

## Decreased echolocation performance following high-frequency hearing loss in the false killer whale (*Pseudorca crassidens*)

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### SUMMARY

Toothed whales and dolphins possess a hypertrophied auditory system that allows for the production and hearing of ultrasonic signals. Although the fossil record provides information on the evolution of the auditory structures found in extant odontocetes, it cannot provide information on the evolutionary pressures leading to the hypertrophied auditory system. Investigating the effect of hearing loss may provide evidence for the reason for the development of high-frequency hearing in echolocating animals by demonstrating how high-frequency hearing assists in the functioning echolocation system. The discrimination abilities of a false killer whale (*Pseudorca crassidens*) were measured prior to and after documented high-frequency hearing loss. In 1992, the subject had good hearing and could hear at frequencies up to 100 kHz. In 2008, the subject had lost hearing at frequencies above 40 kHz. First in 1992, and then again in 2008, the subject performed an identical echolocation task, discriminating between machined hollow aluminum cylinder targets of differing wall thickness. Performances were recorded for individual target differences and compared between both experimental years. Performances on individual targets dropped between 1992 and 2008, with a maximum performance reduction of 36.1%. These data indicate that, with a loss in high-frequency hearing, there was a concomitant reduction in echolocation discrimination ability, and suggest that the development of a hypertrophied auditory system capable of hearing at ultrasonic frequencies evolved in response to pressures for fine-scale echolocation discrimination.

Key words: odontocete, hearing, hearing loss, echolocation.

### INTRODUCTION

Toothed whales and dolphins possess many adaptations that make them well suited to an aquatic lifestyle, including the use of echolocation and the development of high-frequency hearing. Echolocation, or biosonar, independently evolved aurally in bats and aquatically in cetaceans, and both groups developed high-frequency hearing (Busnel and Fish, 1980). The odontocete echolocation system is composed of two parts: the sound generation system and the auditory reception system. To generate sounds, odontocetes produce short, ultrasonic signals that are generated in the nasal complex and focused into a directional signal within the melon (Aroyan et al., 2000; Cranford, 2000). The sounds are received via an auditory system characterized by directional, high-frequency hearing (Renaud and Popper, 1975). Hearing abilities may vary considerably in frequency according to species, and some species may perceive signals of 150 kHz or higher (Kastelein et al., 2002; Nachtigall et al., 1995; Nachtigall et al., 2008). The auditory system of odontocetes is therefore hypertrophied compared with that of most mammals and is characterized by a large auditory nerve, a large volume of nerve fibers in the inner ear and high ganglion cell counts (Ketten and Warzok, 1990).

Underwater auditory structures presumably first evolved for low-frequency, non-directional hearing (Gingerich et al., 1983; Luo, 1998). Over time, fine-detailed echolocation discrimination would have required processes to emerge that allowed for the reception of increased frequency and directionality. The shift from hearing on land to hearing in water is explained by the need of the animal to sense its ambient environment, but the very high-frequency hearing ranges of extant odontocetes suggest additional evolutionary pressures beyond passive hearing (Nummela et al., 2004; Thewissen

and Hussain, 1993). It is reasonable to assume that high-frequency hearing has a value in echolocation, yet it is difficult to interpret this strictly from the fossil record. It has been hypothesized that higher frequencies result in the ability to resolve finer details in echolocation targets (Au, 1993), but it is unknown whether increased echolocation ability is truly linked with high-frequency hearing capabilities.

The underwater use of echolocation has intrigued investigators for over 50 years (e.g. Norris, 1968) and, given the excellent performance of dolphins and small whales in comparison to technological sonar, there have been many attempts to mimic and model biosonar (Busnel, 1966; Nachtigall and Moore, 1988; Moore et al., 1991; Roitblat et al., 1995). Much of this effort has been based on the demonstrated ability of odontocetes to differentiate small differences between arbitrarily constructed echolocation targets, including differences in target size, shape and materials from which they are constructed (Nachtigall, 1980). The full suite of cues that odontocetes use to discriminate targets is unknown, but it is thought that they may use small differences in the complex structure of target echoes to differentiate targets (Branstetter et al., 2007; Gaunard et al., 1998; Muller et al., 2008). The ability of cetaceans to differentiate and recognize the acoustic characteristics of objects using echolocation has an obvious biological benefit. Echolocation appears to be predominantly a foraging tool, but may also have a role in navigation and the avoidance of hazards and predators, especially in low-light or turbid conditions (Norris, 1968; Tyack and Clark, 2000). Conducting a controlled echolocation study in the wild poses many challenges. The use of arbitrarily constructed echolocation targets in the laboratory allows the control and measurement of acoustic cues and fine measurements of discrimination thresholds.

