

1 **Hearing in Cetaceans: From Natural History to Experimental Biology**

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1 *Abstract*

2 Sound is the primary sensory cue for most marine mammals, and this is especially true for  
3 cetaceans. To passively and actively acquire information about their environment, cetaceans  
4 have perhaps the most derived ears of all mammals, capable of sophisticated, sensitive hearing  
5 and auditory processing. These capabilities have developed for survival in an underwater world  
6 where sound travels five times faster than in air, and where light is quickly attenuated and often  
7 limited at depth, at night, and in murky waters. Cetacean auditory evolution has capitalized on  
8 the ubiquity of sound cues and the efficiency of underwater acoustic communication. The sense  
9 of hearing is central to cetacean sensory ecology, enabling vital behaviors such as locating prey,  
10 detecting predators, identifying conspecifics, and navigating. Increasing levels of anthropogenic  
11 ocean noise appears to influence many of these activities.

12       Here we describe the historical progress of investigations on cetacean hearing, with a  
13 particular focus on odontocetes and recent advancements. While this broad topic has been  
14 studied for several centuries, new technologies in the last two decades have been leveraged to  
15 improve our understanding of a wide range of taxa, including some of the most elusive species.  
16 This paper addresses topics including how sounds are received, what sounds are detected,  
17 hearing mechanisms for complex acoustic scenes, recent anatomy and physiology studies, the  
18 potential impacts of noise, and mysticete hearing. We conclude by identifying emerging  
19 research topics and areas which require greater focus.

20

1 **1. INTRODUCTION**

2           Hearing in cetaceans is an impressive process resulting from various adaptations to life  
3 underwater. Some components of the auditory system of mysticetes (baleen whales) are among  
4 the largest of all mammals and some species are likely to hear infrasonic frequencies.  
5 Odontocetes (toothed whales, dolphins, and porpoises) can have extraordinarily broad hearing  
6 ranges, up to 180 kHz in some species. Within this range, most odontocete species have fine-  
7 scale frequency discrimination abilities. They can process sounds rapidly, compensating for both  
8 the faster underwater sound speed and complex requirements for echolocation. Furthermore,  
9 odontocetes have developed a novel mechanism to receive sounds through specialized acoustic  
10 fats associated with their lower jaws.

11           Past investigations of cetacean hearing, particularly those conducted on odontocetes in  
12 the past 50 years, have revealed a significant amount of information about the impressive hearing  
13 abilities of cetaceans. Because cetaceans are primarily offshore, pelagic animals, many of whom  
14 do not maintain well in captivity, audiometry studies typically involve small sample sizes for a  
15 limited subset of species. Consequently, there is still a substantial amount of knowledge to be  
16 gained for most species and with the subject of cetacean hearing.

17           This review addresses what has been learned regarding cetacean hearing, presenting it  
18 within a historical context while incorporating more recent, novel investigations. The review  
19 focuses on odontocetes because the majority of information available examines this suborder  
20 (Figure 1A-C). We also address what little is known about mysticete hearing and suggest future  
21 research areas.

22

23 **2. EARLY INVESTIGATIONS**

1           The study of cetacean hearing started as an observational inquiry, centered on natural  
2 history. One of the notable earlier studies was published by John Hunter in 1787 (Hunter, 1787).  
3 In his lengthy work titled “Observations on the Structure and Oeconomy of Whales”, Hunter  
4 noted that cetacean ears are made of the same structures as quadruped ears including an external  
5 opening, a tympanic membrane, the Eustachian tube, ossicles, cochlea, and semicircular canals.  
6 However, there is no pinna and the ear canal is a long tube taking a “serpentine course” through  
7 the tissues of the head. The bony portion of the ear, composed of the “tympanum” (tympanic)  
8 and the “round, bony process” (periotic) is very hard and is not as integrated into the skull as  
9 other quadrupeds. Regarding how the organ functions, Hunter speculated that the tympanic  
10 cavity amplifies sound through the vibration of bone and these vibrations are directly transferred  
11 to the inner ear.

12           In 1812, Everard Home published an account of the ears of bowhead whales (*Balaena*  
13 *mysticetus*). He noticed the peculiarity of the tympanic membrane in these animals, which is  
14 convex unlike in any other animal and projects into the ear canal (Home, 1812). This derived  
15 tympanic membrane, which is common to mysticetes but not found in odontocetes, is now called  
16 the “glove finger.” Home hypothesized that the bowhead whale hears through vibrations of the  
17 tympanic bone, which are transmitted via another “membrane” stretched across the tympanic  
18 cavity and attaching to the malleus.

19           Remington Kellogg studied the evolution of whales in the 1920’s, comparing currently  
20 existing species to fossil cetaceans and examining various modifications to the skull as cetaceans  
21 evolved to live under water (Kellogg, 1928). In the process, Kellogg elaborated upon previous  
22 descriptions of the auditory anatomy. He noted that the attachment of the tympanic and periotic  
23 bones (housing the middle and inner ears) to the skull differs between toothed whales and baleen

1 whales: the bones are only attached to the skull by ligaments in toothed whales, while the  
2 periotic bones of all living and fossil baleen whales have a long posterior process that is wedged  
3 between the exoccipital and squamosal bones. Kellogg speculated that the dense, heavy, air-  
4 filled tympanic bulla serves as a resonating sounding box, vibrating somewhat independently of  
5 the periotic and transmitting sound along the ossicles. This “resonance theory” seems to have  
6 been a popular viewpoint at this time, as the same mechanism was also described by Claudius  
7 (1858) and Denker (1902)<sup>1</sup> even though they disagreed about the involvement of the ossicles.

8 Various other theories on cetacean sound reception also existed during this time period.  
9 Camper (1762)<sup>1</sup> thought that sperm whales heard through the ear canal. Buchanan (1828) stated  
10 that bowhead whales heard through the Eustachian tube. An unnamed scientist (described in  
11 Kernan, 1919) thought that sound reaches the cochlea directly through vibrations of the periotic  
12 bone, but this was dismissed by Kernan because the cochlear fluid needs to receive an orderly  
13 succession of waves from the ossicles for sensitivity to different frequencies. Kernan (1919)  
14 supported bone conduction, where vibrations from the entire skull are transmitted to the  
15 tympano-periotic complex through a bony outgrowth of the tympanic that may contact the skull.  
16 Yamada (1953) also supported the bone conduction theory, arguing that even if the tympano-  
17 periotic complex lacks bony connections to the skull, fibrous connections prevent acoustic  
18 isolation of the ears. He reasoned that resonance of air in the middle ear cavity cannot be  
19 essential to auditory function because the cavity often fills up with parasites.

20 Yamada also provided a summary of conflicting theories of the time, including  
21 Boenninghaus (1904)’s “sound-funnel” theory. Boenninghaus<sup>1</sup> proposed a soft-tissue pathway  
22 which ends at the tympanic bulla, putting the malleus into motion and thus transferring sounds

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<sup>1</sup> These works are unavailable in English. Therefore, the content was obtained from Yamada (1953)’s descriptions of the theories.

1 via the ossicles to the inner ear. Although he included skin, fat, tongue, and jawbone  
2 musculature in the soft-tissue pathway, this seems to be the theory closest to the current view of  
3 odontocete sound reception described by Norris (1968; see below). However, Yamada noted  
4 that Boenninghaus's work was "really so hard to understand that... a serious confusion was  
5 brought into our field." Yamada concluded his discussion by stating that the experiments  
6 necessary to settle the dispute of how cetaceans receive sound are not yet feasible, but the field  
7 will greatly benefit from technical advances in the future.

8         While the mechanism of hearing remained unclear, the anatomic potential for acute  
9 hearing in cetaceans was becoming evident. Hunter (1787) had noted the well-developed  
10 cochlea relative to the semi-circular canals, an observation repeated by Fraser (1952).  
11 Langworthy (1931)'s study of the central nervous system revealed that the acoustic nerves and  
12 acoustic components of the brain are exceptionally well developed in odontocetes. He  
13 commented that the highly developed odontocete cerebral cortex may have been driven by very  
14 acute hearing and need for acoustic processing, analogous to the rapid growth and differentiation  
15 of the primate cortex as a response to its complex optic structures and binocular stereoscopic  
16 vision. Indeed, researchers began suspecting that odontocetes might echolocate and "see"  
17 through their hearing in 1947 (Schevill and McBride, 1956).

18         The first underwater recordings of cetacean vocalizations were made in the 1940's, which  
19 greatly advanced our understanding of the sounds used by cetaceans (Schevill and Lawrence,  
20 1949). In 1952, Kellogg and Kohler borrowed a transducer from the U.S. Navy for a primitive  
21 behavioral hearing experiment on captive dolphins (Kellogg and Kohler, 1952). Based on the  
22 results, they surmised that dolphins can hear ultrasonic sounds of up to 50 kHz. High frequency

1 hearing in odontocetes was also supported by histological examination of their cochlea (Yamada  
2 and Yoshizaki, 1959).

3           Meanwhile, the controversy on *how* cetaceans received sounds was not yet settled.  
4 Reysenbach De Haan (1957) argued that the cetacean ear canal was vestigial based on  
5 experiments using tissue from blue whales (*Balaenoptera musculus*). He took a section of  
6 blubber which contained the ear canal, immersed it in water, and used hydrophones to show that  
7 sound conductivity was not significantly different through water compared to blubber.  
8 Furthermore, the orientation of the ear canal relative to the sound source made no difference in  
9 sound propagation. Therefore, he concluded that the ear canal could not be a preferential  
10 pathway for sound. Dudok van Heel (1962) supported this view as well. Fraser and Purves  
11 (1960) came to the opposite conclusion by measuring sound waves traveling through a dissected  
12 ear canal compared to the surrounding tissue in fin whales. Because sound was attenuated the  
13 least through the ear canal, they surmised that it is a preferential sound reception pathway.  
14 Regarding the alternate theories, Fraser and Purves stated, “The adaptation of the sound path in  
15 normal terrestrial mammals is, on the face of it, more acceptable than any *de novo* method of  
16 sound conduction in mammals.”

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### 18 **3. KEN NORRIS AND THE “JAW HEARING” HYPOTHESIS**

19           The major breakthrough in the field came in the mid 1960’s. Ken Norris was walking on  
20 a beach in Mexico when he came across a dolphin skeleton. He noticed a region of the lower  
21 jaw which was so thin that it was translucent (Figure 1A). Norris then realized that this is a  
22 common feature to all odontocetes, and that this thin area of bone was overlain with an oval fatty  
23 area which he called the “acoustic window.” According to Norris, sound enters the odontocete

1 head through this oval fat body and goes through the thinnest part of the mandible to the  
2 “acoustic fat” filling the mandibular canal (Figure 1B). While the existence of these mandibular  
3 fat bodies was known since the 1800’s, Norris was the first one to associate them with the  
4 auditory system, observing that they lead directly to the tympanic bulla and may provide a low  
5 impedance pathway to the ears (Figure 1; Norris, 1964; Norris, 1968).

6 Not everyone accepted Norris’s hypothesis immediately. However, Norris’s stimulating  
7 idea led to a series of validation studies, enabled by technological advances of the time. Bullock  
8 *et al.* (1968) conducted physiological recordings from anesthetized dolphins and found the  
9 greatest response when sound was played to the lower jaw. Norris and Harvey (1974) implanted  
10 small hydrophones in various locations of a dead bottlenose dolphin head and found sound to be  
11 concentrated in the proposed sound channel of the jaws. Brill *et al.* (1988) found that a  
12 bottlenose dolphin’s echolocation abilities were greatly reduced when its lower jaws were  
13 covered by an acoustically opaque hood. The authors suggested that the hood prevented the  
14 animal from hearing the returning echoes, thus behaviorally supporting the notion of jaw hearing.  
15 A behavioral hearing test supported these observations in which sound was presented via a  
16 “jawphone,” or a transducer implanted in a suction cup (Brill, *et al.*, 2001). The tests showed that  
17 high frequencies were best detected when sounds were presented along the lower jaw (e.g.,  
18 Figure 1C). However, the dolphin detected lower frequencies better when they were presented  
19 near the meatus. These reports were supported with similar electrophysiological hearing tests  
20 (Møhl, *et al.*, 1999).

21 Scientists from other fields also made significant contributions. For example, Varanasi  
22 and colleagues’ biochemical analysis showed that “acoustic fats” are incredibly specialized,  
23 comprised of endogenously synthesized shorter, branch-chained fatty acids and wax esters not



1 typically found in mammalian adipose tissues (Litchfield, *et al.*, 1975; Morris, 1975; Varansi, *et*  
2 *al.*, 1975; Varansi and Malins, 1972). Recent work by (Koopman, *et al.*, 2006) has revealed a  
3 complex and consistent topographical distribution of lipids within odontocete perimandibular  
4 fats, with the highest relative wax ester concentrations for each species all occurring in the  
5 caudal-most portions of the inner mandibular fat bodies, which connect to the tympano-periotic  
6 complex. This new study confirmed early suggestions of heterogeneity in lipid composition of  
7 odontocete perimandibular fats (Malins and Varanasi, 1975).

8 Koopman *et al.*, (2006) also found that the distribution of fatty acids show consistent  
9 patterns, where the shortest and branched-chain compounds were concentrated in the middle of  
10 the inner fat body and around the tympano-periotic complex. It has been shown that sound  
11 velocity in lipids is a function of their molecular weight and that sound also travels faster through  
12 triacylglycerols than through wax esters (Flewellen and Morris, 1978; Gouw and Vlugter, 1967;  
13 Hustad, 1971). Therefore, the study hypothesized that the topographical arrangement of lipids  
14 within perimandibular fat bodies of odontocetes are arranged so that sound is directed to the ears  
15 as it bends towards the inner low-velocity center of the mandibular fat body, which has a higher  
16 concentration of wax esters and short, branched-chain lipids. Such an acoustic channel has also  
17 been proposed for odontocete melons in previous studies which have found compositional  
18 heterogeneity within the melon (Blomberg and Lindholm, 1976; Litchfield, *et al.*, 1973; Scano,  
19 *et al.*, 2005; Varanasi and Malins, 1972; Wedmid, *et al.*, 1973).

20 Interestingly, Zahorodny *et al.*, (2009) found that the perimandibular fats of the  
21 bottlenose dolphin do not display the same pattern of having an inner low-velocity channel,  
22 although the fats closest to the tympano-periotic complex do follow the pattern of having the  
23 highest wax ester content and shortest, branched-chained fatty acids and fatty alcohols. These

1 differences between species, as well as differences in lipid composition found between age  
2 classes, may reflect the complexity, development and niche related adaptations of the fat  
3 “channels” (Koopman and Zahorodny, 2008). Together, these studies helped establish the  
4 validity of Norris’s unconventional theory, leading to a paradigm shift by uncovering a whole  
5 new mechanism for mammalian hearing.

6

## 7 **4. WHAT ODONTOCETES HEAR**

### 8 **4.1. Basic hearing abilities**

9         The odontocete audiogram, or a plot of frequency vs. detection limit (hearing threshold,  
10 e.g., Figure 2), was first estimated by Johnson (1966; 1967). Using operant-conditioned and a  
11 go/no-go procedure, an 8-9 year old male bottlenose dolphin was trained to press a lever when a  
12 sound was detected (a “go” or positive response). If the animal did not detect a sound it would  
13 remain still (a “no-go”). A staircase method, which steps sound levels up or down based on  
14 correct and incorrect responses, was used to vary sound levels. The animal was given a 90  
15 second time-out for incorrect responses. This work described an auditory range of 75 Hz – 150  
16 kHz and thresholds at or below 50 dB re 1  $\mu$ Pa from approximately 10-115 kHz. Maximal  
17 sensitivity was 40.8 dB at 65 kHz. This broad and sensitive audiogram set a benchmark for  
18 which all other odontocete audiogram have been, and continue to be, compared.

19         This bottlenose dolphin audiogram was soon succeeded by comparative hearing tests in  
20 several other odontocete species including one harbor porpoise (*Phocoena phocoena*), one killer  
21 whale (*Orcinus orca*) and one Amazon river dolphin (*Inia geoffrensis*) (Andersen, 1970; Hall  
22 and Johnson, 1972; Jacobs and Hall, 1972). The hearing tests from each of these animals  
23 produced different audiograms. The harbor porpoise had slightly less sensitive hearing

1 compared to the bottlenose dolphin and its best hearing was found at slightly lower frequencies  
2 (8-32 kHz). The killer whale was most sensitive at even lower frequencies and had a high  
3 frequency cut-off of only 32 kHz. The Amazon river dolphin had a narrow range of “best  
4 sensitivity” (10-50 kHz) and a high frequency limit of 105 kHz. (Note that meaning of “best  
5 sensitivity” can vary between studies; in this case it refers to 20 dB above the lowest threshold).  
6 At the time, it was not clear whether the large variations between these audiograms were due to  
7 species or individual differences.

8           Since these early audiograms, there have been several additions to the roster of species  
9 with hearing tests (Table 1). These now include the: Chinese river dolphin (*Lipotes vexillifer*)  
10 (Wang, *et al.*, 1992); beluga (*Delphinapterus leucas*) (Awbrey, *et al.*, 1988; Klishin, *et al.*, 2000;  
11 Mooney, *et al.*, 2008; White, *et al.*, 1978); false killer whale (*Pseudorca crassidens*) (Thomas, *et*  
12 *al.*, 1988; Yuen, *et al.*, 2005); tucuxi (*Sotalia fluviatilis guianensis*) (Sauerland and Dehnhardt,  
13 1998); Risso’s dolphin (*Grampus griseus*) (Nachtigall, *et al.*, 1995; Nachtigall, *et al.*, 2005);  
14 striped dolphin (*Stenella coeruleoalba*) (Kastelein, 2003); finless porpoise (*Neophocoena*  
15 *phocanoides*) (Popov, *et al.*, 2005); Gervais’ beaked whale (*Mesoplodon europaeus*) (Cook, *et*  
16 *al.*, 2006; Finneran, *et al.*, 2009); *Tursiops truncatus gilli* (Houser, *et al.*, 2008; Ljungblad, *et al.*,  
17 1982); the white beaked dolphin (*Lagenorhynchus albirostris*) (Nachtigall, *et al.*, 2008); long-  
18 finned pilot whale (*Globicephala melas*) (Pacini, *et al.*, 2010); Blainville’s beaked whale  
19 (*Mesoplodon densirostris*) (Pacini, *et al.*, 2011); and the pygmy killer whale, (*Feresa attenuata*)  
20 (Montie, *et al.*, 2011). These audiograms have yielded a substantial amount of information on  
21 odontocete hearing sensitivity.

22           One conclusion that can be derived from the above studies is that there is a huge diversity  
23 in hearing ranges and sensitivities among odontocetes. These disparities appear to be a

1 combination of species differences and individual variation. Increasing sample sizes within a  
2 species has shown that there are many instances of hearing loss. For example, Rigdway and  
3 Carder (1997) demonstrated that hearing loss in bottlenose dolphins appears to be correlated with  
4 age and sex. Older animal were more likely to have high frequency hearing loss compared to  
5 younger individuals. Males had a greater incidence and extent of high frequency hearing loss  
6 compared to females. These results implied that the relatively narrower audiograms in species  
7 such as the killer whale and Risso's dolphin reflected incidences of individual high frequency  
8 hearing loss rather than a species-wide phenomenon (Hall and Johnson, 1972; Nachtigall, *et al.*,  
9 1995). This hypothesis was supported by subsequent tests of both species (Nachtigall, *et al.*,  
10 2005; Szymanski, *et al.*, 1999). For the killer whale, Szymanski *et al.* showed a substantially  
11 greater high frequency limit of 120 kHz, as opposed to 32 kHz (Hall and Johnson, 1972), while  
12 the frequency of best hearing was similar to the previous study (18 and 20 kHz). Nachtigall *et*  
13 *al.*'s (2005) work examined the hearing of a neonate Risso's dolphin (Figure 2). This animal had  
14 a high frequency limit of 150 kHz, instead of 100 kHz, and good sensitivity (< 80 dB) over a  
15 wider range, from 8-110 kHz (Figure 3). Lowest thresholds were 49.5 dB at 90 kHz, instead of  
16 the previously reported threshold at 67 dB at 64 kHz, although these elevated thresholds were  
17 likely masked by the noisy test conditions of Kaneohe Bay (Nachtigall, *et al.*, 1995).

18         While the above studies established that intra-species variation existed, these differences  
19 were examined in greater detail for two subspecies of bottlenose dolphins (*T. truncatus* and *T.*  
20 *truncatus gilli*) (Houser and Finneran, 2006b; Houser, *et al.*, 2008). Variability in the range of  
21 hearing and age-related reductions in sensitivity was consistent between the two bottlenose  
22 dolphin subspecies. However, areas of best sensitivity differed between the two subspecies. The

1 authors suggested that both genetic differences between the subspecies and the background noise  
2 conditions of the populations could be causing these differences.

