

The upper limit of underwater auditory frequency discrimination in the California sea lion

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It was hypothesized that at similar or even greater sensation levels (SLs) the frequency discrimination of the sea lion (*Zalophus californianus*) in water would be much poorer in the range of frequencies between 32 and 48 kHz than it would be between 16 and 28 kHz. Difference limens were estimated for frequencies of 16, 24, 28, 34, and 38 kHz. Results clearly supported this hypothesis. Between 16 and 28 kHz, the Weber ratio ($\Delta F/F$) was 20 or, in other words, *Zalophus* could discriminate frequencies in this range which were 2.0% apart. At 34 kHz, frequency resolution became twice as coarse as it was at 28 kHz. Performance at 38 kHz deteriorated to such an extent that the sea lion was capable of only discriminating frequencies which were 11.2% apart. The present results showing a loss of good frequency resolution much above 32 kHz in *Zalophus* despite increased SL as compared to the loss of frequency resolution in phocids above 60 kHz are consistent with the notion that one of the major differences between the underwater hearing of otariids and phocids is the high-frequency cutoff. Although the sample of species and individuals involved in behavioral comparisons is very small, comparative anatomical evidence supports the idea that in water phocids obtain more spectral information from high frequencies than do otariids.

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INTRODUCTION

Although the use of echolocation for refined target assessment by porpoises had been well documented by 1965,¹ their auditory perception of underwater sound (see, e.g., Refs. 2 and 3) has only recently been found to match their echolocation performances and the frequency spectrum of their echolocation signals.^{4,5} Significantly, both neurophysiological⁶ and behavioral preparations have consistently produced similar results in outlining the auditory features necessary for echolocation in several species of toothed whales. Although recent investigations into the hearing of phocid pinnipeds has also been quite extensive (see, e.g., Refs. 7-10), the research on the underwater sound perception of otariid pinnipeds has been meager.

The only underwater audiogram of an otariid pinniped—the California sea lion (*Zalophus californianus*)—showed a range of maximal sensitivity between 1 and 28 kHz with a loss in sensitivity of 60 dB/oct between 28 and 36 kHz.¹¹ Corresponding audiometric data on three species of phocid pinnipeds (harbor, harp, and ringed seals) showed that their maximal sensitivity lies between 1 and 45 kHz with a loss in sensitivity of 60 dB/oct between 45 and 64 kHz.^{7,10,12} Such steep slopes in the audiogram or rates of loss in sensitivity are indicative of the occurrence of a conventional high-frequency cutoff. However, above 36 kHz, the slope of the sea lion underwater audiogram decreased considerably to about 20 dB/oct and above 64 kHz the slope of the audiograms of all three species of the family *Phocidae* also decreased significantly. Paralleling these slope changes in the underwater audiograms of pinnipeds, ultrasonic bone conduction thresholds in humans also demonstrated a characteristic change in slope from very steep at the lower frequencies to gradual at the higher frequencies.¹³ Human subjects, while capable of discriminating between the intensity of these ultrasonic frequencies, were

incapable of making a frequency discrimination.¹⁴ Similarly, Mohl¹⁵ and Terhune and Ronald¹² found that their phocid pinnipeds could readily distinguish between tonal frequencies in the range of approximately 1-57 kHz but were either incapable or found it extremely difficult to discriminate between frequencies above 60 kHz even though all pulses were at least 30 dB above threshold. On the other hand, all pinnipeds thus far tested have been able to detect relatively intense sounds at or above 90 kHz.^{7,10,11}

On the basis of the frequency-discrimination capabilities of phocids, whose upper limit of hearing is approximately one-half octave higher than *Zalophus*, we predicted that the underwater auditory frequency discrimination of *Zalophus* would be much poorer in the range of frequencies between 32 and 48 kHz than it would be between 16 and 28 kHz, even if pulses at the higher frequencies had a greater intensity above threshold than those of the lower frequencies. More specifically we hypothesized that above 36 kHz, where the underwater audiogram showed that the *rate of hearing loss declined*, frequency discrimination by *Zalophus* would be either nonexistent or very poor, i.e., the difference limens (DLs) would be extremely large.

I. METHOD

A. Subject

The experimental animal (Sam) was an 11-12-year-old male *Zalophus*, weighing about 250 kg. An underwater audiogram on Sam had been obtained when he was six years old¹¹ and most recently he had performed an intensity-discrimination task.¹⁶ On test days the total amount of food consumed by Sam, including reward feeding, was approximately 11 kg of herring. Testing usually occurred in the morning with Sam not having eaten for about 18-20 h.

