

Auditory masking in killer whales (*Orcinus orca*): Critical ratios for tonal signals in Gaussian noise

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ABSTRACT:

Masked detection thresholds were measured for two killer whales (*Orcinus orca*) using a psychoacoustic, adaptive-staircase procedure. Noise bands were 1-octave wide continuous Gaussian noise. Tonal signals extended between 500 Hz and 80 kHz. Resulting critical ratios increased with the signal frequency from 15 dB at 500 Hz up to 32 dB at 80 kHz. Critical ratios for killer whales were similar to those of other odontocetes despite considerable differences in size, hearing morphology, and hearing sensitivity between species. © 2021 Acoustical Society of America.

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I. INTRODUCTION

Killer whales (*Orcinus orca*) are the largest delphinid odontocete, have the most cosmopolitan distribution of all cetaceans, and are a top predator (Baird, 2000). These animals often live in life-long, matrilineal groups (Baird and Whitehead, 2000), where sound is important for individual and group identification (Deecke *et al.*, 2010), conspecific communication, coordinating group behavior, navigation, and finding and capturing prey (Barrett-Lennard *et al.*, 1996). Killer whales can be divided into ecotypes and populations, one of which, the southern resident population, is currently listed as endangered by the United States and Canada (Government of Canada, 2020; National Marine Fisheries Services, 2016). After this population peaked at 98 individuals in 1996, it began a significant decline from which it has struggled to recover (National Marine Fisheries Services, 2016). Anthropogenic noise has been identified as one of three major threats to the recovery of the southern resident population (and other populations), thus warranting the study of how this species perceives sound, particularly in the presence of noise (Holt *et al.*, 2009).

The negative effects of noise on marine mammals are multifaceted and include a reduction in fitness related behavior (Branstetter *et al.*, 2018; Holt, 2008; Houser *et al.*, 2013), masking of biologically relevant acoustic signals (Bain and Dahlheim, 1994; Finneran and Branstetter, 2013), a reduction in hearing sensitivity (Finneran, 2016), and physical pain or death (Parsons, 2017). Auditory masking can be defined as when one sound (often designated as noise) interferes with a listener's ability to detect, discriminate, or recognize another sound (often designated as the signal), resulting in an elevated threshold (Erbe *et al.*,

2016). Auditory masking is complex, where the amount of masking can vary considerably, depending on the signal frequency (Au and Moore, 1990; Fletcher, 1940), how correlated the signal and noise are in space and time (Penner, 1980), and similarity in signal and noise acoustic features such as frequency and temporal structure (Branstetter *et al.*, 2013a; Branstetter *et al.*, 2016; Cunningham *et al.*, 2014). Despite this complexity, when describing the perceptual attributes of auditory masking, the auditory periphery is often modeled as a series of overlapping bandpass filters, where the power of the signal at threshold (P_s) is proportional to the noise power that passed through a hypothetical filter centered on a tonal signal:

$$P_s = K \int_0^{\infty} N(f)W(f)df, \quad (1)$$

where $N(f)$ is the noise power and $W(f)$ is the auditory filter and K is a constant (Patterson and Moore, 1986). If the noise spectral density is flat (i.e., equal energy at all frequencies) and the bandwidth of noise is wider than the auditory filter (i.e., broadband noise), Eq. (1) can be simplified:

$$\Delta f_{ERB} = \frac{P_s}{KN_o}, \quad (2)$$

where N_o is the noise spectral density, K is a constant, and Δf_{ERB} is the equivalent rectangular bandwidth of the auditory filter (Patterson and Moore, 1986). Because of this relationship, the auditory filter bandwidth can be estimated by measuring detection thresholds in broadband noise. If the noise spectral density level and the signal level at thresholds are expressed in dB quantities, the critical ratio (CR) can be calculated by

$$CR = S_{th} - N, \quad (3)$$

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where S_{th} is typically the 50% detection threshold measured in dB re 1 μPa , and N is the pressure spectral density of broadband Gaussian noise measured in dB re 1 $\mu\text{Pa}^2/\text{Hz}$. Critical ratios for mammals, including all odontocetes measured to date, exhibit a stereotypical increase as a function of signal frequency (Branstetter *et al.*, 2017). This pattern is the result of the constant- Q “quality” of auditory filter bandwidths increasing as a function of the center frequency of the filter (f_c), described by

