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Shipboard measurements of the hearing of the white-beaked dolphin *Lagenorhynchus albirostris*

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SUMMARY

This is the first report of an underwater audiogram from a dolphin in a capture-and-release scenario. Two bow-riding white-beaked dolphins *Lagenorhynchus albirostris* (a female and a male) were captured using the hoop-net technique in Faxaflói Bay, Iceland. The dolphins were transferred to a stretcher and hoisted into a plastic research tank on board a small fishing vessel. Two underwater transducers were used to cover the frequency range from 16 to 215 kHz. Two human EEG electrodes mounted in suction cups, one placed near the blow hole and the other on the dorsal fin, picked up bioelectrical responses to acoustic stimuli. Responses to about 1000 sinusoidal amplitude modulated stimuli for each amplitude/frequency combination were averaged and analyzed using a fast Fourier transform to obtain an evoked auditory response. Threshold was defined as the zero crossing of the response using linear regression. Two threshold frequencies at 50 kHz and 64 kHz were obtained from the female. An audiogram ranging from 16 to 181 kHz was obtained from an adult male and showed the typical 'U' shaped curve for odontocetes. The thresholds for both white-beaks were comparable and demonstrated the most sensitive high frequency hearing of any known dolphin and were as sensitive as the harbor porpoise.

Key words: AEP, catch-and-release, dolphin, hearing, Iceland, shipboard.

INTRODUCTION

Atlantic white-beaked dolphins (*Lagenorhynchus albirostris*) do not always have a white beak. Frequently their short, approximately 5 cm long nose is dark or mottled grey (Ellis, 1982; Rasmussen and Miller, 2002). The beak of this fast-swimming dolphin is not the most distinctive characteristic that can be readily seen; instead the large white patch below the dark dorsal fin area may be quickly noticed in a surfacing, jumping or bow-riding animal. The dolphins are found in temperate and subarctic waters of the North Atlantic. They are the most common dolphin species all around Iceland and are frequently seen in the summer in Faxaflói Bay off Keflavík, Iceland, where they often ride the bow wave of vessels (Víkingsson and Ólafsdóttir, 2004; Rasmussen et al., 2006). These dolphins are acoustically active, producing both whistles and clicks (Rasmussen and Miller, 2004). Mitson (Mitson, 1990) recorded white-beaked dolphins feeding on sand-eels and reported energy with frequencies as high as 305 kHz, much above the typical upper hearing frequency limit for odontocetes of about 150 kHz (Nachtigall et al., 2000). Whistles may be used for communication and can presumably be heard at distances over 10 km (Rasmussen et al., 2006), but the hearing thresholds of white-beaked dolphins have not been measured.

Most odontocete audiograms measured up to this point have been collected using behavioral psychophysical procedures in which the animal is captured, kept within a laboratory setting and then trained to respond to the presence or absence of acoustic stimuli. These sorts of hearing measurements are ideally made within the quiet laboratory tank environments, but are occasionally made at oceanaria, in open sea pens, or in tanks above ground (Nachtigall et al., 2000). While these procedures and settings are ideal for obtaining auditory measurements on marine mammals, this quiet sort of laboratory environment is becoming increasingly difficult to obtain. Training and testing with traditional psychophysical procedures is expensive and time consuming. The use of auditory evoked potential (AEP) procedures, in which the animal's hearing is measured by passively receiving the animal's electric potentials from the surface of its skin over its head when in the presence of sound stimuli, provides the opportunity to rapidly test animals outside of normal laboratory circumstances. (Nachtigall et al., 2005). Unlike other large mammals, odontocetes are particularly suited for this quick hearing evaluation because their brain electrical patterns readily follow patterned sound beyond 1000 modulations per second (Dolphin et al., 1995; Supin and Popov, 1995; Mooney et al., 2006). Fortunately, there is good agreement between hearing measurements using the AEP procedure and those collected using traditional behavioral techniques for odontocete cetaceans (Yuen et al., 2005; Houser and Finneran, 2006).