B. Sound equipment and measurement

The experiment was conducted in a $3.5 \times 11.1 \times 1.2$ -m³ concrete pool located above ground. One end of the pool contained the testing platform which housed the test equipment, observation port, and the experimenters.¹⁷ The various pure tones used in the experiment were introduced into the water by either an F-50 or F-41 transducer calibrated by the Underwater Sound Reference Division of the Naval Research Laboratory (USRD/NRL). A general description as well as the specifications and acoustic characteristics are given by Groves.¹⁸ Alongside both transducers was a 150-W flood lamp. Both were mounted on 1.3-cm steel pipe which held them in a fixed position above the bottom of the pool. The water level of the pool was 91.4 cm, and during testing, the transducer was 43.2 cm from the bottom and 172.7 cm from the sides of the pool. The sea lion was required to place his head on a head stand that positioned him at a distance of 3.1 cm directly in front of the transducer, and 43.2 cm above the pool bottom. An Atlantic Research hydrophone (LC-50) monitored the underwater sounds during testing.

The sound field was mapped by transmitting a single-frequency, constant-wave signal from the F-50 or F-41. The transducers were driven across a range of frequencies from 16 to 150 kHz using a McIntosh 75-W audio amplifier to provide a constant-voltage input (20 V p-p) to the transducer. Signals were received by the USRD/NRL-provided hydrophone H-23¹⁸ which was placed at the sea lion's head position. The signal was amplified by a Princeton Applied Research Model CR 4-A low-noise preamplifier, high-pass filtered by a Krohn-Hite active filter model 315A, and the voltage-level data were visually determined using a Tektronix type 564 oscilloscope. Fluctuation in the measured sound pressure levels (SPLs) through the frequency range used in the present experiment was most influenced by standing waves generated primarily by multipath interference and surface-wave action.

The signals used in the frequency-discrimination task were a sequential pair of pure-tone pulses each 1.0 s in duration with a rise-fall time of 100 ms. The first tone of the pair was designated the standard frequency and the

second the comparison. Since primary interest was in those underwater high frequencies in which *Zalophus* showed best sensitivity followed by a rapid loss in sensitivity,¹¹ frequency discrimination ability was tested at the following standard frequencies: 16, 24, 28, 34, and 38 kHz.

The standard frequency was generated by a General Radio model 1312 oscillator, the output of which was fed to one of two inputs of a Grason-Stadler model 829E electronic switch. The comparison tone was generated by an Exact model 129 voltage-controlled oscillator. The output of the Exact was fed to the other channel of the electronic switch.

By controlling the voltage to be fed to the frequency-modulation input of the comparison oscillator, the frequency of the comparison tone could be set to either the standard frequency (a cw trial) or some frequency *below* the standard tone (an FM trial). In order to make valid comparisons of frequency discrimination between each of the standard frequencies, modulation was restricted to downward frequency shifts because at 34 and 38 kHz there was no way of increasing sensation level (SL) of the comparison tone to match the standard tone.¹¹ The amount of control voltage and, therefore, the frequency difference of the comparison oscillator was determined by the setting of a Hewlett Packard model 350C attenuator, the input of which was connected to a precision voltage source and the output to a control box which either shorted the frequency modulation input (selecting a cw trial) or connected the output of the attenuator to the input of the comparison oscillator (selecting an FM trial). The output of both the standard and comparison oscillator were continuously monitored by a Berkeley Beckman model 7350G frequency counter.

The output of the electronic switch was fed via a Davan 2-dB step attenuator to a McIntosh 75-W audio amplifier. The output of the amplifier was connected to either of the transducers, and was calibrated before each session and continuously monitored by a Tektronix model DM64 oscilloscope. All signals were gated on and off at random phase. Calculations of SL were based on the underwater audiogram of *Zalophus* by Schusterman, Balliet, and Nixon.¹¹ The SLs of the standard frequencies are given in Table I. Note that SLs of the two higher frequencies are 10 dB greater than for the lower frequencies. Although the voltage level of the signal was controlled precisely, random wave action on the pool surface produced sound-level fluctuations about the head-stand position. These momentary random variations resulted in fluctuating differences of as much as 13 dB in overall SPL during the signal presentation interval. It is, therefore, unlikely that intensity cues played an important role in controlling the sea lion's responses.¹⁹ Moreover, Verschuure and van Meeteren²⁰ suggest that the effect of pitch induced loudness cues is likely to be minimized in a binaural listening situation. The noise in the tank was measured using a General Radio Company Sound and Vibration Analyzer, type 1554A, in its one-third-octave bandwidth position at frequencies from 1 to 20 kHz. In this bandwidth ambient noise decreased from -27 to -34 dB *re* 1 μ bar.

TABLE I. Relative thresholds for frequency discrimination in California sea lion Sam.

