

Audiogram and auditory critical ratios of two Florida manatees (*Trichechus manatus latirostris*)

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This Corrigendum relates to *J. Exp. Biol.* **215**, 1442-1447.

The authors misunderstood JEB's policies on citing non-peer-reviewed literature, and failed to cite the dissertation of Gerstein (Gerstein, 1999), who also measured critical ratios in two captive manatees.

Gerstein measured critical ratios using both pulsed and continuous (4s) tones in the presence of 1/3-octave wide masking noise using two different noise levels. The critical ratios were lower for the pulsed tones than the continuous tone. Although we did not test the same frequencies, our measurements of critical ratios in two other manatees were similar or lower for similar test frequencies for the continuous tone. For example, we measured critical ratios from two manatees at 4 kHz of 30.8 and 29.9 dB, while Gerstein measured critical ratios at 3 kHz of 31 and 34 dB. At 16 kHz we measured critical ratios of 27.0 and 28.1 dB, while Gerstein measured critical ratios of 38 and 42 dB at 18 kHz. The results Gerstein obtained for the pulsed tones were closer to the critical ratios we measured with the 1 s tone. The differences in results could be due to differences between individuals or methods used in the two studies. They are unlikely to be due to differences in the masking noise, because the bandwidth of masking noise used in our experiments was wider.

The authors apologise to Dr Gerstein, the journal editors and the readership for any inconvenience this may have caused but assure readers that it does not affect the data, results, interpretations or conclusions of the paper.

Publisher's note

The journal received a letter of concern relating to a lack of acknowledgement of a previous body of research in *J. Exp. Biol.* **215**, 1442-1447. After contacting the authors of the paper, the journal asked The University of South Florida, USA, to carry out an investigation. The outcome of this investigation indicated no evidence of misconduct.

Reference

Gerstein, E. R. (1999). Psychoacoustic evaluations of the West Indian manatee. PhD dissertation, Florida Atlantic University, Boca Raton, FL, USA.

RESEARCH ARTICLE

Audiogram and auditory critical ratios of two Florida manatees (*Trichechus manatus latirostris*)

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SUMMARY

Manatees inhabit turbid, shallow-water environments and have been shown to have poor visual acuity. Previous studies on hearing have demonstrated that manatees possess good hearing and sound localization abilities. The goals of this research were to determine the hearing abilities of two captive subjects and measure critical ratios to understand the capacity of manatees to detect tonal signals, such as manatee vocalizations, in the presence of noise. This study was also undertaken to better understand individual variability, which has been encountered during behavioral research with manatees. Two Florida manatees (*Trichechus manatus latirostris*) were tested in a go/no-go paradigm using a modified staircase method, with incorporated 'catch' trials at a 1:1 ratio, to assess their ability to detect single-frequency tonal stimuli. The behavioral audiograms indicated that the manatees' auditory frequency detection for tonal stimuli ranged from 0.25 to 90.5 kHz, with peak sensitivity extending from 8 to 32 kHz. Critical ratios, thresholds for tone detection in the presence of background masking noise, were determined with one-octave wide noise bands, 7–12 dB (spectrum level) above the thresholds determined for the audiogram under quiet conditions. Manatees appear to have quite low critical ratios, especially at 8 kHz, where the ratio was 18.3 dB for one manatee. This suggests that manatee hearing is sensitive in the presence of background noise and that they may have relatively narrow filters in the tested frequency range.

Key words: manatee, sirenian, audiogram, hearing, critical ratio.

INTRODUCTION

Endangered Florida manatees (*Trichechus manatus latirostris*) inhabit rivers, bays, estuaries and coastal areas, where their primary food source, light-dependent vegetation, concentrates them in shallow-water areas. Much of their environment overlaps with humans, and as a result they suffer mortality and injury from boats, water control structures and fisheries gear (US Fish and Wildlife Service, 2001), in addition to a variety of natural causes. Twenty-nine percent of all manatee deaths in the period from 1974 to 2009 were attributable to human-related causes (Florida Fish and Wildlife Conservation Commission, 2011). This is undoubtedly an underestimate of human impact as the cause of 29% of deaths during this period could not be determined, some because of the degree of carcass decomposition. Manatee casualties caused by human activities can be minimized through an understanding of how manatees sense their environment and, in some critical instances, fail to sense it. The Florida Manatee Recovery Plan (US Fish and Wildlife Service, 2001) explicitly recognized this need in calling for study of sensory processes. In the long term, understanding the auditory habitat of manatees will be crucial to their protection. To address the Florida Manatee Recovery Plan sensory objectives, we investigated the hearing ability of manatees in both quiet and noisy settings in a controlled environment in order to understand the factors that influence how well they can detect boats and other sound sources (such as depth finders).