Stranded or newly captured dolphins and small whales normally become quite passive after coming onto a beach or being taken in a net. This passivity provides a unique opportunity to test the hearing of cetaceans using AEP in a catch-and-release scenario. As

a part of an overall project to assess the biology of the white-beaked dolphin, two *Lagenorhynchus albirostris* dolphins were hoop netted, caught, placed in a stretcher, moved to a foam-lined box aboard the converted fishing trawler *Hafborg*, tagged and then released in Faxaflói Bay off Keflavík, Iceland. Once placed in a stretcher in the foam-lined, water-filled box on board the boat, the animals were available for us to measure their ability to hear precalibrated sounds using auditory evoked potential procedures.

MATERIALS AND METHODS

Animals

Dolphins *Lagenorhynchus albirostris* Gray 1846 were readily located in Beaufort Sea, states 1 and 2, when summer winds calmed in Faxaflói Bay of Keflavík, Iceland. The white-beaked dolphin's propensity to bow-ride was essential for hoop-netting them (Fig. 1). As the animals rose to breathe during bow-riding, the 90 cm diameter steel hoop containing a bunched up 'bag' net stretched across the face, was placed directly in front of them. If they jumped forward through the hoop, the net released catching them quickly in the tethered bag net. The boat was immediately stopped and the net, which covered and held the front three quarters of the animal, served to keep the animal in place until a small dingy reached it and it could be placed in a racked stretcher (Fig. 2). Immediately upon being placed within the stretcher the animal was brought to the side of the boat and winched aboard with a hydraulic crane. The animal was placed in a 1×1×3.7 m, 1 cm thick structural constructed plastic box that was lined with 3 cm thick open cell mattress foam. The box was reinforced with a welded steel frame (Fig. 3).

Two animals were caught and measured, a female and a male. The female was not weighed but the male weighed 217 kg. The female was 209 cm from rostrum to fork of tail with a girth of 128 cm just behind the pectoral fins. The male was 224 cm long with a girth of 131 cm behind the pectoral fins. The female appeared to be a young adult while the male appeared to be fully mature. Both animals were caught near the small fishing port of Garður. They were individually placed into the box, and physical measurements were made while the boat motored into the port seeking calm waters for hearing measurements. Calm waters ensured a constant distance from the sound emitting transducers to the animals and a minimum of background acoustic noise.

Two transducers were used to project the underwater stimuli. The first, an ITC-1032 (Santa Barbara, CA, USA), with a resonance frequency of 38 kHz, was used to project stimuli from 16 to 45 kHz. The second transducer was a directional Reson TC 2130 (Slangerup, Denmark) that projected tones from 50 to 215 kHz. When one of the two transducers was in use, it was suspended from an overhead bar that stretched across the tank, and secured at a position 80 cm from the animal's beak and 115 cm to the animal's ear, but near the foam box wall. The transducer was adjusted to hang 30 cm below the water's surface. The animal was positioned in the stretcher hanging from steel suspension bars over the box. A large flap in the stretcher was unzipped in order to permit 'free' sound transmission to the animals' head and lower jaw.

Pre-calibration of foam lined box

Prior to animal expeditions, sound levels of the acoustic stimuli were calibrated to determine the received levels at the animal's head. One transducer, either the ITC or Reson 2130, was lowered 30 cm into the water and projected 19 ms sinusoidally amplitude modulated (SAM) acoustic stimuli, the same signals as for the AEP measurements. Received sound levels were recorded using one of

Fig. 1. Hoop catching method. The dolphin rides the bow and a small net placed in the hoop is put in front of the animal when it comes up to breathe. As it jumps through the hoop it is caught in the small net, which releases immediately from the hoop.

Fig. 2. Maneuvering the female white-beaked dolphin into the stretcher.

two hydrophones: (1) a Reson TC 4013 (sensitivity –211 dB re. 1 V/μPa and frequency response up to 140 kHz) for frequencies up to 50 kHz, and (2) a Reson TC 4034 hydrophone (sensitivity –217 dB re. 1 V/μPa, ±3 dB up to 300 kHz) for frequencies from 64 kHz to 215 kHz. Sound stimuli were recorded using an Etec amplifier (HP at 100 Hz, Etec, Frederiksværk, Denmark), and an AD-Link (Taiwan) 12-bit DAQ card set at 1×10^6 samples s^{-1}. Receiving hydrophones were placed 75 cm from the projector, down the longitudinal axis of the tank and 50 cm from the nearest two tank walls. This position was determined to be the approximate location of the subjects' heads and there was little measurable variation in received levels within a few centimeters of the original hydrophone position. Frequencies calibrated included 16, 32, 45, 50, 64, 90, 128, 152, 181 and 215 kHz. Each of these SAM tones was transmitted in the tank and the received peak-to-peak voltage ($V_{p\text{-}p}$) was measured on the oscilloscope. This $V_{p\text{-}p}$ was converted to root-mean-square voltage (peRMS) by subtracting 15 dB. The

Fig. 3. Experimental plastic tank lined with open cell foam.

