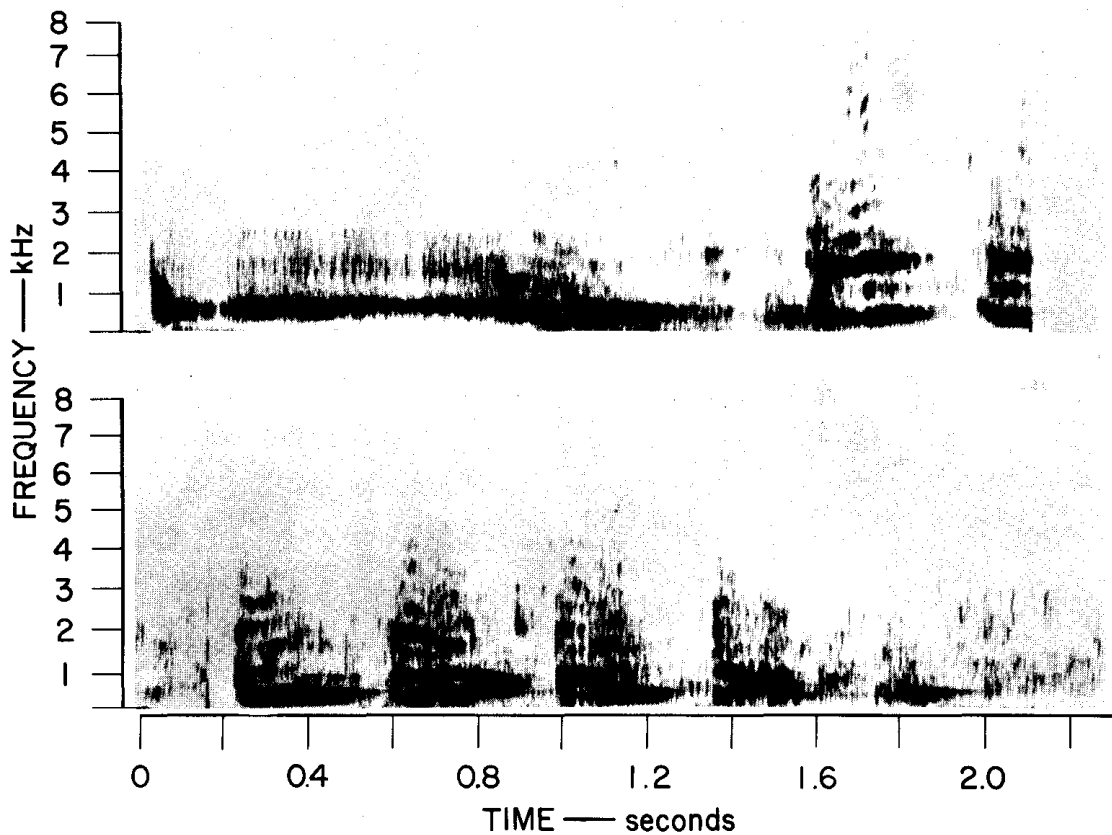
6. Sonogram of clicks produced by a 3-yr-old male California sea lion (Sam) while swimming in the presence of a mirror stimulus (see Section VI, E of text) (narrow band).

Subsequently another short pause occurred and clicking resumed with the dominant frequency at 1250 Hz (c) and a pulse rate as low as 10/sec. Although all the initial clicks covered a frequency spectrum of about 4 kHz, some clicks toward the end of the series showed rather systematic changes in frequency ranges (shown in c); some had a frequency range of less than 1500 Hz.

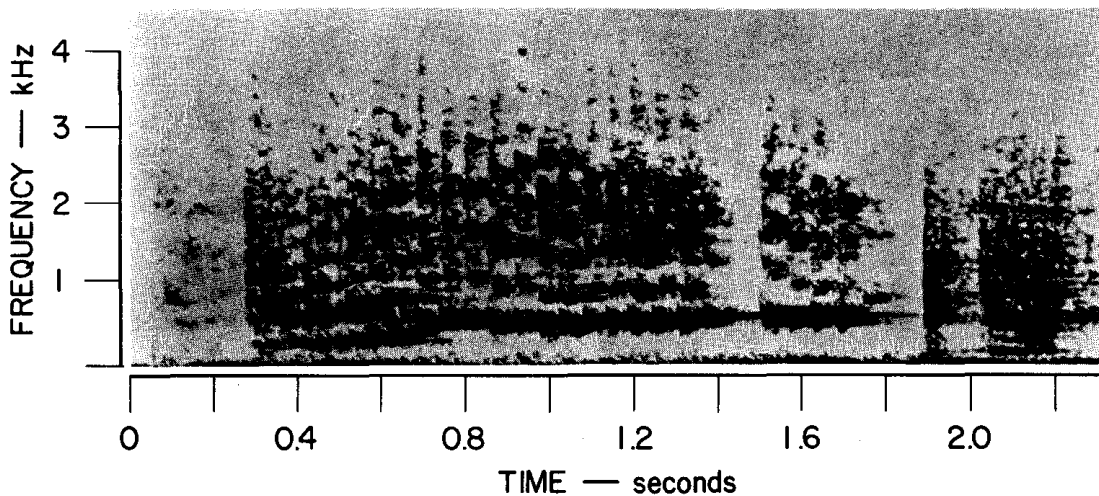
Figure 4 is a sonogram of clicks produced by one sea lion while play-fighting with another sea lion. When the tape which produced this sonogram was replayed, I noted that a popping sound seemed to be superimposed on the clicks. This is indicated on the graph, I believe, by the great variation in the frequency pattern. Such a sound pattern is highly distinctive and has been produced by only one of the animals (Cathy). Figures 5 and 6 present underwater clicks emitted by two male Zalophus and are indicative of two other types of click patterns.

It is important to note that clicking sounds were never emitted at fairly regular intervals by any of the animals under any of the free-swimming conditions. This is in marked contrast to the bottlenose dolphin, which is reported to emit "exploratory" pings every 15 to 20 sec. (32). Such periodic signal emission has been suggested as the sonar equivalent to "glancing" in the field of vision (32).

Barks. This form of underwater vocalization has most of its energy below 3500 Hz, although some energy may be found at frequencies as high as 8 kHz. There is little variation in the duration of any given bark--they generally last from 200 to 300 ms. Barks are sometimes preceded by a series of clicks, as shown in Fig. 7. The sounds shown in this figure were produced by a two-year-old male Zalophus while it was fleeing from the E who was attempting to drive the animal out of the testing tank. During E's initial attempts, the animal swam rather rapidly



7. Sonograms of clicks and barks produced by a 1.5-yr-old male (Tommy) while fleeing from the experimenter (wide band).



8. Sonogram of Bibi's "whinny" vocalization produced during an aggressive encounter with another California sea lion (see Section VI, E of text) (narrow band).

while producing long trains of clicks. As the action became more intense, the clicks shifted into a series of barks. The shifting from clicking to barking under these circumstances suggests that the two types of calls form a single system of vocalization which changes as a function of the level of arousal, with barking indicative of a higher level of arousal than clicking.

"Whinny". A sonogram of this vocalization is shown in Fig. 8. It was frequently produced by a 3.5-year-old female Zalophus (Bibi) during an aggressive encounter. For lack of a better term, we have called it the "whinny" sound since it sounds a little like a horse neighing. This vocalization is often preceded by clicks or a growl sound. The whinny typically lasts for about 1.5 sec. and may be repeated three or four times in succession. The sonogram indicates a fundamental at 500 Hz with harmonics to 3 kHz. The marking on the extreme right of the graph is a water noise. This whinny sound may be the female counterpart of a male bark. However, contrary to another report (11), I have heard females bark both in air and submerged.

"Buzzing". A characteristic "buzz" sound from a sea lion in a social situation is depicted in Fig. 9. This vocalization may actually be a series of discrete sound pulses which occur so rapidly that they take on a buzzing quality.

