

AUDIOMETRIC ASSESSMENT OF NORTHERN FUR SEALS, *CALLORHINUS URSINUS*

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ABSTRACT

Aerial and underwater audiograms for two young female northern fur seals (*Callorhinus ursinus*) and one young female California sea lion (*Zalophus californianus*) were obtained with the same procedure and apparatus. *Callorhinus* hears over a larger frequency range and is more sensitive to airborne sounds than *Zalophus* or any other pinniped thus far tested in the frequency range of 500 Hz to 32 kHz. Sensitivity of *Callorhinus* to waterborne pure tones, ranging from 2 to 28 kHz, is equal or superior to all other pinnipeds tested in this same frequency range. Like *Zalophus*, the upper frequency limit for underwater hearing (as defined by Masterton *et al.* 1969) in *Callorhinus* is about one-half octave lower than the three phocid species thus far tested. *Callorhinus*' upper frequency limit in air is about 36 kHz and under water it is about 40 kHz. Comparison of air and water audiograms shows *Callorhinus* is no exception to previous behavioral findings demonstrating that the "pinniped ear" is more suitable for hearing in water than in air. Similar to *Zalophus* and *Phoca vitulina*, *Callorhinus* shows an anomalous hearing loss at 4 kHz in air. The basis for this insensitivity to airborne sounds at 4kHz and not at lower or higher frequencies is presumably caused by specialized middle ear mechanisms matching impedance for waterborne sounds. Critical ratio curves for *Callorhinus* are similarly shaped to ones obtained for humans but are shifted upwards in frequency. Compared to all other marine mammals thus far evaluated, the critical ratios for *Callorhinus* are the smallest yet reported.

Key words: northern fur seals, aerial audiograms, underwater audiograms, critical ratios, hearing sensitivity, California sea lions, psychophysics, pinniped hearing.

Audition is an extremely important sensory modality for all marine mammals. The highly variable noise background of the sea presents a real and

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ubiquitous detection problem for an individual's hearing system. The animal's ability to extract relevant acoustic information from the noise is likely to have a significant impact on the animal's ability to reproduce successfully, find and capture food prey and to escape and/or avoid predators.

Modern industrial societies have expanded their land-based activities to include the marine environment. To evaluate accurately the effects of noise, whether natural or man-made, on the behavior of marine mammals, basic information on the aerial and underwater hearing abilities of a variety of species is required. In particular, pinnipeds breeding on the offshore islands of California may be quite vulnerable to disturbances produced by man-made devices including overhead aircraft as well as sonic booms (Cooper and Jehl 1980).

One species of concern is the northern fur seal (*Callorhinus ursinus*), an otariid pinniped whose main breeding grounds are the Pribilof Islands in Alaska. The only laboratory research reporting on the hearing abilities of these fur seals is in published abstracts and a brief review (Moore and Schusterman 1978, Schusterman and Moore 1978, 1981, Schusterman 1981). This paper details our methods and results, covers aerial, underwater, and masked auditory thresholds in *Callorhinus* over a wide range of audio frequencies, and generally expands the paltry data base on hearing capabilities of pinnipeds (Watkins and Wartzok 1985). Three experiments are presented and discussed; the work is summarized at the end of this report.

Experiment 1: Aerial Audiograms

The auditory capabilities of phocid pinnipeds, as assessed by behaviorally obtained audiograms or evoked potential audiograms, include both underwater and in-air measurements of a common (harbor) seal (*Phoca vitulina*) (Møhl 1968) and the harp seal (*P. groenlandica*) (Terhune and Ronald 1971, 1972) and underwater audiograms for the ringed seal (*Phoca hispida*) (Terhune and Ronald 1975) and the gray seal (*Halichoerus grypus*) (Ridgway 1975). However, until now auditory capabilities of otariid pinnipeds have been represented by air and water audiograms of only one male California sea lion (*Zalophus californianus*) (Schusterman *et al.* 1972, Schusterman 1974).

To further compare the hearing abilities of phocid *vs.* otariid species, we obtained the first in-air audiograms for northern fur seals (*Callorhinus ursinus*). Moreover, to facilitate a within-family comparison, an in-air audiogram of a female California sea lion was also determined using the same facilities and procedures as with the fur seals.

Although Schusterman (1974) reported an in-air audiogram for *Zalophus*, we felt that a direct comparison of the hearing abilities of the two species, obtained within the same experimental setting, was essential. Furthermore, the previous audiogram had not extended below 4 kHz. Frequencies below 4 kHz represent a significant area of *Zalophus* hearing because many sea lion vocalizations are comprised of frequencies around this value (*see* Schusterman 1978). In the previous in-air audiogram, background noise was considered to be an effective masker below 4 kHz but, as the present study progressed, we con-

cluded that background noise above 4 kHz probably influenced the earlier work published on *Zalophus* sensitivity to airborne sounds.

Subjects—We used three otariid pinniped subjects for these experiments. All were two- to three-year-old females that were experimentally naive. Animals were tested early in the morning and fed in the afternoon; thus, they were not fed for about 18 h prior to testing. Two subjects, Lori and Tobe, were northern fur seals. They weighed 16.1 and 17.5 kg, respectively. Their reward feedings were supplemented to a total daily intake of 1.4 kg. The third subject, Rocky, was a California sea lion. She weighed 26.2 kg and was fed 3.5 kg daily. All subjects were fed cut herring.

Apparatus—The in-air threshold experiments were conducted in a specially constructed acoustic chamber. The entire chamber was a $3.8 \times 1.5 \times 1.8$ m wooden box of post and beam construction; the walls and roof were plywood, 2.5 cm thick, and all joints and seams were reinforced with resin impregnated fiberglass cloth (Fig. 1). The interior of the box consisted of a testing chamber and an experimenter's chamber. The experimenter's chamber was a 96-cm-long segment of one end of the box housing the control equipment and experimenter. All the walls and an access door were lined with 9 cm of fiberglass insulation. The testing chamber interior was $2.9 \times 1.5 \times 1.8$ m, and the walls and ceiling were lined with 8.5-cm-thick convoluted acoustic foam glued to the inside surface. The common wall between the testing chamber and experimenter's chamber was equipped with an observation and feeding port. Entry to the testing chamber was via a 61×67 cm door located in the center of the south wall. A small step was hinged on the inside wall below the door to allow easy access to the chamber and was raised and fixed against the wall during testing (this was also covered with foam).

When the animal entered the chamber, it approached and assumed a stationary position in a nose cup, located 51 cm above the floor, 25 cm out from the north wall and 73 cm from the common wall between the two chambers. The cup was used to assure a fixed head position in the sound field and consisted of a 9 cm cylinder of frosted plexiglass with a cone-shaped hollow center. Embedded in the nose cup were three small lamps that illuminated the device and acted as a trial warning light.

The response paddle was directly opposite the nose cup, 1.0 m away and on the south wall. The paddle was a white, 11.5-cm plexiglass disk mounted 53 cm above the floor, 30 cm from the south wall and 63 cm from the common wall. Depending on the signal frequency, either a Jensen Model 41 moving coil and electrostatic tweeter combination (500 Hz–8 kHz) or a James B. Lansing Model 075 tweeter (16–32 kHz) was used to present the signals. The Jensen Model 41 was located perpendicular to the north wall 1.13 m away from the nose cup. The tweeter was mounted closer (65 cm from the center) and pointing down toward the nose cup, 1.0 m above the floor on the north wall and 1.0 m away from the common wall. The entire testing chamber was kept in semi-darkness, illuminated only by an overhead 25-w lamp and the nose cup lights (during a trial).