$$Q = \frac{f_c}{\Delta f_{ERB}}. \quad (4)$$

Due to their relative simplicity, CRs have been adopted as a metric to measure and predict auditory masking in marine mammals. Critical-ratio measurements have been published for four different odontocete species, including the bottlenose dolphin (*Tursiops truncatus*) (Au and Moore, 1990; Branstetter *et al.*, 2017; Johnson, 1968; Lemonds, 1999), the harbor porpoise (*Phocoena phocoena*) (Kastelein *et al.*, 2009), the beluga whale (*Delphinapterus leucas*) (Johnson *et al.*, 1989), and the false killer whale (*Pseudorca crassidens*) (Thomas *et al.*, 1990). For killer whales, a summary of unpublished CR data were reported (Bain and Dahlheim, 1994), where CR values for 10 and 80 kHz were 20 and 40 dB, respectively. Although details of the experiment were not provided, these data are fairly consistent with CR values from other odontocetes (Branstetter *et al.*, 2017).

Although CRs are a “simple and convenient” metric for predicting auditory masking, CRs may not generalize to all non-Gaussian noise types. Branstetter *et al.* (2013a) demonstrated that different noise types with identical spectral density levels can result in CRs that vary by as much as 22 dB. Many natural and anthropogenic noise types (e.g., coastal noise from snapping shrimp, *Alpheus digitalis*) are broadband and amplitude modulated, resulting in comodulation masking release (Branstetter *et al.*, 2013b; Branstetter and Finneran, 2008; Erbe and Farmer, 1998). Furthermore, the similarity between signal type and noise type (e.g., odontocete whistles and ice squeaks) can have a profound effect on levels of masking (Branstetter *et al.*, 2016; Cunningham *et al.*, 2014). Despite these complexities, CRs are a useful metric for predicting auditory masking and appear to be fairly representative of different masking scenarios (Erbe *et al.*, 2016; Sills *et al.*, 2017).

The objective of this study was to measure CRs using tonal signals embedded in octave-band Gaussian noise and standard psychophysical methods as a first step to characterize effects of noise on hearing in the species. The current study is an extension of Branstetter *et al.* (2017), where the experiments were conducted using the same behavioral methodology with the same trained animal participants.

II. METHODS

A. Subjects

One female and two male adult killer whales participated in this study. However, the female was removed from

the project due to inconsistent hearing-test behavior. The remaining males both had good species-representative hearing with their audiograms and demographic data available in Branstetter *et al.* (2017). The same letter identifiers (C, E) for each whale were used in the current study. The two males’ estimated ages at the time of the current study were 25 yrs (whale C) and 16 yrs (whale E). The whales were housed in a 21 000 m³ complex of interconnected pools at SeaWorld San Diego. The study followed a protocol approved by the Animal Care Review Committee at SeaWorld as well as an Institutional Animal Care and Use Committee at the National Marine Mammal Foundation.

B. Signal and noise generation

Signals were linear, frequency-modulated (FM) sweeps, where the start and stop frequencies corresponded to 10% of the center frequency of the signal. For example, a 10 kHz signal would have start and stop frequencies of 9.5 and 10.5 kHz, respectively. Linear FM sweeps produce equivalent detection thresholds to pure tones but have the advantage of producing a more homogeneous sound field in a reflective pool environment (Finneran and Schlundt, 2007; Sills *et al.*, 2017). Each signal was 500 ms in duration with 10 ms linear onset and offset ramps to reduce spectral splatter. To properly measure CRs, the masking noise bandwidth must be at least as wide as the auditory filter [see Eqs. (1) and (2)]. For human critical-ratio measurements, noise bandwidths typically extend the full range of hearing. For odontocetes with the broadest range of hearing in the animal kingdom, noise bandwidths for CR measurements are typically chosen to exceed a critical bandwidth [e.g., 2/3 octave bandwidth; Kastelein *et al.* (2009)]. Since critical bandwidths have not been measured in killer whales, the current study used 1-octave band Gaussian noise, which was estimated to be considerably wider than any known critical band for any marine mammal (Finneran and Branstetter, 2013). Each tonal signal was centered in a noise band where the start and stop frequencies of the noise were 1/2 octave above and below the signal frequency. For example, the 10 kHz signal was centered in a 1-octave noise band with start and stop frequencies of 7.07 and 14.14 kHz, respectively (Fig. 1). Noise spectral density levels can be found in Table I and were chosen to be approximately 10–20 dB above the animal’s absolute detection threshold for the tonal frequency serving as the signal. Signal and noise frequency were chosen to extend through most of this species’ audible range. Signals and noise bands centered at 20 kHz and above were projected from an ITC-1001 spherical, omnidirectional projector (International Transducer Corporation, Santa Barbara, CA). For signals and noise below 20 kHz, sounds were projected from a Lubell LL916 underwater speaker (Lubell Labs Inc., Whitehall, OH). Due to the resonant frequency of each projector and the sound field of the pool, a software-based (LABVIEW custom software) compensation filter was applied to produce flat-spectrum noise (Fig. 1). The potential for sound conduction from the projectors through