"Bang" or "crack". This sound has thus far been produced by two of our California sea lions (Bibi and Sam). The sound was first heard when Bibi was confronted with its mirror image and was repeated several times over a period of days, usually under the same circumstances. Figure 10 shows a pair of these high-energy "bang" sounds. The sound, which has always been associated with very rapid swimming, appears quite loud and mechanical to the human ear, and, as the sonogram shows,

it is a broad-band pulse with a rapid onset. Apparently, from the description of Caldwell, Haugen and Caldwell (14), Zalophus' "bang" sound is very similar to high-energy "crack" sounds produced by Tursiops truncatus under conditions of fright. We have recently heard similar sounds produced by the Steller sea lion (Eumetopias jubatus) while performing on an underwater visual discrimination task. It is not clear how the "bang" sound of Zalophus is produced, i.e., whether it is made by the sea lion's vocal apparatus, by jaw-clapping, or by some other mechanism such as the front flippers causing an underwater cavitation as they are thrust together and then parted during initiation of a very rapid swim.

Sound production mechanism. Careful observations of Zalophus while it was in the act of emitting underwater clicks have indicated some movement in the area of the throat or larynx; such movement appeared less pronounced when the animal was silent. These preliminary observations implicating the laryngeal area as the underwater sound-producing site of Zalophus have been supported by experimental evidence (T. C. Poulter, personal communication). Using a triangulation technique, Poulter found that the site of underwater barking was the vocal cords on the anterior portion of the larynx and that the apparent point of origin of underwater clicks was posterior to the vocal cords.

All of the underwater vocalizations that have been described can apparently be produced with the mouth and nostrils closed and therefore without the emission of bubbles, or with the mouth and nostrils partially opened and with the emission of bubbles. Moreover, clicks may be produced in air with the mouth closed or with the mouth wide open. Barking sounds seem to show the same basic frequency-intensity structure in air and under water. However, clicking in air is usually less intense and much less

frequent than under water. Although no systematic attempt has yet been made to measure the intensity of Zalophus' underwater clicks, there has been no difficulty in monitoring these sounds even when the background noise was considerable and the animal was as far as 5 to 6 m from the hydrophone. This contrasts with the findings of Schevill, et.al. (57) who state that the underwater sounds of Zalophus were so faint they could not be detected unless the animal was within 3 m of the transducer.

Although there are certain similarities between the sonar signals of the porpoise (Tursiops truncatus) and the clicks of Zalophus californianus, there are also great differences. Whereas the clicks of the porpoise are very narrow columns of noise having their greatest energy up to 30 kHz with smaller energy fractions to 170 kHz (32,47), those sampled from Zalophus thus far often contain a harmonic structure having their greatest energy at 500 Hz to 4 kHz with possibly smaller energy fractions at higher frequencies. Furthermore, regarding the porpoise, Norris reports that "during fine discriminations where sight is impossible, the environment is literally saturated with tiny plosive clicks, up to 500-600 per second." (47, p.320). Such rapid pulsing has not been consistently produced by Zalophus.

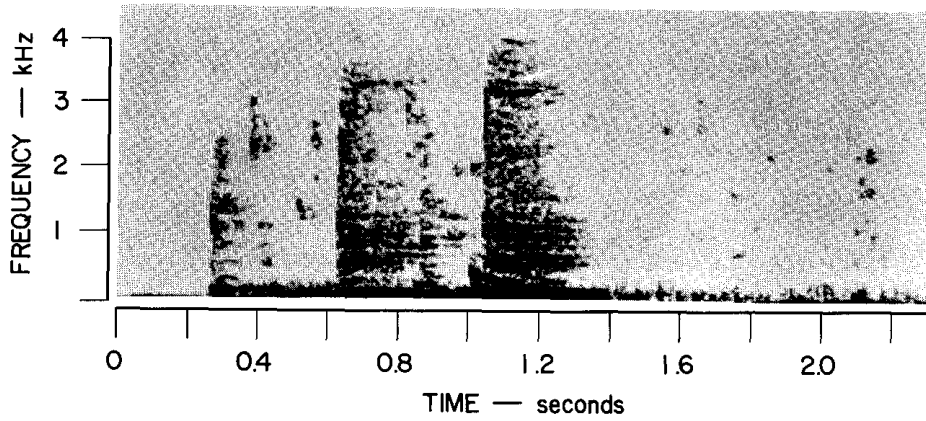
Since a higher vibration rate or sound frequency results in a shorter wavelength between a single compression and rarefaction and therefore a more precise resolution from a reflected echo, the porpoise is theoretically capable of much finer detections and discriminations by means of active sonar than is Zalophus. In fact, by this reasoning, on the basis of the sonograms presented here, Zalophus would be limited to the detection of objects at least 30 to 60 cm in diameter.

IV. Underwater Sound Perception

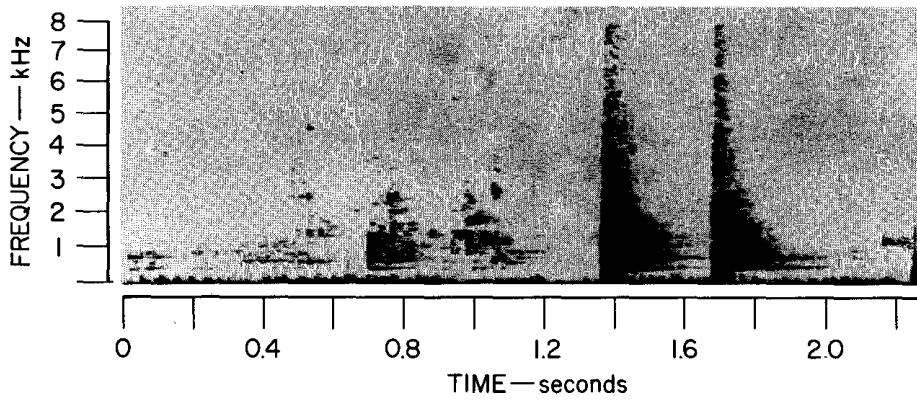
Both Scheffer (55) and King (34) indicate that there is no information of an experimental nature regarding the underwater or in-air hearing of Zalophus, or for that matter of any pinnipeds. There has even been some suggestion that their underwater hearing is "somewhat feeble" (11). However, the general belief of most investigators working with pinnipeds has been that, as in cetaceans, hearing is a very important sensory avenue in seals and sea lions. Our own general impressions tend to support this view. On several occasions, brief sounds have inadvertently been introduced into a testing tank with a submerged California sea lion or harbor seal, invariably resulting in the animal's orientation to the sound source.

In contrast to the very high-frequency hearing of the Atlantic bottlenose porpoise--shown to range between 75 Hz to 150 kHz with peak sensitivity at 50 kHz (30)--preliminary work at our laboratory and by William E. Evans (personal communication) indicates that the upper frequency range of underwater hearing of Zalophus is considerably lower and lies somewhere between 40 and 50 kHz.

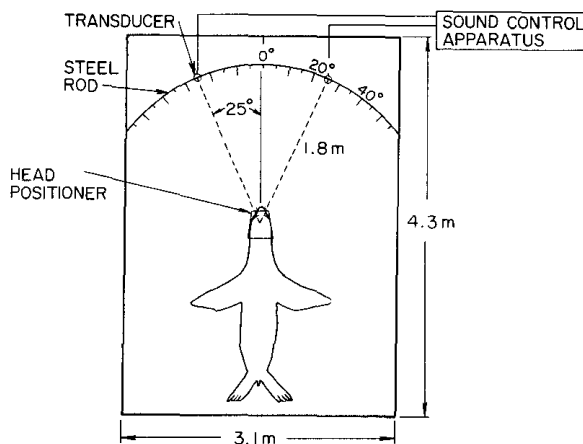
Recent investigations (21,53) on the anatomy and physiology of the cetacean acoustic mechanisms indicate that they are superbly adapted for purposes of underwater hearing with respect to both spectral or frequency analysis and auditory space-perception. A comparable anatomical analysis has yet to be worked out for the pinniped auditory mechanisms. On the other hand, behavioral tests of sea lion's underwater directional hearing, or auditory spatial perception, similar to those conducted by Dudok van Heel (17) with the porpoise, Phocaena phocaena have been conducted at our laboratory by Roger Gentry (23).



