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SHORT NOTE

Behavioral assessment of in-air hearing range for the Pacific walrus (*Odobenus rosmarus divergens*)

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Abstract

The conservation status of wild walruses *(Odobenus rosmarus)* is influenced by rapid warming of the Arctic, loss of seasonal sea ice, and increasing pressures related to anthropogenic activities and associated noise. Few data are available regarding acoustic sensitivity in walruses, although the species is known to be vulnerable to human disturbance. Here, we provide new information to describe the range of sound frequencies that are audible to walruses. These data were obtained through partnership with the Walrus Conservation Consortium and two zoological facilities. Two adult female walruses were trained to cooperate in an auditory detection task by responding to relatively high-amplitude airborne tones of approximately 80 dB re 20 µPa. Once performance was reliable, behavioral responses were generalized to a range of frequencies spanning more than six octaves. The upper- and lower-frequency limits of hearing were determined during audiometric testing with fully calibrated sounds. Results confirmed an audible range of hearing extending from 60 Hz to 23 kHz in air. Hearing range in water is expected to be similar or broader at high frequencies. This study provides evidence that hearing in walruses is different from that of other marine carnivores, including seals, sea lions, and sea otters, and better than suggested by early reports for the species.

Keywords Audiometry · Acoustic · Frequency limits · Pinniped · Odobenid

Introduction

As sea ice retreats, Arctic habitats are confronted with an influx of ocean noise from increased maritime traffic, expanded activities related to oil and gas exploration and production, and escalating military operations (for review see Moore et al. 2012). Among marine mammals inhabiting this region, walruses *(Odobenus rosmarus)* are particularly vulnerable to multiple stressors associated with habitat loss (MacCracken 2012; MacCracken et al. 2017). However, there are limited available data with which to evaluate the environmental effects of underwater noise on this species. Only one study of underwater hearing has been published, based on data for a single adult male walrus (Kastelein et al. 2002). The authors noted some peculiar attributes of the reported hearing sensitivity profile, or audiogram, which differed from similar measurements made in water for other amphibious marine mammals. The walrus exhibited poor hearing ability at both high (> 15 kHz) and low (< 500 Hz) frequencies, an unusual decline in sensitivity around 2 kHz, and relatively low sensitivity overall. It is difficult to derive an evolutionary explanation for this audiogram, because walruses (representing the sole living species in the Family Odobenidae) are not closely related to any mammals, including the other pinnipeds: seals (Phocidae) and sea lions (Otariidae).

Even fewer data are available to describe the hearing abilities of walruses in air. Audiometric testing has been

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conducted over a narrow range of frequencies with one individual trained to listen for tones presented outdoors, either through headphones or in a free field (Kastelein et al. 1996). Threshold measurements for this individual indicated poor sensitivity below 250 Hz and a hearing range extending to at least 8 kHz (higher frequencies were not tested). One field study of hearing has been conducted by observing the spontaneous responses of wild walruses to airborne sounds (Kastelein et al. 1993); this playback study confirmed detection of sounds between 250 Hz and 4 kHz, but did not examine lower or higher frequencies that would suggest a functional range of hearing for the species in air.

In light of the unusual nature of the single audiogram available for this species, renewed interest in the conservation status of wild walruses, and anticipated increases in anthropogenic impacts on walrus habitat, more information about auditory sensitivity is needed. We conducted a simple study with trained walruses living in zoological facilities to expand available audiometric data for the species by measuring the frequency range of hearing in air. Because hearing in air is expected to provide a conservative limit for the frequency range of hearing in water (e.g., Nummela 2008), these data can be used to determine whether the sole underwater audiogram available for the walrus is likely to be representative for the species. More broadly, this effort informs the use of regulatory guidelines for assessing the effects of anthropogenic noise on marine mammals, and suggests priorities for additional bioacoustic research with walruses.

Methods

General approach

Hearing in marine mammals is best studied using behavioral, psychoacoustic methods with trained animals. Under quiet conditions, auditory thresholds can be measured by holding frequency constant while amplitude is progressively lowered until sounds can no longer be detected (Stebbins 1970; Dent 2017). An alternative approach is to hold sound amplitude constant while varying frequency so that the lower- and upper-frequency limits of hearing—or hearing range—can be measured. Because tone amplitude remains relatively high throughout testing, this work can be conducted in outdoor environments without specialized, sound-attenuating acoustic facilities. In the present study, we used this approach to evaluate the frequency range of hearing in air for walruses trained to cooperate in auditory testing procedures. An adaptation of this method was recently used to passively estimate hearing range in sea otters (*Enhydra lutris*), a species for which no auditory information was previously available (Ghoul and Reichmuth 2014a); results were subsequently validated by traditional psychoacoustic testing with trained animals (Ghoul and Reichmuth 2014b).