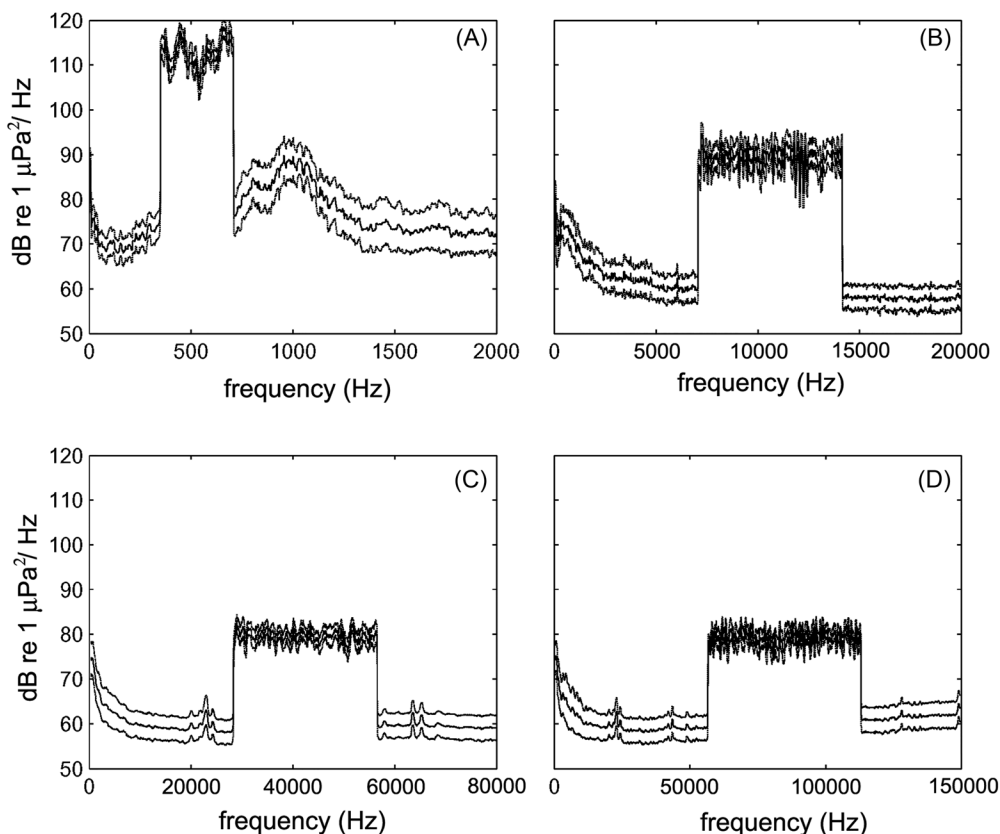


FIG. 1. Examples of 1-octave band masking noise used in the experiment. For each panel, the middle line represents the spectral density of the noise, while the upper and lower lines represent the standard deviation. The figures represent received levels at the hearing test station within the testing pool. Low-pass and high-pass cutoffs are 1/2 octave above and below the signal frequency being tested. (A) 110 dB centered at 500 Hz, (B) 90 dB centered at 10 kHz, (C) 80 dB centered at 40 kHz, and (D) 80 dB centered at 80 kHz.

the stationing device was limited by having the ITC-1001 attached to a polyvinylchloride (PVC) rod, which was attached to the aluminum stationing device with a closed cell neoprene buffer between them (Fig. 2). Furthermore, the tip of the stationing device, where the whale would place its rostrum tip (see Sec. II C), was covered with closed cell neoprene for the whale’s comfort and to further reduce potential sound conduction. The Lubell was attached to a PVC frame, which was suspended from the pool’s gate via rubber hooks (Fig. 2).

