**Title**

Auditory Masking in Sea Lions, Seals, and Walruses

**Author**

Jones, Ryan Alexander

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# AUDITORY MASKING IN SEA LIONS, SEALS AND WALRUSES

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By

**Ryan Alexander Jones**

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The dissertation of Ryan A. Jones is approved by:

Dr. Ari Friedlaender, Chair

Dr. Colleen Reichmuth, Advisor

Dr. Brandon Southall

Dr. Chris Edwards

Peter Biehl
Vice Provost and Dean of Graduate Studies

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# Abstract

## Auditory Masking in Sea Lions, Seals, and Walruses

## Ryan A. Jones

Despite its importance within marine habitats, most of what we know about auditory masking is based on terrestrial species and theoretical assumptions about signal processing in animals. To fill data gaps and improve models that predict active listening space for marine mammals, I have measured hearing thresholds for tonal sounds with highly trained sea lions, walruses, and seals in the presence of precisely and experimentally varied background noise conditions. My aim is to provide empirical measurements of frequency-dependent masking parameters to inform a quantitative understanding of the acoustic scenarios encountered by free-ranging individuals. Three frequency-dependent aspects of masking are considered: critical ratios, critical bandwidths, and masker level effects.

Critical ratios (CR), or the signal-to-noise ratios required for auditory detection of pure tones embedded in controlled, spectrally-flat noise, were measured for sea lion and walrus subjects across a frequency span from 0.2 to 16 kHz. Despite differences in hearing sensitivity, these masking metrics were similar for the subjects and followed expected frequency-dependent trends observed in terrestrial carnivores. When compared to published data for seals, sea lion and walrus CRs were generally higher, indicating that, among these marine Carnivores, seals are especially adapted for hearing in noise. To evaluate how the spectral content of noise contributes to masking, I determined the frequency bandwidth of noise that interferes with the detection of a given tonal signal, the 'critical bandwidth' (CBW). I conducted hearing measurements with three subjects–a

sea lion, walrus, and seal–while varying the frequency content of surrounding noise. The study subjects showed an expected increase in absolute CBW with increasing frequency. While data for the sea lion and walrus were similar, the seal exhibited narrower CBWs that increased as a constant percentage of center frequency, further suggesting additional specialization for hearing in noise for this group. Finally, to explore how noise level contributes to masking, I conducted a series of tone detection measurements with one California sea lion in a highly controlled acoustic environment. Across experimental trials, I gradually increased the amplitude of surrounding noise from a level of no effect to capture masking onset. The data revealed a frequency-and bandwidth-dependent transition zone that occurs before complete masking is evident.

The reported masking parameters provide insight into how some marine mammals hear within noisy conditions. These data, obtained using behavioral, psychoacoustic methods, can be applied to estimate masking effects for amphibious marine carnivores listening in air or water. Further, because they extend to lower frequencies where noise tends to be high and few hearing data are available, these results have clear and actionable outcomes and implications for real-world scenarios and conservation. The findings identify the frequencies where these species are most vulnerable to noise, highlight differences in auditory biology among pinniped lineages, and enable improved predictions of the extent of masking in marine environments dominated by natural and anthropogenic noise.

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The work presented in this dissertation is the result of multiple collaborative efforts that showcased an immense dedication to science and exploration as well as to animal care and research. I feel truly indebted to those who helped me through this process. First, I would like to acknowledge the funding agencies that made this work possible. Thank you to the Navy's Living Marine Resources Program, the US Geological Survey, the US Department of Fish and Wildlife, and the Sooy Family Fellowship Program for their financial support.

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Onwards,

Ry

## Statement of Contribution

The text of this dissertation includes reprints of the previously published material:

**Chapter 1: Jones, R. A.,** Sills, J. M., Synnott, M., Mulsow, J., Williams, R., & Reichmuth, C. (2023). Auditory masking in odobenid and otariid carnivores. *The Journal of the Acoustical Society of America*, *154*(3), 1746-1756.

This manuscript was published open access under a CC-BY license; as such, no permission is necessary, according to the *JASA Editing Team.* This work was original research by Ryan Jones (RJ), with contributions from co-authors as revisions of text or analytical advice. Specifically, RJ conducted all data collection and analyses. RJ, CR, JM and JS assisted in the project concept and design and data. MS served as the lead walrus trainer and liaison between research staff and SeaWorld San Diego. RW provided feedback on the associated manuscript and assisted with the project design.  All authors participated in drafting the manuscript and gave final approval for publication.

# Dedication

I dedicate this dissertation to Jim Finneran.

You changed my entire life, and I will forever be grateful to have you as a mentor and as a friend.

And to my parents, I love you both

## Glossary of Key Terms

**Sound pressure level (SPL) -** decibel measure of sound pressure; unit measure of hearing threshold that can be referenced to 20 μPa (airborne sounds) or 1 μPa (waterborne sounds)

[1]**Power spectral density (PSD) -** distribution of power in a signal versus frequency, where continuously distributed sound (not tones) is the important component. Correct units are watts/Hz but the usual units in acoustics are $\mu Pa^2/Hz$; power is proportional to the mean square pressure and pressure is the measured quantity

[1]**Octave-band level -** the sound pressure level within the frequency band whose upper limit in hertz is twice the lower limit

[1]**Absolute hearing threshold -** minimum sound pressure level that can be perceived by an animal in the absence of significant background noise. Varies with frequency.

[1]**Ambient hearing threshold -** minimum sound pressure level that can be perceived by an animal in the presence of environmental/natural background noise. Varies with frequency.

[1]**Critical Ratio -** difference between sound level for a barely audible tone (in SPL) and the spectrum level of background noise (in PSD) at nearby frequencies

[1]**Critical bandwidth -** frequency band of noise that has strong effects on detection of a sound signal at a particular frequency

**Pinniped -** a clade of amphibious marine Carnivores including the families Otariidae (sea lions and fur seals), Phocidae (true seals), and Odobenidae (walrus). These mammals transitioned to marine living and diverged at least 23 million years ago.

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[1] Adapted from W. H. Richardson et al., (1995) *Marine mammals and noise.* Academic press.

[2] Adapted from Berta, A. (2012) *Return to the sea: the life and evolutionary times of marine mammals*. Univ of California Press.

# General Introduction

In nature, the hearing sense of animals is almost always influenced by surrounding noise. Behavioral measures of absolute sensitivity are the standard for understanding and comparing the hearing abilities of different species, however, whether these measurements are representative of the true acoustic *umwelt* of a listener depends heavily on the subject's environment. Thus, when considering the acoustic world of animals, it becomes imperative to consider the acoustic environments they inhabit and experience.

Sounds from abiotic sources such as wind-driven water motion, surf, and sea ice and biotic contributors such as invertebrates, fish, and mammals combine to establish the overall soundscape of a natural marine habitat (Hildebrand, 2009; Duarte et al., 2021). Identifying relevant sounds within background noise conditions is especially important to marine mammals that rely on acoustic cues for essential life functions such as finding mates, caring for offspring, defending territories, foraging, navigation, and avoiding threats (e.g., Caldwell, 1965; Richardson, 1995; Charrier et al., 2010, Insley et al., 2003).

Marine mammals like seals, porpoises, and whales have adapted over tens of millions of years to operate within typical acoustic scenes (Berta, 2012), but there is a growing understanding that modern ocean environments are getting louder. Human-generated sound from transportation, energy development, naval and survey sonar, construction, and recreational activities alters the amount of invasive noise to which these sensitive species are exposed (Clark et al., 2009; Duarte et al., 2021). The rising contributions of anthropogenic sources to many marine soundscapes have prompted long-standing concern for the potentially harmful effects of noise on marine mammals (e.g., NRC, 2003; Richardson et al., 1995; Southall et al., 2019). Exposure to high levels of noise can cause a range of auditory effects, including physical harm, acute auditory effects such as permanent or temporary hearing loss, or less severe but more pervasive effects such as masking of biologically relevant sounds (Clark, 1991; Kryter, 1994; Erbe, 2022).

Auditory masking occurs when one sound interferes with the synoptic detection of another. The process occurs initially within the peripheral sensory system of a listener where neural transduction of incident acoustic energy occurs; for this reason, the auditory process is sometimes called 'energetic' masking. Just as masking has great relevance for human hearing within noisy backgrounds (Moore, 2012), there have been recent empirical efforts to better understand masking in marine mammals that face similar sensory challenges within the aquatic realm. Marine mammal research on auditory masking to date has been thoroughly reviewed by Erbe et al. (2016) and Branstetter and Sills (2022), who highlight the importance of this topic for different marine mammal groups. There are several available studies of hearing and masking for the three families of semi-aquatic pinnipeds: *Phocidae* (seals), *Otariidae* (sea lions and fur seals), and *Odobenidae* (walruses). Most of these data are focused on absolute (unmasked) hearing profiles and hearing measurements in the presence of controlled masking noise (see Erbe, 2016). Significant knowledge gaps remain, notably in terms of variation in masking stimulus parameters.

The objective of this dissertation is to provide new information that will improve current understanding of auditory masking and hearing in all three pinniped families from the mammalian order Carnivora. Ultimately, this contribution of empirical measurements will enable masking to be considered more substantively and accurately in future ocean noise management efforts.

### *Hearing on land and at sea*

To understand how the amphibious pinnipeds hear on shore and at sea, it is helpful to first review the pathway through which acoustic information is received and processed by terrestrial mammalian carnivores. Acoustic energy in the form of pressure waves is collected by the external pinna before passing through the auditory meatal canal where it stimulates the tympanic membrane. The energy is then amplified within the middle ear by movement of the ossicles—three small bones (malleus, incus, stapes) contained within the auditory bulla. This ossicular amplification is integral in overcoming the impedance mismatch between the air-filled middle ear and the fluid-filled inner ear, as sound energy is lost when transitioning between media. Vibrations of the middle ear bones are transmitted into the fluid of the inner ear through the circular (round) window of the snail-shaped cochlea, where specific receptor cells along the frequency-coded basilar membrane are triggered. Neural conduction of acoustic energy is passed from the sensorineural cells to the auditory nerve leading to higher areas of central auditory processing in the brain, including the auditory somatosensory cortex (Santos-Sacci & Jahn, 1988; Moore, 2012). This ancestral mammalian pathway is apparently used by pinnipeds and other amphibious carnivores when receiving acoustic information in air. However, during submergence in water, alternative hearing pathways are allowed by the impedance matching between the fluid-filled body cavity and the aquatic environment (Møhl, 1964; Numella, 2008; Capshaw et al., 2023).

Given that there is little transmission loss between the aqueous environment and the tissues of the animal, the entire body may act as a conduit for transmitting acoustic energy to the inner ear via bone conduction, although this mode of hearing is poorly understood (Møhl, 1964; Capshaw et al., 2023). To reduce potentially dangerous air-filled spaces within the ear, pinnipeds line the air-filled outer and middle ear cavities with cavernous tissue that swells with blood during diving. The amount, distribution, and functionality of this cavernous tissue varies between the pinniped groups (Numella, 2008). Seals and walruses have cavernous tissue in the middle ear with extra non-cavernous tissue that envelopes the ossicles to protect them during diving (Møhl, 1964). In contrast, sea lions and fur seals have cavernous tissue in portions of the middle ear with non-cavernous tissue stretching across the epitympanic recess to touch only the ventral part of the ossicles (Repenning, 1972). Seals have massive ossicles to further withstand the effects of pressure at depth (King, 1964). Walrus ossicles are not similarly hypertrophied, but since these bones scale allometrically, their large relative size confers the same benefit (Kastelein et al., 1996). Sea lions and fur seals show no substantive ossicular hypertrophy (Repenning 1972). These and other morphological variations related to separation and acoustic isolation of the two ears result in differences in auditory sensitivity and functional hearing range among pinnipeds (see Wartzok & Ketten, 1999, Numella, 2008).

The differences in auditory adaptations between phocid, otariid, and odobenid pinnipeds are unsurprising given their evolutionary relationships. Despite their superficial similarities and shared amphibious life history strategies, each pinniped clade is quite evolutionarily distinct. For example, the odobenid lineage split from the otariids at least 18 million years ago (*see* Berta et al., 2018). Phocids, the most aquatically adapted pinnipeds, diverged from the other amphibious carnivores at least 25 million years ago (*see* Berta et al., 2022). The differences in structure and function paired with the significant evolutionary separation within the three pinniped families are intriguing and make comparative measurements within each group especially important.

### *Measuring the hearing abilities of pinnipeds*

Functional aspects of hearing are evaluated through audiometry (hearing measurements), using either neurophysiological or behavioral methods. Auditory evoked potentials (AEPs) are measured by 'eavesdropping' on the peripheral nervous system, using small electrodes to monitor neural responses to incident sound (Burkhard et al., 2007). AEP's are beneficial in that they can be measured from stranded, wild, or untrained subjects and can sometimes be collected in a single handling session. However, because AEP methods attend only to the electrophysiological response from the peripheral sensory system, they cannot describe what a subject can actually perceive. Furthermore, while AEP methods can effectively measure hearing thresholds in fully-aquatic cetaceans—which possess an enlarged auditory nerve and are sensitive to very high frequency sounds—similar methods have not been developed to evaluate the hearing of pinnipeds in water (e.g., Houser & Finneran, 2006; Mulsow et al., 2012; Schlundt et al., 2007). Behavioral methods of audiometry rely on subjects that learn to perform in psychoacoustic paradigms. These methods can be applied to measure hearing in air or water, and because they include a 'whole animal' response that includes the peripheral and central nervous system, they provide the most accurate measurements of hearing and signal perception. However, behavioral methods are time consuming and require access to trained subjects in managed care as well as to controlled testing environments. The psychophysical approach taken with marine mammals is typically a go/no-go response paradigm where subjects report the presence of a presented signal and are rewarded for correct response with a food reward (Stebbins, 1970). Hearing results are typically presented as a series of detection thresholds—or the lowest amplitude signals audible to the subject—measured across a range of frequencies and plotted as a continuous sensitivity curve, or audiogram. Because of the different pathways by which acoustic energy reaches the inner ear depending on if the listener is under water or in air, both aerial (terrestrial) and in-water audiograms are necessary to gain a full hearing sensitivity profile for amphibious pinnipeds.

Of the three pinniped families, the most well studied in regard to absolute auditory sensitivity (hearing in quiet conditions) are the phocid seals. Published audiograms derived from behavioral audiometry are available for 11 of the 18 seal species in at least one testing medium (air or water). These data reveal that seals have extraordinary hearing abilities, with a range of best hearing from 0.3-60 kHz in water and 0.5 - 14 kHz in air (see Hanke & Reichmuth, 2022). Absolute sensitivity is also well studied in otariids, for which three of 14 species have been tested (two sea lions and one fur seal) and shown to have similar sensitivity between species and within media (Moore & Schusterman, 1987; Mulsow et al., 2012; Reichmuth et al., 2017; Reichmuth & Southall, 2012). The hearing range of otariids is more similar to that of terrestrial carnivores with a region of best hearing between 0.5 – 14 kHz in both air and water (Hanke et al., 2021). Generally, there is a good understanding of hearing sensitivity in these two pinniped groups. There has been contrastingly less hearing work published for the only living odobenid species, the walrus *Odobenus rosmarus*. Most known hearing measurements for walrus come from a single subject tested in both air and water (Kastelein et al., 1996, 2002). Data from this individual suggest that this species is not as sensitive to airborne or waterborne sounds as their distant seal and sea lion relatives. Hearing range is more limited than for either the phocid or otariid pinniped groups, likely attributable to the large body size of walruses (Reichmuth et al., 2020).

Pinnipeds and other mammals only rarely inhabit natural environments that are sufficiently quiet for hearing to be limited by an individual's true sensitivity. These rare cases include sea state conditions where the water's surface is completely calm and there is no biological noise in the frequency region of interest. In most cases, hearing is limited by the background noise of the environment, which can drown out specific sounds of interest. In very noisy conditions, noise can exceed an individual's hearing sensitivity by 10, 20 or more decibels, resulting in reduced ranges over which certain sounds can be heard (Richardson et al., 1995). Thus, measures of absolute sensitivity become less representative of the limits of auditory perception for these species in their natural environment. In order to characterize and quantify the effects of noise on hearing, additional work focused on auditory masking is needed.

### *Auditory masking in pinnipeds*

While quantitative measurements of auditory masking can be obtained using AEP's in some marine mammals, auditory masking data have conventionally been collected from trained subjects using behavioral audiometry procedures (Reichmuth, 2012; Branstetter and Sills, 2022). The study of masking in animals in many ways parallels approaches used to evaluate human hearing in noise (Fay, 1988; Moore, 2012). The classic model of hearing created by Fletcher (1940) helped to explain how the ear processes sounds of different frequencies—pooling signals and noise into different overlapping 'bins' that explain how and when noise interferes with the detection of sounds. This framework has generally been applied to the study of mammalian hearing.

Much of what is assumed about auditory masking was built on Fletcher's work (1940) to define the Power Spectrum Model (PSM) of masking (Moore, 1993). This model makes four primary assumptions: (1) the cochlear membrane, which is lined with frequency-tuned sensorineural cells, can be treated as an array of linear, overlapping bandpass filters, (2) a listener utilizes just one of these filters when detecting a tonal signal in a noise background, (3) only the noise that is able to pass through a given filter will have any effect in masking a given signal, and (4) signal detection thresholds are determined by the amount of noise passing through the auditory filter. While these four assumptions have largely been challenged and none have been found to be entirely valid (see Moore 1993), they serve as an important—albeit often conservative—starting point from which to interpret and predict the masking potential of noise. Further, from these assumptions we can begin to define the primary metrics of auditory masking for humans and other animals: critical ratios and critical bandwidths.

### *Critical Ratios*

A critical ratio is the difference in decibels between the sound pressure level of a tonal signal at detection threshold and the power spectral density level of spectrally flat masking noise centered on the tone frequency (Moore 2013). In simpler terms, this signal-to-noise ratio is the level by which a signal must exceed surrounding noise to be detected by the listener. The degree to which a tonal sound is masked depends on the amount of competing acoustic energy received by the auditory filter centered on the target frequency. The bandwidth of these invisible auditory filters varies by frequency. Narrow filter widths generally occur at lower frequencies and correspond with less competing noise, while filters widen at higher frequencies. Because critical ratios depend on auditory filter widths, they typically increase monotonically with frequency with a consistent slope of about 3 dB/octave (Fay 1988). And because auditory filters operate within the cochlea, the resultant critical ratios are independent of the hearing pathway or medium (air or fluid) in which the sound was received (see Reichmuth, 2012).

As with measures of absolute hearing sensitivity, most available critical ratio data for pinnipeds comes from phocid seals (Branstetter and Sills, 2022). At least some critical ratio data are available for ten seal species (see review in Erbe, 2016). Generally, these data suggest that seals are better at hearing in background noise than other carnivores, as reflected by their relatively low critical ratio values (e.g., Sills et al., 2020). Sparse masking data from two otariid species, the northern fur seal *Callorhinus ursinus* and California sea lion *Zalophus californianus* (Moore & Schusterman, 1987; Southall et. al., 2000; Southall et. al., 2003), are generally consistent with data for other mammalian carnivores like cats and rodents (see Fay, 1988). However, these data are limited and do not conform to expected trends at higher frequencies (Reichmuth, 2012). Currently, there are no critical ratio data available for walruses. As masking values for pinnipeds come from different studies using somewhat different methods, it remains challenging to make direct comparisons of auditory masking for the three primary phylogenetic groupings.

### *Critical Bandwidths*

Another key metric of masking concerns the frequency range of the auditory filters. A critical bandwidth describes the span of noise in hertz (Hz) that influences the detection of a target sound (Moore, 1993). Critical bandwidths are most commonly measured by systematically widening or narrowing the frequency bandwidth of noise surrounding a given signal (Fletcher, 1940; Moore, 1995). As noise bandwidth increases, the masked threshold for the target signal progressively increases as well. The threshold value plateaus at the critical bandwidth, at which point additional frequency content in the noise stimulus will theoretically have no effect on threshold. Like critical ratios, critical bandwidths depend on target frequency. They are narrower at lower frequencies and wider at higher frequencies (Greenwood, 1961). Fletcher (1940) suggested that critical bandwidths (*CB*) could be calculated mathematically using the critical ratio at the target frequency:

$$CB = 10^{CR/10}$$

While this approach provides a conservative estimation of expected trends in the data, it does not accurately identify the frequency range over which masking noise limits the detection of a given signal (Moore 2012). Therefore, direct measurements of critical bandwidth are needed to explain how and when auditory masking occurs relative to surrounding noise conductions

Currently, few critical bandwidth measurements are available for pinnipeds. Southall et. al. (2003) directly measured critical bandwidths using behavioral audiometry in two phocids, the harbor seal *Phoca vitulina* and northern elephant seal *Mirounga angustirostris*, as well as in the California sea lion. Again, there are no such data available for walruses. Furthermore, no critical bandwidth data have been measured in any marine mammal below 2 kHz (see Erbe, 2016; Branstetter and Sills, 2022) where most anthropogenic noise occurs.

*Predicting masking effects*

Critical ratio and critical bandwidth measurements can be used to predict how hearing thresholds change in the presence of surrounding noise. Given both of these biological metrics, along with a characterization of the noise present in terms of spectral, amplitude, and time domains, a masked detection threshold can be estimated. This value is useful to understanding how noise constrains hearing. The loss or change in perceptual space caused by acoustic masking can be explained in terms of the reduction in effective area, or 'acoustic footprint,' of a relevant sound (Clark et al., 2009). Masking predictions may be further enhanced by measuring other biological aspects of auditory processing, such as the relevant temporal windows for signal processing or the effect of noise level on masking onset and growth.

Nearly all studies of auditory masking in humans and other animals are based on highly simplified listening scenarios and involve testing at moderate to higher masker levels. Behavioral audiometry uses standardized stimuli to enable comparisons within and between subjects and species (Stebbins, 1970). Masking studies typically measure detection of tonal sounds in the presence of loud, wide bandwidth, continuous white noise. The use of highly regular tonal sounds and spectrally flat masking noise does not account for masking release that can occur when stimuli are more realistic and complex (*see* Berg et al., 2004; Branstetter et al., 2008). For example, comodulated masking release refers to a reduction in masking in the presence of noise that is coherently amplitude modulated across multiple auditory filters (Verhey et al., 2003). There are limited data that investigate this phenomenon in marine mammals and even fewer that do so in pinnipeds.

Branstetter et. al. (2016) measured masked thresholds in bottlenose dolphins *Tursiops truncatus* in the presence of naturally occurring broadband noise types that included recordings of natural sounds such as ice squeaks and computer-generated sounds. This study also evaluated the detection of complex signals such as dolphin whistles and frequency-modulated sweeps. Results showed that thresholds decreased in the presence of amplitude-modulated noise and for signals that varied in frequency (Branstetter et al., 2016). For pinnipeds, Cunningham et. al. (2014) measured thresholds for complex signals that included frequency and amplitude modulation as well as dynamic harmonic structure. Thresholds were measured for these signals both in the presence of controlled octave-band noise and more variable shipping noise. Results showed that masking release occurred when signal energy could be divided among multiple auditory filters and when noise varied in either frequency or amplitude (Cunningham et al., 2014). Sills et al. (2017) measured thresholds for seals listening for low-frequency tonal signals within seismic pulses recorded 1 and 30 km from an air gun array. The extent of masking was only predicted by critical ratios in certain cases. When noise amplitude varied significantly, the results suggested that there were points where a higher signal-to-noise ratio would present within time windows shorter than the full duration of the signal (Sills et al., 2017). Largely, these studies demonstrate that conventional masking models are not entirely accurate in their predictions of the effects of complex or natural noise in realistic scenarios.

Acoustic masking in nature and in the presence of complex noise can never be perfectly predicted, especially considering what is termed 'informational' masking. Listening is influenced by psychological factors such as stress, attention, confusion, and uncertainty and auditory processing that occurs within the central nervous system (Branstetter et al., 2016). The study of masking that arises from ocean noise is still at an early stage for marine mammals. The gradual refinement of masking parameters is both necessary and possible and will improve our ability to establish conceptual and quantitative models that represent the acoustic world of pinnipeds.

### *Scope of Dissertation*

This dissertation investigates how noise influences the auditory perception of signals in acoustically dependent amphibious carnivores. Several empirical studies aimed to address key data gaps for auditory masking profiles in pinnipeds follow.

In **Chapter One** I report and compare critical ratio values determined for otariid (sea lion) and odobenid (walrus) pinnipeds across a broad frequency range. I use several approaches to validate these data for sea lions and walruses and to examine how well the measured masking parameters predict hearing thresholds in ambient (uncontrolled) noise conditions. These critical ratio measurements resolve data gaps for sea lions and provide entirely new information for walrus. Masking data for these subjects are combined with similar information available for phocid seals to consider hearing more fully within the pinniped lineages. This chapter has been published at the time of dissertation submission (Jones et al., 2023).

In **Chapter Two**, I provide direct critical bandwidth measurements as a function of frequency for representatives of all three pinniped families. This chapter includes auditory measurements for the sea lion, walrus, and bearded seal *Erignathus barbatus*. Prior to this study, no critical bandwidth data were available for any marine mammals below 2 kHz. In addition to filling this data gap for pinnipeds, these directly comparable data reveal key group-level differences and similarities in terms of hearing in noise across a wide range of frequencies.

**Chapter Three** includes an exploration of relatively low-amplitude noise and the onset of auditory masking as noise gradually increases from a level of no effect. This is a topic for which no data are currently available for pinnipeds or any other mammal. The level and frequency band parameters under which masking onset occurs were identified for a single subject at several frequencies to refine functional aspects of the presumed auditory filter model. This approach provides a potential new framework on which to base our understanding of the initial impact of sound source on hearing.

These quantitative measurements are exhaustive and obtained over thousands of trials conducted with healthy, motivated, and experienced individuals. An advantage of these studies is a common approach using standardized behavioral audiometry that enables relevant comparisons within and between subjects. Taken together, these three studies improve our understanding of auditory masking in phocid, otariid, and odobenid pinnipeds and contribute to ongoing efforts to minimize the harmful impacts of anthropogenic noise on these species.

## References

Berg, B. G., & Kong, Y. Y. (2004). Models of commodulation masking release. *The Journal of the Acoustical Society of America*, *116*(4_Supplement), 2624-2624.

Berta, A., & Churchill, M. (2012). Pinniped taxonomy: Review of currently recognized species and subspecies, and evidence used for their description. *Mammal Review*, *42*(3), 207–234. https://doi.org/10.1111/j.1365-2907.2011.00193.x

Berta, A., Churchill, M., & Boessenecker, R. W. (2018). The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences*, *46*(1), 203-228.

Berta, A., Churchill, M., & Boessenecker, R. W. (2022). The origin of phocid seals and evolution of key behavioral character traits. In *Ethology and behavioral ecology of phocids* (pp. 3-30). Cham: Springer International Publishing.

Branstetter, B. K., & Finneran, J. J. (2008). Comodulation masking release in bottlenose dolphins (Tursiops truncatus). *The Journal of the Acoustical Society of America*, *124*(1), 625-633.

Branstetter, B. k., Ketten, D. R., Arruda, J., Cramer, S., & Yamato, M. (2016). Hearing mechanisms and noise metrics related to auditory masking in bottlenose dolphins (*Tursiops truncatus*). In A. N. Popper & A. Hawkins (Eds.), *The Effects of Noise on Aquatic Life II* (pp. 529–538). Springer Science+Business Media, LLC.

Branstetter, B. K., & Sills, J. M. (2022). Mechanisms of auditory masking in marine mammals. *Animal Cognition*, *25*(5), 1029–1047. https://doi.org/10.1007/s10071-

022-01671-z

Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottle-nosed dolphins (*Tursiops truncatus*). *Nature*, *207*(4995), 434–435.

Capshaw, G., Brown, A. D., Peña, J. L., Carr, C. E., Christensen-Dalsgaard, J., Tollin, D. J., ... & McCullagh, E. A. (2023). The continued importance of comparative auditory research to modern scientific discovery. *Hearing Research*, *433*, 108766.

