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Underwater hearing in California sea lions (*Zalophus californianus*): Expansion and interpretation of existing data

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Measurements of underwater hearing sensitivity of pinnipeds have been made for 9 of 33 species, with most studies involving just one or two trained individuals. There is a need to refine and expand this limited knowledge base to improve understanding of hearing and possible anthropogenic noise effects, especially in cases where data may be extrapolated to other species (see National Research Council 2000, Southall *et al*. 2007). Schusterman *et al*. (1972) published what is still the only complete underwater audiogram for a California sea lion (*Zalophus californianus*). The purpose of this brief communication is to present hearing data from another trained California sea lion for comparison with the classic audiogram.

Schusterman *et al.* (1972) originally tested the underwater hearing ability of an adult male sea lion—identified as "Sam"—using an operant conditioning method of vocal response. Sam was trained to either vocalize upon detecting a 500 ms pure tone signal or to remain silent when no signal was detected. The signals were varied in level in an adaptive, up-down fashion to obtain hearing thresholds at frequencies from 0.25 to 64 kHz. Thresholds were defined as the stimulus sound pressure level (SPL) in dB re: 1 μbar corresponding to the 75% correct detection probability at each test frequency.

The underwater hearing sensitivity of another captive California sea lion—an adult female identified as "Rio"—was later evaluated at relatively low frequencies (0.1–6.4 kHz) during similar auditory detection tasks conducted by Kastak and Schusterman (1998) and then again by Southall *et al*. (2005). The absolute threshold measurements obtained in these studies were subsequently extended to cover the full functional hearing range. The higher frequency data for Rio

(6.4–37.2 kHz) are reported here for the first time to allow a complete audiogram for her to be composited and compared to the classic audiogram for Sam.

In total, Rio's hearing sensitivity was measured at 13 frequencies between 0.1 kHz and 37.2 kHz. Rio's hearing above 40 kHz was not tested because Schusterman *et al.* (1972) had previously determined that the hearing thresholds reported for Sam above this frequency were likely a result of ultrasonic bone conduction and not functional hearing (see also Møhl 1967). Like Sam, Rio was trained for audiometric testing using operant conditioning methods. She either touched a target upon detecting a 500 ms pure tone signal or withheld the response when no signal was detected. Correct responses to both signal-present trials and signal-absent trials were similarly reinforced with fish rewards and false detection rates were maintained above 0% and below 25%. Rio's hearing sensitivity at each test frequency was first estimated using an adaptive up-down method over 3–16 test sessions until performance was stable. Thresholds were then measured over 2–5 additional sessions using the method of constant stimuli, in which the test tones were presented in random order at fixed SPLs that surrounded the initial threshold estimate. Final thresholds were defined as the stimulus level in dB re: 1 μPa corresponding to the 50% correct detection probability at each frequency, and were required to have 95% confidence limits within ±3 dB.

Rio completed all three stages of testing while between 7 and 15 yr of age. The thresholds were obtained in the same relatively quiet testing pool using comparable methods, apparatus, and sound generation and calibration equipment. The projecting and receiving transducers used to test Rio's hearing at 6.4 kHz and below are described in Kastak and Schusterman (1998) and Southall *et al.* (2005) where the original data were reported. The higher frequency measurements were obtained during the time interval between the two sets of lower frequency measurements. For these measurements, test signals from 6.4 to 23.1 kHz were transmitted from a Naval Undersea Warfare Center J9 transducer and test signals from 27.9 to 37.2 kHz were transmitted from a Brüel and Kjær 8104 projecting hydrophone. In both cases, an International Transducer Corporation 8212 hydrophone was used to calibrate the test signals prior to and following each session. Ambient noise levels were obtained in the testing enclosure periodically throughout the three stages of testing. These measurements were limited by electrical rather than acoustical noise and thus represent liberal estimates of the background noise present in the pool.

Rio's measured hearing sensitivity at each test frequency is shown in Table 1. The individual values reported for this subject have uniformly low variance (SD $\leq$ 1.6 dB) due to the rigorous threshold determination procedure used throughout testing. As some threshold measurements were repeated across different stages of testing, mean threshold values are also reported. The mean thresholds, based on a minimum of one and a maximum of three independent assessments, were used to generate the composite audiogram that is depicted in Figure 1. This audiogram is shown alongside the original data from Schusterman *et al.* (1972) for Sam in Figure 1 and in Table 1 and is plotted in common units of SPL for ease of comparison. The background noise levels reported for Sam and the maximum background noise levels observed for Rio are provided in Table 1.

Table 1. Underwater hearing thresholds for California sea lions Rio and Sam and corresponding ambient noise spectral density level.

	California sea lion "Rio"					California sea lion "Sam"	
Frequency	Threshold[a]	Threshold[b]	Threshold[c]	Mean threshold[d]	Ambient noise[e]	Threshold[f]	Ambient noise[f]
(kHz)	(dB re:1 μPa)	(dB re:1 μPa)	(dB re:1 μPa)	(dB re:1 μPa)	(dB re:1 μPa^2/Hz)	(dB re: 1 μPa)	(dB re:1 μPa^2/Hz)
0.1	116 (0.6)			116	74		
0.2	100 (0.3)		85 (1.6)	93	67		
0.25						115	51
0.4	89 (0.6)		83 (0.7)	86	66		
0.5						94	53
0.8	84 (0.8)		75 (0.4)	78	54		
1.0						86	47
1.6	69 (0.3)			69	47		
2.0						82	38
3.2			68 (0.6)	68	45		
4.0						87	36
6.4	57 (0.7)	66 (0.7)	63 (0.6)	62	45		
8.0						81	33
8.2		71 (0.7)		71	45		
15.5		68 (1.1)		68	43		
16.0						79	30
23.1		70 (0.8)		70	43		
27.9		78 (0.8)		78	43		
31.6		78 (0.8)		78	43		
32.0						97	
36.0						126	
37.2		113 (0.7)		113	42		
48						138	
64						145	