Analog tonal signals were generated from a 16-bit National Instruments (Austin, TX) USB-6251 multifunction data acquisition (DAQ) card at an update rate of 606 kS/s. Analog noise was generated from a separate 16-bit National Instruments USB-6343 multifunction DAQ card at an update rate of 500 kS/s. The noise was manually attenuated (TDT PA5 signal attenuator; Tucker Davis Technologies, Alachua, FL), added to the signal (TDT SM5; Tucker Davis Technologies), amplified (Hafler P1000; Tempe, AZ), and projected into the water column with the transducers

TABLE I. Spectral density levels, masked detection thresholds, false alarm rates, and CRs for whales C and E.

Parameter	Value							
	0.5	1	5	10	20	40	56	80
Frequency (kHz)								
Whale C								
Noise spectral density level (dB re 1 $\mu\text{Pa}^2/\text{Hz}$)	110	110	90	90	80	80	80	80
Masked threshold (dB re 1 μPa)	127	133	113	117	106	108	108	111
False alarm rate (%)	18.1	10.4	12.9	8.6	10.0	12.4	10.9	10.6
Critical ratio (dB)	17	23	23	27	26	28	28	31
Whale E								
Masked threshold (dB re 1 μPa)	125	131	112	115	106	110	109	112
False alarm rate (%)	0.0	0.0	7.7	6.1	11.8	6.6	7.8	7.7
Critical ratio (dB)	15	21	22	25	26	30	29	32
Mean CR (dB)	16	22	22	26	26	29	29	32

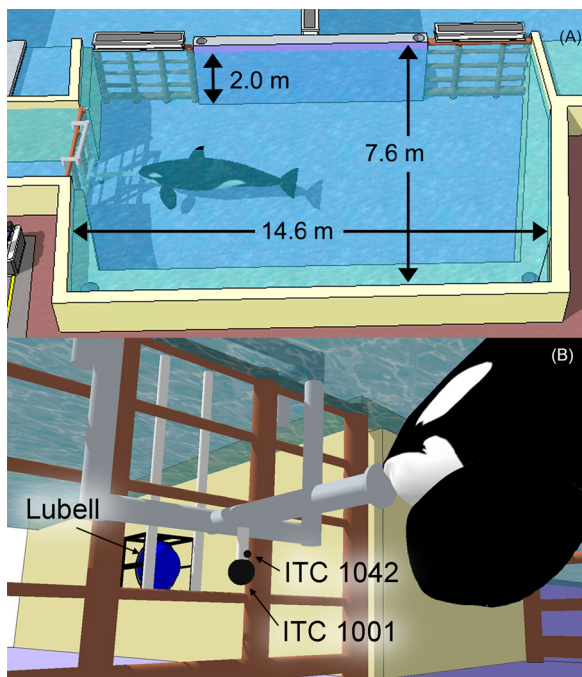


FIG. 2. (Color online) Testing pool and hearing test apparatus. (A) Hearing tests were conducted in an isolated pool 14.6 m long, 7.6 m wide, and 2.0 m deep. (B) The hearing test station was designed to keep the whales at a fixed distance from the sound projectors (Lubell LL916 and ITC-1001). The ITC 1042 projector was not used in this study. [Adapted from [Branstetter et al. \(2017\)](#).]

