Underwater hearing sensitivity of a male and a female Steller sea lion (*Eumetopias jubatus*)

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The unmasked underwater hearing sensitivities of an 8-year-old male and a 7-year-old female Steller sea lion were measured in a pool, by using behavioral psychophysics. The animals were trained with positive reinforcement to respond when they detected an acoustic signal and not to respond when they did not. The signals were narrow-band, frequency-modulated stimuli with a duration of 600 ms and center frequencies ranging from 0.5 to 32 kHz for the male and from 4 to 32 kHz for the female. Detection thresholds at each frequency were measured by varying signal amplitude according to the up–down staircase method. The resulting underwater audiogram (50% detection thresholds) for the male Steller sea lion showed the typical mammalian U-shape. His maximum sensitivity (77 dB *re*: 1 μPa, rms) occurred at 1 kHz. The range of best hearing (10 dB from the maximum sensitivity) was from 1 to 16 kHz (4 octaves). Higher hearing thresholds (indicating poorer sensitivity) were observed below 1 kHz and above 16 kHz. The maximum sensitivity of the female (73 dB *re*: 1 μPa, rms) occurred at 25 kHz. Higher hearing thresholds (indicating poorer sensitivity) were observed for signals below 16 kHz and above 25 kHz. At frequencies for which both subjects were tested, hearing thresholds of the male were significantly higher than those of the female. The hearing sensitivity differences between the male and female Steller sea lion in this study may be due to individual differences in sensitivity between the subjects or due to sexual dimorphism in hearing.

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I. INTRODUCTION

There are nine species of sea lions and fur seals living in both hemispheres. Of these Otariid pinnipeds, the Steller sea lion (*Eumetopias jubatus*) is the largest and shows the most marked sexual dimorphism. Females weigh up to 350 kg and adult males may be up to three times heavier. The Steller sea lion occurs in the subarctic waters of the North Pacific Ocean. It leads an amphibious life and spends much time both resting on land and in the water during activities such as migration, foraging, and courtship (Loughlin, 2002). Since the mid-1970s the western population of Steller sea lions has declined and the species was declared endangered in 1997 (Trites and Larkin, 1996; Merrick *et al.*, 1997). One of the factors causing this decline could be disturbance by increased anthropogenic underwater noise (Akamatsu *et al.*, 1996).

Steller sea lions produce both aerial and underwater vocalizations. The loud aerial vocalizations produced by bulls are described as belches, growls, snorts, scolds, and hisses; these signals seem to have a social function mainly related to territorial behavior during the breeding season. The aerial sounds emitted by females and their pups are described as bellows and as resembling the bleating of sheep (Ono, 1965; Gentry, 1968; Orr and Poulter, 1967). Steller sea lions also produce a large variety of underwater vocalizations described as belching, barking, and clicks (Orr and Poulter, 1967; Schusterman *et al.*, 1970; Poulter and del Carlo, 1971).

To determine the importance of sound for Steller sea lions during activities such as communication, reproduction, predator avoidance, and navigation, and the potential for disturbance by anthropogenic noise, information is needed on the species' hearing sensitivity both in air and underwater. However, neither aerial nor underwater hearing sensitivities of the Steller sea lion have been tested. Underwater audiograms have so far been obtained for only nine of the 34 pinniped species of the three families (*Phocidae, Otariidae*, and *Odobenidae*). To date, hearing profiles are available for only two of nine *Otariids*. These profiles are based on information from only one or two animals per species: a 5–6-

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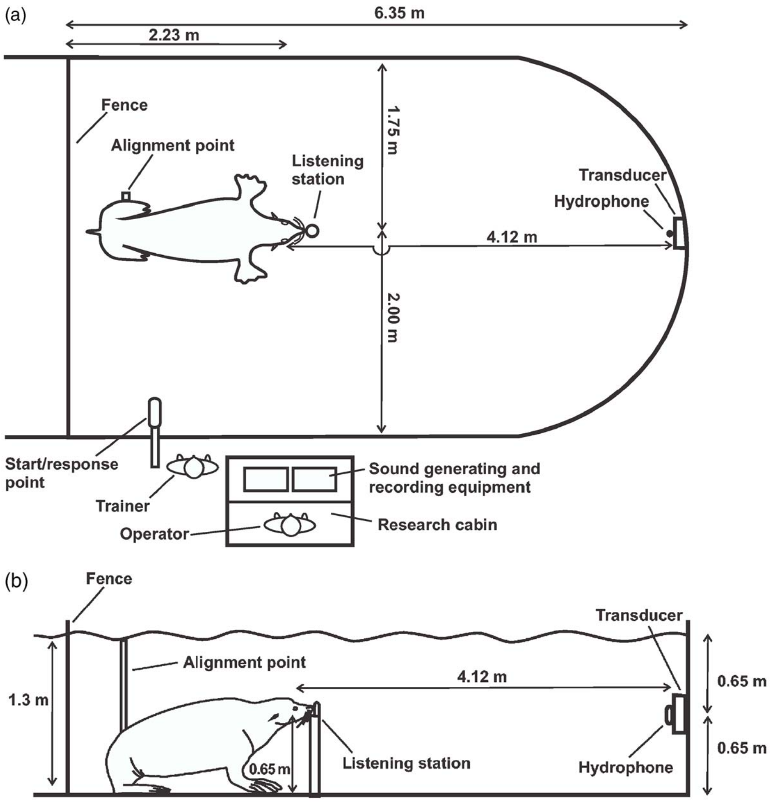