9. Sonogram of a "buzzing" sound emitted by Cathy while swimming with another California sea lion (narrow band).



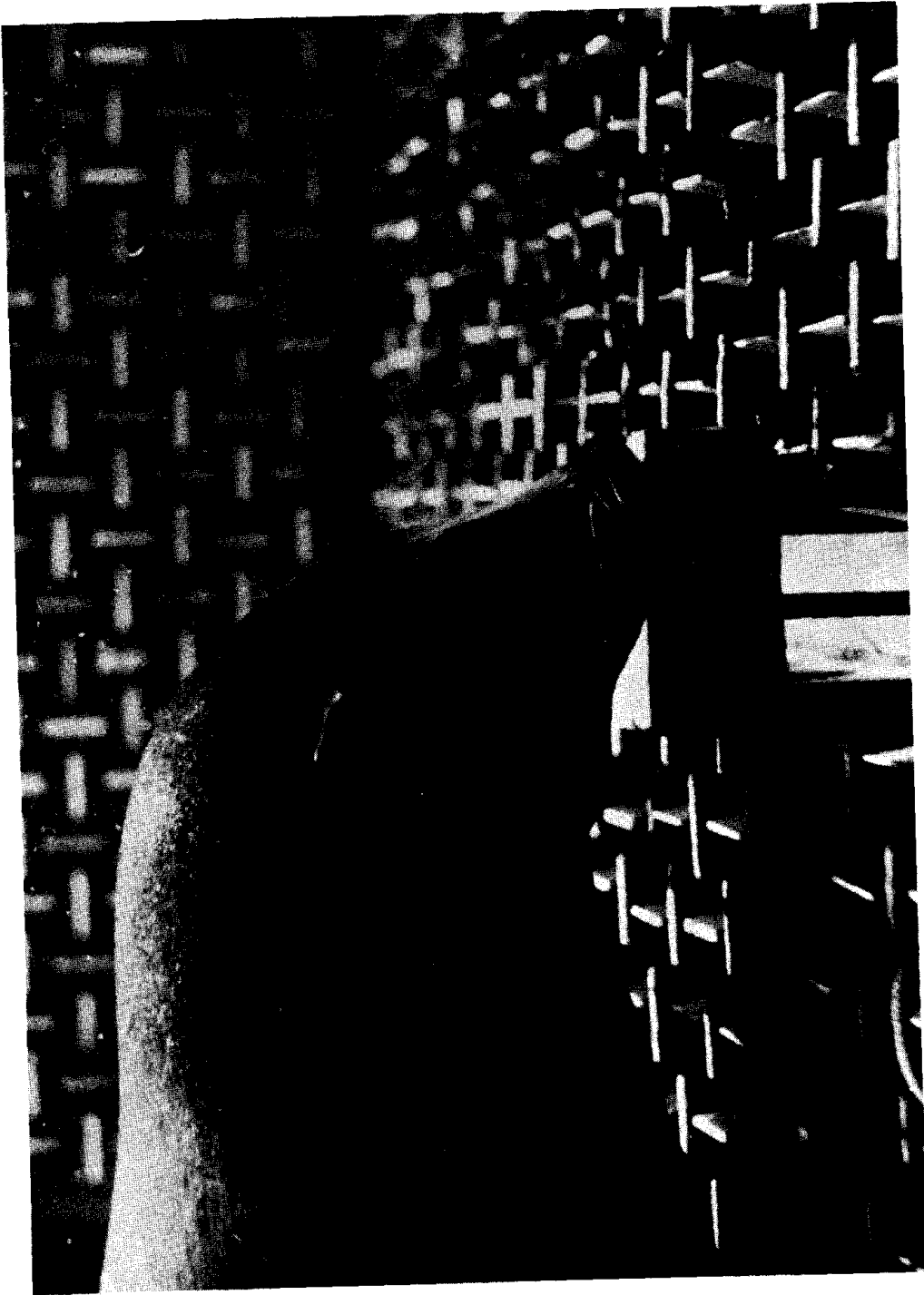
10. Sonogram of two "bang" sounds produced by a 3-yr-old California sea lion (Bibi) while orienting to a submerged mirror (narrow band).



11. Schematic diagram of the tank used to test hearing; shows locations of the sound transducers in regard to position of the sea lion's head.

These tests were carried out in a tank approximately 4.3 m x 3.1 m and 1.5 m deep, made partially anechoic by the placement of 15-cm-long wooden wedges along the walls and floor. At one end of the tank, two barium titanate transducers were suspended 60 cm into the water from a curved metal rod atop the tank. The rod was marked at 5° intervals from 40° left to 40° right azimuth. The median plane of the sea lion's head corresponded to a perpendicular dropped from 0° azimuth. These markings refer to the auditory angle defined as the angle subtended by either of the transducers from the center of the sea lion's head, which was maintained at a fixed position (see Fig. 11). The transducers were attached through a two-place selector switch to a MacIntosh 75-watt amplifier and an HD Model 200 cd wide-band oscillator. A rheostat placed between oscillator and amplifier acted as off-on switch and loudness control for the transducers. To give tones of standard loudness, an Eico Model 460 oscilloscope was attached to a hydrophone hung in the position where the animal's ears would be at the outset of each tone presentation. A rheostat setting was then selected for each frequency and transducer which would give a wave of standard amplitude on the oscilloscope. This was done before each test session. The sound level was + 1 dB (reference ~~1 μ bar~~). To initiate a tone, E selected a transducer and then turned the rheostat quickly to the selected setting and back to zero. Of 90 measured tones produced by this method, 81% had durations between 0.3 and 0.4 sec.

The subject (Growler), a 4-year-old male Zalophus, was trained to lie in a fixed position on the bottom of the tank 1.8 m from the transducers with its head on a wooden block (see Fig. 12). The two-choice discrimination method was used, and the animal was trained to respond to a tone from one of two transducers by swimming to and nose-pressing the manipulandum (a round metal target) spatially contiguous with the

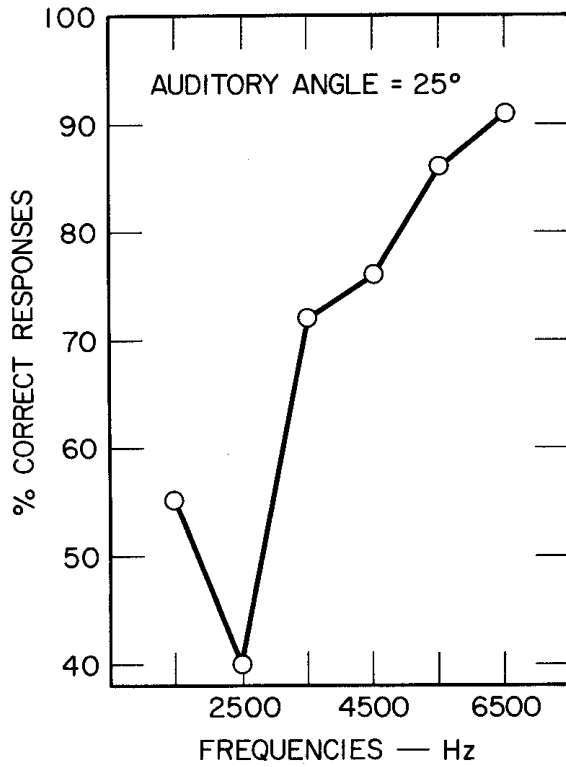


12. A sea lion positioning its head on a wooden block at the bottom of the "anechoic" tank during a test trial of its underwater directional hearing.

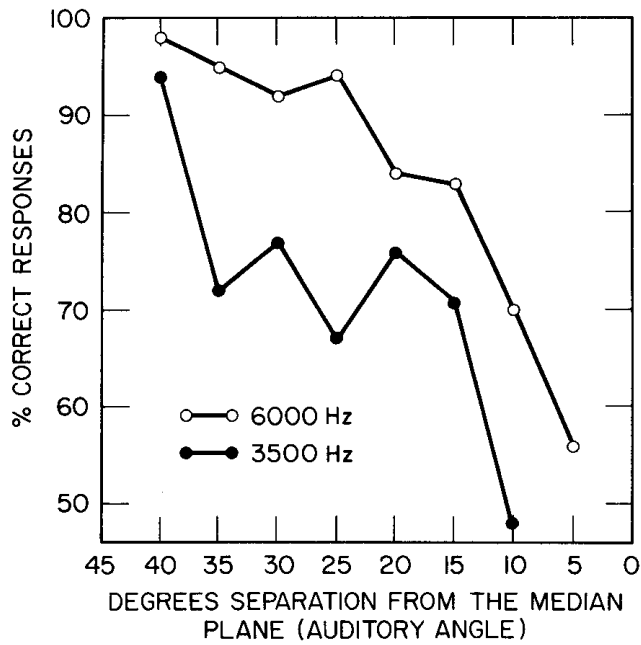
transducer. A correct response consisted of pressing the manipulandum associated with the activated transducer. Each such response was reinforced with a small piece of herring. Errors were never reinforced and a trial terminated with a target press. Activation of the right or left transducer was randomly determined.