3

#### 4 **4.2. Functional explanations for diversity in audiograms**

5         These species differences, and the consistencies in audiogram shape between closely  
6 related species, suggest that there is a genetic component to odontocete hearing (Houser and  
7 Finneran, 2006b; Houser, *et al.*, 2008), which has been observed in other mammals (Vanke,  
8 1980). In general, these differences are often attributed to correlations with the sounds produced,  
9 such as the frequencies of the echolocation clicks of the species.

10         Compared to the average bottlenose dolphin audiogram, the range of best sensitivity (20  
11 dB within the lowest threshold in this case) for killer whales was centered around much lower  
12 frequencies of 12-52 kHz (Szymanski, *et al.*, 1999). The best sensitivities were also  
13 comparatively lower, in the range of 40-50 kHz, for the two beaked whale species measured  
14 (Finneran, *et al.*, 2009; Pacini, *et al.*, 2011). Correspondingly, beaked and killer whale  
15 echolocation click signals are centered at lower frequencies than for clicks produced by  
16 bottlenose dolphins (20-50 kHz vs. 80-130 kHz) (Au, *et al.*, 1974; Au, *et al.*, 2004; Johnson, *et*  
17 *al.*, 2007).

18         Harbor porpoises show a broad range of good sensitivity 16-140 kHz which included  
19 relatively high frequencies (Kastelein, *et al.*, 2002). They are also sensitive up to 180 kHz.  
20 Compared to the bottlenose dolphin, porpoise echolocation pulses are narrow band, high  
21 frequency signals, consistent with their high-frequency hearing (Au, *et al.*, 1999). This is  
22 exceptional for odontocetes with only one other species, white beaked dolphins, detecting signals  
23 at such high frequencies (Nachtigall, *et al.*, 2008).

1 Whistles are presumably just as important, at least to the species that produce them. For  
2 the bottlenose and *Stenella* spp., whistle fundamental frequencies often do not overlap with the  
3 regions of best sensitivity (Johnson, 1967; Kastelein, 2003; Lammers, *et al.*, 2003). However,  
4 whistle harmonics can overlap with “best” hearing ranges, suggesting that their auditory system  
5 is well adapted to detect these components of the communication signals (Lammers, *et al.*, 2003).  
6 Notably, echolocation signals can change with hearing abilities (Ibsen, *et al.*, 2007; Kloepper, *et*  
7 *al.*, 2010). As high frequency hearing is lost, animals seem to alter their echolocation centroid  
8 frequencies to match regions of maximal auditory sensitivity. Thus, there is substantial evidence  
9 that hearing sensitivities match the acoustic signals produced. Echolocation clicks with  
10 substantial sound energies at frequencies beyond the range of best hearing has been found in  
11 only in the white beaked dolphin (Nachtigall, *et al.*, 2008; Rasmussen and Miller, 2002). While  
12 somewhat unexpected, this is probably a function of slight differences in the animals’ auditory  
13 anatomy or physiology. There are several examples of terrestrial animals producing sounds  
14 beyond their hearing range (Pytte, *et al.*, 2004).

15

### 16 **4.3 The auditory evoked potential (AEP) method**

17 Increased audiogram sample sizes, even across different methods and experimental  
18 conditions (Figure 4), have greatly broadened our understanding odontocete hearing sensitivity.  
19 Many of these audiograms were made possible by applying electrophysiological methods to  
20 study hearing. The primary electrophysiological method that has been used is called the auditory  
21 evoked potential method (AEP). AEP provide a noninvasive and rapid way to test hearing by  
22 measuring the small voltages generated by neurons in the auditory system in response to acoustic  
23 stimuli (Figure 3). Voltages in response to sound are often generated in the brainstem and are

1 sometimes referred to as auditory brainstem responses (ABRs). Louder acoustic stimuli lead to  
2 larger amplitudes in the AEP signals. As the stimulus is reduced in intensity, the resulting AEP  
3 signals also become reduced. The intensity at which the AEP signal is no longer detectable is  
4 defined as the hearing threshold. Actual threshold determinations can be conducted in several  
5 ways (Finneran, *et al.*, 2007a; Nachtigall, *et al.*, 2007; Supin and Popov, 2007). The AEP  
6 method requires no training of the subject and is used to assess hearing in a variety of taxa  
7 including other mammals, such as humans (Dolphin and Mountain, 1992; Hecox and Galambos,  
8 1974), birds (Brittan-Powell, *et al.*, 2002), teleost fish (Ladich and Yan, 1998), cartilaginous fish  
9 (Casper, *et al.*, 2003), and invertebrates (Lovell, *et al.*, 2005).

10         Electrophysiological auditory measurement techniques have been established for several  
11 decades in marine mammals. Initially, the methods varied, electrophysiological tools adapted for  
12 marine mammals were not widely available, the experiments were often invasive, and the  
13 methods were not widely applied (Bullock, *et al.*, 1968; Popov and Supin, 1990; Ridgway, *et al.*,  
14 1981). Early studies initially required anesthesia, a major accomplishment for animals which  
15 respire voluntarily (Ridgway and McCormick, 1967). Bullock *et al.* (1968) followed this work  
16 with the first acoustically-stimulated electrophysiological auditory recordings from twenty nine  
17 odontocetes among four species. This was a comprehensive study which addressed waveform  
18 characteristics, temporal resolution, electrode placement, frequency tuning, masking using  
19 background noise, and pure tones vs. modulated stimuli. The study produced an “audiogram”  
20 similar in frequency responses and sound levels to Johnson’s audiogram for the bottlenose  
21 dolphin. Evoked potentials were measured using tungsten and stainless steel electrodes inserted  
22 in several locations, with reliable responses originating from the inferior colliculus.

1 McCormick et al. (1970) followed with an integrative anatomical and  
2 electrophysiological study of the mechanisms of the dolphin middle ear using dissections and  
3 physiologically recording from the inner ear's round window. They concluded that sound will  
4 induce movement of the ossicles (thus a functional middle ear) and be conducted to the inner ear  
5 through the oval window. While still a novel study, the results were slightly limited by the  
6 inevitable surgery and the necessity to make measurements with the animal at the water's surface.  
7 Odontocete middle ear mechanisms are still debated today.

8 The pace of electrophysiological studies in the U.S. slowed after the passage of the  
9 Marine Mammal Protection Act of 1972. However, substantial AEP work was continued by  
10 Soviet scientists (see review by Ridgway, 1980). Advancements included using AEPs to identify  
11 response-generating regions within the cortex and identifying how AEP onset and offset  
12 responses were impacted by frequency and duration (Ladygina and Supin, 1970; Ladygina and  
13 Supin, 1977; Popov and Supin, 1976; Popov and Supin, 1978). The thresholds produced were  
14 similar to prior psychophysical (behavioral) tests (Johnson, 1966). Classical conditioning was  
15 used to measure hearing physiologically by pairing tones with electric shocks, while monitoring  
16 changes in heart rate, respiration and galvanic skin response (Sukhoruchenko, 1971;  
17 Sukhoruchenko, 1973; Supin and Sukhoruchenko, 1970). The experiments detected the upper  
18 limit of hearing and showed that both bottlenose dolphins and porpoises have precise frequency  
19 discrimination abilities across their hearing range. Using operant conditioning, Thompson and  
20 Herman demonstrated that dolphins can distinguish two sounds that differ in frequency by only  
21 0.2-0.3%, displaying remarkably precise frequency analyses (1975).

22 Amongst these early AEP studies was the establishment of non-invasive methods which  
23 recorded responses from the surface of the skin (Seeley, *et al.*, 1976). This method was similar



1 to those used on humans and set the stage for rapid advances in odontocete AEP recordings  
2 (Hecox and Galambos, 1974). Within the last two decades an emphasis on relatively simple,  
3 non-invasive AEP techniques has been developed, providing insights into the auditory systems  
4 of odontocetes (Dolphin, *et al.*, 1995; Nachtigall, *et al.*, 2007; Supin and Popov, 1995; Supin, *et*  
5 *al.*, 2001).

6       Early non-invasive dolphin AEP measurements were stimulated with tone pips and  
7 revealed dolphin AEP responses involving a series of 5-7 neurophysiological “wave” responses  
8 (Popov and Supin, 1985; Popov and Supin, 1990). An efficient and reliable method to obtain  
9 AEP hearing thresholds has used the envelope following response (EFR) or auditory steady state  
10 response (ASSR; Supin and Popov, 1995). In this method the stimulus is a sinusoidally  
11 amplitude modulated tone or a series of clicks (Figure 3). The series of resulting AEP waves are  
12 all visible at the onset of an EFR, but if a stimulus is played at a rapid enough rate, most of the  
13 waves blend together in a sinusoidal fashion. The animal’s EFR is a consequent sinusoidal  
14 “following” of the envelope of the carrier signal; when the animal is able to detect the stimulus,  
15 the AEP recordings contain a sinusoidal signal at the frequency with which the amplitude of the  
16 stimulus is modulated. The results of this method compare favorably to those from behavioral  
17 psychometric audiograms (Houser and Finneran, 2006a; Szymanski, *et al.*, 1999; Yuen, *et al.*,  
18 2005). Other aspects of odontocete AEPs are well-reviewed elsewhere (Nachtigall, *et al.*, 2007;  
19 Supin, *et al.*, 2001).

20

## 21 **5. HEARING MECHANISMS FOR COMPLEX AUDITORY SCENES**

22       While the increasing number and quality of audiograms provide insights into what  
23 odontocetes hear, substantial progress has also been made regarding how odontocete hearing

1 works. For hearing to provide any advantage to an individual listener, an animal must not only  
2 detect, discriminate and recognize sounds, but must also know the sound source location. These  
3 abilities are complicated by the presence of multiple sounds occurring simultaneously in  
4 Euclidean space. An excellent example of a fundamental, but complex auditory task occurs  
5 during cooperative nocturnal feeding by Hawaiian spinner dolphins (*Stenella longirostris*). These  
6 animals are tasked with cooperatively herding a low-density mesopelagic biomass, into a dense  
7 group that is more conducive to feeding. (Benoit-Bird and Au, 2009). Behaviorally, the group  
8 spreads out in a horizontal line and swims towards the low density layer forcing the fish to  
9 coalesce for protection. To accomplish this task, the dolphins must acoustically monitor the  
10 position of group members and coordinate their herding behavior, acoustically monitor the  
11 position and density of their prey, and still remain vigilant for potential predators. Monitoring the  
12 position and direction of movement in group members is likely accomplished by both directly  
13 echolocating on group members as well as passively listening to specific acoustic cues associated  
14 with other group member's directional phonations. Foraging groups in Hawaii typically range  
15 from 16-28 individuals (Benoit-Bird and Au, 2009) meaning that there will be a cacophony of  
16 clicks and echoes coming from many different sources and targets that the dolphin auditory  
17 system must make sense of. Understanding how this is accomplished requires an understanding  
18 of how the dolphin's auditory system segregates and recognizes sounds in complex auditory  
19 scenes.

20

## 21 **5.1 Basic hearing model**

22 The dolphin auditory pathway can be modeled as a series of transfer functions that  
23 convert environmental pressure fluctuations into perception. The primary stages are: the head

1 related transfer function (HRTF), amplification by the middle ear ossicles, spectral  
2 decomposition at the basilar membrane, transduction and amplitude compression at the hair cells,  
3 low pass filtering by the 8<sup>th</sup> nerve and higher auditory areas, and reintegration of the information  
4 from both ears to form a percept. What follows is a review on some of the stages that have been  
5 studied.

6

## 7 **5.2. Head related transfer function**

8 In terrestrial mammals, the primary purpose of the outer ear (i.e., the pinna and meatus) is  
9 to focus sound towards the middle and inner ear. In addition, the complex ridges and folds of the  
10 pinna, as well as the head and torso, also differentially filter sound depending on the source's  
11 location. This is known as a position-dependant spectral filter or a head related transfer function  
12 (HRTF) and aids a listener in determining the location of a sound source, especially in the  
13 vertical plane (Branstetter and Mercado III, 2006). A feature often found in auditory predators  
14 (e.g., the barn owl, *Tyto alba*, (Knudsen, 1981)) is pronounced asymmetry in external auditory  
15 anatomy that results in a HRTF with salient localization cues. In water, the terrestrial pinna loses  
16 its reflective and filtering capabilities due to the density similarity with water. As a result, natural  
17 selection has sacrificed the archetypical odontocete pinna to provide a more streamlined shape  
18 for locomotion. To compensate for the loss of the pinna, the reflective and refractive properties  
19 of internal anatomical structures may function as a pinna analog (Aroyan, 2001; Ketten, 1997).  
20 Like other auditory predators, odontocetes exhibit pronounced asymmetry in anatomical  
21 structures including the skull (Fahlke, *et al.*, 2011; Ness, 1967), soft tissue (Cranford, *et al.*,  
22 1996), and cranial air sacks (Cranford, *et al.*, 1996; Houser, *et al.*, 2004b). To date, a detailed  
23 HRTF of any cetacean has not been measured. However, data from behavioral experiments (Brill,

1 *et al.*, 2001), electrophysiological experiments (Supin and Popov, 1993) and computer models  
2 (Aroyan, 2001) all suggest that odontocetes possess a salient and complex HRTF.

3

### 4 **5.3 Middle ear transfer function**

5         The function of the middle ear in terrestrial animals is to amplify sounds to overcome  
6 impedance mismatch between air and the fluid-filled cochlea. Impedance mismatch between an  
7 ocean environment and the fluid-filled cochlea is minimal, which calls into question the function  
8 of the middle ear in odontocetes. The ossicles of odontocetes are rigid and calcified, lacking the  
9 mobility of their terrestrial ancestors (Ketten, 1997). Nevertheless, mechanical models based on  
10 the anatomy of the tympano-periotic complex suggest the odontocete middle ear functions as a  
11 velocity amplification device using a lever mechanisms (Nummela, *et al.*, 1999). The rigidity of  
12 the system may be a specialization for high frequency hearing associated with echolocation and  
13 the computer models are able to provide reasonable fits to odontocete audiograms (Hemilä, *et al.*,  
14 2001).

15

### 16 **5.4. Frequency and temporal resolution at the auditory periphery**

17         Sound enters the cochlea at the oval window and displaces the differentially stiff basilar  
18 membrane (BM). The odontocete basilar membrane functions on the same principles as  
19 terrestrial mammals. The basal end is stiffer and maximally displaced by shorter wavelength,  
20 high-frequency sounds. The apical end responds to long wavelength, lower frequency sounds  
21 (Ketten and Wartzok, 1990). The basal end of the odontocete basilar membrane is especially  
22 thick (25  $\mu$ ), narrow (30  $\mu$ ) and rigid, consistent with their sensitivities to ultrasonic sounds.  
23 Towards the apex, the thickness decreases (5  $\mu$ ) and the width increases nine fold to increase

1 sensitivity to lower frequencies (Ketten and Wartzok, 1990). Because of the frequency dependent  
2 displacement of the BM, hair cells at specific locations will fire best for a characteristic  
3 frequency. Odontocete hair cell density along the BM appears to be uniform (Ketten and  
4 Wartzok, 1990) as in most terrestrial mammals. Each site along the basilar membrane is tuned to  
5 a specific frequency. Because there is a uniform distribution of hair cells on the BM, but not  
6 uniform displacement (i.e., lower frequencies have longer wavelengths, and thus displace a  
7 larger surface area of the BM) more hair cells are allocated to lower frequencies resulting in finer  
8 frequency resolution.

9         Frequency selectivity has been measured in odontocetes using both electrophysiological  
10 (Popov, *et al.*, 1997) as well as behavioral methods (Au and Moore, 1990; Finneran, *et al.*,  
11 2002a; Lemonds, 1999) in different masking paradigms. One of the most common methods for  
12 measuring frequency selectivity is a band-widening, masking paradigm resulting in a metric  
13 known as the critical band (CB). Listeners are required to detect the presence of a sinusoidal tone  
14 masked by a narrow band of noise centered on the signal frequency. Thresholds are estimated as  
15 a function of increasing bandwidth. A result replicated across many animal species is that  
16 thresholds increase as a function of bandwidth, but only up to a specific bandwidth known as the  
17 critical band. Masking noise beyond this critical band no longer contributes to the masking of the  
18 signal. To account for this result, Fletcher (1940) suggested that the auditory periphery behaves  
19 as a series of overlapping band pass filters. Each filter processes frequency energy within a  
20 limited range while attenuating peripheral frequency energy. A related metric known as the  
21 critical ratio is based on the idea that since only a small band of noise contributes to the masking  
22 of the signal, the auditory filter bandwidth can be estimated by measuring tonal thresholds in  
23 wideband noise. This assumes that the amount of energy in the noise band that masks the signal

1 is equivalent to the signal at thresholds. If the pressure spectral density of the noise (N) and the  
2 signal at threshold ( $S_{th}$ ) are known the CB can be estimated by:

$$\Delta F_{CB} = S_{th}/(K \cdot N), \tag{1}$$

6 where  $\Delta F_{CB}$  is the CB and  $K$  is a constant. If  $K$  is assumed to equal to 1, the equation simplifies  
7 to:

$$\Delta F_{CR} = S_{th}/N, \tag{2}$$

11 Where  $\Delta F_{CR}$  is the critical ratio. If CR is expressed in dB re 1 Hz, the CR can be simplified by  
12 subtracting the pressure spectral density level ( $L_N$ , in dB re 1  $\mu Pa^2/Hz$ ) from the signal SPL at  
13 threshold ( $L_S$ , in dB re 1  $\mu Pa$ ):

$$L_{CR} = L_S - L_N. \tag{3}$$

16 where  $L_{CR}$  is the critical ratio. The CR is the most widely used masking metric for marine  
17 mammals due to the relative ease of data collection (i.e., only one noise bandwidth is required  
18 compared to CBs which require several noise bandwidths). Figure 6 displays CRs for several  
19 odontocete species. A common feature among terrestrial mammals is that CRs increase as a  
20 function of frequency due to increasing bandwidths of auditory filters. The relationship between  
21 the center frequency of a filter and the bandwidth of a filter can be described as a quality factor,  
22 Q:

23

1  $Q = f_o / \Delta f,$   
 2 (4)

3 where  $f_o$  is the frequency of the signal and  $\Delta f$  is the filter bandwidth. Q values for bottlenose  
 4 dolphins have been estimated to be 12.3 for CRs and 2.2 for CBs (Au and Moore, 1990). A  
 5 consequence of a constant-Q filter bank is that higher frequencies associated with wider filters  
 6 will have reduced spectral resolution compared to lower frequencies (see Figure 7). The tradeoff,  
 7 however is that wide, high frequency filters will have excellent temporal resolution (See Figure  
 8 8). A recent reevaluation of Q values for *The bottlenose dolphin* suggest these animals have a  
 9 constant-Q filter bank for lower frequencies (< 40kHz) and a constant bandwidth filter bank for  
 10 frequencies above 40 kHz (Lemons, *et al.*, 2011). Similar constant bandwidth filters have been  
 11 measured in harbor porpoises (Popov, *et al.*, 2006).

12 Auditory filter shapes have been measured using a notched noise methodology for  
 13 bottlenose dolphins and belugas (Finneran, *et al.*, 2002a; Lemonds, 1999). Equation (1) can be  
 14 rewritten as:

15  
 16  $P_s = K \int_{-\infty}^{\infty} N(f)W(f)df,$  (4)  
 17

18 where  $P_s$  is the power of the signal at threshold,  $N(f)$  is the noise power spectral density  
 19 and  $W(f)$  is a weighting function described by the shape of the auditory filter.  $W(f)$  is often  
 20 estimated using a rounded exponential (roex) function:

21  
 22  $W(g) = (1-r)(1+pg)e^{-pg} + r$  (5)  
 23

1 where  $g$  is a normalized frequency deviation [ $g = |f - f_0|/f_0$ , where  $f$  is frequency and  $f_0$  is the  
2 signal frequency], and  $p$  and  $r$  are adjustable parameters

3       Biomimetic models using simulated auditory filters derived from empirical  
4 measurements have proven useful for investigating what time-frequency information is available  
5 to dolphins during echolocation discrimination tasks for artificial targets (Branstetter, *et al.*,  
6 2007b; Roitblat, *et al.*, 1993b) as well as natural fish targets (Au, *et al.*, 2009) and as inputs into  
7 neural network classifiers (Au, *et al.*, 1995; Branstetter and Mercado III, 2006; Roitblat, *et al.*,  
8 1993a). These models attempt to incorporate limitations of the dolphin auditory system with  
9 respect to both frequency and temporal resolution and mimic how this information might be  
10 organized and utilized for classification purposes.

