

Auditory detection of ultrasonic coded transmitters by seals and sea lions

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Ultrasonic coded transmitters (UCTs) are high-frequency acoustic tags that are often used to conduct survivorship studies of vulnerable fish species. Recent observations of differential mortality in tag control studies suggest that fish instrumented with UCTs may be selectively targeted by marine mammal predators, thereby skewing valuable survivorship data. In order to better understand the ability of pinnipeds to detect UCT outputs, behavioral high-frequency hearing thresholds were obtained from a trained harbor seal (*Phoca vitulina*) and a trained California sea lion (*Zalophus californianus*). Thresholds were measured for extended (500 ms) and brief (10 ms) 69 kHz narrow-band stimuli, as well as for a stimulus recorded directly from a Vemco V16-3H UCT, which consisted of eight 10 ms, 69 kHz pure-tone pulses. Detection thresholds for the harbor seal were as expected based on existing audiometric data for this species, while the California sea lion was much more sensitive than predicted. Given measured detection thresholds of 113 dB re 1 μ Pa and 124 dB re 1 μ Pa, respectively, both species are likely able to detect acoustic outputs of the Vemco V16-3H under water from distances exceeding 200 m in typical natural conditions, suggesting that these species are capable of using UCTs to detect free-ranging fish.

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I. INTRODUCTION

Ultrasonic coded transmitters (UCTs) are acoustic tags commonly used in fisheries research. These tags emit a series of short duration, high-frequency pulses containing a signature by which spatially distributed receivers can identify individual tags. In order for receivers to be effective, they must be able to detect signals from tags at relatively long distances. The fact that underwater high-frequency sounds attenuate quickly with distance from the sound source, combined with constraints on receiver placement, necessitates a high sound pressure level (SPL) for tag outputs. Tag acoustic source levels (SPL at 1 m) typically range from 140 to 165 dB re 1 μ Pa. Tag outputs consist of a series of 8–9 discrete, 10 ms pulses with a total duration of approximately 3 s; tags are programmed to emit a single output at a variable delay, usually between 30 and 90 s. The discrete pulses that compose a UCT output consist of a sinusoidal signal in the

frequency range of 50–400 kHz, depending on the tag type and model. Because UCTs are relatively small and inexpensive, they have been widely used for studying fish life history parameters such as behavior, migration patterns, and survivorship.

On the West Coast of the United States, researchers commonly employ UCTs to conduct large-scale survivorship studies on vulnerable, economically important salmonid species. In California alone, thousands of migratory fish are instrumented with 69 kHz tags annually (Moustahfid *et al.*, 2011). A fundamental assumption of these life history studies is that survivorship rates for instrumented fish are similar to those of untagged fish. However, this assumption is inconsistent with recent observations of higher mortality in adult salmon implanted with active acoustic tags relative to those implanted with passive integrated transponder tags, as well as to those implanted with sham acoustic tags having physical characteristics similar to active tags, but producing no output (Wargo-Rub, 2012a,b). One possible explanation for this discrepancy has been termed the “dinner bell” hypothesis: marine mammals that can hear acoustic tag outputs use

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this information to selectively predate tagged fish, thereby skewing survivorship data (Bowles *et al.*, 2010).

While UCT outputs are designed to be above the frequency range thought detectable by most fish, these tags might still be detectable by some marine mammals, including seals, sea lions, and odontocetes. A recent report by Bowles (2010) showed that harbor seals reacted with apparent aversion to 69 kHz acoustic tags, suggesting that the outputs of at least some UCTs are salient to this species. This finding is consistent with pre-existing hearing data for pinnipeds. Using behavioral techniques with captive pinnipeds, Møhl (1968a) determined that a harbor seal could reliably detect an 180 kHz pure-tone with a sound pressure level of 133 dB re 1 μ Pa, and Schusterman *et al.* (1972) reported that a California sea lion could detect a 64 kHz pure-tone with a sound pressure level of 145 dB re 1 μ Pa. Considering these hearing thresholds relative to typical UCT frequencies (50–400 kHz) and source levels (140–165 dB re 1 μ Pa), it becomes apparent that harbor seals should detect all but the highest frequency, lowest SPL UCTs at considerable distances, while California sea lions should detect only the lowest frequency, highest SPL UCTs at close range, if at all.