Frequency (kHz)	Date tested	75% threshold (F/F) $\times 10^3$	SPL (dB <i>re</i> 1 μ bar)	Approximate sensation level (dB)
16 (F-41)	5/13/77	21	-1	20
24	1/11/77	17	4	20
24	1/31/77	16	4	20
28	1/12/77	20	5	20
28	1/24/77	30	5	20
28	1/25/77	20	5	20
34	1/13/77	40	40	30
34	1/26/77	53	40	30
38	1/28/77	112	58	30

C. Procedure

Schusterman *et. al.*¹¹ provides a full description of the equipment controlling the experimental contingencies. A trial started after the sea lion had assumed a fixed position at the head stand. A light served as a warning signal and was presented for a total trial duration of 4.0 s. During the last 2.0 s of the light, the sound stimuli were presented, the light and sound terminated simultaneously. Sam was required to indicate his decision as to the type of trial (cw or FM) any time after the onset of the second tone pulse. An underwater bark signaled an FM trial and remaining silent signaled a cw trial. After either response, Sam swam forward and pressed a paddle indicating the end of a trial. A correct response was rewarded with a piece of cut herring, and if the response was incorrect, no fish was given. (See Schusterman²¹ for greater detail on the training of these behaviors.)

Each daily session consisted of 300 total trials including 50 "warm-up" trials, with an *a priori* probability of presentation for FM and cw trials fixed at 0.50. A modified method of limits similar to the "staircase" method was used to obtain all frequency DLs. Before each session, an attenuator setting was chosen that would produce a large ΔF value for FM trials. If Sam identified eight out of ten trials correctly, the attenuator setting was increased (reducing the ΔF value for FM trials) or, if fewer than eight out of ten were identified, the setting was decreased. After the first 50 "warm-up" trials the criterion was reduced to seven out of ten for the remainder of the session.

II. RESULTS

During each test session the frequency of both standard and comparison tones were monitored and record-

ed for each attenuator setting and the resultant frequency change (ΔF) was calculated. Frequency DLs for each daily test session were estimated by plotting psychophysical functions for each ΔF setting in which 30 or more trials were obtained. A regression line was fitted to the data and the 75% "threshold" was calculated. Signal-detection plots indicated no strong response bias for any of the daily psychophysical functions. (See Schusterman²² for a discussion of response bias in the threshold testing of marine mammals.) The threshold estimates at each of the frequencies tested are expressed in terms of amount of the ratio of the frequency change to each standard frequency multiplied by 10^3 [$(\Delta F/F) \times 10^3$]. Threshold estimates at each standard frequency tested, along with dates of testing, SPLs and SLs are given in Table I. The F-50 transducer was used to obtain all DLs for frequencies between 24 and 38 kHz, while the F-41 was used to obtain the DL at 16 kHz.

Between 16 and 28 kHz the average frequency-discrimination ability of *Zalophus* was 20 [$(\Delta F/F) \times 10^3$] or, in other words, the sea lion could discriminate frequencies in this range which were 2.0% apart. At 34 kHz, frequency resolution became twice as coarse as it was at 28 kHz. Finally, frequency discrimination at 38 kHz deteriorated to such an extent that the sea lion was capable of only discriminating frequencies which were 11.2% apart.

In order to gain a relative appreciation of the degree to which *Zalophus* could differentiate underwater auditory frequencies in the best part of its upper hearing range and to see the extent of the loss of this ability at only slightly higher frequencies, Fig. 1 compares the frequency-discrimination ability of *Zalophus* with that of two phocid pinnipeds *P. vitulina*¹⁵ and *P. hispida*¹² and