Charrier, I., Aubin, T., & Mathevon, N. (2010). Mother-calf vocal communication in Atlantic walrus: A first field experimental study. *Animal Cognition*, *13*(3), 471–482. https://doi.org/10.1007/s10071-009-0298-9

Clark, W. W. (1991). Recent studies of temporary threshold shift (TTS) and permanent threshold shift (PTS) in animals. *The Journal of the Acoustical Society of America*, *90*(1), 155-163.

Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A., & Ponirakis, D. (2009). Acoustic masking in marine ecosystems: Intuitions, analysis, and implication. *Marine Ecology Progress Series*, *395*, 201–222. https://doi.org/10.3354/meps08402

Cunningham, K. A., Southall, B. L. L., & Reichmuth, C. J. (2014). Auditory sensitivity of seals and sea lions in complex listening scenarios. *The Journal of the Acoustical Society of America*, *136*(6), 3410. https://doi.org/10.1121/1.4900568

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., ... & Juanes, F. (2021). The soundscape of the Anthropocene ocean. *Science*, *371*(6529), eaba4658.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin*, *103*(1–2), 15–38. https://doi.org/10.1016/j.marpolbul.2015.12.007

Erbe, C., Dent, M. L., Gannon, W. L., McCauley, R. D., Römer, H., Southall, B. L., ... & Thomas, J. A. (2022). The effects of noise on animals. In *Exploring animal behavior through sound: volume 1: methods* (pp. 459-506). Cham: Springer International Publishing.

Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook* (L. A. Wilber (ed.)). Hill-Fay Associates.

Finneran, J. J., & Houser, D. S. (2006). Comparison of in-air evoked potential and underwater behavioral hearing thresholds in four bottlenose dolphins (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, *119*(5), 3181–3192. https://doi.org/10.1121/1.2180208

Fletcher, H. (1940). Auditory patterns. *Reviews of Modern Physics*, *12*, 47–66. https://doi.org/https://doi.org/10.1103/RevModPhys.12.47

Greenwood, D. D. (1961). Auditory msking and the critical band. *The Journal of the Acoustical Society of America*, *33*(4), 484–502. https://doi.org/10.1121/1.1908699

Hanke, F. D., & Reichmuth, C. (2022). Phocid sensory systems and cognition. In D. P. Costa & E. A. McHuron (Eds.), *Ethology and Behavioral Ecology of Phocids* (pp. 31–68).

Springer Nature Switzerland.

Hanke, F. D., Reichmuth, C., & Cook, P. (2021). The sensory world of otariids. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 305-321). Cham: Springer International Publishing.

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, *395*, 5–20. https://doi.org/10.3354/meps08353

Insley, S., Phillips, A. V., & Charrier, I. (2003). A review of social recognition in pinnipeds. *Aquatic Mammals*, *29*(2), 181-201.

Santos-Sacchi, J., & Jahn, A. F. (Eds.). (1988). *Physiology of the Ear*. Raven Press.

Kastelein, R. A., Dubbeldam, J. L., de Bakker, M. A. G., & Gerrits, N. M. (1996). The anatomy of hte walrus head (*Odobenus rosmarus*). Part 4: The ears and their function in aerial and underwater hearing. *Aquatic Mammals*, *22*(2), 95–125.

Kastelein, R. A., Mosterd, P., Van Ligtenberg, C. L., & Verboom, W. C. (1996). Aerial hearing sensitivity tests with a male Pacific walrus (*Odobenus rosmarus divergens*), in the free field and with headphones. *Aquatic Mammals*, *22*, 81–93.

Kastelein, R. A., Mosterd, P., van Santen, B., Hagedoorn, M., de Haan, D., & Gagedoorn, M. (2002). Underwater audiogram of a Pacific walrus (*Odobenus rosmarus divergens*) measured with narrow-band frequency-modulated signals. *The Journal of the Acoustical Society of America*, *112*(5 Pt 1), 2173–2182. https://doi.org/10.1121/1.1508783

Kryter, K. D. (1994). *The handbook of hearing and the effects of noise*. Brill.

Lucke, K., Popper, A. N., Hawkins, A. D., Akamatsu, T., André, M., Branstetter, B. K., Lammers, M., Radford, C. A., Stansbury, A. L., & Aran Mooney, T. (2016). Auditory sensitivity in aquatic animalsa). *The Journal of the Acoustical Society of America*, *139*(6), 3097–3101. https://doi.org/10.1121/1.4952711

Mohl, B. (1967). Seal ears. *Science,* 157 (3784): p. 99-115.

Moore, B. C. J. (1993). Frequency analysis and pitch perception. In W. A. Yost, A. N. Popper, & R. R. Fay (Eds.), *Human Psychophysics, Springer Handbook of Auditory Research* (Issue 1940, pp. 56–115).

Moore, B. C. J. (1995). Frequency Analysis and Masking. In B. C. J. Moore (Ed.), *Hearing* (pp. 161–200). Academic Press, Harcourt Brace & Company.

Moore, P. W. B., & Schusterman, R. J. (1987). Audiometric assessment of northern fur seals, Callorhinus ursinus. *Marine Mammal Science*, *3*(1), 31–53. https://doi.org/10.1111/j.1748-7692.1987.tb00150.x

Moore, S. E., Reeves, R. R., Southall, B. L., Ragen, T. J., Suydam, R. S., & Clark, C. W. (2012). A new framework for assessing the effects of anthropogenic sound on marine mammals in a rapidly changing Arctic. *BioScience*, *62*(3), 289-295.

Mulsow, J., Reichmuth, C., Houser, D., & Finneran, J. J. (2012). Auditory evoked potential measurement of hearing sensitivity in pinnipeds. In A. N. Popper & A. Hawkins (Eds.), *The Effects if Noise on Aquatic Life. Advances In Experimental Medicine and Biology* (Vol. 730). Springer. https://doi.org/10.1007/978-1-4419-7311-5_16

Numella, S. (2009). Hearing. In W. F. Perrin, B. Wursig, & T. J.G.M. (Eds.), *Encyclopedia of Marine Mammals* (2nd ed., pp. 553–562). Academic Press.

Reichmuth, C. (2012). Psychophysical studies of auditory masking in marine mammals: key concepts and new directions. In A. N. P. Popper & A. Hawkins (Eds.), *The Effects of Noise on Aquatic Life* (pp. 23–27). Springer-Verlag. https://doi.org/10.1007/978-1-4419-7311-5_4

Reichmuth, C., Sills, J. M., Brewer, A., Triggs, L., Ferguson, R., Ashe, E., & Williams, R. (2020). Behavioral assessment of in-air hearing range for the Pacific walrus (*Odobenus rosmarus divergens*). *Polar Biology*, *43*(6), 767–772. https://doi.org/10.1007/s00300-020-02667-6

Reichmuth, C., Sills, J. M., & Ghoul, A. (2017). Psychophysical audiogram of a California sea lion (*Zalophus californianus*) listening for airborne tonal sounds in an acoustic chamber. *Proceedings of Meetings on Acoustics*, *30*, 010001. https://doi.org/10.1121/2.0000525

Reichmuth, C., & Southall, B. L. B. L. (2012). Underwater hearing in California sea lions (*Zalophus californianus*): Expansion and interpretation of existing data. *Marine Mammal Science*, *28*(2), 358–363. https://doi.org/10.1111/j.1748-7692.2011.00473.x

Repenning, C. A. (1972). Underwater hearing in seals: Functional morphology. In R. Harrison (Ed.), *Functional Anatomy of Marine Mammals: Vol 1* (pp. 307–331). Academic Press.

Richardson, W. J., Greene, C. R., Malme, C. I., & Thomson, D. H. (1995). *Marine*

*Mammals and Noise*. Academic Press, Harcourt Brace & Company.

Schlundt, C. E., Dear, R. L., Green, L., Houser, D. S., & Finneran, J. J. (2007). Simultaneously measured behavioral and electrophysiological hearing thresholds in a bottlenose dolphin (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, *122*(1), 615–622. https://doi.org/10.1121/1.2737982

Sills, J. M., Reichmuth, C., Southall, B. L., Whiting, A., & Goodwin, J. (2020). Auditory biology of bearded seals (*Erignathus barbatus*). *Polar Biology*, *43*, 1681–1691. https://doi.org/10.1007/s00300-020-02736-w

Sills, J. M., Southall, B. L., & Reichmuth, C. (2017). The influence of temporally varying noise from seismic air guns on the detection of underwater sounds by sealsa). *Journal of the Acoustical Society of America*, *141*(2), 996–1008. https://doi.org/10.1121/1.4976079

Southall, B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., Nowacek, D. P., & Tyack, P. L. (2019). Marine Mammal Noise Exposure Criteria: Updated Scientific Recommendations for Residual Hearing Effects. *Aquatic Mammals*, *45*(2), 125–232. https://doi.org/10.1578/AM.45.2.2019.125

Southall, B. L., Schusterman, R. J., & Kastak, D. (2000). Masking in three pinnipeds: underwater, low-frequency critical ratios. *The Journal of the Acoustical Society of America*, *108*(3 Pt 1), 1322–1326. https://doi.org/10.1121/1.1288409

Southall, B. L., Schusterman, R. J., & Kastak, D. (2003). Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements. *J Acoust Soc Am*, *114*(3), 1660–1666. https://doi.org/10.1121/1.1587733

Stebbins, W. C. (1970). Principles of animal psychophysics. In W. C. Stebbins (Ed.), *Animal Psychophysics: the Design and Conduct of Sensory Experiments* (pp. 1–19). Appleton-Century-Crofts.

Verhey, J. L., Pressnitzer, D., & Winter, I. M. (2003). The psychophysics and physiology of comodulation masking release. *Experimental Brain Research*, *153*(4), 405–417. https://doi.org/10.1007/s00221-003-1607-1

Wartzok, D., & Ketten, D. R. (1999). Marine mammal sensory systems. In J. E. Reynolds & S. A. Rommel (Eds.), *Biology of Marine Mammals* (pp. 117–175). Smithsonian Institution.

# Chapter 1: Auditory masking in odobenid and otariid carnivores

Ryan A. Jones[1], Jillian M. Sills[2], Mitzi Synnott[3], Jason Mulsow[4], Rob Williams[5], and Colleen Reichmuth[2,a]

[1]*Department of Ocean Sciences, University of California Santa Cruz, Santa Cruz, California 95064, USA*

[2]*Institute of Marine Sciences, Long Marine Laboratory, University of California Santa Cruz, Santa Cruz, California 95060, USA*

[3]*SeaWorld San Diego, San Diego, California 92109, USA*

[4]*National Marine Mammal Foundation, San Diego, California 92109, USA*

[5]*Oceans Initiative, Seattle, Washington 98102, USA*

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Running title: Masking in walruses and sea lions

## ABSTRACT

As the only living species within the odobenid lineage of carnivores, walruses (*Odobenus rosmarus*) have no close relatives from which auditory information can be extrapolated. Sea lions and fur seals in the otariid lineage are the nearest evolutionary outgroup. To advance understanding of odobenid and otariid hearing, we conducted behavioral testing with two walruses and one California sea lion (*Zalophus californianus*). Detection thresholds for airborne sounds were measured from 0.08 to at least 16 kHz in ambient noise conditions, and then re-measured in the presence of octave-band white masking noise. Walruses were more sensitive than the sea lion at lower frequencies and less sensitive at higher frequencies. Critical ratios for the walruses ranged from 20 dB at 0.2 kHz to 32 dB at 10 kHz, while critical ratios for the sea lion ranged from 16 dB at 0.2 kHz to 35 dB at 32 kHz. The masking values for these species are comparable to one another and to those of terrestrial carnivores, increasing by about 3 dB per octave with increasing frequency. Despite apparent differences in hearing range and sensitivity, odobenids and otariids have a similar ability to hear signals in noisy conditions.

## Introduction

Concern for rising levels of noise in ocean ecosystems has prompted many recent studies of marine mammal hearing. Several comprehensive reviews reveal significant knowledge gains as well as important data gaps (e.g., Erbe et al., 2016; Mooney et al., 2012; Nummela, 2008; Southall et al., 2019) Among amphibious marine mammals, the best studied with respect to hearing are the phocid carnivores. These 'true seals' are linked within a common phylogenetic lineage that exhibits a broad frequency range of sensitive hearing and notable auditory adaptations to support marine living (see Hanke and Reichmuth, 2022). By comparison, the auditory biology of the otariid (sea lions and fur seals) and odobenid (walrus) carnivore lineages is lesser known and would benefit from further investigation.

The otariid carnivores, or 'eared seals,' include 14 living species. Their auditory anatomy is similar to that of terrestrial carnivores but with reduced and rolled pinnae, notable changes in bony structure related to sound conduction in water, and soft tissue adaptations including the presence of cavernous tissue and the thickening of cartilaginous structures to protect the ear during diving (see Nummela, 2008; Repenning, 1972). Otariids rely on sound for orientation, social communication, and threat assessment both in air and in water (see Charrier et al., 2021). Most sound production is airborne and occurs on terrestrial haulouts, but males in particular are known to emit barks and clicks under water (Schusterman and Balliet, 1969).

Terrestrial and aquatic hearing have been studied in three otariid species (see Hanke et al., 2021). Behavioral audiometric data are available for northern fur seals *Callorhinus ursinus* (Babushina et al., 1991; Moore and Schusterman, 1987), California sea lions *Zalophus californianus* (Cunningham and Reichmuth, 2016; Kastak and Schusterman, 1998, 2002; Kastelein et al., 2022a, 2022b; Moore and Schusterman, 1987; Mulsow et al., 2011; Reichmuth et al., 2013; Reichmuth et al., 2017; Reichmuth and Southall, 2012; Schusterman, 1974; Schusterman et al., 1972) and Steller sea lions *Eumetopias jubatus* (Kastelein et al., 2005; Mulsow and Reichmuth, 2010). While these species span the extremes of size and phylogenetic distance among otariids, they have similar auditory profiles, suggesting the available measurements are representative of otariids as a group (Mulsow et al., 2012). The functional frequency range of hearing (measured at the 60 dB re 20 μPa level) is about 0.2 to 38 kHz in air, with hearing capabilities extending slightly higher in water. The range of best hearing (measured at 20 dB re minimum threshold) occurs from 1 to 23 kHz in air, and over an even wider range of 0.35 to 37 kHz in water. Auditory masking has been evaluated in California sea lions and northern fur seals at frequencies between 0.5 and 32 kHz (Moore and Schusterman, 1987; Southall et al., 2000, 2003). However, there are inconsistencies between the limited available data and expected frequency-dependent masking patterns for mammalian carnivores.

Odobenid carnivores are represented by only one extant species of walrus, *Odobenus rosmarus*, which has no close living relatives. This species last shared a common ancestor with otariids more than 24 million years ago, and is even further removed from the phocid lineage and all other carnivores (Berta et al., 2018; Boessenecker and Churchill,

2018) Compared to otariids—which are found in most temperate oceans in areas of high productivity—walruses have a restricted geographic range limited to the shallow continental shelf areas of Arctic and sub-Arctic seas (Bonnell and Ford, 1987; Fay, 1982). Walruses lack external pinnae and have small ear openings, as well as significantly enlarged ear drums, middle ear cavities, and ossicles (Kastelein et al., 1996b; Repenning, 1972). While they share some morphological adaptations with phocids, their auditory structures are also similar to those of otariids, leading to a somewhat 'intermediate' ear type (see Numella, 2008; Repenning, 1972). Walruses are among the most vocal of the pinnipeds (the sub-order comprising phocid, otariid, and odobenid carnivores). In contrast to other species, they produce a wide range of social sounds in air and under water year round (see Miller and Kochnev, 2021; Mouy et al., 2012), and observations from passive acoustic monitoring suggest they also use underwater sounds in non-social contexts (Mouy et al., 2012).

Understanding of hearing ability in the walrus is limited, with measures of auditory sensitivity available from one adult male Pacific walrus (*O. r. divergens*) tested both under water and in air. This male had a demonstrated hearing range from 0.125 to just 15 kHz in water (Kastelein et al., 2002), with worse sensitivity than both phocids and otariids. The same individual tested with airborne sounds in outdoor conditions exhibited poor sensitivity (> 60 dB re 20 µPa) from 0.125 to 8 kHz; however, higher frequencies were not tested due to equipment limitations and the authors report that measurements were likely constrained by environmental noise (Kastelein et al., 1996a). Playback studies with wild Atlantic walruses (*O. r. rosmarus*) on terrestrial haulouts confirmed responses to tonal stimuli within the same frequency range (Kastelein et al., 1993). More recently, Reichmuth et al. (2020) determined that the audible range of terrestrial hearing in walruses extends from at least 0.06 to 23 kHz—broader than previously tested but still narrow in comparison to other carnivores. While a coarse understanding of their auditory biology is emerging, there are no available measures of auditory masking for walruses.

For regulatory and management purposes related to anthropogenic acoustic exposures, odobenids are typically grouped into the same category with otariid carnivores (Finneran, 2015; Southall et al., 2019), along with one mustelid (sea otter, *Enhydra lutris*) and one ursid carnivore (polar bear, *Ursus maritimus*). The separation of these 'other marine carnivores' from phocid carnivores is based mostly upon aspects of auditory biology that set the phocids apart. Exploring finer scale similarities and differences in hearing ability among marine carnivores will address outstanding questions concerning species- and taxa-specific auditory adaptations. Some applied information such as onset thresholds for temporary or permanent hearing loss will be difficult or impossible to gather from multiple species. Other relevant aspects of hearing such as metrics of auditory masking can be more readily studied within a comparative framework.

Auditory masking—which occurs when one sound interferes with the detection of another—can be studied in relatively simple conditions (*i.e.*, without the need for specialized testing rooms or pools) where a controlled noise background can be generated. Several quantitative studies of masking in marine mammals have addressed the challenges of receiving biologically relevant cues within noisy backgrounds (see

Branstetter and Sills, 2022; Erbe et al., 2016). The most fundamental metric of masking, the critical ratio, describes the difference in decibels between the sound pressure level of a tonal signal at detection threshold and the power spectral density level of spectrally flat masking noise centered on the tone frequency (Fletcher, 1940; Moore, 1993). These frequency-dependent signal-to-noise ratios describe the level by which a given signal must exceed surrounding noise to be detected by a listener. Critical ratios vary across species with different hearing profiles (Fay, 1988). Significantly, they are independent of the hearing pathway and medium (air or fluid) in which sound is received (see Reichmuth, 2012), allowing for empirically determined critical ratio values to be applied to both environments utilized by amphibious pinnipeds.

Here, we provide measures of hearing and masking for otariid and odobenid subjects trained to listen for airborne tones both in ambient outdoor conditions and within a background of spectrally flat masking noise. Detection thresholds and critical ratios are compared between sea lions and walruses and to data currently available for related species.

## Methods

### *Subjects*

Audiometric testing was conducted at SeaWorld San Diego (San Diego, CA, USA) and Long Marine Laboratory at the University of California Santa Cruz (Santa Cruz, CA, USA). Subjects were in good health with no known otological problems or prior exposure to ototoxic medications. Odobenid subjects were an adult female and a sub-adult male Pacific walrus identified as *Chou Chou* (11-12 y) and *Mitik* (9 y). Neither had prior experience with audiometry. The otariid subject was an adult female California sea lion identified as *Ronan* (NOA0006602; 13-14 y). This sea lion had participated in several audiometric studies, including measures of in-air and underwater sensitivity as a function of frequency (Reichmuth et al., 2013; Reichmuth et al., 2017), ultrasonic hearing and masking trials (Cunningham and Reichmuth, 2016), and auditory assessments using complex stimuli (Cunningham et al., 2014a, 2014b). Testing for all subjects occurred between May 2021 and December 2022 during three rounds of data collection following intermittent training over the preceding 18 months.

Cooperative behavior for husbandry and research tasks was established using operant conditioning methods and positive reinforcement (fish, clam, or squid). Individual diets were pre-determined by veterinary and animal care staff to maintain optimal health and weight. Animal diets were not constrained for research purposes and subjects were offered their scheduled diet daily regardless of performance during auditory tasks.

In addition to the primary animal subjects, the hearing of one adult male human (21 y) was tested using the same equipment and environment as the sea lion to validate the experimental procedure through comparison to published hearing and masking thresholds (see SuppPub1).

### *Environment and Apparatus*

Auditory testing with walruses was conducted outdoors in the Wild Arctic facility at SeaWorld San Diego in a 7 m x 4 m pen adjacent to the primary living enclosure. The floor and two side walls were cement while the front and back walls were enclosed by metal bars spaced 50 cm apart. The top of the pen was open to the environment but shaded by tarpaulin. The testing apparatus comprised a station marker and response target that were positioned at the bars facing a walkway. The white 15 cm x 15 cm square station was firmly affixed to a metal bar at the height of the center of the subject's head while in a relaxed sitting posture – 0.84 m elevation for the female, 1.0 m elevation for the male. A black 15 cm x 15 cm square response target was mounted to another bar 0.5 m to the subject's left side at the same height. The speaker used to project auditory stimuli was affixed on a tripod in the walkway, 1.0 m directly in front of the station and 1.2 m from the center position of the subject's head during testing. The station, response target, and speaker were in the same horizontal plane for each walrus.

The sea lion and human subject were tested in a similar setup at Long Marine Laboratory. Trials were conducted in an outdoor 5 m x 3.5 m holding pen, with two walls of vinyl-coated chain link fencing to the front and left side of the subject and two rigid walls of synthetic HDPE at the subject's right and rear. The top of the enclosure was covered with shade cloth. Similar to the walrus configuration, a white station and black response target were attached to the fence at the height of the subject's head (0.84 m) in a relaxed position, 50 cm apart. The speaker was positioned in the adjacent walkway 1.0 m in front of the station and 1.2 m from the center position of the subject's head during testing.

In both facilities, the trainer and experimenter were concealed from the subject's view during audiometric testing. The experimenter was positioned behind a visual barrier, while the trainer stepped behind a nearby blind at the start of each trial. The instrumentation used to generate acoustic stimuli (Section II.C) was configured within a waterproof case placed behind a barrier and linked to the speaker via a cable. A Hero8 video camera (GoPro, San Mateo California) was securely placed in the walkway to record each session.

Ambient noise was measured daily in test-ready conditions with a calibrated, self-powered 2250 Sound Level Meter (Sampling rate 48 kHz; Brüel & Kjær A/S, Nærum, Denmark) with a free-field 1/2" type 4966 microphone. The microphone was placed at the center position of the subject's head during testing. Noise power spectral density levels (PSD, dB re (20 μPa)$^2$/Hz) for frequencies from 0.0125 – 20 kHz were calculated from the median of 1-min, unweighted third-octave band 50th percentile measurements (L50) obtained throughout testing. Noise above 20 kHz was less than 0 dB re 20 μPa, as measured with an MK301 microphone capsule (0.005–100 kHz, ± 2 dB; Microtech Gefell GmbH, Gefell, Germany) with a C617 body (Josephson Engineering, Santa Cruz, CA, USA) and BPS-1 power supply (Stewart Electronics, Rancho Cordova, CA, USA) linked to a battery-powered Fostex FR-2 Field Memory Recorder (Fostex Company, Tokyo, Japan).

### *Stimulus generation and calibration*

Test frequencies were 0.08, 0.1, 0.2, 0.5, 1, 2, 4, 10 and 16 kHz for the walruses; this range was extended to include 32 kHz for the sea lion based on expected differences in high-frequency hearing limits (Reichmuth et al., 2020; Reichmuth et al., 2017). The human subject was tested at a subset of these frequencies as well as 8 kHz to align with available critical ratio data (*e.g.* Hawkins and Stevens, 1950). Signals were 1-s pure tones with 50-ms linear ramps generated (1 MHz update rate) from a PC laptop computer in LabVIEW (NI, Austin, TX, USA) using Hearing Test Program (HTP) software (Finneran, 2003). Signals passed through an NI USB-6251 data acquisition board, a 0.1–250 kHz bandpass active filter module (Krohn-Hite, Brockton, MA, USA), and a 2-channel Mix 2:1 passive mixer (Radial Engineering, Vancouver, B.C.) before being projected through a KH 80 DSP powered studio monitor with internal amplifier (0.057–21 kHz, +/- 3 dB; Neumann, Berlin, Germany). The filter module was bypassed to enable testing at low frequencies (0.08 and 0.1 kHz). For testing at 32 kHz, filtered signals were mixed using a TDT signal ladder (Tucker-Davis Technologies, Alachua, FL, USA) before passing through a NX100 2-channel power amplifier (Behringer, Illich, Germany) and were projected through a Vifa ultrasonic dynamic speaker (Avisoft Bioacoustics, Glienicke/Nordbahn, Germany).

To confirm a stable received sound field, audiometric signals at each test frequency were spatially mapped within a 3 cm x 3 cm x 3 cm area surrounding (and including) the position of each ear. Maximum variability in received sound pressure level (SPL, dB re 20 μPa) relative to ear position was +/- 2 dB. Test signals were calibrated before each session at the right or left ear position, whichever was associated with the greater received level during sound field mapping. Signals were inspected as waveforms and spectrograms at a range of amplitudes to confirm the absence of artifacts. Spectra of the signals used for audiometry are provided in SuppPub2. During mapping and calibration between 0.08 and 16 kHz, signals were received by the 2250 Sound Level Meter and 4966 microphone and passed through the same NI USB data acquisition board used for signal generation before being measured in HTP software. At 32 kHz, signals were received by the Microtech Gefell MK301 microphone capsule with the Josephson C617 body and Stewart BPS-1 power supply and passed through the same data acquisition hardware and software used for the lower frequencies.

Masking stimuli were continuous, octave-wide bands of Gaussian (white) noise centered at each test frequency from 0.1 to 10 kHz for walruses and from 0.2 to 32 kHz for the sea lion. Masking noise was generated and spectrally flattened in the testing environment prior to each session using a custom LabVIEW virtual instrument which compensated for the frequency response of the outgoing equipment chain and environment. During testing, masking noise was sent from the computer sound card using Audacity(R) software (Version 3.0.0), mixed with the signal at the passive mixer, and projected through the same Neumann KH 80 speaker. For testing at 32 kHz, masking noise and filtered signals were mixed using the TDT signal ladder before passing through the NX100 2-channel power amplifier and being projected through the ultrasonic Vifa speaker.

Maskers were spatially mapped across the same grid described previously, with maximum variability in octave-band SPL relative to ear position of +/- 2 dB. Masking noise was calibrated before each session to ensure that the noise was spectrally flat, with the SPL of each 1/3-octave band within 1 dB of the center band and center band SPL within 1 dB of target level. Spectra of maskers used for audiometry are provided in

SuppPub2. To ensure appropriate masking conditions at each frequency, the target PSD of the masking noise was set either equal to or 5 dB above the SPL of the corresponding ambient threshold value. This masker level always exceeded the ambient noise in the surrounding third octave band. The same incoming equipment chain was used for mapping and calibration of masking stimuli as for the pure-tone signals, along with the LabVIEW virtual instrument used for generating masking noise.

### *Audiometry*

Audiometric protocols were the same for all subjects. The auditory task consisted of both signal-present and signal-absent trials in a go/no-go signal detection paradigm (Stebbins, 1970) similar to that used in previous behavioral studies of walrus hearing (Kastelein et al., 2002; Kastelein et al., 1996a; Reichmuth et al., 2020). For each trial, correct responses (remaining still at the station when no signal was presented or touching the response target when a signal was presented) were marked with a conditioned acoustic reinforcer (a verbal "OK" or whistle bridge) followed by a food reward delivered near the station. Correct responses to signal-present and signal-absent trails were reinforced equally. Incorrect responses (misses on signal-present trials and false detections on signal-absent trials) were not reinforced and the subject was re-prompted to the station before moving on to the next trial.

During each session, signal frequency was held constant while signal amplitude was varied based on subject performance using an adaptive staircase method (Stebbins, 1970). The first signal-present trial in a session contained an easily detectable signal, after which amplitude was decreased by 2-4 dB following each correct detection until the first miss. Signal amplitude was then increased by 6 dB after each miss and decreased by 2 dB after each correct detection until 3-8 descending (hit-to-miss) transitions were obtained. The larger ascending step size minimized consecutive errors, while the smaller descending step size enabled precise determination of hit-to-miss transitions. The session ended with several easily detectable signals following the last miss to maintain stimulus control on the task.