As a preliminary step, the psychophysical method of limits was used in order to obtain a range of auditory angle settings with a constant tone of 6 kHz. Following this, formal tests were made by the psychophysical method of constants with tones of 6 kHz and 3.5 kHz. On the basis of the preliminary results, eight auditory angle settings were selected, ranging from 40° to 5° in intervals of 5° . Six such settings were presented for 15 consecutive trials at each test session until a total of 105 trials had been presented at each of the eight auditory angles. Randomized sequences of settings were given from session to session. The results of this experiment are depicted in Fig. 13, which shows correct responses as a function of auditory angle with frequency as a parameter. The results indicate that the California sea lion can reliably locate an underwater sound source at a minimum auditory angle of 10° when a 6 kHz tone is used, and at 15° when a 3.5 kHz tone is used.

In order to test hearing directionality over a wider frequency spectrum range, a second experiment was conducted in which the auditory angle remained at a constant 25° and the frequency varied from 1.5 kHz to 6.5 kHz in increments of 1 kHz. Again the psychophysical method of constants was used with six frequency settings presented for 15 consecutive trials at each test session until a total of 105 trials had been presented at each frequency. The results, illustrated in Fig. 14, show that at a constant auditory angle of 25° , performance of the California sea lion improved as a direct function of increasing frequencies up to 6.5 kHz.



13. Performance on an underwater audio-direction task as a function of auditory angle and sound frequency.



14. Performance on an underwater audio-direction task as a function of sound frequency.

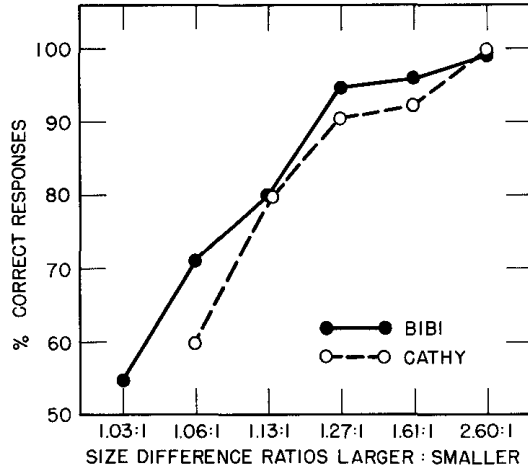
The data points at 1.5 kHz and 2.5 kHz do not differ significantly from chance. Apparently, even at an angle as wide as 25° , Zalophus cannot locate a sound at frequencies much below 3.5 kHz. The reason for this is not as yet clear, and obviously more data are needed. It may, however, be a function of a decreased sensitivity of Zalophus to low-frequency sounds or an unfavorable signal to noise ratio at the low end of the spectrum. Interestingly, Dudok van Heel (17) also found that the porpoise, Phocaena phocaena, was not proficient at localizing a 2 kHz tone.

The present data indicate that, under water, Zalophus and Phocaena have nearly the same degree of acuity of audio-direction at similar frequencies. At 6 kHz, the minimum auditory angle for the porpoise was 8° and for Zalophus it was 10° . At 3.5 kHz, the minimum angle increased for both species-- 12° for the porpoise and 15° for Zalophus. It may be concluded that the California sea lion is as capable as Phocaena in locating the direction of underwater sound.

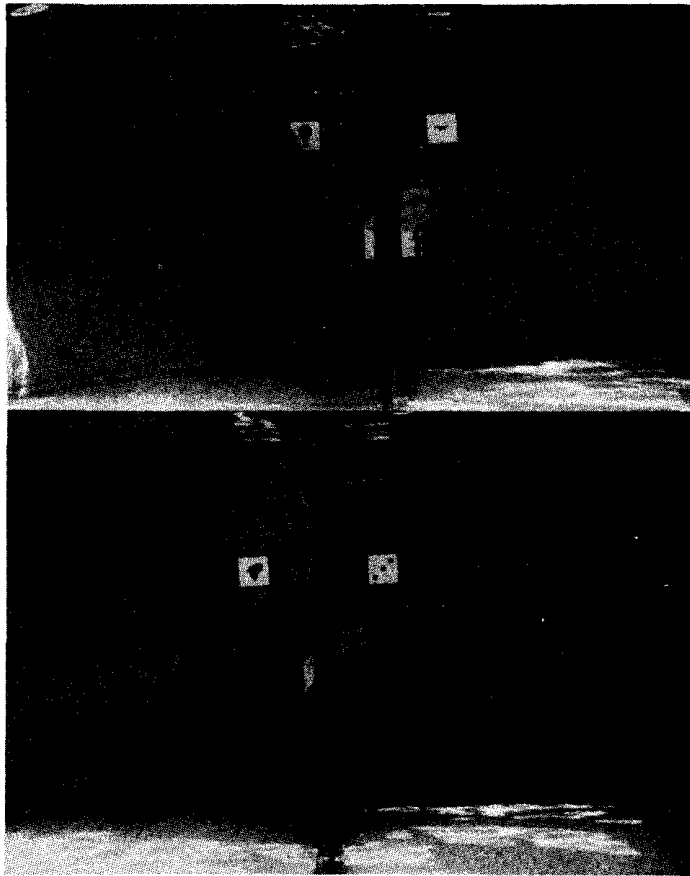
It should be noted that subsequent to the undertaking of these directional hearing experiments with Zalophus, we became aware of Møhl's (43) recent findings showing that under water the harbor seal (Phoca vitulina) can reliably locate the direction of a 2 kHz tone at 3.1° azimuth from the median plane.

V. Underwater Visual Perception

Anatomical evidence suggests that pinnipeds have compensated for the loss of the refractive power of the cornea under water by having a large spherical lens which produces enough accommodation to form a reasonably well-defined image on the retina (70). Recent behavioral data on the underwater size discrimination ability of two California sea lions have confirmed this anatomical evidence (62). Differential



15. Performance curves of two sea lions on a size-discrimination task.



16. A California sea lion (a) indicating its choice on a pattern discrimination task, and (b) swimming toward a new stimulus pattern display. Note the relatively low position of the animal.

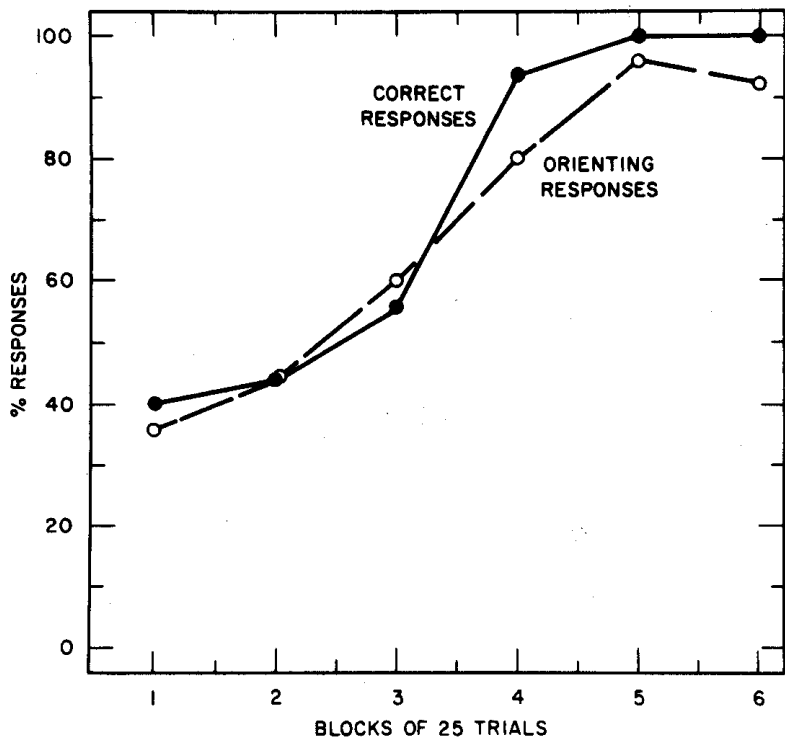
size-thresholds were obtained by the psychophysical method of constant stimuli. The two sea lions (Bibi and Cathy) were always required to respond to the smaller of two triangular or circular targets, and were forced to make a decision at least 1.2 m prior to giving an indicator response. Results of this experiment are presented in Fig. 15, which shows that as the magnitude of the size-difference ratios increased, there was a corresponding increase in correct responses. The figure also reveals that both animals were capable of discriminating a size-difference ratio as small as 1.06:1. Additional data with the Steller sea lion and the harbor seal indicate that these two species of pinnipeds are also capable of discriminating a size-difference ratio of about 1.06:1. If the discrimination of size-differences may be taken as a gross measure of visual acuity, then Zalophus and other species of Pinnipedia may be said to have good underwater visual acuity. Indeed, comparison of Zalophus' results with those of such "visual" animals as the Java monkey (35), and the squirrel monkey (63) reveals little difference in the size-discrimination ability of these divergent mammalian forms.