Bowles *et al.* (2010) estimated detection ranges for pinnipeds and small cetaceans to certain UCTs. In order to accomplish this, transmission loss for a tag output was directly measured as a function of distance in a nearshore marine environment. This transmission loss function was then used to determine the distance that a UCT output could travel before its SPL fell below the auditory threshold of a hypothetical listener. Auditory thresholds for UCT outputs were derived from the available literature on detection of high-frequency signals by marine mammals, as well as from related studies on auditory summation and pulsatile (brief) stimuli. This source-path-receiver analysis indicated that harbor seals should detect a 69 kHz tag output with a source level of 140 dB re 1 μ Pa at a minimum distance of 25 m and a maximum distance of 200 m. A similar analysis indicated that the 69 kHz tag output would likely be inaudible to a California sea lion at distances greater than 1 m. Note that these calculations assume that the ambient noise in the frequency range of the UCT output is at least one critical ratio lower than the detection threshold. This is a safe assumption given that ambient noise in the habitats of interest (i.e., large rivers where resident pinnipeds prey on spawning salmonids) tends to decrease with increasing frequency, to the point where the spectrum level of the noise is much lower than pinniped detection thresholds (Vračar and Mijić, 2011).

The aim of the present study was to directly measure pinniped hearing capabilities at 69 kHz, a common operational frequency for UCTs, creating a basis for detection range estimates. Auditory threshold measurements were made for two common predators of salmonids on the West Coast of the United States: the Pacific harbor seal and the California sea lion. To ensure adequate understanding of the influence of signal frequency and duration on signal detectability, hearing thresholds were measured for a trained individual from each species to an extended (500 ms) narrowband 69 kHz stimulus, a brief (10 ms) narrowband

69 kHz stimulus, and a series of eight 10 ms, 69 kHz pure-tone pulses recorded directly from a Vemco V16-3H UCT. These auditory data were used to empirically refine the earlier predictions by Bowles *et al.* (2010), and to test the viability of the “dinner bell” hypothesis with direct hearing measurements.

II. METHODS

A. Experimental design

This study was designed to test the ability of a trained harbor seal and a trained California sea lion to detect the acoustic output of a Vemco V16-3H UCT. The Vemco V16-3H projects a series of eight 10 ms pulses over an interval of approximately 3.5 s. Each pulse comprises a 69 kHz pure tone within a 10 ms envelope including a brief linear ramp up and down, and has an SPL of 165 dB re 1 μ Pa at 1 m.

Auditory measurements were conducted in three matched phases with each phase employing a unique stimulus. The three stimuli, in the order tested, were: treatment 1, a 500 ms, 10% linear frequency-modulated (FM) sweep centered around 69 kHz; treatment 2, a 10 ms, 2% FM sweep centered around 69 kHz; and treatment 3, the recorded output of the tag itself. Narrowband FM sweeps were used for synthesized signals because these types of stimuli result in detection thresholds similar to pure-tone signals, but tend to exhibit less spatial variation in SPL when presented in a reverberant testing environment (Finneran and Schlundt, 2007; Kastelein *et al.*, 2002). A duration of 500 ms was used for treatment 1 so as to be greater than the estimated temporal integration time at 69 kHz (Kastelein *et al.*, 2010; Holt *et al.*, 2012), resulting in detection thresholds that represent maximum sensitivity at this frequency.

The stimuli used in treatments 1, 2, and 3 had rise times of 25, 5, and approximately 0.1 ms, respectively. Because rise times and signal duration can affect signal bandwidth and lead to spectral energy at frequencies distant from the center frequency, received signals for all three treatments were analyzed across the functional range of hearing for these species. No low-frequency energy was detected above the noise floor of the test environment for the range of signal SPLs used during behavioral testing. Received spectrum levels, relative to ambient noise levels in the testing environment, are depicted for each treatment in Fig. 1.

The experimental progression from treatment 1 to treatment 2 to treatment 3 was chosen for two reasons. First, both animal subjects had prior experience working with 500 ms, 10% FM stimuli as used in treatment 1. Therefore, this experimental design allowed the subjects to transition from the most familiar type of stimulus to the least familiar. Second, because different features of the stimulus changed between treatments, this design allowed for a better understanding of which aspects of the signal influenced changes in threshold. That is, the difference between treatments 1 and 2 is mainly duration, while the difference between treatments 2 and 3 is mainly the number of pulses presented. Hence, any observed threshold change between the first two stimuli is likely due to decreased duration, and similarly, any threshold change