FIG. 1. The study area, showing one of the Steller sea lions under water in the correct position at the listening station. (a) top view and (b) side view, both to scale.

year-old male California sea lion, *Zalophus californianus* (Schusterman *et al.*, 1972), a 12-year-old male California sea lion (Kastak and Schusterman, 2002) and two 2–3-year-old female Northern fur seals, *Callorhinus ursinus* (Moore and Schusterman, 1987). Due to the small sample size per species, very little is known about the hearing demographics in pinniped species including differences between individuals that might be related to age, size, and sex. Steller sea lion hearing may not resemble that of the *Otariids* which have been tested. A recent study of the underwater hearing sensitivity of the large Pacific walrus (*Odobenus rosmarus divergens*) shows a limited frequency hearing range for this species (Kastelein *et al.*, 2002). The limited frequency range may be due to the large size of the hearing organ structures in the walrus (Kastelein *et al.*, 1996) compared to those of the smaller pinniped study subjects of which the hearing sensitivity has been tested. Because Steller sea lions show a large sexual difference in body size, large differences in the sizes of the structures of the hearing organs probably exist. This may lead to sexual differences in hearing sensitivity or frequency range of hearing, as is found in terrestrial mammals (Heffner *et al.*, 2001). It is not clear if sizes of the middle and inner ears are related to the hearing sensitivity in marine mammals.

In order to measure hearing sensitivity of Steller sea lions, and to evaluate how hearing sensitivity varies between individuals of different sizes and sexes, we tested, under identical conditions, the underwater hearing (frequency range of hearing and frequencies of best hearing sensitivity) of two captive Steller sea lions of similar age: an adult male and an adult female.

II. MATERIALS AND METHODS

A. Study animals

The study animals were a male (code EjZH021) and a female (code EjZH022) Steller sea lion which were collected for research purposes in British Columbia, Canada, at the age of a few weeks and housed at the Vancouver Aquarium until the age of 4 years, after which they were sent to Dolfinarium Harderwijk, The Netherlands. During the current experiment, the animals were healthy. The male was 8 years old and his body weight varied between 590 and 960 kg depending on the season. The female was 7 years old and her body weight varied between 213 and 228 kg. Veterinary records showed that the animals had not been exposed to ototoxic medication. The male received between 20 and 40 kg and the female between 7 and 15 kg of thawed fish (herring, *Clupea harengus*; mackerel, *Scomber scombrus*; scad, *Trachurus trachurus*, and sprat, *Sprattus sprattus*) per day depending on the season (Kastelein *et al.*, 1990), divided over four to seven meals.

B. Study area

The experiment was conducted at one end of a C-shaped outdoor concrete pool with an adjacent haul-out space. The portion of the pool used for the experiment was 9 m(l) ×3.75 m(w), 1.3 m deep (Fig. 1). The water level was kept constant. The average monthly water temperature varied between 3 and 22 °C, and the salinity was approximately 2.5% NaCl. The water circulation pump was switched off 10 min before and during sessions, so that there was no pump noise or water current in the pool during the experiments. No other

TABLE I. The mean 50% detection thresholds of an 8-year-old male Steller sea lion for eight narrow-band FM signals (based on total number of reversals), mean session threshold range, number of sessions conducted, number of reversals used to calculate the mean detection threshold, and prestimulus response rate based on the number of prestimulus responses in all trials (signal-present+signal-absent trials). SPL in dB *re*: 1 μPa, rms.

Center frequency (kHz)	Frequency modulation range (kHz)	Mean 50% detection threshold (SPL)	Mean session threshold range (SPL)	No. of sessions	Total no. of reversals	Prestimulus response rate (%)
0.5	0.495–0.505	100	93–107	4	40	23
1	0.99–1.01	77	72–80	10	122	16
2	1.98–2.02	81	77–83	10	176	7
4	3.96–4.04	82	77–89	10	150	7
8	7.92–8.08	87	78–92	5	58	4
16	15.84–16.16	85	77–88	6	76	3
25	24.75–25.25	90	86–92	4	70	2
32	31.68–32.32	99	94–101	3	40	4

animals were present in the pool during the tests, as the one or two pool mates (one of which was the other study subject) were trained to stay ashore during sessions. The equipment used to produce the sound stimuli was housed out of sight (above) of the study animals, in an observation and data collection cabin that was located 4 m away from the animals and trainer (Fig. 1).