Within a session, signal-present and signal-absent trials were presented in a predetermined, pseudorandom order at a ratio of 70:30. The interval of each trial was 6 s, during which signal onset could be varied. Approximately 40 trials were conducted per session, depending on the subject's motivation. Subjects participated in 1-2 sessions per day with the duration of each session kept within the optimal attention span of each subject, and without exceeding 15 minutes. False alarm rates were determined for each session as the proportion of false detections on signal-absent trials.

### *Ambient Hearing Thresholds*

Data collection at each frequency began by measuring hearing thresholds in the ambient conditions of the testing environment, with frequencies tested to completion in a shuffled order. Ambient hearing thresholds were collected over 2-3 sessions and calculated from 9 to 15 consecutive, stable (standard deviation < 3) hit-to-miss transitions. Thresholds were estimated as the average of these hit-to-miss transitions.

### *Masked Hearing Thresholds and Critical Ratios*

Masked hearing thresholds were measured at each frequency following threshold measurements in ambient conditions. Masking noise was played throughout the session to establish a uniform, artificial noise floor; auditory fatigue during a session was not expected due to the relatively low masking noise levels used (*e.g.* Houser 2021; Smith, 1934). Testing was conducted using the same method described for ambient thresholds. Masked thresholds were determined from 15 stable (standard deviation < 2 dB) hit-to-miss transitions obtained over 2-4 consecutive sessions. Critical ratios for each frequency were calculated as the difference (in dB) between the SPL of the masked hearing threshold and the mean PSD level of the octave-band masker.

After data collection was completed, critical ratios were added to corresponding noise spectral density levels measured during ambient threshold testing. This provided an estimate of the lowest threshold that could be measured at each frequency in this testing environment (Kastelein et al., 2005). These theoretical lowest thresholds were compared to ambient threshold measurements to evaluate whether the measured hearing thresholds were constrained by environmental noise.

## Results

### *Ambient noise conditions*

Ambient noise levels in both outdoor testing environments were highest at low frequencies and declined with increasing frequency, as expected (Table I, Fig. 1). At

SeaWorld San Diego, ambient noise spectral density levels ranged from 47 dB re (20 μPa)$^2$/Hz at 0.08 kHz to -10 dB re (20 μPa)$^2$/Hz at 16 kHz. At Long Marine Laboratory, outdoor noise levels ranged from 33 dB re (20 μPa)$^2$/Hz at 0.08 kHz to -24 dB re (20 μPa)$^2$/Hz or less at and above 16 kHz. Ambient noise conditions were, on average, 15 dB lower at Long Marine Laboratory compared to SeaWorld San Diego

### *Ambient hearing thresholds*

Ambient hearing thresholds for walruses were collected at nine frequencies from 0.08 to 16 kHz (Table I, Fig. 1 upper panel). These were similar (within 4 dB) for both individuals at the five common test frequencies. Best sensitivity (lowest threshold) was 35 dB re 20 μPa at 10 kHz. Below 10 kHz, ambient thresholds increased gradually to 74 dB re 20 μPa at 0.08 kHz. The high-frequency roll off was effectively captured for both subjects above 10 kHz, where sensitivity declined by approximately 15 dB within a half octave. Hearing thresholds were 57 and 53 dB re 20 μPa for the two subjects at 16 kHz, just below the nominal high-frequency hearing limit of 60 dB (as defined by Heffner and Heffner, 2008). False alarm rates were similar across subjects and frequencies: 0.16 (range: 0.06 – 0.24) for female *Chou Chou* and 0.20 (range: 0.18 – 0.27) for male *Mitik*. Threshold-to-noise offsets—measured as the difference between hearing threshold and ambient noise at each frequency—varied between 16 and 34 dB, except at 16 kHz where the offset was 63 dB. Walrus ambient thresholds were consistent with previously reported detection thresholds for the species (Kastelstein et al., 1996a); the low- and high-frequency roll offs also aligned with a prior estimate of hearing range (Reichmuth et al., 2020).

Ambient hearing thresholds for the California sea lion were collected at ten frequencies from 0.08 to 32 kHz (Table I, Fig. 1 lower panel). Consistent with a prior evaluation of this subject's absolute hearing (Reichmuth et al., 2017), the sea lion showed best sensitivity at 16 kHz, with a lowest measured threshold of 4 dB re 20 µPa. Low-frequency sensitivity rolled off to 83 dB re 20 µPa at 0.08 kHz, while high-frequency sensitivity declined by 43 dB over one octave, to 47 dB re 20 µPa at 32 kHz. Offsets between measured thresholds and associated ambient noise ranged from 23 to 50 dB, and were greatest at the lowest and highest frequencies tested. The sea lion's mean false alarm rate across all frequencies was 0.12 (range: 0.07 – 0.25), similar to that of the two walrus subjects.

### *Masked Thresholds and Critical Ratios*

Walrus critical ratios were calculated from masked thresholds at frequencies from 0.2 to 10 kHz (Table II, Fig. 2). Masked thresholds were not measured at 0.08, 0.1, or 16 kHz, as the required stimulus levels (based on ambient thresholds) exceeded the capabilities of the equipment. Critical ratios generally increased with increasing frequency from 17 dB at 0.5 kHz to 32 dB at 10 kHz. There was a slight upward inflection at 0.2 kHz with a critical ratio of 20 dB. At the four frequencies where both individuals were tested, critical ratios were within 2 dB of one another. False alarm rates were again similar: 0.23 (range: 0.20 – 0.29) for the female *Chou Chou* and 0.21 (range: 0.17 – 0.24) for the male *Mitik*

Critical ratios for the sea lion were evaluated at frequencies from 0.2 to 32 kHz. Masked thresholds at 0.08 and 0.1 kHz could not be measured. The critical ratios ranged from 18 at 0.2 kHz to 34 dB at 32 kHz (Table II, Fig. 2). The linearity of the observed trend (i.e., in dB with the logarithm of frequency) is notable. The mean false alarm rate for the sea lion was 0.14 (range: 0.06 – 0.23).

Critical ratios for both species were similar and showed a predictable increase of about 3 dB per octave with increasing frequency (Fig. 2). While there are no comparable data available for odobenid carnivores, these values are consistent with those previously reported for otariids at frequencies below 2 kHz (Southall et al., 2003, 2000). Critical ratios were higher than existing data for otariids at frequencies above 2 kHz (Moore and Schusterman, 1987; Southall et al., 2003). Validation data obtained for the human subject in the same test conditions generated frequency-dependent critical ratios (SuppPub1) that were within a few dB of most previously published values (Hawkins and Stevens, 1950; Hienz and Sachs, 1987; Houtsma, 2005). Therefore, the results obtained in this masking study can be considered comparable to those obtained in traditional auditory testing conditions.

### *Theoretical Lowest Threshold Values*

Ambient thresholds that were likely constrained by environmental noise were revealed through *post hoc* comparison to theoretical lowest threshold values (Fig. 3). For walruses, ambient thresholds at frequencies from 0.08 to 10 kHz were similar to the corresponding theoretical values, suggesting that measured thresholds in this range were masked by background noise. At 16 kHz, ambient thresholds for both walrus subjects were well above theoretical lowest values, indicating that these were valid measurements of absolute hearing sensitivity. For the sea lion, ambient hearing thresholds from 1 to 16 kHz were similar to theoretical lowest values. At lower and higher frequencies, ambient thresholds exceeded theoretical lower limits and were not influenced by ambient noise. For the human subject, measured thresholds < 8 kHz were masked in outdoor ambient conditions based on comparison to theoretical lowest threshold values.

## Discussion

### *Hearing in Ambient Conditions*

Auditory thresholds were measured with a California sea lion in ambient outdoor conditions to provide information for subsequent masking experiments. These ambient thresholds followed expected trends in sensitivity across the frequency range of hearing. Thresholds were elevated at some frequencies relative to those previously measured for the same subject in the quiet conditions of an hemi-anechoic chamber (Reichmuth et al., 2017) and those obtained for another sea lion tested using headphones in semi controlled conditions (Mulsow et al., 2011). Comparison of these datasets indicates that background noise in the outdoor testing environment predictably constrained hearing thresholds in this study from 0.5 to 10 kHz. There was near-perfect correspondence between the thresholds reported here and those measured for the same individual in quiet conditions at 0.1 kHz (the lowest frequency previously tested), 16 kHz (in the range of best hearing), and 32 kHz (the highest frequency tested). Hearing at 32 kHz was also similar to that measured by (Mulsow et al., 2011). While no comparative auditory data were available below 0.1 kHz, the measured threshold of 83 dB re 20 μPa at 0.08

kHz follows the subject's previously reported low-frequency roll off (Reichmuth et al., 2017).

*Post-hoc* evaluation of theoretical lowest thresholds derived from ambient noise and critical ratios confirmed that hearing thresholds for the sea lion from 0.5 to 10 kHz were masked, while hearing thresholds at 0.08, 0.1, 0.2 and 32 kHz were absolute (unmasked) measures of hearing. The lowest ambient threshold of 4 dB re 20 µPa at 16 kHz was near the theoretical limit but is assumed to be an absolute measure of hearing due given the direct agreement with data for the same subject obtained in quiet conditions (Reichmuth et. al. 2017). These absolute and masked auditory thresholds conform to available and predicted data for this individual and for this better-studied species, validating the behavioral audiometric approach taken here. Thus, findings for the California sea lion increase confidence in the interpretation of hearing and masking data collected using the same methods for the walruses in this study.

Ambient threshold data for walruses collected in outdoor conditions are consistent with the few available auditory data reported for trained (Kastelein et al., 1996a) and free-ranging walruses (Kastelein et al., 1993). The better sensitivity values measured for the individuals in this study may be attributable to methodological differences or lower background noise levels. Even so, ambient thresholds for the walruses in the present student were constrained by background noise at all frequencies except 16 kHz—based on comparison to theoretical lowest thresholds. Thus, walrus absolute hearing thresholds at and below 10 kHz are expected to be lower than the values reported here. Thresholds at 16 kHz are well above the noise and are unmasked, capturing the high-frequency roll-off in auditory sensitivity for these individuals. The apparently poor high-frequency hearing ability of these walruses is consistent with findings from Reichmuth et al. (2020) and Kastelein et al. (2002) that suggest an upper-frequency limit of hearing near 20 kHz in air and water for this species. This upper-frequency limit is lower than for phocid and otariid pinnipeds, as well as terrestrial carnivores that hear up to at least 30 kHz (Fay, 1988; Heffner and Heffner, 2008; Reichmuth et al., 2013). This corresponds well with the bandwidth of aerial sound production in walruses (from 0.2 to at least 20 kHz) (Charrier, 2010; Miller, 1985). Anatomical studies confirm adaptations, such as hypertrophy of the ossicular bones and a large interaural distance (Kastelein et al., 1996b; Nummela, 2008), that may constrain high-frequency hearing ability and potentially improve hearing at lower frequencies. In fact, despite background noise being higher in the walrus testing environment, walrus ambient thresholds were 9 dB lower than the sea lion's absolute threshold at 0.08 kHz and 14 dB lower at 0.1 kHz. Given that walrus hearing thresholds were noise limited below 16 kHz, it is possible that their true low-frequency hearing ability is even better than described here.

For all three subjects, elevated ambient thresholds at most frequencies highlight the necessity of using specialized sound-attenuating facilities to fully characterize absolute hearing sensitivity. Such quiet conditions, however, are not required to effectively evaluate auditory masking.

### *Hearing in Noise*

Reliable masked hearing measurements were obtained in ambient outdoor conditions by artificially elevating and flattening the noise floor over which audiometric signals were presented. This made it possible to evaluate walrus hearing in a zoological facility without a specialized environment for audiometric testing. This approach was validated with critical ratios collected for a person that were consistent with data previously reported for human subjects (as shown in SuppPub1).

Critical ratio values for the marine mammal subjects were comparable to or higher than those previously published for other otariids and were more similar to those of terrestrial carnivores than to phocid seals (see Erbe et al., 2016; Fay, 1988; Reichmuth, 2012). Despite demonstrated differences in overall hearing sensitivity for sea lions and walruses, the ability to detect signals in noise was similar for both species. Furthermore, critical ratios for these subjects were generally comparable to published data for mammalian species including other otariids, terrestrial carnivores, (Erbe et al., 2016; Fay, 1988; Hawkins and Stevens, 1950; see SuppPub1), though they were slightly (5 dB) higher relative to those reported for phocid seals (see Erbe et al., 2016). The sea lion dataset reported here provides masking information across a wider frequency span than was previously available for otariids, supplementing the limited available data for this group. In particular, this study provides previously unavailable masking data for otariids at lower frequencies (< 500 Hz), and the only data for auditory masking in odobenid carnivores. Overall, good agreement across a variety of mammalian species of differing sizes and degrees of evolutionary relatedness indicates that many have evolved similarly in terms of their ability to extract signals from noise, despite species differences in absolute hearing sensitivity.

Several factors may help to reconcile the observed differences (highlighted in Fig. 2) between the critical ratio measurements presented here and those previously published for otariids (Moore and Schusterman, 1987; Southall et al., 2003, 2000). In the current study, critical ratios were obtained using equalized, spectrally white noise floors that exceeded environmental noise, which controlled for any variability within the octave band surrounding the test frequency. The equalization procedure precisely controlled the spectral ‘flatness’ of the masker, likely to a greater degree than in previous studies. While the present study used continuous rather than intermittent masking noise, there was no evidence of auditory fatigue or loudness adaptation based on within-session performance. The masking stimuli in the current study were set equal to or just above ambient threshold values, allowing signals to be presented at lower levels than in many other studies. Often, critical ratios are measured in the presence of noise that exceeds the subject's ambient or unmasked detection threshold by 10 – 20 dB (Holt and Schusterman, 2006; Reichmuth et al., 2013; Southall et al., 2003). The relatively quieter masker levels used in the present study ensured that audiometric stimuli were also of lower amplitude and minimized potential amplitude-related artifacts, such as transient harmonics or spectral splatter, that could result in artificially low masked thresholds.

### *Applications to Predicting Noise Effects*

Psychoacoustic measures of auditory masking are often based on detection of pure-tone stimuli in the presence of band-limited white noise, which is not necessarily representative of *in situ* listening scenarios. While this caveat remains true in the present study, theoretical lowest threshold calculations were able to approximate ambient detection thresholds for all three subjects listening in the complex noise conditions of their respective outdoor testing environments. In practice, critical ratios paired with ambient noise measurements likely provide a more accurate representation of hearing than absolute threshold measurements, because noise in most natural environments is usually high enough to influence hearing (Dooling and Blumenrath, 2013). Thus, masking parameters are particularly useful for understanding hearing in the real world. If ambient noise levels exceed absolute detection thresholds in a given environment—as they did at most frequencies in both test facilities used in this study—hearing thresholds for both walruses and sea lions could be determined based on noise measurements and critical ratios alone. In such sufficiently noisy environments, the agreement between walrus and sea lion critical ratio values would result in predicted thresholds to be similar for both species—despite apparent differences in their species-specific unmasked hearing limits. Further, as auditory masking is a cochlear phenomenon (at least in terms of the energetic masking tested here), it is independent of hearing pathway and medium (see Reichmuth, 2012; Erbe et al., 2016; Branstetter and Sills, 2022). As a result, critical ratios of amphibious marine mammals are the same in air and under water, despite their differences in absolute sensitivity between the two media (Renouf, 1980; Sills et al., 2014; Southall et al., 2003; Turnbull and Terhune, 1990). The masking data provided in this study can therefore be applied to estimate listening space, communication ranges, and zones of influence around human-generated noise sources in both aerial and underwater environments.

Using critical ratios paired with ambient noise measurements to predict what an individual can hear in a given environment is effective when applied to relatively stable noise backgrounds. However, this approach may overestimate the extent of masking when noise is spectrally complex, temporally structured, or highly variable (e.g., Branstetter and Sills, 2022; Erbe et al., 2016; Klump and Langemann, 1995). Empirical masking studies using complex signals in the presence of non-Gaussian noise can be used to better predict detection thresholds for animals operating in time-varying natural environments (see Branstetter et al., 2013; Cunningham et al., 2014b). Masking predictions can also be further enhanced through the measurement of critical bandwidth at which masking occurs and a better understanding of the effects of noise level on auditory masking.

### *Conclusions*

Among marine mammals, walruses have been understudied from the standpoint of hearing and noise. The present study includes confirmation of enhanced low-frequency hearing and constrained/limited high-frequency hearing in air and provides critical ratio measurements applicable in air or water across most of the hearing range. It is apparent that an absolute (completely unmasked) in-air audiogram for walruses would require testing in an acoustically controlled, artificially quiet environment. However, this method of estimating critical ratios in outdoor conditions—validated through testing of human and sea lion subjects—can be applied to collect masking data from species such as the walrus that cannot easily be tested in ideal conditions. As marine mammal hearing is often limited by ambient noise in nature, both in air and under water, a robust understanding of auditory masking is a conservation priority.

Despite apparent differences in hearing ability both species are similarly able to detect signals within sufficiently noisy conditions. Overall, placing odobenid with otariid carnivores in the same functional hearing group is a pragmatic, conservative management approach. However, additional protection may be warranted for walruses at low frequencies, where most anthropogenic noise occurs.

## Supplementary Material

See supplementary material for validation masking data with a human subject (SuppPub1) and spectra of the signals and maskers used for audiometry (SuppPub2).

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## Author Declarations

### *Conflict of Interest*

The authors have no conflicts of interest to disclose.

### *Ethics Approval*

Federal permission for access to the walruses was granted under public display authorization to SeaWorld San Diego by the United States Fish and Wildlife Service. Auditory trials were conducted with the approval of the Animal Welfare Committee at SeaWorld San Diego. Federal authorization for sea lion research was granted by the United States National Marine Fisheries Service under marine mammal research permits 18902 and 23554. Animal research at both facilities was conducted with approval and oversight by the Institutional Animal Care and Use Committee at the University of California Santa Cruz. The participation of the undergraduate student volunteer in auditory trials met the ethical criteria specified in the Belmont Report (1978).

## Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## REFERENCES

Babushina, Y. S., Zaslavski, G. L., and Yurkevich, L. I. (**1991**). "Air and underwater hearing characteristcs of the Northern fur seal: Audiograms, frequency and differential thresholds," Psychophysics, 36, 909–913.

Berta, A., Churchill, M., and Boessenecker, R. W. (**2018**). "The origin and evolutionary biology of pinnipeds: Seals, sea lions, and walruses," Annu. Rev. Earth Planet. Sci., 46, 203–228. doi:10.1146/annurev-earth-082517-010009

Boessenecker, R. W., and Churchill, M. (**2018**). "The last of the desmatophocid seals: A new species of Allodesmus from the upper Miocene of Washington, USA, and a revision of the taxonomy of Desmatophocidae," Zool. J. Linn. Soc., 184, 211–235. doi:10.1093/zoolinnean/zlx098

Bonnell, M. L., and Ford, R. G. (**1987**). "California sea lion distribution : A statistical analysis of aerial transect data" 28-06," J. Wildl. Manage., 51, 13–20.

Branstetter, B. K., and Sills, J. M. (**2022**). "Mechanisms of auditory masking in marine mammals," Anim. Cogn., doi: 10.1007/s10071-022-01671-z.

Charrier, I., Aubin, T., & Mathevon, N. (**2010**). Mother–calf vocal communication in Atlantic walrus: a first field experimental study. Anim. Cog., 13, 471-482.

Charrier, I. (**2021**). "Vocal communication in otariids and odobenids. In Ethology and behavioral ecology of otariids and the odobenid" (pp. 265-289). Cham: Springer International Publishing.

Cunningham, K. A., Hayes, S. A., Michelle Wargo Rub, A., and Reichmuth, C. (**2014a**). "Auditory detection of ultrasonic coded transmitters by seals and sea lions," J. Acoust. Soc. Am., 135, 1978–1985. doi:10.1121/1.4868371

Cunningham, K. A., and Reichmuth, C. (**2016**). "High-frequency hearing in seals and sea lions," Hear. Res., 331, 83–91. doi:10.1016/j.heares.2015.10.002

Cunningham, K. A., Southall, B. L., and Reichmuth, C. (**2014b**). "Auditory sensitivity of seals and sea lions in complex listening scenarios," J. Acoust. Soc. Am., 136, 3410–3421. doi:10.1121/1.4900568

Dooling, R. J., and Blumenrath, S. H. (**2013**). "Avian sound perception in noise," In H. Brumm (Ed.), Anim. Commun. Noise. Anim. Signals Commun., Springer Berlin Heidelberg, pp. 229–250. doi:10.1007/978-3-642-41494-7

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (**2016**). "Communication masking in marine mammals: A review and research strategy." Marine pollution bulletin, 103(1-2), 15-38.

Fay, F. H. (**1982**). "Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens*" Illiger. North American Fauna, (74), 1-279.

Fay, R. R. (**1988**). "Comparative psychoacoustics," Hear. Res., 34, 295–306. doi:0378-5955

Finneran, J. J. (**2003**). "An integrated computer-controlled system for marine mammal auditory testing." SSC San Diego, San Diego, CA, 1-107.

Finneran, J. J. (**2015**). "Noise-induced hearing loss in marine mammals: A review of temporary threshold shift studies from 1996 to 2015," J. Acoust. Soc. Am., 138, 1702–1726. doi:10.1121/1.4927418

Hanke, F. D., & Reichmuth, C. (**2022**). "Phocid sensory systems and cognition." In Ethology and behavioral ecology of phocids (pp. 31-68). Cham: Springer International Publishing.

Hanke, F. D., Reichmuth, C., & Cook, P. (**2021**). "The sensory world of otariids." In Ethology and Behavioral Ecology of Otariids and the Odobenid (pp. 305-321). Cham: Springer International Publishing.

Hawkins, T. E., and Stevens, S. S. (**1950**). "The masking of pure tones and of speech by white noise," J. Acoust. Soc. Am., 22, 6–13. doi:10.1121/1.1906581

Heffner, H. E., and Heffner, R. S. (**2008**). "High-frequency hearing," Handb. Senses

Audit., pp. 55–60.

Hienz, R. D., and Sachs, M. B. (**1987**). "Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) and pigeons (*Columba livia*).," J. Comp. Psychol., 101, 16–24. doi:10.1037/0735-7036.101.1.16

Holt, M. M., and Ronald J. Schusterman (**2006**). "Spatial release from masking of aerial tones in pinnipeds," J. Acoust. Soc. Am., , doi: 10.1121/1.2404929. doi:10.1121/1.2404929

Houser, D. S. (**2021**). "When is temporary threshold shift injurious to marine mammals?," J. Mar. Sci. Eng., 9 (7), 757 , doi:10.3390/jmse9070757

Houtsma, A. J. M. (**2005**). "A note on pure-tone masking by broadband noise under free-field and insert-phone conditions (L)," Cit. J. Acoust. Soc. Am., 117, 490. doi:10.1121/1.1841611

Kastak, D., and Schusterman, R. J. (**1998**). "Low-frequency amphibious hearing in pinnipeds: Methods, measurements, noise, and ecology," J. Acoust. Soc. Am., 103, 2216–2228. doi:10.1121/1.421367

Kastak, D., and Schusterman, R. J. (**2002**). " Changes in auditory sensitivity with depth in a free-diving California sea lion (*Zalophus californianus*) ," J. Acoust. Soc. Am., 112, 329–333. doi:10.1121/1.1489438

Kastelein, R. A., Mosterd, P., van Ligtenberg, C. L., and Verboom, W. C. (**1996a**). "Aerial hearing sensitivity tests with a male Pacific walrus (*Odobenus rosmarus divergens*), in the free field and with headphones," Aquat. Mamm., 22, 81–93.

Kastelein, R. A., Mosterd, P., van Santen, B., Hagedoorn, M., and de Haan, D. (**2002**). "Underwater audiogram of a Pacific walrus (*Odobenus rosmarus divergens*) measured with narrow-band frequency-modulated signals ," J. Acoust. Soc. Am., 112, 2173–2182. doi:10.1121/1.1508783

Kastelein, R. A., van Schie, R., Verboom, W. C., and de Haan, D. (**2005**). " Underwater hearing sensitivity of a male and a female Steller sea lion (*Eumetopias jubatus*)," J.

Acoust. Soc. Am., 118, 1820–1829. doi:10.1121/1.1992650

Kastelein, R. a, Van Ligtenberg, C. L., Gjertz, I., and Verboom, W. C. (**1993**). "Free field hearing tests on wild Atlantic walruses (*Odobenus rosmarus rosmarus*) in air," Aquat. Mamm., 19, 143–148.

Kastelein, R., Dubbeldam, J., M.A.G, de B., and Gerrits N.M. (**1996b**). "The anatomy of the walrus head (*Odobenus rosmarus*). Part 4: The ears and their function in aerial and underwater hearing," Aquat. Mamm., 22.2, 95–125.

Miller, E. H. (**1985**). "Airborne acousitic communication in the walrus *Odobenus rosmarus*" Natl. Geogr. Res., 1, 124–145.

Mooney, T. A., Yamato, M., and Branstetter, B. K. (**2012**). "Hearing in cetaceans: From natural history to experimental biology", Adv. Mar. Biol., Elsevier Ltd., 1st ed., Vol. 63, 197–246 pages. doi:10.1016/B978-0-12-394282-1.00004-1

Moore, P. W., & Schusterman, R. J. (**1987**). "Audiometric assessment of Northern fur seals, *Callorhinus ursinus*." Mar. Mammal Sci., 3(1), 31-53.

Mouy, X., Hannay, D., Zykov, M., & Martin, B. (**2012**). "Tracking of Pacific walruses in the Chukchi Sea using a single hydrophone." J. of the Acoust. Soc. of Am., 131(2), 1349-1358.

Mulsow, J., Finneran, J. J., Houser, D. S., Street, H., Diego, S., and Houser, D. S. (**2011**). "California sea lion (*Zalophus californianus*) aerial hearing sensitivity measured using auditory steady-state response and psychophysical methods," , doi: 10.1121/1.3552882.

Mulsow, J., and Reichmuth, C. (**2010**). " Psychophysical and electrophysiological aerial audiograms of a Steller sea lion (*Eumetopias jubatus*) ," J. Acoust. Soc. Am., 127, 2692–2701. doi:10.1121/1.3327662

Mulsow, J., Reichmuth, C., Houser, D., Houser, D., and Finneran, J. J. (**2012**). "Auditory evoked potential measurement of hearing sensitivity in pinnipeds 3: Development of noninvasive audiometric methods," Adv. Exp. Med. Biol., 730, 978–1.

doi:10.1007/978-1-4419-7311-5

Nummela, S. (**2008**). "Hearing in aquatic mammals," Sens. Evol. Treshold Adapt. Second. Aquat. Vertebr., pp. 211–224.

Rawdon Smith, A. F. (**1934**). "Auditory fatigue," Br. J. Psycology, 1, 77–85.

Reichmuth, C. (**2012**). "Psychophysical studies of auditory masking in marine mammals: Key concepts and new directions.," Adv. Exp. Med. Biol., 730, 23–27. doi:10.1007/978-1-4419-7311-5_4

Reichmuth, C., Holt, M. M., Mulsow, J., Sills, J. M., and Southall, B. L. (**2013**). "Comparative assessment of amphibious hearing in pinnipeds," J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol., 199, 491–507. doi:10.1007/s00359-013-0813-y

Reichmuth, C., Sills, J. M., Brewer, A., Triggs, L., Ferguson, R., Ashe, E., and Williams, R. (**2020**). "Behavioral assessment of in-air hearing range for the Pacific walrus (*Odobenus rosmarus divergens*)," Polar Biol., 43, 767–772. doi:10.1007/s00300-020-02667-6

Reichmuth, C., Sills, J. M., and Ghoul, A. (**2017**). "Psychophysical audiogram of a California sea lion listening for airborne tonal sounds in an acoustic chamber," Proc. Meet. Acoust., , doi: 10.1121/2.0000525. doi:10.1121/2.0000525

Reichmuth, C., and Southall, B. L. (**2012**). "Underwater hearing in California sea lions (*Zalophus californianus*): Expansion and interpretation of existing data," Mar. Mammal Sci., 28, 358–363. doi:10.1111/j.1748-7692.2011.00473.x

Repenning, C. A. (**1972**). "Underwater hearing in seals: Functional morphology," Funct. Anat. Mar. Mamm., United States Geological Survey, Branch of Paleontology and Stratigraphy, Menlo Park, California, USA, pp. 307–331.