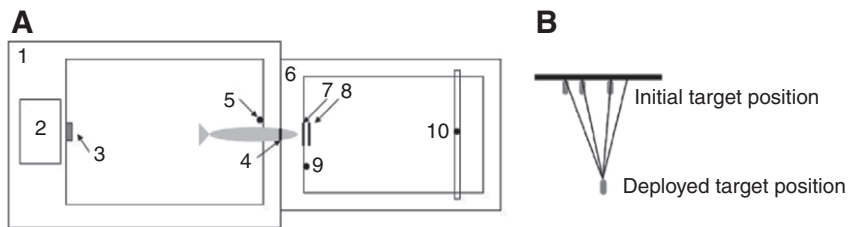


Fig. 1. (A) Experimental setup. 1, Experimental pen; 2, experimental shack; 3, stationing pad; 4, hoop; 5, response paddle; 6, target pen; 7, acoustic baffle; 8, visual screen; 9, monitoring camera; 10, target deployer. (B) Detail of target deployer, a V-shaped device that allows targets to be deployed at the same location and depth in the water.

The linkage of high-frequency hearing and echolocation discrimination performance has not previously been examined empirically. Recent evidence of age-related high-frequency hearing loss (presbycusis) in a false killer whale (*Pseudorca crassidens*) from previous echolocation discrimination experiments provided a model system for investigating the link between high-frequency hearing and echolocation discrimination performance. Prior audiometric studies on the animal used in these experiments indicate that the whale previously had good hearing up to 100 kHz (Thomas et al., 1990). Recent audiogram analyses show a reduction in frequency hearing capabilities of approximately 60 kHz over 15 years (Yuen et al., 2005). The echolocation discrimination abilities of this whale were previously quantified, but unpublished, 15 years ago. The comparison of echolocation performance before and after high-frequency hearing loss allows for direct testing of target-discrimination abilities and a comparison between periods of good and reduced high-frequency hearing. This provides the opportunity to investigate whether an increased ability to discriminate targets is linked with high-frequency hearing capabilities and whether a reduction in high-frequency hearing results in poorer discrimination performance.

Here, we report the wall-thickness discrimination abilities of a female false killer whale at two different time periods: in 1992, when the subject had good high-frequency hearing, and in 2008, after the subject had lost a significant portion of her high-frequency hearing. The results show that a reduction in high-frequency hearing causes a reduction in echolocation discrimination performance. We discuss the possible mechanisms for this loss in performance and provide a hypothesis for the role of high-frequency hearing in echolocation.

## MATERIALS AND METHODS

### Experimental subject and equipment

Two experiments were completed: one in 1992 and one in 2008. Both experiments were conducted in floating pens in Kaneohe Bay, Oahu, Hawaii, USA, with a female false killer whale [*Pseudorca crassidens* (Owen 1846)] named Kina. The exact age of the whale is unknown, although she was brought to Hawaii as an adult in 1987 and has been used extensively in published echolocation work (e.g. Supin et al., 2008). In 1992, the subject measured 3.6 m and weighed 389 kg. In 2008, the subject measured 3.9 m and weighed 453 kg.

The setup for both experiments was nearly identical. Although the pen configuration was moved between experiments, both were conducted within Kaneohe Bay (Fig. 1A). During each experiment, the subject remained stationary to examine echolocation targets by placing her head within a hoop that was 1 m below the water surface. An underwater camera (SCS Enterprises, Montebello, NY, USA) was used to monitor her positioning behavior within the hoop station. An acoustically opaque screen was placed in front of the subject to prevent her from echolocating prematurely on the targets.