Subjects

Two adult female Pacific walruses (*Odobenus rosmarus divergens*) at Point Defiance Zoo and Aquarium (PDZA, Tacoma, Washington) and Six Flags Discovery Kingdom (SFDK, Vallejo, California) were enrolled in the study. These individuals (identified as *Joan* and *Uquq*) were 23 years old at the time of testing and in generally good health. Cooperative behavior for husbandry and research was established using operant conditioning methods and positive (fish, clam, or squid) reinforcement. Animal diets were pre-determined by the veterinary and animal care staff at the host facility, and were not limited for experimental purposes. Training took place opportunistically over a period of up to 6 months, followed by a testing period of 2–3 days.

Procedure

The auditory task involved presenting a walrus with both tone-present and tone-absent trials in a go/no-go signal detection paradigm (Stebbins 1970). Each walrus was trained to place her head at a specific position (a white station, Fig. 1a) affixed in her living enclosure until she detected a tone. The subject reported detection of the auditory signal by moving from this station to touch a black response target placed 50 cm to the left of the station (Fig. 1b). Both the station and the response target were mounted at eye level

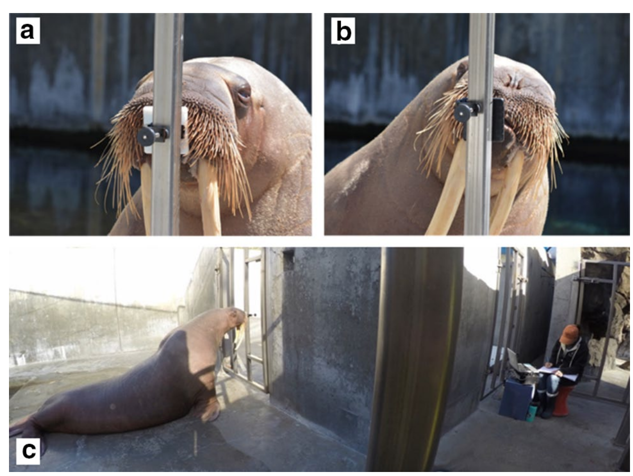

Fig. 1 Audiometric testing configuration used for Pacific walrus (*Odobenus rosmarus divergens*) *Uquq* at Six Flags Discovery Kingdom. The walrus moves from the white station (**a**) to touch the black response target to her left upon detecting a tone (**b**). During testing, both the trainer and the experimenter were out of view of the subject (**c**). Tones were projected from a transducer positioned 1 m in front of the station as shown in Online Resource 1

(approximately 1 m from the ground) on a vertical gate formed from steel bars with openings 10–30 cm wide. This configuration enabled the walrus to position at the station while hauled out on one side of the gate, while the trainer was positioned on the other side of the gate.

The walrus was rewarded for correct responses (either remaining still at the station position when no tone was presented, or touching the response target when a tone was presented) on both trial types. Correct responses were marked by a conditioned reinforcer followed by a food reward; the food reward was equivalent for all correct trials. Incorrect responses (misses and false detections) were not reinforced and the subject was prompted to return to the station to proceed to the next trial. A walrus typically participated in two audiometric sessions per day, each of which contained 20–60 individual trials. Training was conducted with sounds of fixed duration and level covering a frequency range from 200 Hz to 15 kHz. Testing was conducted over a wider frequency range with pure tones of 2-s duration and 50-ms rise and fall times, presented at a constant sound pressure level (SPL) of 80 dB re 20 µPa. The interval within which a tone could occur on a given trial was 6 s following the subject's calm positioning at the station. During testing, tones were presented on ~ 50% of trials. To prevent behavioral cueing, both the experimenter and the trainer remained out of view of the walrus until each trial was complete and the trainer moved from behind a visual barrier to provide reinforcement (Fig. 1c; Online Resource 1).