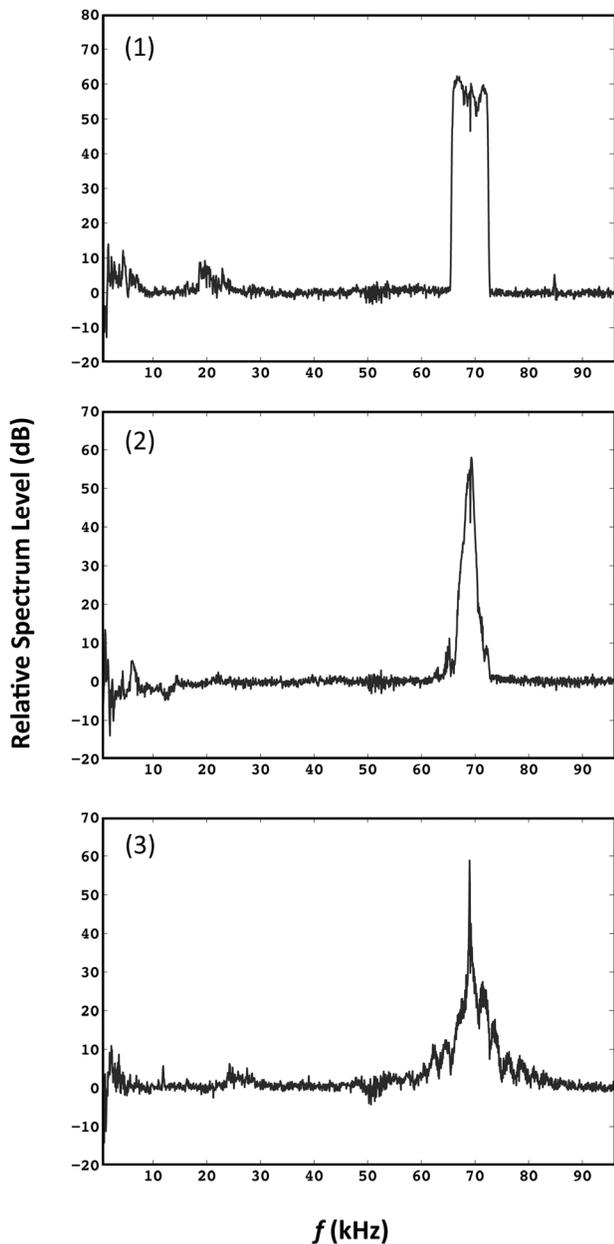


FIG. 1. Received spectra for (1) a 500 ms, 10% linear frequency-modulated (FM) sweep centered around 69 kHz, (2) a 10 ms, 2% FM sweep centered around 69 kHz, and (3) the recorded output of a Vemco V16-3H UCT. Signals were recorded at the position of the test subject's head and spectrum levels are normalized to the ambient noise in the test environment recorded immediately prior to signal projection (figures show the difference in decibels between the received spectrum level for the signal-plus-ambient and the spectrum level for the ambient noise alone). Note the absence of any low-frequency components above the noise floor in all three stimuli. In the 100–72 000 Hz range, average ambient noise spectrum levels in the test environment tend to decrease with increasing frequency, ranging from 74 dB re $(1 \mu\text{Pa})^2/\text{Hz}$ at 100 Hz to 28 dB re $(1 \mu\text{Pa})^2/\text{Hz}$ at 72 000 Hz.

between the second two stimuli is likely due to the number of available pulses.

B. Test subjects

Two subjects participated in this study: a 24 year-old male harbor seal identified as *Sprouts* (NOA0001707) and a 3 year-old female California sea lion identified as *Ronan* (NOA0006602). Both subjects had multiple years of

experience participating in psychophysical hearing studies and both have measured audiograms that demonstrate species-typical hearing (Reichmuth *et al.*, 2013). Testing was conducted at Long Marine Laboratory in Santa Cruz, California.

C. Testing procedure

Animal testing took place at a depth of 1 m in an outdoor circular, concrete test pool (7.6 m diameter, 1.8 m depth) filled with natural seawater at temperatures between 10 °C to 15 °C. Signals were projected from an ITC 1042 hydrophone mounted on PVC pipe and suspended into the test pool. Outgoing signals were bandpass filtered with a Krohn-Hite 3364 analog filter, attenuated by 10 dB using a TDT PA5 programmable attenuator, and amplified using a Hafler P1000 amplifier when necessary. Analog to digital conversion was performed through a National Instruments USB-6259 data acquisition system at a sampling rate of 500 kHz. Signals were calibrated and the received sound fields mapped using a Reson 4032 hydrophone and custom software (HTP; Finneran, 2003). HTP software was also used to generate the FM sweep stimuli used in treatments 1 and 2. The tag stimulus used in treatment 3 was recorded without environmental influence by coupling the Vemco V16-3H to an ITC 1042 hydrophone via ultrasound gel in air. This method effectively eliminated multipath reflections and produced a recording representative of the projected tag signal with a high signal-to-noise ratio.