Procedure—At the start of a session the test animal entered the chamber and

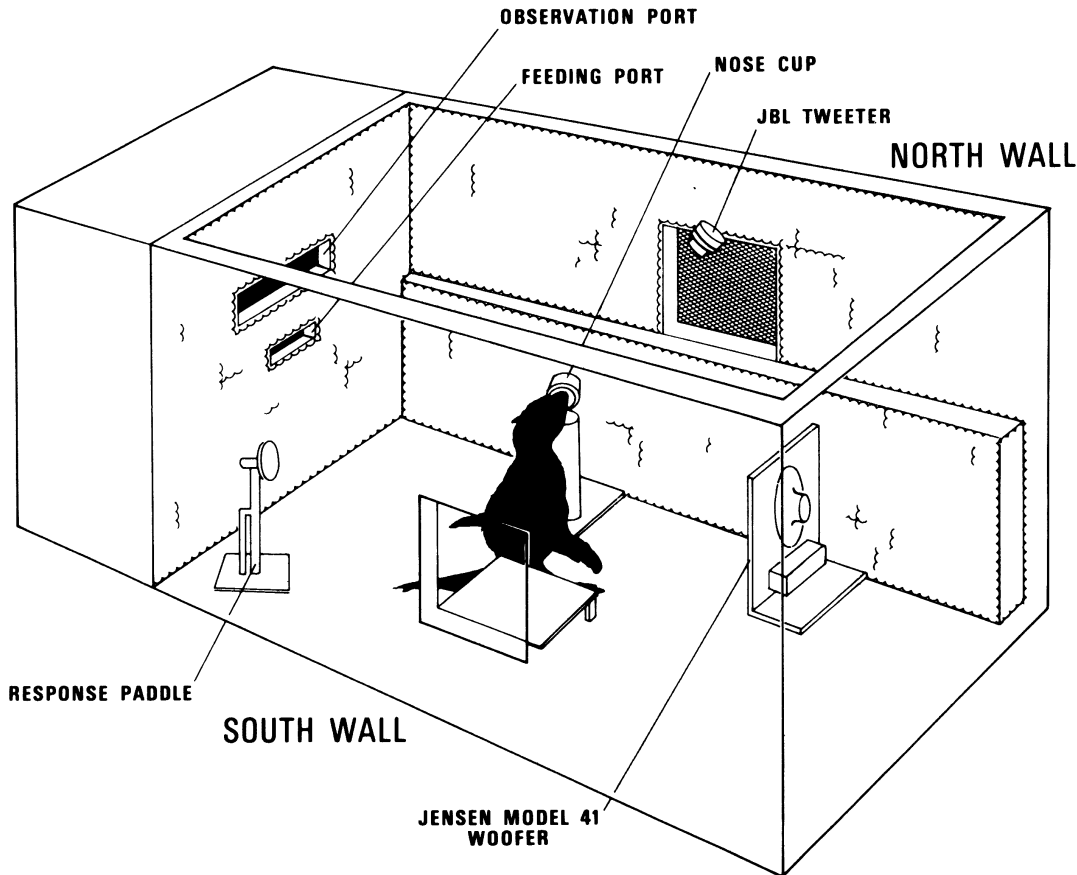


Figure 1. Schematic drawings of the acoustic test chamber showing placement of transducers, nose cup and response paddle.

assumed its position in the nose cup. The experimenter then pressed the trial start switch, which illuminated the nose cup for a total duration of 6.0 sec. If a signal trial was selected, a 0.5 sec tone occurred 2.0 sec after the nose cup was lit. A correct response to a signal trial or a "hit" was defined as leaving the nose cup and pressing the paddle. For a non-signal (noise trial), remaining in the nose cup until the light went out constituted a correct response or a "correct rejection." All correct responses were rewarded with a piece of cut herring; incorrect responses were not reinforced (Rocky and Tobe) or resulted in a 1-min timeout (Lori).

The psychophysical procedure used was a "threshold tracking" or "up-down staircase" technique. A threshold testing session usually consisted of 20 "warm-up" trials followed by at least 50 "threshold" trials and terminated with 10 "cool-off" trials. Warm-up and cool-off trials were trials in which the intensity of the signal was selected to be at least 10–15 dB above the animal's threshold and were used to assess the degree of stimulus control over the animal both before and after a testing session. If the animal failed to maintain 85 percent or better detection performance during the warm-up section, the session was used for training and not counted as data. If the animal failed to maintain 90 percent or better detection during cool-off, the session was declared invalid and

omitted from the data base. Signal and noise trials were presented randomly with an *a priori* probability of 0.50 (Gellerman 1933) for either type of trial. If the animal passed the warm-up criterion, testing began and the signal level was reduced by 2-dB increments until the first incorrect response to a signal trial (miss) occurred, after which the sound pressure level was increased in 1.0-dB steps until the animal again made a correct response to a signal trial (hit). Throughout the remainder of the session, 1.0-dB steps were used for ascending and descending runs. False alarms (*i.e.*, leaving the nose cup and pressing the paddle when a sound source was not activated) and correct rejections (*i.e.*, remaining in the nose cup if a sound was not presented) did not modify signal levels. The first miss following a series of hits was considered the beginning of the first run. A run was defined as a series of attenuator changes in one direction, *i.e.*, increments or decrements, contingent on the animal's responses to signal trials. For example, a single run started with the signal level of the last hit (correct response to signal-peak) and terminated with the signal level of the next subsequent miss (incorrect response to signal and noise-valley). Threshold estimates (50 percent level) were obtained by averaging the peaks and valleys for each frequency tested (Gelfand 1981). The minimum number of runs for threshold estimates at a given frequency was arbitrarily set at 20. Generally, this took at least two or three daily sessions.

Because the sea lion (Rocky) exhibited high false alarm rates (0.20), this animal's signal-trial *a priori* presentation probability was decreased to maintain consistent low false alarm rates among all three subjects. Threshold estimates were obtained for frequencies of 0.5 kHz (Tobe only) 1.0, 2.0, 4.0, 8.0, 16.0, 24.0 and 32.0 kHz.

Stimuli—A Hewlett-Packard (H.P.) Model 200 CD oscillator was used to generate the pure tone stimuli, the output was monitored by an H.P. Model 400D voltmeter. The output of the oscillator was also fed to an electronic switch, which gated the tone. The tone's duration was 0.5 sec and rise/fall time was 40 msec. The output of the switch was fed to an H.P. 350 C attenuator and then to a Dynaco Model 120 amplifier (for frequencies below 16 kHz) or southwest Technical Products Model 140 CX amplifier (for frequencies of 16 kHz and above).

At the beginning of the experiment, the intensity of the tonal stimuli was measured at the head stand position with a Bruel and Kjaer Model 2203 Precision sound level meter, a 1613 octave filter set and a 4145 or 4135 condenser microphone. A General Radio Model 1982 precision sound level meter and analyzer with a 1962-9601 electric condenser microphone was also used. Both instruments were periodically checked using a General Radio 1567 sound-level calibrator.

Signal frequencies from 500 Hz to 16 kHz were measured using both sound level meters, but beyond 16 kHz only the Bruel and Kjaer with 4135 (6.4 mm) microphone was used. Both the signals and background noise were measured in octave bands and a Krohn-Hite Model 3550 filter set was used in place of the internal filters for 24, 28 and 32 kHz measurements. Ten successive measurements were taken and the mean assumed to be the true signal level.

Table 1. Frequency thresholds, standard deviation and percent false alarms for the fur seals and sea lion of this study. T threshold, SD standard deviation, FA percent false alarms.

Frequency kHz		Air dB re: 0.0002 dynes cm ²			Underwater dB re: 1 μB	
		Lori	Tobe	Rocky	Lori	Tobe
0.5	T	27	—	—	—	—
	SD	2	—	—	—	—
	FA	16	—	—	—	—
1.0		30	28	41	-4	-7
		4	4	3	4	2
		12	9	4	5	11
2.0		10	8	19	-32	-30
		3	2	3	2	2
		14	8	5	1	9
4.0		21	23	26	-42	-40
		6	6	2	5	2
		16	1	8	7	4
8.0		15	11	16	-42	-35
		5	4	2	3	7
		17	14	10	9	11
16.0		6	7	28	-37	-34
		3	6	3	5	7
		9	4	7	9	6
24.0		23	20	37	—	—
		3	3	3	—	—
		4	23	7	—	—
28.0		—	—	—	-35	-44
		—	—	—	2	5
		—	—	—	0	2
32.0		40	27	61	-24	-23
		3	2	2	2	3
		17	3	6	2	11
42.0 ^a		—	—	—	28	17
		—	—	—	3	3
		—	—	—	2	11

^a Averaged threshold obtained with the J9 and F41 transducers underwater.

The ambient noise levels were measured inside the chamber at the nose cup position in octave bands at 0.5, 1, 2, 4, 8, 16 and 32 kHz and the levels were 16, 14, 10, 9, 9 and 11 dB re: 0.0002 dynes/cm² respectively. The levels beyond 2 kHz are more likely peak levels because of the limitation of the instruments.