specified above. The signal and noise were always projected from the same transducer during a testing session. Signal and noise received levels were measured with a Reson TC4033 hydrophone (Teledyne Reson, Slangerup, Denmark) coupled to a Reson VP1000 pre-amp (Teledyne Reson) while the test subjects were in a different pool. The location of the Reson TC 4033 was 57 cm from the tip of the stationing device [Fig. 2(B)], which is the approximate midpoint between the whales' auditory meatuses during a hearing test. Signal calibrations consisted of measuring the signal voltage (V) generated by the computer and the resulting received level (dB re 1 μ Pa), for all signal levels that would be used during a hearing test session and then fitting a linear model to the data, resulting in an input-output function (received level as a function of input voltage). The validity of the linear model was tested before (pre-calibration) and after (post-calibration) a hearing test by measuring the mean difference between the predicted received levels from the model and the actual received level in the pool. If the absolute mean difference was greater than 6 dB for either the pre- or post-calibrations, data from that hearing test session were rejected. This occurred only once. For noise calibrations, the average spectral density (dB re 1 μ Pa²/Hz) within the noise band was adjusted by manual attenuation to be within 1 dB of the desired level prior to the hearing test. The noise was measured again after the hearing test, and the session's data were rejected if the absolute difference was greater than 4 dB. This occurred only once. No attempt was made to characterize the entire sound field

of the testing pool, since these measurements would likely be altered after the added presence of a large whale. However, the use of a linear FM signal, the compensation filter applied to the noise, and both the noise and signal being projected from the same transducer were all measures used to approximate a stable and homogeneous sound field.

C. Procedure

Behavioral hearing tests were conducted in an isolated medical pool at SeaWorld San Diego under similar conditions as [Branstetter et al. \(2017\)](#) using the same apparatus (Fig. 2). During each session, the whale participant would voluntarily swim into the pool and station in front of its trainer. The gates were temporarily closed to prevent the other whales from physically interrupting the hearing tests. Sound could freely travel between the interconnected pools. If non-participating whales were vocalizing, trainers would interact with these animals, which generally reduced or ceased vocalizations. For each threshold estimation procedure, continuous masking noise would be turned on for the duration of a dive, which is defined at the interval between two breaths. The noise would be turned off after each dive. At a hand signal from the trainer, the whale would dive and station its rostrum on the stationing device (Fig. 2). The stationing device was designed to keep the whale at a fixed distance from the sound projectors, thus keeping the received levels under experimental control. Once stationed on the device, the whales would typically exhale (buoyancy control), which would signal the experimenter to begin a series of trials for that dive. The number of trials during a single dive randomly varied between one and ten. A go, no-go response procedure was used, where the whale was trained to produce a "raspberry" vocalization if the whale heard a tonal signal on a tone trial or remain silent otherwise ([Branstetter et al., 2017](#)). The raspberry vocalization was produced by forcing air from its blow hole to produce a low-frequency, embouchure-type sound; thus, there was both an acoustic indicator and a visual bubble indicator of a response. The acoustic response was monitored by a speaker attached to a listening hydrophone (Reson TC 4033). During each trial, there was a stimulus period (500 ms) followed by a 2-s response interval. During the stimulus period, the whale was randomly presented with a tone-in-noise interval (tone trial) or noise-alone interval (catch trial) chosen at random (50% probability) by the computer software. Trainers had no knowledge of trial types. If the whale responded correctly to the tone before the end of the response interval, an experimenter who was running the computer software would inform the trainer to produce a conditioned reinforcer (i.e., a whistle bridge) that provided feedback to the whale of its correct response, and a "hit" was logged by the computer. If the whale failed to produce a vocal response, no whistle feedback was given, and a "miss" was logged. If a response occurred after the end of the response window (i.e., late response), a miss was logged. During a catch trial, if the whale remained silent, a whistle bridge was given, and a

“correct rejection” was logged. If the whale produced a vocal response to a catch trial, no whistle bridge was given, and a “false alarm” (FA) was logged. In addition, any vocal response that occurred outside of the response window was logged as a FA. After one to ten trials were completed, another conditioned reinforcer was given, a sound produced by tapping a bucket lid on the wall (i.e., terminal bridge). This signaled the end of a dive and for the whale to return to the trainer’s station for primary (fish) reinforcement or secondary (ice cubes, snow, tactile rub down) reinforcement following a variable ratio with reinforcement variety schedule (Lawrence *et al.*, 2016). Terminal bridges only occurred following a correct response. The masking noise was turned off after the terminal bridge, which typically coincided with the animal rising to the surface for a breath of air.