Daily signal calibration was performed at the position of the center of the subject's head during testing. The calibration routine tested linear attenuation of the signal and mean error across the desired range of SPLs. For all stimuli, SPL was calculated relative to the root-mean-square pressure over the full duration of the signal, except in the case of treatment 3, where the SPL was calculated over the full duration of the first pulse within the eight-pulse sequence. During daily calibration, received signals were visually inspected in the time and frequency domains for temporal distortions as well as for any energy at frequencies other than 69 kHz. For each treatment, SPLs were measured at 24 positions within a $3 \times 3 \times 3$ cubic grid encompassing the position of the subject's head during testing. Points on the grid were separated by 7 cm, making the outer dimensions of the grid 14 cm \times 14 cm \times 14 cm. The criterion for acceptable spatial variability in received sound fields was ± 3 dB at all measured positions; if this criterion was not met, the transducer was repositioned until a suitable configuration was obtained.

The psychoacoustic procedures were the same for all treatments. A standard go/no-go procedure was used. First, the subject swam down to a listening station, which provided a fixed location for the animal to rest its head, and waited for an underwater light to come on indicating the beginning of the trial. The light would remain on for a four-second trial duration, during which a signal might be presented at any time. The subject had been previously trained to move from the listening station and touch its nose to a target positioned at the left of the station when a signal was presented. Correct responses occurred when the subject touched the target after

a signal had been presented, but before the trial interval ended (termed a “hit”), or when the subject remained positioned at the station for the full trial interval when no signal (i.e., an output of 0 V) was presented. Correct responses were marked by a brief buzzer sound followed by a fish reward delivered by a trainer who was blind to the trial condition. No reward was given and the subject was recalled to the surface when it either touched the target when no signal had been presented (“false alarm”), or when it failed to touch the target when a signal had been presented (“miss”).

Signal-present and signal-absent trials were presented in a pseudorandom sequence with a maximum run length of four for either trial type. On signal-present trials, HTP was used to adjust the outgoing signal voltage (and consequently the received signal SPL) in between trials using an adaptive staircase procedure (Cornsweet, 1962). Testing began at an SPL approximately 20 dB above threshold, estimated from either pre-existing audiometric data or preliminary performance on the task. The stimulus amplitude was decreased in 4 dB steps following each correct detection, until the subject failed to detect a signal. The amplitude was then increased in 4 dB steps until the subject successfully detected the signal, at which point the amplitude was decreased by 2 dB steps until the subject again failed to detect the signal. This 4 up/2 down procedure was continued until the subject demonstrated consistent performance through five consecutive hit-to-miss transitions, after which the subject was given several supra-threshold level trials that were approximately 20 dB above threshold. A stable response bias was maintained by adjusting the ratio of signal-present to signal-absent trials in between sessions as necessary. As a result, the proportion of signal-absent trials within a session varied between 35 and 50 %.

D. Threshold analysis

From each session, thresholds were estimated in terms of SPL by taking the mean of the last five hit-to-miss transitions. The criterion to finish testing for a given treatment was three sessions with estimated thresholds within 3 dB of one another, all with false alarm rates greater than 0% but less than 30% for the trials encompassing the last five hit-to-miss transitions. Probit analysis (Finney, 1947) was then used to fit a Gaussian distribution to the proportional response data pooled across these three sessions. The cumulative distribution function of this Gaussian distribution is equivalent to the psychometric function. Final thresholds were defined as the SPL corresponding to the 50% detection probability as determined by taking an inverse prediction from this psychometric function.

III. RESULTS

For synthesized stimuli (treatments 1 and 2), as well as for the stimulus recorded directly from the VEMCO V16-3H (treatment 3), received signals contained no significant energy outside of the 69 kHz frequency region within the range of SPLs used in this study. Further, for brief stimuli (treatments 2 and 3), energy occurring at times beyond the duration of the projected signal due to reflections was

minimal. A small amount of energy due to acoustic reflection appeared between 15–25 ms after the initial projection of the signal; however, the energy contained in this interval was 10 dB less than the energy contained within the 0–10 ms period. Therefore, the signals received by the subject were similar to those that would be received from an acoustic tag in a free-field.

For treatment 1, the calculated detection threshold for the harbor seal was 106 dB re 1 μ Pa, and for the California sea lion it was 112 dB re 1 μ Pa. Because treatment 1 employed a narrowband stimulus with duration much greater than the expected temporal integration time (Kastelein *et al.*, 2010; Holt *et al.*, 2012), these results can be construed as data points in an audiogram. Figure 2 depicts these data points along with pre-existing audiogram data for these subjects, as well as for other individuals from these species. The threshold for the harbor seal agrees well with the available species data in this frequency range and appears to fall