Schusterman, R. J. (**1974**). "Auditory sensitivity of a California sea lion to airborne sound," J. Acoust. Soc. Am., 56, 1248–1251.

Schusterman, R. J., and Balliet, R. F. (**1969**). "Underwater barking by male sea lions (*Zalophus californianus*)," Nature,. doi:10.1038/2221179a0

Schusterman, R. J., Balliet, R. F., and Nixon, J. (**1972**). "Underwater audiogram of the California sea lion by the conditioned vocalization technique," J. Exp. Anal. Behav., 17, 339–350. doi:10.1901/jeab.1972.17-339

Sills, J. M., Southall, B. L., and Reichmuth, C. (**2014**). "Amphibious hearing in spotted seals (*Phoca largha*): underwater audiograms, aerial audiograms and critical ratio measurements," , doi: 10.1242/jeb.097469.

Sills, J. M., Southall, B. L., and Reichmuth, C. (**2017**). "The influence of temporally varying noise from seismic air guns on the detection of underwater sounds by seals," J. Acoust. Soc. Am., 141, 996–1008. doi:10.1121/1.4976079

Southall, B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., et al. (**2019**). "Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects," Aquat. Mamm., 45, 125–232. doi:10.1578/AM.45.2.2019.125

Southall, B. L., Schusterman, R. J., and Kastak, D. (**2000**). "Masking in three pinnipeds: Underwater, low-frequency critical ratios," J. Acoust. Soc. Am., 108, 1322. doi:10.1121/1.1288409

Southall, B. L., Schusterman, R. J., and Kastak, D. (**2003**). "Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements," J. Acoust. Soc. Am., 114, 1660–1666. doi:10.1121/1.1587733

Stebbins, W. C. (**1970**). "Principles of animal psychophysics," In W. C. Stebbins (Ed.), Anim. Psychophys. Des. Conduct Sens. Exp., Appleton-Century-Crofts, New York, pp. 1–19.

Turnbull, S. D., & Terhune, J. M. (**1990**). White noise and pure tone masking of pure tone thresholds of a harbour seal listening in air and underwater. Can. J. Zoo., 68(10), 2090-2097.

## Chapter 1: Auditory Masking in Odobenid and Otariid Carnivores

Figures, tables, and figure captions

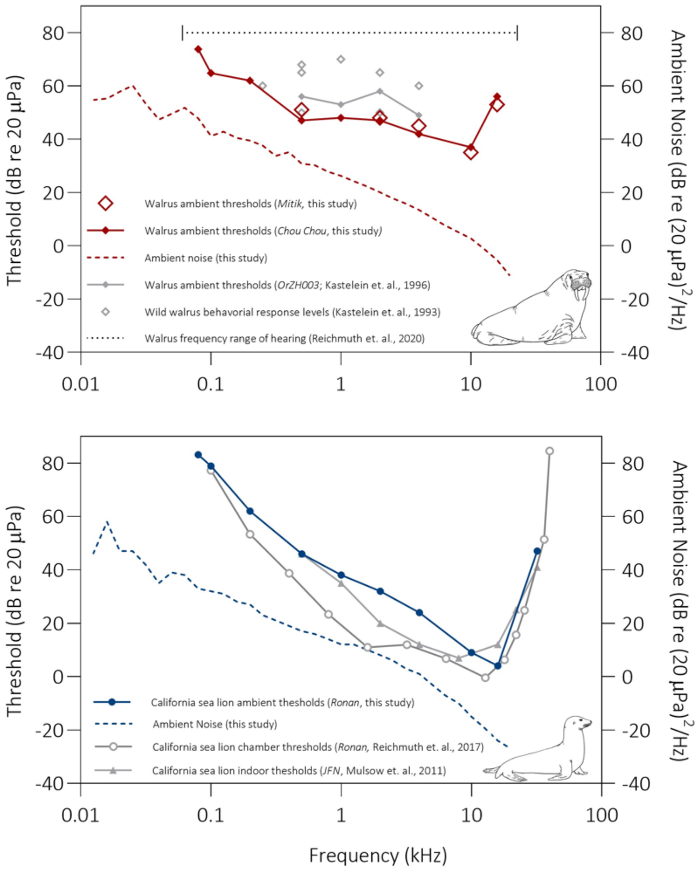


FIG 1. (Color online). Ambient hearing thresholds are shown for two Pacific walruses (*Chou Chou*, *Mitik*, upper panel) and one California sea lion (*Ronan*, lower panel) for frequencies between 0.08 and 16 kHz or 32 kHz, respectively. Associated mean noise levels (L50) are plotted as dashed lines corresponding to the right-hand y-axes. For comparison to the walrus data, ambient thresholds collected previously with a single adult male walrus (Kastelein et al., 1996), behavioral response measurements with wild walruses (Kastelein et al., 1993; n=5), and the frequency range of hearing for two adult female walruses at 80 dB (Reichmuth et al., 2020; n=2) are provided. For comparison to the sea lion data, absolute (unmasked) thresholds measured in a hemi-anechoic chamber are shown for the same sea lion subject (Reichmuth et al., 2017) along with data collected with another individual in a controlled environment (Mulsow et al., 2011).

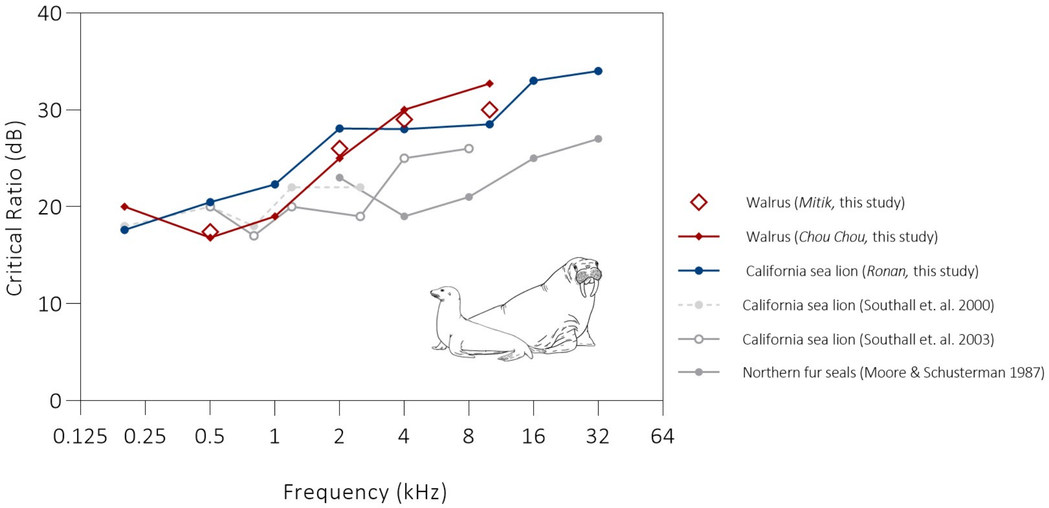


FIG 2. (Color online). Auditory critical ratios measured in air for two Pacific walruses (*Chou Chou*, *Mitik*) and one California sea lion (*Ronan*) for frequencies between 0.2 and 10 or 32 kHz, respectively. Also shown are critical ratios reported previously for otariids: California sea lions (Southall et al., 2000, n=1; Southall et al., 2003, n=1) and northern fur seals (Moore and Schusterman, 1987; n=2).

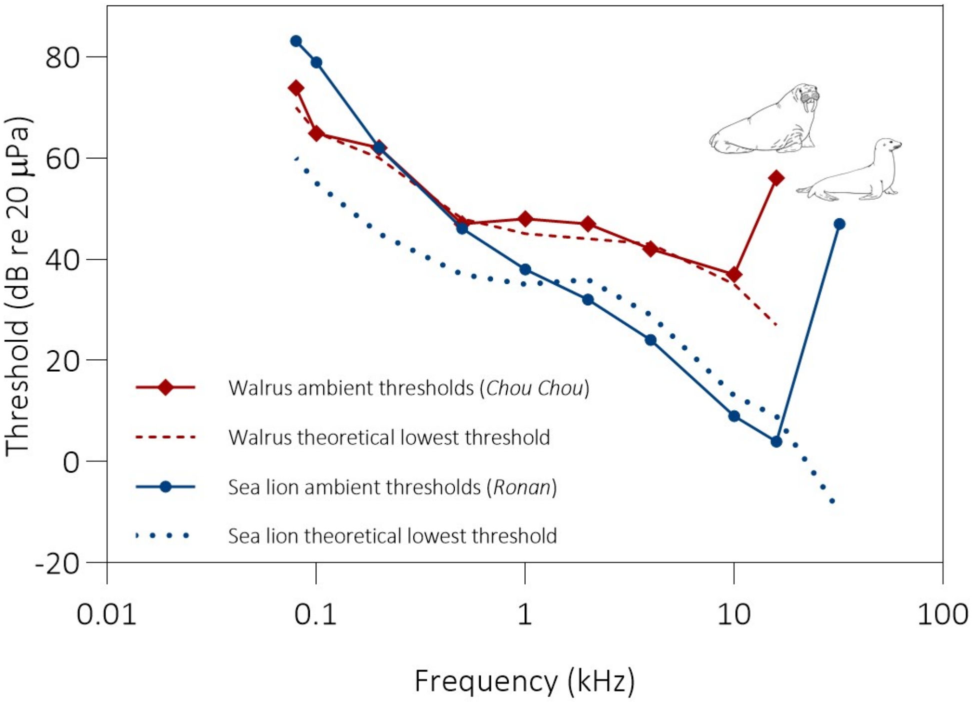


**FIG 3.** Ambient hearing thresholds are shown for Pacific walrus *Chou Chou* and California sea lion *Ronan* for frequencies between 0.08 and 16 or 32 kHz, respectively. Theoretical lowest thresholds calculated by adding the ambient noise spectral density level to the critical ratio measured at each test frequency are shown as dotted or dashed lines. Theoretical lowest thresholds at 0.1 and 0.08 were estimated by extrapolation from critical ratio data collected at higher frequencies. Thresholds that fall above their corresponding dashed lines are more likely to reflect absolute hearing sensitivity; those that fall near or below the dotted line are likely constrained by background noise.

**TABLE I.** Ambient hearing thresholds for airborne tones for two Pacific walruses (*Chou Chou, Mitik)* and one California sea lion (*Ronan*), along with corresponding false alarm rates and noise levels in the outdoor testing environment. Detection thresholds at each frequency were calculated as the average of the hit-to-miss transitions[a]. False alarm rates were calculated as the proportion of responses on signal-absent trials (>25 trials per frequency). Ambient noise levels in the third-octave band surrounding the test frequency were measured prior to each session and are presented as median (50th percentile) spectral density levels.

| Species | Subject | Tone frequency | Test order | Ambient noise | Outdoor ambient threshold | Standard deviation | Hit-to-miss transitions | False alarm rate | Threshold-to-noise offset |
|---|---|---|---|---|---|---|---|---|---|
| | | kHz | | dB re (20 μPa)$^2$/Hz | dB re 20 μPa | | n | | dB |
| Pacific walrus | *Chou Chou* | 0.08 | 9 | 48 | 74 | 1.7 | 15 | 0.21 | 26 |
| | | 0.1 | 8 | 41 | 65 | 2.0 | 15 | 0.22 | 24 |
| | | 0.2 | 3 | 40 | 62 | 3.0 | 10 | 0.24 | 22 |
| | | 0.5 | 5 | 31 | 47 | 1.5 | 10 | 0.18 | 16 |
| | | 1 | 2 | 26 | 48 | 1.4 | 9 | 0.22 | 22 |
| | | 2 | 7 | 20 | 47 | 1.0 | 12 | 0.06 | 27 |
| | | 4 | 4 | 14 | 43 | 1.5 | 10 | 0.19 | 29 |
| | | 10 | 1 | 3 | 37 | 1.2 | 9 | 0.06 | 34 |
| | | 16 | 6 | -6 | 57 | 1.3 | 10 | 0.10 | 63 |
| | *Mitik* | 0.5 | 2 | 31 | 51 | 1.2 | 13 | 0.27 | 20 |
| | | 2 | 4 | 20 | 48 | 1.0 | 10 | 0.15 | 28 |
| | | 4 | 1 | 14 | 45 | 1.3 | 12 | 0.18 | 31 |
| | | 10 | 5 | 3 | 35 | 1.3 | 10 | 0.21 | 32 |
| | | 16 | 3 | -6 | 53 | 1.2 | 15 | 0.23 | 59 |
| California sea lion | *Ronan* | 0.08 | 10 | 33 | 83 | 1.3 | 15 | 0.19 | 50 |
| | | 0.1 | 7 | 32 | 79 | 2.1 | 15 | 0.25 | 47 |
| | | 0.2 | 3 | 27 | 62 | 2.7 | 15 | 0.13 | 35 |
| | | 0.5 | 6 | 17 | 46 | 0.9 | 15 | 0.07 | 29 |
| | | 1 | 2 | 12 | 38 | 2.5 | 15 | 0.08 | 26 |
| | | 2 | 8 | 8 | 32 | 1.8 | 15 | 0.12 | 24 |
| | | 4 | 4 | 1 | 24 | 1.2 | 15 | 0.22 | 23 |
| | | 10 | 1 | -15 | 9 | 2.0 | 15 | 0.13 | 24 |
| | | 16 | 5 | -24 | 4 | 1.3 | 15 | 0.13 | 28 |
| | | 32 | 9 | < 0 | 47 | 1.3 | 15 | 0.11 | > 47 |

[a] Initial ambient threshold measurements at 4 kHz were unexpectedly high for both walrus subjects. Testing at this frequency was repeated for both subjects after the completion of primary data collection.

**TABLE II.** Masked in-air hearing thresholds and critical ratios for two Pacific walruses (*Chou Chou, Mitik)* and one California sea lion (*Ronan*), shown with false alarm rates and spectral density levels for flat-spectrum, octave-band masking noise. Masker spectral density level for each frequency was set at or +5 dB above the corresponding ambient threshold for each subject.[b] Masked thresholds were calculated as the average of the hit-to-miss transitions. False alarm rates were calculated as the proportion of responses on signal-absent trials (>37 trials per frequency).

| Species | Subject | Tone frequency | Test order | Masker level | Masked threshold | Standard deviation | Hit-to-miss transitions | False alarm rate | Critical ratio |
|---|---|---|---|---|---|---|---|---|---|
|  |  | kHz |  | dB re (20 μPa)$^2$/Hz | dB re 20 μPa |  | n |  | dB |
| Pacific walrus | *Chou Chou* | 0.2 | 3 | 62 | 82 | 1.5 | 15 | 0.26 | 20 |
|  |  | 0.5 | 5 | 52 | 69 | 1.5 | 15 | 0.20 | 17 |
|  |  | 1 | 2 | 48 | 66 | 1.7 | 15 | 0.21 | 19 |
|  |  | 2 | 6 | 47 | 71 | 1.5 | 15 | 0.21 | 25 |
|  |  | 4 | 4 | 57 | 87 | 1.4 | 15 | 0.29 | 30 |
|  |  | 10 | 1 | 37 | 69 | 2.0 | 15 | 0.24 | 32 |
|  | *Mitik* | 0.5 | 2 | 56 | 73 | 1.4 | 15 | 0.17 | 17 |
|  |  | 2 | 3 | 48 | 74 | 1.0 | 15 | 0.22 | 26 |
|  |  | 4 | 1 | 45 | 86 | 1.5 | 15 | 0.22 | 29 |
|  |  | 10 | 4 | 35 | 65 | 1.5 | 15 | 0.24 | 30 |
| California sea lion | *Ronan* | 0.2 | 3 | 62 | 80 | 0.9 | 15 | 0.14 | 18 |
|  |  | 0.5 | 6 | 52 | 72 | 1.8 | 15 | 0.13 | 20 |
|  |  | 1 | 2 | 38 | 60 | 1.6 | 15 | 0.19 | 23 |
|  |  | 2 | 7 | 38 | 66 | 1.7 | 15 | 0.09 | 28 |
|  |  | 4 | 4 | 24 | 53 | 1.8 | 15 | 0.18 | 28 |
|  |  | 10 | 1 | 9 | 37 | 1.3 | 15 | 0.23 | 28 |
|  |  | 16 | 5 | 9 | 42 | 1.3 | 15 | 0.14 | 33 |
|  |  | 32 | 8 | 46 | 80 | 1.0 | 15 | 0.06 | 34 |

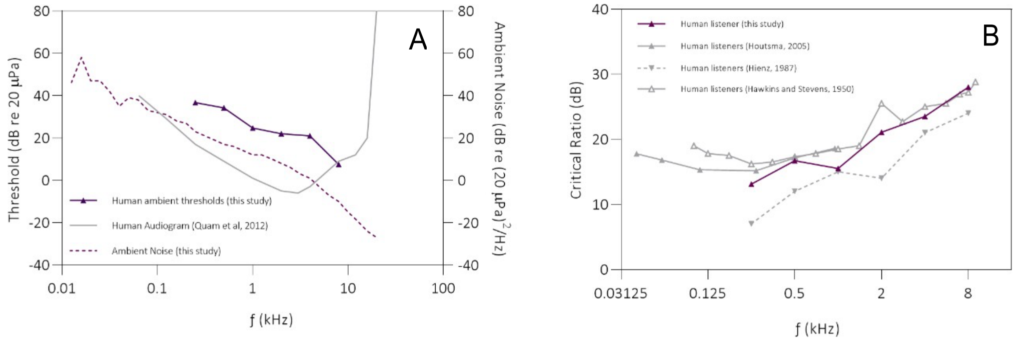
[b] The masking noise target spectral density level at 4 kHz was set based on initial (unexpectedly high) ambient threshold measurements for walrus *Chou Chou* and was therefore 14 dB higher than the reported ambient threshold. This masker level is not expected to influence the corresponding critical ratio value.

## Auditory masking in odobenid and otariid carnivores

*The Journal of the Acoustical Society of America*

Ryan A. Jones, Jillian M. Sills, Mitzi Synnott, Jason M. Mulsow, Rob Williams, and Colleen Reichmuth

**Supplement 1.** Comparative ambient hearing thresholds and critical ratio data for a human subject



The hearing capabilities of one adult male human subject were measured to validate the audiometric procedure used in this study. The undergraduate student volunteer was tested with the same equipment and psychophysical methods as those applied with the walrus and California sea lion subjects, and in the same outdoor testing environment that was used for the sea lion at Long Marine Laboratory in Santa Cruz, California. The subject was 21 years old with apparently normal hearing. His participation met the ethical criteria specified in the Belmont Report.[1]

**Panel A.** Ambient hearing thresholds are provided for the human subject, along with a composite human audiogram measured in an acoustic chamber. Auditory data are shown on the left y-axis and corresponding background noise levels from the present study are shown on the right y-axis. The subject's ambient hearing thresholds were largely constrained by environmental noise in the outdoor testing facility. The threshold measured at 8 kHz was consistent with published data collected in a quiet environment and likely reflects absolute hearing sensitivity. Thresholds at 0.25, 0.5, 1, and 4 kHz were approximately one critical ratio above the ambient noise, and thus are assumed to be masked.

**Panel B.** Auditory critical ratios for the human subject. Masked thresholds were measured outdoors at 0.25, 0.5, 1, 2, 4, and 8 kHz in the presence of octave-band, spectrally flat noise set 5 dB above the corresponding ambient hearing threshold. Critical ratios were calculated as the difference between the SPL of the masked threshold and the PSD of the masking noise. Critical ratio values were 13, 17, 15, 21, 23, and 28 dB at the ascending target frequencies. Critical ratios increased predictably with frequency and were consistent with data published for other human subjects.[2,3,4] The consistency between the critical ratio data collected here and critical ratio values published previously for human subjects validate the experimental approach taken in this study. These findings confirm that accurate measures of auditory masking in outdoor facilities are possible with calibrated and spectrally-flattened masking stimuli that exceed the ambient noise background.

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[1] Quam, R., Ramsier, M., Fay, R., and Popper, A. (**2017**). *Primate Hearing and Communication*, Vol. 63, 141–174 pages. Retrieved from http://link.springer.com/10.1007/978-3-319-59478-1

[2] Hawkins, T. E., and Stevens, S. S. (**1950**). "The Masking of Pure Tones and of Speech by White Noise," J. Acoust. Soc. Am., **22**, 6–13. doi:10.1121/1.1906581

[3] Hienz, R. D., and Sachs, M. B. (**1987**). "Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater)* and pigeons (*Columba livia*)," J. Comp. Psychol., **101**, 16–24. doi:10.1037/0735-7036.101.1.16

[4] Houtsma, A. J. M. (**2005**). "A note on pure-tone masking by broadband noise under free-field and insert-phone conditions (L)," J. Acoust. Soc. Am., **117**, 490–491. doi:10.1121/1.1841611

**Auditory masking in odobenid and otariid carnivores**

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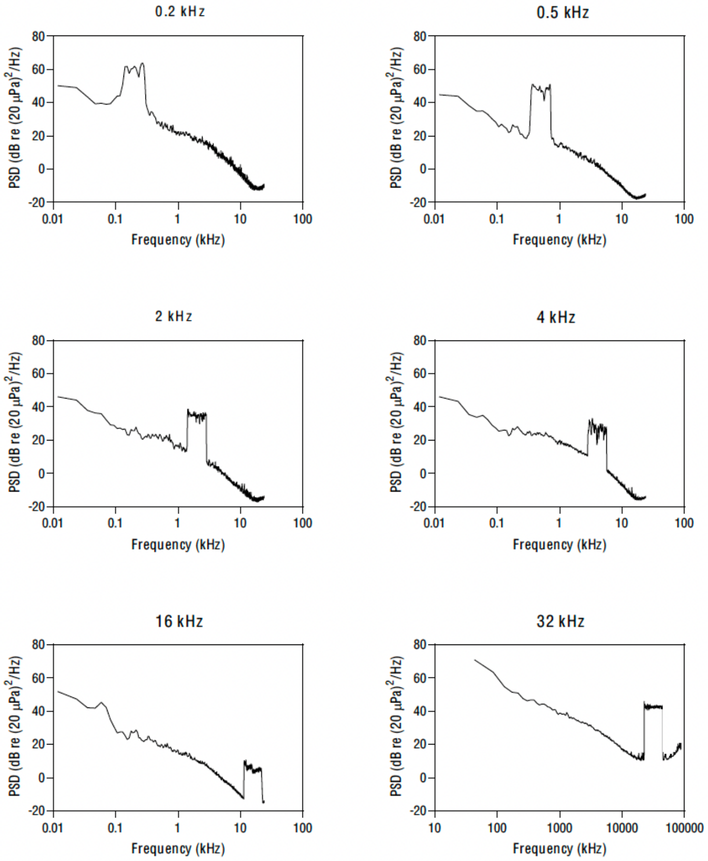
Ryan A. Jones, Jillian M. Sills, Mitzi Synnott, Jason M. Mulsow, Rob Williams, and Colleen Reichmuth

**Supplement 2b.** Representative masker spectra used in audiometry. Spectrally flattened octave-band masking noise centered at the test frequency was recorded at the calibration position in the absence of the subject. Maskers were recorded at representative levels used for the California sea lion. Spectra are plotted from .wav recordings using a hamming window and an FFT size of 4096. Maskers are shown within the actual ambient noise background of the testing environment at Long Marine Laboratory.



# Chapter 2: Direct Critical Bandwidth Measurements in Pinnipeds

## Abstract

Auditory masking occurs when one sound interferes with the detection of another. While knowledge of this sensory phenomenon is growing, much of our understanding is theoretical or based on terrestrial models. Empirical data become especially important when considering hearing in marine mammals that are largely reliant on acoustic cues for foraging, communication, and avoiding predation. To better understand how anthropogenic noise can influence hearing in otariid, odobenid, and phocid pinnipeds, detection thresholds for tonal sounds were measured for a trained California sea lion, Pacific walrus, and bearded seal within noise of progressively constrained spectral content. The frequency bandwidth of noise that contributed to the masking of a given tone (the 'critical bandwidth') was identified at up to seven frequencies across the functional hearing range of each individual. These data confirmed that absolute critical bandwidth values increased with increasing frequency, although species-level trends were apparent. The sea lion and walrus subjects were shown to be similarly adapted to hearing in noise. The seal critical bandwidths were narrower, suggesting additional auditory specialization—particularly at lower frequencies.

Key words: Masking, frequency resolution, constant Q, sea lion, walrus, seal

## Introduction

Animals that rely on sound for various life processes must be able to efficiently extract relevant acoustic cues from their environment. This environment is often saturated with competing biotic (animal-produced) and abiotic (environmental or anthropogenic) noise that may limit an individual's ability to hear important sounds. Mammals in particular have developed complex and sensitive auditory systems that allow them to thrive in acoustically dynamic environments. The frequency selectivity of the mammalian auditory system is fundamental to this group's overall high auditory acuity. Functionally, the mammalian ear segregates incoming acoustic signals into a series of overlapping bandpass filters (Fletcher, 1940). The frequency span of each auditory filter determines the listener's degree of frequency selectivity. The detectability of a given signal is only impeded, or masked, by competing noise that falls within the upper and lower cutoff frequencies of the relevant auditory filter—that is, the spectral region termed the critical bandwidth. Comparative studies that include such frequency-dependent metrics improve our understanding of auditory masking and thus our ability to predict the noise conditions in which it occurs.

Predictive models of auditory masking rely on frequency-dependent parameters that are appropriate for a given species or species grouping. Among mammals, these masking parameters vary depending on the level of specialization for processing certain target signals. For example, bats and dolphins show a high degree of frequency specificity corresponding to the ultrasonic spectral range relevant to biosonar (Moss et al., 2023). In contrast, most carnivores seem to be generalists, with no apparent frequency-specific specialization for hearing in noise (*see* Fay, 1988).

Critical bandwidths and critical ratios are the frequency-dependent parameters most relevant to auditory masking. When combined with the traditional power spectrum model of masking (*see* Erbe et al., 2016; Moore, 1993), these metrics can be used to predict how specific noise sources will interfere with the detection of important sounds. This approach generates reasonable masking estimates for signal and noise sources that are relatively stable over time (*see*, e.g., Dooling et al., 2013; Branstetter et al., 2013; Sills et al., 2017; Jones et al., 2023).

Critical ratios, the signal-to-noise ratios required for detection of tonal signals embedded in wide-band, spectrally flat noise, can be measured relatively easily with trained subjects. In contrast, direct critical bandwidth measurements require significantly more experimental effort. As a result, critical bandwidths are often estimated in place of direct measurements. Fletcher (1940) proposed the equal power assumption of masking, which suggests that critical bands can be calculated indirectly using the following equation (01):

$$It \ = \ kN_0 \, x \, \Delta \mathrm{f}$$

where the intensity of the tone at threshold ($I_t$) is equal to a constant (k) multiplied by the noise spectral density at threshold ($N_0$) and the bandwidth of the auditory filter at the tone frequency ($\Delta f$). The equation can be simplified as follows (Eq.02):

$$\Delta f = 10^{CR/10}$$

where the estimated critical bandwidth ($\Delta f$) is equal to ten raised to the power of the critical ratio divided by ten. There is a strong relationship between $\Delta f$ and the critical ratio. Both relate directly to the amount of summed energy being processed by the auditory filter and how this impacts hearing: a lower critical ratio implies a narrower filter bandwidth. This method of estimating critical bandwidths has proven to be useful but varyingly inaccurate compared to direct measurements of auditory performance—estimated critical bands are often, but not always, narrower than predicted values (Egan and Hake, 1950; Schafer et al., 1950; Hamilton, 1957; Zwicker et al., 1957; Patterson, 1976). While no exact correlation applies to all mammals, critical bandwidth estimates can be corrected for human subjects by multiplying the constant 'k' by a factor of 2.5 (see Moore et al., 1993; Erbe et al., 2016). There are no similar correction factors available for other mammalian species. Consequently, empirical measurements obtained in behavioral (psychophysical) studies remain the most accurate approach to determining critical bands for non-human species.