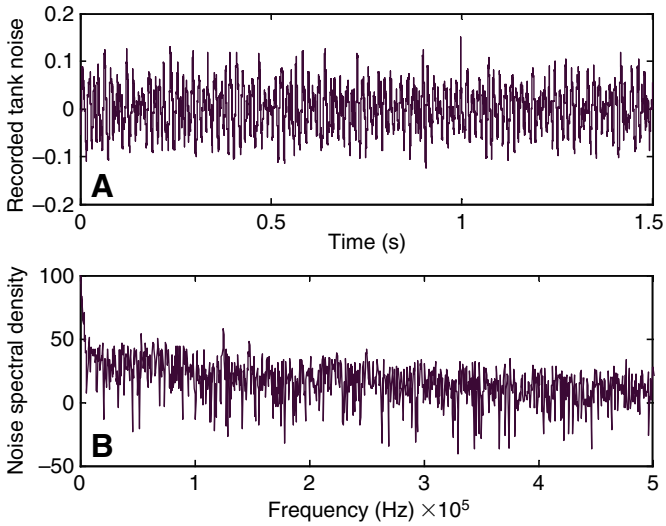

Fig. 4. Ambient noise in the tank. (A) Waveform of the measured noise in a 1.5 s segment. (B) Noise spectral density (dB re. 1 μpa^2/Hz) from 1 Hz to –500 kHz using a 1024-point FFT. The peak at 125 kHz and harmonics of this are weak system noise artifacts.

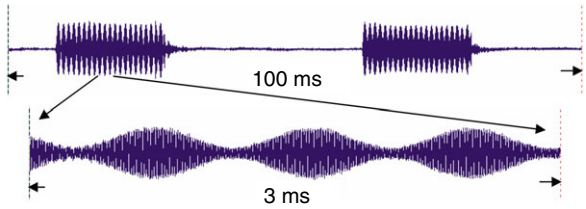

Fig. 5. Sinusoidal amplitude modulated (SAM) stimulus recorded near the lower jaw of the male white-beaked dolphin during audiogram acquisition. The 181 kHz SAM stimulus was filtered between 10 and 200 kHz.

peRMS was taken as the RMS voltage and used to calculate the sound pressure level (SPL) for that frequency. Due to the extremely short nature of the SAM tone bursts, reflections were highly unlikely. However, as a precautionary measure the received signals were simultaneously recorded using a CS12 miniature hydrophone (Derell Engineering, Virum, Denmark): sensitivity –210 dB re. 1 V/μPa and frequency response up to 150 kHz, placed about 25 cm from the lower jaw of the animal. Acoustic stimuli were amplified 70 dB (Etec, Frederiksværk, Denmark) (high pass 100 Hz) and sampled at 1 MHz (AD Link 12-bit, Taiwan, Formosa) to determine the spectrum and ensure that no competing signals or reflections existed.

Background noise level measurements were also recorded using the Reson TC 4032 hydrophone (sensitivity –170 dB re. 1 V/μPa, ±3 dB up to 120 kHz), Etec amplifier (HP at 100 Hz), and an AD-Link (Taiwan) 12-bit DAQ card set at 1×10^6 samples s^{-1}. The noise level in the tank on board ship was 118 dB re. 1 μPa RMS (band width, BW=100 Hz to 120 kHz, τ=2.3 s). The system noise was 102 dB re. 1 μPa RMS (BW=100 Hz to 120 kHz, τ=881 ms). Fig. 4 shows an example of tank noise.