11

## 12 **5.5. Transduction and low-pass filtering**

13       In addition to resolving characteristics of the auditory filters, hair cell transduction and  
14 low pass-filtering of the 8<sup>th</sup> nerve (and beyond) will also affect how sounds are perceived. Little  
15 is known about hair cell transduction in any marine mammal. However, hair cell anatomy  
16 appears to be similar to terrestrial mammals. One striking difference is that odontocetes have a  
17 high density of afferent innervations with up to 2900 ganglion cells, 100 inner hair cells (IC), and  
18 300 outer hair cells / mm (Ketten, 1997). There are about three times as many ganglion cells /  
19 IC in some odontocetes compared to humans (Ketten, 1997). Hair cells behave as non-linear,  
20 half-wave rectifiers (Berg, 1996; Branstetter, *et al.*, 2007b) that can be described by a simple  
21 model:

$$22 \quad f_{rect}(t) = \left( f(t) + \sqrt{f(t)^2} \right) / 2 \quad (6)$$



1 Where  $t$  is the instantaneous amplitude of the time domain waveform. Another characteristic of  
2 hair cell response is amplitude compression, which is partially responsible for the broad range in  
3 amplitude sensitivity of mammalian listeners (Regan, 1994). Input-output functions describing  
4 amplitude compression have not been estimated in cetaceans. Unlike typical neurons, hair cells  
5 do not have refractory periods, which make them extremely fast. However, ganglion cells are  
6 much more sluggish and behave as low-pass filters which can be described with an exponential  
7 decay function:

8

$$9 \quad h(t) = ke^{-t/\tau} \quad (7)$$

10 Where  $k$  is a constant,  $t$  is units of time and  $\tau$  is the critical interval or integration time constant  
11 (Berg, 1996). The critical interval ( $\tau$ ) for transient signals appears to be around 264  $\mu$ sec (Moore,  
12 *et al.*, 1984; Vel'min and Dubrovskii, 1976). For tonal signals, the integration time constant  
13 appears to be governed by a different mechanism than transient signals. Time constant are  
14 frequency-dependent and much longer in duration. For example, the integration time constants  
15 are approximately 200 and 100 ms for a 10 kHz and 20 kHz tone respectively. The time constant  
16 for a 100 kHz tone is less than 10 ms. Differences in integration times for tonal signals and  
17 transient signals may be the result of compartmentalized hearing abilities for communication  
18 signals and echolocation signals, respectively.

19

## 20 **5.7. Auditory masking with complex stimuli**

21 The auditory masking experiments previously described (CBs, CRs, and filter shape  
22 measurements) were all conducted with Gaussian noise maskers. The primary finding of these  
23 studies is that only noise within a single auditory filter centered on the signal frequency

1 contributes to the masking of the signal. This finding is a special case of masking that applies to  
2 Gaussian noise but fails to generalize to more complex sounds animals might encounter in the  
3 ocean. In natural auditory scenes, sounds are often amplitude and frequency modulated and the  
4 auditory system can use common modulation patterns to segregate sound sources (Bregman,  
5 1990). This has been demonstrated in dolphins in what is called comodulation masking release or  
6 CMR (Branstetter and Finneran , 2008). When broadband noise is coherently amplitude  
7 modulated across frequency regions, a release from masking as large as 17 dB has been reported,  
8 compared to Gaussian noise of equal pressure spectral density (Figure 9). An important feature  
9 of CMR is that the effect is most salient when noise bandwidths exceed an auditory filter  
10 bandwidth (Branstetter and Finneran, 2008a; Hall and Grose, 1990). In other words, more total  
11 noise power equals less masking. Several acoustic variables contribute to CMR. Wide band  
12 noise (i.e., greater than an auditory filter bandwidth) produces a systematic decrease in masking.  
13 In addition, lower AM rates produce greater amounts of CMR (Branstetter and Finneran, 2008a).  
14 A similar release from masking has been demonstrated for natural sounds including ice-cracking  
15 noise (Erbe, 2008) and snapping shrimp noise (Trickey, *et al.*, 2011), both of which are also  
16 coherently amplitude modulated across frequency regions (Figure 10).

17

## 18 **5.8. Sound localization**

19       Due to limited visibility, locating prey, predators, conspecifics, or any other biologically  
20 relevant object or event is often accomplished through sound. To localize sounds in the  
21 horizontal plane, humans and animals have been shown to exploit binaural stimulus differences  
22 related to loudness, temporal onset and phase. Because the cetacean auditory system evolved  
23 from the archetypal terrestrial auditory system, changes in anatomy and physiology occurred to

1 compensate for a dense aquatic medium where sound travels almost five times faster than in air.  
2 For terrestrial animals, interaural loudness differences (ILDs) are created by sound shadowing  
3 due to the impedance mismatch between the air medium and an animal's head. In water,  
4 terrestrial animals lose ILDs due to the density similarity of the head and water. For odontocetes,  
5 ILDs are created not by external anatomy, but by internal structures of varying density. The  
6 dense tympano-periotic complex, which houses the middle and inner ear, is completely separated  
7 from the skull by a matrix of air sinuses, lipids and vascularization collectively called the  
8 albuminous foam (Ketten, 1992). The foam, along with additional structures such as cranial air  
9 sacks and mandibular fats, collectively function to acoustically isolate each ear and produce  
10 ILDs in excess of 20 dB (Supin and Popov, 1993). Sensitivity to ILDs has been measured in the  
11 bottlenose dolphin to be less than 1 dB (Moore, *et al.*, 1995). Interaural time differences (ITD)  
12 will be five times smaller in aquatic environments due to increased sound speed in water relative  
13 to air. However, dolphins are still capable of exploiting ITD and have demonstrated sensitivity to  
14 ITDs as small as 7  $\mu$ sec (Moore, *et al.*, 1995). In terrestrial mammals, the use of interaural phase  
15 differences (IPD) decreases with an increase in frequency because the wavelengths get smaller.  
16 While it is unlikely that odontocetes use IPDs for higher frequencies, it has not been tested. IPDs  
17 could be exploited by mysticetes, which have large heads and use low-frequency sounds.

18 ILDs and ITDs only provide source information in the horizontal plane. However,  
19 dolphins have excellent localization abilities not only in the horizontal plane, but also in the  
20 vertical plane. The minimum audible angle (MAA) for the bottlenose dolphin is 0.9 and 0.7 in  
21 the horizontal and vertical planes respectively (Renaud and Popper, 1975). The fact that the  
22 bottlenose dolphin can localize as well (if not slightly better) in the vertical plane despite the lack  
23 of ITDs and ILDs is remarkable, and suggests an additional mechanism exists for vertical

1 localization. As mentioned previously, dolphins likely have a salient HRTF due to the  
2 pronounced asymmetry of cranial structures. Position-dependent spectral cues related to the  
3 dolphin's HRTF may be providing the dolphin with fine vertical localization abilities. Although  
4 a detailed HRTF for an odontocete has not been measured, receiving beam patterns have been  
5 measured for the bottlenose dolphin for a few frequencies, resulting in a complex pattern. The 3  
6 dB beam widths for 30, 60, and 120 kHz were measured to be 59.1, 32.0, and 13.7 degrees  
7 respectively in the horizontal plane and 30.4, 22.7, and 17.0 degrees in the vertical plane (Au and  
8 Moore, 1984). Receiving beam patterns are more directional for higher frequencies, which likely  
9 aid the animal in localizing sounds during echolocation. The ability of the bottlenose dolphin to  
10 echoically discriminate horizontal angular differences has been measured to be about 0.9-1.5  
11 degrees (Branstetter, *et al.*, 2007a; Branstetter, *et al.*, 2003) which is significantly smaller than  
12 the receiving 3 dB beam width, but similar to the dolphin's MAA. The receiver beam width  
13 likely aids in gross localization as well as attenuating off-axis signals during echolocation.

14

## 15 **6. ADVANCED ANATOMICAL AND PHYSIOLOGICAL STUDIES**

### 16 **6.1. Anatomy**

17 The recent use of computerized tomography (CT) has proven useful to study in-situ  
18 auditory anatomy of odontocetes. (Cranford, *et al.*, 2008; Houser, *et al.*, 2004a; Ketten, 1994;  
19 Ketten and Wartzok, 1990; Montie, *et al.*, 2011; Soldevilla, *et al.*, 2005). These imaging  
20 techniques are particularly valuable for studying fatty sound reception pathways since these  
21 unique fats have a low melting temperature, are soft at room temperature, and liquid at body  
22 temperatures for at least some species (Norris, 1968), making them difficult to study via  
23 dissection. Dissection also prevents the study of the in-situ geometries of these fats. In fact, a

1 magnetic resonance imaging (MRI) study by Ketten (1994) led to the finding of a new funnel-  
2 shaped fat channel lateral to the tympano-periotic complex in some odontocetes (*Delphinus*  
3 *delphis*, *Lagenorhynchus acutus*, and *Tursiops truncatus*) that may serve as a “second acoustic  
4 window” for lower frequency sounds to reach the ears (Popov, *et al.*, 2008).

5 Live cetaceans were CT scanned for the first time by Houser *et al.* (2004a) using  
6 bottlenose dolphins trained by the U.S. Navy’s Marine Mammal Program. The use of live  
7 animals was a significant improvement since it prevented post-mortem changes in air space  
8 volumes and tissue characteristics from potentially affecting the data. This study also  
9 incorporated functional investigations of auditory and sound production tissues through single  
10 photon emission computed tomography (SPECT) and positron emission tomography (PET),  
11 identifying extensive blood flow in the lower jaw and melon fats. Since these tissues are  
12 relatively metabolically inert, the authors hypothesized that the blood flow served as a  
13 thermoregulatory control of lipid density, optimizing the acoustic fats for sound reception and  
14 propagation. The application of such advanced functional imaging techniques to fully aquatic,  
15 live mammals may have seemed inconceivable to most researchers before this study.

16 An equally challenging and exciting idea for the future was presented by Moore *et al.*  
17 (2011b), who developed a hyperbaric computed tomography technique for investigating the  
18 effect of pressure on lung compression in postmortem marine mammals. The paper concludes  
19 with potential modifications of the system for application to live animals in the future. If this  
20 technique can actually be used on live animals, it may enable investigations on changes in  
21 middle ear air volumes and tissues relevant to the auditory system with simulated depth.

22 Applying biomedical imaging techniques to cetaceans has also enabled the modeling of  
23 sound reception pathways in odontocete heads. One type of modeling technique that is often

1 used is called the Finite Element Method (FEM). In FEM, a model is constructed by defining a  
2 set of mathematical equations in a continuous domain. For example, to model sound propagation  
3 through a dolphin head, the mathematical model is the wave equation together with a set of  
4 boundary conditions. The domain, which in this case corresponds to the dolphin head and the  
5 surrounding medium, is discretized into small connected “elements” creating what is called the  
6 finite element mesh. By employing structural data from CT and material properties from  
7 different types of tissues like bone, muscle, and fats, the acoustical power flow of both isolated  
8 anatomical structures and whole multi-tissue systems can be modeled to estimate optimal  
9 impedance paths for sounds from internal or external sources. While computer models of  
10 odontocete sound production had been developed earlier (Aroyan *et al.*, 1992), the application of  
11 FEM and related methods to odontocete sound reception has seen much progress over the past  
12 decade (Aroyan, 2001; Cranford, *et al.*, 2010; Cranford, *et al.*, 2008; Krysl, *et al.*, 2006).

13

## 14 **6.2. AEPs in hearing tasks**

15 As described above, there are many types of studies which address hearing in odontocetes.  
16 However, a large proportion of them now involve AEP measurements (Figure 4). AEP is an  
17 appealing method because data can be gathered rapidly with minimal or no animal training  
18 investment. A complete audiogram can be obtained in an untrained animal in less than twenty  
19 minutes, enabling hearing tests even during situations where time is severely limited (Nachtigall,  
20 *et al.*, 2004; Nachtigall, *et al.*, 2005). Recording times can be dramatically decreased by  
21 simultaneously recording responses to multiple frequencies (Finneran and Houser, 2007) and  
22 using automated methods of response detection (Finneran, *et al.*, 2007a).

1           One advantage of AEP related methodology has been to opportunistically measure the  
2 hearing of stranded animals, thus broadening the number of individuals and species tested  
3 (André, *et al.*, 2007; Ridgway and Carder, 2001). Early attempts at recording AEPs from  
4 stranded animals were conducted at rehabilitation facilities and produced mixed results  
5 (Ridgway and Carder, 2001). The animals tested were large and included a pigmy sperm whale  
6 (*Kogia breviceps*), a gray whale (*Eschrichtius robustus*) calf and a neonate sperm whale  
7 (*Physeter macrocephalus*). The response records were somewhat noisy and full audiograms  
8 were not acquired, perhaps because the large size of animals reduced signal-to-noise ratios of the  
9 AEP (Houser, *et al.*, 2007; Szymanski, *et al.*, 1999). However, the study produced novel records,  
10 showed the efficacy of the technique, and laid substantial groundwork for future research.

11           Improvements in methods and equipment between 2001 and 2005 led to successful AEP  
12 recordings from a stranded neonate Risso's dolphin (*Grampus griseus*), producing a full  
13 audiogram and an estimate of temporal resolution (Mooney, *et al.*, 2006; Nachtigall, *et al.*, 2005).  
14 This animal had sensitive and broadband hearing, discounting suggestions that there may have  
15 been permanent auditory damage due to a potential noise-induced stranding event (Figure 2).  
16 However, "profound" hearing loss has been found in other stranded odontocetes including pilot  
17 whales, bottlenose dolphins and rough-toothed dolphins (Mann, *et al.*, 2010). The authors  
18 speculated that the causes of hearing loss vary and could include congenital defects, chemical  
19 contaminants, and normal presbycusis.

20           A major advance in AEP technology is the development of portable systems which can  
21 be applied in field situations (Delory, *et al.*, 2007; Finneran, 2009; Ridgway and Carder, 2001;  
22 Taylor, *et al.*, 2007). The AEP test on the stranded Risso's dolphin involved flying a desktop  
23 computer from Hawaii to Portugal and was conducted over 5 days. Since these tests, AEP

1 systems have been reduced in size to laptop-based systems and audiograms are collected much  
2 more rapidly. To date, AEP recordings in the field have been made with catch-and-release  
3 procedures on white-beaked dolphins (Nachtigall, *et al.*, 2008) and beach-stranded delphinids  
4 (Moore, *et al.*, 2011a), showing promising results despite logistical challenges.

5         Recent, novel AEP experiments have combined AEPs with morphological studies to  
6 address form-and-function questions. Montie *et al.* (2011) examined the hearing of two stranded  
7 pygmy killer whales. They moved electrode locations and created 3-D reconstructions of the  
8 brain from CT images, while concurrently measuring the amplitude of the ABR waves. Their  
9 results provided evidence that the neuroanatomical sources of ABR waves I, IV and VI were the  
10 auditory nerve, inferior colliculus and the medial geniculate body, respectively. Other studies  
11 have combined AEP with CT and MRI to examine the hearing pathways of odontocetes  
12 (Mooney, *et al.*, 2011). Using a jawphone transducer to present stimuli, Mooney *et al.* showed  
13 that AEP responses can be generated from multiple locations on the head and body. Jawphones  
14 placed at the mandibular fat bodies (identified from MRI and CT) tended to produce higher  
15 amplitude AEPs, lower thresholds, and faster responses, although this was somewhat frequency  
16 dependent (Figure 4C). Thus, the head anatomy receives and guides sound in multiple ways,  
17 confirming earlier findings by Mohl *et al.* (1999) which mapped the areas of best sensitivity in the  
18 bottlenose dolphin head using AEPs and jawphone-presented stimuli. These areas of best  
19 sensitivity differ slightly between the few species examined (bottlenose dolphin, beluga, finless  
20 porpoise; Figure 4C, D), suggesting that the diverse morphologies found among odontocete  
21 species affects how each of them receives sound (Mooney, *et al.*, 2008).

22

### 23 **6.3. AEPs during echolocation**



1           Bullock and Ridgway (1972) had discovered that AEP responses varied based on whether  
2 they were induced from self-generated clicks or simulated clicks presented by the researchers,  
3 laying the groundwork for substantial future developments of hearing protection and auditory  
4 gain control. Since then, AEPs have been used to measure hearing during echolocation,  
5 addressing auditory gain control and how ears are adapted to hear quiet echoes which occur  
6 immediately after loud clicks (Nachtigall and Supin, 2008; Supin, *et al.*, 2003). These studies  
7 methodically addressed this issue by training a false killer whale to echolocate on cylinder  
8 targets while AEPs were concurrently measured (Figure 4B). The earliest work established that  
9 far-field evoked potential methods can be used to record AEPs in response to both outgoing  
10 clicks and returning echoes (Supin, *et al.*, 2003). The click and echo AEPs had similar  
11 amplitudes, despite substantial (40 dB) differences in the relative stimulus intensity levels.  
12 Impressively, these results suggested either an “attenuation of sound transmission from the sound  
13 generator to the ears and/or a neurophysiological mechanism of releasing responses to echoes  
14 from masking by loud emitted clicks.”

15           In two succeeding experiments the authors varied the target distance and length (i.e., the  
16 target strength), thus varying the intensity of the returning echoes. The amplitudes of echo-  
17 generated AEPs were independent of the variables. The click-generated AEPs were dependent on  
18 target strength, but not distance (Supin, *et al.*, 2004; Supin, *et al.*, 2005). The sound pressure  
19 levels of the outgoing clicks did not vary based on target strength, which suggested that the  
20 differences in AEP amplitude were due to changing hearing sensitivities as the animal  
21 echolocated – a fascinating finding. Supin et al. (2006) sorted AEPs relative to the SPL of the  
22 outgoing click and compared these responses from simulated clicks of varying amplitude.  
23 Evoked potential amplitudes, and thus hearing of these clicks, were dependent on target presence,

1 target absence, and passive hearing vs. echolocation. Thus, this whale adjusted its hearing based  
2 on the context of the experiment (Supin, *et al.*, 2006).

3 Adjustments and recovery from auditory dampening of loud echolocation clicks appeared  
4 to be based on both the distance of a target (i.e., the time interval between the outgoing click and  
5 the incoming echo) and the intensity of the click (Supin, *et al.*, 2007). The use of electronically  
6 simulated phantom echoes allowed the “echo” amplitude and distance to be adjusted. In both  
7 behavioral and electrophysiological studies, echo thresholds or response levels appear dependent  
8 on distance of the target. As the time between click and echo increased, hearing ability improved,  
9 suggesting that the protection of ears during echolocation may somewhat mask the hearing of  
10 clicks; however this forward masking was released as time increased (Supin, *et al.*, 2008; Supin,  
11 *et al.*, 2009). Follow-up studies in a standard echolocation task showed that while echo  
12 generated AEPs were constant with target distance, click generated AEPs increased. The results  
13 indicated that control of hearing during echolocation served as a way to keep sensitivities of  
14 echoes constant, perhaps as a means to compensate for natural echo attentions, and improve  
15 hearing abilities of quiet echoes, at greater distances (Supin, *et al.*, 2010). These hypotheses were  
16 confirmed by subsequent phantom echo studies (Supin, *et al.*, 2011). Overall, these novel  
17 investigations revealed much regarding the active process of odontocete hearing and their  
18 impressive echolocation capabilities. While few studies have addressed parallel investigations in  
19 “standard” hearing tests, it is possible that odontocetes may also adjust reception or sensitivities  
20 when not producing sounds.

21 This work has expanded recently with comparative studies in the bottlenose dolphin and  
22 the harbor porpoise. The porpoise showed that it alters its outgoing click amplitudes as well as its  
23 click AEP levels (Linnenschidt, *et al.*, 2012). Like Supin, the authors supposed that these gain

1 controls maximized detection of quiet echoes. In similar experiments, Li et al. found the  
2 bottlenose dolphin may enact direct control over both the click and echo (Li, *et al.*, 2010). Echo-  
3 generated AEP amplitudes increased with target distance, suggesting an “overcompensation” of  
4 echo hearing. This was unlike the porpoise and false killer whale studies, but it was not clear  
5 whether these were species, individual, or anatomical differences. It is also notable, that these  
6 mechanisms are not only means to improve echo detection but a way to protect sensitive ears  
7 from repeated, intense echolocation clicks (Li, *et al.*, 2011).