Critical bandwidths can be directly measured through a number of psychophysical approaches. The most common is a band-widening procedure (Fletcher, 1940). Here, the subject listens for a target tone in the presence of controlled masking noise with a steadily increasing bandwidth. When the noise bandwidth is narrow and tightly surrounding the signal, little to no masking of the tone occurs. As the masker bandwidth is widened, the masking of the tone increases until the critical bandwidth is reached. At this point, any further increase in noise bandwidth has no additional effect on signal detectability.

Direct measures of critical bandwidths can be represented as Q values, calculated as the center frequency (fc) divided by the measured critical bandwidth ($\Delta f$), shown in the following equation (03):

$$Q = \frac{f_c}{\Delta f}$$

Q values, the expression of critical bandwidth as a proportion of center frequency, are assumed to be relatively constant for most mammals around 23% (or one third of an octave). This is denoted as a constant Q (or constant quality) model. Critical bandwidths that fit the constant Q model increase proportionally as a function of center frequency.

Models of auditory masking are becoming increasingly important for marine mammals due to the increasing noise levels in the ocean (Duarte et al., 2023). Erbe et al. (2016) summarized the available frequency-specific masking parameters available for marine mammals and identified significant data gaps for marine carnivores. Audiometric studies of terrestrial carnivores (including bears, felines, canines, and weasels) suggest members of this Order are hearing generalists with no apparent specialization at any particular frequency (*see* Fay, 1988)., which aligns with the constant Q model of hearing

Within the Order *Carnivora*, pinnipeds (sea lions, walruses, and seals) offer a compelling model for studies of hearing in noise, given their need to discern biologically important information in two disparate media (air and water). Some critical ratio measurements are now available for ten species of pinnipeds. These include seven phocid (true seal) species (see review in Erbe et al., 2016), two otariids (sea lions and fur seals) (Moore & Schusterman, 1987; Southall et al., 2000, 2003; Jones et al., 2023), and the only living odobenid species, the walrus (Jones et al., 2023). At least a few of these species have been tested across a fairly broad frequency range (*e.g.* Sills et al., 2015; 2020). In contrast, critical bandwidths have only been measured for three pinniped species: two phocids and one otariid (Turnbull & Turhune, 1990; Southall et al., 2003). Notably, no critical bandwidth measurements are available below 2 kHz for any pinniped, or for any other marine mammals (Erbe et al., 2016; Branstetter & Sills, 2022).

The limited critical bandwidth data for pinnipeds show no apparent frequency-specific specialization, although available measurements cover a narrow frequency range that does not extend below 2500 Hz (Turnbull & Turhune, 1990; Southall et al., 2003). Critical ratio data collected in phocid seals (e.g., Sills et al., 2020; *see* Erbe et al., 2016) show that northern species–such as bearded and spotted seals–have consistently lower critical ratios than their otariid (sea lion) and odobenid (walrus) counterparts. This is particularly true at lower frequencies (see Jones et al. 2023, Sills et al., in *prep*), suggesting that these species may display additional frequency specialization at frequencies that have not yet been tested.

This data gap is substantial given that most environmental and anthropogenic noise overlaps with many pinniped vocalizations at the mid and low frequencies (*e.g.* Richardson, 1995). Consequently, pinnipeds are at a higher risk of exposure to pervasive noise within their frequency range of biological relevance and may possess some derived adaptation for extracting important acoustic cues from noisy environments.

Currently, the mammalian auditory system is generally understood to have critical bandwidths that are about equal to a third of an octave at all frequencies. The present study seeks to evaluate this assumption in pinnipeds. To do this, we obtain direct critical bandwidth measurements from three pinnipeds trained for cooperative auditory testing: a sea lion, a walrus, and a true seal. To consider potential frequency specialization, we provide these parameters across frequency spans between 100 Hz and 16 kHz. These findings will build on the limited data available for pinnipeds and improve the current understanding of which noise sources may have more or less masking potential.

## Methods

### *General Approach*

Direct critical bandwidth measurements were obtained for three pinniped subjects trained to participate in behavioral audiometry. Detection thresholds for each subject were measured for tonal signals in the presence of masking noise of varying bandwidths. At each test frequency, the bandwidth of the masking stimulus was systematically varied from wide (one octave band) to narrow (1/9th of an octave) to determine the point at which signal-to-noise ratios (SNRs) at threshold ceased to increase as a function of noise bandwidth.

*Subjects*

Animal subjects comprised one representative species from each of the three pinniped families. The otariid (eared seal) subject was an adult female California sea lion (*Ronan*, *Zalophus californianus*, NOA0006602, 14-15 y), the phocid (true seal) was an adult male bearded seal (*Noatak*, *Erignathus barbatus*, NOA0010270, 8 y), and the odobenid (walrus) was an adult female Pacific walrus (*Chou Chou*, *Odobenus rosmarus*, 12 y). Operant conditioning methods and positive (fish) reinforcement were used to establish cooperative behavior for audiometry sessions. Each subject had prior experience performing psychophysical hearing and masking tasks (e.g., Reichmuth et al., 2017, Sills et al., 2020; Jones et al., 2023). All subjects were in good health at the time of testing and had no known otological issues or prior exposure to ototoxic medications. Animal diets were not constrained for experimental purposes.

Authorization for this study was granted under US National Marine Fisheries Service marine mammal research permit 23554. Animal research was reviewed and approved by the Institutional Animal Care and Use Committees at the University of California Santa Cruz and SeaWorld San Diego. Further, research for the bearded seal was conducted with expressed support from the Ice Seal Committee, a tribally authorized Alaska Native co-management organization.

*Environment and Apparatus*

The sea lion and seal were tested outdoors at Long Marine Laboratory in Santa Cruz, California. Sea lion trials were conducted in a 5 m x 3.5 m holding pen with two walls of synthetic high-density polyethylene (HDPE) at the subject's right and rear and two walls of vinyl-coated chain link fencing to the subject's left and front. A white station marker was attached to the fence at the height of the subject's nose when relaxed. A black response target was mounted 0.5 m to the left of this station. The speaker was positioned on a tripod the other side of the acoustically transparent fencing, 1.2 m from the center of the subject's head when positioned at the station.

The seal was tested in the open doorway of his home enclosure with one wall of HDPE to his immediate right and a wall of plexiglass to his left. The seal performed the task in a prone position, with his head resting in a chin cup station secured to the decking, and a response target positioned 0.1 m to his left. The speaker was positioned on the deck 1 m in front of and on axis with the subject's head. A piece of neoprene was placed between the deck and the speaker to reduce unintentional somatosensory cues.

The walrus was tested in a 4 m x 7 m pen adjacent to her home enclosure in the Wild Arctic Exhibit of SeaWorld San Diego in San Diego, California. The front and back of the pen were enclosed by metal bars, and the side walls were made of cement. Similar to the sea lion testing configuration at LML, a white station, and black response target were affixed to the front-facing bars. The tripod-mounted speaker was positioned 1.2 m in front of the center of the subject's head, on the opposite side of the barrier.

Ambient noise in each test location was measured with a calibrated, self-powered 2250 sound level meter (sampling rate 48 kHz; Brüel and Kjaer A/S, Naerum, Denmark) with a free-field ½-in type 4966 microphone. A 1-min, unweighted noise measurement was taken in test-ready conditions in the position of the subject's head immediately preceding each data collection session. For each experimental condition, masking noise levels exceeded the surrounding ambient noise levels.

*Stimulus Generation and Calibration*

Test frequencies were chosen to extend across each subject's functional hearing range based on published audiograms for each species (Reichmuth et al., 2017, Sills et al., 2020, Reichmuth et al., 2020). The sea lion and seal were tested at 200, 500, 4000, 10000, and 16000 Hz; the seal was also tested at 100 Hz. The walrus was tested at a subset of these frequencies:  200, 4000, and 10000 Hz; fewer conditions were evaluated due to the subject's high-frequency hearing limit, equipment limitations, and subject availability.

Test signals were 1-s pure tones with 50-ms linear onset/offset ramps that were generated (1 MHz update rate) using the Hearing Test Program (HTP) LabVIEW (NI) software (Finneran, 2003). Digital signals were converted to analog signals via an NI USB-6251 data acquisition board (NI, Austin, TX) and then passed through a 0.1—250 kHz bandpass active filter module (Krohn-Hite, Brockton, MA) and a two-channel passive mixer (Mix 2:1, Radial Engineering, Vancouver, Canada). The signal was projected through either a KH80 DSP-powered studio monitor with an internal amplifier (0.057–21 kHz, 63 dB; Neumann, Berlin, Germany) or a Vifa ultrasonic dynamic speaker with a portable ultrasonic power amplifier (1–120 kHz, Avisoft Bioacoustics, Glienicke/Nordbahn, Germany).

Masking stimuli were Gaussian (white) noise bands centered around the test frequency. A maximum of nine noise bandwidth conditions were generated for each test frequency, ranging from a full octave band to 1/9th of an octave band. The noise stimuli were generated using a custom LabVIEW virtual instrument and were calibrated before each session to ensure the masker was spectrally flat and that the masker's power spectral density (PSD) level was within 1 dB of the desired target level. Masker amplitude remained constant for each frequency and bandwidth condition. During testing, masking noise was projected continuously using Audacity® software (version 3.0.0) through the computer's internal sound card and mixed with the test tone using the two-channel passive mixer before transmitting through the same speaker used to project the tonal signals.

Stimuli were mapped prior to testing at each frequency within a 3 cm x 3 cm x 3 cm area surrounding the expected position of the subject's ears when at the station. The maximum sound pressure level (SPL, dB re 20 μPa) deviation from the calibration position allowed to meet criteria was +/- 3 dB for both the test tones and maskers. Audiometric signals and maskers at each frequency were calibrated daily and spatially mapped using the same sound level meter used to characterize the ambient noise (Brüel and Kjaer A/S, Naerum, Denmark). Calibration occurred in the position of the subject's left or right ear depending on frequency–whichever side had the louder received level during mapping.

### *Audiometry*

Hearing thresholds were measured at each test frequency, first in the ambient noise environment of the test enclosures and then again with the masking stimulus projected throughout the session. In both cases, trial conditions were set by an operator obscured from the subject's view. A trainer who was unaware of individual trial conditions provided support when instructed by the operator to reinforce or reset the subject. A Hero8 video camera (GoPro, San Mateo, CA) recorded each session.

The audiometric protocol consisted of a go/no-go signal detection paradigm (Stebbins, 1970) with signal-present and signal-absent trials. Signal onset occurred randomly within the 6 s trial window. Subjects reported detection of the tone stimulus on signal-present trials by moving from the station to touch the response target with their nose within the trial window. On signal-absent trials, the subject remained on the station for the full 6-s trial window. Correct responses were marked with a conditioned acoustic reinforcer (either a verbal or whistle cue) followed by a food reward delivered by the trainer. Incorrect responses (misses on signal-present trials or false detections on signal-absent trials) were not reinforced, and the subject was prompted to the station before moving on to the subsequent trial.

Within each session, the test frequency and noise bandwidth remained constant. Signal amplitude varied from trial to trial according to the subject's performance via an adaptive staircase method (Stebbins, 1970). The signal level started at an easily detectable amplitude and decreased by 2-4 dB after each correct detection until the first miss. Signal amplitude was then increased by 4 dB after every miss and decreased by 2 dB after each correct detection. This sequence was repeated until 3-8 descending hit-to-miss transitions were obtained. The session ended with several suprathreshold signals to maintain stimulus control for the task. Subjects were first tested at each frequency in ambient (no-masker conditions).

For masking sessions, the target level of the noise was equal to or 5 dB above the subject's corresponding ambient hearing threshold. Subjects were exposed to one noise bandwidth condition per session in a modified band-widening method (Greenwood, 1961), where conditions were shuffled in pseudorandom session blocks. Subjects were tested at each noise bandwidth once per block, and blocks were repeated until sufficient reversal data were collected for threshold determination (see below). Initial testing with the sea lion at 500, 4000, and 16000 Hz was completed with bandwidth conditions that included: 1-octave, 2/3-octave,1/2-octave, 1/3-octave, 1/4-octave, 1/6-octave, and 1/9-octave. For subsequent testing at 200 and 10000 Hz, data were collected at a subset of these bandwidth conditions. Bandwidths were selected to best capture a gradual release from masking in each case, with at least one point demonstrating full masking and one indicating complete masking release (e.g. when the threshold is unaffected by the masking stimulus). Intermediate bandwidths were added as needed to increase resolution by ensuring that at least two transitional points showed partial masking release at each frequency. This more efficient and targeted method was later applied to testing with the seal and walrus subjects (see Table 1).

Subjects participated in 1-2 audiometric sessions per day with approximately 40 trials per session. Within each session, signal-present and signal-absent trials were presented in a predetermined, pseudorandom order at a ratio of 70:30. False alarm rates determined as the proportion of false detections on the signal-absent trials were calculated for each condition.

### *Threshold Determination*

Ambient thresholds measured in outdoor conditions and masked thresholds for each noise bandwidth condition were estimated in SPL as the average of 15 hit-to-miss transitions obtained over 2-4 sessions. Thresholds met criteria when the pooled hit-to-miss transitions for a condition had a standard deviation of less than or equal to 2, and a corresponding false alarm rate between 1 and 30%. Additionally, the SNRs at threshold was determined for each masking condition as the difference (in dB) between the masked threshold and masking noise power spectral density level.

### *Critical Ratio Validation*

SNRs measured in the wide-band noise conditions (octave and ⅔ -octave bands) were compared to published critical ratios for each subject (Sills et al., 2020; Jones et al., 2023). To maximize data collection with the walrus participant, the octave band was not tested (if the ⅔ -octave band SNR at threshold was within 2 dB of her published critical ratio) and the previously published value was used in the determination of the critical bandwidth.

### *Critical Bandwidth Determination*

For each subject, measured SNRs at threshold were plotted as a function of noise bandwidth for each frequency. Two linear regressions were applied: (1) to the 2-3 transitional points that displayed masking release (i.e., SNRs at threshold that were more than 2 dB lower than the critical ratio) and (2) to the points where maximal masking effect was noted (i.e. SNRs at threshold within 2 dB of the critical ratio). The critical bandwidth was estimated as the value (in Hz) corresponding to the intersection between these two regression lines. Additionally, Fletcher critical bands were estimated from critical ratio at each frequency using Eq. 02. Critical ratios for this calculation were identified as the SNR determined from thresholds collected in the presence of the widest band noise conditions.

## **Results**

### *Ambient and Masked Thresholds*

Ambient (unmasked) auditory thresholds obtained for airborne tonal sounds in outdoor conditions were predictably elevated compared to those reported in highly controlled conditions for the sea lion and other seal species (Table I; Jones et al, 2023; Reichmuth et al., 2017; Reichmuth et al., 2013). These values were used to establish the noise levels for masking trials presented to each subject, ensuring complete masking for wideband noise conditions.

Masked thresholds and associated SNRs obtained for each frequency-bandwidth condition are summarized for all subjects in Table 01. Signal-to-noise ratios for thresholds collected in the presence of octave-band or ⅔-octave band noise were similar (within 2 dB) of published critical ratio values for all three subjects (Figure 1; Sills et al., 2020; Jones et al., 2023) (Fig 1).

For the sea lion, thresholds measured in the presence of the narrowest band noise (1/6 or 1/9 octave band) were within 1 dB of the subject's measured threshold in ambient (no masker) conditions at all frequencies, demonstrating a full release from masking. Consequently, these noise conditions did not provide informative data and were not tested with the walrus and seal subjects to increase the efficiency of testing (these points are not included in the linear regression used to determine the critical bandwidth).

Average false alarm rates were 0.18, 0.21, and 0.16 for the sea lion, walrus, and seal, respectively. The similar rates suggest similar response bias for these individuals. There was no relationship between measured false alarm rates and either test frequency or noise bandwidth condition. Standard deviations of false alarm rates were less than 1.8 dB for all subjects (Table I.

*Critical Bandwidths*

Critical bandwidths were determined at up to five frequencies for each subject (Table II; representative data shown in Fig. 2). The sea lion and seal were tested at 200, 500, 4000, 10000, and 16000 Hz, while the walrus was tested at 200, 4000, and 10000 Hz. Additionally, the seal was tested at 100 Hz. A minimum of two fully masked thresholds (where SNR is equal to the critical ratio) and two partially masked thresholds (where SNR is still increasing as a function of noise bandwidth) were used to run the linear regression analysis.

Absolute critical bandwidth values (measured in Hz) increased reliably with increasing frequency (Figure 3, Table II). The narrowest critical bandwidths were measured at 200 Hz and were 70, 29, and 100 Hz for the sea lion, seal, and walrus. The widest critical bands were measured at the highest frequency tested: 16000 for the sea lion and seal and 10000 Hz for the walrus. These critical bandwidths were 1319, 487, and 1585 Hz for the sea lion, seal, and walrus, respectively.

Critical bandwidth as a percentage of center frequency was calculated using Eq 03 (Table II). Sea lion Q values were 0.35, 0.33, 0.19, 0.18, and 0.16 at 200, 500, 4000, 10000, and 16000 Hz. Seal Q values were 0.14, 0.14, 0.20, 0.24, and 0.18 at 200, 500, 4000, 10000, and 16000 Hz. Walrus Q values were 043, 0.27, and 0.20 and 200, 4000, and 10000 Hz (Figure 4).

Direct critical bandwidth measurements were compared to estimated Fletcher critical bands calculated using Eq 02 (Table II). These estimated bandwidths did not consistently predict direct critical bandwidths, with differences ranging from 2 Hz at 200 Hz for the seal subject to 2901 Hz at 4000 Hz for the walrus subject.

## Discussion

The standardized auditory thresholds obtained from highly experienced animals in the presence of spectrally flat masking noise allowed for the determination of frequency-dependent masking parameters including critical ratios and critical bandwidths. Critical ratios and critical bandwidths were obtained at up to five frequencies for sea lion, walrus, and seal subjects. These frequencies cover a broad range, from within the known or presumed range of most sensitive hearing (10000 to 16000 Hz) to a few hundred Hz. The critical ratio data confirm previously published values for the same species (Jones 2023, Sills 2020) demonstrating the validity of this approach. The critical bandwidth data are both novel and comparative for these marine carnivores. Such information has been previously unavailable for any marine mammal at frequencies below 2000 Hz, which are most relevant for many sources of ocean noise.

### *Masked Thresholds and Critical Ratios*

Masked thresholds measured for all three subjects showed low variance (standard deviation < 2 dB) regardless of noise bandwidth condition. This may be a result of the projected maskers creating uniform noise backgrounds, thus limiting the influence of time-varying external and internal noise on measured detection thresholds. Further, the observed consistency in performance reflects the expert nature of the three test subjects. Comparison with prior measures of hearing for these individuals and conspecifics suggests that they are reliable representatives of their respective species (Reichmuth et al., 2013, Reichmuth et al., 2017, Sills et al., 2020, Jones et al., 2023).

The strong agreement between measured thresholds measured in wide-band (octave- and ⅔-octave band) conditions confirms that these SNRs, obtained outdoors in air, can be considered reliable critical ratios. For the sea lion and walrus subjects, critical ratios were previously collected using octave-band noise in the same testing environments with the same airborne tonal signals, equipment, and methods (Jones et al., 2023). The current critical ratios fall within 4 dB of those previously reported, indicating a high degree of replicability in these measurements. Importantly, the critical ratio values used for comparison for the seal subject were collected using an entirely different apparatus and were collected in water (Sills et al., 2020), further validating that these masking parameters are independent of medium (*see* Erbe et al., 2016).

### *Critical Bands*

The absolute critical bands estimated by linear regression increased as a function of center frequency for all three subjects. At the higher and mid-range frequencies (between 4000 and 16000 Hz), absolute critical bandwidth values were similar for each individual. This finding is consistent with the critical bandwidth data collected by Southall et al. (2003), where critical bands for two seals and one sea lion were measured at 2500, 4000, and 8000 Hz. However, at the lower frequencies tested (500 Hz and 200 Hz), the seal's critical bands were substantially narrower than those estimated for the sea lion and walrus. This relatively enhanced frequency resolution is consistent with the markedly lower critical ratios of most northern seals compared to those of otariids, odobenids, and terrestrial carnivores (*see* Erbe et al., 2016; Sills et al., 2020).

The consistent increase in critical bandwidth with increasing frequency observed in the present study confirms that pinnipeds as a group are hearing generalists when it comes to hearing in noise. This lack of narrowband frequency specialization is not surprising given that it has only been observed in echolocators that rely heavily on signal detection at a narrow range of frequencies, such as the horseshoe bat and porpoises (Vater & Duifhuis, 1986; Lemmonds, 2011). However, the seal's relatively narrower absolute critical bandwidths across lower frequencies stand out as a possible specialization. This trend suggests that seals are generally very well adapted to detect signals within noise in this frequency range when compared to other pinnipeds.

When considered in terms of Q value (or as a proportion of center frequency), the critical bands are similar above 500 Hz for the sea lion, seal, and walrus. Across the mid and high frequencies, all subjects' Q values are near 0.20, which fits the traditional constant Q model and is consistent with the conclusion that these species are, like other carnivores, hearing generalists (*see* Fay 1988; Southall, 2003). At 500 Hz and below, the seal's Q values remain close to 0.20 and even decreased to 0.14, while the sea lion and walrus Q values increased to above 0.30. While the constant Q model is applicable to all three species at the higher and mid-frequencies, at lower frequencies it apparently only applies to the seal's data. There is some indication that seal critical bandwidths and associated Q values increase below 200 Hz (Sills et al., *in prep*). This is further supported by the critical ratio data, which show that critical ratios cease to decrease at the predicted 3 dB per octave and instead begin to increase below 200 Hz (Sills et al., 2020). Regardless, it is apparent that seals maintain a higher frequency resolution across a wider portion of their hearing range than do sea lions and walruses. More data are needed at low frequencies to fully evaluate frequency-dependent trends in making parameters for these species, as there are very few available critical bandwidth data below 500 Hz from which to draw a comparison.

Fletcher critical band estimations were not able to accurately predict absolute critical bandwidths for any subject at any frequency, highlighting the need for direct measurements with trained subjects. There was no evidence that a simple correction factor could be applied to improve the Fletcher estimates.

Evolutionary drivers could be the cause for the extended frequency selectivity observed among phocids. For example, the breeding systems of many northern seals require a fair amount of long-distance acoustic communication–either to attract mates or deter competitors through vocal displays of reproductive fitness (*e.g.* Miksis-Olds et al., 2011; Mizuguchi, 2016; Sills et al., 2022). These calls have many low-frequency components that enable signals to travel over longer distances. In this scenario, it becomes important for conspecifics to be able to extract the relevant information over these greater distances, where important signal characteristics may be more susceptible to encountering competing noise. Unlike their Arctic phocid counterparts, walruses and sea lions aggregate in large social groups. While this introduces more noise into their immediate environment, it removes the need for long-distance acoustic communication that is required of the northern seals.

### *Implications for Management*

These direct measurements of critical bandwidth, including at relatively low frequencies, can be applied to improve masking models for pinnipeds. The same critical ratios and critical bandwidths can be used as frequency-specific masking parameters in scenarios involving airborne or waterborne noise. Reported critical bandwidths indicate the relevant frequency span for evaluating noise effects as a function of frequency. It can be concluded that while sea lions and walruses show a similar degree of frequency resolution compared to their terrestrial counterparts, seals appear to have high-frequency resolution throughout a wider portion of their functional hearing range. Further, while the present study fills several data gaps with respect to auditory masking parameters for pinnipeds, there is still much that is unknown about frequency resolution and masking in these species at low frequencies.

From these data, it becomes clear that the commonly used approach of modeling the mammalian auditory system as a bank of filters that are approximately a third of an octave wide is only applicable to sea lions and walruses at frequencies of 500 Hz and above. In this way, these marine carnivores are similar to terrestrial carnivores (references). While there are few comparative data available at lower frequencies, these pinniped species are considerably worse at extracting signals from noise at lower frequencies and will be more sensitive to noise impacts at lower frequencies than traditionally expected.

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## References

Branstetter, B. K., & Sills, J. M. (2022). Mechanisms of auditory masking in marine mammals. *Animal Cognition*, *25*(5), 1029–1047. https://doi.org/10.1007/s10071-022-01671-z

Branstetter, B. K., Trickey, J. S., Bakhtiari, K., Black, A., Aihara, H., & Finneran, J. J. (2013). Auditory masking patterns in bottlenose dolphins ( *Tursiops truncatus* ) with natural, anthropogenic, and synthesized noise. *The Journal of the Acoustical Society of America*, *133*(3), 1811–1818. https://doi.org/10.1121/1.4789939

Dooling, R. J., & Blumenrath, S. H. (2013). Avian Sound Perception in Noise. In H. Brumm, V. M. Janik, & P. McGregor (Eds.), *Animal Communication and Noise, Animal Signals and Communication 2* (pp. 229–250). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-41494-7_8

Duifhuis, H., & Vater, M. (1986). On the Mechanisms of the Horshoe Bat Cochlea. In S. A. Levin, J. B. Allen, A. E. Hubbar, S. T. Neely, & A. Tubis (Eds.), *Peripheral Auditory Mechnanisms* (pp. 89–96). Springer-Verlag Berlin Heidelberg GmbH. https://doi.org/10.1007/978-3-642-50038-1

Egan, J. P., & Hake, H. W. (1950). On the Masking Pattern of a Simple Auditory Stimulus. *Journal of the Acoustical Society of America*, *22*(5), 622–630. https://doi.org/10.1121/1.1906661

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin*, *103*(1–2), 15–38. https://doi.org/10.1016/j.marpolbul.2015.12.007

Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook* (L. A. Wilber (ed.)). Hill-Fay Associates.

Fletcher, H. (1940). Auditory Patterns. *Reviews of Modern Physics*, *12*, 47–66. https://doi.org/https://doi.org/10.1103/RevModPhys.12.47

Greenwood, D. D. (1961). Auditory Masking and the Critical Band. *The Journal of the Acoustical Society of America*, *33*(4), 484–502. https://doi.org/10.1121/1.1908699

Hamilton, P. M. (1957). Noise Masked Thresholds as a Function of Tonal Duration and Masking Noise Band Width. *Journal of the Acoustical Society of America*, *29*(4), 506–511. https://doi.org/10.1121/1.1908942

Jesus, S. M., Duarte, R., Spadoni, G., Soares, C., & Fernandez, M. (2023). Assessing Risk of Noise Pressure on Marine Life Using Bayes Estimator. In A. N. Popper, J. Sisneros, A. D. Hawkins, & F. Thomsen (Eds.), *The Effects of Noise on Aquatic Life* (pp. 1–13). Springer Nature Switzerland AG 2023. https://doi.org/10.1007/978-3-031-10417-6_43-1

Jones, R. A., Sills, J. M., Synnott, M., Mulsow, J., Williams, R., & Reichmuth, C. (2023). Auditory masking in odobenid and otariid carnivores. *The Journal of the Acoustical Society of America*, *154*(3), 1746–1756. https://doi.org/10.1121/10.0020911

Lemonds, D. W., Kloepper, L. N., Nachtigall, P. E., Au, W. W. L., Vlachos, S. A., & Branstetter, B. K. (2011). A re-evaluation of auditory filter shape in delphinid odontocetes: Evidence of constant-bandwidth filters. *The Journal of the Acoustical Society of America*, *130*(5), 3107–3114. https://doi.org/10.1121/1.3644912

Miksis-Olds, J. L., & Parks, S. E. (2011). Seasonal trends in acoustic detection of ribbon seal (*Histriophoca fasciata*) vocalizations in the Bering Sea. *Aquatic Mammals*, *37*(4), 464–471. https://doi.org/10.1578/AM.37.4.2011.464

Mizuguchi, D., Tsunokawa, M., Kawamoto, M., & Kohshima, S. (2016). Underwater vocalizations and associated behavior in captive ringed seals (*Pusa hispida*). *Polar Biology*, *39*(February), 659–669. https://doi.org/10.1007/s00300-015-1821-x

Moore, B. C. J. (1993). Frequency analysis and pitch perception. In *Human Psychophysics* (Issue 1940, pp. 56–115).