C. Test stimuli production and calibration

Narrow-band sinusoidal frequency-modulated (FM) signals were produced by a waveform generator (Hewlett Packard, model 33120A). The modulation range of the signal was ±1% of the center frequency (the frequency around which the signal fluctuated symmetrically), and the modulation frequency was 100 Hz. For example, if the center frequency was 10 kHz, the frequency fluctuated 100 times per second between 9.9 and 10.1 kHz. Tables I and II show the frequency ranges of the signals.

In most previous studies of pinniped hearing, except in an experiment in which the hearing sensitivity of a Pacific walrus was tested (Kastelein *et al.*, 2002), pure tones have been used as test signals. In the present study, narrow-band FM signals were used because such signals reduce the level of constructive and destructive interference effects (standing waves) on the signals reaching the animal in a reverberant pool. Sound measurements showed that the exposure level was more constant when using FM signals than when using pure tones. Within a measurement session, the maximum variation between SPL measurements of the FM signals varied per frequency between 0.2 and 6 dB, but was generally around 3 dB. In humans, FM signals tend to have a slightly higher arousal effect than pure tones, which may lead to slightly lower (<5 dB depending on center frequency and modulation frequency) hearing thresholds (Morgan *et al.*, 1979). The test signals had no harmonics with sound pressure levels (SPLs) near the sea lions' hearing thresholds.

A modified audiometer used for testing human aerial hearing (Midimate, model 602) was used to control the duration and amplitude of signals (Fig. 2). During the experiment, the stationary portion of the signal was 600 ms in duration. The onset and offset of the signal were delayed with a rise and fall time (each 50 ms) to prevent transients. This signal duration was expected to be acceptable in relation to the hearing system's integration time (based on the integration time of the harbor seal, *Phoca vitulina*; Terhune, 1988). The SPL at the sea lion's head while at the listening station could be varied in 5-dB increments (this step size was determined by the audiometer; 5-dB steps are generally used in human audiometry). Before each session the sound generating system was checked in two ways. The voltage output

TABLE II. The mean 50% detection thresholds of a 7-year-old female Steller sea lion for five narrow-band FM signals (based on total number of reversals), mean session threshold range, number of sessions conducted, number of reversals used to calculate the mean detection threshold, and prestimulus response rate based on the number of prestimulus responses in all trials (signal-present+signal-absent trials). SPL in dB *re*: 1 μPa, rms.

Center frequency (kHz)	Frequency modulation range (kHz)	Mean 50% detection threshold (SPL)	Mean session threshold range (SPL)	No. of sessions	Total no. of reversals	Prestimulus response rate (%)
4	3.96–4.04	81	76–83	3	38	11
8	7.92–8.08	80	78–82	2	24	2
16	15.84–16.16	79	72–83	2	22	0
25	24.75–25.25	73	71–74	2	24	2
32	31.68–32.32	79	77–80	2	24	7

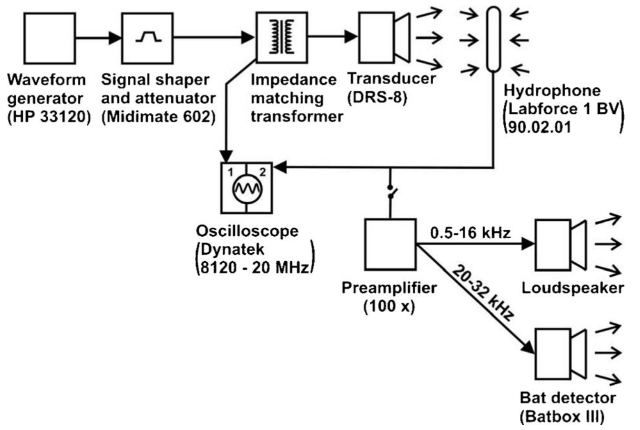

FIG. 2. Block diagram of the signal generation and listening system used in the Steller sea lion underwater hearing study.

level of the system, at the input of the impedance-matching transformer (while the attenuator was at the same setting as during calibrations), was checked with an oscilloscope (Dynatek 8120, 20 MHz; Fig. 2). In addition, the voltage output of a hydrophone (Labforce 1 BV, model 90.02.01) placed in front of the transducer was checked when a signal was produced.

The signals were projected by an underwater piezoelectric transducer (Ocean Engineering Enterprise, model DRS-8; 25 cm diameter) with its impedance-matching transformer (Fig. 2). The transducer was fixed to the pool wall in a protective stainless-steel cage during the entire study period. It was 4 m in front of the study animals when they were positioned at the listening station. The transducer was positioned with the acoustic axis of the projected sound beam pointed at the center of the animal's head.

The male Steller sea lion's underwater hearing sensitivity was measured for signals with center frequencies of 0.5, 1, 2, 4, 8, 16, 25, and 32 kHz. The female's hearing was tested for signals with center frequencies of 4, 8, 16, 25, and 32 kHz. The female's hearing was tested for fewer frequencies than the male's because she gave birth and therefore had to be separated from the male.