Results and discussion—The average of the daily-session threshold estimates for each frequency tested are presented in Table 1, and the aerial audiograms are shown in Figure 2. The fur seal audiograms show a high degree of similarity between 1.0 and 24 kHz; however, at 32 kHz, a 12-dB difference between thresholds exists. This difference in sensitivity at 32 kHz may be an actual individual difference of the upper limit of hearing, an effect of learning (*i.e.*,

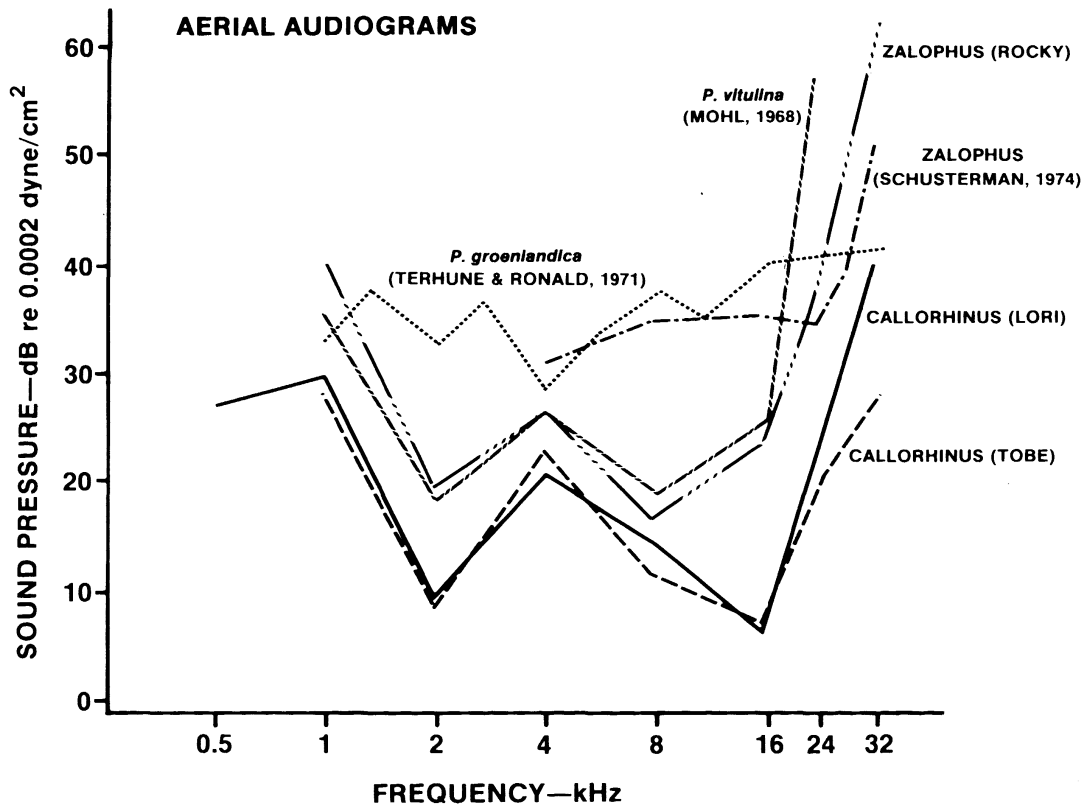


Figure 2. Comparative aerial audiograms of the two *Callorhinus* and *Zalophus* of this study and *Phoca* (Møhl 1968), *Zalophus* (Schusterman 1974) and *P. groenlandica* (Terhune and Ronald 1971).

selecting a more advantageous listening posture) or a combination of both effects. Although the stationing nose cup was fixed and the animals were required to assume a steady position in the device, differences in muzzle size and animal height caused a less than perfect fit for all the subjects. An intensive search of the sound field at 16 kHz and above was conducted using the Bruel and Kjaer sound level meter, with the 6.4 mm microphone on a tripod mount. The sound field was sampled above, below, to the right, and left and along the axis of the nose cup, in 2.5-cm increments, from the cup's front face to 15.2 cm from the face along the center axis. Measurements indicated that at 32 kHz a 5.0 to 7.0 dB advantage in sound pressure level could be gained (due to standing waves) by a 2.5 cm vertical adjustment in the head position. Medical histories of the animals indicated that no ototoxic drugs had been administered to Lori, so the difference in thresholds measured at 32 kHz was probably a combination of learned head placement and individual sensitivity.

The fur seal and sea lion audiograms of this study (Fig. 2) show the same general functions: a 20 dB/octave increase in sensitivity between 1 and 2 kHz, and a decrease in sensitivity between 2 and 4 kHz. For Lori, Tobe and Rocky, the decrease was 12, 15 and 7 dB/octave, respectively. From 4 and 16 kHz, both fur seals show a rather linear increase in sensitivity of approximately 7.5 dB/octave with the function reversing at a best frequency of 16 kHz. The sea

lion audiogram also shows an increase in sensitivity of 10 dB, but only for one octave, between 4 and 8 kHz, with the function reversing at a best frequency of 8 kHz.

The concomitance of the fur seals and sea lion audiograms of this study between 1 and 8 kHz suggested that perhaps the 21 dB difference in sensitivity at 16 kHz was an artifact. However, we retested Rocky at 16 kHz one month later, after we tested the sea lion at 24 and 32 kHz. The results showed no change in Rocky's threshold (+1.0 dB). Had Rocky been able to gain an advantage in the testing by changing her head posture, the retesting results at 16 kHz would have shown increased sensitivity. Since the two tests results were consistent, we felt confident that the 16 kHz threshold value as measured was accurate. From 16 to 32 kHz all three subjects show a sharp decrease in sensitivity of 40, 34 and 21 dB/octave for Rocky, Lori and Tobe, respectively. These steep slopes in the audiogram are typical and indicate a conventional high-frequency sensitivity limit (as defined by Masterton *et al.* 1969).

The outstanding feature that distinguishes the northern fur seal's audiogram from that of the California sea lion is a general decrease in sensitivity of the sea lion, ranging from 10 dB at 1.0 and 2.0 kHz, reaching a minimum of 4.0–5.0 dB between 4.0 and 8.0 kHz with increasing insensitivity of 17 dB at 16 kHz to a maximum measured difference of 30 dB at 32 kHz. Although the absolute values indicate that the sea lion was generally less sensitive throughout the entire frequency range tested, an argument could be made that the procedural differences (*i.e.*, no timeouts for Tobe *vs.* 1-min timeout for Lori *vs.* a 70/30 presentation schedule for Rocky) could have resulted in the observed increase in threshold across frequencies for Rocky as compared to Lori and Tobe. However, it is the concomitance of all the subjects' audiograms that suggests similar hearing mechanisms.

All three audiograms show a notable peak hearing loss at 4.0 kHz. Figure 2 shows aerial audiograms for the three subjects of the present study along with those for a California sea lion (Schusterman 1974), harbor seal (Møhl 1968) and a harp seal (Terhune and Ronald 1971).

Møhl's (1968) audiogram of a harbor seal closely resembles the audiogram for Rocky, the sea lion of this study, in that the two audiograms remain within 2.0 dB in the range 1.0–16.0 kHz. Beyond 16.0 kHz, however, the two differ markedly; the harbor seal shows a hearing loss of 32 dB at 22.5 kHz, but the California sea lion loses only 9 dB out to 24.0 kHz. This accelerated rate of hearing loss for a harbor seal as compared to a sea lion and fur seals suggests that the effective upper limit of aerial hearing for phocids may be about 20 kHz (as defined by Masterton *et al.* 1969). At 22.5 kHz, the seal's threshold is 58 dB re: 0.0002 dynes/cm², but the sea lion doesn't reach this value until 32 kHz. Thus, these data indicate California sea lions and northern fur seals have at least ½ octave superiority in terms of high frequency hearing compared to a harbor seal. Both the harbor seal and sea lions are less sensitive than the fur seals throughout the hearing range tested and the three species showed a common insensitivity peak at 4.0 kHz.

In comparison, however, the aerial audiograms previously reported for a

California sea lion (Schusterman 1974) and the harp seal (Terhune and Ronald 1971) do not exhibit the same general trend as the audiograms from animals tested in this study. The differences between our results with Rocky and those reported for the previously tested California sea lion (Schusterman 1974) were most likely due to noise. Noise effectively raised the thresholds between 4 and 24 kHz in the earlier study of the California sea lion. Between 24 and 32 kHz, the fact that the audiograms start rising steeply close to the same frequency indicate similar upper limits of hearing (*see* Fig. 2).