Moore, P. W. B., & Schusterman, R. J. (1987). Audiometric assessment of northern fur seals, *Callorhinus ursinus*. *Marine Mammal Science*, *3*(1), 31–53. https://doi.org/10.1111/j.1748-7692.1987.tb00150.x

Moss, C. F., Ortiz, S. T., & Wahlberg, M. (2023). Adaptive echolocation behavior of bats and toothed whales in dynamic soundscapes. *Journal of Experimental Biology*, *226*(9). https://doi.org/10.1242/jeb.245450

Patterson, R. D. (1976). Auditory filter shapes derived with noise stimuli. *The Journal of the Acoustical Society of America*, *59*(3), 640–654. https://doi.org/10.1121/1.380914

Reichmuth, C., Sills, J. M., Brewer, A., Triggs, L., Ferguson, R., Ashe, E., & Williams, R. (2020). Behavioral assessment of in-air hearing range for the Pacific walrus (*Odobenus rosmarus divergens*). *Polar Biology*, *43*(6), 767–772. https://doi.org/10.1007/s00300-020-02667-6

Reichmuth, C., Sills, J. M., & Ghoul, A. (2017). Psychophysical audiogram of a California sea lion (*Zalophus californianus*) listening for airborne tonal sounds in an acoustic chamber. *Proceedings of Meetings on Acoustics*, *30*, 010001. https://doi.org/10.1121/2.0000525

Richardson, W. J., Greene, C. R., Malme, C. I., & Thomson, D. H. (1995). *Marine*

*Mammals and Noise*. Academic Press, Harcourt Brace & Company.

Schusterman, R. J., Kastak, D., Levenson, D. H., Reichmuth, C. J., & Southall, B. L. (2000). Why pinnipeds don't echolocate. *Journal of the Acoustical Society of America*, *107*(4), 2256–2264. https://doi.org/10.1121/1.428506

Sills, J. M., & Reichmuth, C. (2022). Vocal behavior in spotted seals (*Phoca largha*) and implications for passive acoustic monitoring. *Frontiers in Remote Sensing*, *3*(May), 1–14. https://doi.org/10.3389/frsen.2022.862435

Sills, J. M., Reichmuth, C., Southall, B. L., Whiting, A., & Goodwin, J. (2020). Auditory biology of bearded seals (*Erignathus barbatus*). *Polar Biology*, *43*, 1681–1691. https://doi.org/10.1007/s00300-020-02736-w

Southall, B. L., Schusterman, R. J., & Kastak, D. (2003). Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements. *J Acoust Soc Am*, *114*(3), 1660–1666. https://doi.org/10.1121/1.1587733

Stebbins, W. C. (1970). Principles of animal psychophysics. In W. C. Stebbins (Ed.), *Animal Psychophysics: the Design and Conduct of Sensory Experiments* (pp. 1–19). Appleton-Century-Crofts.

Turnbull, S. D., & Terhune, J. M. (1990). White noise and pure tone masking of pure tone thresholds of a harbour seal listening in air and underwater. *Canadian Journal of Zoology*, *68*(10), 2090–2097. https://doi.org/10.1139/z90-291

Zwicker, E., Flottorp, G., & Stevens, S. S. (1957). Critical Band Width in Loudness Summation. *The Journal of the Acoustical Society of America*, *29*(5), 548–557. https://doi.org/10.1121/1.1908963

## Chapter 2: Direct Critical Bandwidth Measurements in Pinnipeds

Figures, tables, and figure captions

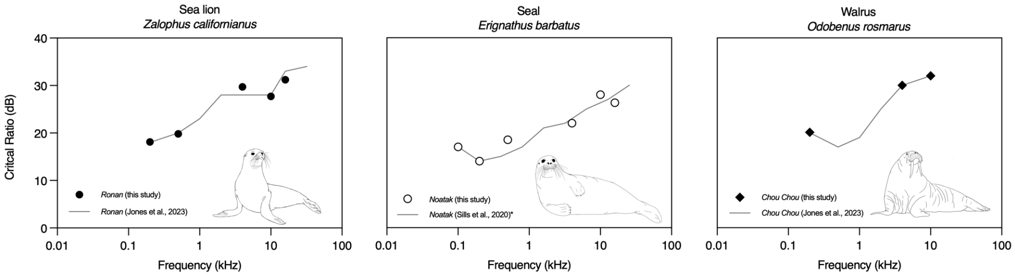


FIG. 1. Auditory critical ratios measured in the presence of wide-band, Gaussian (white) noise for a sea lion, seal, and walrus (n=1 for each species). Critical ratios represented by symbols were collected in air as part of the current study. Sea lion and walrus critical ratios are plotted alongside data collected for the same subjects in the same outdoor testing environment about one year prior (Jones et al., 2023). Seal critical ratios are shown with those obtained for the same subject in water four years prior to the present study (Sills et al., 2020).

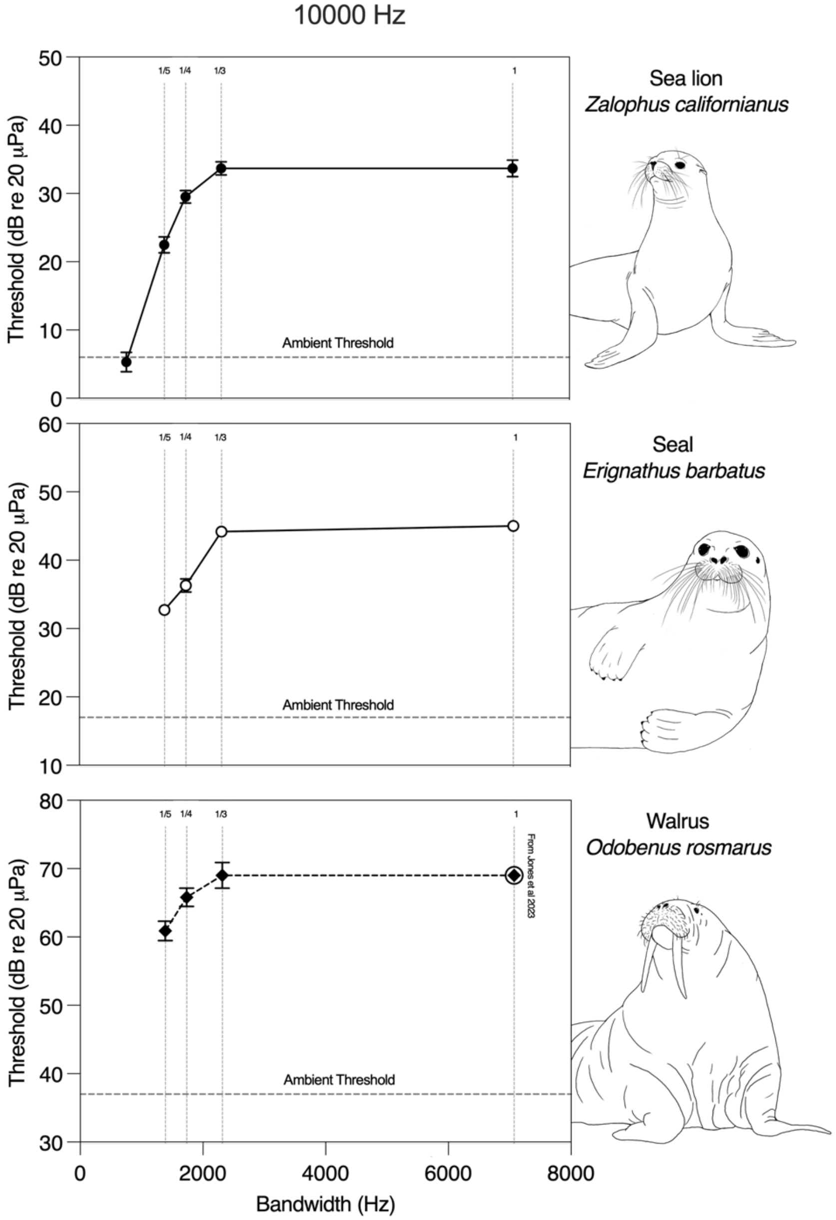


FIG. 2. Auditory thresholds for a sea lion, seal, and walrus subject collected in air in the presence of variable-bandwidth masking stimuli. Thresholds increased as a function of masking noise bandwidth until the noise band was sufficiently wide (*i.e.*, when the noise band exceeded the critical bandwidth). Critical bandwidths were estimated from these data via linear regression. Data shown here are for a single representative frequency (10000 Hz). Threshold data for all frequencies and bandwidths are provided in Table I and Supplement 1.

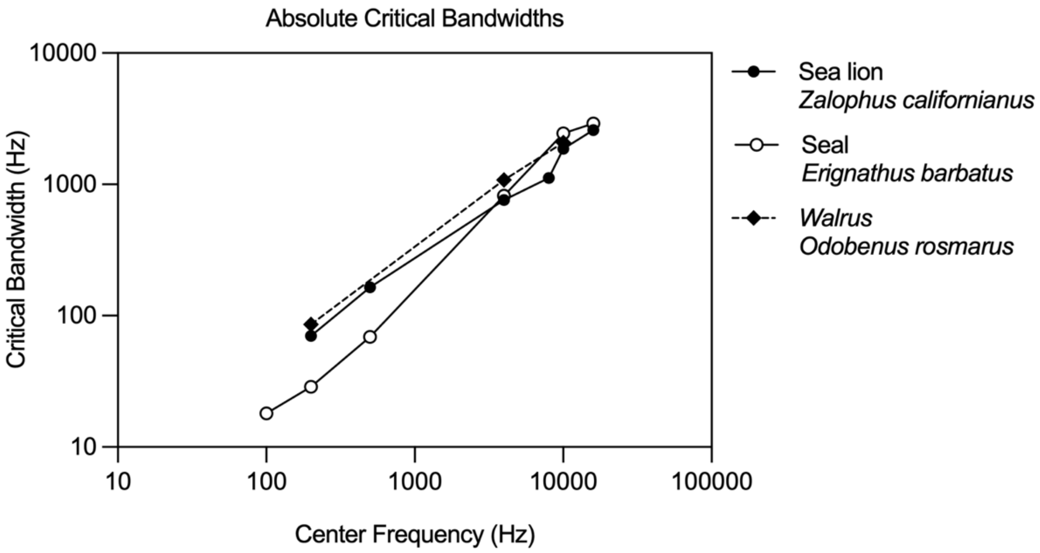


FIG. 3. Absolute critical bandwidths (Hz) plotted together as a function of center frequency for a sea lion, seal, and walrus subject. Data used to determine critical bands were collected in air using a band-widening technique. Critical bandwidths increase reliably with frequency for all subjects.

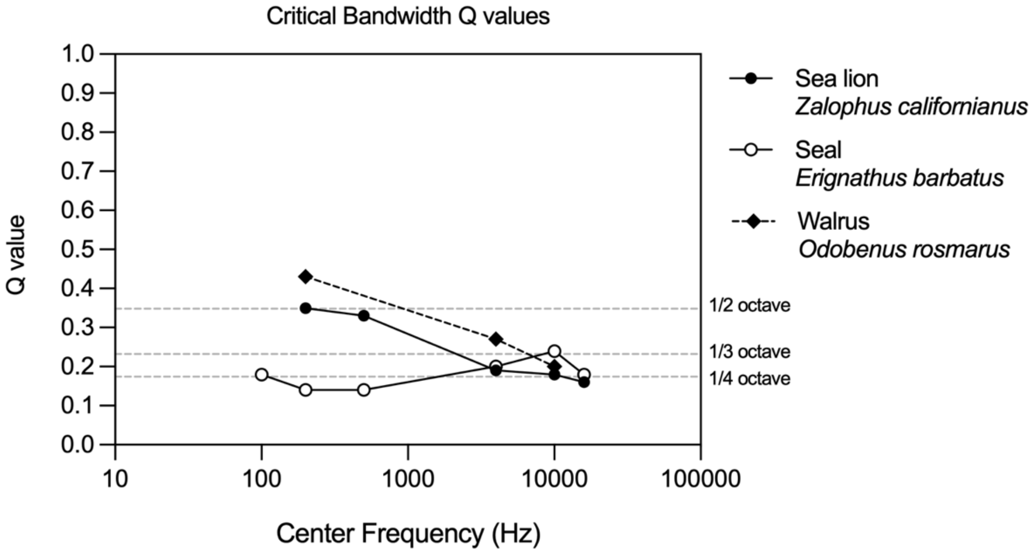
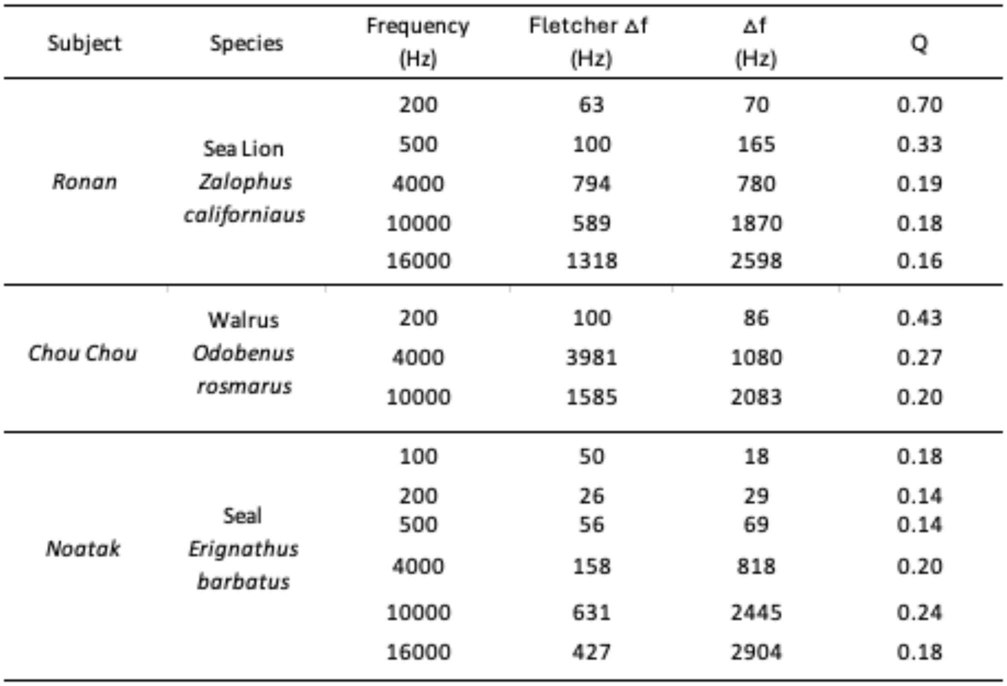


FIG. 4. Q values for a sea lion, seal, and walrus subject are shown as a function of frequency. . These Q values were determined by dividing each estimated critical bandwidth by the corresponding center frequency (see Eq. 03). Dashed horizontal lines denote the Q values corresponding to ½-, ⅓-, and ¼-octave bands.

|  |  |  | *Ronan*<br>Sea lion, *Zalophus californianus* |  |  | *Chou Chou*<br>*Odobenus rosmarus* |  |  | *Noatak*<br>*Erignathus barbatus* |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Frequency Hz | Noise condition | Bandwidth Hz | Threshold dB re 20 µPa | Stdev | SNR dB | Threshold dB re 20 µPa | Stdev | SNR dB | Threshold dB re 20 µPa | Stdev | SNR dB |
| 100 | Ambient | - |  |  |  |  |  |  | 50 | 1.79 | 20 |
|  | 1 | 71 |  |  |  |  |  |  | 67 | 1.83 | 16 |
|  | 1/3 | 23 |  |  |  |  |  |  | 66 | 1.44 | 15 |
|  | 1/4 | 17 |  |  |  |  |  |  | 63 | 1.67 | 12 |
|  | 1/6 | 12 |  |  |  |  |  |  | 63 | 1.06 | 12 |
|  | 1/8 | 9 |  |  |  |  |  |  | 53 | 1.66 | 3 |
| 200 | Ambient | - | 62 | 1.35 | 35 | 62 | 2.00 | 22 | 45 | 1.36 | 18 |
|  | 1 | 141 | 80 | - | 18 | 82 | - | 20 | 59 | 1.57 | 14 |
|  | 2/3 | 93 | - | - | - | 82 | 1.49 | 20 | - | - | - |
|  | 1/2 | 70 | 80 | 1.49 | 18 | - | - | - | - | - | - |
|  | 5/12 | 58 | 74 | 1.80 | 12 | 75 | 2.03 | 13 |  |  |  |
|  | 1/3 | 46 | 68 | 1.28 | 6 | 72 | 1.83 | 10 | - | - | - |
|  | 1/4 | 35 | - | - | - | - | - | - | 59 | 1.51 | 14 |
|  | 1/6 | 23 | - | - | - | - | - | - | 59 | 1.7 | 14 |
|  | 1/7 | 20 | - | - | - | - | - | - | 52 | 2.2 | 7 |
|  | 1/9 | 15 | 63 | 2 | 1 | - | - | - | 48 | 1.80 | 3 |
| 500 | Ambient | - | 45 | 0.90 | 29 |  |  |  | 36 | 1.79 | 20 |
|  | 1 | 354 | 69 | 1.31 | 20 |  |  |  | 54 | 1.41 | 18 |
|  | 2/3 | 233 | 69 | 2.00 | 20 |  |  |  | - | - | - |
|  | 1/2 | 174 | 69 | 1.40 | 20 |  |  |  | - | - | - |
|  | 5/12 | 145 | 63 | 0.89 | 14 |  |  |  | - | - | - |
|  | 1/3 | 116 | 49 | 1.67 | 0 |  |  |  | - | - | - |
|  | 1/4 | 87 | 45 | 1.41 | -4 |  |  |  | 54 | 1.49 | 17 |
|  | 1/5 | 69 | - | - | - |  |  |  | 53 | 1.28 | 16 |
|  | 1/6 | 58 | 44 | 0.89 | -6 |  |  |  | 50 | 1.41 | 13 |
|  | 1/9 | 39 | 44 | 1.10 | -5 |  |  |  | 43 | 1.35 | 6 |
| 4000 | Ambient | - | 24 | 1.23 | 23 | 42 | 1.5 | 29 | 20 | 1.54 | 19 |
|  | 1 | 2828 | 60 | 1.45 | 29 | 73 | - | 36 | 43 | 1.07 | 22 |
|  | 2/3 | 1865 | 59 | 1.41 | 29 | - | - | - | - | - | - |
|  | 1/2 | 1393 | 59 | 1.28 | 29 | - | - | - | - | - | - |
|  | 1/3 | 926 | 59 | 1.28 | 29 | 73 | 1.41 | 36 | 42 | 1.23 | 21 |
|  | 7/24 | 810 | 55 | 1.41 | 25 | 68 | 1.10 | 31 | 40 | 1.60 | 19 |
|  | 1/4 | 694 | 50 | 1.41 | 21 | 65 | 1.67 | 28 | 34 | 1.41 | 13 |
|  | 1/5 | 555 | - | - | - | - | - | - | 24 | 1.23 | 3 |
|  | 1/6 | 462 | 24 | 1.63 | -5 | - | - | - | - | - | - |
|  | 1/9 | 308 | 24 | 1.23 | -5 | - | - | - | - | - | - |
| 10000 | Ambient | - | 6 | 1.40 | 21 | 37 | 1.20 | 34 | 17 | 1.23 | 32 |
|  | 1 | 7071 | 34 | 1.23 | 28 | 69 | - | 32 | 45 | 1.51 | 28 |
|  | 1/3 | 2316 | 34 | 0.98 | 28 | 69 | 0.94 | 32 | 44 | 1.26 | 23 |
|  | 1/4 | 1735 | 30 | 0.92 | 24 | 65 | 1.35 | 28 | 36 | 0.98 | 15 |
|  | 1/5 | 1387 | 22 | 1.19 | 16 | 61 | 1.41 | 24 | 33 | 1.49 | 12 |
|  | 1/9 | 770 | 5 | 1.28 | -1 | - | - | - | - | - | - |
| 16000 | Ambient | - | 4 | 1.30 | 21 |  |  |  | 17 | 1.46 | 34 |
|  | 1 | 11314 | 40 | 1.03 | 31 |  |  |  | 43 | 1.28 | 26 |
|  | 2/3 | 7460 | 40 | 1.45 | 31 |  |  |  | - | - | - |
|  | 1/2 | 5573 | 40 | 1.49 | 31 |  |  |  | - | - | - |
|  | 1/3 | 3705 | 40 | 1.41 | 31 |  |  |  | 44 | 1.67 | 27 |
|  | 1/4 | 2776 | 39 | 1.67 | 30 |  |  |  | 41 | 1.63 | 23 |
|  | 9/40 | 2498 | 37 | 1.19 | 28 |  |  |  | 36 | 1.41 | 19 |
|  | 1/5 | 2220 | 30 | 1.49 | 21 |  |  |  | 29 | 1.19 | 12 |
|  | 1/6 | 1849 | 4 | 1.03 | -5 |  |  |  | - | - | - |
|  | 1/9 | 1232 | 4 | 1.47 | -5 |  |  |  | - | - | - |

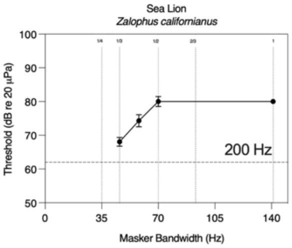
Table I. Ambient thresholds, masked thresholds, standard deviations, and signal-to-noise ratios (SNRs) at masked threshold collected in air for three pinniped subjects. Masking noise used for each threshold varied in bandwidth between 1/9-octave and 1-octave-band, with up to nine bandwidth conditions tested per frequency. Average false alarm rates were 0.18, 0.21, and 0.16 for the sea lion, walrus, and seal, respectively.

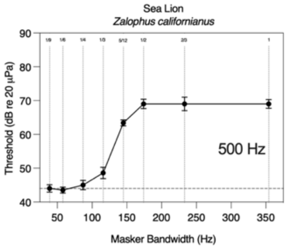


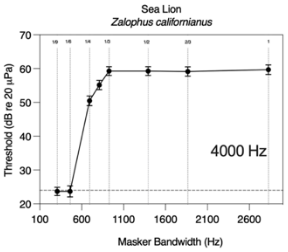
| Subject | Species | Frequency (Hz) | Fletcher Δf (Hz) | Δf (Hz) | Q |
|---|---|---|---|---|---|
| *Ronan* | Sea Lion<br>*Zalophus californiaus* | 200 | 63 | 70 | 0.70 |
| | | 500 | 100 | 165 | 0.33 |
| | | 4000 | 794 | 780 | 0.19 |
| | | 10000 | 589 | 1870 | 0.18 |
| | | 16000 | 1318 | 2598 | 0.16 |
| *Chou Chou* | Walrus<br>*Odobenus rosmarus* | 200 | 100 | 86 | 0.43 |
| | | 4000 | 3981 | 1080 | 0.27 |
| | | 10000 | 1585 | 2083 | 0.20 |
| *Noatak* | Seal<br>*Erignathus barbatus* | 100 | 50 | 18 | 0.18 |
| | | 200 | 26 | 29 | 0.14 |
| | | 500 | 56 | 69 | 0.14 |
| | | 4000 | 158 | 818 | 0.20 |
| | | 10000 | 631 | 2445 | 0.24 |
| | | 16000 | 427 | 2904 | 0.18 |

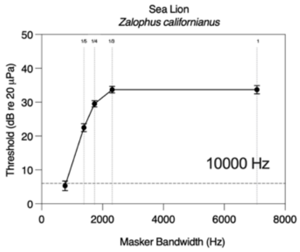
Table II. Critical bandwidths and Q values determined for up to six frequencies for a sea lion, seal, and walrus subject. Direct measures of critical bandwidth ($\Delta f$) were determined from masking data in this study using linear regression; for comparison, indirect estimates obtained from critical ratio data using Fletcher's (1940) equation (Eq. 02) are also shown (Fletcher $\Delta f$). Q values were calculated (Eq. 03) from the direct critical band measurements.

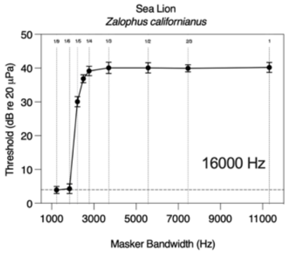
# *Supplement 1.* Masked thresholds, all subjects

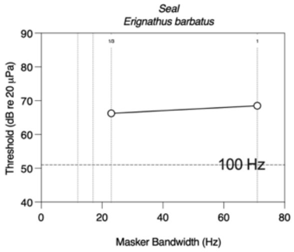


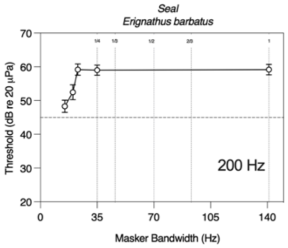


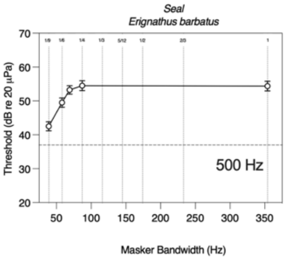


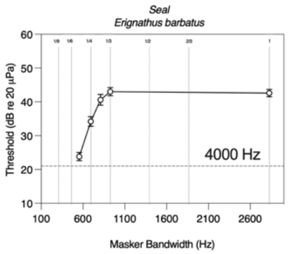


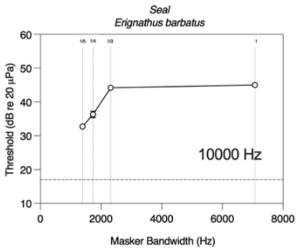


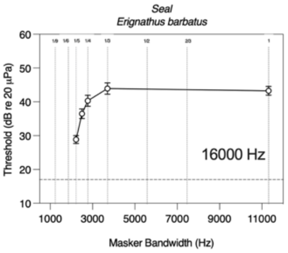


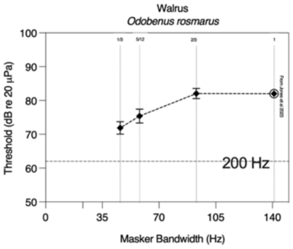


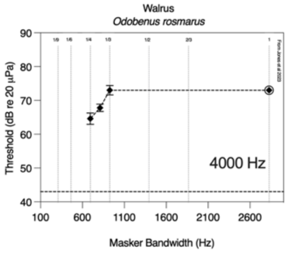


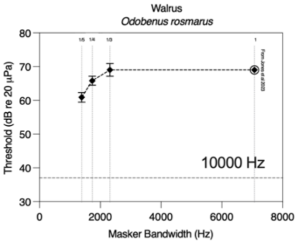




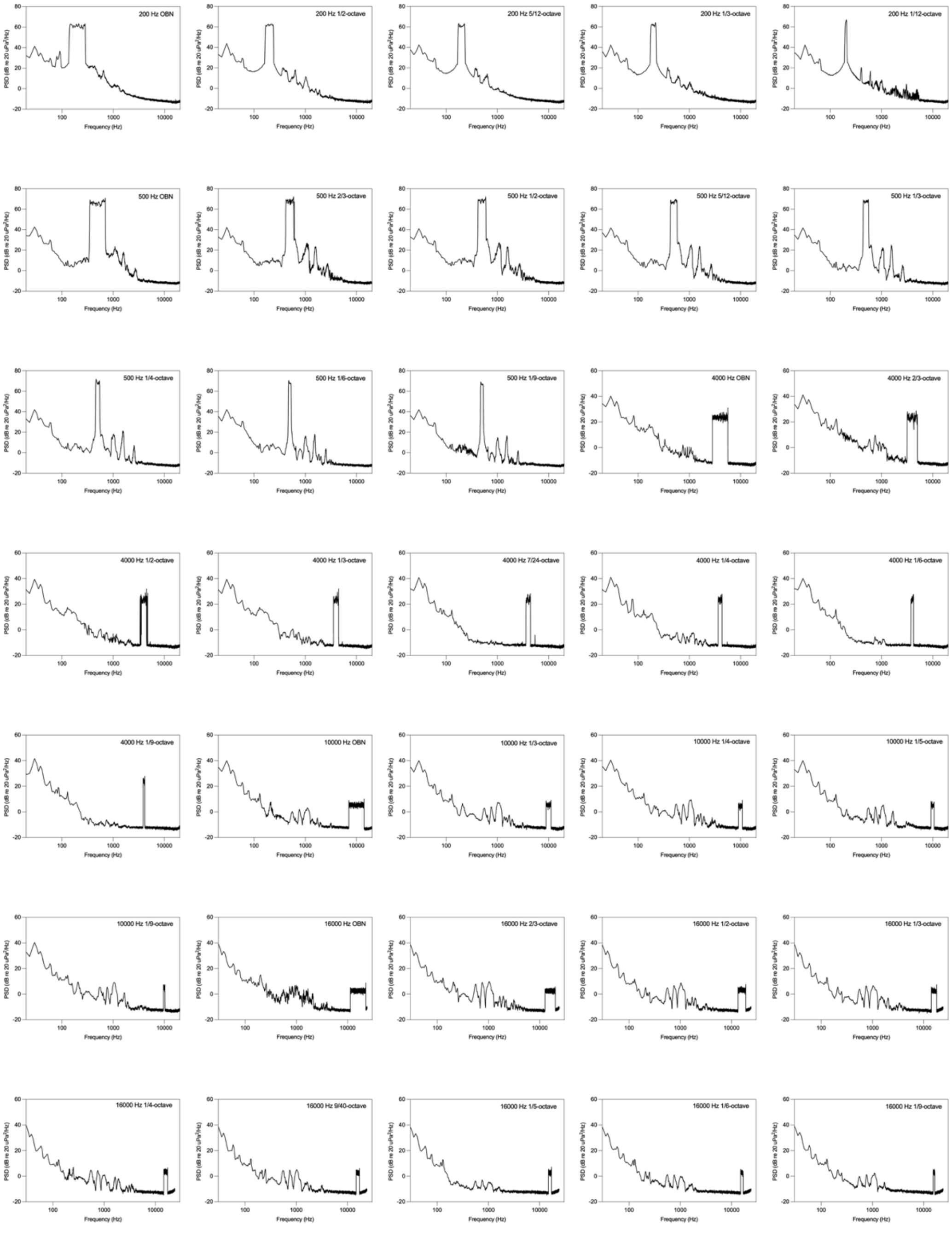








## *Supplement 2.* Exemplar spectra of maskers used for sea lion subject



## Chapter 3: Masking Onset in a California Sea Lion (*Zalophus californianus*)

### Abstract

Despite long-standing interest in auditory masking and the effects of noise on marine mammals, the level at which noise begins to impede the hearing of a listener remains unknown. To investigate the onset of masking as a function of noise level, the hearing of one California sea lion (*Zalophus californianus*) was tested in a hemi-anechoic testing chamber in the presence of generated octave-band, white noise of gradually increasing amplitude. Auditory detection thresholds for pure tone signals were measured in the presence of systematically varied noise amplitude at 0.5, 4, and 16 kHz. Additional measurements were obtained to evaluate the contribution of noise bandwidth to masking onset. Data revealed a frequency-dependent transition zone between the no masking and full masking effect. Further, the degree of masking onset depended on both noise level and noise bandwidth. These findings improve our understanding of auditory masking and inform efforts to accurately predict masking zones in the marine environment.