Before each session, the test signal (at a sufficient SPL) was checked aurally by the signal operator via the hydrophone which was mounted just in front of the transducer. The hydrophone's output was connected to an amplifier and loudspeaker or, for the ultrasonic signals (>20 kHz), to a bat detector (Batbox III; Stag Electronics, Steyning, UK).

The root-mean-square (rms) SPL (dB *re*: 1 μPa) of each test frequency was measured approximately once each month at the sea lions' typical head position when the animals were at the listening station during the tests (Fig. 1). The sea lions were not in the pool during these calibrations. During trials, the location of the sea lion's head (while at the listening station) relative to the transducer was carefully checked by the trainer to ensure that head position was consistent to within a few centimeters.

The calibration equipment used for all signals consisted of a broadband hydrophone [Brüel & Kjaer (B&K) 8101], with flat frequency response (within 1 dB) in the tested frequency range, a conditioning amplifier (B&K, Nexus 2690), a computer with a data acquisition card (National Instruments, PCI-MIO-16E-1, 12-bit resolution), and a coaxial module to receive the input signals (National Instruments, model BNC-2090). The system was calibrated with a pistonphone (B&K, 4223). The signals were digitized at a sample rate of 512 kHz and fast Fourier transformed (FFT) into the frequency domain using a Hanning window. The highest peak in the spectrum was selected to determine the SPL, and five consecutive 0.2-s time blocks were used to calculate the average SPL per calibration session. The maximum SPL variation between calibration sessions varied per frequency between 0 and 4 dB, but was generally around 2 dB. The average SPL per frequency was calculated based on all calibration sessions. These averages were used to determine the session thresholds. The SPLs 20 cm in all six directions from the auditory meatus of the animals varied by 0–2 dB.

The SPL was calibrated at a level 10–30 dB above the threshold levels found in the present study. The linearity of the attenuation of the audiometer was checked three times during the study and was precise. The spectra of the signals were monitored to detect potential surface reflections causing cancellations. Multipath arrivals and standing waves introduce both temporal and spatial variations in the observed SPL at the listening station. The use of frequency-modulated stimuli generally resulted in smaller amplitude variations (generally 3 dB) at the listening station than pure tones.

D. Background noise

No activity took place near the pool during sessions, and the water pump in a nearby engine room was switched off. Underwater background noise levels were measured under the same conditions as during the sessions.

The equipment used to measure the background noise in the pool differed from the equipment used to calibrate the signals. The equipment consisted of a broadband (0–100 kHz) hydrophone (B&K, 8101), a voltage amplifier system (TNO TPD, 0–300 kHz), and an analyzer system (Hewlett Packard 3565, controlled by a Toshiba Pro 4200 notebook computer; frequency range 0–80 kHz, sample frequency 260 kHz, $df=31$ Hz, FFT measurement converted to 1/3-octave bandwidths). The total system was calibrated with a pistonphone (B&K, 4223) and a white noise "insert voltage signal" into the hydrophone preamplifier. Measurements were corrected for the frequency sensitivity of the hydrophone and the frequency response of the measurement equipment.

Background noise levels are given as "equivalent sound-pressure spectrum levels" (L_{eq} method), i.e., the time-averaged levels of the fluctuating noise (Hassall and Zaveri, 1988). An equivalent sound-pressure level would produce the same acoustic energy, over a stated time period, as a specified time-varying noise. Background noise was converted to "spectrum level" (dB *re*: 1 μPa/$\sqrt{\text{Hz}}$) using the formula $L_{sp}=L_{eq}-10\log \text{BW}$, in which L_{sp}=equivalent sound spectrum level (in dB *re*: 1 μPa), L_{eq}=equivalent sound pressure level, and BW=bandwidth of 1/3-octave bands (in Hz). Figure 3 shows the background noise levels in the pool, converted to spectrum level (L_{eq}, 1-Hz bandwidth,