Equipment

Testing was conducted within a calibrated sound field. The speaker was placed 1 m directly in front of the station, at a distance of 1.2 m from the listening position (defined as the center of the subject's head between the ears). Audiometric signals were generated using AudioTest software (Katsura Shareware) on a battery-powered laptop computer and passed through a Radio Shack MPA-50 40-W amplifier. Low-frequency signals were then projected through a 2245H JBL Incorporated low-frequency speaker. This 46 cm diameter speaker was mounted in a wooden frame with its center point 40 cm above the ground, at an angle of about 30 degrees relative to the subject's head; this was the optimal output orientation of the speaker. During calibration, low-frequency signals were measured and recorded at the listening station with a 4189 free-field microphone (6 Hz–20 kHz) and a calibrated Brüel and Kjaer 2250 Sound Level Meter (linear weighting). To support the production of high-frequency signals, an external Roland Quad Capture sound card (24-bit, 192 kHz) was used in line between the laptop and the amplifier. Sounds were projected through a Fostex FT96H tweeter with 6.8 cm diameter. The tweeter was positioned at the height of the station, on-axis to the subject's head in both the vertical and horizontal planes. High-frequency signals were recorded at the listening position with a Microtech Gefell MK301 microphone (5 Hz–100 kHz, ± 2 dB) in a Josephson C617 body linked to a Stewart PBS-1 power supply and Fostex FR2 field recorder (24-bit, 192 kHz). Recorded sounds were referenced to a known calibration tone. Tones were calibrated in situ in the absence of animals before and after each testing session, in 10 Hz frequency steps below 100 Hz and in 1 kHz steps above 18 kHz. Tones were inspected as both waveforms and spectrograms to confirm the absence of artifacts that could potentially influence the animals' responses.

Acoustic environment

Ambient noise measurements were obtained repeatedly in each testing environment to ensure that responses to the 80 dB re 20 µPa airborne tones were not constrained by background noise. To accomplish this, 1 min, unweighted, third-octave band measurements (50th percentile, L50) were obtained with the self-powered Brüel and Kjaer 2250 Sound Level Meter and converted to power spectral density units (dB re (20 µPa)^2 Hz^{-1}) that could be directly compared to the SPL of the tonal stimuli used during testing.

Hearing range determination

Within a given testing session, either the lower- or upper-frequency limit of hearing was evaluated. Low-frequency testing began with easily discernible tones of 800 Hz. The frequency of the test tone was then decreased over successive trials following each correct detection: in octave steps to 100 Hz, and then 10 Hz steps below 100 Hz. Following a failure to detect (miss), the subsequent signal was increased in frequency to 100–200 Hz. This repeated descending staircase procedure (Stebbins 1970) was used to estimate the lower-frequency limit of hearing, identified as the frequency beyond which the animal's performance fell below reliable levels of detection. The high-frequency hearing limit was measured in a similar fashion; sessions began with easily detectable tones of 8 kHz, after which frequency was increased following each correct detection in 2 kHz steps up to 18 kHz, and by 1 kHz steps above 18 kHz. Following each miss, the frequency of the subsequent signal was decreased to 18–20 kHz to establish the repeated staircase procedure.

Results

Both walruses successfully completed audiometric training and participated in formal testing to determine the frequency limits of hearing in air. Testing was conducted with *Joan* at PDZA and with *Uquq* at SFDK during May and June 2018.

The broadest frequency range of detectable sounds across both subjects was 60 Hz–23 kHz at an SPL of approximately 80 dB re 20 µPa (Table 1).

The upper- and lower-frequency limits of hearing for *Joan* were independently estimated over 15 transitions from signal detections to signal misses as the frequency of the tone was varied towards the extremes of her hearing range (Table 1). Performance was stable in the high-frequency region of her hearing range, indicating an upper-frequency hearing limit of 23 kHz. *Joan* reliably detected all signals that were < 23 kHz, detected 23 kHz tones on 13 of 15 presentations, and failed to detect 24 kHz tones on 13 of 13 presentations. At low frequencies, *Joan* reliably detected signals > 60 Hz, successfully detected 60 Hz tones on 8 of 14 trials, and failed to detect 50 Hz tones on 8 of 8 trials. *Joan* demonstrated good stimulus control throughout data collection; her false detection rate during testing was 13% (12 of 91 tone-absent trials). Based on her performance, we confirm an audible frequency range for *Joan* of 60 Hz–23 kHz.