Key words: Pinnipeds, audiometry, hearing, low-amplitude noise, critical ratio

## Introduction

Measuring the effects of noise on marine mammal hearing has been a focus of research in recent decades due to its implications for mitigating anthropogenic disturbance in the ocean (Southall, 2019). Regulatory efforts have primarily focused within two categories: (1) noise exposures that cause behavioral responses of varying severity and (2) noise exposures that induce temporary or permanent reductions in auditory sensitivity (Southall et al., 2007; Southall et al., 2019). Of these possible effects, temporary changes in hearing sensitivity (temporary threshold shifts, TTS) are most readily measured through behavioral or physiological studies with trained animals. In these experiments, marine mammal subjects are intentionally exposed to high-intensity sounds, and their resulting auditory loss and recovery are documented through progressive hearing tests. The results of such studies are used to inform acoustic exposure guidelines for marine mammal species that may be exposed to harmful sound either under water or in air (*see* Long, 2011; Erbe, 2013; Finneran et al., 2015; Lucke et al., 2016; National Marine Fisheries Service, 2018, Tougaard et al., 2022).

While an emphasis on higher-order auditory effects is important to avoid sound exposures that may cause physical harm to free-ranging marine mammals, the acoustic environment of a listener is often significantly altered long before TTS has occurred. Auditory masking, which is when one sound impedes the concurrent detection of another, is a far more pervasive noise effect that is not considered in most noise mitigation criteria (*see* Erbe, 2013; National Marine Fisheries Service, 2018; Southall, 2019). However, while less relevant to current regulatory standards, measuring the specific exposure conditions under which masking occurs is essential to understanding acoustic habitat degradation that results from anthropogenic noise (Erbe et al., 2016).

Biological metrics for describing auditory masking include the critical ratio and the critical bandwidth. These species- and frequency-dependent parameters are reflective of the frequency coding along the basilar membrane within the mammalian cochlea. Fletcher (1940) first described the basilar membrane as an overlapping series of auditory band-pass filters, with the upper and lower bounds of each filter corresponding to the range of sound frequencies that would contribute to masking a pure tone at the center of the band. These critical bandwidths can be considered a functional proxy for the adjacent sound frequencies that are processed together and have the ability to interfere with one another (Fletcher, 1940; Moore 1993). In contrast, critical ratios are the signal-to-noise ratios (SNRs) required for a listener's detection of a pure tone in surrounding noise that is wider than or as wide as the critical band (Fletcher, 1940). This value is a constant that scales with increasing noise level. Put another way, to be detected, the energy of the pure tone at the subject's masked threshold must exceed the energy contained within the critical bandwidth by a frequency-dependent critical ratio.

Unlike measures of TTS, masking parameters including critical bandwidths and critical ratios can be reliably measured in the presence of relatively low-amplitude noise, (Moore, 1975). Although such masking parameters are relatively easy to measure with trained marine mammals, many data gaps still exist, particularly for amphibious pinnipeds (seals, sea lions, and walruses). Several reviews of available masking studies for marine mammals have identified needs for additional high-resolution information to improve understanding of auditory masking (Reichmuth, 2012; and Erbe et al. 2016; Branstetter and Sills, 2022). Currently, masking in the environment is predicted using the targeted species' hearing thresholds and critical ratios and the estimated received level of the noise source(s) in question (see Erbe et al. 2016; Moore, 1993). These predictions would benefit from quantitative research that focuses on the functionality of these masking metrics in various noise scenarios. For example, because previous studies started testing at higher amplitudes, the exposure level at which noise begins to affect hearing (the noise level associated with the onset of masking) is not well understood. Furthermore, as noise increases beyond the level of masking onset, it is unclear how the growth of masking behaves or if the critical ratio is immediately applicable. This operational understanding of hearing is limited not only for marine mammals but for all mammals.

An informed consideration of the full spectrum of auditory masking is ultimately going to be most valuable when considered in the context of other noise effects. When evaluating the effects of a particular sound source,  its degree of impact ranges from audibility up to discomfort or physical injury (Richardson et al., 1995). The potential for auditory masking and varying degrees of behavioral response (*i.e.* avoidance or cessation of foraging; *e.g.* Blackwell et al. 2015) also exist along this continuum. Audiometric data from trained subjects have established the conditions under which TTS (and by extrapolation, permanent threshold shift or PTS) is expected to occur for many species of odontocetes (toothed whales) and pinnipeds (*see* Southall et al., 2019). These findings contribute an important anchoring point for policy makers, and provide an upper bound for other noise effects (e.g. masking). However, empirical data describing lower order noise effects– including the onset of auditory masking–are imperative to further enrich and anchor these predictive models with empirical data and improve predictive models and characterize the zones of masking surrounding sound sources in the environment.

Here, masking as a function of noise level is measured and reported for one highly trained subject, a California sea lion (*Zalophus californianus*). While many individuals across taxa would need to be tested to definitively describe this masking phenomenon in marine mammals, this foundational study allows for exploration of low-amplitude noise effects and their consideration in the context of other frequency-dependent masking parameters (i.e., critical bandwidths and critical ratios). Because auditory masking occurs at the level of the cochlea, masking parameters are the same regardless of the peripheral sound pathway. Thus, these data collected with airborne sounds are applicable to masking predictions in both terrestrial and marine environments and should support an improved understanding of hearing in this species. Further, the quantitative description of the onset of masking can inform aspects of both auditory and behavioral criteria for noise exposure mitigation efforts.

## Methods

### *General Approach*

Hearing thresholds were measured for the sea lion in air at three frequencies (0.5, 4, and 16 kHz) in quiet conditions to determine absolute (unmasked) thresholds, as well as in the presence of masking noise at varying levels. Signal-to-noise ratios were calculated at the sea lion's threshold for each frequency-level combination to determine the relative level at which wideband noise begins to influence hearing.

### *Subject*

The subject was a 15-year-old female California sea lion (*Ronan*, NOA0006602) with no known otological problems and no previous exposure to ototoxic medications. She had previously participated in several behavioral auditory studies, including similar masking trials. These studies were conducted both with airborne sounds (Cook et al., 2013; Reichmuth et al., 2017; Rouse et al., 2017; Jones et al., 2023) and waterborne sounds (Reichmuth et al., 2013; Cunningham et al., 2014a, 2014b; Cunningham 2016; Sills et. al, *in prep*). *Ronan* was trained to voluntarily enter an acoustic testing chamber along with her trainer to participate in cooperative hearing tests using a go/no-go paradigm as in Reichmuth et al. (2017).

Research was conducted without harm using operant conditioning methods and positive reinforcement. The sea lion's scheduled diet was not constrained for experimental purposes. Research was authorized by the United States National Marine Fisheries Service under marine mammal research permit 23554. Animal protocols were reviewed and approved by the Institutional Animal Care and Use Committee at the University of California Santa Cruz.

### *Test Environment*

Audiometric testing at 0.5 kHz occurred outdoors in the subject's holding enclosure. Her relatively high hearing threshold at this frequency (44 dB re 20 µPa; Jones et al., 2023) and typical ambient noise in the surrounding ⅓ octave band (17 dB re 20μPa2/Hz) provided a sufficiently quiet environment for the presentation of planned masking noise levels. The enclosure included a station marker and response target for the sea lion. The experiment was controlled by an operator positioned out of view of the sea lion. The outdoor enclosure and the testing configuration for *Ronan* are described in detail in Jones et al. (2023) and Chapter 2 of this dissertation.

Given the sea lion's more sensitive hearing at higher frequencies, audiometric testing at 4 and 16 kHz was conducted in a modified hemi-anechoic acoustic chamber (Eckel Industries, Cambridge, MA, USA) that contained a 3.3 × 2.3 × 2.2 m testing room with double-paneled stainless-steel walls and ceiling lined with sound-attenuating, fiberglass-filled aluminum wedges. The solid floor of the acoustic chamber was covered with 4 cm thick foam mats. Typical ambient noise levels in the chamber were < -23 dB re 20 μPa2/Hz and < 28 dB re 20 μPa2/Hz at these at 4 and 16 kHz, providing a threshold-to-noise offset of > 28 and > 33 dB at these frequencies. The experiment was controlled remotely from an adjacent, sound-isolated room where the operator could monitor surveillance cameras in the test enclosure while remaining out of view. During testing, a trainer was positioned in the test room with sea lion *Ronan*. The trainer was blind to the experimental conditions and wore noise-canceling, over-the-ear headphones during testing to obscure any acoustic stimuli and to receive instructions from the operator. *Ronan* used a similar station and response target in the chamber as in the outdoor condition. At the start of each trial presented during a session, the trainer prompted *Ronan* to place her chin on the station placed 0.6 m above the floor and 1.2 m from the sound projector. *Ronan* reported the presentation of a test tone by pressing a response target 0.5 m to her left.

### *Test Stimuli and Apparatus*

Tonal signals were 1-s sinusoids with 50-ms linear ramps that were generated using the Hearing Test Program (HTP) LabVIEW (NI) software (Finneran, 2003). The digital signals were converted to analog via a NI USB-6251 (NI, Austin, TX) data acquisition board and then passed through a 0.1—250 kHz bandpass active filter module (Krohn-Hite, Brockton, MA) and a two-channel passive mixer (Mix 2:1, Radial Engineering, Vancouver, Canada). The 0.5 kHz signals were projected from a KH80 DSP-powered studio monitor with an internal amplifier (0.057–21 kHz, Neumann, Berlin, Germany) while the 0.4 and 16 kHz signals were projected from a Vifa ultrasonic dynamic speaker with a portable ultrasonic power amplifier (Avisoft Bioacoustics, Glienicke/Nordbahn, Germany).

Masking stimuli were octave-band Gaussian noise maskers centered around each test frequency. They were generated using a custom LabVIEW virtual instrument and calibrated before every session to ensure the masker was spectrally flat and that the masker's power spectral density level was within 1 dB of the desired target level. During testing, this masking noise was projected continuously during the session using Audacity® software (version 3.0.0) through the computer's internal sound card. It was mixed with the test tone by a two-channel passive mixer before being transmitted through the designated speaker (Figure 1).

Audiometric signals and maskers at each frequency were calibrated daily using a B&K 2250 sound level meter (Brüel and Kjær A/S, Naerum, Denmark) linked to the same LabVIEW virtual instruments used to generate the signals. The sea lion's head at the station was set in a reliable position for each trial. The tonal and masking stimuli were calibrated at the position of the sea lion's left or right ear depending on frequency (whichever side had the louder received level). Signal and noise stimuli were spatially mapped prior to testing at each frequency within a 3 cm x 3 cm x 3 cm area to ensure that the maximum deviation from the calibration position was +/- 3 dB.

While the noise maskers were calibrated using the spectral density level, the ⅓ octave-band level of received noise surrounding the test frequency for each noise condition was calculated *post-hoc* as:

$$BL = PSD + 10\text{Log}(BW)$$

where BL is the noise band level (dB re 20 µPa), PSD the noise power spectral density (dB re (20 µPa)$^2$/Hz), and BW the noise bandwidth (Hz).

*Audiometry*

The sea lion's absolute (unmasked) hearing thresholds at 0.5, 4, and 16 kHz were measured using a go/no-go signal detection paradigm (Stebbins, 1970) that consisted of signal-present and signal-absent trials in a predetermined, pseudorandom order at a ratio of 70:30. On each trial, *Ronan* positioned at the station for a 6-s interval. She reported detection of the tone stimulus on signal-present trials by moving from the station to press the response target with her nose. Signal onset varied between 1 and 5 s during each 6-s trial window. On signal-absent trials, *Ronan* remained at the station for the full 6-s trial window to report that no signal was detected. Correct responses were marked with a conditioned acoustic reinforcer (a buzzer) activated by the operator followed by a food (fish) reward delivered by the trainer. Incorrect responses (misses on signal-present trials and false detections on signal-absent trials) were not reinforced, and the trainer reset the sea lion at the station and stepped out of view before moving on to subsequent trials.

The absolute thresholds were determined for each frequency using an adaptive staircase method (Stebbins, 1970). A session began with the signal amplitude set at a suprathreshold level and decreased by 2 dB after each correct detection and increased by 4 dB after each miss. Sessions ended after 3-5 descending hit-to-miss transitions were obtained (15-40 trials). Thresholds were determined as the average of 15 stable hit-to-miss transitions across 2-5 sessions (standard deviation < 2 dB), with 1-2 sessions conducted per day. False alarm rates were determined as the proportion of false detections on signal-absent trials. False alarm rates > 0 and ≤ 0.3 were considered acceptable and comparable across conditions.

Masked hearing thresholds were measured for the same tonal signals in the presence of noise of varying levels. Seven noise level conditions were generated for each frequency to capture the onset of masking as noise level increased. Masking levels, measured in terms of power spectral density, were -20, -15, -10, -5, +0, +5, and +10 dB relative to the subject's measured absolute threshold. Within each audiometry session, noise level was held constant. Across sessions, noise level conditions were shuffled in pseudorandom blocks. Ronan was tested at each noise condition once per block, and these session blocks were repeated until a final threshold was determined for each frequency-masking level condition.

Following planned masked threshold measurements with spectrally flat, octave-band wide noise, an additional set of masking measurements were completed for the 16 kHz stimuli. Masked thresholds were re-measured with the same seven masking noise levels, this time in the presence of 1/4-octave band noise, which approximates the sea lion's critical bandwidth (measured in Chapter 2). We did this to assess whether the noise band being set equal to the critical bandwidth would produce different results than wider band noise in terms of masking onset for these low-amplitude stimuli.

## Results

### *Absolute and masked thresholds*

The sea lion's absolute thresholds at 0.5, 4, and 16 kHz (Table I) were as predicted with low variance (std dev < 2 dB) and consistent response bias (false alarm rates 0.12-0.27). Measured hearing thresholds were within 2 dB of those measured previously in the same enclosures (Reichmuth et al., 2017, Jones et al. 2023), confirming this subject's behavioral reliability during audiometry.

Masked thresholds were measured at the same frequencies in the presence of octave-band noise at seven noise level conditions (Table I). These masked thresholds showed similar low variance (std dev < 2 dB) and response bias (false alarm rates 0.08-0.28) across the frequency-noise level combinations.

*Masking onset*

Threshold values as a function of noise level show similar patterns of masking onset at frequencies of 0.5, 4, and 16 kHz (Table 1, Figure 2). Thresholds collected in the lowest amplitude noise conditions (-20 dB and -15 dB re: threshold) were equal to the subject's absolute thresholds at each frequency and were considered unmasked. At the highest amplitude noise conditions (+0 dB, +5 dB, and +10 dB re: threshold), signal-to-noise ratios at threshold were 20, 28, and 33 dB for the 0.5, 4, and 16 kHz conditions, respectively. These values are within 1 dB of previously published critical ratio values for this subject (Jones et al. 2023), demonstrating full masking in these noise conditions..

At each frequency, masked thresholds began to increase as a function of noise level when the noise PSD was 10 to 5 dB below the subject's hearing threshold, as shown in Figure 2. In the -10 dB noise masker condition, thresholds were elevated by 4, 8, and 15 dB for the 0.5, 4, and 16 kHz conditions obtained with wider (octave) band noise. When the masking noise at 16 kHz was narrowed to ¼ of an octave band, the threshold elevation for the -10 dB masker declined from 15 to 6 dB. There was no apparent pattern masking onset relative to the ⅓ octave-band level. However, when masking noise PSD was high (0 to 10 dB above absolute threshold), the subject's masked threshold was always similar (within 2 dB) to the ⅓ octave-band noise level.

## Discussion

The relationship between masking noise level and hearing threshold was revealed through behavioral measurements obtained with one California sea lion. Audiometric testing conducted at 0.5, 4, and 16 kHz spanned a five-octave range that included the sea lion's region of best hearing sensitivity in air (near 12 kHz; Reichmuth et al., 2017) and the region of typical sound production (near 8 kHz, *see* Southall et al., 2019). The onset and growth of auditory masking was captured as noise amplitude was gradually increased. No masking effect was observed when the PSD of surrounding noise was 15 dB or more below the corresponding absolute hearing threshold. A transition zone where partial masking effect was observed occurred when noise PSD was set 5 to 10 dB below the corresponding hearing threshold. Full masking effect occurred at higher masker amplitudes, when noise PSD was set equal to or above the subject's absolute hearing threshold. From this point on, the threshold-to-noise offset was equal to the critical ratio and remained consistent as noise level increased. The same pattern was evident at each of the frequencies evaluated.

These results are generally consistent with Fletcher (1940), who stated that a tonal signal would need to exceed the PSD of surrounding noise by a stable critical ratio to be detected under full masking effect. Furthermore, we observed that full masking effect occurred when the 1/3 octave-band sound pressure level of the noise was equal to the subject's masked hearing threshold. This confirms that the sea lion's critical bandwidths at these frequencies can be reasonably approximated as 1/3 of an octave wide. Direct critical bandwidth measurements for this subject (*see* Chapter 2) show this approximation to be most applicable at 4 and 16 kHz, where measured critical bands are about 23% of center frequency, or 1/3 octave. This approximation was less accurate at 0.5 kHz, where the measured critical band was somewhat wider. Despite these general consistencies with traditional theories of masking, there was a significant deviation in terms of masking onset. Specifically, Fletcher's model would predict no masking within the transitional zone observed in this study.

For the sea lion, the amount of masking observed at onset (the initial increase in threshold with increasing noise level) was greatest at higher frequencies. Within the zone of partial masking, increases in noise level also resulted in more masking at higher frequencies, prior to reaching a stable plateau when noise PSD reached or exceeded the absolute (unmasked) hearing threshold. This effect could be explained by the equal power spectrum model of masking (Moore, 1996), which describes how the energy contained within the target signal must exceed the energy contributed by the masking stimulus within the critical band in order to be detected by a listener. A wider critical band (i.e., 2560 Hz for 16 kHz vs 165 Hz for 500 Hz for a sea lion; see Chapter 2) corresponds to a greater amount of competing energy and a larger increase in masking potential with each incremental increase in noise level.

The specific effect of noise bandwidth on masking onset was tested at 16 kHz, where thresholds were measured with wider (1-octave) band noise and narrower (¼-octave) band noise approximating the critical bandwidth for this subject (Chapter 2). For these two noise bandwidth conditions, onset of partial masking occurred at the same noise level: 10 dB below the absolute threshold determined at 16 kHz. However, the amount of masking observed was greater in the wider noise bandwidth condition. The initial growth in masking as a function of increasing noise level was also greater for the wider-band noise condition. These differences in masking effect as a function of noise bandwidth could be explained by an upward spread of masking. In this process, low-frequency noise outside the critical band contributes to the overall masking potential of a wider band noise stimulus (Moore, 1995). This is surprising in the present case given that the upward spread of masking is typically only considered to be relevant when noise amplitude is exceedingly high (Fletcher, 1940). Here, even when the noise level was relatively low, as long as the noise bandwidth was wider than the critical bandwidth, the lower frequency components of the noise apparently contributed to the overall masking effect. When the noise PSD was equal to or exceeded the absolute threshold, the bandwidth of the noise no longer influenced the amount of masking observed; threshold-to-noise offsets were constant (equal to the critical ratio) regardless of increasing noise level.

These data describing the onset and growth of masking in the presence of low-amplitude noise for one expert subject provide a helpful perspective when considering the area of influence surrounding a given noise source or the degree of auditory impact on a listener. Taking partial masking into account affects the area over which masking would be expected. When using methods that apply hearing thresholds to determine active space (e.g., Southall et al., 2003; Jensen et al., 2012; Erbe et al., 2016), the zone of influence surrounding a particular noise source may be underestimated since an exposure level below the threshold for the target species is not considered. For example, in this study, noise with a PSD 5 dB below the sea lion's absolute threshold at 16 kHz resulted in a masked threshold elevated by 25 dB–in this scenario, it would have been assumed that the surrounding noise would not alter this subject's hearing. Further, when the noise was 5 dB PSD below threshold at 0.5 kHz, the sea lion's hearing threshold was increased by 4 dB. While this is a comparatively small increase in threshold, this difference may be enough to keep the listener from interpreting necessary information within a biologically important signal (see Dooling et al., 2009; Branstetter et al., 2016). These findings highlight our somewhat limited ability to make accurate masking estimates given the available operational understanding of hearing in noise–even when key masking parameters are defined. However, these findings also provide some quantitative basis for practical evaluations of real-world noise exposure scenarios

The results of this exploratory study indicate that auditory masking is not expressed as a simple step function, where a signal is either unaltered or completely masked by noise–with detection thresholds one critical ratio above the noise. Rather, the fine-scale measurements from this individual show the complex transition zone between absolute and fully masked detection thresholds for relevant acoustic cues. Put another way, we show here that the growth of masking occurs gradually and that the critical ratio does not apply in all noise scenarios. This description of masking onset in relatively low-noise conditions is most applicable in very quiet or pristine acoustic environments–which are rare in nature. Thus, the applied value of these measurements lies in identifying the conditions under which a noise source starts to affect hearing (*i.e.* the edge of the zone of masking). This new metric of masking onset provides an objective anchoring point that defines the lower bound of noise exposure and can be quantitatively linked to the characterization of higher-level noise impacts like TTS (see Pirotta, 2022a). Currently, this anchoring point is defined from ambient noise metrics that are much more subjectively determined–i.e. the noise band, location,  or ambient noise percentile level (see Pirotta et al., 2022b). Models that predict the probability of behavioral changes in response to a noise source can instead be bracketed between masking onset and TTS, metrics that are both rooted in empirical, taxa-specific data.

It is important to note that the data presented here describe masking onset for one expert subject. The results are consistent and–while their underlying explanations remain, in some cases, unknown–the data demonstrate reliable patterns in masking effects for this individual. While this study suggests how the active space of an acoustic stressor may be misrepresented in current models, additional work is needed to increase sample size for this species, include other species, and expand to evaluate additional frequencies and noise bandwidths. Even so, the present work contributes to a refined understanding of the noise conditions that affect hearing, which can improve estimations for zones of influence surrounding human-generated noise sources.

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## References

Blackwell, S. B., Nations, C. S., McDonald, T. L., Thode, A. M., Mathias, D., Kim, K. H., ... & Macrander, A. M. (2015). Effects of airgun sounds on bowhead whale calling rates: evidence for two behavioral thresholds. PloS one, 10(6), e0125720.

Branstetter B k., Ketten DR, Arruda J, et al (2016) Hearing mechanisms and noise metrics related to auditory masking in bottlenose dolphins (*Tursiops truncatus*). In: Popper AN, Hawkins A (eds) The Effects of Noise on Aquatic Life II. Springer Science+Business Media, LLC, New York, pp 529–538

Branstetter, B. K., & Sills, J. M. (2022). Mechanisms of auditory masking in marine mammals. Animal Cognition, 25(5), 1029-1047.

Clark CW, Ellison WT, Southall BL, et al (2009) Acoustic masking in marine ecosystems: Intuitions, analysis, and implication. Mar Ecol Prog Ser 395:201–222. https://doi.org/10.3354/meps08402

Cook P, Rouse A, Wilson M, Reichmuth C (2013) A California sea lion (Zalophus californianus) Can Keep the Beat: Motor Entrainment to Rhythmic Auditory Stimuli in a Non Vocal Mimic. J Comp Psychol 127:412–427. https://doi.org/10.1037/a0032345

Cunningham KA, Hayes SA, Wargo Rub AM, Reichmuth C (2014a) Auditory detection of ultrasonic coded transmitters by seals and sea lions. J Acoust Soc Am 135:1978–85. https://doi.org/10.1121/1.4868371

Cunningham KA, Reichmuth C (2016) High-frequency hearing in seals and sea lions. Hear Res 331:83–91. https://doi.org/10.1016/j.heares.2015.10.002

Cunningham KA, Southall BLL, Reichmuth CJ (2014b) Auditory sensitivity of seals and sea lions in complex listening scenarios. J Acoust Soc Am 136:3410. https://doi.org/10.1121/1.4900568

Dooling RJ, Blumenrath SH, Smith E, Fristrup K (2013) NOISE-CON 2013 Evaluating Anthropogenic Noise Effects on Animal Communication. In: Noise-Con2013. Denver, Co., p August 26-28

Erbe C, Reichmuth C, Cunningham K, et al (2016) Communication masking in marine mammals: A review and research strategy. Mar Pollut Bull 103:15–38. https://doi.org/10.1016/j.marpolbul.2015.12.007

Finneran JJ (2003) An Integrated Computer-Controlled System for Marine Mammal Auditory Testing, Technical Document 3159. San Diego, CA

Finneran JJ, Schlundt CE, Branstetter BK, et al (2015) Effects of multiple impulses from a seismic air gun on bottlenose dolphin hearing and behavior. J Acoust Soc Am 137:1634–1646. https://doi.org/10.1121/1.4916591

Fletcher H (1940) Auditory Patterns. Rev Mod Phys 12:47–66. https://doi.org/https://doi.org/10.1103/RevModPhys.12.47

Jones RA, Sills JM, Synnott M, et al (2023) Auditory masking in odobenid and otariid carnivores. J Acoust Soc Am 154:1746–1756. https://doi.org/10.1121/10.0020911

Lucke, K., Scowcroft, G., Winter, H. V., Knowlton, C., Lam, F. P. A., Hawkins, A., & Popper, A. N. (2016, July). International harmonization of approaches to define underwater noise exposure criteria and needs of the international regulatory community. In Proceedings of Meetings on Acoustics (Vol. 27, No. 1). AIP Publishing

Long, R. (2011). The Marine Strategy Framework Directive: a new European approach to the regulation of the marine environment, marine natural resources and marine ecological services. Journal of Energy & Natural Resources Law, 29(1), 1-44.