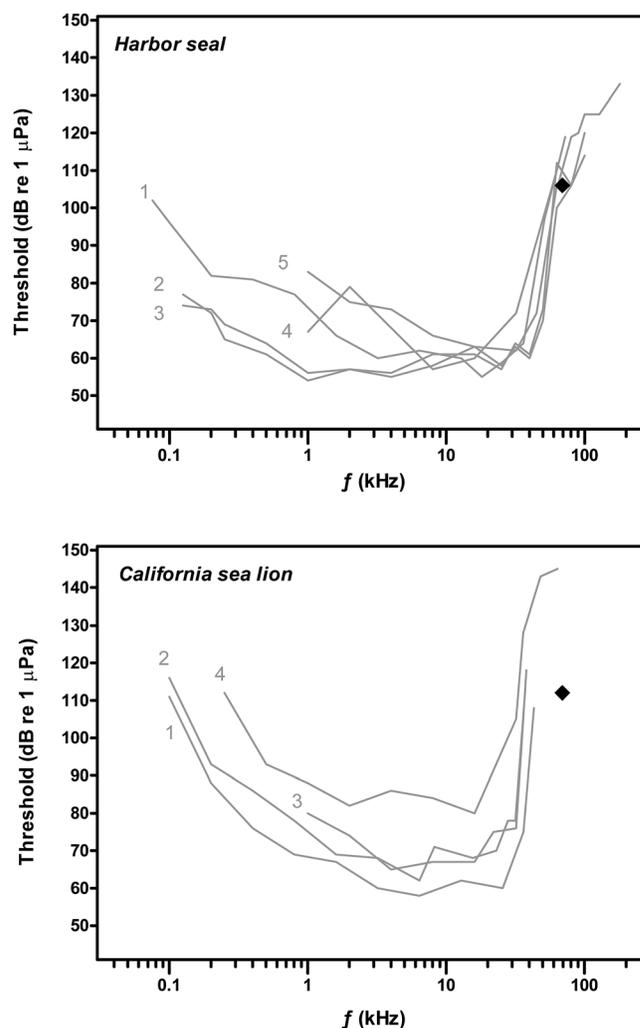


FIG. 2. Auditory detection thresholds for a 69 kHz (500 ms) narrowband signal from this study (◆) for a harbor seal and a California sea lion as compared to published audiograms for these species. Note that lower detection thresholds indicate better auditory sensitivity. Harbor seal references: 1 (Reichmuth *et al.*, 2013); 2, 3 (Kastelein *et al.*, 2009); 4 (Terhune, 1988); 5 (Möhl, 1968a). California sea lion references: 1 (Reichmuth *et al.*, 2013); 2 (Reichmuth and Southall, 2012); 3 (Mulsow *et al.*, 2012); 4 (Schusterman *et al.*, 1972).

TABLE I. Directly measured and estimated auditory detection thresholds for an extended (500 ms) 69 kHz tone, the increase in threshold for a brief (10 ms) 69 kHz tone, the decrease in threshold when multiple (8) pulses are available, as well as detection thresholds for a Vemco V16-3H UCT. Estimated values (those not from this study) and the corresponding references are from [Bowles et al. \(2010\)](#).

	Detection threshold at 69 kHz (dB re 1 μ Pa)	Threshold increase for 10 ms signal (dB)	Threshold decrease for multiple pulses (dB)	Threshold for VEMCO V16-3H (dB re 1 μ Pa)
Harbor seal	106 ^a 109–112 ^{b,c}	+9 ^a +6–10 ^{d,e}	–2 ^a –1 ^f	113 ^a 114–121 ^g
California sea lion	112 ^a 145 ^h	+15 ^a	–3 ^a	124 ^a 150–154 ^g

^aThis study.

^bMøhl, 1968a.

^cKastelein et al., 2009.

^dTerhune, 1988; 64 kHz.

^eKastelein et al., 2010; 40 kHz.

^fTurnbull and Terhune, 1993.

^gCalculated by combining estimates of 69 kHz sensitivity, duration effect, and multiple pulse effect from existing literature (columns 1, 2, and 3). For this calculation, estimates of duration effect and multiple pulse effect were based on harbor seal studies for both the harbor seal and sea lion.

^hSchusterman et al., 1972; 64 kHz.

within the region of the audiogram where sensitivity is decreasing rapidly with increasing frequency, i.e., the high-frequency roll-off. There is limited pre-existing data in this frequency range for the California sea lion; however, the threshold determined in this study is 33 dB lower than the lone existing data point in this range (64 kHz, [Schusterman et al., 1972](#)) and appears to fall beyond the high-frequency roll-off region of the audiogram.

For treatment 2, the calculated threshold for the harbor seal was 115 dB re 1 μ Pa, and for the California sea lion it was 127 dB re 1 μ Pa. For the stimuli used in treatments 1 and 2, both narrowband FM sweeps with center frequencies of 69 kHz, but with durations of 500 and 10 ms, respectively, the difference in threshold was calculated to be +9 dB for the harbor seal and +15 dB for the sea lion.