A one-down, one-up, adaptive-staircase procedure (Levitt, 1971) was used to titrate the level of the signal during the hearing tests [see Branstetter *et al.* (2017)] (Fig. 2). During each threshold estimation procedure, the level of the signal would typically start 15–20 dB above the whale’s estimated threshold. The initial descending step size was 5 dB but switched to 2 dB after the first reversal (miss) and remained 2 dB for all subsequent step sizes. A minimum of 11 reversals were completed during each test. Thresholds were calculated by averaging the last ten reversals. One to six thresholds were estimated during each day testing occurred. The same signal frequencies were not tested on the same day. Data were rejected if (1) the FA rate exceeded 30%, (2) the standard deviation of reversals exceeded 3 dB, or (3) a total of 11 reversals failed to be acquired. FA rate is defined as the total number of FAs divided by the total number of catch trials that occurred. Data collection for each specific frequency was considered complete if the standard deviation for three consecutive thresholds did not exceed 3 dB.

III. RESULTS

Data were collected between July 12, 2019 and November 19, 2020. A hiatus in data collection occurred between March 22, 2020 and September 2, 2020 due to a temporary closure of SeaWorld San Diego due to the COVID-19 pandemic. Table I displays spectral density levels of the masking noise, average detection thresholds, average FA rates, and CRs for each frequency tested. Figure 3(A) displays CRs for the two killer whale subjects plotted as a function of frequency. Each data point represents the mean for the last three thresholds collected if more than three threshold sessions were conducted. The standard deviation for each data point was 3 dB or less (thus, error bars are not included). Figure 3(B) displays CRs for all odontocete subjects tested to date. The killer whale CR values are consistent with other odontocetes. Killer whale aggregate data and odontocete aggregate data were fit with the power equation:

$$CR = a[\log_{10}(f)]^b + c, \tag{5}$$

where a, b, and c were fitting parameters. Parameter values are found in Figs. 3(A) and 3(B).

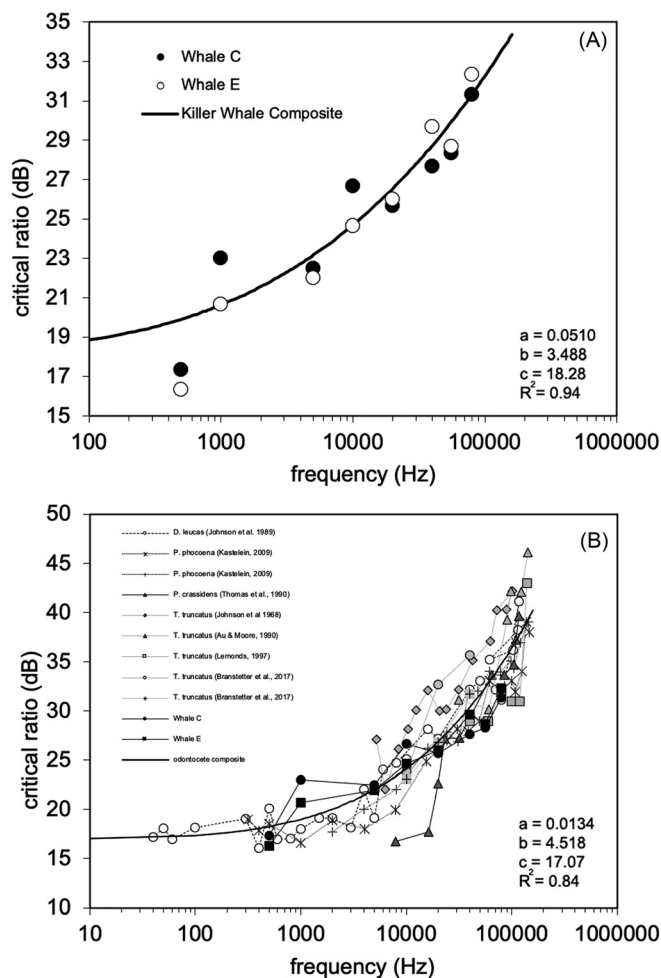


FIG. 3. Critical ratios. (A) Critical ratios for the two killer whale participants (C and E) in the current study. (B) Critical ratios for odontocetes. Lines in both panels represent model fits for aggregate data [Eq. (5)]. Parameter values for model fits are displayed in the lower right-hand corner of each panel.