Frequency hearing limits for *Uquq* were estimated over 10 transitions from signal detections to signal misses at low frequencies, and 11 transitions from signal detections to signal misses at high frequencies (Table 1). At high frequencies, *Uquq* reliably detected tones < 20 kHz, she successfully detected 20 kHz tones on 8 of 10 presentations, and she failed to detect 21 kHz tones on 8 of 8 presentations. At low frequencies, her performance was more variable. While she readily responded to tones at 200 Hz and higher, and a few tones presented at 90 and 80 Hz, her ability to respond to tones at 100 Hz was unreliable (2 strong responses over 8 presentations). *Uquq* had a higher rate of false detections when compared to *Joan*: 29% (15 of 51 tone-absent trials). Based on her performance, we confirm an audible frequency range for *Uquq* of at least 200 Hz–20 kHz.

While the performance of both walruses may have improved with additional training at the frequency extremes of their hearing range, and testing in more controlled conditions than was possible here, it is apparent that walruses are capable of detecting tonal sounds as low as 60 Hz and as high as 23 kHz at relatively high exposure levels in air (80 dB re 20 µPa).

Calibration and inspection of the tones used during testing confirmed that received signal levels at the position of the head were within 3 dB of 80 dB re 20 µPa for frequencies at and below 100 Hz, and at and above 18 kHz. The bandwidth of each tone used during testing remained within the surrounding 1/3-octave band. While there were faint harmonics for high-frequency signals at twice the test frequency, these were well above the testing range and there was no energy present below the frequency of the test tone.

Ambient noise in the testing environment was louder at low frequencies than at high frequencies, as is typical of outdoor environments. The noise floors were similar at both facilities (Fig. 2); ambient levels were at least 30 dB lower than the 80 dB re 20 µPa tones used during testing at low frequencies, and more than 80 dB lower than the test tones at high frequencies. While there are no auditory masking data available for walruses, this offset between signal and noise

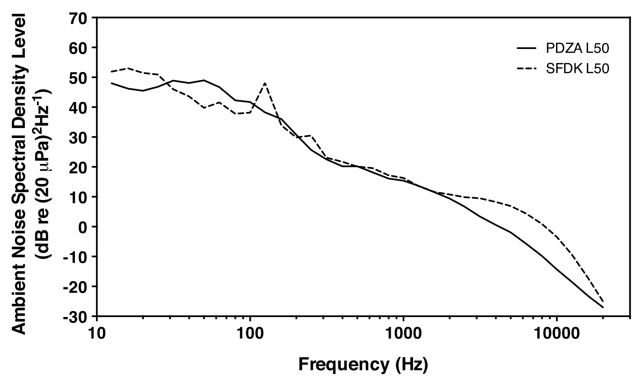

Fig. 2 Ambient acoustic conditions in the testing enclosures at Point Defiance Zoo and Aquarium (PDZA) and Six Flags Discovery Kingdom (SFDK). Noise spectral density levels were calculated from the median of L50 1/3-octave band levels associated with each testing session

Table 1 Performance data for two Pacific walruses (*Odobenus rosmarus divergens*) during auditory testing at the extremes of the hearing range

Frequency	*Joan* Correct/Total (%)	*UqUq* Correct/Total (%)	Frequency	*Joan* Correct/Total (%)	*Uquq* Correct/Total (%)
200 Hz	–	9/11 (82%)	18 kHz	–	8/8 (100%)
100 Hz	15/15 (100%)	2/8 (25%)	19 kHz	–	10/10 (100%)
90 Hz	15/15 (100%)	2/2 (100%)	20 kHz	15/15 (100%)	8/10 (80%)
80 Hz	14/15 (93%)	1/2 (50%)	21 kHz	15/15 (100%)	0/8 (0%)
70 Hz	14/14 (100%)	0/1 (0%)	22 kHz	15/15 (100%)	0/1 (0%)
60 Hz	8/14 (57%)	–	23 kHz	13/15 (87%)	–
50 Hz	0/8 (0%)	–	24 kHz	0/13 (0%)	–

Trials in the low-frequency and high-frequency portions of test sessions are shown for each subject as correct out of total trials, including % correct responses. Performance between 200 Hz and 18 kHz was near perfect for both subjects throughout training and testing should have provided sufficiently quiet conditions for detection of the 80 dB re 20 µPa tones at all of the test frequencies used, based on general patterns of hearing in mammals (Fay 1988). There were occasional low-frequency sounds present during testing (e.g., noise generated by distant airplanes, vehicles, and machinery); while these sounds did not mask the audiometric tones, they may have influenced failures to detect signals as well as false detection rates.