### Target characteristics

For each target discrimination task, two sets of targets were used. Each set consisted of one standard target and six or seven comparison

targets. The standard target was a hollow aluminum cylinder 12.7 cm long with an outer diameter of 37.85 mm, an inner diameter of 25.15 mm and a wall thickness of 6.35 mm. The cylinders were hollow so that they filled with water when submerged. Comparison targets had the same length and outer diameter as the standard target but differed in inner wall thickness by  $\pm 0.076$ ,  $\pm 0.152$ ,  $\pm 0.229$ ,  $\pm 0.305$ ,  $\pm 0.406$  and  $\pm 0.813$  mm. Thus, the experiment utilized a set of targets thicker than the standard and a set of targets thinner than the standard. In 2008, an additional target of  $\pm 0.203$  mm was used, and in 1992 a comparison target of  $\pm 1.600$  mm was initially used, but detailed results are not reported here owing to consistently perfect performance.

Targets were hung from a monofilament line 8 m away from the subject at a depth of 1 m using a target deployer to avoid cueing effects. The target deployer was a V-shaped device that allowed the experimenter to control target deployment remotely from the experimental shack. The deployer held up to four targets at one time and allowed each target to be lowered at the same location and to the same depth in the water (Fig. 1B).

### Experimental procedure

Prior to the start of a trial, the subject remained stationed on a vertically placed pad on the side of the pen near the trainer. When cued, she swam into a hoop up to her pectoral flippers to remain stationary for the trial. A target was placed into the water using the deployer, and the acoustic baffle was lowered, providing the subject with acoustic access to the target. The subject ensounded the target and was trained to provide a response to the standard target that differed from the response required for all other objects. If the target was a standard target (a 'go'), the subject backed out of the hoop and touched a response paddle with her rostrum. If the target was a comparison target (a 'no go'), the subject remained in the hoop until signaled out by the trainer. The subject was rewarded with fish for correct responses. Incorrect responses resulted in no fish reward. Thus, the general form of the procedure was a 'go'/no-go' response paradigm (Schusterman, 1980).

Each session consisted of 50 experimental trials. Target presentation order was determined using a modified method of constants, and each session was broken into five 10-trial blocks. During each block, the subject discriminated between the standard target and one comparison target. A modified Gellermann series (Gellermann, 1933), with no more than three types of trials in a row, was used for target presentation order. Each block contained an equal number of standard and comparison targets.

Both experiments were broken down into cycles. Each cycle consisted of multiple blocks of trials for each comparison target within one target set (thicker only or thinner only). Initially, each cycle was composed of 10–15 blocks (100–150 trials) but, as the experiment progressed and the animal gained more experience with the task, the cycles were reduced to 5–10 blocks (50–100 trials) for each comparison target. After a cycle was completed, the target sets were switched so that the subject alternated between cycles of thinner targets only or thicker targets only.

Table 1. Model parameters and Akaike's information criterion results

Model parameters	d.f.	N	AIC
Wall thickness	604	1	2.14E+03
Wall thickness + target set	603	2	2.11E+03
Wall thickness + experimental year	603	2	1.62E+03
Wall thickness + cycle	601	2	2.09E+03
Wall thickness + target set + experimental year	602	3	1.62E+03
Wall thickness + target set + cycle	600	3	2.06E+03
Wall thickness + experimental year + cycle	600	3	1.59E+03
Wall thickness + target set + experimental year + cycle	599	4	1.58E+03

N, number of parameters; AIC, Akaike's information criterion.

In 1992, a total of 3200 experimental trials was conducted: four cycles with the thicker target set and three cycles with the thinner target set. The first 10-trial block of each session always consisted of the standard plus the comparison target of the largest wall-thickness difference ( $\pm 1.600$  mm) as a warm-up for the subject prior to testing. To control for possible cueing, 20 sessions were run with a segment of blind controls, 10 sessions were run with a different experimenter and two sessions were run with modified protocols.