IV. DISCUSSION

The CRs determined for the two killer whales in the current study are typical of odontocete cetaceans and mammals in general, where CRs increase with signal frequency. Critical ratios ranged from approximately 16 dB for the lowest frequency tested (500 Hz) up to 32 dB for the highest frequency tested (80 kHz). Odontocete CRs appear to be very similar across species despite considerable differences in functional head size (Heffner and Heffner, 2008), ear morphology (Ketten, 1998), and frequency sensitivity between species (NOAA Fisheries, 2018). The use of biosonar is the primary evolutionary driver for odontocete high-frequency hearing capabilities with anatomical modifications supporting high-frequency listening originating at the middle ear (Nummela *et al.*, 1999a; Nummela *et al.*, 1999b) and basilar membrane (Ketten, 1992). The mechanisms for auditory masking can be traced to the mechano-transduction level of the cochlea (Recio-Spinoso and Cooper, 2013). Odontocete basilar membranes can be divided into two types called type I and type II, based on the ratio of the thickness and width

of the membrane (Ketten, 1992). Killer whales, the largest member of the family Delphinidae, are mid-frequency listeners (NOAA Fisheries, 2018) with type II basilar membranes. In contrast, harbor porpoises are high-frequency listeners with type I basilar membranes. Despite clear difference in hearing capabilities and cochlear morphology between odontocete species (Mooney *et al.*, 2012), masking patterns appear remarkably similar. This is a peculiar result, considering auditory filter shapes have been measured for *T. truncatus* (Finneran *et al.*, 2002; Lemonds, 1999; Lemonds *et al.*, 2011), *D. leucas* (Finneran *et al.*, 2002), and *P. phocoena* (Popov *et al.*, 2006), resulting in *Q*-values and auditory filter bandwidths that are quite different. Auditory filter shapes have yet to be measured in killer whales.

Killer whales are exposed to a variety of noise sources, including shipping, construction, petroleum exploration, naval operations, and tourism-based watercraft (Holt, 2008; Richardson *et al.*, 1995). Impacts related to auditory masking can be modeled as population consequences (Thompson *et al.*, 2013) due to a reduction in communication space and the inability to acoustically locate prey (Clark *et al.*, 2009; Erbe *et al.*, 2016). Communication space models rely on species-specific parameters, many of which must be assumed due to a lack of empirical data. For killer whales, CRs at communication frequencies [1.5–12 kHz; Williams *et al.* (2014)] are between 22 and 26 dB. An additional 4 dB can be added if recognition thresholds are to be estimated, which is a more biologically relevant metric (Branstetter *et al.*, 2016), suggesting that acoustic signals would need to be at least 26–30 dB above the spectral density level of Gaussian noise sources for recognition to occur.

Masking predictions based on CRs are useful but should be made with the appropriate caveats. Environmental noise will likely have a much more complex spectral-temporal structure than flat-spectrum, Gaussian noise (Branstetter *et al.*, 2013a). Tonal signals used in laboratory hearing experiments are narrowband and fit nicely within a single auditory filter. However, typical calls emitted by killer whales in noisy environments are broadband with multiple harmonics that extend into several, non-overlapping critical bands (Holt *et al.*, 2011). How detection thresholds for broadband vs narrowband signals differ is unknown for odontocetes. When estimating auditory masking, additional variables should also be considered, including (1) the spectral-temporal structure of the signal (Cunningham *et al.*, 2014) and noise (Branstetter *et al.*, 2013a; Branstetter and Finneran, 2008), (2) the relative positions of the signal and noise sources (Holt and Schusterman, 2007), and (3) whether recognition of a sound is more meaningful than detection alone (Branstetter *et al.*, 2016). Many of these variables have yet to be measured for odontocetes, and none have been measured for mysticetes.

V. CONCLUSIONS

Critical ratios for killer whales ranged between 16 and 32 dB between the frequencies of 500 Hz and 80 kHz. The

increase in CRs as a function of signal frequency was similar to that in other odontocetes despite differences in cochlear morphology and hearing abilities. For communication frequencies between 1.5 and 15 kHz, signals would need to be approximately 22–26 dB above the spectral density of the background noise to be detected.

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