8

## 9 **7. THE IMPACTS OF NOISE**

10 As discussed above, odontocetes may have a mechanism to protect their sensitive ears  
11 from their own loud echolocation clicks. However, these mechanisms may not be sufficient to  
12 overcome the constant exposure to human-made sound. The effects of noise on marine  
13 mammals have been a substantial topic of concern for researchers, policy makers, and the public.  
14 Much of these interests stem from beaked whale strandings that were associated with high-  
15 amplitude naval sonar (Balcomb and Claridge, 2001; Evans, *et al.*, 2001; Frantzis, 1998). The  
16 actual sonar-induced physiological or behavioral effects on the stranded animals have been  
17 extensively debated (Brownell, *et al.*, 2009; Cox, *et al.*, 2006; Fernandez, *et al.*, 2005; Jepson, *et*  
18 *al.*, 2003; Southall, *et al.*, 2006). Furthermore, the reality is that ocean noise is diverse, including  
19 shipping and vessel traffic, construction of wind farms, air guns related to seismic exploration,  
20 construction, and scientific surveys. These sounds can be broadly grouped into noise categories  
21 of (i) continuous (or near-continuous) such as shipping, (ii) impulse sounds such as seismic air  
22 guns or military munitions, and (iii) intermittent noise like construction or sonar. Behavioral

1 changes in response to elevated noise conditions from these various sources have caused alarm  
2 (e.g., Holt, *et al.*, 2009; Miller, *et al.*, 2000; Parks, *et al.*, 2009).

3 In terrestrial mammals, a well-established and primary concern of noise exposure is  
4 noise-induced hearing loss (Kryter, 1994; Ward, *et al.*, 1958). Over exposure to noise can induce  
5 both temporary and permanent hearing loss, also referred to as temporary or permanent threshold  
6 shifts. For marine mammals, a wide array of data are needed to predict potential occurrences of  
7 noise impacts. The necessary research efforts to address noise impacts on marine mammals have  
8 been addressed by four National Research Council reports and a more recent report by Southall  
9 *et al.*, to establish a science-based, noise exposure criteria (National Academy of Sciences, 1994;  
10 2000; 2003; 2005; Southall, *et al.*, 2007). Hearing related recommendations include: establishing  
11 baseline hearing sensitivities in a greater number of species and individuals, investigating  
12 auditory scene analyses in regards to how cetaceans process and evaluate multiple acoustic cues  
13 simultaneously, determining the levels and effects of auditory masking, and the sounds and  
14 conditions which induce temporary and permanent threshold shifts (i.e., temporary and  
15 permanent hearing loss). These previous documents provide comprehensive reviews of this  
16 specific subject, addressing behavioral, physiological, and anatomical noise impacts; thus we  
17 will only briefly address hearing and noise exposures here to provide an update on the data since  
18 this report, and place these data in the context of past results and conclusions.

19 Temporary threshold shifts (TTSs) have received substantial experimental attention in  
20 recent years. It was first established in cetaceans (five bottlenose dolphins and two belugas)  
21 using 1 s pure tones across a range of frequencies (0.4 – 75 kHz) (Schlundt, *et al.*, 2000). Shifts  
22 of 6-17 dB re 1  $\mu$ Pa were measured at exposure levels generally between 192 and 201 dB, but  
23 TTS was also documented for fatiguing stimuli as low as 182 dB. Shortly thereafter, intense

1 impulse sounds (226 dB<sub>(peak-peak)</sub> re 1 μPa and a sound exposure level of 186 dB re 1 μPa<sup>2</sup>•s)  
2 from a seismic watergun were used as the fatiguing noise to induce TTS (Finneran, *et al.*, 2002b).

3 The sound exposure level (SEL) can be calculated by:

$$4 \quad SEL = 10 \log_{10} \left( \int_0^T \frac{p^2(t)}{p_0^2 t_0} dt \right),$$

5 Where  $t_0$  is the reference time of 1 sec,  $p(t)$  is the instantaneous sound pressure of the signal, and  
6  $p_0$  is the reference pressure of 1 μPa. This metric is useful because it integrates the squared  
7 pressure over the total duration of the signal and is often used to predict TTS due to multiple  
8 exposures of varying duration. Threshold shifts were induced in the beluga tested, but not in the  
9 bottlenose dolphin. A subsequent study used increased duration, lower amplitude, broadband  
10 noise (4-11 kHz, 179 dB re 1 μPa and 55 min) to induce TTS in a bottlenose dolphin.  
11 (Nachtigall, *et al.*, 2003). Shifts were variable between sessions from (-1 to 18 dB). These early  
12 studies were pivotal in multiple respects. Not only did they establish that TTS can occur by  
13 multiple types of noise exposure, there were substantial differences regarding whether TTS was  
14 actually induced within replicate conditions, the amount of TTS induced varied between the  
15 species tested and within individuals. The variations and covariates revealed the mountainous  
16 task of predicting auditory noise impacts.

17 Subsequent work has improved the methods for measuring TTS, addressed means to  
18 bridge some of these variables, and filled in key data gaps. Since the 2007 Southall *et al.*  
19 publication, Finneran and colleagues used AEP technology to measure TTS at multiple  
20 frequencies simultaneously, making it possible to rapidly determine at which frequencies TTS is  
21 induced (Finneran, *et al.*, 2007b). Several research groups have also addressed how best to  
22 predict situations that may induce TTS (Finneran, *et al.*, 2005; Mooney, *et al.*, 2009a). Recent  
23 work has shown that if the fatiguing noise type is constant, but duration and amplitude are varied,

1 TTS onset is well predicted by SEL (Finneran, *et al.*, 2010; Mooney, *et al.*, 2009a). In other  
2 words, shorter duration sounds require greater energy to induce TTS compared to longer duration  
3 signals. Note that these studies did not investigate impulse sounds such as seismic air guns,  
4 which may have entirely different effects (Ward, 1997). The TTS growth in dolphins was also  
5 correlated with SEL and TTS exposure duration continued to play a greater influence in  
6 generating TTS compared to SPL (Finneran, *et al.*, 2010). These results have several  
7 implications. First, TTS onset and growth data are better represented as functions of SPL and  
8 duration rather than SEL alone. Second, short duration signals such as most sonar must be of  
9 very high received intensity to induce TTS (Mooney, *et al.*, 2009b). These situations are  
10 probably rare because they would usually require the animal to be close to the sound source.  
11 Third, longer duration sounds such as constant shipping or snapping shrimp noise may induce  
12 TTS at much lower intensity and sensation levels (the SPL relative to threshold). These chronic  
13 exposures, such as shipping noise, may induce quite different impacts compared to the brief,  
14 intense exposures. The impacts of these chronic exposures are a growing area of concern.

15       Hearing thresholds were comparatively examined using noise exposures with a mid and a  
16 higher frequency tone (3 and 20 kHz) to address the impacts of hearing sensitivities on TTS  
17 (Finneran and Schlundt, 2010). The results showed that at 20 kHz TTS not only began at a lower  
18 exposure level compared to the 3-kHz exposures, but also grew at a faster rate. Repeated  
19 exposures also increased noise impact susceptibility (Finneran and Schlundt, 2010). The results  
20 clearly demonstrated auditory impact risk criteria must take exposure frequency, hearing  
21 sensitivity and prior experience into account.

22       While these prior studies addressed auditory physiology, they did not address the  
23 perception of sound intensity, or loudness. Equal loudness contours provide a comparison of

1 tones that are perceived at the same sound level, providing a means to modify acoustic damage  
2 risk criteria by placing greater emphasis on sensitive frequencies. The first of these studies in a  
3 non-human animal was conducted with a bottlenose dolphin (Finneran and Schlundt, 2011). The  
4 animal was trained to perform a loudness comparison test, where it indicated which of two  
5 sequential tones was perceived as louder. The resulting equal loudness contours were similar in  
6 shape to the dolphin audiogram. As in humans, the contours became flatter at higher SPLs  
7 (Finneran and Schlundt, 2011). Based on these data, the authors were able to provide modified  
8 auditory weighting functions which provided greater insight into the frequencies dolphins may  
9 be most sensitive. In general, there was an inverse relationship between sensitivity and hearing  
10 thresholds, with similar loudness responses ( $\pm 2.5$  dB) from approximately 6-100 kHz. These  
11 weighting functions were substantially different from those proposed by Southall *et al.*, (2007),  
12 reflecting the need for management practices that can adapt to the growing literature of best  
13 available data

14

## 15 **8. HEARING IN MYSTICETES**

16 In contrast to the immense amount of progress that has been made on hearing in  
17 odontocetes, the study of mysticete hearing has been more stagnant over the past several decades.  
18 Mysticetes are large, rarely kept in captivity, and have never been trained, making them more  
19 difficult to study. Therefore, several indirect methods have been applied to gain information  
20 about mysticete hearing. One method is based on vocalization data, based on the premise that  
21 animals typically vocalize at frequencies audible to conspecifics. Recordings of mysticete  
22 vocalizations conducted since 1951 suggest that baleen whales use and hear low frequency

1 sounds (Watkins and Wartzok, 1985). Vocalizations down to 12 Hz have been recorded in the  
2 blue whale (Cummings and Thompson, 1971).

3 Anatomical studies of middle and inner ear structures afford another way to understand  
4 what kinds of sounds mysticetes may hear. Yamada and Yoshizaki (1959) noted the lack of  
5 high-frequency specializations in mysticete cochleae, in contrast to the cochleae of odontocetes.  
6 Mysticetes also possess massive, loosely-joined ossicles and wide basilar membranes, consistent  
7 with low-frequency hearing (Ketten, 1994). Parks et al. (2007) predicted that the total possible  
8 hearing range for the North Atlantic right whale (*Eubalaena glacialis*) is approximately 10 Hz to  
9 22 kHz, based on measurements of their basilar membranes. Using FEM, Tubelli *et al.*, (2011)  
10 recently estimated the middle ear transfer function of the minke whale to have a best frequency  
11 range between approximately 100 Hz and 75 kHz, depending on the location of the stimulus  
12 input location (Tubelli, *et al.*, 2011). These anatomical studies are promising for studying  
13 hearing in rare and inaccessible species, especially if they can be validated by future  
14 physiological studies.

15 A third method for deducing what types of sounds mysticetes may hear is the playback  
16 technique, in which a range of naturally recorded or artificially generated sounds are presented to  
17 wild animals. An acoustic stimulus that elicits a behavioral response from an animal is presumed  
18 to be audible to the animal. While most playback studies on mysticetes are not designed to test  
19 their hearing, they support the hypothesis that mysticetes are able to hear and differentiate  
20 vocalizations of conspecifics (Clark and Clark, 1980; Mobley, *et al.*, 1988; Parks, 2003; Tyack,  
21 1983). In a study of minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*),  
22 humpback (*Megaptera novaeangliae*), and right whales near Cape Cod, Watkins (1986) found  
23 that most whales reacted to human-made sounds between 15 Hz and 28 kHz, whereas higher



1 frequency sounds between 36 and 60 kHz elicited no response. These data also support the  
2 notion that mysticetes are sensitive to lower frequencies. Yet, an individual may not always  
3 respond to an audible sound and the received levels of the sounds are often unknown, limiting  
4 the effectiveness of playback studies as a method for studying hearing.

5         The ultimate goal for understanding what mysticetes hear is to obtain audiograms  
6 showing hearing sensitivity as a function of frequency. Behavioral tests using trained, captive  
7 animals are unlikely, as mentioned above. However, AEP testing may be a possibility in the  
8 future. As noted earlier, Ridgway and Carder (2001) attempted to record AEPs from a stranded  
9 gray whale calf which was rehabilitated at Sea World of San Diego between January 1997 and  
10 March 1998. While some preliminary AEPs were recorded, an audiogram could not be produced.  
11 Besides the rarity of opportunities to conduct AEP testing, a major obstacle in applying current  
12 AEP methods to mysticetes is that mysticetes are generally larger and also have very different  
13 cranial morphologies compared to odontocetes. It is likely that customized equipment needs to  
14 be developed based on the auditory anatomy and sound reception mechanisms of mysticetes.

15         This leads us to the other fundamental question about mysticete hearing: *how* do baleen  
16 whales receive sound? There is still no consensus regarding how the auditory system of baleen  
17 whales function, and this question has not received much attention for the past 50 years.  
18 Interestingly, Yamato *et al.* recently described a potential fatty sound reception pathway in the  
19 minke whale (Yamato *et al.*, submitted). Combining CT, MRI, and dissections, the authors  
20 found a well-formed fat body adjacent to the mandibular ramus and lateral to the tympano-  
21 periotic complex (Figure 10). This fat body inserts into the tympano-periotic complex at the  
22 juncture between the tympanic and periotic bones and is in contact with the ossicles. Preliminary  
23 dissections of fin and humpback whales also indicate that they possess fat bodies associated with

1 the ears, suggesting that fatty sound reception pathways may not be a unique feature of  
2 odontocete cetaceans.

3

#### 4 **9. CONCLUSIONS AND FUTURE WORK**

5 Our knowledge of cetacean hearing has substantially increased in recent years. Through  
6 technology advancements such as AEPs and FEM, there are a greater number of research  
7 questions which can be addressed. This provides an improved understanding of how and what  
8 many species hear, as well as their sophisticated acoustic processing abilities. Much of this work  
9 has been in applied research to determine noise impacts, but have also yielded more basic  
10 information in auditory scene processing and mammalian hearing. These developments have  
11 also made clear several data gaps and research priorities.

12 Mysticete hearing abilities have been predicted from a variety of studies but there has yet  
13 to be an audiogram established. While AEPs will be difficult to measure for some species, the  
14 method has potential for smaller animals such as minke whale or juvenile whales. Entangled or  
15 stranded situations might offer reasonable test scenarios. This would not only establish the sound  
16 sensitivity of a “great” whale but also empirically test the current auditory models for future  
17 applications to other species.

18 There are also quite a few odontocete species for which audiograms also need to be  
19 established. Measuring the audiogram for these species provides data-based methods to evaluate  
20 potential noise impacts. This would also provided much needed information the diversity of  
21 auditory capabilities. Acquiring these data likely requires the continual advancement of AEP  
22 technologies for field situations, and perhaps even integrating them into non-invasive tagging  
23 tools. Such tools would not only produce audiograms, but will also enable the study of auditory

1 gain control mechanisms and hearing during echolocation in natural situations. A tag-based  
2 technology would also greatly increase study sample sizes, a clear limitation for many cetacean  
3 audiometric studies.

4         Investigations of a greater number of species would also address the subtle differences  
5 found between taxa. There are clear morphological and behavioral differences between species,  
6 suggesting subtle auditory physiological differences as well. A clear way to investigate this is  
7 through research which addresses classic form-and-function questions, combining anatomical  
8 studies with physiological, experimental research. We may also find that species adapt to noise  
9 impacts in different manners, since some animals seem particularly sensitive to sound. For  
10 odontocetes which are high-frequency specialists, high frequency hearing loss which is typical in  
11 mammals may have unique impacts. Physiological investigations of hearing loss and auditory  
12 protective mechanisms may further our understanding of how or whether certain animals can  
13 reduce the impacts of noise exposure.

14         Despite the recent advancements there is continual room for improvements in  
15 understanding of basic hearing abilities. As anthropogenic use of aquatic environments increases,  
16 so does the need for empirical studies on sensory ecology. Information regarding the overlap  
17 between human and cetacean acoustic habitats is crucial to evaluate the potential impacts on  
18 these sound-sensitive marine animals. Ultimately, these studies will further our understanding of  
19 the evolution of mammalian hearing and the adaptations acquired for sophisticated auditory  
20 systems which process and cope with complex auditory scenes.

21

22

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1 **REFERNECES**

- 2 Andersen, S. (1970). The auditory sensitivity of the harbor porpoise, *Phocoena phocoena* in  
3 Pilleri, G. (Ed), *Investigations on Cetacea*, Berne-Bumpliz, pp. 255-259.
- 4 André, M., Delory, E., Degollada, E., Alonso, J. M., del Río, J., van der Schaar, M., Castell, J. V.  
5 and Morell, M. (2007). Identifying cetacean hearing impairment at stranding sites.  
6 *Aquatic Mammals* **33**, 100-109.
- 7 Aroyan, J. L. (2001). Three-dimensional modeling of hearing in *Delphinus delphis*. *Journal of*  
8 *the Acoustical Society of America* **110**, 3305-3318.
- 9 Au, W. W. L., Andersen, L. N., Rasmussen, A. R., Roitblat, H. L. and Nachtigall, P. E. (1995).  
10 Neural network modeling of a dolphin's sonar discrimination capabilities. *Journal of the*  
11 *Acoustical Society of America* **98**, 43-50.
- 12 Au, W. W. L., Branstetter, B. K., Benoit-Bird, K. J. and Kastelein, R. A. (2009). Acoustic basis  
13 for fish prey discrimination by echolocating dolphins and porpoises. *Journal of the*  
14 *Acoustical Society of America* **126**, 460–467.
- 15 Au, W. W. L., Floyd, R. W., Penner, R. H. and Murchison, A. E. (1974). Measurement of  
16 echolocation signals of the Atlantic bottlenose dolphin *Tursiops truncatus* Montague, in  
17 open waters. *Journal of the Acoustical Society of America* **56**, 280-290.
- 18 Au, W. W. L., Ford, J., Horne, J. and Newman, K. (2004). Echolocation signals of free-ranging  
19 killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon  
20 (*Oncorhynchus tshawytscha*). *Journal of the Acoustical Society of America* **115**, 901–909.
- 21 Au, W. W. L., Kastelein, R. A., Rippe, H. T. and Schooneman, N. M. (1999). Transmission  
22 beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*).  
23 *Journal of the Acoustical Society of America* **106**, 3699-3705.

- 1 Au, W. W. L. and Moore, P. W. B. (1984). Receiving beam patterns and directivity indices of the  
2 Atlantic bottlenosed dolphin (*Tursiops truncatus*). *Journal of the Acoustical Society of*  
3 *America* **75**, 255-262.
- 4 Au, W. W. L. and Moore, P. W. B. (1990). Critical ratio and critical bandwidth for the Atlantic  
5 bottlenose dolphin. *Journal of the Acoustical Society of America* **88**, 1635-1638.
- 6 Awbrey, F. T., Thomas, J. A. and Kastelein, R. A. (1988). Low-frequency underwater hearing  
7 sensitivity in belugas, *Delphinapterus leucas*. *Journal of the Acoustical Society of*  
8 *America* **84**, 2273-2275.
- 9 Balcomb, K. C. and Claridge, E. (2001). A mass stranding of cetaceans caused by naval sonar in  
10 the Bahamas. *Bahamas Journal of Science* **8**, 2-12.
- 11 Benoit-Bird, K. and Au, W. W. L. (2009). Cooperative prey herding by the pelagic dolphin,  
12 *Stenella longirostris*. *Journal of the Acoustical Society of America*, 125-137.
- 13 Berg, B. G. (1996). On the relationship between comodulation masking release and temporal  
14 modulation transfer functions. *Journal of the Acoustical Society of America* **100**, 1013-  
15 1023.
- 16 Blomberg, J. and Lindholm, L.-E. (1976). Variations in lipid composition and sound velocity in  
17 melon from the North Atlantic pilot whale, *Globicephala melaena melaena*. *Lipids* **11**,  
18 153-156.
- 19 Boenninghaus (1904). Das Ohr des Zahnwales. *Zool. Jahrb., Abt. Anat. u. Ontog.* **19**, 189-360.
- 20 Branstetter, B. and Mercado III, E. (2006). Sound localization by cetaceans. *International*  
21 *Journal of Comparative Psychology* **19**, 26-61.

1 Branstetter, B., Mevissen, S. J., Pack, A. A., Herman, L. M., Roberts, S. R. and Carsrud, L. K.  
2 (2007a). Dolphin (*Tursiops truncatus*) echoic angular discrimination: Effects of object  
3 separation and complexity. *Journal of the Acoustical Society of America* **121**, 626-635.

4 Branstetter, B. K. and Finneran, J. J. (2008a). Comodulation masking release in bottlenose  
5 dolphins (*Tursiops truncatus*). *Journal of the Acoustical Society of America* **124**, 625-33.

6 Branstetter, B. K. and Finneran, J. J. (2008b). Comodulation masking release in bottlenose  
7 dolphins (*Tursiops truncatus*). *Journal of the Acoustical Society of America* **124**, 623-633.

8 Branstetter, B. K., Mercado, E. and Au, W. W. L. (2007b). Representing multiple discrimination  
9 cues in a computational model of the bottlenose auditory system. *Journal of the*  
10 *Acoustical Society of America* **122**, 2459-2468.

11 Branstetter, B. K., Mevissen, S. J., Herman, L. M., Pack, A. A. and Roberts, S. P. (2003).  
12 Horizontal angular discrimination by an echolocating bottlenose dolphin *Tursiops*  
13 *truncatus*. *The International Journal of Sound and Its Recording* **14**, 15-34.