Blind controls consisted of a target with dimensions identical to the standard target being substituted for a comparison target. The substitution was unknown to the experimenter, who rewarded the subject as if the blind control were a comparison target. If the subject perceived the blind control to be the same as the standard, she responded as a 'go' and received no reward. Thus, perfect performance on blind control trials resulted from the subject choosing to 'go' on all trials, which would appear to the experimenter as 50% performance. Blind controls were conducted to ensure the subject used wall thickness to conduct discrimination and not some other characteristic specific to the standard target.

Modified protocols consisted of different placement of the stationing pad and response paddle. Conducting sessions with modified protocols and conducting sessions with a different experimenter ensured that the subject was not cueing off anything other than the target itself when performing the discrimination task.

In 2008, a total of 3640 experimental trials were conducted: four cycles with the thicker target set and three cycles with the thinner target set. The first 10-trial block of each session was a warm-up for the subject, consisting of the standard plus the largest comparison target ( $\pm 0.813$  mm). The comparison targets used in the remaining blocks were randomized, and a two-trial cool-down of the standard plus the largest comparison target ( $\pm 0.813$  mm) was included. To test for possible cueing, four sessions were run with a segment of blind controls, different experimenters were used and 20 sessions were run with modified protocols.

Performance on each target was recorded as the percentage of correct responses that the subject achieved in each block of trials. Performances were calculated from binomial data (correct or incorrect) and averaged for all 10 trials in one block. Targets were normalized by reporting the comparison targets as the absolute difference between the comparison targets and the standard target.

#### Data analysis

Analysis of the subject's performance was conducted using generalized linear models (GLMs) (glmfit; Matlab, MathWorks, Natick, MA, USA) to model the probability of a correct response as a function of wall thickness, target set (thicker *versus* thinner), experimental year and cycle. The performance of the subject was calculated from binomial data (correct or incorrect) and a logit link function was used for analysis. Target set, experimental year and cycle were treated as categorical variables for analysis. Akaike's information criterion (AIC) was used to select the best-fitting model. Pairwise *t*-tests were conducted to test the significance between performances on individual target types.

## RESULTS

### Echolocation discrimination performance

To ensure that the subject was discriminating wall thickness, and not characteristics specific to the standard target, blind controls were conducted in which the subject discriminated between two standard targets. These trials averaged 54.0% performance, which was not statistically ( $t_{19}=1.57$ ,  $P=0.07$ ,  $N=40$ ) different from the expected performance for blind control trials of chance, or 50.0%.

Comparison of models using AIC showed that a model that included wall thickness, experimental year, target set and cycle was the best fit for predicting performance (Table 1). The GLM output of the best-fitting model is shown in Table 2. Both target wall thickness and experimental year were significant predictors of performance (wall thickness,  $P<0.001$ ,  $N=606$ ; experimental year,

Table 2. Generalized linear model of wall thickness, experimental year, target set and cycle on performance

Parameter	Coefficient	s.e.m.	<i>t</i>	<i>P</i>
Wall thickness	4.448	0.843	5.275	1.33E-07
Target set=thick	0	–	–	–
Target set=thin	–0.192	0.254	–0.752	0.452
Experimental year=2008	0	–	–	–
Experimental year=1992	1.839	0.299	6.15	7.77E-10
Cycle=1	0	–	–	–
Cycle=2	0.344	0.316	1.086	0.277
Cycle=3	0.51	0.314	1.626	0.104
Cycle=4	0.727	0.424	1.713	0.087

Deviance=–745.97; d.f.=599

Target set, experimental year and cycle were tested as categorical variables, so the first parameter coefficient in each category was set to zero. The results for subsequent parameters in each category were tested as the effect of switching from the first category to the second category.