Experimental design and stimulus presentation

The acoustic stimuli were sinusoidally amplitude modulated (SAM) tone-bursts, digitally synthesized with a customized LabView data acquisition program that was created with a National Instruments (Austin, TX, USA) PCMCIA-6062E DAQ card implemented into a laptop computer. Each SAM tone-burst was 19 ms long, with an update rate of 200 kHz for carrier tones less than 64 kHz, and 800 kHz for carrier frequencies equal to or above 64 kHz. The carrier frequencies were modulated at a rate of 1125 Hz, with a modulation depth of 100%. This modulation rate was chosen based on ideal measurement modulation rates for similar odontocetes and a pre-established modulation rate transfer function to be published independently for the white-beaked dolphin (Dolphin et al., 1995; Supin et al., 2001; Mooney et al., 2006). A 30 ms break of no sound was alternated between the 19 ms stimulus presentations (see Fig. 5). The stimuli were sent from the computer to a custom built signal shaping box that could attenuate the tone bursts in 1 dB steps. An EZ OS-310M battery-powered digital oscilloscope (Puchonsi, Kyunggi-do, Republic of Korea) was used to monitor the outgoing stimuli from the signal-shaping box to the projecting hydrophones.

AEP measurements

AEP responses were collected from two gold, passive electrode sensors embedded in rubber suction cups. The electrodes were standard 10 mm EEG electrodes, the same type used for human EEG collection. The suction cups were easily placed on the animal at the beginning of each session with standard conductive gel. The active electrode was attached about 3–4 cm behind the blowhole, slightly off to the right and over the brain, while the reference electrode was attached on the dorsal fin. We chose the dorsal fin because there are few muscles and noise producing nerves. The animal was rested in the stretcher at the surface with most of its head underwater to receive sound input through the major tissue routes to the ears (Møhl et al., 1999; Ketten, 2000) while the suction cups, with the embedded electrodes, remained in the air to maximize signal strength. The animals were continuously visually monitored, breaths were counted and a heart rate monitor kept track of heart rate.

An Iso-Dam Isolated Biological Amplifier (Sarasota, FL, USA) amplified the AEP responses from the electrodes by ×10 000. The Iso-Dam as well as a Krohn-Hite Filter Model 3103 (Brockton, MA, USA) with a bandpass of 300–3000 Hz, filtered the responses for anti-aliasing protection. The amplified and filtered responses were transferred to an analog input of the same DAQ card in the same laptop computer. The received signal was digitized at a rate of 16 kHz in order to extract the recorded AEP from noise, and the entire trial was extended to about 1 min by averaging 1000 samples so that the stimuli were presented at a rate of 20 s^{-1}.

The general procedure used to estimate a hearing threshold for each frequency was to pre-select a carrier frequency, determine the initial stimulus presentation level to be used for that frequency, and then to present a series of trials with progressively decreasing stimulus amplitudes. Because this was the first audiogram of a white-beaked dolphin, stimulus presentation levels were based on previously published audiograms of other odontocetes. Stimulus levels began 20–30 dB above the lowest threshold levels of the preceding measured thresholds. Carrier frequencies were tested ranging from 16 to 215 kHz.

Stimuli with carrier frequencies of 50 and 64 kHz were first tested with the female; however, given the fact that white-beaked dolphins had not previously been examined or caught, we became concerned when the animal's breathing rate became irregular and the mean heart rate increased. The animal was taken out of the test chamber, tagged with an acoustic tag on a suction cup, and released back into the bay, resulting in only two thresholds for the female dolphin. The male proved a bit more robust. Breathing remained regular throughout 90 min of testing and frequencies of 16, 32, 45, 64, 90, 128, 152, 181 and 215 kHz were presented. Noise on the boat and from one of our amplifiers proved problematic and unfortunately we were unable to measure frequencies lower than 16 kHz.

The amplitudes of the transmitted SAM tone-bursts for the various carrier frequencies were reduced in 5–10 dB steps, until the envelope following responses (EFR) could no longer be distinguished from the background noise. Step size was based on the intensity of the signal and the animal's neurological response. Where behavioral tests normally use 3 dB steps, 5–10 dB steps may be used in evoked potential work because thresholds are estimated by extrapolation. An average of eight stimulus intensity levels was presented for each of the nine different frequencies. Recordings of SAM stimuli taken near the lower jaw of the animal during experimentation showed no obvious reverberations, as shown in Fig. 5.