Early reports of manatee hearing using auditory evoked potential (AEP) techniques suggested that manatees had greatest hearing sensitivity at lower frequencies (Bullock et al., 1980; Bullock et al., 1982). Anatomical analysis (Ketten et al., 1992) also indicated adaptations for low-frequency hearing. More recent reports of AEP studies of both West Indian and Amazonian manatees (*Trichechus inunguis*) indicate higher-frequency hearing, with the greatest sensitivity in the 10–25 kHz range and upper limits as high as 60 kHz (Klishin et al., 1990; Mann et al., 2005; Popov and Supin, 1990). A behavioral audiogram for two West Indian manatees reported by Gerstein et al. (Gerstein et al., 1999) was consistent with the high-frequency ranges found in the later AEP studies. Some of the discrepancy between the early and later studies might be accounted for by differences between in-air measures, such as those used by Bullock et al. (Bullock et al., 1980; Bullock et al., 1982), which appear to yield lower frequency detection estimates, and in-water measures. The question of frequency sensitivity remains open because of the small sample sizes (usually one to two animals) and potential variability among techniques.

Important issues include the ability of manatees to detect and localize boat engine noise, and the frequencies that are best detected. Recently, the ability of manatees to localize sounds in a four-speaker, 180 deg array was assessed (Colbert et al., 2009). In general, it was found that manatees were quite good at localizing broadband stimuli,

but quite poor at determining the direction of unmodulated tonal sounds. The manatee body provides substantial sound shadowing over a broad frequency range, which may allow for the optimization of localization cues. Many aspects of detection remain to be explored, such as hearing in noise that is more typical of the natural environment.

The critical ratio is a measure of the detectability of a tone in noise calculated in dB as the difference in sound level of the just detectable tone (dB re. $1\mu\text{Pa}$) and the spectrum level background noise (i.e. the background noise with equivalent 1 Hz resolution) (dB re. $1\mu\text{Pa}^2\text{Hz}^{-1}$) (Hawkins and Stevens, 1950; Watson, 1963). As manatee vocalizations are often tonal in nature (Schevill and Watkins, 1965; Nowacek et al., 2003; O'Shea and Poché, 2006), critical ratio data are important for understanding how manatees hear and communicate in areas where they often encounter boat noise (Bengtson and Fitzgerald, 1985).

The goals of this study were to measure the behavioral audiograms and critical ratios of two captive manatees. This doubles the number of manatees for which a behavioral audiogram has been measured, while also extending the frequency range tested.

MATERIALS AND METHODS

Subjects

The subjects were two male Florida manatees, *Trichechus manatus latirostris* (Harlan 1824), housed at Mote Marine Laboratory and Aquarium. The manatees, Buffett and Hugh, were 19 and 22 years old, respectively, at the start of testing. Both subjects had extensive training backgrounds. They have participated in multiple sensory and physiological research studies (Colbert et al., 2001; Bauer et al., 2003; Mann et al., 2005; Colbert et al., 2009; Bauer et al., 2012), as well as trained to voluntarily participate in all veterinary procedures.