Table 3. Performance values for the thicker and thinner target sets in each cycle

Thicker comparison targets					Thinner comparison targets				
$\Delta$ Target (mm)	1st cycle	2nd cycle	3rd cycle	4th cycle	$\Delta$ Target (mm)	1st cycle	2nd cycle	3rd cycle	4th cycle
A. 1992 experiment									
0.813	99.00 $\pm$ 3.16	99.09 $\pm$ 2.87	–	–	0.813	99.00 $\pm$ 3.16	–	–	–
0.406	100.00 $\pm$ 0.00	100.00 $\pm$ 0.00	–	–	0.406	97.00 $\pm$ 4.83	–	–	–
0.305	99.00 $\pm$ 3.16	99.09 $\pm$ 2.87	99.29 $\pm$ 2.67	98.75 $\pm$ 3.54	0.305	94.00 $\pm$ 6.99	97.27 $\pm$ 6.17	94.44 $\pm$ 7.26	–
0.229	91.00 $\pm$ 11.01	94.55 $\pm$ 12.33	100.00 $\pm$ 0.00	98.75 $\pm$ 3.54	0.229	64.00 $\pm$ 14.30	96.36 $\pm$ 8.81	90.00 $\pm$ 10.54	–
0.152	–	–	98.00 $\pm$ 4.14	100.00 $\pm$ 0.00	0.152	–	91.82 $\pm$ 10.29	94.00 $\pm$ 6.99	–
0.076	–	–	70.67 $\pm$ 17.92	92.50 $\pm$ 7.07	0.076	–	86.36 $\pm$ 15.53	78.00 $\pm$ 20.98	–
B. 2008 experiment									
0.813	91.00 $\pm$ 5.68	95.56 $\pm$ 5.27	96.67 $\pm$ 5.00	–	0.813	96.51 $\pm$ 5.59	96.25 $\pm$ 5.18	95.00 $\pm$ 8.50	95.56 $\pm$ 7.26
0.406	78.33 $\pm$ 9.83	92.00 $\pm$ 13.04	92.50 $\pm$ 9.57	–	0.406	78.33 $\pm$ 16.02	84.00 $\pm$ 15.17	82.00 $\pm$ 13.04	94.00 $\pm$ 8.94
0.305	66.00 $\pm$ 11.40	78.00 $\pm$ 10.95	96.00 $\pm$ 8.94	–	0.305	71.67 $\pm$ 18.35	77.50 $\pm$ 17.08	86.00 $\pm$ 11.40	78.00 $\pm$ 19.24
0.229	70.00 $\pm$ 20.00	84.00 $\pm$ 8.94	70.00 $\pm$ 15.81	–	0.229	73.33 $\pm$ 13.66	75.00 $\pm$ 12.91	80.00 $\pm$ 0.00	86.00 $\pm$ 11.40
0.203	65.71 $\pm$ 12.72	68.33 $\pm$ 19.41	71.67 $\pm$ 13.29	–	0.203	51.25 $\pm$ 20.31	55.00 $\pm$ 17.32	71.67 $\pm$ 24.01	75.00 $\pm$ 16.04
0.152	63.75 $\pm$ 15.06	61.43 $\pm$ 16.76	63.33 $\pm$ 12.11	–	0.152	62.50 $\pm$ 11.65	63.33 $\pm$ 12.11	72.50 $\pm$ 13.89	60.00 $\pm$ 17.89
0.076	60.00 $\pm$ 8.94	46.67 $\pm$ 5.16	61.11 $\pm$ 12.69	–	0.076	56.25 $\pm$ 13.02	55.00 $\pm$ 13.78	55.00 $\pm$ 17.73	65.00 $\pm$ 16.43

$P < 0.001$ ,  $N = 606$ ) but target set and cycle did not predict performance (Table 2). For all combinations of experimental year, target set and cycle, the subject performed better as the difference between the wall thickness of the standard target and the comparison target increased. For table purposes only, performances were averaged for each cycle and wall thickness and were grouped according to target set and experimental year. Discrimination performance was initially high in the 1992 experiment, with the subject performing well above 75.0% for the majority of the cycles (Table 3). Performance was lower on targets in the 2008 data set, with performance below 75.0% on about half the comparison targets.