[a]Hearing thresholds (shown with SDs) for Rio at age 7–9 yr, from Kastak and Schusterman (1998).
[b] Hearing thresholds (shown with SDs) for Rio at age 13 yr, previously unpublished data.
[c] Hearing thresholds (shown with SDs) for Rio at age 14 yr, from Southall *et al.* (2005).
[d] Mean hearing thresholds for Rio across all stages of testing.
[e] Maximum background noise measured for Rio across all stages of testing.
[f] Hearing thresholds for Sam at age 5–6 yr, reported with corresponding background noise levels, converted to common units from Schusterman *et al.* (1972).

Rio's hearing thresholds are lower than Sam's at every frequency tested when compared in common units of SPL. This is especially evident across the broad range of best sensitivity between 0.4 kHz and 32 kHz, where Rio's thresholds are about 10 dB lower than Sam's. Rio's overall best sensitivity is 62 dB re: 1 μPa at 6.4 kHz compared to Sam's best sensitivity of 79 dB re: 1 μPa at 16 kHz. While the overall

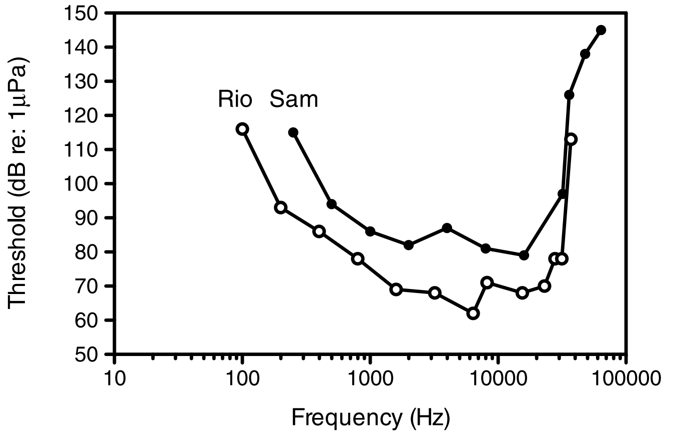

Figure 1. Underwater audiogram for California sea lion Rio compared to the original audiogram reported for sea lion Sam by Schusterman *et al.* (1972). Note that Sam's hearing thresholds are converted from the original unit of dB re: 1 µbar to dB re: 1 µPa.

shape of the audiogram and the high frequency roll-off are quite similar between subjects, Rio's low frequency roll-off extends more than an octave below Sam's.

The considerable differences in sensitivity between the two animals can be attributed in part to the difference in the psychometric calculation of thresholds. For Sam, threshold determination at the 75% correct detection probability rather than at the 50% probability more commonly used in hearing studies would theoretically result in more conservative measures of sensitivity. That is, higher hearing thresholds would be expected based solely on how thresholds were defined. The actual differences between the corresponding threshold values can be evaluated to some extent, as Schusterman *et al.* (1972) provide partial psychometric functions from which the 75% threshold criteria were derived. If these functions are reassessed closer to the 50% correct detection probability to normalize the data for the two subjects, Sam's thresholds decrease by 5–10 dB to within a few decibels of Rio's at nearly all frequencies. The only notable difference between the two sea lions then occurs at 0.25 kHz, the lowest frequency tested by Schusterman *et al*. (1972). While the ambient noise levels measured in the testing environments appears to have been sufficiently low to obtain unmasked thresholds for both subjects (see Southall *et al.* 2000), Rio's superior hearing below 0.25 kHz suggests that Sam's threshold at this frequency may have been compromised in some way. It is unlikely that acoustic near field effects can explain this difference as the transducer was placed much farther from Rio (5 m) than to Sam (1 m) during testing.

In summary, this report provides a description of underwater hearing sensitivity in an adult female California sea lion, which raises the number of individuals tested across their frequency range of hearing from one to two. This audiogram is consistent with a revised interpretation of the Schusterman *et al*. (1972) description of hearing for this species, as the functional hearing capabilities of both of the sea lions tested are similar when their hearing thresholds are compared using the same criterion. The results indicate relatively acute underwater hearing sensitivity (62–86 dB re: 1 μPa) across at least six octaves (0.4–32 kHz), with a steep loss in high frequency sensitivity above 32 kHz and a gradual low frequency roll-off extending to at least 0.1 kHz. We suggest that this updated audiometric assessment be used, rather than the classic audiogram, when hearing data for California sea lions are applied in biological and regulatory contexts or compared to other species tested with similar methods.

While it is clear from earlier work that differences in psychophysical methods and parameters heavily influence threshold measurements (see Levitt 1970, Schusterman and Johnson 1975), this issue is often overlooked in reviews of marine mammal hearing. The current case supports the view that when audiograms are evaluated comparatively, methodological variables should be considered prior to assessing species or individual differences. While a detailed understanding of hearing demographics in marine mammals as a function of variables such as age, sex, and species awaits more comprehensive studies, this effort illustrates the value of comparing data appropriately and expanding sample sizes, even marginally, to enhance understanding of species-typical hearing capabilities.

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