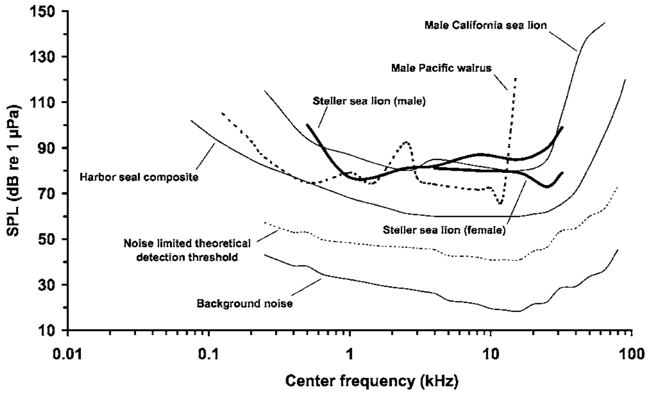

FIG. 3. The mean 50% detection thresholds in dB *re*: 1 μPa (rms) for narrow-band FM signals obtained for the male and female Steller sea lion in the present study (for details, see Tables I and II). Also shown are the underwater audiograms of a harbor seal [a composite of data from Møhl (1968a), Turnbull and Terhune (1990), and Kastak and Schusterman (1998), with potentially masked thresholds adapted], a California sea lion (Schusterman *et al.*, 1972), and a male Pacific walrus (Kastelein *et al.*, 2002). The background noise in the pool of the present study between 250 Hz and 80 kHz is plotted in dB *re*: 1 $\mu\text{Pa}/\sqrt{\text{Hz}}$ (derived from 1/3-octave band levels). Also shown is the noise-limited theoretical detection threshold level based on the background noise level, an estimated sea lion critical ratio (derived from Moore and Schusterman, 1987; Southall *et al.*, 2000, 2003) and an assumed directivity index for sea lions.

range 250 Hz–80 kHz). Also shown in this figure is the noise-limited theoretical detection threshold curve based on the background noise level in the pool, an estimated sea lion critical ratio [derived from Moore and Schusterman, 1987 (Northern fur seal), and Southall *et al.*, 2000, 2003 (California sea lion)] and an assumed directivity index for sea lions. (The noise-limited theoretical detection threshold = background noise + critical ratio − directivity index).

E. Experimental procedure

Training the sea lions for the go/no-go underwater hearing procedure took 1 month. Operant conditioning using positive reinforcement was used to condition the animals to produce a response (go) in the presence of a signal and to withhold the response (no-go) in the absence of the signal. Experimental sessions consisted of multiple trials. A trial began when one of the animals was positioned at a start and response point on land next to the trainer [Fig. 1(a)]. When the trainer gave the animal the vocal command accompanied by a gesture (pointing downward), the animal descended to the listening station (a nylon ball on a wooden pillar), so that its external auditory meatus was 412 cm from the sound source and about 65 cm below the water surface [Fig. 1(b)]. Each animal was trained to position its nose against the listening station so that its head axis was in line with the projected beam axis. To assist them to reach the correct alignment with the transducer's beam, the animals were trained to put their left hind flipper against a bar on a fence behind them.

Two trial types were presented during each experimental session: signal-present trials and signal-absent trials. In signal-present trials, the stimulus was presented unpredictably between 4 and 10 s after the animal was positioned correctly at the listening station. A minimum waiting time of 4 s was chosen because it took about 4 s for the waves, created by the animal's descent, to dissipate. If the animal detected the sound, it responded by leaving the listening station (go response) at any time during the signal's duration and returning to the start and response point [Fig. 1(a)]. The signal operator then informed the trainer (via a headset radio) that the response was correct (a hit), after which the trainer gave a vocal signal and the sea lion received a fish reward. If the animal did not respond to the signal, the signal operator informed the trainer that the animal had failed to detect the signal (a miss). The trainer then signaled to the animal (by tapping the fish bucket on the floor) that the trial had ended, thus calling the animal back to the start and response point. No reward was given following a miss. If the animal moved away before a signal was produced (a prestimulus response or false alarm), the signal operator told the trainer to end the trial without reinforcement.

On signal-absent, or catch trials, the signal operator told the trainer to end the trial after a random interval of 4 to 10 s after the sea lion had stationed. The trial was terminated when the trainer blew a whistle. If the animal responded correctly by remaining at the listening station until the whistle was blown (a correct rejection), it then returned to the start and response point and received a fish reward. If the sea lion left the listening station before the whistle was blown (a prestimulus response or false alarm), the signal operator told the trainer to end the trial without rewarding the animal. The same amount of fish was given as a reward for correct go and no-go responses. In both signal-present and signal-absent trials, the trainer was unaware of the trial type until the animal had responded.

A session generally consisted of 20–24 trials and lasted for about 20 min. Each session consisted of 50% signal-present and 50% signal-absent trials presented in random order based on a pseudorandom series table (Gellermann, 1933; maximum of three consecutive similar trials), with the modification that the first trial in a session was always a signal-absent trial. Each day one of four data collection sheets with different random series was used. Over the 18-month study, six different sets of four data collection sheets were used.

In each session, the signal frequency was held constant and the signal amplitude was varied according to a modified up/down staircase psychometric technique (Robinson and Watson, 1973). This is a variant of the method of limits, which results in a 50% correct detection threshold (Levitt, 1971). Prior to testing at a given frequency, an estimated threshold was determined during preliminary sessions, in which the rough hearing threshold per test frequency was determined using the up–down staircase method.

During subsequent experimental sessions, the starting SPL of the signal was 10–15 dB above the estimated threshold. Following each hit, the signal amplitude on the next signal-present trial was reduced by 5 dB. Following each miss, the signal level was increased on the next signal-present trial by 5 dB. Prestimulus responses (false alarms) did not lead to a change in signal amplitude for the next trial.

TABLE III. Two-way ANOVA to test for differences in hearing sensitivity between the male and female Steller sea lion. There is a significant difference between the hearing thresholds of the two sea lions, and the signal frequency has a significant effect on the hearing threshold.