For treatment 3, the calculated threshold for the harbor seal was 113 dB re 1 μ Pa, and for the California sea lion it was 124 dB re 1 μ Pa. The primary difference between treatments 2 and 3 was the number of pulses within the employed stimuli (1 and 8, respectively), and the difference in thresholds between these treatments was calculated to be –2 dB for the harbor seal and –3 dB for the California sea lion.

Measured thresholds for both subjects and all three treatments are summarized in Table I, along with threshold estimations based on [Bowles et al. \(2010\)](#) for comparison. False alarm rates for each of the three treatments were between 10 and 15 % for both subjects.

By combining the calculated detection thresholds for the Vemco V16-3H (treatment 3) with a propagation model, detection ranges can be estimated for both species relative to the output of this tag. This is accomplished using the equation

$$DT = SL - 15 \log(r) - \alpha r, \quad (1)$$

where DT is the detection threshold, SL is the tag source level, r is the distance from the source in meters, and α is the attenuation coefficient in dB/m. The $15 \log(r)$ term serves as an estimate of the spreading loss and is halfway between spherical and cylindrical spreading. The αr term accounts for

loss of energy due to absorption. The value of α is based on the Francois–Garrison model of acoustic absorption and is a function of frequency, temperature, depth, salinity and pH ([Francois and Garrison, 1982a,b](#)). For any given distance, the transmission loss estimated by this model will be higher than that estimated by the model of [Bowles et al. \(2010\)](#), which was developed based on direct transmission loss measurements of a 69 kHz Vemco tag. Consequently, the detection ranges generated by Eq. (1) are conservative relative to empirical measurements of transmission loss.

Two sets of input values were used to calculate values for α . The first set was selected to represent a large riverine habitat such as the Columbia River and is particularly relevant for this study as this is the type of environment where pinnipeds may selectively predate tagged fish. The second set of values was chosen to represent a mid-latitude, coastal marine environment, where acoustic tags are used on a variety of fish species (e.g., [Zimmerman et al., 2013](#)). Chosen environmental input parameters and the corresponding values for α are summarized in Table II.

Using the propagation model from Eq. (1) with the empirical auditory detection threshold of 113 dB re 1 μ Pa for the harbor seal, and a source level of 165 dB re 1 μ Pa for the VEMCO V16-3H, yields detection ranges of 933 and 501 m in the hypothetical riverine and coastal marine environments respectively. Similarly, the auditory threshold of 124 dB re

TABLE II. Input values used to estimate the attenuation coefficient (α) for a representative riverine environment and a marine environment. Riverine values were approximated for the Columbia River and marine values for a typical nearshore, mid-latitude environment.

	Frequency (kHz)	Temperature (°C)	Depth (m)	Salinity (psu)	pH	α (dB/m)
Riverine ^a	69	12	30	10	8	0.008
Marine ^b	69	14	100	35	8	0.023

^aTemperature and pH values estimated from [Führer et al. \(1996\)](#). Salinity values are heavily dependent on location as well as tides. Conservative values resulting in a larger value for α were chosen for salinity and depth.

^bTemperature, salinity and pH estimated from [Kennish \(2001\)](#).

1 μPa for the California sea lion yields detection ranges of 352 and 236 m for the riverine and marine environments. For comparison purposes, detection ranges for the VEMCO V16-3H were also calculated using seal and sea lion auditory thresholds estimated from Bowles *et al.* (2010) combined with Eq. (1). Both sets of detection ranges—those based on the estimated detection thresholds and those based on the directly measured detection thresholds—are summarized in Table III.

IV. DISCUSSION

When compared with relevant existing data, the auditory detection thresholds determined in this study for extended (500 ms) and brief (10 ms) 69 kHz stimuli were as expected for the harbor seal, but much lower than expected for the California sea lion. Treatment 1, which produced standard audiometric data for the relatively long duration 69 kHz signal, confirmed the sensitivity of a harbor seal at this high frequency. The measured threshold was 106 dB re 1 μPa , similar to the available threshold measurements of 106 dB re 1 μPa at 64 kHz (Møhl, 1968a) and 106–109 dB re 1 μPa at 63 kHz (Kastelein *et al.*, 2009). Data in this high-frequency range are much scarcer for the California sea lion because the upper functional hearing limit for this species has generally been considered to be around 32 kHz (Mulsow *et al.*, 2012) and testing has rarely occurred at frequencies higher than this. The calculated threshold for the current study was 112 dB re 1 μPa , 33 dB lower than the one previously existing data point in the frequency range of interest (64 kHz, Schusterman *et al.*, 1972). This 33 dB difference in absolute sensitivity is the major factor driving the large discrepancy in the predicted Vemco V16-3H detection threshold for the California sea lion estimated from Bowles *et al.* (2010) versus the empirical threshold from this study.