Experiment I – behavioral audiogram

A Clark Synthesis Aquasonic underwater speaker (AQ339, Littleton, CO, USA) was used to present tonal sounds of 16 kHz and below. An International Transducer Corporation transducer (ITC-1042, Santa Barbara, CA, USA) was used to produce tonal stimuli of 16 kHz and above. The manatees' responses to the 16 kHz stimuli demonstrated no difference between the speaker and transducer. Signals were generated digitally by a Tucker-Davis Technologies Real-Time Processor (TDT RP2.1, Alachua, FL, USA) at a sample rate of 195,312 Hz, attenuated with a programmable attenuator (TDT PA5) to control level, and amplified with a Hafler Power Amplifier (P1000, Tempe, AZ, USA). A digital output on an RP2.1 was used to control the light indicating the start of a trial. A separate D/A channel was used to generate the signal to a speaker at the manatee start station. All experiments were programmed in MATLAB (The MathWorks, Natick, MA, USA) with a graphical user interface. All signals had a 10 ms rise–fall time to eliminate transients. Sound levels were calibrated at the position of the head of the manatee when the manatee was not present using a calibrated pressure hydrophone, Reson TC-4013 with VP 1000 amplifier (Slngerup, Denmark), with a flat frequency response from 1 Hz to 170 kHz. The signals received by the manatees were also recorded for all experiments with a calibrated hydrophone (HTI-96, High Tech, Inc., Gulfport, MS, USA) located on the stationing apparatus. The software reported the sound level for each trial.

Subjects were trained using standard conditioning techniques (Colbert et al., 2001). They were rewarded for desired responses on a continuous reinforcement schedule with favored food items, such as beets, apples, carrots and monkey biscuits. Undesirable responses were ignored. Each subject was trained to position itself

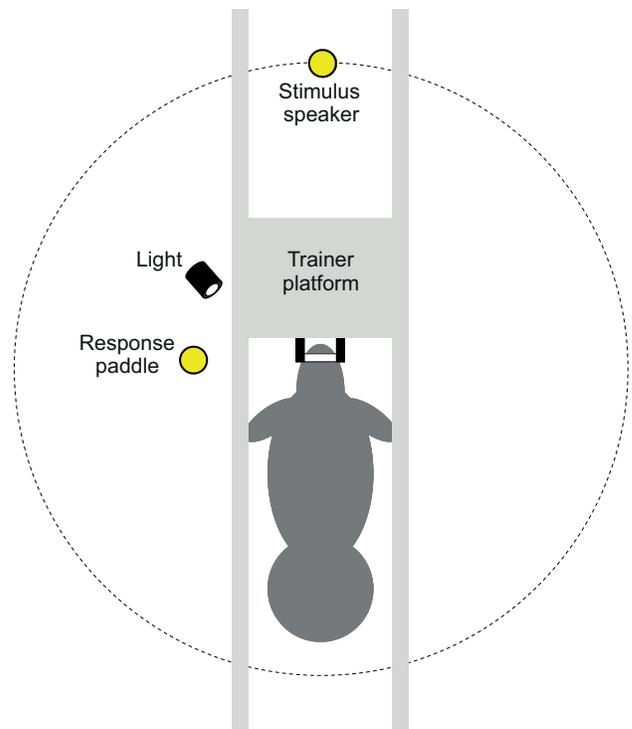


Fig. 1. Experimental arrangement (overhead view). The manatee is stationed at a depth of 1 m below the water surface, facing the speaker/transducer, which is located 3 m from the stationing bar.

at a central station 1 m below the water surface for the start of a trial by pressing the post-nasal crease underneath a polyvinyl chloride (PVC) horizontal bar. The start of a trial was indicated by playing a subject-specific pulsed tone from a dedicated speaker on the stationing apparatus (Fig. 1). This horizontal stationing bar was positioned 3 m in front of an independently mounted transducer, which presented the test stimuli. A cluster LED signaled (1 s in duration) the subject that a stimulus window would begin 2 s from onset in which a tonal stimulus would be presented or not presented. Sound stimuli were 2 s in duration, which video analysis indicated did not allow subjects to move from the stationing bar before the signal termination.

A staircase method (Cornsweet, 1962) determined the presentation of stimulus levels. For each tone frequency, testing started at a sound pressure level that was easily detectable (e.g. 15 dB above estimated threshold) based on previous published reports and AEP studies with Buffett and Hugh. After a correct response to a presentation trial, the sound intensity was decreased 6 dB. After an error, sound intensity was increased 3 dB, followed by 3 dB drops for all subsequent correct responses. The tonal sounds were delivered on quasi-random schedules in which half the trials were sound present and half were sound absent, a proportion designed to prevent a response bias based on the probability of sound presentation. A session consisted of eight to 10 sound intensity reversals. A threshold was defined as two consecutive sessions with mean amplitude levels of reversals differing by no more than 6 dB. If thresholds differed by more than 6 dB, a third session was conducted and the three interpolated thresholds were averaged.