The audiogram of the harp seal (Terhune and Ronald 1971) shows little detail similarity with the audiograms of the present study or of the harbor seal (Møhl 1968) between 1.0 and 8.0 kHz. This lack of similarity could be due to a truly different hearing function in harp seals or to methodological differences although Møhl (1968) also used punishment, in the form of an air blast, for incorrect responses. We suspect the differences to be due to background noise, limiting performance between 1.0 to 8.0 kHz. In the harp seal's aerial audiogram, the thresholds from 1 to 32 kHz never differ by more than 13 dB, making the threshold values somewhat suspect. Terhune and Ronald (1971) report spectrum level background noise averaging 23.0 dB greater than that of the present study for frequencies between 1.0 and 4.0 kHz and 15 dB greater between 4.0 and 8.0 kHz. Figure 3 shows comparative audiograms and $\frac{1}{3}$ octave band background noise levels for the fur seals from the present study and for the harp seal from Terhune and Ronald (1971), with the reported background noise from the harp seal study converted from spectrum level to $\frac{1}{3}$ octave band noise levels.

The dissimilarity between the fur seal and harp seal audiograms above 4.0 kHz is not explainable by noise limiting for the harp seal at these higher frequencies. Since Terhune and Ronald (1971) report no accelerated rate of hearing loss at high frequency, we believe the aerial high frequency cut-off for the harp seal has not been established.

The peak of hearing loss at 4.0 kHz demonstrated by the subjects of the present study and by Møhl's (1968) harbor seal may be caused by differences in the sound route for air *vs.* water media. Møhl's (1968) harbor seal *underwater* audiogram does not show this insensitivity peak at 4.0 kHz nor does Schusterman *et al.*'s (1972) *underwater* audiogram for the California sea lion.

Experiment 2: Underwater Audiograms

In this study, we obtained the underwater audiograms of the two fur seals using the same basic procedures we used for the aerial audiograms. Differences between the studies are reported below.

Subjects—The subjects for this experiment were the same two *Callorhinus* used in the aerial study. The animals' underwater hearing thresholds were obtained after the in-air tests. When testing began, the animals weighed about 19 kg each. Tests were given in the morning after the fur seals had eaten 18 h earlier. Daily food intake, including reinforcements earned during a test session, was about 1.5 kg.

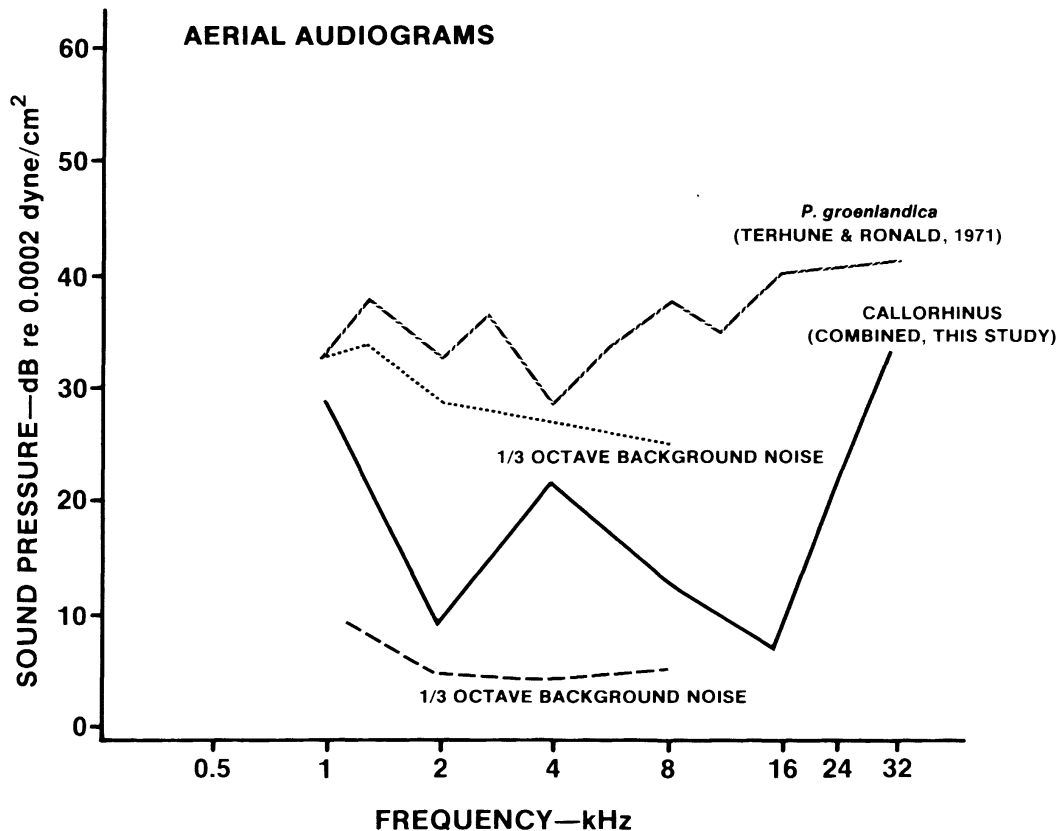


Figure 3. Background noise ($1/3$ octave) and combined aerial audiogram of the fur seal (this study) shown against that of the harp seal, *P. groenlandica* (Terhune and Ronald 1971).

Apparatus—Underwater hearing thresholds were obtained in a 3.5 m \times 11.1 m \times 1.2 m above-ground concrete tank. Schusterman *et al.* (1975) describe the pool design, the location of experimental equipment, and the acoustical properties of the pure tones used in testing.

Stimuli—The various pure tones used in the experiment were projected into the water by either a J-9 or F-41 transducer. The transducers were calibrated by the Underwater Sound Reference Division of the Naval Research Laboratory (USRD/NRL). The transducers' description, specifications and acoustic characteristics are given by Groves (1974). Alongside each transducer was a 150-w flood lamp mounted on 1.3-cm pipe, which held the lamp and transducer in a fixed position above the bottom of the pool. The water level of the pool was 91 cm and, during testing, the transducer was 43 cm from the bottom and 173 cm from the sides of the pool. Each fur seal was required to place its nose in a nose cup mounted on a stand (the same nose cup used in the in-air study, modified for underwater use), which assured a fixed position in the sound field.

The sound field was measured by transmitting pure tones from the J-9 or the F-41 (1–42 kHz, depending on frequency) transducer. Signals were received by a USRD/NRL-provided H-23 hydrophone (Groves 1974), which was placed at the fur seal's head position. The signal was high-pass filtered (Krohn-

Hite Model 3350) and the voltage-level data were visually determined using a Tektronix Type 564 oscilloscope.

A General Radio Model 1312 oscillator generated the test tones. The output of the oscillator was fed to an electronic switch, which gated the tone on and off with a duration of 0.5 sec and a rise-decay time of 40 msec. The output of the switch was fed to a H.P. 350 C attenuator and then to the McIntosh amplifier, which led directly to either of the underwater projectors. Voltage across the projector was calibrated before each test session and was continuously monitored using the Tektronix oscilloscope.

The ambient noise in the tank was measured at the head stand using a General Radio Company Sound and Vibration Analyzer, type 1554A, in $\frac{1}{3}$ octave bands for frequencies from one to 20 kHz. In this range, ambient noise decreased from -27 to -34 dB re: $1 \mu\text{B}$. The corresponding *spectrum levels* of ambient noise decreased from -50 to -71 dB re: $1 \mu\text{B}$.

Procedure—Since both fur seals had learned to respond to tones in air during their aerial audiometric assessment, the transfer to such sounds in water was immediate.

We used the same testing procedures for obtaining underwater audiograms as we had for the air audiograms. Soon after the animal entered the water, it assumed its position with nose firmly in the nose cup. The experimenter then pressed a switch, which initiated the trial. A trial consisted of the same sequence of light and tone durations used in the aerial study with half the trials consisting of light-only trials (noise trials) randomly interspersed with light-tone trials (signal trials). A correct response to a signal (hit) occurred when the fur seal left the nose cup following signal onset, swam forward about 2 m and pressed an underwater paddle. A correct response on a noise trial (correct rejection) occurred when the fur seal remained in the nose cup during the entire duration of a trial, *i.e.*, from light onset to light offset.

The experimenter worked from behind an opaque screen (with viewing port) and presented all trials by means of a remote switch. The experimenter reinforced all correct responses by throwing a small piece of cut herring to the fur seal. If the fur seal pressed the paddle on a noise trial (false alarm), the response was not reinforced and a 1-min timeout (both animals) was taken prior to starting the next trial. If the fur seal remained in the nose cup on a signal trial (miss), no reinforcement was given and there was no timeout. The inter-trial interval was approximately 10–15 sec. If the fur seal left the nose cup during the first 2 sec of a trial, the trial was aborted. This behavior rarely occurred.

Results and discussion—Results from the underwater tests are shown in Table 1. The false alarm levels were low for both animals at all frequencies so the thresholds presented are probably conservative estimates of the fur seal's sensitivity over this frequency range.