Source of variation	Degrees of freedom	Adjusted means square	Test statistic (F)	Probability (P)
Sea lion	1	9147.6	292.89	0.000
Signal frequency	4	734.3	23.51	0.000
Sea lion × signal frequency	4	1239.3	39.68	0.000
Error	500	31.2		
Total	509			

A switch in the sea lion's response from a detected signal (a hit) to an undetected signal (a miss), or vice versa, is called a reversal.

Thresholds were determined for eight frequencies for the male sea lion and five frequencies for the female sea lion. In order to prevent the animals' learning process from affecting the shape of the audiogram, the test frequency was varied from session to session. The sequence of frequencies, tested in successive sessions, were neighbors in the following list: 0.5, 1, 2, 4, 8, 16, 25, and 32 kHz. This way, the difference in frequency between sessions was limited, reducing the potential need for adaptation to the frequency.

One experimental session was conducted daily (maximum 5 days/week) during the first meal of the day between 0800 and 0820 h, when the sea lions had not been fed for 16 h, and the park was still closed to visitors. Data for the male were collected between June and August 2001, and between May and November 2002. Both years, no tests were conducted during the Steller sea lion's rutting period in July due to loss of food motivation (Kastelein *et al.*, 1990). Data for the female were collected between July and August 2001. It was the intention to conduct at least ten sessions per frequency and to test frequencies below 0.5 kHz and above 32 kHz. However, the study period was shorter than previously planned because access to the animals for research was not granted after October 2002.

F. Analysis

Sound levels at which reversals took place were taken as data points. The mean 50% detection threshold per frequency was defined for each animal as the mean amplitude of all the reversal data points obtained in all available sessions after the mean session thresholds leveled off, which usually occurred after two or three sessions. Sessions with more than 20% prestimulus responses (four out of the usual 20 trials per session) were not included in this analysis. These occurred only about ten times during the entire study, and usually coincided with obvious transient background noises.

The hearing thresholds obtained for each animal were compared across frequencies using a one-way ANOVA to evaluate within-subject effects of signal frequency on sensitivity. Tukey tests were used to compare sensitivities at the various signals frequencies. The hearing thresholds of the two animals at the five frequencies they both were tested for were compared using a two-way ANOVA to identify individual differences in sensitivity.

All statistical analysis was carried out on MINITAB for Windows version 13 (Ryan and Joiner, 1994) with a significance level of 5%, using the hearing threshold as the dependent variable. Test assumptions were met in all tests (Zar, 1984).

III. RESULTS

The underwater audiogram (50% detection thresholds) for the male Steller sea lion shows the typical mammalian U-shape (Fig. 3 and Table I). His maximum sensitivity (77 dB *re*: 1 μPa, rms) occurred at 1 kHz. The range of best hearing (10 dB from the maximum sensitivity) was from 1 to 16 kHz (4 octaves), and sensitivity fell below 1 kHz and above 16 kHz. After the initial two or three sessions of a frequency, which were not included in the analysis, the animal's sensitivity for each test frequency was stable over the 1.5-year study period. The male's average prestimulus response rate (for both signal-present and signal-absent trials) varied between 2% and 23%, depending on the frequency (Table I). Most prestimulus responses occurred during tests with low-frequency signals. There was a significant difference in the hearing threshold of the male Steller sea lion due to frequency ($F_{7,724}=164.15, P<0.001$). Tukey tests showed that the thresholds for the frequencies could be ordered as follows: $1<2=4<16=8<25<32=0.5$ kHz.

The female's maximum sensitivity (73 dB *re*: 1 μPa, rms) occurred at 25 kHz (Fig. 3 and Table II). After the initial two or three (depending on the test frequency) sessions, which were not included in the analysis, the female's sensitivity for each test frequency was stable over the 3-month study period. The female's average prestimulus response rate (for both signal-present and signal-absent trials) varied between 0% and 11%, depending on the frequency (Table II). There was a significant difference in the hearing threshold of the female Steller sea lion due to frequency ($F_{4,111}=9.67, P<0.001$). Tukey tests showed that the thresholds fell into two significantly different groups, such that the threshold for 25 kHz was significantly lower than that for 4, 8, and 32 kHz. The threshold for 16 kHz was not significantly different from those of either group.

At frequencies for which both subjects were tested, hearing thresholds of the male were significantly higher than those of the female (Table III).

IV. DISCUSSION AND CONCLUSIONS

A. Evaluation of the data

It is important to know whether the audiograms of the present study are absolute audiograms or if the signals were masked by the ambient noise in the pool. A calculation [detection threshold=background noise+critical ratio −directivity index] shows that the audiograms found in the present study are considerably (more than 10 dB) above the noise limited theoretical detection threshold, and thus represent absolute audiograms (Fig. 3).