The subjects were tested using a go/no-go response procedure (Schusterman, 1980). They were reinforced for touching a response paddle when a sound was presented or for remaining at station for

Table 1. Behavioral audiogram measurements for the two Florida manatees (*Trichechus manatus latirostris*) in the present study, Buffett and Hugh

Frequency (kHz)	Threshold dB level (dB re. 1 μ Pa)	False alarm rate
Buffett		
0.25	116.1	0.09
0.5	103.4	0.12
1	99.7	0.20
2	96.4	0.12
4	86.7	0.10
8	70.3	0.11
16	60.7	0.18
22.627	64.3	0.15
32	63.7	0.16
64	105.1	0.15
76.1093	128.4	0.17
90.5	141.1	0.11
Hugh		
0.25	125.6	0.15
0.5	112.9	0.16
1	104.9	0.12
2	97.0	0.17
4	78.6	0.13
8	71.7	0.19
16	70.7	0.18
22.627	71.0	0.19
32	97.6	0.13
38.0546	121.3	0.10

The frequency is the test frequency. The threshold dB level is the average across multiple sessions of interpolated hearing thresholds at the specific frequency. The false alarm rate is the proportion of sound absent trials that the manatee incorrectly responded to as if sound were present.

10 s if no sound was presented. After a correct response, the subject returned to the central station to be fed by a trainer who was ‘blind’ to the test condition. The ‘blind’ status of the trainer was maintained by wearing headphones playing masking noise. If an incorrect response was made, the subject was called back to the central station for the next trial, to be initiated no sooner than 30 s (the minimum inter-trial interval) after the end of the previous trial.

The location of the subject at the central station was monitored by overhead video to assess exact head position. Only trials where head position remained 3 m from the speaker during a test sound were kept for analysis. Position was monitored by both the person

controlling sound playback and the animal trainer. All responses were automatically recorded and stored so that an ongoing record of correct trials and latencies (time from test signal to speaker touch) could be retained. To control for motivational and performance artefacts, blocks of test trials were preceded by four ‘warm-up’ trials. The sound stimuli for these trials were easily detected training stimuli (e.g. 15 dB above estimated threshold). Performance accuracy of 75% on ‘warm-up’ trials was required to keep session trials for analysis. Otherwise, a session was abandoned or data were not used for detection analysis. Sessions were also rejected if false alarms (incorrect go responses) exceeded 25%.

Buffett was tested on tonal frequencies ranging from 0.2 to 90.5 kHz. Hugh was tested on frequencies from 0.2 to 38.0546 kHz. Neither manatee responded to the 0.2 kHz sound; therefore, only results from 0.25 kHz and greater are reported. Tests at frequencies higher than 38.0546 kHz were attempted for Hugh, but they were not successful; he either performed at chance levels or refused to respond.

Experiment II – critical ratios

The same subjects and testing procedures were used as in Experiment I. The test stimuli were a subset of the frequencies used for the audiogram (Experiment I), measured in low background noise conditions. One-octave wide noise bands centered on the test tone frequency were used as maskers, with the spectrum sound level 7–12 dB above the thresholds from the behavioral audiogram. The same speaker/transducer was used to present the masking noise continuously during the session and the tonal stimuli during each trial. The tone and masking signals were mixed by a summer (TDT SM5) before playing. The noise used in masking experiments was normalized by a second RP2.1 running a 100-tap FIR filter so that it was flat across the frequency spectrum.

RESULTS

Experiment I – behavioral audiogram

The behavioral audiogram data for Buffett and Hugh are presented in Table 1 and Figs 2 and 3. Table 1 includes the false alarm rates (incorrect on signal absent trials), which were below 25% for included data.