In addition, preliminary data (59) demonstrating accurate discriminations by Zalophus under darkened conditions (discriminations which could not be made in the same period of time by the human observer) combined with the anatomical evidence indicating the apparent nocturnal adaptations of the pupil, retina and choroid of the pinniped eye (70) suggest that in dim illumination the visual acuity of Zalophus may be superior to that of man. Furthermore, a recent study of underwater discrimination and transfer by the California sea lion revealed remarkably efficient discrimination of stimulus figures differing only with regard to shape (61). Most of these discriminations were maintained near or at a perfect level of accuracy even when positive, negative or both shapes underwent changes

in orientation of 45° , 90° or 180° . Moreover, some unpublished experiments by the author suggest that Zalophus may be capable of solving a wide range of visual discrimination problems of the types shown in fig. 16 after only a single information trial. In line with Hobson's (28) recent observations regarding the tendency of seals and sea lions to approach from below and silhouette their prey (fish) against the ambient surface light even at night, all animals tested thus far approached stimulus targets from a position considerably beneath the lower edge of the targets (see Fig. 16).

From data such as these, it may be expected that Zalophus and some other pinniped forms would rely strongly on visual cues for the detection and discrimination of underwater objects. Further evidence supporting this viewpoint was obtained in an experiment dealing with the gross orienting responses of Zalophus (58). Orienting responses were defined as postural changes of the head or body occurring within approximately 2 m of the stimulus display.

Following a demonstration of perfect discrimination in clear water between a large black circular disk (736.1 cm^2 in area) and a small black circular disk (16.1 cm^2 in area), sea lion Cathy was confronted with the identical discrimination task in turbid water. A harmless vegetable dye (see Schusterman, 1966) was poured into the water so that visibility was attenuated to a distance of approximately 2.8 m, i.e., the maximum distance at which a skin diver was capable of perceiving the larger target. Presumably the animal was unable to perceive the stimulus display when it began its approach approximately 6 m away. Following 150 training trials in turbid water, Cathy was tested alternately in clear water and turbid water. Figure 17 presents the effects of reduced underwater visibility on Cathy's performance. Even though the discrimination had been perfected prior to making the water turbid, and despite the fact



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17. Acquisition of orienting and correct responses in turbid water.

that visibility under water had not prohibited discriminability in advance of the choice point (approximately 1.2 to 1.5 m), Cathy averaged less than 60% correct responses during the first 75 trials. As the figure clearly shows, the acquisition curve for correct responses is closely paralleled by the acquisition curve for orienting responses. This experiment was replicated with two other California sea lions with essentially the same results.

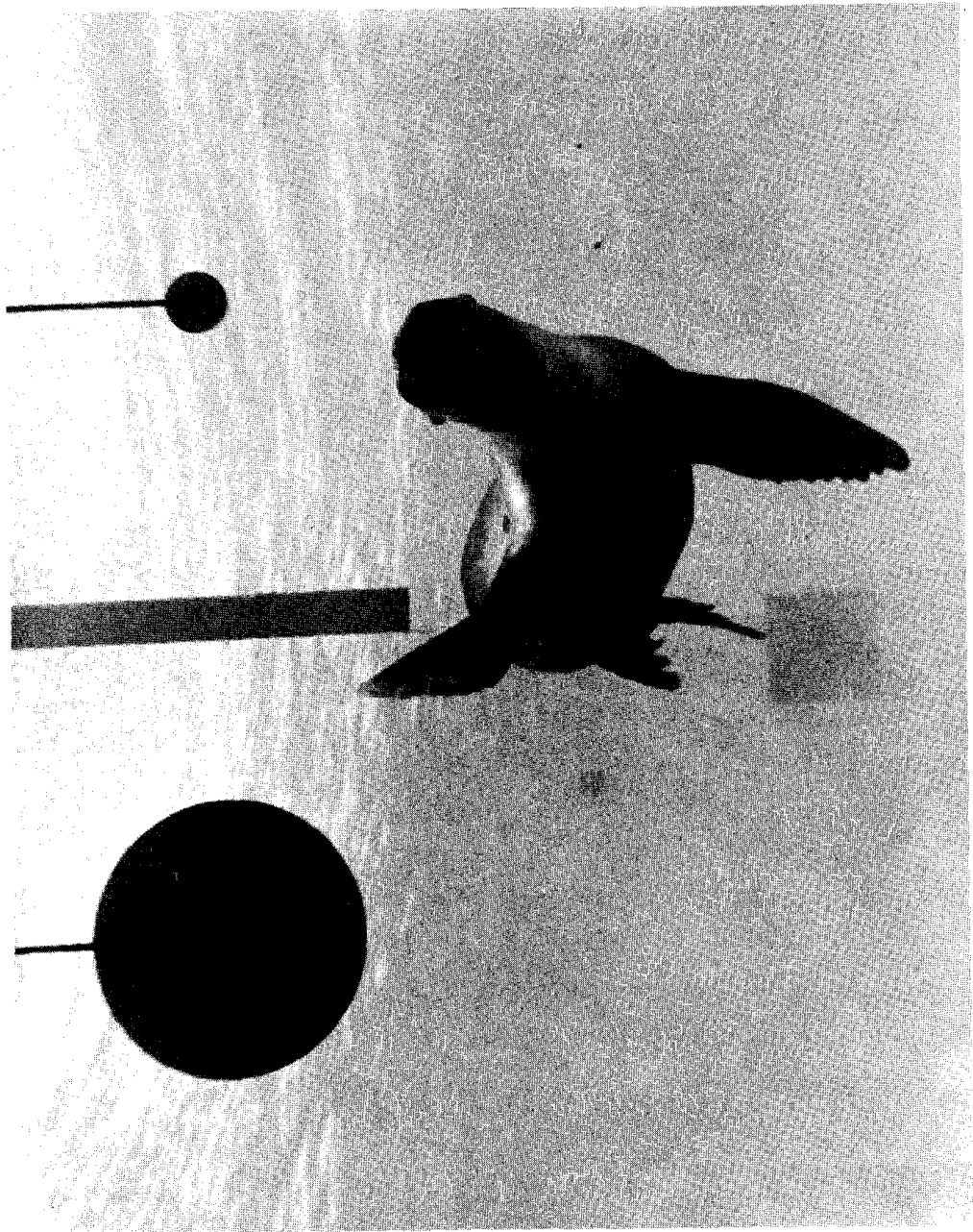
Thus, sea lions swimming in mildly turbid water--which completely occluded their vision as they began their approach toward a stimulus display--learned orienting responses of the head and body in order to discriminate visually between two target stimuli. Discrimination performance remained perfect in both clear and turbid water, but orienting responses remained highly probable only during the latter condition. These results suggest that sea lions rely primarily on postural adjustments and fixating responses of the head and eyes in order to discriminate effectively between two different size objects.