In contrast to the slightly lower hearing thresholds found in humans when using FM signals instead of pure-tone signals (Morgan *et al.*, 1979), the use of FM signals instead of pure tones probably had little effect on the thresholds found in the present study. This assumption is based on the results from a hearing test with 250-Hz signals on a Pacific walrus. No difference was found in thresholds between the same narrow-band FM signals as used in the present study (frequency modulation only 1% of the center frequency), and pure-tone signals (Kastelein *et al.*, 2002). In addition, a study with California sea lions, in which much wider band FM signals were used (1-octave sweeps in 10–50 ms: 3.2 →6.4 kHz and 6.4→3.2 kHz; 5-ms rise and fall times), showed similar evoked potential thresholds to those obtained with pure tones (Bullock *et al.*, 1971).

Signal duration can influence hearing thresholds. In humans, for instance, aerial hearing thresholds begin to increase when signal duration drops below a certain value. However, several threshold durations are mentioned in literature: 10 s (Garner, 1947); 1 s (Plomp and Bouman, 1959); 300 ms (Watson and Gengel, 1969). From Johnson (1968) 1 s can be derived as the relevant value for bottlenose dolphins (*Tursiops truncatus*). In harbor seals, phocid pinnipeds, sharp increases in hearing thresholds only occur when signal duration becomes less than 50 ms (Terhune, 1988; 1989). Kastelein *et al.* (2002) found no statistical differences between hearing thresholds in a Pacific walrus for signals of 1500 and 300 ms. The integration time of the walrus is probably also shorter than 300 ms. As the hearing system integration time is frequency dependent and decreases for increasing frequencies, it may be expected that the 600-ms signal duration used in the present study was more than the integration time of the Steller sea lion's hearing system. A short test signal duration (but above the integration time) has two advantages: it reduces the chance of the animal being able to adjust the position of its head in order to find regions of slightly higher SPL due to multipath effects, and it reduces the chance of the animal producing a false alarm during signal presentations below the hearing threshold. The 600-ms signal used in the present study was long enough to yield an accurate best hearing sensitivity curve but short enough to avoid the disadvantages of longer signals.

For some frequencies the sample size was relatively small due to the unexpected early termination of the study. However, when the study was interrupted for 6 months and then resumed, the mean hearing thresholds of the male from before the break were similar to those after the break (varying 2–4 dB depending on the test frequency).

B. Comparison with other pinniped hearing studies

Comparing the findings of the present study to those of other pinniped hearing studies is difficult, since the accuracy of the studies often cannot be established. Information on the calibration methodology, threshold calculation, and variation in the threshold data between sessions is often limited, and results are not always free from masking influences. In addition, most studies have used different methodology, stimuli parameters such as signal type (pure tone versus FM signal) and signal duration, ways to report SPL (peak-to-peak or rms, causing a 9-dB difference), the level calculation method is often not specified, and the studies were conducted at different depths. Also, the physical effort an animal has to exert to show response probably affects the threshold level. In some cases animals only had to press a pedal next to them as a response, while in the present study the sea lion had to move its entire body several meters. This probably led to a conservative audiogram, but most other audiograms on pinniped underwater hearing are probably conservative as well.

Despite these limitations, general comparisons can be made between the underwater audiogram of the Steller sea lions and the underwater audiograms of the other pinnipeds of which the underwater hearing has been tested. This is the case for two *Otariid* species: California sea lion (Schusterman *et al.*, 1972; Kastak and Schusterman, 1998; 2002), Northern fur seal (Schusterman and Moore, 1978; Moore and Schusterman, 1987), six *Phocid* species: harbor seal (Møhl, 1968a, b; Terhune, 1988; Terhune and Turnbull, 1995; Turnbull and Terhune, 1994; Kastak and Schusterman, 1998), ringed seal, *Pusa hispida* (Terhune and Ronald, 1975), harp seal, *Pagophilus groenlandicus* (Terhune and Ronald, 1972), gray seal, *Halichoerus grypus* (Ridgway and Joyce, 1975), Hawaiian monk seal, *Monachus schauinslandi* (Thomas *et al.*, 1990), Northern elephant seal, *Mirounga angustirostris* (Kastak and Schusterman, 1998; 1999), and one *Odobenid* species: the Pacific walrus, *Odobenus rosmarus divergens* (Kastelein *et al.*, 2002). Of these studies, the latter was conducted with the same equipment and methodology as the present study and can therefore easily be compared.

The hearing sensitivity of the male Steller sea lion in the present study is fairly similar to that of the male California sea lion tested by Schusterman *et al.* (1972). However, the hearing sensitivity of the female Steller sea lion in the present study was higher than that of the male California sea lion for frequencies above 20 kHz (Fig. 3). For the frequencies that were tested in both species, the hearing sensitivity of the two much smaller female Northern fur seals (Moore and Schusterman, 1987) was higher than that of the female Steller sea lion in the present study. At 1 kHz, the hearing of the male Steller sea lion in the present study was 10–20 dB better than that of the male California sea lion and the female Northern fur seals (Schusterman *et al.*, 1972; Schusterman and Moore, 1978; Moore and Schusterman, 1987; Kastak and Schusterman, 1998). In three studies with seals (ringed seals, harp seals, and a female Northern elephant seal), the underwater hearing sensitivity was tested for frequencies below 1 kHz (Terhune and Ronald, 1972; 1975; Kastak and Schusterman, 1998). The Northern elephant seal can hear lower frequencies better than the smaller *Phocids* that have been tested, and, at least the female Northern elephant seal, can hear high frequencies well (Kastak and Schusterman, 1998; 1999).