14 Bregman, A. S. (1990). *Auditory Scene Analysis: The Perceptual Organization of Sound*. The  
15 MIT Press.

16 Brill, R. L., Moore, P. W. B., Helweg, D. A. and Dankiewicz, L. A. (2001). Investigating the  
17 dolphin's peripheral hearing system: Acoustic sensitivity about the head and lower jaw,  
18 SSC, pp. 20.

19 Brill, R. L., Sevenich, M. L., Sullivan, T. J., Sustman, J. D. and Witt, R. E. (1988). Behavioral  
20 evidence for hearing through the lower jaw by an echolocating dolphin (*Tursiops*  
21 *truncatus*). *Marine Mammal Science* **4**, 223–230.

- 1 Brittan-Powell, E. F., Dooling, R. J. and Gleich, O. (2002). Auditory brainstem responses (ABR)  
2 in adult budgerigars (*Melopsitacus undulatus*). *Journal of the Acoustical Society of*  
3 *America* **112**, 999-1008.
- 4 Brownell, R. L., Ralls, K., Baumann-Pickering, S. and Poole, M. M. (2009). Behavior of melon-  
5 headed whales, *Peponocephala electra*, near oceanic islands. *Marine Mammal Science* **25**,  
6 639-658.
- 7 Buchanan, T. (1828). Physiological illustrations of the organ of hearing in Longman, Rees, Orme,  
8 Brown and Green (Eds), pp. 100-103.
- 9 Bullock, T. H., Grinnell, A. D., Ikezono, F., Kameda, K., Katsuki, Y., Nomoto, M., Sato, O.,  
10 Suga, N. and Yanagisava, K. (1968). Electrophysiological studies of the central auditory  
11 mechanisms in cetaceans. *Zeitschrift fur Vergleichende Physiologie* **59**, 117-156.
- 12 Bullock, T. H. and Ridgway, S. H. (1972). Evoked potentials in the central auditory system of  
13 alert porpoises to their own and artificial sounds. *Journal of Neurobiology* **3**, 79-99.
- 14 Camper, P. (1762). Abhandlg. uber d. Gehor d. Caschalotts (Boenninghaus).
- 15 Casper, B. M., Lobel, P. S. and Yan, H. Y. (2003). The hearing sensitivity of the little skate, *Raja*  
16 *erinacea*: a comparison of two methods. *Environmental Biology of Fishes* **68**, 371-379.
- 17 Clark, C. W. and Clark, J. M. (1980). Sound playback experiments with Southern right whales  
18 (*Eubalaena australis*). *Science* **207**, 663-665.
- 19 Claudius (1858). *Physiologische Betrachtungen uber das Gehorogan der Cetaceen und das*  
20 *Labyrinth der Saugethiere*. Schwers'sche Buchbaudlung.
- 21 Cook, M. L. H., Verela, R. A., Goldstein, J. D., McCulloch, S. D., Bossart, G. D., Finneran, J. J.,  
22 Houser, D. S. and Mann, D. A. (2006). Beaked whale auditory evoked potential hearing



1 measurements. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral*  
2 *Physiology* **192**, 489-495.

3 Cox, T. M., Ragen, T. J., Read, A. J., Vos, E., Baird, R. W., Balcomb, K. C., Barlow, J.,  
4 Caldwell, J., Cranford, T. W., Crum, L., D'Amico, A., D'Spain, G., Fernandez, A.,  
5 Finneran, J. J., Gentry, R. L., Gerth, W., Gulland, F., Hildebrand, J. A., Houser, D. S.,  
6 Hullar, T., Jepson, P. D., Ketten, D. R., MacLeod, C. D., Miller, P. J., Moore, S. E.,  
7 Mountain, D. C., Palka, D. L., Ponganis, P., Rommel, S. A., Rowles, T., Taylor, B. L.,  
8 Tyack, P. L., Wartzok, D., Gisiner, R., Mead, J. G. and Benner, L. (2006). Understanding  
9 the impacts of anthropogenic sound on beaked whales. *Journal of Cetacean Research*  
10 *Management* **7**, 177-187.

11 Cranford, T. W., Amundin, M. and Norris, K. S. (1996). Functional morphology and homology  
12 in the odontocete nasal complex: implications for sound generation. *Journal of*  
13 *Morphology* **228**, 223-285.

14 Cranford, T. W., Krysl, P. and Amundin, M. (2010). A new acoustic portal into the odontocete  
15 ear and vibrational analysis of the tympanoperiotic complex. *PLoS ONE* **5**, e11927.

16 Cranford, T. W., Krysl, P. and Hildebrand, J. A. (2008). Acoustic pathways revealed: simulated  
17 sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*).  
18 *Bioinspiration and Biomimetics* **3**, 1-10.

19 Cummings, W. C. and Thompson, P. O. (1971). Underwater sounds from the blue whale,  
20 *Balaenoptera musculus*. *Journal of the Acoustical Society of America* **50**, 1193-1198.

21 Delory, E., Rio, J. d., Castell, J., Schaar, M. v. d. and André, M. (2007). OdiSEA: An  
22 autonomous portable auditory screening unit for rapid assessment of hearing in cetaceans  
23 *Aquatic Mammals* **33**, 85 - 92.

- 1 Denker, A. (1902). Anatomie des Gehororgans der Cetacea. *Anat. Hefte* **19**, 424-448.
- 2 Dolphin, W. F., Au, W. W. L., Nachtigall, P. E. and Pawloski, J. L. (1995). Modulation rate  
3 transfer functions to low frequency carriers by three species of cetaceans. *Journal of*  
4 *Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology* **177**, 235-245.
- 5 Dolphin, W. F. and Mountain, D. C. (1992). The envelope following response: Scalp potentials  
6 elicited in the mongolian gerbil using sinusoidally AM acoustic signals. *Hearing*  
7 *Research* **58**, 70-78.
- 8 Dudok Van Heel, W. H. (1962). Sound and cetacea. *Netherlands Journal of Sea Research* **1**,  
9 407-507.
- 10 Erbe, C. (2008). Critical ratios of beluga whales (*Delphinapterus leucas*) and masked signal  
11 duration. *Journal of the Acoustical Society of America* **124**, 2216-2223.
- 12 Evans, D. L., England, G. R., Lautenbacher, C. C., Livingstone, S. M., Hogarth, W. T. and  
13 Johnson, H. T. (2001). *Joint Interim Report: Bahamas Marine Mammal Stranding, Event*  
14 *of 15-16 March 2000*. U.S. Department of Commerce / United States Navy.
- 15 Fahlke, J. M., Gingerich, P. D., Welsh, R. C. and Wood, A. R. (2011). Cranial asymmetry in  
16 Eocene archaeocete whales and the evolution of directional hearing in water. *PNAS* **108**,  
17 14545-14548.
- 18 Fernandez, A., Edwards, J. F., Rodriguez, F., Espinosa, A., Herraiez, P., Castro, P., Jaber, J. R.,  
19 Martin, V. and Arbelo, M. (2005). "Gas and fat embolic syndrome" involving a mass  
20 stranding of beaked whales (Family Ziphiidae) exposed to anthropogenic sonar signals.  
21 *Veterinary Pathology* **42**, 446-457.

- 1 Finneran, J. J. (2009). Evoked response study tool: A portable, rugged system for single and  
2 multiple auditory evoked potential measurements. *Journal of the Acoustical Society of*  
3 *America* **126**, 491–500.
- 4 Finneran, J. J., Carder, D. A., Schlundt, C. E. and Dear, R. (2010). Growth and recovery of  
5 temporary threshold shift at 3 kHz in bottlenose dolphins: Experimental data and  
6 mathematical models. *Journal of the Acoustical Society of America* **127**, 3256–3266.
- 7 Finneran, J. J., Carder, D. A., Schlundt, C. E. and Ridgeway, S. H. (2005). Temporary threshold  
8 shift in bottlenose dolphins (*Tursiops truncatus*) exposed to mid-frequency tones. *Journal*  
9 *of the Acoustical Society of America* **118**, 2696-2705.
- 10 Finneran, J. J. and Houser, D. S. (2007). Bottlenose dolphin (*Tursiops truncatus*) steady-state  
11 evoked responses to multiple simultaneous sinusoidal amplitude modulated tones.  
12 *Journal of the Acoustical Society of America* **121**, 1775–1782.
- 13 Finneran, J. J., Houser, D. S., Mase-Guthrie, B., Ewing, R. Y. and Lingenfelter, R. G. (2009).  
14 Auditory evoked potentials in a stranded Gervais' beaked whale (*Mesoplodon europaeus*).  
15 *Journal of the Acoustical Society of America* **126**, 484–490.
- 16 Finneran, J. J., Houser, D. S. and Schlundt, C. E. (2007a). Objective detection of bottlenose  
17 dolphin (*Tursiops truncatus*) steady-state auditory evoked potentials in response to  
18 AM/FM tones. *Aquatic Mammals* **33**, 43-54.
- 19 Finneran, J. J. and Schlundt, C. E. (2010). Frequency-dependent and longitudinal changes in  
20 noise-induced hearing loss in a bottlenose dolphin (*Tursiops truncatus*) (L). *Journal of*  
21 *the Acoustical Society of America* **128**, 567–570.

1 Finneran, J. J. and Schlundt, C. E. (2011). Subjective loudness level measurements and equal  
2 loudness contours in a bottlenose dolphin (*Tursiops truncatus*). *Journal of the Acoustical*  
3 *Society of America* **130**, 3124–3136.

4 Finneran, J. J., Schlundt, C. E., Branstetter, B. K. and Dear, R. (2007b). Assessing temporary  
5 threshold shift in a bottlenose dolphin (*Tursiops truncatus*) using multiple simultaneous  
6 auditory evoked potentials. *Journal of the Acoustical Society of America* **122**, 1249-1264.

7 Finneran, J. J., Schlundt, C. E., Carder, D. A. and Ridgway, S. H. (2002a). Auditory filter shapes  
8 for the bottlenose dolphin (*Tursiops truncatus*) and the white whale (*Delphinapterus*  
9 *leucas*) derived with notched noise. *Journal of the Acoustical Society of America* **112**,  
10 322-328.

11 Finneran, J. J., Schlundt, C. E., Dear, R., Carder, D. A. and Ridgway, S. H. (2002b). Temporary  
12 shift in masked hearing thresholds in odontocetes after exposure to single underwater  
13 impulses from a seismic watergun. *Journal of the Acoustical Society of America* **111**,  
14 2929-2940.

15 Flewellen, C. G. and Morris, R. J. (1978). Sound velocity measurements on samples from the  
16 spermaceti organ of the sperm whale (*Physeter catodon*). *Deep Sea Research* **25**, 269-277.

17 Frantzis, A. (1998). Does acoustic testing strand whales. *Nature* **392**, 29.

18 Fraser, F. C. (1952). *Handbook of R. H. Burne's Cetacean Dissections*. British Museum (Natural  
19 History).

20 Fraser, F. C. and Purves, P. E. (1960). Hearing in cetaceans: Evolution of the accessory air sacs  
21 and the structure and function of the outer and middle ear in recent cetaceans. *Bulletin of*  
22 *the British Museum (Natural History)* **7**, 140.

- 1 Gouw, I. R. T. H. and Vlugter, I. R. J. C. (1967). Physical properties of triglycerides III:  
2 Ultrasonic sound velocity. *Fette, Seifen, Anstrichmittel* **69**, 159-164.
- 3 Hall, J. D. and Johnson, C. S. (1972). Auditory thresholds of a killer whale, *Orcinus orca*  
4 Linnaeus. *Journal of the Acoustical Society of America* **51**, 515-517.
- 5 Hall, J. W. and Grose, J. H. (1990). Effects of flanking band proximity, number, and modulation  
6 pattern on comodulation masking release. *Journal of the Acoustical Society of America*  
7 **87**, 269-282.
- 8 Hecox, K. and Galambos, R. (1974). Brain stem auditory evoked responses in human infants and  
9 adults. *Archives of Otolaryngology* **99**, 30-33.
- 10 Hemilä, S., Nummela, S. and Reuter, T. (2001). Modeling whale audiograms: effects of bone  
11 mass on high-frequency hearing. *Hearing Research* **151**, 221-226.
- 12 Holt, M. M., Noren, D., Veirs, V., Emmons, C. K. and Veirs, S. (2009). Speaking up: Killer  
13 whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. *JASA*  
14 *Express Letters* **25**, EL27-32.
- 15 Home, E. (1812). An Account of Some Peculiarities in the Structure of the Organ of Hearing in  
16 the Balaena Mysticetus of Linnaeus. *Philosophical Transactions of the Royal Society of*  
17 *London* **102**, 83-89.
- 18 Houser, D. S., Crocker, D. E., Reichmuth, C. J., Mulsow, J. and Finneran, J. J. (2007). Auditory  
19 evoked potentials in northern elephant seals (*Mirounga angustirostris*). *Aquatic Mammals*  
20 **33**, 110-121.
- 21 Houser, D. S., Finneran, J., Carder, D., Van Bonn, W., Smith, C., Hoh, C., Mattrey, R. and  
22 Ridgway, S. (2004a). Structural and functional imaging of bottlenose dolphin (*Tursiops*  
23 *truncatus*) cranial anatomy. *Journal of Experimental Biology* **207**, 3657-3665.

- 1 Houser, D. S. and Finneran, J. J. (2006a). A comparison of underwater hearing sensitivity in  
2 bottlenosed dolphins (*Tursiops truncatus*) determined by electrophysiological and  
3 behavioral methods. *Journal of the Acoustical Society of America* **120**, 1713-1722.
- 4 Houser, D. S. and Finneran, J. J. (2006b). Variation in the hearing sensitivity of a dolphin  
5 population determined through the use of evoked potential audiometry. *Journal of the*  
6 *Acoustical Society of America* **120**, 4090-4099.
- 7 Houser, D. S., Finneran, J. J., Carder, D. A., Van Bonn, W., Smith, C., Hoh, C., Mattrey, R. and  
8 Ridgway, S. H. (2004b). Structural and functional imaging of bottlenose dolphin  
9 (*Tursiops truncatus*) cranial anatomy. *The Journal of Experimental Biology* **207**, 3657-  
10 3665.
- 11 Houser, D. S., Gomex-Rubio, A. and Finneran, J. J. (2008). Evoked potential audiometry of 13  
12 Pacific bottlenose dolphins (*Tursiops truncatus gilli*). *Marine Mammal Science* **24**, 28-41.
- 13 Hunter, J. (1787). Observations on the Structure and Oeconomy of Whales. *Philosophical*  
14 *Transactions of the Royal Society of London* **77**, 371-450.
- 15 Hustad, G. O. (1971). Acoustic properties of some lipids. *Chemistry and physics of lipids* **7**, 61.
- 16 Ibsen, S. D., Au, W. W. L., Nachtigall, P. E., DeLong, C. M. and Breese, M. (2007). Changes in  
17 signal parameters over time for an echolocating Atlantic bottlenose dolphin performing  
18 the same target discrimination task. *Journal of the Acoustical Society of America* **122**,  
19 2446–2450.
- 20 Jacobs, D. W. and Hall, J. D. (1972). Auditory thresholds of a freshwater dolphin, *Inia*  
21 *geoffrensis* Blainville. *Journal of the Acoustical Society of America* **51**, 530-533.
- 22 Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A. P., Castro, P., Baker, J. R., Degollada, E.,  
23 Ross, H. M., Herraiez, P., Pocknell, A. M., Rodreguez, F., Howie, F. E., Espinosa, A.,

- 1 Reid, R. J., Jaber, J. R., Martin, V., Cunningham, A. A. and Fernandez, A. (2003). Gas-  
2 bubble lesions in stranded cetaceans. *Nature* **425**, 575-576.
- 3 Johnson, C. S. (1966). Auditory thresholds of the bottlenosed porpoise (*Tursiops truncatus*,  
4 Montagu), U.S. Naval Ordnance Test Station, pp. 1-28.
- 5 Johnson, C. S. (1967). Sound detection thresholds in marine mammals in Tavolga, W. N. (Ed),  
6 *Marine bioacoustics*, Pergamon Press, pp. 247-260.
- 7 Johnson, M., Madsen, P. T., Zimmer, W. M. X., Aguilar de Soto, N. and Tyack, P. L. (2007).  
8 Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click  
9 types matched to different phases of echolocation. *Journal of Experimental Biology* **209**,  
10 5038-5050.
- 11 Kastelein, R. A. (2003). Audiogram of a striped dolphin (*Stenella coeruleoalba*). *Journal of the*  
12 *Acoustical Society of America* **113**, 1130-1141.
- 13 Kastelein, R. A., Bunscoek, P., Hagedoorn, M., Au, W. W. L. and de Haan, D. (2002).  
14 Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band  
15 frequency-modulated signals. *Journal of the Acoustical Society of America* **112**, 334-344.
- 16 Kellogg, R. (1928). The history of whales - their adaptation to life in the water (concluded). *The*  
17 *Quarterly Review of Biology* **3**, 174-208.
- 18 Kellogg, W. N. and Kohler, R. (1952). Reactions of the porpoise to ultrasonic frequencies.  
19 *Science* **116**, 250-252.
- 20 Kernan, J. D. (1919). Bone conduction of sound in cetacean and its relation to increased bone  
21 conduction in human beings. *The Laryngoscope* **29**, 510-521.

- 1 Ketten, D. R. (1992). The marine mammal ear: specializations for aquatic audition and  
2 echolocation in Webster, D. B., Fay, R. J. and Popper, A. N. (Eds), *The evolutionary*  
3 *biology of hearing*, Springer-Verlag, pp. 717-750.
- 4 Ketten, D. R. (1994). Functional analyses of whale ears: Adaptations for underwater hearing.  
5 *I.E.E.E. Proceedings in Underwater Acoustics* **1**, 264-270.
- 6 Ketten, D. R. (1997). Structure and function in whale ears. *Bioacoustics* **8**, 103-135.
- 7 Ketten, D. R. and Wartzok, D. (1990). Three-dimensional reconstructions of the dolphin ear in  
8 Thomas, J. A. and Kastelein, R. A. (Eds), *Sensory abilities of cetaceans*, Plenum Press,  
9 pp. 81-105.
- 10 Klishin, V. O., Popov, V. V. and Supin, A. Y. (2000). Hearing capabilities of a beluga whale,  
11 *Delphinapterus leucas*. *Aquatic Mammals* **26**, 212-228.
- 12 Kloepper, L., Nachtigall, P. E. and Breese, M. (2010). Change in echolocation signals with  
13 hearing loss in a false killer whale (*Pseudorca crassidens*). *Journal of the Acoustical*  
14 *Society of America* **128**, 2233-2237.
- 15 Knudsen, E. (1981). The hearing of the barn owl. *Scientific American* **245**, 113-125.
- 16 Koopman, H. N., Budge, S. M., Ketten, D. R. and Iverson, S. (2006). Topographic distribution of  
17 lipids inside the mandibular fat bodies of odontocetes: Remarkable complexity and  
18 consistency. *IEEE Journal of Oceanic Engineering* **31**, 95-106.
- 19 Koopman, H. N. and Zahorodny, Z. P. (2008). Life history constrains biochemical development  
20 in the highly specialized odontocete echolocation system. *Proceedings of the Royal*  
21 *Society of London. Series B: Biological Sciences* **275**, 2327-2334.
- 22 Krysl, P., Cranford, T. W., Wiggins, S. M. and Hildebrand, J. A. (2006). Simulating the effect of  
23 high-intensity sound on cetaceans: Modeling approach and a case study for Cuvier's



1 beaked whale (*Ziphius cavirostris*) *Journal of the Acoustical Society of America* **120**,  
2 2328-2339.

3 Kryter, K. D. (1994). *The handbook of hearing and the effects of noise: Physiology, psychology,*  
4 *and public health.* Academic Press.

5 Ladich, F. and Yan, H. Y. (1998). Correlation between auditory sensitivity and vocalization in  
6 anabantoid fishes. *Journal of Comparative Physiology A* **182**, 737-746.

7 Ladygina, T. F. and Supin, A. Y. (1970). The acoustic projection in the dolphin cerebral cortex.  
8 *Fiziol. Zh. SSSR im. I. M. Schenova* **56**, 1554.

9 Ladygina, T. F. and Supin, A. Y. (1977). Localization of sensory projection zones in the cerebral  
10 cortex of the bottlenosed dolphin, *Tursiops truncatus*. *Zh. Evolutsionnoy Biokhimii I*  
11 *Fiziol.*

12 Lammers, M. O., Au, W. W. L. and Herzing, D. L. (2003). The broadband social acoustic  
13 signaling behavior of spinner and spotted dolphins. *Journal of the Acoustical Society of*  
14 *America* **114**, 1629-1639.