Data analysis

Fourier transforms were calculated for a 16 ms window of the average evoked response recorded at each intensity level for each frequency in order to quantitatively estimate the animal's hearing threshold. This window contained a whole number of response cycles to the stimulus. The 256-point Fast Fourier transforms (FFT) provided response frequency spectra of the data where a peak reflected energy received, or the animal's physiological following response, to the 1125 Hz modulation rate. Thus a larger EFR response was reflected as a higher peak value. The peak FFT amplitude at the modulation rate was used to estimate the magnitude of the response evoked by the SAM stimulus.

The values of these peaks were then plotted as response intensity against sound pressure level (SPL) of the stimulus. A regression line addressing the data points was hypothetically extended to zero, the theoretical point where there would be no response to the stimulus and the arbitrary definition of threshold. With the stimulus SPL value at the zero response, it was possible to estimate the threshold for each of the frequencies presented to the animal as described in Supin et al. (Supin et al., 2001). Analysis was conducted using EXCEL, MatLAB and MINITAB software.

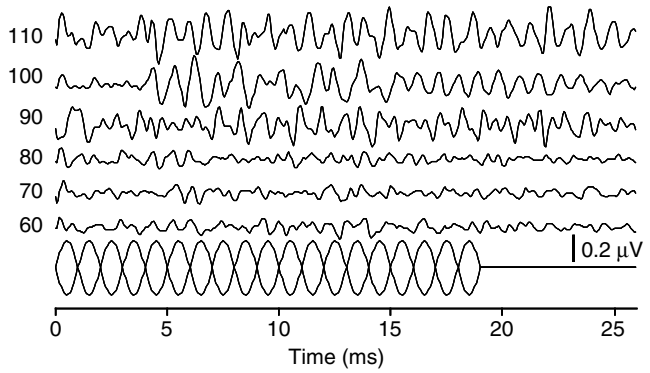

Fig. 6. Sinusoidal envelope of a stimulus (lowest trace) and envelope following response of a 16 kHz tone from 110 dB to 60 dB re. 1 μPa in 10 dB steps (upper traces).

RESULTS

The unusual environment of the foam-lined plastic tank chamber on-board a fishing vessel provided an excellent opportunity to obtain threshold values without natural background noise interference. The animals' EFR above threshold values were clearly observed as the data were collected (Fig. 6). The AEP response showed a temporal lag of around 4–5 ms compared to both the onset and offset of the tone-burst stimulus. This lag was the result of the latency of the evoked potential following the presentation of the stimulus. This was not an artifact, but rather it served as a predictable electrophysiological feature demonstrating that the brainwave recording occurred in direct response to the SAM acoustic stimulus. When stimulus intensities were high relative to threshold, EFRs were discernable well above the noise level (Fig. 6). As the measurements approached the auditory threshold levels, the decreasing EFR magnitudes reflected the synchronously decreasing SPL of the stimuli.

In determining threshold values, these EFRs were Fast Fourier transformed (FFT) to obtain the frequency spectrum of the animal's evoked response (Fig. 7). The consistent peak at 1125 Hz reflected the animal's EFR, and thus neurophysiological 'following' of the carrier tone modulated at an 1125 Hz rate. The strength of the evoked response was reflected in the amplitude of the peak at the modulation frequency; as stimulus level was decreased, the peak amplitude decreased correspondingly. Fig. 7 illustrates a typical peak at 16 kHz carrier frequency that decreases as the stimulus intensity was attenuated. At the lowest stimulus intensity of 60 dB, the peak of the response spectra was no different from the background physiological noise. The intensity of each of the spectrum peaks was plotted as a function of stimulus SPL, and linear regression lines were drawn to calculate the theoretical zero response value, which is defined as threshold for that frequency. Therefore, for a stimulus of 16 kHz, the threshold is estimated in Fig. 8 to be 70 dB. Threshold values for other frequencies are given in Table 1.

The hearing threshold for each of the carrier frequencies was determined in the same manner, with thresholds calculated as the stimulus level predicted to generate a response amplitude of zero.