The results of the audiogram with Buffett and Hugh represent the means of at least two staircase runs. The one exception is at 90.5 kHz, where the result from Buffett is from one staircase. After

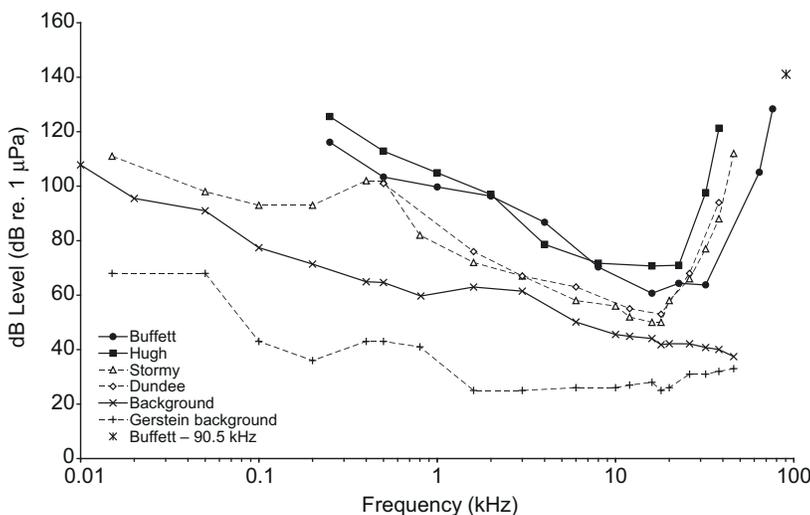


Fig. 2. Behavioral audiograms of Buffett (solid line, circles) and Hugh (solid line, squares) (*Trichechus manatus latirostris*). Note Buffett’s threshold at 90.5 kHz, which is based on one staircase (asterisk). Background noise levels are denoted by crosses. Dashed lines depict the behavioral audiograms of Stormy (open triangles) and Dundee (open diamonds) from a previous study by Gerstein et al. (Gerstein et al., 1999). Background noise in the Gerstein study is represented by plus signs.

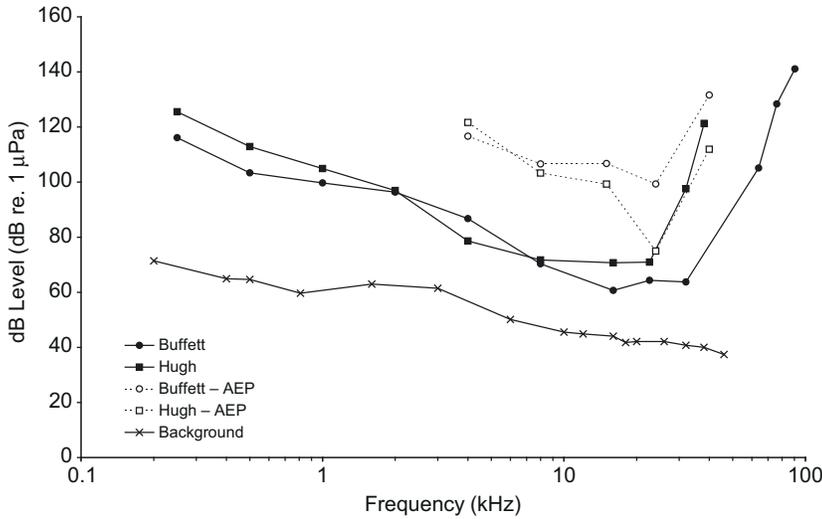


Fig. 3. Behavioral audiograms of Buffett (solid line, circles) and Hugh (solid line, squares) (*Trichechus manatus latirostris*) plotted with the evoked potential audiograms of Buffett (dotted line, open circles) and Hugh (dotted line, open squares) (Mann et al., 2005) for comparison. Background noise present in the test tank as a result of the life support systems and surrounding habitats during the Hugh/Buffett audiograms is represented by crosses.

the first staircase, Buffett stationed and responded correctly to catch trials, but the presentation of the test sounds elicited a leave response and a failure to re-station. Given the aversive response, the decision was made to stop testing at this frequency. Buffett and Hugh had similar sensitivity, with the best sensitivity for Buffett between 16 and 22.627 kHz and the best sensitivity for Hugh between 8 and 22.627 kHz. The audiograms also show sensitivity down to 250 Hz. Fig. 2 includes the behavioral audiogram for two previously tested manatees, Stormy and Dundee, reported by Gerstein et al. (Gerstein et al., 1999). Fig. 3 displays the AEP audiogram of the two test subjects for comparison (Mann et al., 2005).