15 Langworthy, O. R. (1931). Central nervous system of the Porpoise *tursiops truncatus*. *Journal of*  
16 *Mammalogy* **12**, 381-389.

17 Lemonds, D. W. (1999). Auditory filter shapes in an Atlantic bottlenose dolphin (*Tursiops*  
18 *truncatus*), *Psychology*, University of Hawaii, pp. 74.

19 Lemonds, D. W., Kloepper, L., Nachtigall, P. E., Au, W. W. L., Vlachos, S. and Branstetter, B.  
20 K. (2011). A re-evaluation of auditory filter shape in delphinid odontocetes: Evidence of  
21 constant-bandwidth filters. *Journal of the Acoustical Society of America* **135**, 3107–3114.

- 1 Li, S., Nachtigall, P. E. and Breese, M. (2010). Dolphin hearing during echolocation: evoked  
2 potential responses in an Atlantic bottlenose dolphin (*Tursiops truncatus*). *Journal of*  
3 *Experimental Biology* **214**, 2027-2035.
- 4 Li, S., Nachtigall, P. E. and Breese, M. (2011). Dolphin hearing during echolocation: evoked  
5 potential responses in an Atlantic bottlenose dolphin (*Tursiops truncatus*). *Journal of*  
6 *Experimental Biology* **214**, 2027-2035.
- 7 Linnenschidt, M., Beedholm, K., Wahlberg, M., Hojer-Kristensen, J. and Nachtigall, P. E. (2012).  
8 Keeping returns optimal: gain control exerted through sensitivity adjustments in the  
9 harbour porpoise auditory system. *Proceedings of the Royal Society of London, B.*  
10 *Biological Science* **on line**.
- 11 Litchfield, C., Greenberg, A. J., Caldwell, D. K., Caldwell, M. C., Sipos, J. C. and Ackman, R. G.  
12 (1975). Comparative lipid patterns in acoustical and nonacoustical fatty tissues of  
13 dolphins, porpoises and toothed whales. *Comparative Biochemistry and Physiology B-*  
14 *Biochemistry & Molecular Biology* **50**, 591-597.
- 15 Litchfield, C., Karol, R. and Greenberg, A. J. (1973). Compositional topography of melon lipids  
16 in the Atlantic bottlenosed dolphin *Tursiops truncatus*: Implications for echo-location.  
17 *Marine Biology* **23**, 165-169.
- 18 Ljungblad, D. K., Scoggins, P. D. and Gilmartin, W. G. (1982). Auditory thresholds of a captive  
19 Eastern Pacific bottle-nosed dolphin, *Tursiops* spp. *Journal of the Acoustical Society of*  
20 *America* **72**, 1726-1729.
- 21 Lovell, J. M., Findlay, M. M., Moate, R. M. and Yan, H. Y. (2005). The hearing abilities of the  
22 prawn *Palaemon serratus*. *Comparative Biochemistry and Physiology, Part A* **140**, 89-  
23 100.

- 1 Malins, D. C. and Varanasi, U. (1975). Cetacean biosonar part II: The biochemistry of lipids in  
2 acoustic tissues in Sargent, D. C. M. a. J. R. (Ed), *Biochemical and Biophysical*  
3 *Perspectives in Marine Biology*, Academic Press, pp. 237-290.
- 4 Mann, D., Hill-Cook, M., Manire, C., Greenhow, D., Montie, E., Powell, J., Wells, R., Bauer, G.,  
5 Cunningham-Smith, P., Lingenfelter, R., DiGiovanni, R., Stone, A., Brodsky, M.,  
6 Stevens, R., Kieffer, G. and Hoetjes, P. (2010). Hearing loss in stranded odontocete  
7 dolphins and whales. *PLoS ONE* **5**, e13824.
- 8 McCormick, J. G., Wever, E. G., Palin, J. and Ridgeway, S. H. (1970). Sound conduction in the  
9 dolphin ear. *Journal of the Acoustical Society of America* **48**, 1418-1428.
- 10 Miller, P. J. O., Biassoni, N., Samuels, A. and Tyack, P. L. (2000). Whale songs lengthen in  
11 response to sonar. *Nature* **405**, 903-4.
- 12 Mobley, J., Herman, L. M. and Frankel, A. S. (1988). Responses of wintering humpback whales  
13 (*Megaptera novaengliae*) to playback recordings of winter and summer vocalizations and  
14 of synthetic sound. *Behavioral Ecology and Sociobiology* **23**, 211-223.
- 15 Møhl, B., Au, W. W. L., Pawloski, J. L. and Nachtigall, P. E. (1999). Dolphin hearing: relative  
16 sensitivity as a function of point of application of a contact sound source in the jaw and  
17 head region. *Journal of the Acoustical Society of America* **105**, 3421-3424.
- 18 Montie, E. W., Manire, C. A. and Mann, D. A. (2011). Live CT imaging of sound reception  
19 anatomy and hearing measurements in the pygmy killer whale, *Feresa attenuata*. *Journal*  
20 *of Experimental Biology* **214**, 945-955.
- 21 Mooney, T. A., Li, S., Ketten, D. R., Wang, K. and Wang, D. (2011). Hearing pathways in the  
22 finless porpoise, *Neophocaena phocaenoides*, and implications for noise impacts. *Journal*  
23 *of the Acoustical Society of America* **129**, 2431.

1 Mooney, T. A., Nachtigall, P. E., Breese, M., Vlachos, S. and Au, W. W. L. (2009a). Predicting  
2 temporary threshold shifts in a bottlenose dolphin (*Tursiops truncatus*): the effects of  
3 noise level and duration. *Journal of the Acoustical Society of America* **125**, 1816–1826.

4 Mooney, T. A., Nachtigall, P. E., Castellote, M., Taylor, K. A., Pacini, A. F. and Esteban, J.-A.  
5 (2008). Hearing pathways and directional sensitivity of the beluga whale, *Delphinapterus*  
6 *leucas*. *Journal of Experimental Marine Biology and Ecology* **362**, 108–116.

7 Mooney, T. A., Nachtigall, P. E. and Vlachos, S. (2009b). Sonar-induced temporary hearing loss  
8 in dolphins. *Biology Letters* **5**, 565-567.

9 Mooney, T. A., Nachtigall, P. E. and Yuen, M. M. L. (2006). Temporal resolution of the Risso's  
10 dolphin, *Grampus griseus*, auditory system. *Journal of Comparative Physiology. A,*  
11 *Sensory, Neural, and Behavioral Physiology* **192** 373-380.

12 Moore, K. M. E., Sharp, S. M., Charles, H. T., Hoppe, J. M., Moore, M., Niemeyer, M. E.,  
13 Finneran, J. J. and Houser, D. S. (2011a). Field use of auditory evoked potential  
14 technology to acquire audiograms from stranded odontocetes. *19th Biennial Conference*  
15 *on the Biology of Marine Mammals. Tampa, FL.*

16 Moore, M. J., Hammar, T., Arruda, J., Cramer, S., Dennison, S., Montie, E. and Fahlman, A.  
17 (2011b). Hyperbaric computed tomographic measurement of lung compression in seals  
18 and dolphins. *The Journal of Experimental Biology* **214**, 2390-2397.

19 Moore, P. W. B., Hall, R. W., Friedl, W. A. and Nachtigall, P. E. (1984). The critical interval in  
20 dolphin echolocation: What is it? *Journal of the Acoustical Society of America* **76**, 314-  
21 317.

22 Moore, P. W. B., Pawloski, D. A. and Dankiewicz, L. (1995). Interaural time and intensity  
23 difference thresholds in the bottlenose dolphin (*Tursiops truncatus*) in Kastelein, R. A.,

1 Thomas, J. A. and Nachtigall, P. E. (Eds), *Sensory Systems of Aquatic Mammals*, De Spil  
2 Publishers.

3 Morris, R. J. (1975). Further studies into the lipid structure of the spermaceti organ of the sperm  
4 whale (*Physeter catodon*). *Deep Sea Research and Oceanographic Abstracts* **22**, 483-489.

5 Nachtigall, P. E., Au, W. W. L., Pawloski, J. L. and Moore, P. W. B. (1995). Risso's dolphin  
6 hearing thresholds in Kaneohe Bay, Hawaii in Kastelein, R. A., Thomas, J. A. and  
7 Nachtigall, P. E. (Eds), *Sensory Systems of Aquatic Mammals*, DeSpil, pp. 49-53.

8 Nachtigall, P. E., Mooney, T. A., Taylor, K. A., Miller, L. A., Rasmussen, M., Akamatsu, T.,  
9 Teilmann, J., Linnenschidt, M. and Vikingsson, G. A. (2008). Shipboard measurements  
10 of the hearing of the white-beaked dolphin, *Lagenorhynchus albirostris*. *Journal of*  
11 *Experimental Biology* **211**, 642-647.

12 Nachtigall, P. E., Mooney, T. A., Taylor, K. A. and Yuen, M. M. L. (2007). Hearing and  
13 auditory evoked potential methods applied to odontocete cetaceans. *Aquatic Mammals* **33**,  
14 6-13.

15 Nachtigall, P. E., Pawloski, J. L. and Au, W. W. L. (2003). Temporary threshold shifts and  
16 recovery following noise exposure in the Atlantic bottlenosed dolphin (*Tursiops*  
17 *truncatus*). *Journal of the Acoustical Society of America* **113**, 3425-3429.

18 Nachtigall, P. E. and Supin, A. Y. (2008). A false killer whale adjusts its hearing when it  
19 echolocates *Journal of Experimental Biology* **211**, 1714-1718.

20 Nachtigall, P. E., Supin, A. Y., Pawloski, J. L. and Au, W. W. L. (2004). Temporary threshold  
21 shifts after noise exposure in the bottlenose dolphin (*Tursiops truncatus*) measured using  
22 evoked auditory potentials. *Marine Mammal Science* **20**, 673-687.

1    Nachtigall, P. E., Yuen, M. M. L., Mooney, T. A. and Taylor, K. A. (2005). Hearing  
2            measurements from a stranded infant Risso's dolphin, *Grampus griseus*. *Journal of*  
3            *Experimental Biology* **208**, 4181-4188.

4    National Academy of Sciences (1994). *Low frequency sound and marine mammals: current*  
5            *knowledge and research needs*. National Academy Press.

6    National Academy of Sciences (2000). *Marine mammals and low frequency sound: Progress*  
7            *since 1994*. National Academy Press.

8    National Academy of Sciences (2003). *Ocean noise and marine mammals*. National Academies  
9            Press.

10   National Academy of Sciences (2005). *Marine mammal populations and ocean noise:*  
11            *Determining when noise causes biologically significant effects*. National Academies Press.

12   Ness, A. R. (1967). A measure of asymmetry of the skulls of odontocete whales. *Journal of*  
13            *Zoology* **153**, 209-221.

14   Norris, K. S. (1964). Some problems of echolocation in cetaceans in Tavolga, W. N. (Ed),  
15            *Marine Bioacoustics*, Pergamon, pp. 316-336.

16   Norris, K. S. (1968). The evolution of acoustic mechanisms in odontocete cetaceans in Drake, E.  
17            T. (Ed), *Evolution and environment*, Yale University Press, pp. 297-324.

18   Norris, K. S. and Harvey, G. W. (1974). Sound transmission in the porpoise head. *Journal of the*  
19            *Acoustical Society of America* **56**, 659-664.

20   Nummela, S., Reuter, T., Hemilä, S., Holmberg, P. and Pauku, P. (1999). The anatomy of the  
21            killer whale middle ear (*Orcinus orca*). *Hearing Research* **133**, 61-70.

22   Pacini, A. F., Nachtigall, P. E., Klopper, L. N., Linnenschmidt, M., Sogorb, A. and Matias, S.  
23            (2010). Audiogram of a formerly stranded long-finned pilot whale (*Globicephala melas*)

1 measured using auditory evoked potentials. *Journal of Experimental Biology* **213**, 3138-  
2 3143.

3 Pacini, A. F., Nachtigall, P. E., Quintos, C. T., Schofield, T. D., Look, D. A., Levine, G. A. and  
4 Turner, J. P. (2011). Audiogram of a stranded Blainville's beaked whale (*Mesoplodon*  
5 *densirostris*) measured using auditory evoked potentials. *Journal of Experimental*  
6 *Biology* **214**, 2409-2415.

7 Parks, S., Ketten, D. R., O'Malley, J. T. and Arruda, J. (2007). Anatomical predictions of hearing  
8 in the North Atlantic right whale. *The Anatomical Record* **290**, 734-744.

9 Parks, S. E. (2003). Response of North Atlantic right whales (*Eubalaena glacialis*) to playback of  
10 calls recorded from surface active groups in both the North and South Atlantic. *Marine*  
11 *Mammal Science* **19**, 563-580.

12 Parks, S. E., Urazghildiiev, I. and Clark, C. W. (2009). Variability in ambient noise levels and  
13 call parameters of North Atlantic right whales in three habitat areas. *Journal of the*  
14 *Acoustical Society of America* **125**, 1230-1239.

15 Popov, V., Supin, A., Wang, D. and Wang, K. (2006). Nonconstant quality of auditory filters in  
16 the porpoises, *Phocoena phocoena* and *Neophocaena phocaenoides* (Cetacea,  
17 Phocoenidae). *Journal of the Acoustical Society of America* **119**, 3173-3180.

18 Popov, V. V. and Supin, A. Y. (1976). Responses of the dolphin auditory cortex to complex  
19 acoustic stimuli. *Fiziol. Zh. SSSR im. I. M. Schenova* **62**, 1780.

20 Popov, V. V. and Supin, A. Y. (1978). Electrophysiological studies of the auditory system of the  
21 *Tursiops truncatus*, *Morskiye Mlekopitayushchiye. Resul'taty i Metody Issledovaniya*,  
22 Isdatel'stvo Nauka.

- 1 Popov, V. V. and Supin, A. Y. (1985). Determining the hearing characteristics of dolphins  
2 according to brainstem evoked potentials. *Dokl Biol Sci* **283**, 524-527.
- 3 Popov, V. V. and Supin, A. Y. (1990). Auditory brainstem responses in characterization of  
4 dolphin hearing. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral*  
5 *Physiology* **166**, 385-393.
- 6 Popov, V. V., Supin, A. Y. and Klishin, V. O. (1997). Frequency tuning of the dolphin's hearing  
7 as revealed by auditory brain-stem response with notch-noise masking. *Journal of the*  
8 *Acoustical Society of America* **102**, 3795-3801.
- 9 Popov, V. V., Supin, A. Y., Klishin, V. O., Tarakanov, M. B. and Plentenko, M. G. (2008).  
10 Evidence for double acoustic windows in the dolphin, *Tursiops truncatus*. *Journal of the*  
11 *Acoustical Society of America* **123**, 552-560.
- 12 Popov, V. V., Supin, A. Y., Wang, D., Wang, K., Xiao, J. and Li, S. (2005). Evoked-potential  
13 audiogram of the Yangtze finless porpoise *Neophocaena phocaenoides asiaeorientalis*  
14 (L). *Journal of the Acoustical Society of America* **117**, 2728-2731.
- 15 Pytte, C. L., Ficken, M. S. and Moiseff, A. (2004). Ultrasonic singing by the blue-throated  
16 hummingbird: a comparison between production and perception. *Journal of Comparative*  
17 *Physiology A* **190**, 665-673.
- 18 Rasmussen, M. and Miller, L. A. (2002). Whistles and clicks from white-beaked dolphins,  
19 *Lagenorhynchus albirostris*, recorded in Faxaflói Bay, Iceland. *Aquatic Mammals* **28.1**,  
20 78-89.
- 21 Regan, M. P. (1994). Linear half-wave rectification of modulated sinusoids. *Applied*  
22 *Mathematics and Computation* **62**, 61-79.



- 1 Renaud, D. L. and Popper, A. N. (1975). Sound localization by the bottlenose porpoise *Tursiops*  
2 *truncatus*. *The Journal of Experimental Biology* **63**, 569-585.
- 3 Reysenbach De Haan, F. W. (1957). Hearing in whales. *Acta oto-laryngologica. Supplementum*  
4 **134**, 1-114.
- 5 Ridgway, S. H. (1980). Electrophysiological experiments on hearing in odontocetes in Bushnel, R.  
6 G. and Fish, J. F. (Eds), *Animal Sonar Systems*, Plenum Publishing Corporation, pp. 483-  
7 493.
- 8 Ridgway, S. H., Bullock, T. H., Carder, D. A., Seeley, R. L., Woods, D. and Galambos, R.  
9 (1981). Auditory brainstem response in dolphins *Proceedings of the National Academy of*  
10 *Sciences of the United States of America* **78**, 1943-1947.
- 11 Ridgway, S. H. and Carder, D. A. (1997). Hearing deficits measured in some *Tursiops truncatus*  
12 and discovery of a deaf/mute dolphin. *Journal of the Acoustical Society of America* **101**,  
13 590-594.
- 14 Ridgway, S. H. and Carder, D. A. (2001). Assessing hearing and sound production in cetaceans  
15 not available for behavioral audiograms: Experiences with sperm, pygmy sperm, and  
16 gray whales. *Aquatic Mammals* **27**, 267-276.
- 17 Ridgway, S. H. and McCormick, J. G. (1967). Anesthetization for porpoises for major surgery.  
18 *Science* **158**, 510-512.
- 19 Roitblat, H. L., Moore, P. W. B., Helweg, D. A. and Nachtigall, P. E. (1993a). Representation  
20 and processing of acoustic information in a biomimetic neural network in Meyer, J.-A.,  
21 Roitblat, H. L. and Wilson, S. W. (Eds), *Animals to Animats 2: Stimulation of Adaptive*  
22 *Behavior*, MIT press., pp. 1-10.

- 1 Roitblat, H. L., Moore, P. W. B., Helweg, D. A. and Nachtigall, P. E. (1993b). Representation of  
2 acoustic information in a biomimetic neural network in Meyer, J. A., Wilson, S. W. and  
3 Roitblat, H. L. (Eds), *From Animals to Animats 2: Simulation of Adaptive Behavior*, MIT  
4 Press, pp. 90-99.
- 5 Sauerland, M. and Dehnhardt, D. (1998). Underwater audiogram of a Tucuxi (*Sotalia fluviatilis*  
6 *guianensis*). *Journal of the Acoustical Society of America* **103**, 1199-1204.
- 7 Scano, P., Maxia, C., Maggiani, F., Crnjar, R., Lai, A. and Sirigu, P. (2005). A histological and  
8 NMR study of the melon of the striped dolphin (*Stenella coeruleoalba*). *Chemistry and*  
9 *Physics of Lipids* **134**, 21-28.
- 10 Schevill, W. E. and Lawrence, B. (1949). Underwater listening to the white porpoise  
11 (*Delphinapterus leucas*). *Science* **109**, 143-144.
- 12 Schevill, W. E. and McBride, A. F. (1956). Evidence for echolocation by cetaceans. *Deep Sea*  
13 *Research* **3**, 153-154.
- 14 Schlundt, C. E., Finneran, J. J., Carder, D. A. and Ridgway, S. H. (2000). Temporary shift in  
15 masked hearing thresholds of bottlenose dolphins, *Tursiops truncatus*, and white whales,  
16 *Delphinapterus leucas*, after exposure to intense tones. *Journal of the Acoustical Society*  
17 *of America* **107**, 3496-3508.
- 18 Seeley, R. L., Flanigan, W. F. and Ridgway, S. H. (1976). A technique for rapidly assessing the  
19 hearing of the bottlenosed porpoise *Tursiops truncatus*. *Naval Undersea Center TP 552*,  
20 San Diego, CA.
- 21 Soldevilla, M. S., McKenna, M. F., Wiggins, S. M., Shadwick, R. E., Cranford, T. W. and  
22 Hildebrand, J. A. (2005). Cuvier's beaked whale (*Ziphius cavirostris*) head tissues:

1 physical properties and CT imaging. *The Journal of Experimental Biology* **208**, 2319-  
2 2332.

3 Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene Jr, C. R.,  
4 Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A.  
5 and Tyack, P. L. (2007). Marine mammal noise exposure criteria: Initial scientific  
6 recommendations. *Aquatic Mammals* **33**.

7 Southall, B. L., Braun, R., Gulland, F. M. D., Heard, A. D., Baird, R. W., Wilkin, S. and Rowles,  
8 T. (2006). *Hawaiian melon-headed whale (Peponocephala electra) mass stranding even*  
9 *of 3-4 July 2004*. NOAA Technical Memorandum NMFS-OPR-31.

10 Sukhoruchenko, M. N. (1971). Upper limit of hearing of dolphins with reference to frequency.  
11 *Tr. Akust. Institute, Moscow* **17**, 54.