The combined underwater audiogram for the fur seal is presented in Figure 4. In general, the underwater audiograms are similar to one another and show that the range of maximal sensitivity for *Callorhinus* lies between 2 and 28 kHz. Between 28 and 42 kHz, the hearing loss is about 120 dB/octave, which indicates an effective upper limit of hearing (Masterton *et al.* 1969) at about

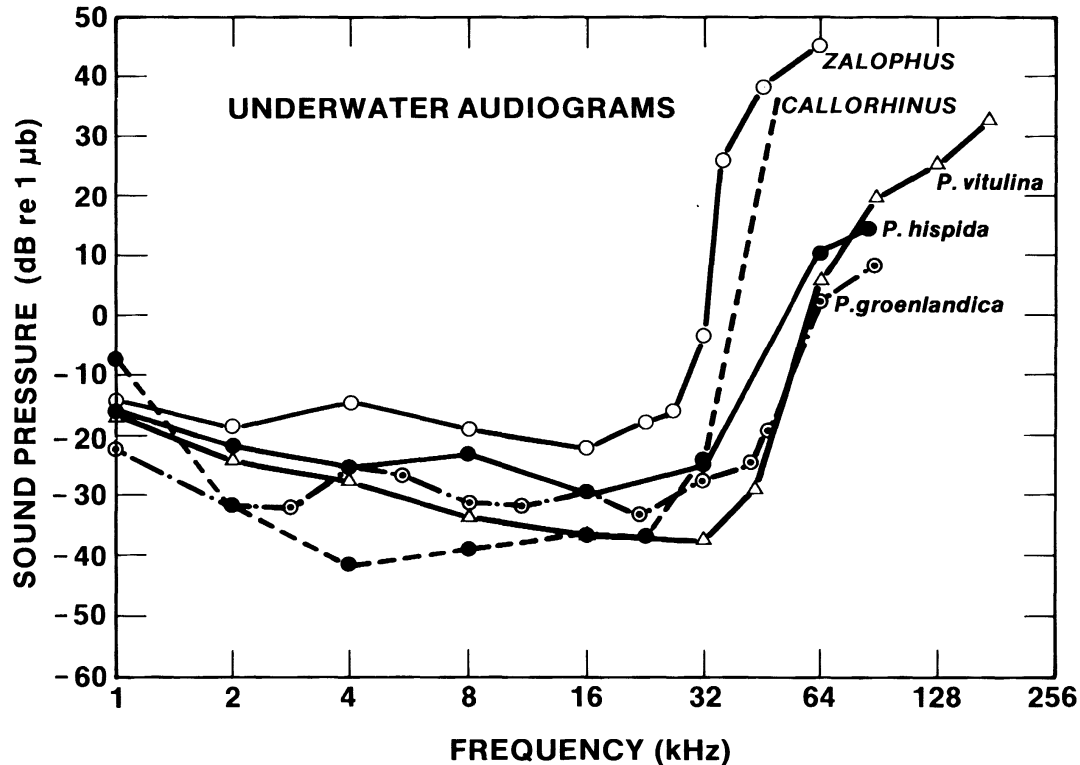


Figure 4. Combined underwater audiogram of the fur seal as derived from this study plotted against underwater audiograms of *Zalophus* (Schusterman *et al.* 1975) *P. hispida* (Terhune and Ronald 1975) *P. groenlandica* (Terhune and Ronald 1972) and *P. vitulina* (Møhl 1968).

40 kHz. Surprisingly, the audiograms indicate that *Callorhinus* is not very sensitive to underwater sounds at 1 kHz and, presumably, frequencies below 1 kHz.

Underwater audiograms for various pinnipeds are also presented in Figure 4. The figure shows that below 32 kHz sensitivity does not differ greatly among species. Also, the upper frequency cut-off is probably the same for the two otariid species. The absolute sensitivity for *Callorhinus* appears to be about 10 dB better than *Zalophus* for frequencies between 2 and 28 kHz. The northern fur seals also appear to be more sensitive than all phocids for a limited range of frequencies. At 2.0 kHz *P. groenlandica* and *Callorhinus* are equally sensitive; however, above 2.0 kHz *Callorhinus* is more sensitive than all previously tested phocid seals and maintains that increased sensitivity up to 16 kHz where *Callorhinus* and *P. vitulina* hearing functions follow each other to 28 kHz.

To assess the degree of adaptability of the fur seal's hearing for specific media, both aerial and underwater audiograms were converted to dB re: $1 \mu\text{W}/\text{cm}^2$. This conversion corrects for differences in the specific acoustic impedance of the two media and produces directly comparable audiometric functions. The converted thresholds for each animal are in Figure 5. Some interesting features arise from this comparison. From 1.0 to 2.0 kHz, there seems to be little or no difference in hearing ability for either animal, and both show a sharp increase

in sensitivity from 1 to 2 kHz. Beyond 2 kHz, the functions diverge for both animals and show radical differences in hearing ability in air and water. At 4.0 kHz, there is a 20 dB or more insensitivity peak in air as compared to water. Above 4 kHz, the functions reconverge and at 16 kHz, they are only 2 to 4 dB different. Beyond 16 kHz, the accelerated hearing losses occur and may begin at a slightly lower frequency in air than water. A prominent feature of the audiograms is the disparity that occurs between aerial and aquatic functions at 4.0 kHz. Like all other pinnipeds that have been tested, overall, the northern fur seal demonstrates an aquatically adapted ear that is more sensitive to sound intensity in the water than air. The upper limit of hearing appears to be quite close in both media, with the underwater frequency range appearing slightly greater than that in air.

An examination of Møhl's (1968) harbor seal data indicates a similar disparity between air and water audiograms. However, Møhl (1968) interpreted the disparity as a "dip in the audiogram at 2.0 kc/s." Møhl suggests that the seal air/water disparity is a result of resonance effect in the external auditory meatus. He calculated 43 mm tube length, which is a little shorter than the actual length of seal meatus casts he made.

Our interpretation follows Møhl and is also based on physiological rather than neurological mechanisms. Examination of the aerial audiograms of the harbor seal, sea lion and fur seal in Figure 2 all show a peak of insensitivity at 4 kHz, but the corresponding underwater audiograms lack this dramatic discrepancy, showing a relatively shallow 4–5 dB/octave increase in sensitivity for the harbor seal, about a 5 dB increase in sensitivity for the fur seal and a mild 2–3 dB decrease in sensitivity for the sea lion. The difference between these aerial and underwater audiograms at 4.0 kHz may be due to several adaptations for better hearing in water. The atrophy of the pinna in the fur seal and sea lion and its absence in the phocids are attributed to specialization as a valve and "undoubtedly reduce the sensitivity of hearing in air by pinnipeds" (Repenning 1972). In water, these animals hear by sound transmission from water through the skin and fatty layers to the inner ear, a sound route that bypasses the outer ear and is commonly referred to as bone conduction. Bone-conducted sound can reach the cochlear capsule by two different means; however, since the routes between air and water are different, this seems to be the most concise explanation for differences between aerial and water audiograms. This occurrence at 4.0 kHz may be due to the altering of both the pinna and the ear canal in these species. In humans, the general shape of the audiogram between 3.0 to 5.0 kHz, an area of maximal sensitivity, is derived in part from the resonant properties of the pinna and ear canal and can account for as much as a 15 dB augmentation in sensitivity (*see* Moore 1982). Since the pinna and ear canal are radically modified in pinnipeds (Repenning 1972), this may explain, in part, why this particular insensitivity peak occurs at 4.0 kHz.