VI. Factors Influencing Production of Clicks and Other Underwater Vocalizations

A. Visibility

Previous exploratory studies have shown that when a captive California sea lion is confronted with an underwater discrimination task, permitting little visibility of the stimuli, it produces clicking sounds and tends to increase the amount of these vocalizations as a function of the degree of water turbidity (59).

Although these quantitative studies were carried out in the laboratory with a single animal, the results have been corroborated by observations on two other California sea lions in another laboratory setting and in the open sea (Evans, personal communication).



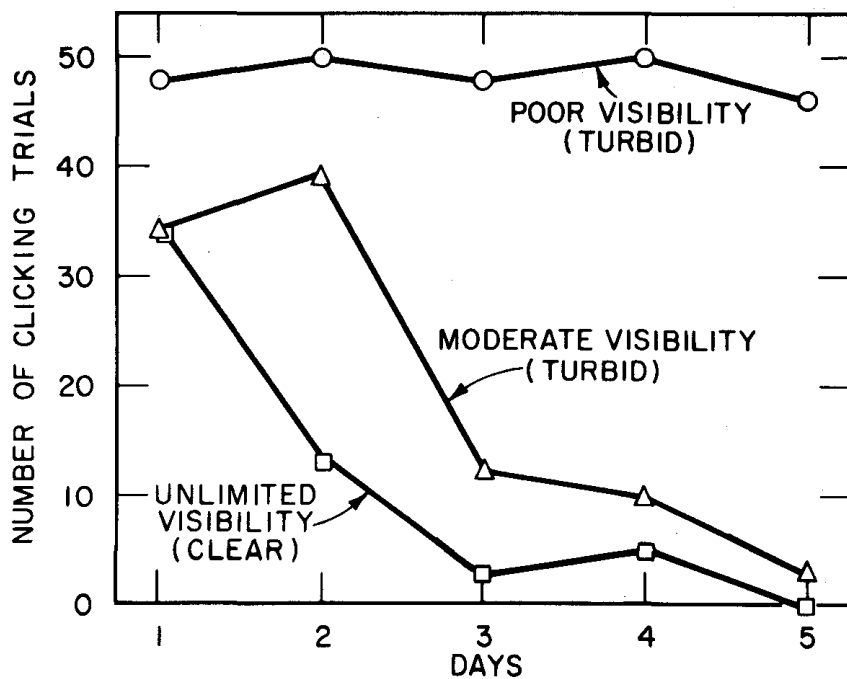
18. A sea lion approaching the smaller of two targets.

On the basis of these results, a hypothesis was formulated suggesting that in addition to being related to the animal's general arousal level, underwater clicking by the California sea lion may be an information-seeking response and thus may be one component of the orienting reflex in this particular species of pinniped.

Thus far, there has been no systematic attempt to vary the degree of underwater visibility over a relatively long period of time in order to determine the joint effect of trials and visibility on the probability of clicking. The following study was designed to do just that and was carried out until the frequency with which a sea lion produced a series of clicks reached asymptotic values under three conditions of visibility (clear water or unlimited visibility and maximum visibilities of 2.7 to 2.8 m and 0.74 to 0.81 m). Since sea lion Bibi had been clicking on virtually every trial under an extremely low visibility condition just prior to this experiment (59), it was hypothesized that the animal would continue its high level of clicking under similar conditions of the present experiment and demonstrate habituation of clicking following a relatively high probability of clicking during the initial trials of the clear-water condition.

Sea lions Bibi and Cathy participated in the experiment. Previously they had both received training on a size discrimination task in clear water and most recently had been tested in turbid water in attempts to demonstrate their "active sonar" capabilities (59). During the latter experiments Cathy received only a few hundred test trials without ever producing a vocalization of any kind, as compared to more than 2500 trials received by Bibi, who made clicking sounds during most of the trials.

Under all three visibility conditions, the animals were required to respond in accordance with their most recent training, Bibi to the larger of two targets and Cathy to the smaller (736.1 cm^2 - 16.1 cm^2 in area).



19. Underwater click vocalizations as a function of visibility conditions and test sessions or days. The ordinate shows the number of trials during which a sea lion produced a train of clicks.

Table 1

Response Latencies (in seconds) as a Function of Visibility Conditions

Condition	Sea Lions			
	Bibi		Cathy	
	Median	Range	Median	Range
Unlimited visibility (clear)	2.9	2.2 - 3.8	3.0	2.1 - 4.2
2.7-2.8 meter visibility (turbid)	3.2	2.3 - 4.5	3.5	2.3 - 4.8
0.74-0.81 meter visibility (turbid)	3.9	2.9 - 5.4	4.5	3.2 - 5.8

The targets were black circles made of 20-gauge steel. Figure 18 shows the type of discrimination used in this study. For the two limited visibility conditions the water was made turbid by means of a vegetable dye. A standard sequence was used each day in a pre- and post-test design. The sequence on each of five consecutive days was as follows:

1. Pre-test. Twenty-five trials of unlimited visibility (clear water).
2. Moderate visibility. Fifty trials with a maximum visibility of from 2.7 to 2.8 m.
3. Poor visibility. Fifty trials with a maximum visibility of from 0.74 to 0.81 m.
4. Post-test. The tank was emptied and refilled with clear water, and the sea lions received 25 additional trials under the unlimited visibility condition.

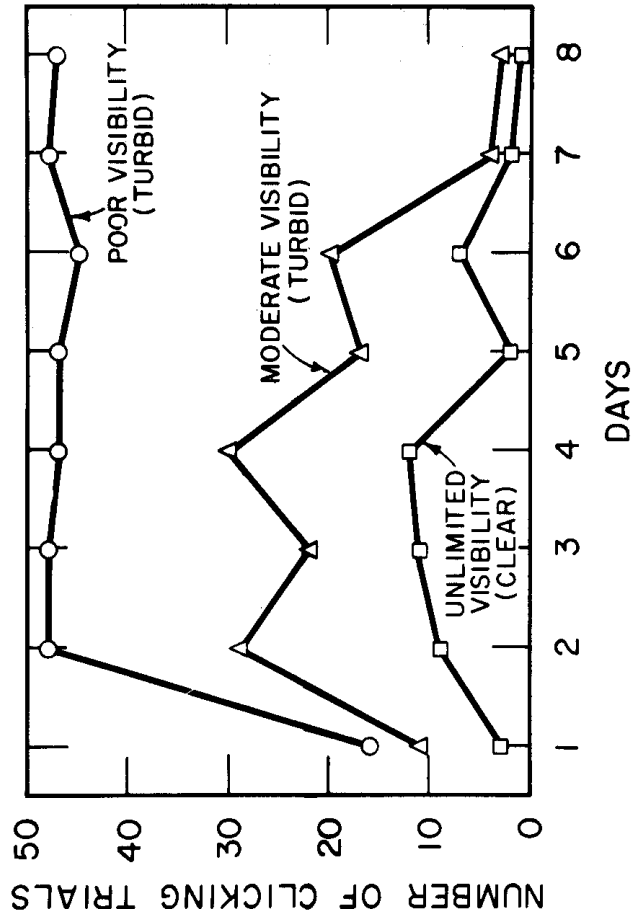
In order to minimize the use of visual cues under the poorest condition of visibility, an earlier series of exploratory studies suggested the use of a 1.2-m divider or barrier (extending outward between the target stimuli) and a procedure whereby an incorrect response could be scored when an animal's nose was just past the side of the barrier on which the incorrect target was located. Since the maximum visibility under the most turbid water condition was considerably less than the distance that the barrier extended outward between the targets, it was assumed that the animals had to make a decision prior to giving the indicator response (pressing the target) at a distance from the stimulus display which afforded virtually no visual information.

Results. There was no difference in the pre- and post-tests; therefore, these results were combined into one condition (unlimited visibility). The main results are presented in Fig. 19. Since Cathy remained silent

throughout the entire experiment, results of this animal are not represented in the figure, which shows that the frequency with which Bibi made clicking vocalizations varied as a joint function of the visibility conditions and the length of time it experienced each of the conditions. As expected, although both animals made almost no errors under the unlimited and moderately limited visibility conditions, they performed near chance when visibility was very poor.