12 Sukhoruchenko, M. N. (1973). Frequency discrimination fo dolphin (*Phocoena phocoena*).  
13 *Fiziol. Zh. SSSR im. I. M. Schenova* **59**, 1205.

14 Supin, A. Y., Nachtigall, P. E., Au, W. W. L. and Breese, M. (2004). The interaction of outgoing  
15 echolocation pulses and echoes in the false killer whale's auditory system: Evoked-  
16 potential study. *Journal of the Acoustical Society of America* **113**, 3218-3225.

17 Supin, A. Y., Nachtigall, P. E., Au, W. W. L. and Breese, M. (2005). Invariance of echo-  
18 responses to target strength and distance in an echolocating false killer whale: evoked  
19 potential study. *Journal of the Acoustical Society of America* **117**, 3928-3935.

20 Supin, A. Y., Nachtigall, P. E. and Breese, M. (2006). Source-to-sensation level ratio of  
21 transmitted biosonar pulses in an echolocating false killer whale. *Journal of the*  
22 *Acoustical Society of America* **120**, 518-526.

- 1 Supin, A. Y., Nachtigall, P. E. and Breese, M. (2007). Evoked-potential recovery during double  
2 click stimulation in a whale: A possibility of biosonar automatic gain control. *Journal of*  
3 *the Acoustical Society of America* **121**, 618–625.
- 4 Supin, A. Y., Nachtigall, P. E. and Breese, M. (2008). Forward masking as a mechanism of  
5 automatic gain control in odontocete biosonar: A psychophysical study. *Journal of the*  
6 *Acoustical Society of America* **124**, 648–656.
- 7 Supin, A. Y., Nachtigall, P. E. and Breese, M. (2009). Forward-masking based gain control in  
8 odontocete biosonar: An evoked-potential study. *Journal of the Acoustical Society of*  
9 *America* **125**, 2432–2442.
- 10 Supin, A. Y., Nachtigall, P. E. and Breese, M. (2010). Target distance-dependent variation of  
11 hearing sensitivity during echolocation in a false killer whale. *Journal of the Acoustical*  
12 *Society of America* **127**, 3830-3836.
- 13 Supin, A. Y., Nachtigall, P. E. and Breese, M. (2011). Interaction of emitted sonar pulses and  
14 simulated echoes in a false killer whale: An evoked-potential study. *Journal of the*  
15 *Acoustical Society of America* **130**, 1711-1720.
- 16 Supin, A. Y., Nachtigall, P. E., Pawloski, J. L. and Au, W. W. L. (2003). Evoked potential  
17 recording during echolocation in a false killer whale *Pseudorca crassidens* (L). *Journal*  
18 *of the Acoustical Society of America* **113**, 2408-2411.
- 19 Supin, A. Y. and Popov, V. V. (1993). Direction-dependent spectral sensitivity and interaural  
20 spectral difference in a dolphin: Evoked potential study. *Journal of the Acoustical*  
21 *Society of America* **93**, 3490-3495.
- 22 Supin, A. Y. and Popov, V. V. (1995). Envelope-following response and modulation rate transfer  
23 function in the dolphin's auditory system. *Hearing Research* **92**, 38-45.

- 1 Supin, A. Y. and Popov, V. V. (2007). Improved techniques of evoked potential audiometry in  
2 odontocetes. *Aquatic Mammals* **33**, 14-23.
- 3 Supin, A. Y., Popov, V. V. and Mass, A. M. (2001). *The sensory physiology of aquatic mammals*.  
4 Kluwer Academic Publishers.
- 5 Supin, A. Y. and Sukhoruchenko, M. N. (1970). The determinatino of auditory threshold in  
6 *Phocoena phocoena* by the method of skin galvanic reaction. *Tr. Akust. Institute, Moscow*  
7 **12**, 194.
- 8 Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S. and Henry, K. R. (1999).  
9 Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral  
10 audiograms. *Journal of the Acoustical Society of America* **106**, 1134-1141.
- 11 Taylor, K. A., Nachtigall, P. E., Mooney, T. A., Supin, A. Y. and Yuen, M. M. L. (2007). A  
12 portable system for the evaluation of auditory capabilities of marine mammals. *Aquatic*  
13 *Mammals* **33**, 6-13.
- 14 Thomas, J. A., Chun, N., Au, W. W. L. and Pugh, K. (1988). Underwater audiogram of a false  
15 killer whale (*Pseudorca crassidens*). *Journal of the Acoustical Society of America* **84**,  
16 936-940.
- 17 Thompson, R. K. R. and Herman, L. M. (1975). Underwater frequency discrimination in the  
18 bottlenose dolphin. *Journal of the Acoustical Society of America* **57**, 943-948.
- 19 Trickey, J. S., Branstetter, B. K. and Finneran, J. J. (2011). Auditory masking with  
20 environmental, comodulated, and Gaussian noise in bottlenose dolphins (*Tursiops*  
21 *truncatus*). *Journal of the Acoustical Society of America* **128**.

- 1 Tubelli, A. A., Zosuls, A., Ketten, D. R. and Mountain, D. C. (2011). The effects of mechanical  
2 property manipulatoin on minke whale hearing sensitivity. *19th Biennial Conference of*  
3 *the Biology of Marine Mammals*, 296.
- 4 Tyack, P. (1983). Differential response of humpback whales, *Megaptera novaeangliae*, to  
5 playback of song or social sounds. *Behavioral Ecology and Sociobiology* **13**, 49-55.
- 6 Vanke, W. J. (1980). Evaluating hearing programs: The significance of race and sex.  
7 *Occupational Health and Safety* **49**, 44-48.
- 8 Varanasi, U. and Malins, D. C. (1972). Triacylglycerols characteristics of porpoise acoustic  
9 tissues: Molecular structures of diisoovaleroylglycerides. *Science* **176**, 926-928.
- 10 Varansi, U., Feldman, H. R. and Malins, D. C. (1975). Molecular basis for formation of lipid  
11 sound lens in echolocating cetaceans. *Nature* **255**, 340-343.
- 12 Varansi, U. and Malins, D. C. (1972). Triacylglycerols characteristics of porpoise acoustic  
13 tissues: Molecular structures of diisoovaleroylglycerides. *Science* **176**, 926-928.
- 14 Vel'min, V. A. and Dubrovskii, N. A. (1976). The critical interval of active hearing in dolphins.  
15 **22**, 622-623.
- 16 Wang, D., Wang, K., Ziao, Y. and Sheng, G. (1992). Auditory sensitivity of a Chinese river  
17 dolphin (*Lipotes vexillifer*) in Thomas, J. A., Kastelein, R. A. and Supin, A. Y. (Eds),  
18 *Marine mammal sensory systems*, Plenum Press, pp. 213-221.
- 19 Ward, W. D. (1997). Effects of high-intensity sound in Crocker, M. (Ed), *Encyclopedia of*  
20 *acoustics*, John Wiley and Sons, Inc., pp. 1497-1507.
- 21 Ward, W. D., Glorig, A. and Sklar, D. L. (1958). Dependence of temporary threshold shift at 4  
22 kcon intensity and time. *Journal of the Acoustical Society of America* **30**, 944-954.

- 1     Watkins, W. A. (1986). Whale reactions to human activities in Cape Cod waters. *Marine*  
2             *Mammal Science* **2**, 251-262.
- 3     Watkins, W. A. and Wartzok, D. (1985). Sensory biophysics of marine mammals. *Marine*  
4             *Mammal Science* **1**, 219-260.
- 5     Wedmid, Y., Litchfield, C., Ackman, R. G., Sipos, J. C., Eaton, C. A. and Mitchell, E. D. (1973).  
6             Heterogeneity of lipid composition within the cephalic melon tissue of the pilot whale  
7             (*Globicephala melaena*). *Biochimica et biophysica acta* **326**, 439-447.
- 8     White, J., M.J., Norris, J. C., Ljungblad, D. K., Barton, K. and di Sciara, G. N. (1978). Auditory  
9             thresholds of two beluga whales (*Delphinapterus leucas*), *Hubbs/Sea World Research*  
10            *Institute Technical Report*, Hubbs Marine Research Institute, pp. 78-109.
- 11    Yamada, M. (1953). Contribution to the anatomy of the organ of hearing of whales. *Scientific*  
12            *Reports of the Whale Research Institute* **8**, 1-79.
- 13    Yamada, M. and Yoshizaki, F. (1959). Osseous labyrinth of Cetacea. *Scientific Reports of the*  
14            *Whale Research Institute* **14**, 291-304.
- 15    Yamato, M., Ketten, D. R., Arruda, J. and Cramer, S. (2008). Biomechanical and structural  
16            modeling of hearing in baleen whales. *Bioacoustics* **17**, 100-102.
- 17    Yuen, M. M. L., Nachtigall, P. E., Breese, M. and Supin, A. Y. (2005). Behavioral and auditory  
18            evoked potential audiograms of a false killer whale (*Pseudorca crassidens*). *Journal of*  
19            *the Acoustical Society of America* **118**, 2688-2695.
- 20    Zahorodny, Z. P., Koopman, H. N. and Budge, S. M. (2009). Distribution and development of  
21            the highly specialized lipids in the sound reception systems of dolphins. *Journal of*  
22            *Comparative Physiology B-Biochemical Systemic and Environmental Physiology* **179**,  
23            783-798.

1

2



1  
2 Figure 1. (A) The lower jaws of a harbor porpoise (MH416Pp), posterior view. Note the  
3 enlarged mandibular foramen on the medial side, which is a common feature to all odontocetes  
4 and is filled with fats associated with sound reception. The thin “pan bone” area which Norris  
5 proposed as the acoustic window is labeled PB. (B) Proposed sound pathways in a porpoise  
6 head showing incoming sounds traveling through the lower jaw (Norris, 1964). (C) Coronal slice  
7 of a dolphin head, modified from Ridgeway (1999). FB, fat body in the lower jaw; BUL,  
8 tympanic bulla. (D) A 3-D reconstruction of the bottlenose dolphin auditory system based on CT  
9 data, ventral view. The bone is off-white, “acoustic fats” are yellow, the tympano-periotic  
10 complex is shown in purple, and the vestigial ear canal is blue. From Yamato *et al.* (2008).

11  
12 Figure 2. Audiograms of two Risso’s dolphins. One was collected behaviorally and the  
13 other using AEP methods. The dashed audiogram was measured from an older animal with high-  
14 frequency hearing loss. The solid audiogram was measured for a neonate animal which  
15 presumably had more “normal” hearing.

16  
17 Figure 3. (A) AEP waveforms to a click stimulus. Two responses are overlaid on top of each  
18 other. Note the series of waves responses generated from the multiple generators of the auditory  
19 system, from the 8<sup>th</sup> nerve up through the brainstem. (B) EFRs or ASSRs to 16 kHz amplitude  
20 modulated stimuli (top trace). The EFRs decrease in amplitude as stimulus amplitude  
21 correspondingly decreases.

22

1 Figure 4. Various hearing test studies and animal examinations. (A) a bottlenose dolphin during  
2 an auditory evoked potential (AEP) hearing test in the free field. The dolphin is stationed in a  
3 hoop 1 m below the surface and 2 m from the sound generator. Note the AEP electrodes on the  
4 head and back of the dolphin. (B) A false killer whale positively responding during a combined  
5 psychoacoustic and electrophysiological task. The animal responds that it detects an object by  
6 touching a yellow ball with its rostrum. The stimulus in this case was the echolocation detection  
7 of cylinder target. In hearing tests tasks, reporting the detection of a tone would generate a  
8 similar response. (C) Measuring the hearing of a finless porpoise out of water using a suction-  
9 cup jawphone transducer placed on the pan bone region of the lower jaw. Responses are measured  
10 using AEPs. A suction-cup electrode is visible on top of the head, just behind the blowhole. (D)  
11 Beluga whale during an AEP hearing test to examine directional sensitivity (from Mooney, *et al.*,  
12 2008)

13  
14 Figure 5. Critical ratios for several odontocete species as a function of frequency. From  
15 Finneran and Branstetter (in press).

16  
17 Figure 6. Frequency response of a gamma-tone filter bank (Branstetter, *et al.*, 2007b) that was  
18 fit from notched-noise masking data (Lemonds, 1999). Frequency resolution is sharper for lower  
19 frequencies.

20  
21 Figure 7. Impulse response of the gamma-tone filter bank (from Figure 6) which illustrates the  
22 high degree of temporal resolution at the higher frequencies and the “ringing” at the lower  
23 frequencies (Branstetter, *et al.*, 2007b) .

24

1 Figure 8. Thresholds for a 10 kHz tone as a function of masker bandwidth for comodulated noise  
2 (CM) and uncomodulated (UC) or Gaussian noise. Both noise types had a flat noise spectral  
3 density of 95 dB re 1  $\mu\text{Pa}^2/\text{Hz}$ . A processing transition can be seen at 1 kHz (the critical  
4 bandwidth for a 10 kHz tone) where thresholds asymptote for UC noise while thresholds  
5 decrease for CM noise (Branstetter and Finneran, 2008b).

6  
7  
8 Figure 9. Thresholds for a 10 kHz tone masked by three broadband noise types (UC = Gaussian,  
9 CM = comodulated, and environmental = snapping shrimp). A release from masking is present  
10 for CM and environmental noise (Trickey, *et al.*, 2011).

11

12 Figure 10. Three-dimensional reconstructions of the auditory system of the minke whale based  
13 on CT data, showing fat bodies associated with the ears. The fats are shown in yellow, the  
14 tympano-periotic complex (ears) in purple, and bone in off-white. (a) Ventral view. (b) Lateral  
15 view (Yamato *et al.*, submitted.)

16

## TIMELINE

- 1762: Camper claims that whales hear through the ear canal, as in terrestrial mammals.
- 1787: Hunter speculates that the tympanic cavity amplifies sound through vibration of bone, and these vibrations are directly transferred to the inner ear.
- 1858: Claudius says vibrations in water are accepted by whole head, and air space resonances are transmitted to the inner ear.
- 1904: Boenninghaus proposes a general soft-tissue sound reception pathway in odontocetes (toothed whales).
- 1919: Kernan proposes bone conduction as the hearing mechanism.
- 1957: Reysenbach de Haan supports a soft tissue sound reception pathway.
- 1958: Kellogg publishes experimental evidence supporting echolocation in odontocetes.
- 1962: Dudok van Heel argues that the ear canal is vestigial.
- 1964: Norris speculates that odontocetes may receive sounds through “acoustic fats” located within and surrounding the lower jaws.
- 1966: Purves and colleagues still maintain that the ear canal is functional.
- 1968: Evoked potential experiments by Bullock *et al.*, support Norris’s hypothesis.
- 1970: McCormick *et al.*, record cochlear potentials from anesthetized dolphins. They argue that the ear canal is not functional and support bone conduction.
- 1974: Norris and Harvey use hydrophones implanted in dead porpoise heads to support the lower jaw acoustic fat theory.
- 1975: The biochemical uniqueness of “acoustic” fats is demonstrated by Varanasi *et al.*
- 1976: Seeley, Ridgway and colleagues record AEPs from dolphins non-invasively
- 1988: Brill finds that an acoustically opaque hood on the lower jaw of dolphins decreases hearing ability. Norris’s hypothesis is more widely accepted as evidence accumulates in support of it.
- 1995: Supin *et al.*, establish the EFR in dolphin AEPs and are rapidly progressing AEP methods
- 2000: Schludt *et al.*, demonstrate TTS in odontocetes

- 2001: Navy sonar is correlated with a Bahamas beaked whale stranding event fueling the growing concern for noise impacts on marine mammals.
- 2001: Ridgway and Carder record AEPs from large, stranded cetaceans showing the techniques possibilities.
- 2003: Supin and Nachtigall initiate their experiments on hearing during echolocation.
- 2005: Nachtigall *et al.*, collect an AEP audiogram from a stranded Risso's dolphin showing the efficacy of the technique in strandings, greater species and high frequency hearing loss.
- 2006: Houser and Finneran demonstrate the variation in dolphin audiograms through hearing examinations of a population of bottlenose dolphins.
- 2007: Finneran and Houser record AEPs to multiple simultaneous sinusoidal amplitude modulated tones.

**Table 1.** Odontocete audiograms chronologically from initial tests on the species.

Species	n	Hearing range (kHz)	Best sensitivity (kHz)	Method	Reference
<i>T. truncatus</i>	1	0.75 - 150	7 - 130	behavior	Johnson, 1966; 1967
	42	10 - 150	10 - 80 <sup>†</sup>	physiology	Houser and Finneran, 2006
<i>P. phocoena</i>	1	1 - 150	2 - 140	behavior	Andersen, 1970
	1	0.250 - 180	4 - 150	behavior	Kastelein <i>et al.</i> , 2002
<i>O. orca</i>	1	0.5 - 31	5 - 30	behavior	Hall and Johnson, 1972
	2	4 - 100	12 - 52	behavior	Szymanski <i>et al.</i> , 1999
	same <sup>#</sup>	1 - 100	16 - 45	physiology	Szymanski <i>et al.</i> , 1999
<i>I. geoffrensis</i>	1	1 - 105	10 - 50	behavior	Jacobs and Hall, 1972
<i>D. leucas</i>	2	1 - 130	15 - 110	behavior	White, <i>et al.</i> , 1978
	4	0.125 - 8*	4 - 8	behavior	Awbrey, <i>et al.</i> , 1988
	1	8 - 128	27 - 107	physiology	Klishin, <i>et al.</i> , 2000
	2	2 - 130	14 - 90	behavior	Finneran <i>et al.</i> , 2005
	1	8 - 128	22 - 90	physiology	Mooney, <i>et al.</i> , 2008
<i>T. truncatus gilli</i>	1	2 - 135	25 - 110	behavior	Ljungblad, <i>et al.</i> , 1982
	13	10 - 150	20 - 130 <sup>†</sup>	physiology	Houser, <i>et al.</i> , 2008
<i>P. crassidens</i>	1	2 - 115	16 - 64	behavior	Thomas, <i>et al.</i> , 1988
	1	4 - 45	7 - 27	behavior	Yuen, <i>et al.</i> , 2005
	same <sup>#</sup>	4 - 45	6.7 - 27	physiology	Yuen, <i>et al.</i> , 2005
<i>L. vexillifer</i>	1	1 - 200	10 - 65	behavior	Wang, <i>et al.</i> , 1992
<i>G. griseus</i>	1	1.6 - 110	4 - 80	behavior	Nachtigall, <i>et al.</i> , 1995
	1	4 - 150	8 - 108	physiology	Nachtigall, <i>et al.</i> , 2005
<i>S. fluviatilis guianensis</i>	1	4 - 135	16 - 105	behavior	Sauerland and Dehnhardt, 1998
<i>S. coeruleoalba</i>	1	32 - 120	0.5 - 160	behavior	Kastelein <i>et al.</i> , 2003
<i>N. phocanoides</i>	2	8 - 152	32 - 139	physiology	Popov, <i>et al.</i> , 2005
<i>M. europaeus</i>	1	10 - 80	40 - 80	physiology	Cook <i>et al.</i> , 2006
	1	20 - 90	20 - 80	physiology	Finneran <i>et al.</i> , 2009
<i>L. albirostris</i>	2	16 - 181	32 - 128	physiology	Nachtigall, <i>et al.</i> , 2008
<i>G. melas</i>	1	22.5 - 50	4 - 100	physiology	Pacini, <i>et al.</i> , 2010

<i>S. bredanensis</i>	14	10 -120	unclear	physiology	Mann <i>et al.</i> , 2010
<i>M. densirostris</i>	1	5.6 - 160	40 - 50	physiology	Pacini, <i>et al.</i> , 2011
<i>F. attenuata</i>	2	5 - 120	20 - 60	physiology	Montie, <i>et al.</i> , 2011

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\*did not establish upper limit

#same animal tested

†greatly varied depending on sex and age

Noted: Bullock et al., 1968 published hearing ranges and relative responses, but not calibrated audiograms

Figure 1.