Experiment II – critical ratios

The results of the critical ratio measurements are listed in Table 2 and are shown in Fig. 4. The 10% energy curve that is plotted on the graph is approximately followed by most mammals for which there are critical ratio measurements compiled in Fay (Fay, 1988). The critical ratios for the ringed seal (*Pusa hispida*), bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*) and harbor porpoise (*Phocoena phocoena*) are shown for comparison (Terhune and Ronald, 1975; Johnson, 1968; Thomas et al., 1990; Kastelein et al., 2009). Manatees possess critical ratios that are relatively quite low, with most below the 10% energy curve, especially at 8 kHz.

DISCUSSION

The shape of the behavioral audiogram is similar to that reported by Gerstein et al. (Gerstein et al., 1999), with the exception of

considerably higher frequency detection by one of our subjects. In general, we found higher threshold levels, which might be attributable to higher background noise levels and masking at some frequencies. The elevated background noise level was generated primarily by the life support systems of the manatee habitat and surrounding exhibits. One manatee (Buffett) refused to participate in subsequent sessions when the 90.5 kHz stimulus was being tested, suggesting an issue with the presence of the sound rather than the inability to detect it. The other test subject did not respond to the test signal at levels above 38.0546 kHz. These relatively high frequencies of sensitivity suggest that manatees may be able to detect ultrasonic fish finders, when used at their lower frequency settings (up to 50 kHz).

Gerstein et al. (Gerstein et al., 1999) were able to measure a threshold to 0.015 kHz, which they speculated may actually be in response to detecting acoustic particle motion with the tactile hairs. Manatee tactile hairs are unique among marine mammals in that they are found all over the body, have heightened blood supply and innervation, and appear to have specialized cortical representations like barrels seen in terrestrial mammals (Reep et al., 2002). The lack of response to 200 Hz in our study may be due to differences in the setup between the two studies. The manatee was positioned 1.5 m from the speaker in Gerstein et al. (Gerstein et al., 1999), whereas in the present study the manatee was positioned 3 m from the speaker. Positioning closer to the speaker would result in higher particle motion for the same acoustic pressure.

The critical ratio experiment allows for an examination of the manatee’s hearing ability in a more naturalistic setting. The low

Table 2. Critical ratio measurements for Buffett and Hugh (*Trichechus manatus latirostris*)

Frequency (kHz)	Masked threshold level (dB re. 1 μPa)	Background noise level (dB re. 1 μPa ² Hz ⁻¹)	Critical ratio (dB)
Buffett			
4	123.8	93	30.8
8	103.8	82	21.9
16	99.6	73	27.0
22.627	107.0	76	31.0
32	98.2	70	28.2
Hugh			
4	114.9	85	29.9
8	102.3	84	18.3
16	105.1	77	28.1
22.627	110.1	76	34.1

The frequency is the test frequency. The masked threshold is the threshold measured in presence of the background noise. The background noise level is the spectrum level background noise centered at the test frequency. Only data with a false alarm rate <25% are included in this table.

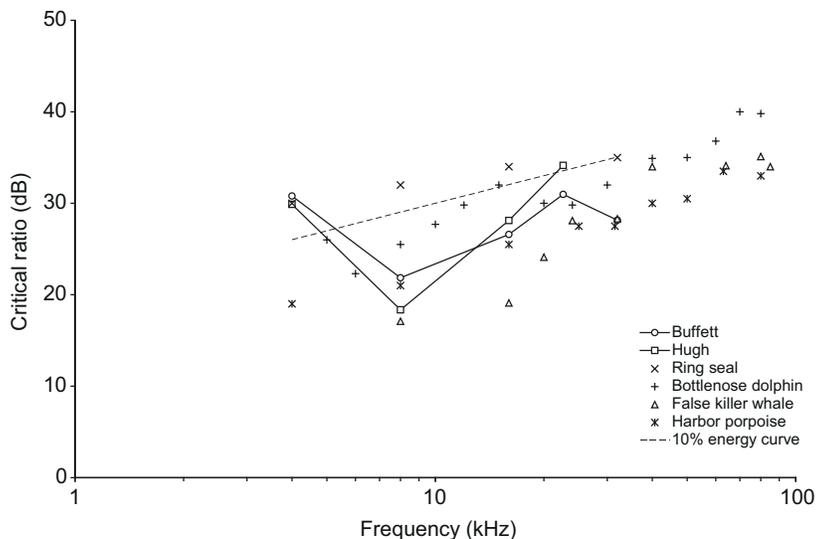


Fig. 4. Critical ratios of Buffett (open circles) and Hugh (open squares) (*Trichechus manatus latirostris*). Also shown for comparison are the critical ratios for ringed seal (crosses) (Terhune and Ronald, 1975), bottlenose dolphin (plus signs) (Johnson, 1968), false killer whale (open triangles) (Thomas et al., 1990) and harbor porpoise (asterisks) (Kastelein et al., 2009). The dashed line represents the 10% energy level, calculated as $10 \times \log(\text{frequency} \times 0.1)$.