The actual bone conduction route may also contribute to the difference between underwater audiograms of the pinniped species. Two different types of bone conduction have been described: (1) inertial, involving relative motion between the ossicular chain and the oval window, and (2) compressional, en-

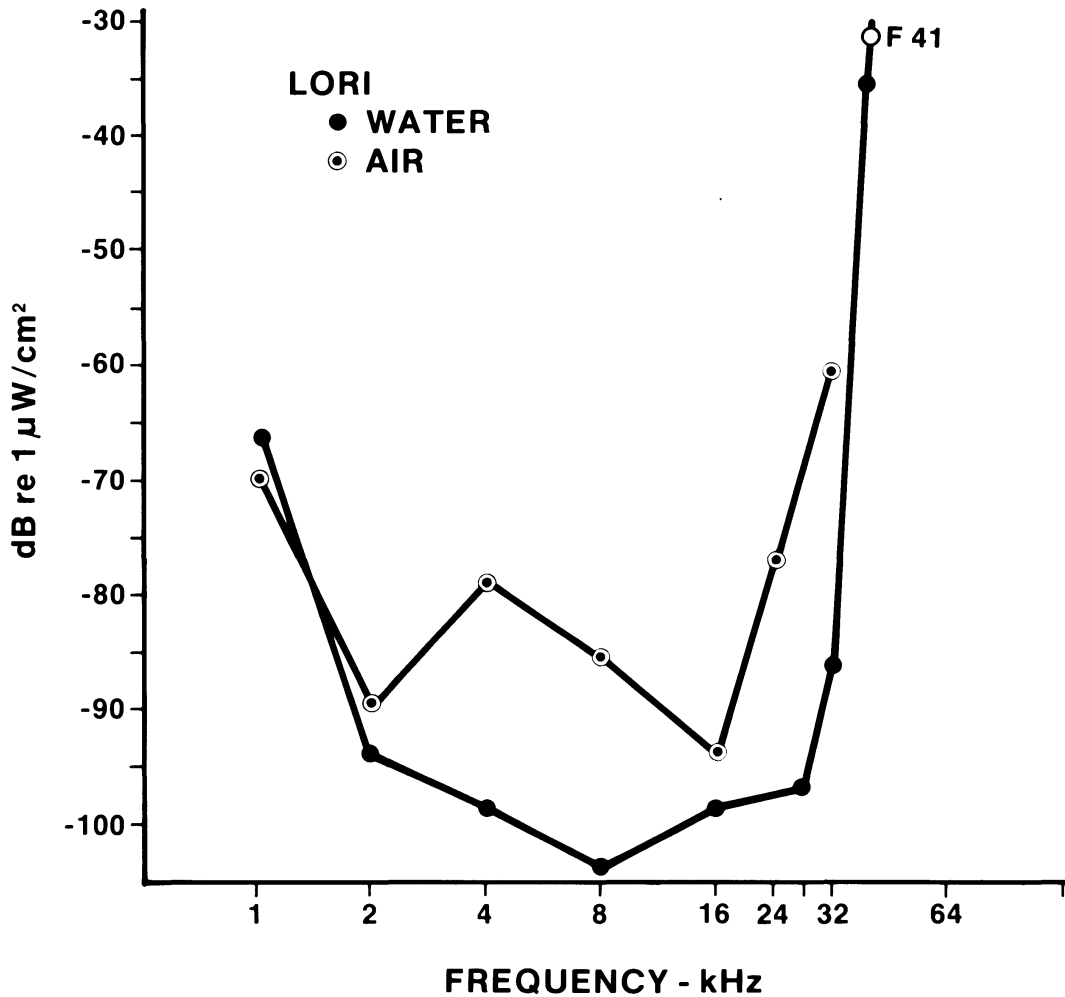


Figure 5. Comparison of air and water audiograms for both subjects converted to dB re: $1 \mu\text{W}/\text{cm}^2$.

tailing alternating compression and expansion of the cochlear capsule from exposure to sound (Tonndorf 1972). Both types of bone conduction depend on different properties of the morphology of the ear and comprise complicated events. Given the inventory of morphological differences that exist between the ears of the pinniped species (Repenning 1972), the exact proprieties that may contribute to these differences can only be speculative.

Based on our data, the notion that otariids differ from phocids both in upper hearing ability *and* overall sensitivity is not generally supported. The thresholds show that both Otariidae have an upper limit of hearing at about 40 kHz where phocid upper limits are about 60 kHz. However, the fur seals show equal or greater sensitivity to underwater sound between 2.0 and 32.0 kHz. Until additional comparative data are available, differences in hearing between the species may simply be a matter of range.

Experiment 3: Underwater Critical Ratios

An animal's ecological niche is limited and defined by sensory capabilities. An animal cannot orient towards sounds it cannot hear nor react differently to

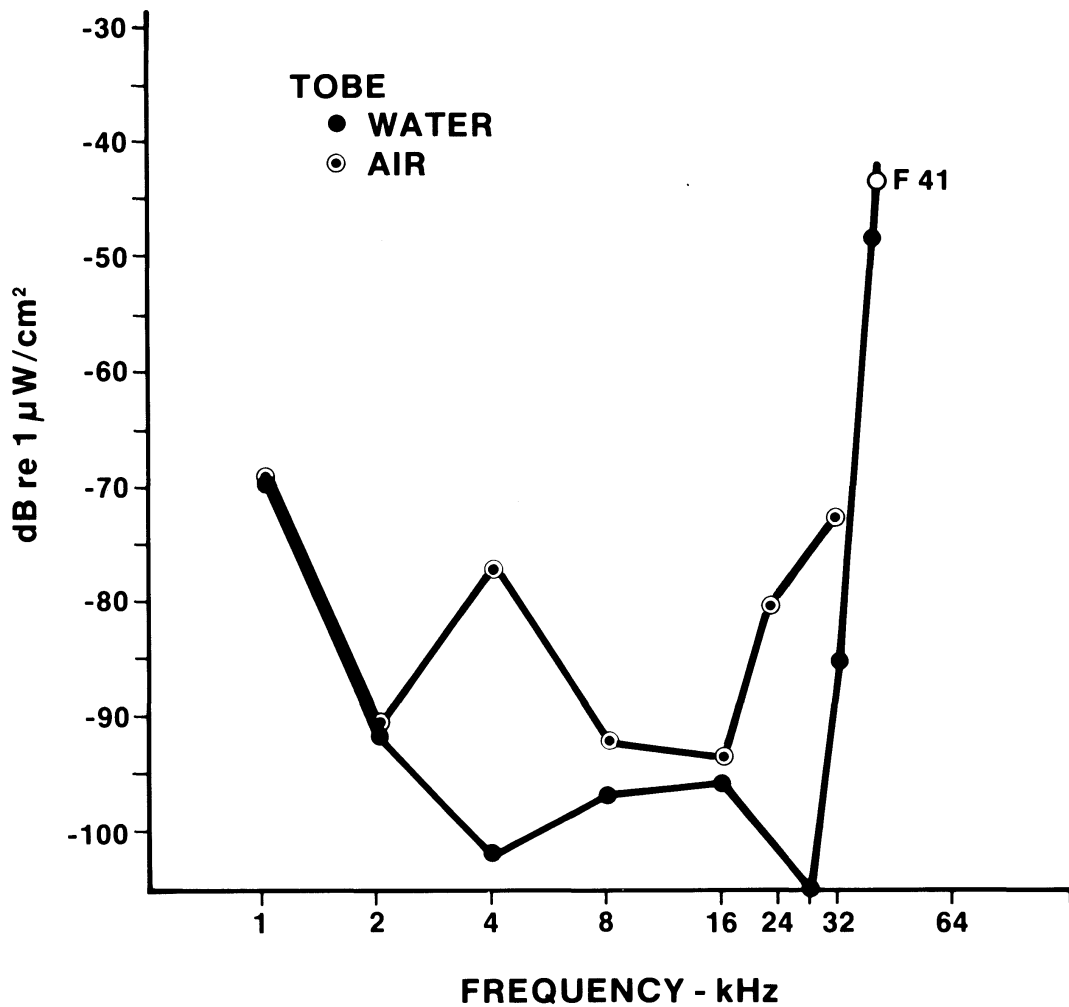


Figure 5. Continued.

sounds that are perceived to be the same. The audiogram describes the levels, range and frequency of sounds that an animal can detect; however, the environment contains many sounds that interfere with an animal's ability to detect and discriminate useful sounds. The interference effect is known as masking and refers to the phenomenon whereby one sound presented to the ear can make another sound difficult or impossible to hear. Experimentally, masking is defined as the difference, in decibels, between the absolute threshold of the signal measured in quiet and the threshold of the signal in the presence of noise or masking stimulus. Masking is often used to study the auditory system's ability to analyze frequency.