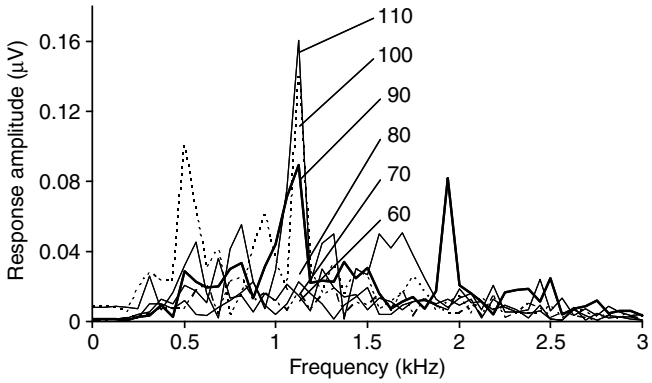

Fig. 7. FFT of the envelope following response amplitudes of a white-beaked dolphin. Response (μV rms) is to a sinusoidal amplitude modulated (SAM) tone presented at a 16 kHz carrier frequency, a 1125 Hz modulation rate and stimulus intensities from 110 to 60 dB re. 1 μPa shown to the right of the graph.

Table 1. Auditory evoked potential thresholds at each frequency tested

Frequency (kHz)	Threshold (dB re. 1 μPa)
16	69.7
32	59.8
45	45.3
64	47.8
90	45.5
128	52.4
152	99.8
181	120.7
215	140; no obvious response

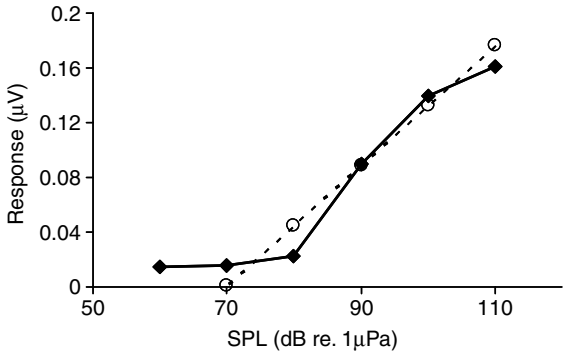

Fig. 8. Intensity of spectrum peaks of a 16 kHz tone (solid line, diamonds) at 1125 Hz at various pressure levels (SPL). Each point (diamond) represents an average of 1000 stimulus presentations. The linear regression of the spectrum peaks (broken line, open circles) is based on points from 70–110 dB. The threshold for the tone is defined as the point where the regression line crosses zero on the response scale, in this case 69.8 dB.

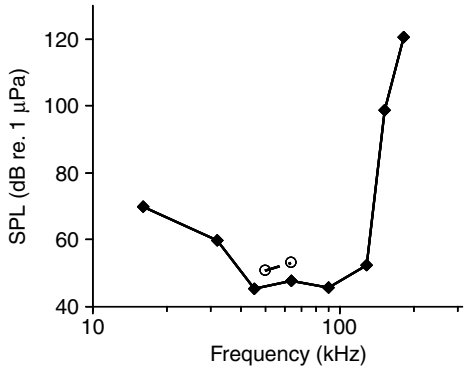

Fig. 9. Partial and entire evoked potential audiogram of two white beaked dolphins, *Lagenorhynchus albirostris*. Female dolphin: broken line with open circles; male dolphin: solid line with black diamonds. The values above 100 kHz are 128 kHz, 152 kHz and 181 kHz.

Results of the threshold calculations are depicted as an audiogram in Fig. 9. Only two thresholds were obtained from the first-caught female white-beaked dolphin. Those thresholds for 50 and 64 kHz carrier frequencies were computed in the same way. They are also presented in Fig. 9 (open circles).

The white-beaked dolphin's AEP audiogram's general shape was a typical mammalian U-shape. At very high frequencies the slope of thresholds increased steeply beyond 128 kHz at a rate of 95 dB/octave. Maximum sensitivity was shown between 50 and 64 kHz. Measured areas of best sensitivity were between 45 and 128 kHz. Unfortunately no measures were made for frequencies lower than 16 kHz. The audiogram of the white-beaked dolphins showed lower thresholds for high frequencies compared with other dolphin species. The adult male white-beaked dolphin was 20 dB more sensitive at 150 kHz than an infant Risso's dolphin (Nachtigall et al., 2005).