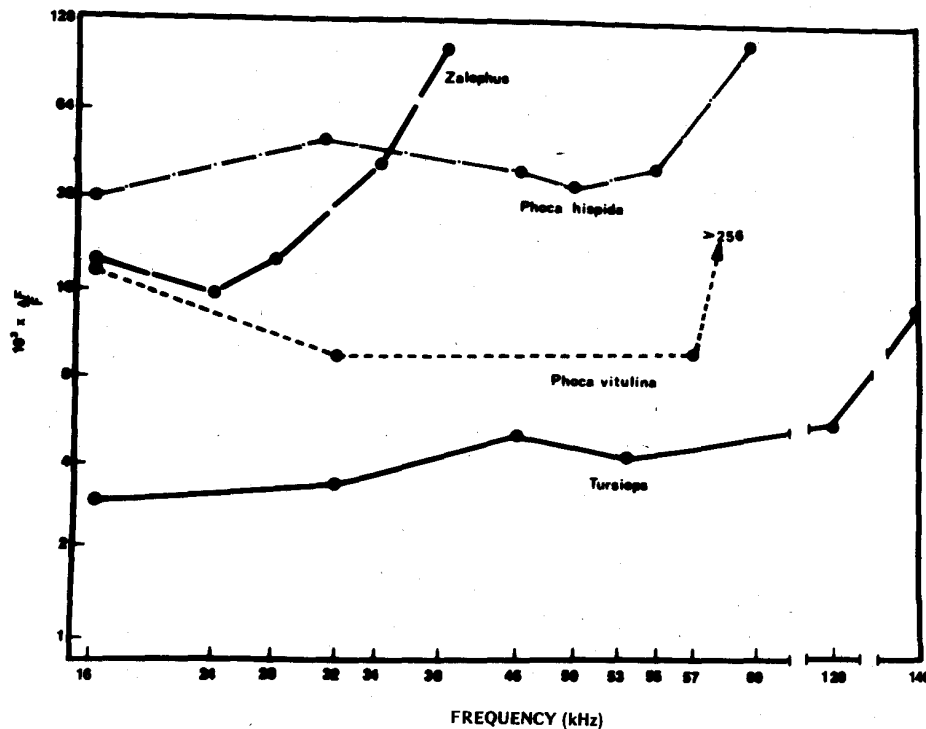


FIG. 1. Comparison of frequency difference thresholds $[(\Delta F/F) \times 10^3]$ of three species of pinnipeds, including *Zalophus* (this study), *Phoca vitulina*,¹⁵ *Phoca hispida*,¹² and one odontocete cetacean, *Tursiops truncatus*.³

the Atlantic bottlenosed porpoise *Tursiops truncatus*³ at frequencies above 16 kHz. The figure shows that the three species of pinniped have Weber ratios ($\Delta F/F$) ranging between approximately 1.8% and 5.4%, i.e., relative discrimination values of 18 and 54 ($\Delta F/F$) $\times 10^3$, over a frequency range of 16 to 32 kHz while the Weber fraction for the porpoise averaged only 0.33% over the same frequency range.

III. DISCUSSION

Thus, the underwater frequency-discrimination abilities of four specimens of three pinniped species (one *Zalophus*, one *P. vitulina*, and two *P. hispida*) are much inferior to the one porpoise species.²³ Moreover, although the upper frequency-discrimination limit of *Zalophus* is 34 kHz, the effective upper limit of frequency discrimination for both phocids is 60 kHz. In contrast to both types of pinnipeds the porpoise still showed excellent frequency discrimination even at a center frequency of 140 kHz. Any notion that *Zalophus* can echolocate on fish prey²⁴ is not supported by the present results since the system would have to operate at frequencies below 34 kHz and the long wavelengths of these frequencies in water would likely prohibit detection of fish prey. Moreover, this low-frequency range may be masked by a variety of meteorological and man-made noises.²⁵

The present behavioral results confirm the evoked potential work of Bullock, Ridgway, and Suga²⁶ who found that compared to pure tones, frequency-modulated tones were considerably more effective in evoking midbrain responses in porpoises than in *Zalophus*. The evoked potential work with *Zalophus* was accomplished by frequency shifts between about 3 and 6 kHz.

As previously noted, audiometric data on pinnipeds suggests that the upper frequency limit of conventional hearing under water appears to be considerably higher in the family *Phocidae* than in the family *Otariidae*. The present results are consistent with the notion that the major difference between the hearing of the otariid and phocid pinnipeds is their high-frequency cutoff. Although the sample of species and individuals involved in behavioral comparisons of the upper limit of hearing in diving pinnipeds is very small, comparative anatomical evidence also tends to support the notion that under water phocids obtain more spectral information from high frequencies than do otariids.²⁷

It appears likely that in water the path of sound reception in all pinnipeds is by some type of bone conduction (e.g., the inertial mode) with the middle-ear system playing a role in the sound route.⁸ At high frequencies, behavioral underwater audiograms from three species of phocid^{7,8} and one otariid species¹¹ have shown a characteristic change in the slope from a very sharp rise to a moderate one which closely resembles the human threshold curve for bone conducted tones in the upper sonic and ultrasonic region.¹³ The loss of effective frequency discrimination by *Zalophus* in the present study occurred at 38 kHz, which is just beyond that portion of the audiogram where the slope changes from a sharp rise to a moderate one. The loss of frequency discrim-

ination in two species of phocid and in the bone-conducted hearing of humans^{14,28} also occurs just beyond the steep portion of their audibility curves, i.e., beyond the point at which the rate of loss in sensitivity indicates the existence of a conventional high-frequency cutoff. Therefore, it seems that the basilar membrane can differentiate bone-conducted sounds up to a given frequency beyond which intense sounds may be detected but spectral information is lost.

Finally, it should be noted that if SL is maintained at a minimum of 20 or 30 dB, then above 1 or 2 kHz and throughout the middle and conventional upper range of hearing all mammalian species thus far tested (approximately 15 species including *Zalophus*) show $\Delta F/F$'s which remain relatively constant.^{29,30} As Fay²⁹ has pointed out, these kind of data support the notion that all mammals make use of a similar mechanism for frequency analysis despite different cochlear lengths, overall hearing bandwidth and modes of sound transmission.

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