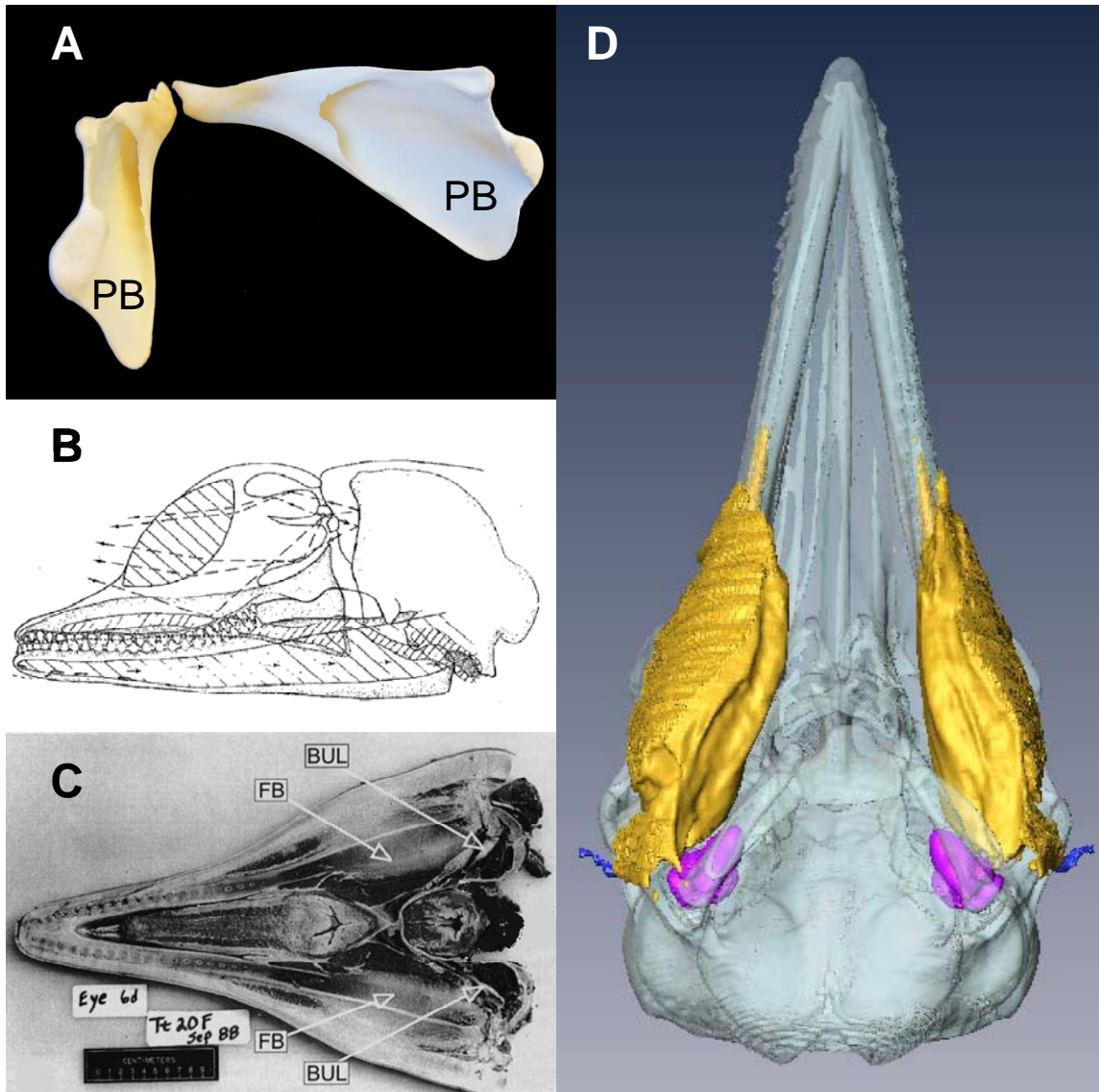




Figure 2.

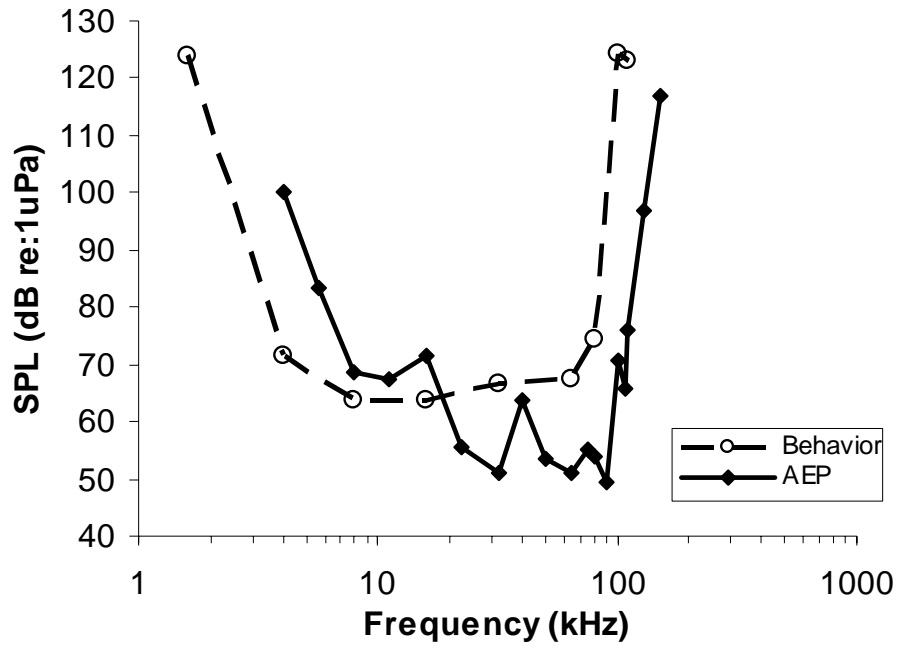


Figure 3.

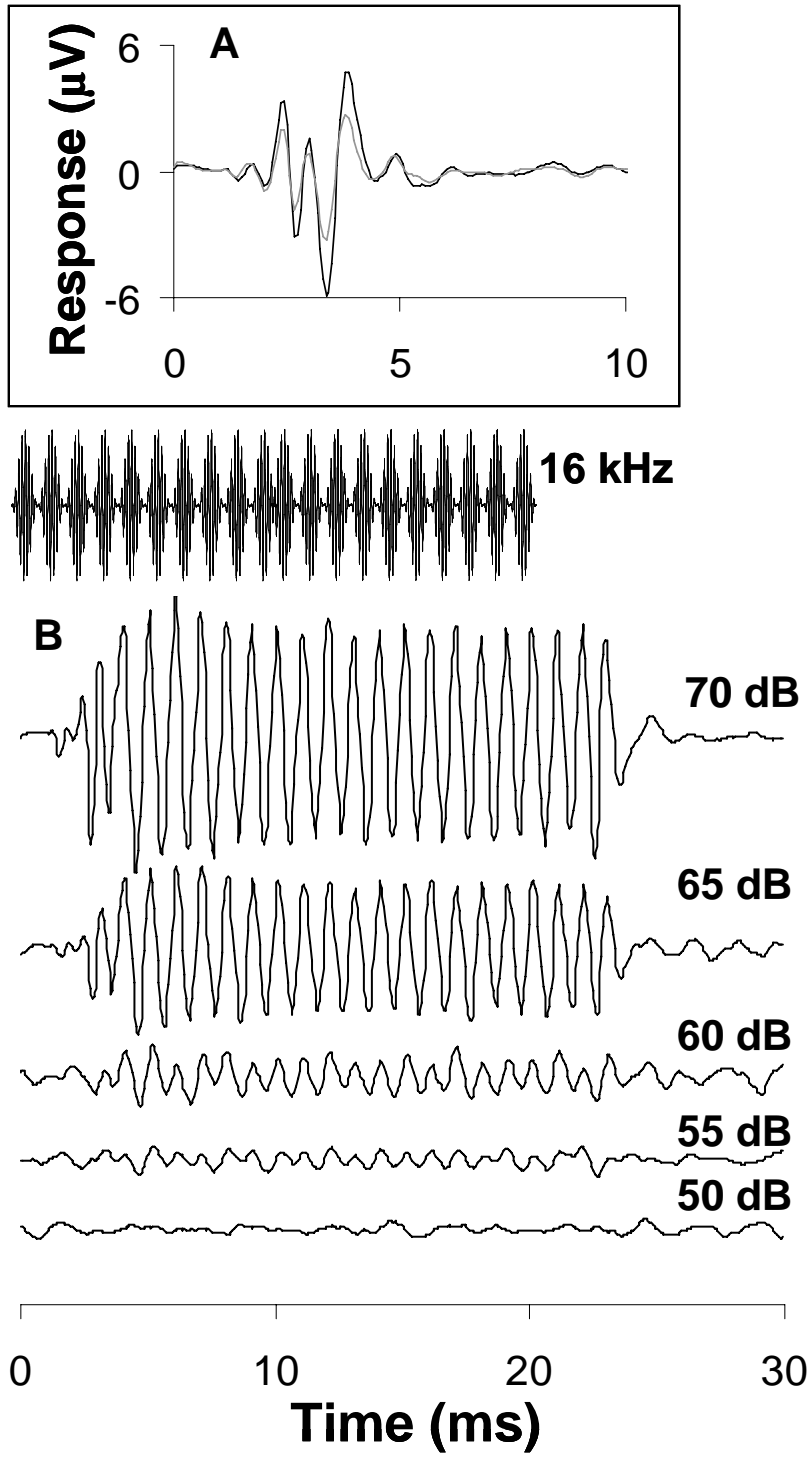


Figure 4.

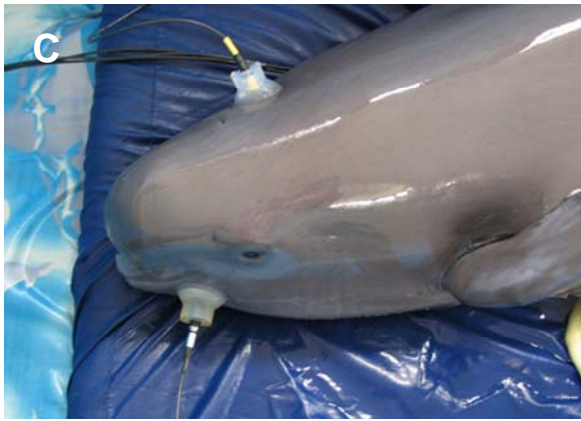
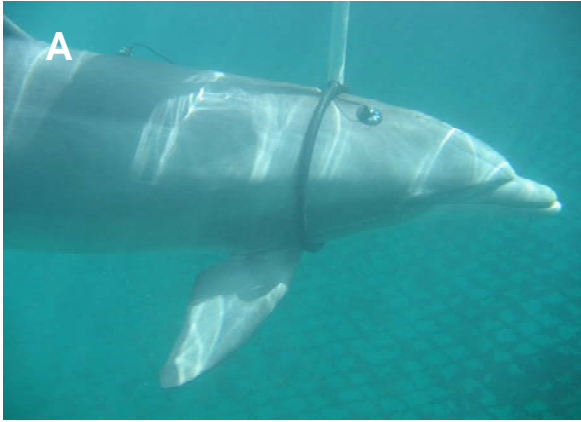


Figure 5.

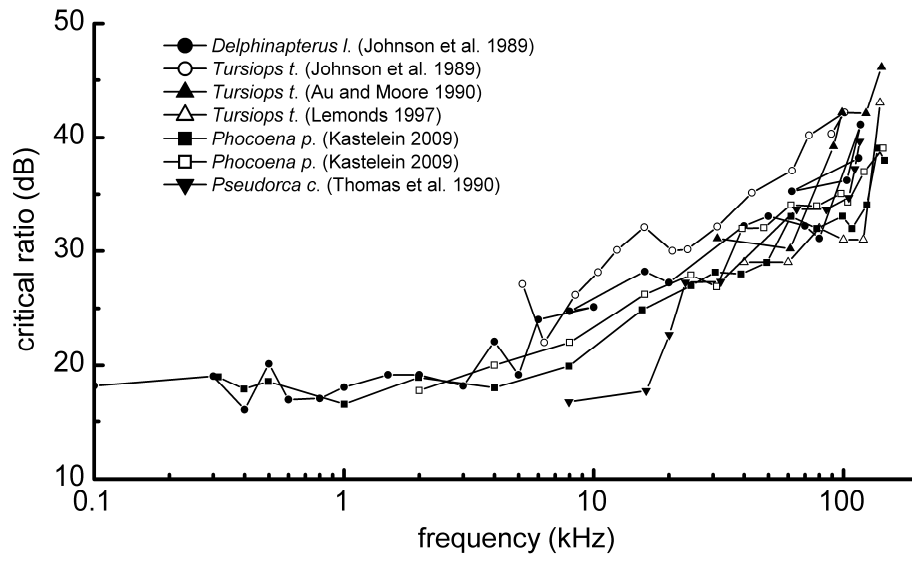


Figure 6.

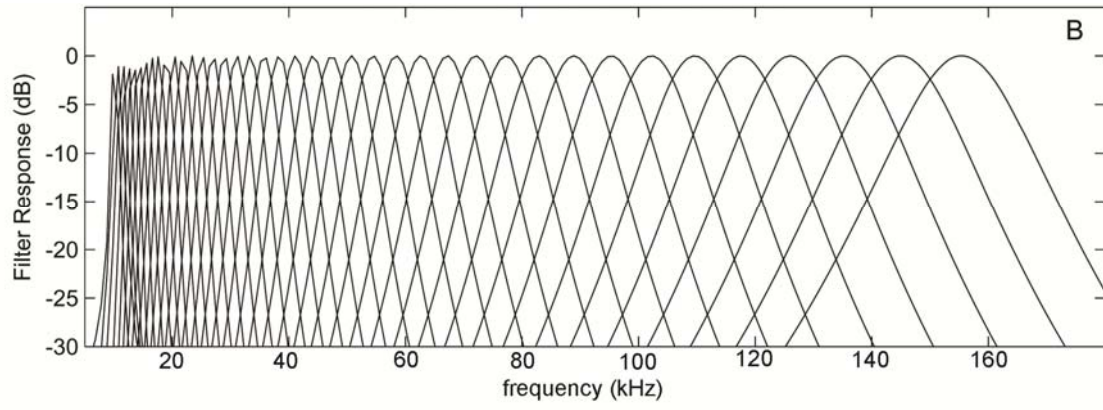


Figure 7.

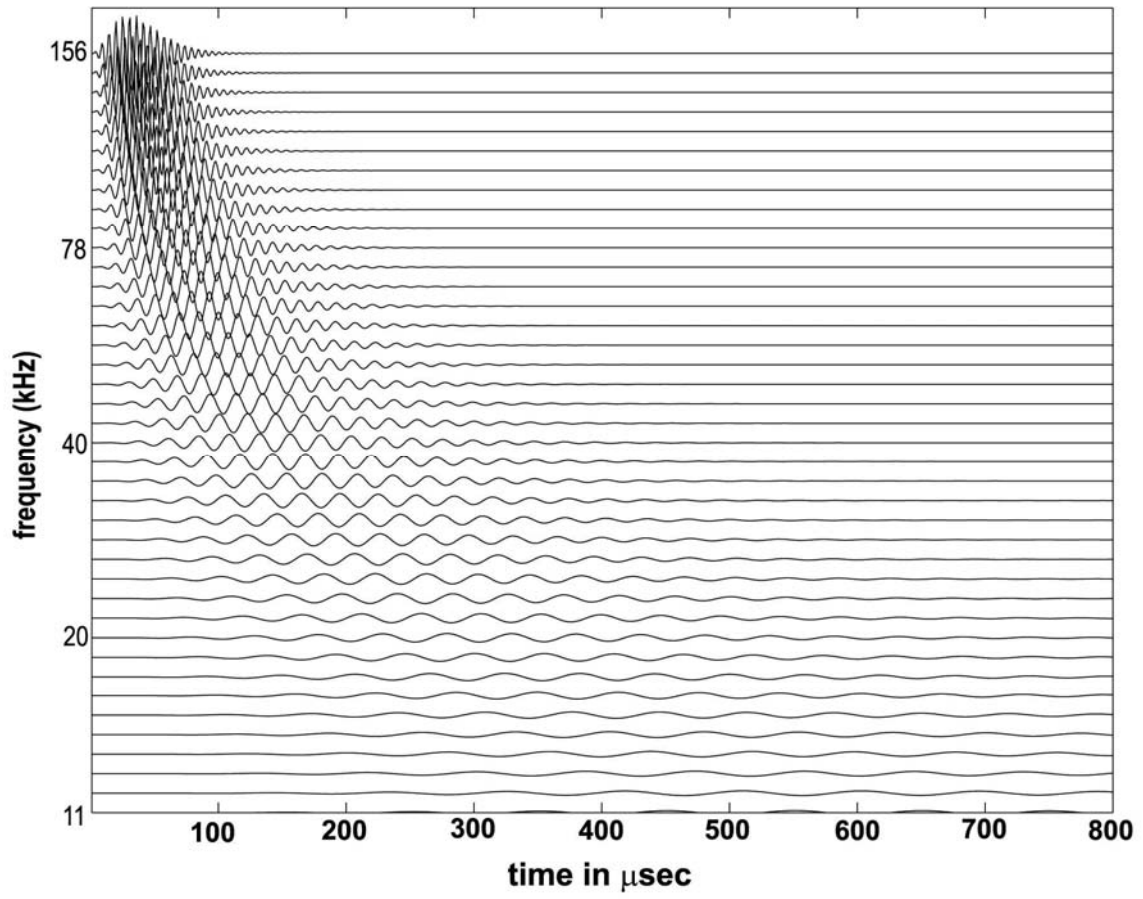


Figure 8.

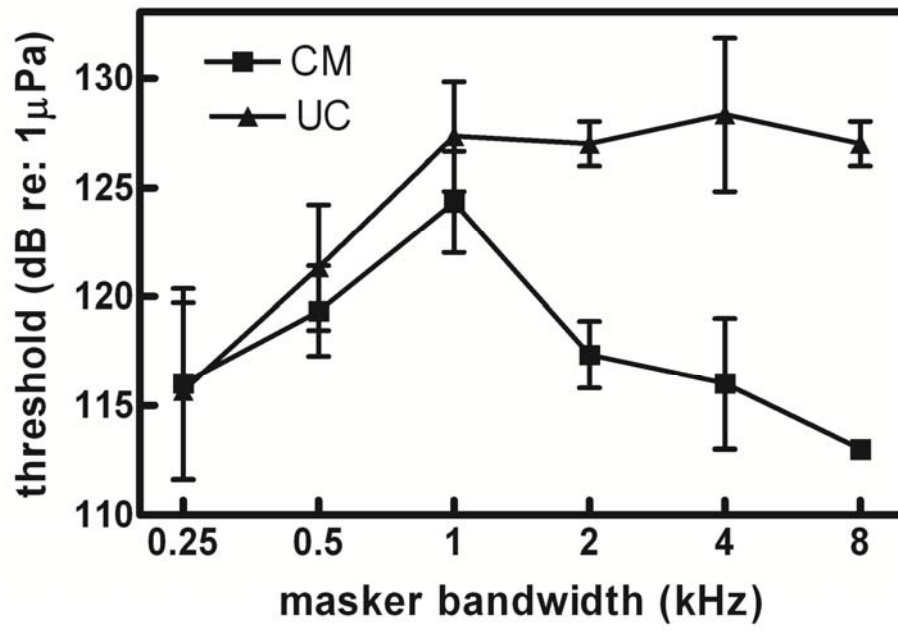


Figure 9.

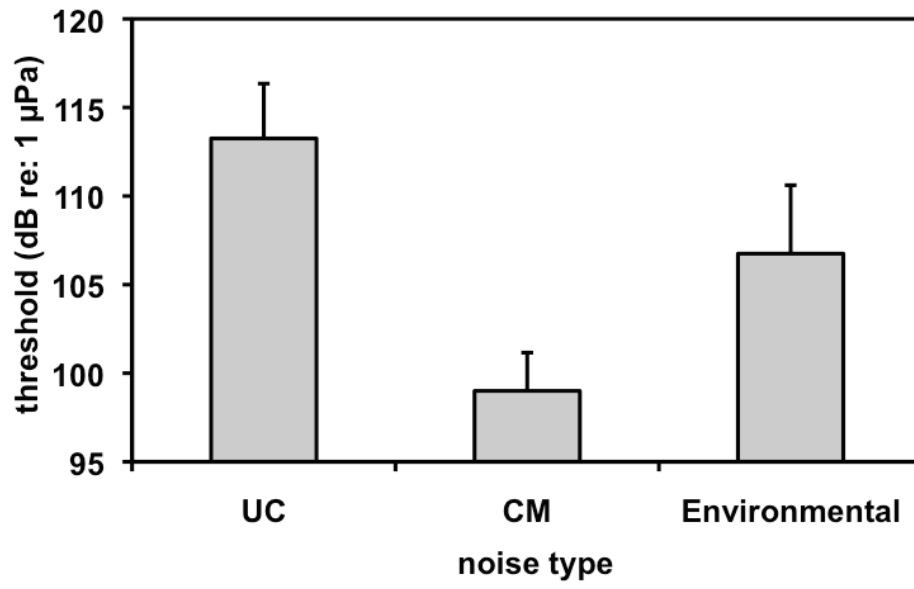




Figure 10.