One known contributor to the higher threshold reported by Schusterman *et al.* (1972) versus the threshold determined for the sea lion in this study is a methodological difference in the manner in which thresholds were calculated. In the present study, thresholds were determined at the 50% correct response rate, where in Schusterman *et al.* (1972), thresholds were determined at the 75% correct response rate. However, based on the psychometric function provided by

TABLE III. Estimated detection ranges for the VEMCO V-16 3H UCT for harbor seals and California sea lions based on the auditory detection thresholds estimated from Bowles *et al.* (2010) or on the detection thresholds directly measured in this study. Detection range estimates are given for representative riverine and nearshore marine environments using Eq. (1), with the absorption coefficients provided in Table II, and a tag source level of 165 dB re 1 μPa .

Environment		Detection range	Detection range
		based on Bowles <i>et al.</i> (2010)	based on this study
Harbor seal	Riverine	478–867 m	933 m
	Marine	299–473 m	501 m
California sea lion	Riverine	0–10 m	352 m
	Marine	0–10 m	236 m

Schusterman *et al.* (1972), this contribution accounts for a difference of approximately 5 dB, a small portion of the total discrepancy (see Reichmuth and Southall, 2012 for a complete discussion of differences in psychophysical methods). How to account for the remaining discrepancy is unclear, but given the limited number of subjects tested thus far, individual variation in absolute sensitivity at high frequencies should be considered a potentially important factor.

In addition to potential differences in high-frequency hearing between individuals within a species, there are documented differences in the auditory capabilities of otariid (sea lion and fur seal) versus phocid (true seal) species. Particularly, the functional hearing ranges of phocids tend to include a broader range of frequencies relative to otariids, the largest differences occurring at the upper frequency range of hearing (Reichmuth *et al.*, 2013). However, the shape of the underwater audiograms of both phocids and otariids share certain characteristics at higher frequencies. For both, when frequencies increase beyond a critical point, sensitivity decreases dramatically with increasing frequency (known as the high-frequency roll-off). This critical point occurs around 32 kHz for the California sea lion, and around 40 kHz for the harbor seal (e.g., Mulsow *et al.*, 2012; Reichmuth *et al.*, 2013).

A critical point followed by a dramatic high-frequency roll-off is characteristic not only of pinniped underwater audiograms, but also of the aerial audiograms of many terrestrial mammals, including humans (Masterton *et al.*, 1969). However, pinniped underwater audiograms deviate from the standard mammalian aerial template at frequencies more than one octave above this critical point. At these ultra-high frequencies, the rate of decrease in sensitivity relative to the increase in frequency is much less, i.e., the slope of the audiogram is shallower (Møhl, 1968a; Schusterman *et al.*, 1972). This phenomenon can be seen in the audiometric data summarized for harbor seals and California sea lions in Fig. 2. For harbor seals, sensitivity decreases dramatically with increasing frequency in the 40–80 kHz range, but after 80 kHz, sensitivity decreases less rapidly with increasing frequency. For California sea lions, the initial sharp decrease in sensitivity occurs in the 32–50 kHz range, but in the two studies that tested at higher frequencies (Schusterman *et al.*, 1972 and this study), this decrease appears much less dramatic above 50 kHz. It is this pattern of decreased slope at ultra-high frequencies that allows for the audibility of sufficiently high level sounds well above the nominal high-frequency hearing limit under water. Interestingly, a similar pattern holds for the audiograms of human subjects listening via a bone vibrator directly coupled to the skull leading to the ability of these subjects to detect tones at frequencies well above the expected upper frequency limit of 20 kHz (Corso, 1963). Further, this ability to detect high-intensity tones at frequencies above 20 kHz is also found in humans immersed in an underwater sound field (Deatherage *et al.*, 1954), suggesting similar mechanisms for humans listening via a bone vibrator, humans listening under water, and pinnipeds listening under water.