auditory critical ratios of the manatees suggest that their auditory system has relatively narrow filters in this frequency range. In comparison to other animals with larger critical ratios, manatee hearing thresholds would not be as elevated by the presence of background noise. Because the same speaker is used to present the masking noise and the test tone, it is not possible that they are obtaining spatial masking release. It is also interesting to note that many manatee vocalizations are tonal harmonic complexes that often include a tonal component in the 4–8 kHz range (Schevill and Watkins, 1965; Nowacek et al., 2003; O'Shea and Poché, 2006). Thus, this sensitivity may be an adaptation specifically related to detecting conspecific vocalizations. Gerstein et al. (Gerstein et al., 1999) have speculated that the high frequency sensitivity of the manatee may be an adaptive response to the Lloyd mirror effect, in which low-frequency long-wavelength signals are effectively cancelled near the water surface. This raises the question, what can manatees hear when they are at the surface? Are underwater acoustic signals conducted through the body and still detectable, as hypothesized by Chapla et al. (Chapla et al., 2007)?

The manatee's critical ratio at 8 kHz is among the lowest measured in mammals. The manatee cochlea appears to be substantially different in terms of changes in base to apex width in comparison to other mammals: manatee basilar membranes are threefold wider at the basal end of the cochlea (Ketten et al., 1992). In contrast, cetaceans have a ninefold to 14-fold change in width, and humans have a sixfold increase (Ketten et al., 1992). Despite this relatively narrow range of variation in the cochlea, the manatee did show relatively high frequency hearing, exceeding the high-frequency range of human hearing. It is possible that the cochlea has specialized in the manatee for detection of its narrow-band communication signals, and that the narrow range of variation in the basilar membrane is related to higher frequency tuning.

The auditory evoked potential audiogram performed with the same animals as the behavioral audiogram had the same general shape, but was approximately 20 dB higher in sensitivity, providing the only comparable examination with manatees (Mann et al., 2005). These data are also useful for interpreting potential mechanisms for directional hearing (Colbert et al., 2009) because they confirm that manatees have relatively high frequency hearing, which could allow them to use frequency-specific shadowing cues to determine the direction of a sound. It would be instructive to measure the critical

bandwidth of the manatee and compare this with the critical ratio. The critical bandwidth measures tonal thresholds with varying bandwidths of noise. In other species, such as dolphin, the critical bandwidth is often wider than what is suggested by the critical ratio (Au and Moore, 1990).

We predict that manatees are capable of hearing nearby boats as long as the noise they generate exceeds the background noise within their hearing range, which is very broad. Gerstein (Gerstein, 2002) presents data from recordings of two boat passes at different speeds and argues that manatees may be less able to detect slow-moving boats compared with fast-moving boats, and suggests that boat impacts may be caused to slow-moving boats. However, most documented boat strikes on manatees are due to fast-moving boats (Calleson and Frohlich, 2007). The audiogram of the manatee supports the idea that in many coastal areas where there is elevated background noise because of biological sound sources, such as snapping shrimp, manatee hearing is limited by background noise. However, in other locations, such as rivers, where manatees seek refuge in cold winter months, the background noise levels are much lower and approach the manatee hearing thresholds. In these environments and in the documented boat strikes, it is clear that manatees ought to be able to detect and even localize broadband boat sounds (Colbert et al., 2009). Yet manatees are still impacted by boats in these environments. Observational studies of behavioral responses to boat approaches show that if a manatee is in shallow water, and a deep-water channel is nearby, the manatee is likely to head towards deeper water (Nowacek et al., 2004). This response may lead to the manatee crossing a boat path, and is supportive of boat slow speed zones in manatee habitat, so that if there is a collision, it is less likely to result in death (Calleson and Frohlich, 2007).

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