Although AIC predicts cycle to be an important parameter in the model, performances on individual target wall thicknesses did not significantly change across all cycles. The only significant change in performance was between the 1st and 2nd cycles for the 0.229 mm target in the thinner target set for 1992 ( $t_{18} = 6.90$ ,  $P = 0.001$ ,  $N = 21$ ) and the 1st and 2nd cycles for the 0.076 mm target and the 1st and 3rd cycles for the 0.305 mm target in the thicker target set for 2008 ( $t_{10} = 3.16$ ,  $P = 0.01$ ,  $N = 12$ ;  $t_8 = 4.63$ ,  $P = 0.002$ ,  $N = 10$ ). As most of the performances did not exhibit a significant change according to cycle, performances on all cycles were pooled for further analysis. A comparison of the average performance for each target wall thickness and target set shows a significant reduction in performance between the 1992 and 2008 experiments for most targets (Fig. 2). Performance decreased from 96.9 to 63.9%, with the biggest reduction in performance occurring for targets with a small difference in wall thickness between standard and comparison targets.

#### Loss of high-frequency hearing

Previous studies (using audiograms and masked hearing thresholds) that document hearing loss with the subject are presented in Fig. 3. Unfortunately, no corresponding audiogram is available for the subject for 1988, but masked hearing thresholds were collected and published. In 1988, the subject's hearing thresholds were measured while in the presence of 75 dB of masking noise (Thomas et al., 1990). The audiogram collected in 2004 using evoked potential methods was conducted in Kaneohe Bay, with no additional masking noise (Yuen et al., 2005). Absolute hearing thresholds for audiograms are typically conducted in the presence of little to no background noise, so it is difficult to extrapolate absolute hearing thresholds from the masked hearing data obtained in 1988. Although direct comparisons between the two studies cannot be made,

information on hearing abilities can be extrapolated from the data. In 1988, the subject demonstrated a sharp rise in threshold, or a reduction in hearing sensitivity, at frequencies above 100 kHz. In 2004, this rise in threshold occurred at 34 kHz. Both studies were conducted in the presence of the ambient noise of Kaneohe Bay. At frequencies above 32 kHz, the subject had substantially lower threshold values, or better hearing sensitivities, in 1998 than in 2004. Even in the presence of added background masking noise, the subject heard better at higher frequencies in 1988 than in 2004.

#### DISCUSSION

The loss in wall-thickness discrimination performance between the 1992 and 2008 experiments means that the subject lost some level of fine-scale discrimination ability. Performance for all targets was worse in 2008 than in 1992, with reductions in performance of up to ~36% (Fig. 2). However, for most of the targets, the subject demonstrated a slight improvement in performance over time, although this change

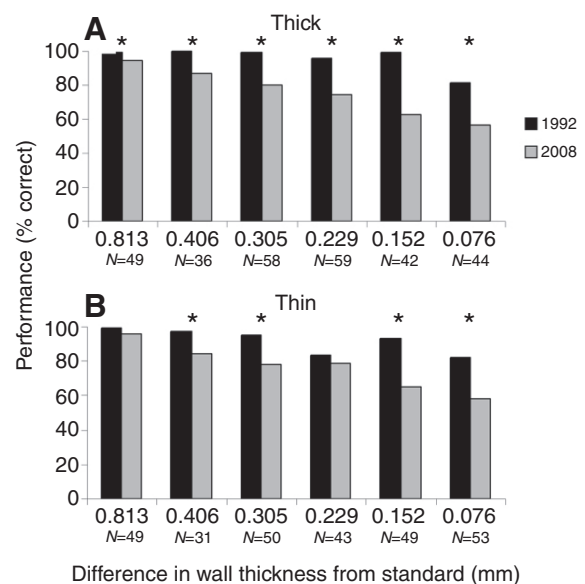


Fig. 2. Change in performance for the wall-thickness measurements for (A) the thicker target set and (B) the thinner target set between the 1992 and 2008 experiments. Asterisks indicate a significant ( $P < 0.001$ ) reduction in performance between the two experiments.