While ultra-high frequency tones can be heard under water at high intensities, pitch discrimination is either

severely impaired or non-existent within the frequency range where the slope of the audiogram levels off in both pinniped and human listeners (Schusterman and Moore, 1978; Möhl, 1968b; Deatherage *et al.*, 1954). This suggests that although the end of the tonotopic map on the basilar membrane has been reached, energy is somehow still reaching hair cells near the basal end of the membrane. Because energy at these frequencies does not seem to stimulate the basilar membrane during conventional aerial hearing, it has been hypothesized that a pathway other than the traditional in-air route (through the meatus and middle ear) is involved in the transmission of energy to the cochlea for underwater hearing at these ultra-high frequencies. This phenomenon is known as bone conduction and a variety of mechanisms have been proposed (see Hood, 1962 for review of bone conduction in humans; Repenning, 1972 for discussion of possible mechanisms in pinnipeds). Further research is needed to determine the precise mechanism of hearing at these ultra-high frequencies. However, it is apparent that when underwater hearing is involved, the fact that the frequency of a signal is above the nominal high-frequency hearing limit for a species is insufficient to rule out the possibility that the signal is detectable, as demonstrated by the much lower than expected detection thresholds for the California sea lion in all three treatments of the current experiment.

It is important to note that the lower than predicted threshold for the sea lion listening for a 500 ms narrowband signal with a rise time of 25 ms (treatment 1) minimizes the potential relevance of any low-frequency energy resulting from the brief rise time and duration of the amplitude envelope of acoustic tag outputs. Bowles *et al.* (2010) speculated that a low-frequency click associated with the envelope of VEMCO tag pulses may be audible to sea lions when the 69 kHz signal is not. However, the experimental design used here shows that not only is the detection threshold for the California sea lion listening for the recorded tag stimulus (treatment 3) around 30–35 dB lower than expected, so is the sea lion threshold for the long duration stimuli with a 25 ms rise time (treatment 1). This indicates that increased sensitivity at 69 kHz is the major factor in the discrepancies between the observed and predicted thresholds for all three treatments, not a low-frequency click. This observation is entirely consistent with the observed absence of low-frequency energy for all three stimuli at the SPLs used in this experiment, indicating that any low-frequency energy associated with the envelope was below the noise floor of the testing environment.

In order for seals and sea lions to effectively use high-frequency acoustic cues from UCTs as an aid in foraging, these cues must be detectable at ecologically relevant distances. The calculated Vemco V16-3H detection ranges for the harbor seal based on this study are similar to the detection ranges calculated based on pre-existing data. In both cases, data indicate that the harbor seal would be able to detect this tag at distances on the order of hundreds of meters in both marine and riverine environments. This suggests that, for this species, signals from the tag are cues that could increase foraging success. For the California sea lion, the estimated detection ranges are much greater when based on data from this

study versus previously existing data. Based on previously existing data, the maximum detection range would be only 10 m for this tag. It is unclear whether this close-range information would be useful in foraging. In contrast, the results of the present study indicate that detection ranges for the sea lion would exceed 200 m in both environments, indicating that these signals may indeed be useful as foraging cues.

In the absence of direct measurements of signal propagation in the environment of interest, it should be noted that the detection ranges calculated here are rough estimates. However, when compared with empirical measurements of transmission loss of a similar Vemco 69 kHz UCT by Bowles *et al.* (2010), the propagation model used in this study is conservative. It should also be noted that, given the large discrepancy in sea lion detection thresholds for stimuli in the 64–69 kHz range between this study and Schusterman *et al.* (1972), a considerable degree of individual variation in sensitivity at ultra-high frequencies above the nominal high-frequency hearing limit may exist. It is possible that the data reported here for a young, female subject are not typical of all California sea lions.

In summary, this study confirms the viability of the “dinner bell” hypothesis relative to the hearing capabilities of both harbor seals and California sea lions. Prior to this study, existing data showing poor auditory sensitivity around 69 kHz in California sea lions implied that these animals could likely not detect UCT outputs at distances that would be useful in foraging. In contrast, this study indicates that high-frequency sensitivity, and consequently detection ranges for 69 kHz UCTs, may be much greater than previously thought, presumably due to bone conduction of high-frequency sounds under water. The sensory capabilities of harbor seals and California sea lions, combined with the fact that both harbor seals and California sea lions are creative and opportunistic foragers, make it likely that these animals exploit signals from UCTs when foraging. This would logically lead to the selective predation of acoustically tagged fish, and might explain the anomalies in survivorship data for many vulnerable and economically important fish species.

These findings are also relevant to recent studies deploying high-frequency transceivers (tags that act as both transmitters and receivers of ultrasonic coded signals) on free-ranging pinnipeds to track encounters with conspecifics or other tagged species (Lidgard *et al.*, 2012; Hayes *et al.*, 2013). Our results indicate that the output of a UCT transmitter physically attached to a seal or sea lion would be perceptually quite loud and, as such, could alter the normal behavior of the tagged animal as well as other animals within the vicinity. Future research should focus on seal and sea lion hearing capabilities in the 100–400 kHz frequency range so as to better understand the capacity of these animals to detect a wide variety of UCTs, as well as on the ability of these animals to localize tag outputs in three-dimensional aquatic environments.

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