Both sea lions frequently displayed orienting responses of the head or body within 2 m of the stimulus display under both turbid water conditions, but rarely showed such activity in clear water. This behavior is reflected in the response latencies of both animals as shown in Table 1. Predictably, on the basis of the ease of target discriminability, response latency increased as visibility decreased. Latency scores within each of the conditions showed only minor fluctuation from session to session. It should be noted that response latencies for the poorest visibility treatment were based on correct-response and not incorrect-response trials, since targets were usually withdrawn from the water as soon as an animal passed the barrier on the side of the negative target.

Discussion. Although Cathy proved to be a nonvocal animal in each underwater discrimination task, regardless of the degree of visibility, the frequency with which Bibi made clicking vocalizations as a function of visibility was shown to depend upon the length of time this sea lion experienced each of the visibility conditions. Thus, Bibi's results confirmed the initial hypothesis that although underwater clicking during a discrimination task may persist under a continuing state of impoverished visual information, the vocalizations have a higher probability of occurrence during the initial stages of unlimited visibility, habituating at a negatively accelerated rate until there is virtually no clicking at all. Conditioning could not have been a factor since reinforcement was more

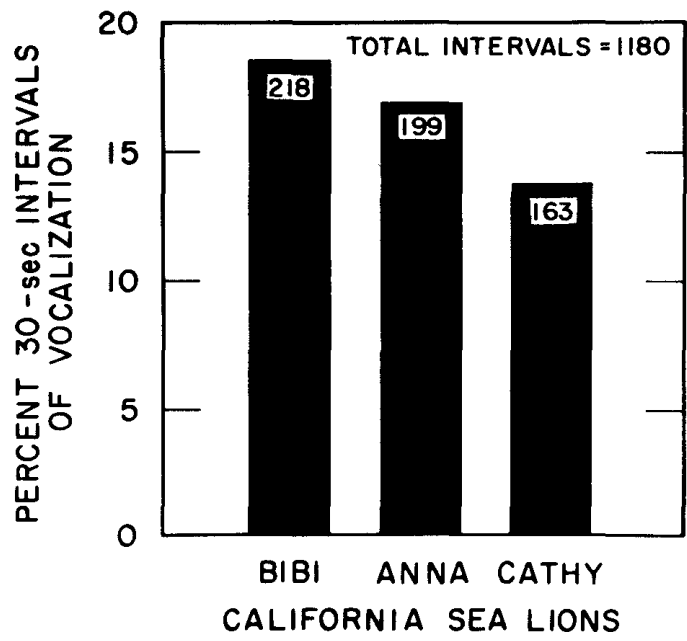


20. Underwater click vocalizations under three conditions of visibility following habituation of clicks in clear water.

probable under conditions of unlimited visibility than under conditions of poor visibility.

Of particular interest was the unpredicted finding that, although the early stages of testing resulted in a higher probability of clicking in moderately turbid water than in clear water, the decline in clicking was more rapid in the former condition, so that the curves describing the clicking probability functions for the two conditions eventually converge at a value near zero.

Since the target stimuli were invisible when an animal began its approach in mildly turbid water, but became visible well in advance of the choice point, it seems likely that the sea lion gradually learned to anticipate target discriminability under this condition. On the basis of this assumption, this animal's results suggest that underwater clicking, rather than being directly related to the turbidity of water as such, depends upon the degree of certainty with which a sea lion can make a decision at the choice point prior to its giving an indicator response. Thus, a clicking vocalization as one aspect of information-seeking behavior does not habituate under conditions of uncertainty which induce and maintain a constant state of conflict and arousal (poor visibility condition), but does habituate under conditions offering little uncertainty. This is so either because the animal can readily distinguish between the food-signalling-stimulus and the nonfood-signalling-stimulus and thus respond appropriately (unlimited visibility condition) or because, by gradually learning, the animal comes to anticipate eventual signal detectability and discriminability prior to making an indicator response (moderate visibility condition). Such an interpretation is consistent with Berlyne's (9) notions relating the influence of conflict induction to the arousal properties of the organism and concomitant information-seeking behavior. Furthermore, if underwater clicking by



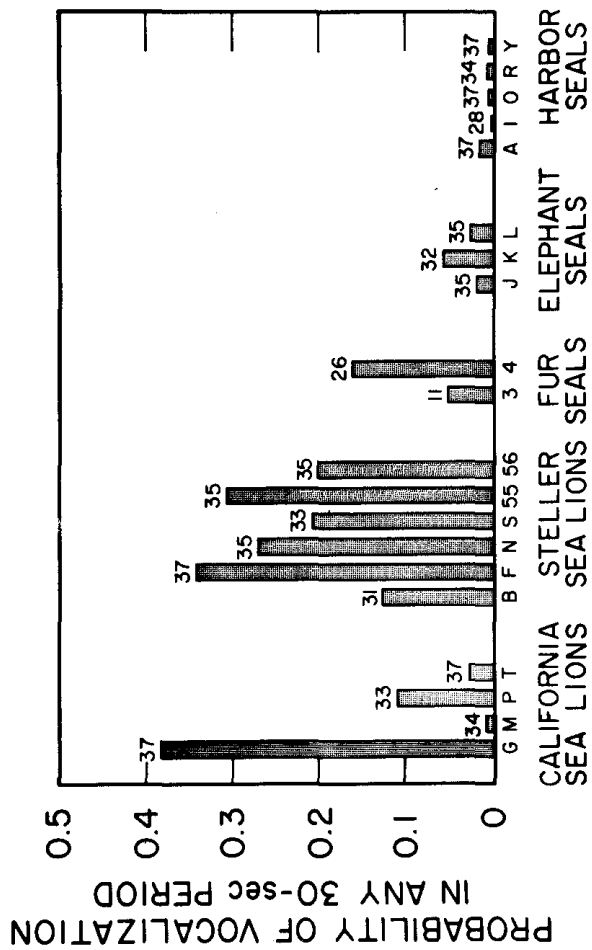
21. Percentage of 30-sec. intervals in which three females emitted any type of airborne vocalization. The number of intervals in which an animal vocalized appears at the top of each column.

Zalophus is in fact one aspect of an orienting reaction, then the persistence of such a reaction is not unexpected. For example, Berlyne, in summarizing the Russian work relating properties of the orienting reflex to stimuli with signal value, states that "the orienting reaction will be singularly intense and last more or less indefinitely if a stimulus with signal value is hard to detect, e.g., because it is near the absolute threshold." (9, p.88).

Although the data from one animal, Bibi, are quite reliable, the fact that Cathy produced no clicking vocalizations under nearly identical conditions discourages any broad generalizations deriving from these results. However, in order to check the reliability of these data even further, a second similar experiment was performed with Bibi. Prior to the initiation of the experiment proper, the animal received approximately 400 trials on a simple size discrimination in clear water and remained relatively silent during each of the trials. On the basis of the previous results and the suggestions formulated from those results, it was predicted that the likelihood of clicking would remain low in clear water, increase to a probability of close to 1.00 under conditions of poor visibility, and increase to some moderate value and then decline to a near-zero value under conditions of moderate visibility. As Fig. 20 shows, the predictions were confirmed. Again, performance in terms of correct responses was perfect in clear water and near chance when visibility was poor.

B. Degree of Airborne Vocalization

The individual differences of the last experiment raise an interesting question concerning the relationship of clicking under water to the general vocalness of a sea lion in air. As a result of general observations made during the course of maintaining three California sea lions (including the two used in the last experiment), it was noted that Cathy appeared to



22. The degree of airborne vocalizations emitted by 20 seals and sea lions. The number of observation sessions for each animal appears at the top of each column.