was not significant owing to high variance levels (Table 3). Learning is thought to be the mechanism behind this improvement; through repeated exposure to the standard and comparison targets, the subject solidifies the internal representation of the stimulus and gains more experience with the task. The improvement is most striking for targets with intermediate wall thickness in each set; in the 2008 thinner target data set, performance increased from 73.3 to 86.0% on the 0.229 mm target and from 51.3 to 75.0% on the 0.203 mm target (Table 3). Conversely, the subject showed little improvement at targets with a wall thickness closest to that of the standard target. This lack of improvement in performance with targets below the threshold verifies that the subject was not able to identify the standard target using features other than its wall-thickness signature in the returning echo. If the subject was using a feature other than wall thickness during discrimination, we would expect an increase in performance over time for all comparison targets. That is, using a unique identifier of the standard target other than wall thickness, the subject would have correctly responded to all comparison targets by using the absence of the cue that distinguished the standard from all other targets as an alternative to wall thickness for discriminating the two classes of targets (standard and non-standard).

The subject continued to perform slightly better on targets with intermediate wall thickness, but did not significantly improve on targets with wall thicknesses similar to that of the standard target. Thus, thresholds did not significantly improve over time. This indicates that the subject would not achieve better discrimination performances with more practice and that we were testing the true discrimination abilities of the subject.

During the time period between the two experiments, the subject also demonstrated a sharp reduction in hearing frequency capabilities (Fig. 3). Hearing loss has been previously documented in marine mammals (Ridgway and Carder, 1997; Houser and Finneran, 2006) and can be the result of acoustic trauma, ototoxic drug exposure or presbycusis. Excessive noise or acoustic impulse may result in damage to tissues of the inner ear, and acoustic trauma has been suggested as a factor leading to stranding events with odontocetes (Evans and England, 2001). Ototoxic drugs such as aminoglycosidic antibiotics cause damage to the hair cells of the cochlea and can result in hearing loss (Aran et al., 1999; Finneran et al., 2005). Presbycusis is the most common cause of hearing loss in older mammals. Over time, degeneration of hair cells in the cochlea results in a gradual inability to hear at high frequencies. In odontocetes, presbycusis has been best studied in bottlenose dolphins (*Tursiops truncatus*). Typically, presbycusis begins to occur around age 20–30 for *T. truncatus*, with males experiencing presbycusis earlier than females (Houser et al., 2008). In one case, a male *T. truncatus* had good high-frequency hearing at age 13 but, by age 26, had lost the ability to hear at frequencies above 60 kHz (Ridgway and Carder, 1997). The hearing loss demonstrated by the subject in the current experiment is most likely the result of presbycusis. Since 1988, the subject has been under veterinary care with no ototoxic drug exposure. Additionally, the subject has not been exposed to acoustic trauma that would result in acute damage to the inner ear. Thus, presbycusis is the most logical explanation for the hearing loss. The subject is located in Kaneohe Bay, an acoustic environment that is dominated by snapping shrimp noise and is considered to be one of the world's noisiest underwater environments (Albers, 1965). Presbycusis is often accelerated with extended exposure to high levels of background noise, so the environment of the test subject may have contributed to her presbycusis.

Although the subject's documented high-frequency hearing loss occurred in concert with the reduction in discrimination abilities, is

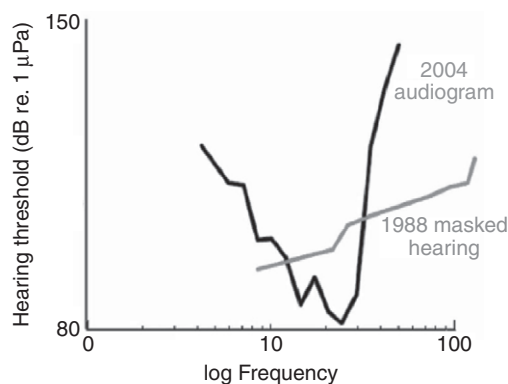


Fig. 3. Comparison of audiogram and masked hearing measurements for the subject demonstrates loss of high-frequency hearing. Masked hearing tests show that the subject heard better at higher frequencies in 1988 than she did in 2004. Audiogram measurements are from Yuen et al. (Yuen et al., 2005) and masked hearing results are from Thomas et al. (Thomas et al., 1990).

this the only possible explanation for the change in performance? The subject probably relies on multiple cues at many frequencies from the target echo to conduct discrimination. Although there may be many cues that odontocetes use for target discrimination (Branstetter et al., 2007; Gaunard et al., 1998; Muller et al., 2008), the use of high frequencies is very likely to be the most important, and the link between high-frequency hearing loss and a reduction in discrimination performance cannot be ignored. These data strongly suggest that the high-frequency component of echoes provides a great deal of information for fine-scale discrimination.