Maybe per pinniped group and within species a correlation exists between body size and hearing sensitivity. The differences in hearing sensitivity between the male and the female Steller sea lion in the present study may be due to individual differences in sensitivity between the subjects or due to sexual dimorphism in hearing. In the latter, the hearing differences may be due to differences in the sizes of structures in the hearing organs. This idea is based on the limited hearing range found in the largest pinniped of which the hearing has been tested so far: a male Pacific walrus (Kastelein *et al.*, 2002). The walrus has large middle- and inner-ear structures compared to the other pinnipeds of which the hearing has been tested (Kastelein and Gerrits, 1990; Kastelein *et al.*, 1996). The physics of sound may relate to the size of ear structures; the larger the size, the more suitable for low-frequency sound reception (Wartzok and Ketten, 1999). It would therefore be of interest to test the underwater hearing sensitivity of an adult male Northern elephant seal, which is the only pinniped in which the male is as big as, or bigger than, an adult male walrus.

C. Ecological significance and suggestions for future research

The frequency range of underwater vocalizations made by Steller sea lions is unknown, as the equipment used by earlier investigators could only record audible sounds up to 20 kHz or less (Orr and Poulter, 1967; Schusterman *et al.*, 1970; Poulter and del Carlo, 1971). However, the maximum underwater hearing sensitivity range (800 Hz–25–30 kHz) obtained in the present study for Steller sea lions overlaps with the frequency range of the underwater vocalizations recorded in those studies. Vocalizations and hearing in males are very important during territorial disputes in the breeding season. One could speculate that for this reason their hearing is more tuned to low-frequency sounds. Females need to find their pups among many other pups in a breeding colony when they return from feeding trips at sea. One could speculate that their hearing is more tuned towards the higher frequencies of pup calls.

The hearing range found in the present study also suggests that Steller sea lions can hear many of the social calls of one of their two main predators, the killer whale (*Orcinus orca*), which are between 500 Hz and 35 kHz (Schevill and Watkins, 1966; Awbrey *et al.*, 1982; Ford, 1989). Steller sea lions can probably also hear some of the killer whale's echolocation clicks which are between 4 and 50 kHz (Schevill and Watkins, 1966; Diercks *et al.*, 1971; Awbrey *et al.*, 1982; Barrett-Lennard *et al.*, 1996). In addition, the frequency of the click repetition rate of killer whales' echolocation signals (10–330 Hz) may sometimes be within the Steller sea lion's range of hearing. It is possible that the relatively high-frequency underwater hearing is related to predator avoidance rather than communication between conspecifics.

Most anthropogenic noise contains energy up to 1 kHz. The lower-frequency components of anthropogenic noise travel further than the higher components. The results from the present study show that Steller sea lions can hear some underwater anthropogenic noise. The effect of audible anthropogenic noise on marine mammals is highly variable in type and magnitude (Severinsen, 1990; Cosens and Dueck, 1993; Richardson *et al.*, 1995), and Steller sea lions are sensitive to acoustic disturbance in certain contexts (Hoover, 1988). A controlled acoustic experiment showed that Steller sea lions sometimes hauled out of the water as a reaction to certain loud sounds (Akamatsu *et al.*, 1996). Anthropogenic noise might reduce the time Steller sea lions forage in particular areas, thus reducing the physiological condition of the animals, and thus their reproductive success.

Therefore, bottom trawl fishing, tanker routes, and drilling platforms should be planned far enough away from areas that are important in Steller sea lion ecology. In addition to the hearing sensitivity of the Steller sea lion, the radius of the discomfort zone depends on several other factors such as the general ambient noise level, water depth, ocean floor sediment, and the spectrum, source level, and duration of the anthropogenic noise. Pinniped hearing is generally more sensitive to anthropogenic noise than is odontocete hearing, which is more sensitive to higher frequencies. This is because odontocetes use echolocation.

To estimate at what distances Steller sea lions can hear conspecifics, echolocation clicks of killer whales, and anthropogenic noise, additional information is needed. Information needs to be obtained on how Steller sea lions hear in the presence of masking noise (critical ratios, critical bands), how they hear sounds of different durations (especially pulsed sounds), and how they perceive the spatial positioning of sounds coming from different directions (receiving beam pattern). Also, the effect of loud pulsed signals on hearing thresholds for pure tones could be studied, as has already been done with California sea lions (Finneran *et al.*, 2003). The effect of loud noise on Steller sea lion hearing should also be tested as has already been done in three other pinniped species (Kastak *et al.*, 1999)

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