Fletcher (1940) demonstrated that not all the noise in a wideband noise masker actually contributed to the masking effect, but only a narrow band centered about the stimulus frequency. He proposed that the band of noise that actively contributed to the masking effect could be measured and he hypothesized that the power in the signal to be detected would be equal to the power of the noise in the masking band when the signal was at the just-masked threshold. This ratio of signal power to noise power as a measure of the critical

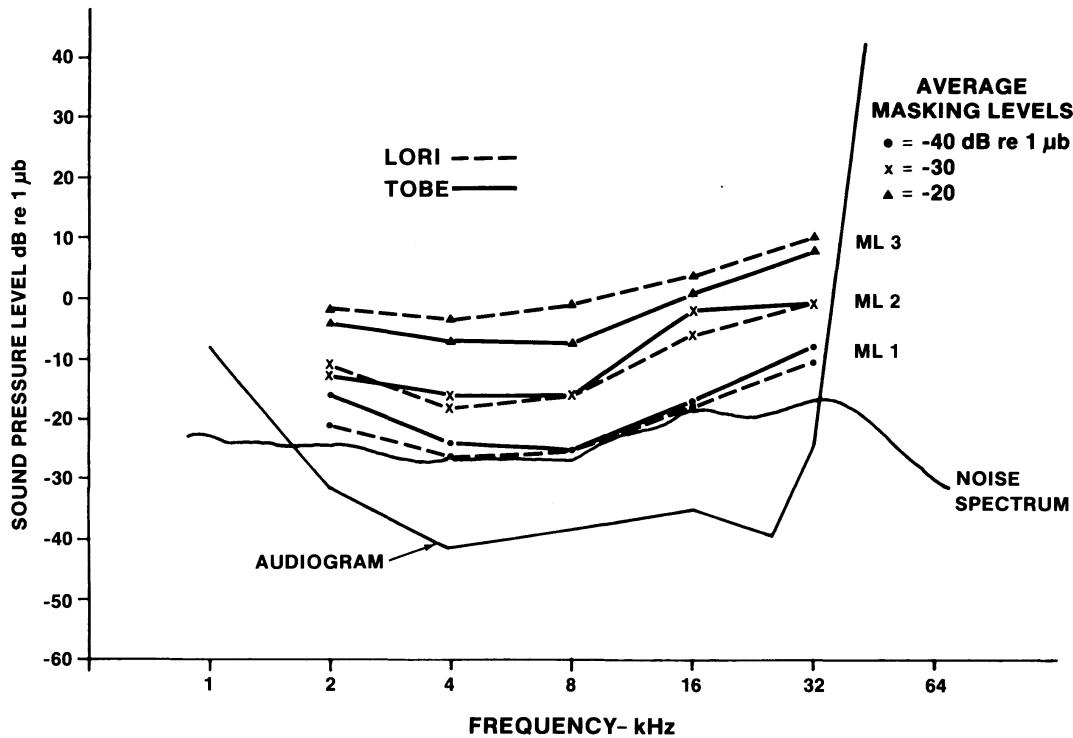


Figure 6. Underwater audiogram of the fur seals plotted with the masked thresholds of both subjects at the three different masking levels. Spectrum of the noise is shown from 1.0 to 64.0 kHz.

band has become known as the critical ratio. Although the critical ratio has been shown to be only an estimate of the actual critical band, the experimental procedure for measuring it is much less complicated than the task of directly measuring the critical band. This relative ease makes the critical ratio the procedure of choice for obtaining initial auditory measures of previously untested wild animals.

Subjects—The subjects were the same two fur seals used in the first two studies. The masked thresholds were a continuation of the underwater testing and animal food intake and weight were about the same. Testing was also conducted in the morning after the animals had eaten 18 h earlier.

Apparatus—The experimental tank and testing apparatus was the same as used in the threshold studies. For the masking measurements, additional equipment was required to introduce and control the masking noise. The masking noise was generated by H. H. Scott (Model 811-B) random noise generator. The output of the noise generator was passed to a second H.P. 305 C attenuator, which controlled the noise level, and fed to a mixer that combined the noise and pure tone signal. The rest of the signal presentation equipment was the same as used in the threshold tests.

The spectrum of the masking noise was measured at the headstand position with the H-23 hydrophone. The masking noise and pure tones were projected from the J-9 or F-41 transducer (depending on frequency). The masking noise level was measured from 1 to 50 kHz in 1.0-kHz increments and converted

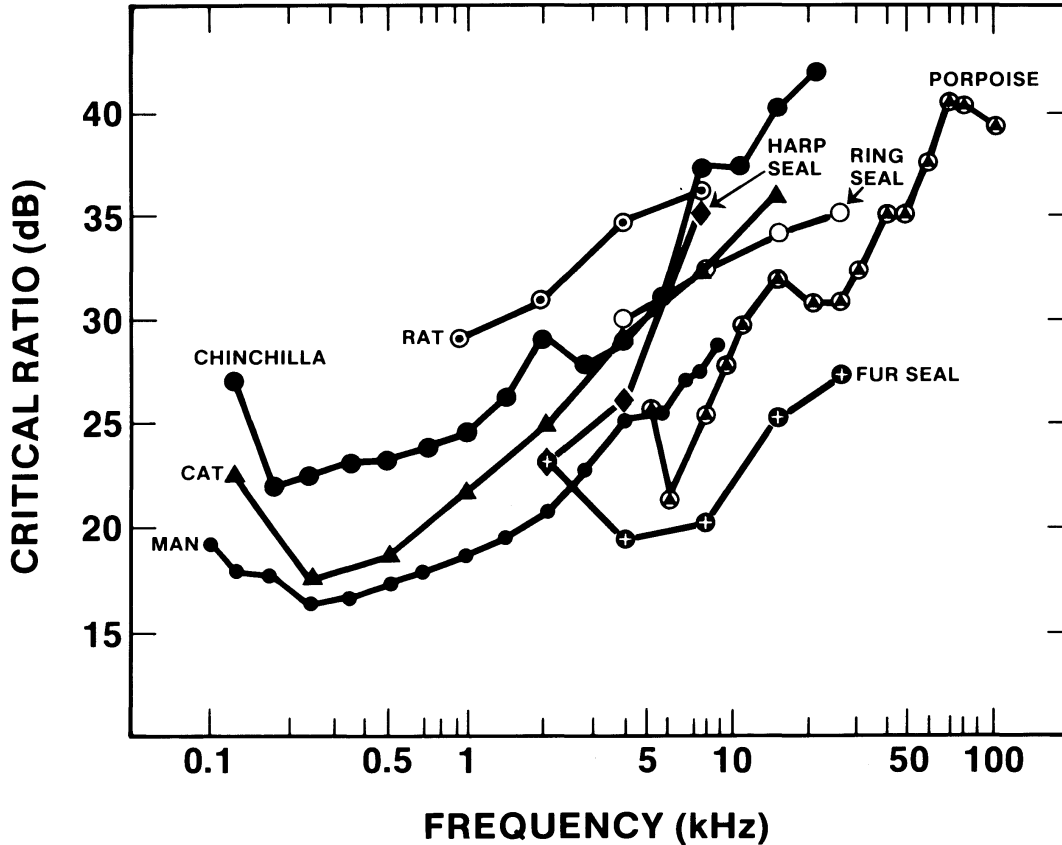


Figure 7. Critical ratio functions measured for the fur seal (this study) porpoise (Johnson 1968), humans (Hawkins and Stevens 1950), cat (Watson 1963), ringed seal (Terhune and Ronald 1975), harp seal (Terhune and Ronald 1971), chinchillas (Miller 1964) and rat (Gourevitch 1965).

to spectrum levels. The plot in Figure 6 shows the noise spectrum along with the combined audiogram for the two fur seals. The noise was flat ± 2 dB to about 8 kHz then increased 7 dB to peak at 32 kHz.

Procedure—The masking study stimulus presentation and response paradigms were the same as used in the other tasks. Masked thresholds were determined at three continuous broadband masking noise levels for frequencies of 2, 4, 8, 16 and 32 kHz. The overall level of the masking noise measured at the nose cup position was -20 dB re: $1 \mu\text{B}$ (spectrum level) for the lowest masking level (ML1). Noise levels for ML2 and ML3 were 10 and 20 dB greater respectively.

Results and discussion—Masked thresholds for the three different masking levels for each animal are shown in Table 2 and plotted with the combined fur seal aquatic audiogram in Figure 6. The thresholds for all three masking levels follow the audiogram between 2 kHz and 4 kHz; masking is somewhat higher at 2 kHz than at 4 kHz, even at the highest masking noise level. Except for the highest masking level at 8 kHz, thresholds at 4 and 8 kHz are similar and within a few dB of each other; with the loudest masking level at 8 kHz, the difference between the two animals' thresholds is about 7 dB. Masked thresholds at 16 and 32 kHz are also consistent within each masking level and follow

Table 2. Masked underwater threshold data for two northern fur seals for three masking levels.