Part of the explanation for a reduction in discrimination abilities may also be attributable to the second part of the odontocete sonar system: the click production mechanism. High-frequency echolocation clicks may provide the opportunity for better target resolution than low-frequency clicks (Au, 1993), and recent analyses indicate that the subject no longer utilizes high-frequency clicks during echolocation (Supin et al., 2008). Previous data demonstrate that, in 1992, the subject used echolocation clicks with most peak frequencies between 40 and 104 kHz (Au et al., 1995). Masked hearing thresholds indicate that the subject had relatively good hearing in this frequency range during this time (Thomas et al., 1990). Current work shows that the subject uses echolocation clicks with peak frequencies between 27 and 32 kHz (Supin et al., 2008). Because the subject currently cannot hear well at frequencies above 34 kHz, it would be disadvantageous for her to produce clicks with frequencies outside this range. However, since lower frequency clicks are presumed to result in poorer target-resolution capabilities, the shift to producing clicks in range of best hearing would naturally result in poorer echolocation abilities. The subject currently emits clicks with peak frequencies in the upper range of good hearing, which may indicate a strategy of producing clicks with the highest audible frequencies possible to maximize target-resolution capabilities.

Another explanation for the reduction in target discrimination capabilities may result from the bandwidth of the echolocation signals. During echolocation, the spectral content of the returning echoes is one of the main cues used in target discrimination (Hammer and Au, 1980). The production and perception of large bandwidth signals utilized by delphinid odontocetes may provide the opportunity for greater target information. Empirical studies with both broad-band dolphin-like clicks and narrow-band porpoise-like clicks show that broad-band signals provide more echo highlights of prey, and thus greater range resolution, than narrow-band signals

(Au et al., 2007). Measurements of echolocation signals from wild *P. crassidens* show -3 dB bandwidths between 15 and 76 kHz, with an average bandwidth of 35 kHz (Madsen et al., 2004). These animals also produced echolocation clicks with a mean peak frequency of 40 kHz, ranging from 26 to 79 kHz. Previous echolocation studies with our experimental subject do not report bandwidth measurements (Au et al., 1995), so a direct comparison is not possible. The reduction in peak frequency, however, suggests that our subject currently produces clicks with bandwidths smaller than those reported from free-ranging *P. crassidens* (Madsen et al., 2004). Even if our subject still produced clicks with wide bandwidths, if she cannot hear frequencies within the signals, a large proportion of her bandwidth is nonfunctional. In essence, a reduction in high-frequency hearing can result in an auditory processing mechanism more similar to narrow-band signals than broad-band signals. Thus, a reduction in hearing can result in a reduction in discrimination and range resolution of prey.

This shift in frequency content of outgoing clicks is likely to be a constant gradual process. Over time, as an animal loses the ability to hear at certain frequencies, those frequencies are dropped out of its outgoing signal. Any frequencies produced outside the range of hearing may simply be artifacts of the click-production mechanism. Continued measurements of hearing, echolocation click parameters and discrimination abilities may show temporal trends in the linkage between hearing sensitivities, echolocation frequency content and echolocation discrimination (Ibsen et al., 2009).

The data from the present study demonstrate that high-frequency hearing is beneficial to the process of discriminating the fine details of echolocation targets. The loss of high-frequency hearing resulted in a decrement in the ability to distinguish fine-scale differences in echolocation targets. Given that both echolocating bats and odontocetes developed the ability to hear high frequencies as they evolved, it seems apparent that one of the primary reasons for the development of high-frequency hearing is for the discrimination of fine detail during echolocation.

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