Moore BCJ (1993) Frequency analysis and pitch perception. In: Yost WA, Popper AN, Fay RR (eds) Human Psychophysics, Springer Handbook of Auditory Research. New York, NY, pp 56–115

Moore BCJ (1995) Frequency Analysis and Masking. In: Moore BCJ (ed) Hearing. Academic Press, Harcourt Brace & Company, San Diego, CA, pp 161–200

National Marine Fisheries Service (2018) 2018 Revisions to: Technical Guidance for assessing the effects of anthropogenic sound on marine mammal hearing (Version 2.0): Underwater acoustic thresholds of permanent and temporary threshold shifts. NOAA Technical Memorandum NMFS-OPR-59, U.S. Dept. of Commerce, NOAA

Pirotta, E., Thomas, L., Costa, D. P., Hall, A. J., Harris, C. M., Harwood, J., ... & Tyack, P. L. (2022a). Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. Science of the Total Environment, 821, 153322.

Pirotta, E., Booth, C. G., Calambokidis, J., Costa, D. P., Fahlbusch, J. A., Friedlaender, A. S., ... & Southall, B. L. (2022b). From individual responses to population effects: Integrating a decade of multidisciplinary research on blue whales and sonar. Animal Conservation, 25(6), 796-810.

Reichmuth C (2012) Psychophysical studies of auditory masking in marine mammals: key concepts and new directions. In: Popper ANP, Hawkins A (eds) The Effects of Noise on Aquatic Life. Springer-Verlag, Berlin, pp 23–27

Reichmuth C, Holt MMMM, Mulsow J, et al (2013) Comparative assessment of amphibious hearing in pinnipeds. J Comp Physiol A Neuroethol Sensory, Neural, Behav Physiol 199:491–507. https://doi.org/10.1007/s00359-013-0813-y

Reichmuth C, Sills JM, Ghoul A (2017) Psychophysical audiogram of a California sea lion (Zalophus californianus) listening for airborne tonal sounds in an acoustic chamber. Proc Meet Acoust 30:010001. https://doi.org/10.1121/2.0000525

Rouse AAAA, Cook PFPF, Large EW, Reichmuth C (2016) Beat keeping in a sea lion as coupled oscillation: Implications for comparative understanding of human rhythm. Front Neurosci 10:1–12. https://doi.org/10.3389/fnins.2016.00257

Southall EL, Finneran JJ, Reichmuth C, et al (2019) Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. Aquat Mamm 45:. https://doi.org/10.1578/AM.45.2.2019.125

Stebbins WC (1970) Principles of animal psychophysics. In: Stebbins WC (ed) Animal Psychophysics: the Design and Conduct of Sensory Experiments. Appleton-Century-Crofts, New York, pp 1–19

Tervo OM, Christoffersen MF, Simon M, et al (2012) High source levels and small active space of high-pitched song in bowhead whales (*Balaena mysticetus*). PLoS One 7.

Tougaard, J., Beedholm, K., & Madsen, P. T. (2022). Thresholds for noise induced hearing loss in harbor porpoises and phocid seals. The Journal of the Acoustical Society of America, 151(6), 4252-4263.

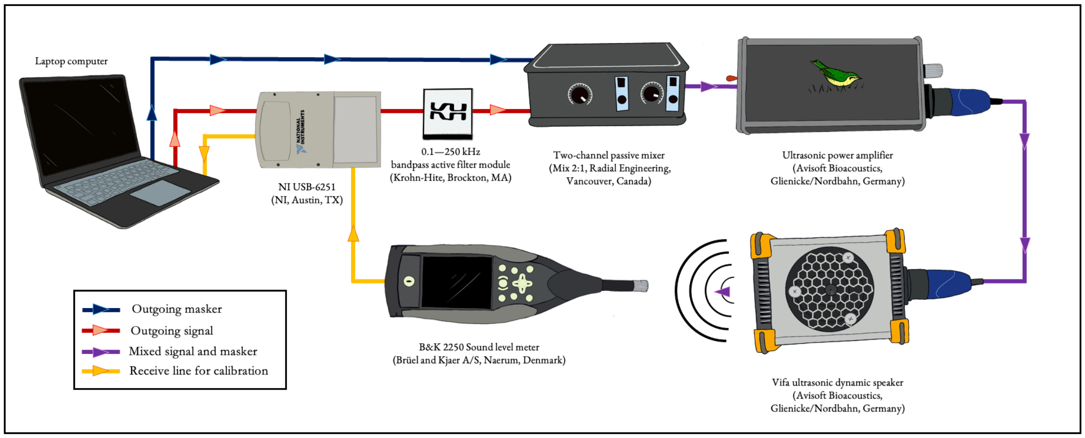
# Chapter 3. Masking onset in a California sea lion (*Zalophus californianus*)

## Figures and Tables

| | 0.5 kHz | | | 4 kHz | | | 16 kHz (OBN) | | | 16 kHz (QOBN) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Noise Condtion dB re: threshold | Threshold dB re 20 uPa | Stdev | SNR dB | Threshold dB re 20 uPa | Stdev | SNR dB | Threshold dB re 20 uPa | Stdev | SNR dB | Threshold dB re 20 uPa | Stdev | SNR dB |
| -20 | 45 | 1.35 | 21 | 10 | 1.23 | 13 | 5 | 0.83 | 20 | 5 | 1.53 | 20 |
| -15 | 44 | 1.03 | 15 | 10 | 1.26 | 19 | 5 | 1.77 | 15 | 5 | 1.31 | 15 |
| -10 | 48 | 0.83 | 14 | 18 | 1.47 | 18 | 20 | 0.98 | 15 | 11 | 1.51 | 6 |
| -5 | 55 | 1.21 | 16 | 25 | 1.35 | 20 | 30 | 1.01 | 30 | 25 | 1.69 | 25 |
| +0 | 64 | 1.03 | 20 | 38 | 1.45 | 28 | 38 | 1.03 | 33 | 39 | 1.49 | 34 |
| +5 | 69 | 1.31 | 20 | 44 | 1.63 | 29 | 43 | 1.69 | 33 | 44 | 1.41 | 34 |
| +10 | 74 | 1.13 | 20 | 48 | 2.00 | 28 | 48 | 1.23 | 33 | 49 | 1.35 | 34 |
| Absolute threshold | 44 | 1.23 | 27 | 10 | 1.23 | 35 | 5 | 1.77 | 33 | - | - | - |

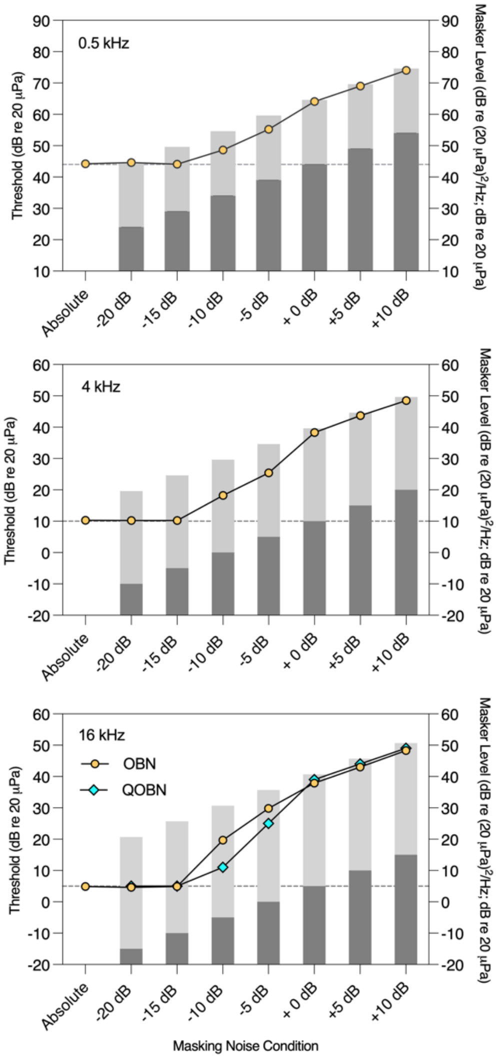
Table I. Absolute and masked thresholds and associated standard deviations (Stdev) and signal-to-noise ratios (SNR) for one California sea lion. Masking noise conditions ranged from 20 dB PSD to 10 dB PSD above below the subject's measured threshold.

FIG 1. Experimental equipment schematic



* For testing conducted at 0.5 kHz, the ultrasonic power amplifier and Vifa speaker were replaced by a KH-80 studio speaker.

FIG 2. Hearing thresholds for one California sea lion measured at three frequencies in the presence of varied masking noise levels and bandwidths. Noise conditions on the x-axis are spectral density levels referenced to the subject's absolute threshold, which is plotted and marked by the horizontal dashed line. Masking noise levels on the right y-axis are presented in two metrics: power spectral density (dark gray bars) and 1/3 octave-band level (light gray bars). Measured thresholds are shown as filled symbols corresponding to the left y-axis were calculated from 15 hit-to-miss transitions. Each threshold had a standard deviation < 2 and false alarm rates across all frequencies were < 0.3. The subject was tested at 16 kHz twice, once in the presence of an octave-band noise masker (OBN, circle symbols) and again with a 1⁄4 octave-band noise masker (QOBN, diamond symbols). At each frequency, masking onset occurred when noise PSD was 10 dB below the subject's measured threshold. Once the noise PSD was equal to absolute threshold (+0 dB masking noise condition), the signal-to-noise ratio at threshold was always equivalent to the critical ratio.



## General Discussion

The objective of this dissertation was to improve understanding of auditory masking in pinnipeds and other marine mammals. The studies presented herein include representatives of all three pinniped families, filling data gaps for sea lions, walruses, and seals with high-resolution hearing data. With a more complete understanding of auditory masking in pinnipeds, key similarities and differences between these evolutionarily distinct groups of amphibious carnivores have been revealed. The results obtained in each of these auditory masking experiments also have practical applications, allowing for the implementation of more accurate masking models for free-ranging pinnipeds.

### *Contributions to knowledge of pinniped hearing*

In a review of available masking data for marine mammals, Erbe et al. (2016) outlined key knowledge gaps for pinnipeds, including limited critical ratio and critical bandwidth data for otariids (sea lions and fur seals), a complete lack of masking data for odobenids (walruses), and minimal critical bandwidth measurements for phocids (true seals). Without comprehensive descriptions of masking parameters in these species, it is difficult or impossible to predict the extent of masking experienced by pinnipeds exposed to different levels of natural and anthropogenic noise.

The critical masking ratios provided in Chapter 1 resolved inconsistencies in prior critical ratio data for sea lions and related otariids–which did not fit expected trends noted in other mammalian carnivores (Moore and Schusterman 1987; Southall et al. 2000, 2003)—and produced a single dataset extending across each subject's hearing range.

Similarly, the critical bandwidths described in Chapter 2 extended the available data for otariids down to 200 Hz and up to 10 kHz. These measurements were generally consistent with those presented for a single sea lion in Southall et al. (2003) that was not tested below 2 kHz. The results from this study showed that sea lion Q values (or critical bandwidths as a proportion of center frequency) follow expected trends for mammals between 4 and 10 kHz and equal approximately 0.23 in this range. At lower frequencies (< 0.5 kHz), critical bandwidths apparently begin to widen. This is inconsistent with a constant Q model (see, e.g., Lemonds et al. 2011) and has important implications for the evaluation of masking by low-frequency anthropogenic noise.

Hearing data previously available for walruses were limited to four studies: an in-water audiogram (Kastelein et al. 2002), an in-air audiogram (Kastelein et al. 1996), a free-field behavioral response study (Kastelein et al. 1993), and an assessment of in-air hearing range (Reichmuth et al. 2020). The data presented here do not provide a full terrestrial hearing profile for walruses but do provide threshold measurements across their functional range of hearing and reveal some key aspects of their absolute sensitivity. For example, the walrus high-frequency roll off in sensitivity to airborne sounds was determined to fall just above 10 kHz markedly lower than for other pinnipeds. Further, despite background noise being higher in the walrus testing environment, walrus ambient thresholds reported in Chapter 1 were lower than the sea lion's absolute thresholds at the lowest frequencies tested (0.08 kHz and 0.1 kHz). Because the walrus thresholds were noise-limited in this range, is possible that their true low-frequency hearing ability is even better than described here.

In terms of auditory masking, the critical ratio data provided in Chapter 1 and the critical bandwidth data provided in Chapter 2 showed that walruses and sea lions are similarly able to extract pure tones from white noise. Since there were no published masking data for walruses prior to this study, walruses have been grouped with sea lions, fur seals, and sea otters in the 'other marine carnivores' category for noise management efforts (Southall et al. 2019). This designation seems reasonable based on the results of this dissertation.  Despite apparent differences in absolute hearing sensitivity, walruses show a similar degree of frequency selectivity to sea lions. Overall, the solid agreement in auditory masking parameters between sea lions and walruses indicates that the more readily testable sea lions appear to be an appropriate representative species for the "other marine carnivore" group.

Finally, among the pinnipeds, seals were the best studied in terms of masking parameters, particularly with respect to critical ratio values. However, only two previous studies evaluated critical bandwidths in seals (Turnbull and Terhune 1990; Southall et al. 2003). These data, as with all other critical bandwidth studies in marine mammals, did not include testing below 2 kHz. The critical bandwidth data presented in Chapter 2 are consistent with previous critical band estimations and extend the available data across a much broader frequency range, extending from 100 Hz and up to 10 kHz. When compared to other pinnipeds, seals maintain a surprisingly consistent degree of frequency selectivity through lower frequencies–in other words, their auditory filters align with the constant Q model down to at least 100 Hz. Together, these data suggest that seals are especially well adapted to extracting signals from noise.

In Chapters 1 and 2, audiometric data were collected for the representative pinnipeds in the ambient noise environments of the subjects' home enclosures as opposed to controlled environments like an acoustic testing chamber. This non-traditional approach to audiometry resulted in reliable data with consistently low variance and allowed us access to trained walruses that, among pinnipeds, are some of the most data-deficient species. Given their large body size, walruses could not have been otherwise included in these comparative experiments. The high quality of the resulting data for all subjects, despite uncontrolled ambient noise environments, is encouraging when considering existing knowledge gaps for other data-deficient groups. These results show that certain types of data–specifically those describing hearing in noisy environments–can be readily obtained in ambient noise environments for species that are difficult to study in specialized laboratory conditions.

The series of experiments described in this dissertation were all conducted with cooperative animal subjects that were trained over months to years to be eager and active participants in audiometric research. From these four individuals, I have been able to obtain valuable, high-resolution masking data that can be applied to better understand the effects of noise in otariid, odobenid, and phocid groups. The far-reaching implications of data collected from these few expert subjects highlights the importance of research-focused animal training at specialized facilities as well as in partnerships with zoos and aquariums to benefit wild populations.

### *Masking predictions for free-ranging pinnipeds*

Masking parameters are especially influential when estimating the zones of influence of an anthropogenic noise source or the detection ranges of biologically relevant sounds for pinnipeds in natural habitats. The frequency-dependent and species-specific masking metrics described in this dissertation are not directly applicable to current management strategies that focus on more acute, harmful effects of noise on the auditory system (i.e., temporary and permanent threshold shifts). However, masking metrics are paramount to our understanding of how the introduction of noise alters the acoustic environment in which these animals operate. In Chapter 1, it was demonstrated that critical ratios can be used to reliably determine masked hearing thresholds in stable or averaged noise conditions. For animals that live in relatively noisy environments, like many species of pinnipeds do, these data provide an *in situ* representation of their hearing sensitivity in a given noise background. The critical ratios and critical bandwidths obtained in Chapters 1 and 2 can be applied directly in masking models for pinnipeds under different noise conditions. The masking onset data presented in Chapter 3 provide information about when a noise source may begin to affect hearing and enable more accurate predictions of masking potential for a particular source and provide an objective anchoring point that that can help predict the probability of behavioral changes in response to a noise source.

To illustrate how these data can be applied to real-world acoustic scenarios, consider a sea lion in Monterey Bay listening for a potential predator while foraging at sea. Here, we can use sea lion the masking data collected in this dissertation to estimate the active space of underwater sounds with the following equation:

$$\mathrm{DT} = \mathrm{SL} - 20\log(r) - \alpha r$$

where DT (detection threshold) is either the sea lion’s absolute hearing threshold at the nearest frequency (if ambient noise is sufficiently low) or the noise amplitude plus the critical ratio (if hearing is limited by ambient noise); SL (source level) is the sound pressure level of the target sound within the 1/3-octave band containing peak frequency; 20log(r) is an estimate of sound propagation in the environment through spherical spreading loss; r is the detection distance from the source; and α is the attenuation coefficient of seawater ($\alpha = 0.036 f^{1.5}$ dB km−1, where $f$ is the peak vocal frequency in kHz; *see* Richardson et al. 1995).

In this simplified example, the sea lion is listening for the tonal S1 call of a killer whale with peak energy near 2 kHz and an SL of approximately 150 dB re 1 µPa (Holt et al., 2009) [1]. The sea lion’s underwater hearing  sensitivity in this frequency range is 67 dB re 1 µPa (Reichmuth et al., 2013) and the critical ratio at 2 kHz is 28 dB (Chapter 1, Jones et al., 2023). The detection range can be compared in ‘low’ and ‘high’ noise environments, with ambient levels estimated from field measurements reported by Casey

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[1] These estimations use broadband source level, and we assume that the source level within the peak 1/3-octave band is also 150 dB re 1 µPa. As source levels within the peak ⅓-OB are likely to be somewhat lower, the true active space is likely to be smaller. However, the relative changes in detection range are representative of the *in situ* effects of increasing noise levels in the marine environment.

et al. (2017). In the low-noise scenario, we have an ambient noise level of approximately 50 dB re (1 μPa$^2$)/Hz. The masking onset data presented in Chapter 3 showed us that noise PSD more than 10 dB below threshold can be effectively ignored[2]. Therefore, in the low-noise environment, DT can be approximated using the absolute hearing threshold for a sea lion in water. Conversely, in a high-noise environment with an ambient level of 80 dB re (1 μPa$^2$)/Hz, the sea lion listener is masked. In this case, DT can be estimated instead by adding the sea lion critical ratio to the noise spectral density level in the surrounding 1/3-octave band. The critical bandwidth for a sea lion near 2 kHz is about 27% of center frequency (Chapter 2), confirming that the ⅓-octave band is the appropriate analysis bandwidth for this calculation.

In the low-noise scenario (50 dB re (1 μPa$^2$)/Hz), the sea lion listener would be able to detect the killer whale call at a range of about 11.6 km. When the noise level is increased to 80 dB re (1 μPa$^2$)/Hz, the detection range for the call falls to 125 m. In this case, the increase in noise results in a reduction in active space for the listener of over 10 km, reducing the listener's detection range for a potential predator by 99%. This example shows how relatively modest increases in the noise background can dramatically alter the acoustic information a listener can extract from their environment. Such reductions in listening space have major consequences when we consider how anthropogenic noise in the marine environment has steadily risen for decades (Duarte et al., 2021). However,

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[2] Typically, with a noise value falling less than one critical ratio below threshold, DT would be approximated by adding the critical ratio to the noise PSD (*e.g.,* Sills et al., 2017). In this case, the masking onset data enable a more accurate estimate of detection range.

putting these masking estimates into the proper ecological context is also important. For instance, while the relative change in detectability for the killer whale call in this example is significant, it is unclear whether a sea lion needs to detect such a call from over 10 km away. These hypothetical listening scenarios should ultimately be compared to how animals behave in their natural environments.

Whether masking metrics or absolute hearing sensitivity are most applicable depends entirely on the acoustic habitat of the listener. For example, animals like walruses and sea lions spend a significant portion of their time in large social groups on coastal terrestrial haulouts (Campagna et al., 2021). Here, in the cacophony of biotic and abiotic noise, an individual must extract relevant signals from conspecifics such as a mother, a pup, or a competitor (Charrier, 2021). In these instances, sea lion and walrus hearing will be often limited by noise, and masking metrics paired with noise measurements would provide the best estimation of hearing. Contrastingly, an Arctic seal's hearing may, in some instances, be best represented by its absolute sensitivity during quieter seasons and by masking data during breeding seasons when multitudes of species are calling in tandem (Southall et al., 2020). Wholly, the utility of the masking data presented here largely depends on the life histories of the species they are being applied to.

### *Future Research*

The behavioral data presented in these three chapters employ classical psychophysical methods that have been used to assess hearing and masking in animals for decades (*see*

Stevens, 1958; Fay, 1988). Testing marine mammals using this approach is labor and time intensive as well as financially demanding, often times relying on very few but reliable and expert subjects. Other methods that use auditory evoked potentials to measure the neurological response to sound stimuli have been developed for use on naïve or stranded marine mammal subjects. However many limitations—such as the frequencies able to be tested—are still being resolved (*see* André et al., 2007). As it currently stands, psychophysical measurements remain the 'gold standard' for measuring sensory perception in marine mammals.

There are many possible directions for future research that build upon the psychoacoustic work presented in this dissertation. First, it is important to increase the sample size of test subjects in order to strengthen the conclusions of each chapter. While it is common for psychophysical studies with trained marine mammals to test one or two individuals, increased sample sizes would provide additional confirmation that the reported masking data are representative of these species and species groupings. Further, the experiments in this dissertation used tonal signals in the presence of controlled, spectrally flattened, white noise. These are simple stimuli that only approximate masking in an environment that is far more complex. Future studies should continue to examine the utility of these masking parameters by comparing masking to those obtained with increasingly complex signal and noise stimuli (as in, *e.g.*, Branstetter et al. 2013; Cunningham et al. 2014). Such efforts could be paired with studies aimed at quantifying differences in detection, discrimination, and recognition thresholds for pinnipeds, which would further enhance active space estimations as it has for cetaceans and birds (e.g.

Branstetter et al. 2016; Dooling 2019). Additionally, to go beyond simple masking metrics like critical ratios and critical bandwidths, exploratory studies measuring the effects of noise outside the critical band on detection thresholds (off-band masking) and the effects of masking noise on cognitive or physiological function would help expand this field of study. Continued efforts to improve our understanding of auditory masking in marine mammals are imperative to enable the consideration of masking in future management efforts.

The information provided in this dissertation significantly advances our understanding of pinniped hearing in noisy environments, filling existing data gaps and enabling improved predictions of the effects of noise on wild marine mammals. Despite these steps forward, there is still much work to be done and exciting prospects for future research.

## References

André, M., & Nachtigall, P. E. (2007). Electrophysiological measurements of hearing in marine mammals. *Aquatic Mammals*, *33*(1), 1.

Branstetter B k., Ketten DR, Arruda J, et al (2016) Hearing mechanisms and noise metrics related to auditory masking in bottlenose dolphins (Tursiops truncatus). In: Popper AN, Hawkins A (eds) The Effects of Noise on Aquatic Life II. Springer Science+Business Media, LLC, New York, pp 529–538

Branstetter BK, Trickey JS, Bakhtiari K, et al (2013) Auditory masking patterns in bottlenose dolphins ( *Tursiops truncatus* ) with natural, anthropogenic, and synthesized noise. J Acoust Soc Am 133:1811–1818. https://doi.org/10.1121/1.4789939

Campagna, C., & Harcourt, R. (Eds.). (2021). *Ethology and behavioral ecology of Otariids and the Odobenid*. New York: Springer.

Casey C, Sills JM, Reichmuth C (2017) Source level measurements for harbor seals and implications for estimating communication space. Proc Meet Acoust 010034:010034. https://doi.org/10.1121/2.0000353

Charrier, I. (2021). Vocal communication in otariids and odobenids. In *Ethology and behavioral ecology of otariids and the odobenid* (pp. 265-289). Cham: Springer International Publishing.

Cunningham KA, Southall BLL, Reichmuth CJ (2014) Auditory sensitivity of seals and sea lions in complex listening scenarios. J Acoust Soc Am 136:3410. https://doi.org/10.1121/1.4900568

Dooling RJ (2019) The Impact of Urban and Traffic Noise on Birds. Acoust Today 15:19. https://doi.org/10.1121/at.2019.15.3.19

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., ... & Juanes, F. (2021). The soundscape of the Anthropocene ocean. *Science*, *371*(6529), eaba4658.

Erbe C, Reichmuth C, Cunningham K, et al (2016) Communication masking in marine mammals: A review and research strategy. Mar Pollut Bull 103:15–38. https://doi.org/10.1016/j.marpolbul.2015.12.007

Fay, R. R. (1988). Comparative psychoacoustics. *Hearing research*, *34*(3), 295-305.

Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K., & Veirs, S. (2009). Speaking up: Killer whales (Orcinus orca) increase their call amplitude in response to vessel noise. The Journal of the Acoustical Society of America, 125(1), EL27-EL32.

Jones RA, Sills JM, Synnott M, et al (2023) Auditory masking in odobenid and otariid carnivores. J Acoust Soc Am 154:1746–1756. https://doi.org/10.1121/10.0020911

Kastelein RA, Mosterd P, Van Ligtenberg CL, Verboom WC (1996) Aerial hearing sensitivity tests with a male Pacific walrus (Odobenus rosmarus divergens), in the free field and with headphones. Aquat Mamm 22:81–93

Kastelein RA, Mosterd P, van Santen B, et al (2002) Underwater audiogram of a Pacific walrus (Odobenus rosmarus divergens) measured with narrow-band frequency-modulated signals. J Acoust Soc Am 112:2173–2182. https://doi.org/10.1121/1.1508783

Kastelein RA, van Ligtenberg CLL, Gjertz I, Verboom WCC (1993) Free field hearing tests on wild Atlantic walruses (Odobenus rosmarus rosmarus) in air. Aquat Mamm 19:143–148

Lemonds DW, Kloepper LN, Nachtigall PE, et al (2011) A re-evaluation of auditory filter shape in delphinid odontocetes: Evidence of constant-bandwidth filters. J Acoust Soc Am 130:3107–3114. https://doi.org/10.1121/1.3644912

Moore PWB, Schusterman RJ (1987) Audiometric assessment of northern fur seals, Callorhinus ursinus. Mar Mammal Sci 3:31–53. https://doi.org/10.1111/j.1748-7692.1987.tb00150.x

Reichmuth C, Sills JM, Brewer A, et al (2020) Behavioral assessment of in-air hearing range for the Pacific walrus (Odobenus rosmarus divergens). Polar Biol 43:767–772. https://doi.org/10.1007/s00300-020-02667-6

Richardson WJ, Greene CR, Malme CI, Thomson DH (1995) Marine Mammals and Noise. Academic Press, Harcourt Brace & Company, San Diego, CA

Southall BL, Schusterman RJ, Kastak D (2000) Masking in three pinnipeds: underwater, low-frequency critical ratios. J Acoust Soc Am 108:1322–1326. https://doi.org/10.1121/1.1288409

Southall BL, Schusterman RJ, Kastak D (2003) Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements. J Acoust Soc Am 114:1660–1666. https://doi.org/10.1121/1.1587733

Southall EL, Finneran JJ, Reichmuth C, et al (2019) Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. Aquat Mamm 45:. https://doi.org/10.1578/AM.45.2.2019.125

Southall, B. L., Southall, H., Antunes, R., Nichols, R., Rouse, A., Stafford, K. M., ... & Rosenbaum, H. C. (2020). Seasonal trends in underwater ambient noise near St. Lawrence Island and the Bering Strait. *Marine Pollution Bulletin*, *157*, 111283.

Stevens, S. S. (1958). Problems and methods of psychophysics. *Psychological bulletin*, *55*(4), 177.

Turnbull SD, Terhune JM (1990) White noise and pure tone masking of pure tone thresholds of a harbour seal listening in air and underwater. Can J Zool 68:2090–2097.