Frequency (kHz)	Masking level dB	No. of runs	Thresholds (mean)	Critical ratio (dB)			
(S1 Tobe)							
2	-44	42	-16	28			
4	-46	32	-24	21			
8	-46	52	-25	21			
16	-41	26	-18	24			
32	-37	33	-8	29			
2	-34	28	-13	21			
4	-36	31	-17	19			
8	-36	32	-17	19			
16	-31	29	-3	29			
32	-27	30	0	27			
2	-24	22	-4	20			
4	-26	32	-7	18			
8	-26	21	-8	18			
16	-21	22	2	23			
32	-17	26	9	26			
(S2 Lori)							
2	-44	40	-21	23			
4	-46	25	-27	18			
8	-46	48	-25	21			
16	-41	29	-19	22			
32	-37	32	-10	27			
2	-34	33	-11	23			
4	-36	30	-19	17			
8	-36	37	-16	20			
16	-31	28	-7	25			
32	-27	30	-1	26			
2	-24	25	-2	22			
4	-26	25	-3	22			
8	-26	28	-1	25			
16	-21	28	4	26			
32	-17	27	9	26			
Pooled critical ratios for both fur seals							
	S1			S2			
	ML1	ML2	ML3	ML1	ML2	ML3	C.R.
2	28	21	20	23	23	22	23 dB
4	21	19	18	18	17	22	19 dB
8	21	19	18	21	20	25	21 dB
16	24	29	23	22	25	26	25 dB
32	29	27	26	27	26	26	27 dB

both the threshold in quiet and the shape of the noise, which showed an increase in level between 8 and 34 kHz. Also, at 4, 8 and 16 kHz, the thresholds for the lowest masking level follow the noise spectrum.

Critical ratios for the fur seal were obtained by pooling the data for both animals at each frequency. Critical ratios were 23, 19, 21, 25 and 27 dB for 2, 4, 6, 18 and 32 kHz respectively. These values are plotted in with other critical ratio data in Figure 7.

Of the species shown in Figure 7, man has the lowest critical ratio about 300 Hz. The shape of the human function, an initial decline followed by an increase in critical ratio value, is reflected in the critical ratio functions for the fur seal, dolphin, chinchilla and cat (*see* caption for references). However, of the marine mammals only dolphins and, to a much greater degree, fur seals, reflect this same shape about 1.5 octaves higher than man. The ringed seal (Terhune and Ronald 1975) values seem to be extraordinarily large and, to a lesser extent, so do those of the harp seal (Terhune and Ronald 1971). At face value, the fur seal critical ratios do not support the previous assumption that Phocidae have better hearing abilities generally than the Otariidae (Schusterman *et al.* 1972).

These results should also not be taken as an indication of superior critical bandwidth. The underlying assumption that the critical ratio is a measure of the critical band, either directly or indirectly, is not at all resolved (Bilger 1976). Green (1976) suggests the "General consensus is that the critical ratio approach is largely arbitrary and should be given little weight as a critical band estimate." We agree that these measures do have some, as yet not fully understood, relation to the frequency resolving capacity of the ear and concur with Long (1977) that "Until more studies have been made in which both measures have been obtained from the same species caution must be exercised in using critical ratios to estimate critical band widths of frequency discrimination capacity based on the relationships found in man." She also points out that "Comparisons of critical ratio measurements from different species without making any assumptions as to their relationship to their critical bands is, however interesting in itself" (Long 1977). More to the point, it has been recently shown that basilar membrane length and the number of spiral turns *are not* related. However, the number of cochlear turns is strongly related to octave hearing range (West 1985).

Given the similarity of the functions for the previously tested dolphin and the fur seal, various alternatives could explain the difference between phocidae critical ratio function and those of other mammals. The range of frequencies tested may have been too limited and further assessment of critical ratio values at lower frequencies would produce functions more similar to the other mammals. Alternatively, the critical ratio estimates for the dolphin, ringed seal and harp seal may have been based on noise-limited thresholds. Methodological differences in sound measuring techniques used to determine the sound fields for the ringed seal, coupled with differences of masker bandwidth (wideband noise from 1 to 50 kHz used in this study compared to "shaped bands of noise" [Terhune and Ronald 1975] for the ringed seal) or aurally obtained

critical ratios for the harp seal, may all have contributed to the disparity between the results of this study and other pinniped critical ratio estimates.

Of these alternatives, we believe that noise-limited thresholds and methodological differences to be more likely candidates for the discrepancies. Aquatic audiograms show that the Phocidae are as sensitive to absolute sound pressure levels and have higher frequency sensitivity than the Otariidae. However, the in-air audiograms reported for the harp seal (Terhune and Ronald 1971) and the sea lion (Schusterman 1974) are most likely masked. Thus, in water, the critical ratios for Phocidae should be close to those of the Otariidae and not 9 to 11 dB inferior, as indicated by reported data for the ringed seal (Terhune and Ronald 1975).

Accurate measurements of acoustic sensitivity require detailed attention to the sound field. Influences of the test environment can be reduced via two procedures: (1) Using a stationing device to restrict, as much as possible, the subject's movement in the field during listening (*see* Moore 1975, Moore and Au 1975, Moore and Schusterman 1976 for details of stationing apparatus) and (2) accurately mapping the signal level and using methods to minimize the effects of reverberation and standing wave patterns on a particular test environment. Given acoustically improved testing situations, remeasurements of both dolphin and other pinniped critical ratios would probably produce functions close to those of the fur seal.

Unfortunately, comparative data are limited. The general notion that *all* Otariidae are less sensitive than Phocidae both in absolute sensitivity and frequency range may be valid, but more and better threshold measurements are needed to extend both the range and number of pinnipeds tested. Critical ratio measures on otariidae extended to lower frequencies and generally increasing the number of both pinniped and cetacean audiograms would be especially fruitful.

We have stated (Schusterman and Moore 1980) that individual fitness in all species of pinnipeds depends to a great extent on the transmission and reception of acoustic information in both air and water. The audiometric data of the northern fur seal suggest that, in comparison with other pinnipeds thus far assessed, members of this taxa are among the most sensitive to airborne sound. Although the critical ratios are smaller than any other previously tested marine mammal species, the superior critical ratios may be a result of better and more accurately measured acoustic surrounds. The limited, comparative data indicate that the northern fur seal is a highly developed acoustic animal, one in which noise disturbance might have an important impact on a variety of adaptations within a wide range of contexts.

SUMMARY AND CONCLUSIONS

We experimentally determined the audiograms of two female northern fur seals both in air and under water. Based on the results of the aquatic threshold, we measured the masked thresholds and determined their critical ratios. In

addition, we measured the aerial audiogram of a California sea lion so that direct comparisons with the fur seals would be possible without complicating differences in experimental design or acoustic environments. The results of the aerial audiograms indicate the two otariid species have very similar functions; however, northern fur seals are 5–10 dB more sensitive to airborne sound than California sea lions throughout the frequency range tested and the upper frequency limit for fur seals is approximately 0.5 octave higher than for sea lions. These tests also indicate that the previous aerial audiogram of the sea lion (Schusterman 1974) was masked below 18 kHz. Of all the pinniped species tested, fur seals are the most sensitive to airborne sound. Audiograms of the harp seal (Terhune and Ronald 1971) match that of the masked audiogram previously reported for the sea lion (Schusterman 1974). Based on the aerial audiograms, the two otariid species are more sensitive than the phocids tested to date, not only in absolute sensitivity but also in the range of frequencies detected. To date, pinnipeds produce audiometric functions that parallel each other but differ based on what appear to be specific adaptations. Further studies are required to explore if there are universal differences in aerial auditory capabilities between phocids and otariids.

Aquatic audiograms of the fur seal indicate best sensitivity between 2.0 and 32.0 kHz and an effective upper limit of hearing at about 40.0 kHz. For both the Otariidae, the upper limit of hearing occurs at a lower frequency than for the Phocidae tested. The fact that the fur seal shows better sensitivity at frequencies of 4.0 and 8.0 kHz as compared to the Phocidae and the only other Otariidae suggests that northern fur seals are different from the California sea lions and more like the Phocidae in absolute sensitivity. This finding may modify the past assumption about differences in aquatic hearing abilities between the Phocidae and Otariidae and support the notion that the true seals differ only in higher upper hearing limit. This position is supported by the fur seal critical ratios, which are the smallest of any previous tested pinnipeds and even the dolphin. The data argue that the difference may be an effect of better behaved acoustic environments for the northern fur seal measurements rather than true species differences, and our position is that these audiometric results spring from exceptionally good testing environments coupled with well-developed methods and practiced animal subjects. For this to be demonstrated, further data must be obtained and physiologic examinations and comparisons of the fur seal cochlea need to be made.

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