Table 2

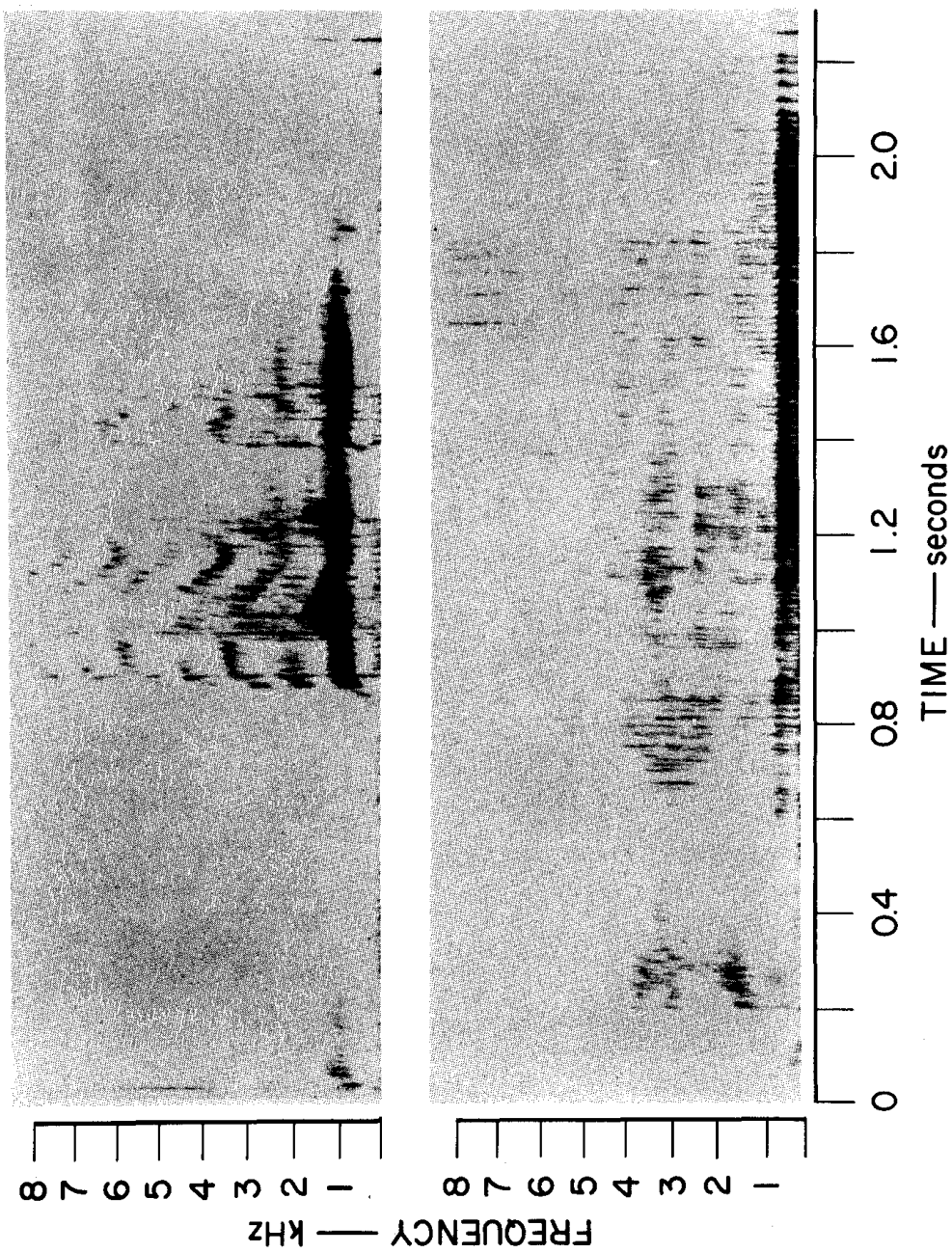
<u>Characteristics of Seals and Sea Lions used in the Vocalization Survey</u>					1.
<u>Animal</u>	<u>Species</u>	<u>Sex</u>	<u>Approximate Age (at time of survey)</u>	<u>Capture Age</u>	
G	<u>Zalophus californianus</u> (California Sea Lion)	M	4.5 yr.	3.5 yr.	2.
M	"	M	4.5 yr.	3.0 yr.	3.
P	"	M	1.5 yr.	1.0 yr.	
T	"	M	1.5 yr.	1.0 yr.	4.
B	<u>Eumetopias jubatus</u> (Steller Sea Lion)	M	1.5 yr.	< 1 mo.	
F	"	M	1.5 yr.	< 1 mo.	5.
N	"	M	1.5 yr.	< 1 mo.	
S	"	F	1.5 yr.	< 1 mo.	6.
55	"	M	5 mo.	< 1 mo.	
56	"	F	5 mo.	< 1 mo.	
3	<u>Callorhinus ursinus</u> (Northern Fur Seal)	M	3 mo.	< 1 mo.	7.
4	"	M	3 mo.	< 1 mo.	
J	<u>Mirounga angustirostris</u> (Northern Elephant Seal)	M	1.0 yr.	1 mo.	8.
K	"	M	1.0 yr.	1 mo.	
L	"	F	1.0 yr.	1 mo.	
A	<u>Phoca vitulina</u> (Harbor Seal)	F	Adult	Adult	9.
1	"	F	7 mo.	1 day	
O	"	M	1.5 yr.	1 mo.	10.
R	"	F	1.5 yr.	1 wk.	
Y	"	F	1.5 yr.	< 1 mo.	11.

be the least vocally responsive animal of the group. This observation offered the obvious suggestion that Cathy's threshold for underwater click vocalizations may have been considerably higher than that for Bibi. Fortunately, a check on this suggestion was available in the form of previously collected data dealing with the social behavior of three captive California sea lions. Behaviors, including virtually all vocalizations, were recorded by 30-sec. intervals on a time-ruled check sheet from May to August, 1964. The data dealing with the vocalizations are presented in Fig. 22; they support the suggestion that Cathy's low level of vocalization in air may have been partly responsible for its previous lack of underwater clicking.

If the degree of sound production in pinnipeds is similar both in air and under water, then an estimate of in-air calling may be helpful in predicting whether one or another species will be more or less vocal under water. Therefore, a preliminary survey of the in-air vocalizations of 20 seals and sea lions, representing five species of Pinnipedia was undertaken in November, 1965 and lasted approximately five weeks. The characteristics of the animals used in the survey are listed in Table 2.

The animals lived together in a large compound with a pool and were usually fed prior to the observation sessions, which took place twice daily--at 1:30 P.M. and 4:30 P.M. Vocalizations were recorded at 30-sec. intervals on a time-ruled check sheet. Vocalization of any sort was scored only once during a 30-sec. period. Each observation session lasted 10 minutes.

The results are presented in Fig. 22. From these data, it would be predicted that both the Steller and California sea lions would be considerably more vocal under water than would the harbor seal with the northern elephant seal occupying an intermediate position. Barking was the dominant vocalization of the California sea lion and clicking and hissing the



23. (a) Sonogram of an airborne "distress" cry from a captive one-month-old northern elephant seal (wide band). (b) Sonogram of an airborne "belch-roar" from a captive yearling northern elephant seal (wide band).

the dominant vocalization of the Steller. The harbor seals were relatively silent; their predominant vocalization being a growl, sometimes followed by a pulsed snorting sound from the nose. This sound is typically used in the harbor seal threat pattern. There were two distinct types of elephant seal calls. The predominant one was a shrill "distress" cry, sometimes with a hodeling quality which is typical of pups in the wild as described by Bartholomew and Collias (8). A highly pulsed call began to emerge in early December, 1965 which was similar to the "belch-roar" of the yearling as described by Bartholomew and Collias (8). Sonograms of these two calls are shown in Fig. 23. It is probable that the distress cry was yielding to the belch-roar as the pups reached yearling status. Since these animals had been in the presence of yearlings and adult elephant seals only for a brief time after birth (about one month) and since that time had been in the company of California and Steller sea lions as well as harbor seals, it is unlikely that the acquisition of the belch-roar was learned. Rather, the evidence suggests that the development of this vocalization is genetically acquired.

C. Conflict and Frustration

An organism is said to be in conflict when two or more incompatible response tendencies are aroused simultaneously (9). Frustration is often a consequence of conflict since the conflicting response tendencies may be a factor in blocking the organism from acquiring an incentive or goal object such as food. In previous experiments, it was indicated that underwater clicking may be evoked as a component of the orientation reflex by a stimulus situation which is relevant to conflict and/or frustration. Evidence supporting this point of view is now presented with a second California sea lion (Sam, a 3-year-old male). Since some of the procedural details of this experiment are not relevant to the present discourse and in fact have been partially presented elsewhere (61), only pertinent