Discussion

The in-air hearing range of 60 Hz–23 kHz measured for an adult female walrus extends the previously confirmed audible range of 250 Hz–8 kHz for this species (Kastelein et al. 1996). This indicates that walruses are more sensitive to both lower- and higher-frequency airborne sounds than previously thought. This wider hearing range corresponds well with the bandwidth of acoustic communication in this species (for review, see Southall et al. 2019). However, the upper-frequency cutoff near 23 kHz in air is still lower than that observed in other terrestrial (Fay 1988) and marine carnivores (Reichmuth et al. 2013; Ghoul and Reichmuth 2014b), which can typically hear airborne sounds above 30 kHz. This could be related to hypertrophy of auditory structures in walruses that may impose inertial constraints on hearing in air (see Hemilä et al. 1995; Supin et al. 2001). Even so, the finding that walruses are capable of detecting a broad range of infrasonic to ultrasonic sounds indicates that airborne anthropogenic noise in the range of at least 60 Hz–23 kHz may disturb wild individuals.

The hearing range for airborne sounds can also be referenced to the single underwater audiogram presently available for the species (Kastelein et al. 2002). As hearing range in water is expected to be the same or broader at high frequencies compared to hearing range in air (Hemilä et al. 2006; Nummela 2008; Reichmuth et al. 2013), it is possible that the underwater audiogram may extend to frequencies above 23 kHz in some individuals of this species. On the low-frequency end, it is also likely that some walruses can detect sounds as low as 60 Hz in water; however, auditory sensitivity to such low frequencies is notoriously difficult to test in pools, making this hypothesis challenging to confirm.

At present, walruses are considered within a regulatory framework for marine mammal acoustic exposures under the grouping of *other marine carnivores* (Finneran 2016; National Marine Fisheries Service 2018; Southall et al. 2019). This distinction assumes that walruses are less sensitive to sound than seals—both in air and under water—and more similar to sea lions and sea otters with respect to their amphibious hearing abilities. While walruses have worse high-frequency hearing than other marine carnivores, the current study does not change this interpretation. Despite differences in the morphological and life history traits of walruses (Fay 1982; Garlich-Miller et al. 2011), along with their extreme phylogenetic isolation (Berta and Churchill 2012), our findings suggest that auditory data for otariid pinnipeds can serve as a reasonable, conservative proxy for walruses in the absence of additional information.

By contributing new information concerning hearing range for two female walruses, we conclude that the available underwater audiogram for the species (Kastelein et al. 2002) somewhat underestimates the frequency range of hearing for the species. While it is unlikely that this the discrepancy can be explained by testing medium (air versus water), individual or methodological variables (e.g., subject sex or history, testing environment) could account for the differences in hearing range observed between studies. As the current study evaluates only hearing range in air—rather than frequency-specific hearing sensitivity in water—it cannot be used to determine whether or not the available sensitivity thresholds for the species are representative. Additional auditory measurements obtained in quiet and masked conditions are needed to support a better understanding of auditory abilities and sensitivities at a species level. However, such studies are expensive, time consuming, and require access to specialized testing facilities that may not be possible with the small number of individuals currently living in human care.

Several options for next steps could be considered. One would be to conduct a study of hearing with trained animals in the presence of masking noise in air or in water. This would provide the first data on auditory masking for the species (Erbe et al. 2016). Further, the results would be relevant to predicting hearing and noise impacts in both terrestrial and aquatic natural environments (see e.g., Dooling et al. 2013) and the use of controlled background noise would preclude the need for specialized testing facilities or very quiet conditions. Another practical option would be to measure the hearing range of walruses in water using an approach similar to the one reported here. Given the use of high-amplitude tones to conduct this research, this study could be accomplished efficiently in a relatively uncontrolled zoological setting. The optimal solution would be to conduct a comprehensive study of underwater hearing with one or two individuals in a quiet research environment. This option would be challenging—and costly with respect to time and resources—but would provide the most useful and direct data concerning auditory biology for the species (see, e.g., Williams et al. 2015). Finally, thoughtful risk assessments (using wider, more precautionary hearing ranges, or explicit auditory data if possible) should be conducted to evaluate population-level exposures of specific sources of acoustic disturbance to walruses.

The current study highlights the ability of scientists to work closely and successfully with zoological partners to obtain information relevant to walrus conservation that cannot be obtained from free-ranging individuals.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. Animal research was conducted in accordance with the ethical standards of the Animal Welfare Committees at Point Defiance Zoo and Aquarium and Six Flags Discovery Kingdom. Research activities were further reviewed and approved by the Institutional Animal Care and Use Committee at the University of California Santa Cruz. Federal Authorization for research with walruses was granted under public display authorizations by the United States Fish and Wildlife Service.

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