DISCUSSION

While most healthy young odontocetes hear frequencies up to 150 kHz (Johnson, 1966; Nachtigall et al., 2000; Nachtigall et al., 2005; Nachtigall et al., 2007), Mitson reported that white-beaked dolphin clicks contained energy up to about 305 kHz (Mitson, 1990). Later Rasmussen and Miller (Rasmussen and Miller, 2002) showed that clicks could have a secondary energy peak at 250 kHz. Assuming these dolphins can hear what they produce, we were therefore prepared to measure hearing up to 250 kHz. We presented signals at 215 kHz and did not receive AEPs in response. Given that most mammalian audiograms are U-shaped we did not present higher frequencies. It is, however, very interesting to note that in this fully adult male we measured a threshold near 100 dB at 152 kHz and 121 dB at 181 kHz. These are very high frequency thresholds especially if one considers Yuen et al.'s findings (Yuen et al., 2005) that AEP measures of hearing do not yield as sensitive a measure as behavioral thresholds. Thresholds gathered using behavioral methods (Yuen et al., 2005) were usually about 10 dB more sensitive than those obtained using AEPs with the same technique as that used in the present study. If that 'correction factor' were extrapolated here, one might obtain white-beaked behavioral thresholds of 90 and 111 dB at 152 and 181 kHz, respectively. If those 'corrected' numbers were then compared to the behaviorally examined harbor porpoise, which heard 160 and 180 kHz signals with 50% mean detection thresholds of 91 and 106 dB, respectively (Kastelein et al., 2002), then the white-beaked dolphin has a very similar high frequency sensitivity.

The audiometric data collected from the two white-beaked dolphins are unusual in that they were collected from healthy animals that were caught and then released. The animals' hearing was measured on board the boat and underwater in a plastic tank lined with foam (Fig. 3). While others (Cook and Mann, 2004) have quickly screened the hearing of bottlenosed dolphins between 5 and 80 kHz using jawphones applied to dolphins laying on mats in a

boat, no one has previously measured the underwater audiogram of an odontocete in a planned catch-and-release program. We hoop-netted the dolphins, brought them on board the vessel in a pre-calibrated acoustic chamber, measured their hearing with evoked auditory potential procedures and then released them. This procedure can be further used in the future to solve two problems associated with the measurement of hearing in cetaceans. The first of these problems is that too few species have been measured. Of the 85 species of cetaceans we now have audiograms on 12 of those species (Nachtigall et al., 2007). The catch-and-release effort allows temporary removal of the animal from its environment to collect hearing data and immediate return to its environment and population. The known audiometrics of cetacean species can be greatly increased using this technique. The second problem is that multiple measures of a population are needed. There are normally large individual differences in the normal hearing parameters of any population of animals within a species. The catch- and-release technique allows the measurement of increased numbers of animals from a given population. The US National Research Council (National Research Council, 1994; National Research Council, 2000) has recommended that population level audiograms be obtained in order to discover population audiometrics and to determine normal hearing loss levels for marine mammals. AEP measurements can be effectively used to quickly measure groups of odontocetes (Popov et al., 2007), and the catch-and-release procedure, combined with hearing tests using the AEP technique, provides a method for fulfilling those recommendations.

These data therefore provide two new important pieces of information about the general hearing of marine mammal species. (1) White-beaked dolphins hear high frequencies underwater as well as the harbor porpoise (Kastelein et al., 2002), which is the animal shown to hear the highest frequencies to date, and (2) a catch-and-release method can be used to temporarily hold dolphins in a water-filled chamber on a boat so that the underwater hearing of healthy wild dolphins and whales can be measured using the measurements of electrophysiological magnitudes (Stevens, 1970).

Our studies were performed in accordance with Icelandic National Regulation No. 279/2002 on animal experiments with permission of the Icelandic National Animal Research Committee, permit no. 0706-2701, and with the full approval of the University of Hawaii Institutional Animal Care and Utilization Committee protocol number 06-036. We wish to thank the Danish Natural Science Research Council for major financial support. Monitoring of animal health and safety and the research cruise were facilitated by the dedicated work of Jeff Foster, Gulli Bjarnason, Kitti Bjarnason and Katja Vinding Peterson. Marlee Breese was helpful in developing the stretcher and others at the Marine Mammal Research Program were valuable in technical support. This is contribution number 1298 of the Hawaii Institute of Marine Biology.

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