CHARACTERISTICS OF HEARING AND ECHOLOCATION IN UNDER-STUDIED ODONTOCETE SPECIES

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ABSTRACT

All odontoctes (toothed whales and dolphins) studied to date have been shown to echolocate. They use sound as their primary means for foraging, navigation, and communication with conspecifics and are thus considered acoustic specialists. However, the vast majority of what is known about odontocete acoustic systems comes from only a handful of the 76 recognized extant species. The research presented in this dissertation investigated basic characteristics of odontocete hearing and echolocation, including auditory temporal resolution, auditory pathways, directional hearing, and transmission beam characteristics, in individuals of five different odontocete species that are understudied. Modulation rate transfer functions were measured from formerly stranded individuals of four different species (*Stenella longirostris, Feresa attenuata, Globicephala melas, Mesoplodon* densirostris) using non-invasive auditory evoked potential methods. All individuals showed acute auditory temporal resolution that was comparable to other studied odontocete species. Using the same electrophysiological methods, auditory pathways and directional hearing were investigated in a Risso's dolphin (*Grampus griseus*) using both localized and far-field acoustic stimuli. The dolphin's hearing showed significant, frequency dependent asymmetry to localized sound presented on the right and left sides of its head. The dolphin also showed acute, but mostly symmetrical, directional auditory sensitivity to sounds presented in the far-field. Furthermore, characteristics of the echolocation transmission beam of this same individual Risso's dolphin were measured using a 16 element hydrophone array. The dolphin exhibited both single and dual lobed beam shapes that were more directional than similar measurements from a bottlenose dolphin, harbor porpoise, and false killer whale.

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CHAPTER 1

INTRODUCTION

1.1 General evolutionary history of cetaceans

The term "marine mammals" is a broad categorization used to describe a polyphyletic group of mammals that have evolved amphibious or obligate aquatic lives. The term generally refers to five primary groups, including the suborder Mysticeti (baleen whales), Odontoceti (toothed whales and dolphins), order Sirenia (manatees and dugongs), suborder Pinnipedia (seals, sea lions, walruses) and polar bears (*Ursus maritimus*). The former three groups have evolved to be completely dependent on an aquatic environment for survival, whereas the latter groups are amphibious and lead only partially aquatic lifestyles. Odontocetes, together with Mysticetes, are suborders that form the order *Cetacea*, or cetacean marine mammals.

Modern cetaceans evolved from a group of primitive whales called Archaeocetes that lived between 55-33 million years ago. Archaeocetes first diversified in near-tropical shallow waters around 45-53 million years ago and spread into temperate waters around 40 million years ago. In the five identified archaeocete families (Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae; Williams 1998), the ancestral transition from animals that are amphibious to those that are fully aquatic is evident in their body forms. Earlier archeocetes exhibit four strong external limbs and narrow tails, while later archeocetes begin to show shorter limbs, often significantly reduced hind limbs, and stronger tails with flattened vertebra (Fordyce and Barnes 1994). Additionally, the skull began to el0ngate and the nostrils begins to migrate dorso-caudally along the top of the skull in a process known as telescoping (Rommel et al. 2009) At this time, the radiation of these animals included shifts from riverine and near shore environments to fully oceanic habitats. It is believed that this initial radiation was influenced primarily by local marine productivity (Gingerich 2005) and possibly the need for protection (Thewissen et al. 2007). A second major radiation occurred 37 to 27 million years ago involving the fully aquatic Neoceti, or the crown group Cetacea. It is during this radiation that filter feeding arose in mysticete cetaceans with the progressive evolution of baleen (Fordyce and Barnes 1994) and echolocation arose in odontocetes. These feeding strategies have not been documented in the preceding archaeocetes. Around the same time, the ancient supercontinent of Gondwana was breaking up, the Southern Ocean was opening, and there was an increased temperature gradient forming from the tropic to polar regions, suggesting that the radiation of cetaceans and the evolution of echolocation and filter-feeding strategies arose as a response to new ecological opportunities (Thewissen and Hussain 1998; Lindberg and Pyenson 2007; Berger 2007). A third major radiation approximately 10 to 12 million years ago brought about the existence of "modern" mysticetes and odontocetes. The extant suborder Mysticeti is comprised of four families, encompassing 14 currently identified species. In contrast, the extant suborder Odontoceti is more diverse, comprised of 10 families and at least 76 identified species across three primary clades (Bannister 2009; Fordyce 2009; Hooker 2009; Committee on taxonomy 2014)

While most terrestrial mammals and, likely, cetacean terrestrial ancestors, utilize olfaction and vision as their primary sensory modalities, light attenuates very quickly in water and airborne odors are likely irrelevant to an animal that lives and feeds underwater. In contrast, the increased density of water causes sound to travel more quickly and to attenuate less than sounds traveling through air (Urick 1983). As cetacean ancestors adapted to obligate aquatic lives to exploit marine resources, the utilization of visual and olfactory sensory systems became less essential, while exploitation of the favorable acoustic properties of water became more advantageous. Thus, cetaceans have evolved to be acoustic specialists. This is particularly evident in odontocetes, the only marine mammal group that possess the capability to echolocate, which they use as their primary mean for foraging, orientation, and navigation. As a result, odontocetes have undergone the most extensive adaptation to exploit the favorable properties of acoustic transmission in water and are the focus of this dissertation.

1.2 Odontocete hearing

Odontocetes exhibit a range of auditory adaptations to accommodate acoustic signal reception in water, which places different constraints due to increased pressure and sound speed of water over air. To better illustrate the adaptive changes that the odontocete auditory system has undergone in relation to terrestrial mammals, a basic review of the typical process of hearing in terrestrial mammals is useful. A commonly used definition of "hearing" is given by Wever (1976) as "...the response of an animal to sound vibrations by means of a special organ for which such vibrations are the most effective stimulus." In a typical terrestrial mammal, pressure changes in air are funneled via external auditory pinnae into the outer ear canal and vibrate the tympanic membrane. In turn, tympanic vibrations cause coupled vibrations of the middle ear bones (maleus, incus, and stapes), which vibrate the oval window at the base of the fluid filled inner ear. The resulting vibrations in the fluid of the inner ear cause deformations and vibrations along the basilar membrane inside the cochlea, which cause inner hair cells to fire at specific locations, generating a electric nerve potential that propagates along the auditory nerve (also called the VIII nerve) and the auditory centers of the brain where the nerve potentials are processed and perceived by the animal.

While much of this hearing process is conserved in odontocetes, they exhibit extensive differentiating adaptations for hearing in water which are most evident in their gross anatomy (Ketten 1992). All parts of the outer, middle, and inner odontocete ear have undergone modification. External pinnae are absent in odontocetes. The outer ear canal, also called the auditory meatus, is filled in with cellular debris and dense cerumen and ends in a blind caecum that is not connected with the tympanic membrane or ossicles. The cetacean ear is comprised of two connected bony bulla that together form the tympano-periodic complex and house the middle and inner ears. In odontocetes, the tympano-periodic complex is attached to the outside of the skull with suspensory ligaments. No bony connections to the skull are present, in contrast to other mammals. Together with the thickening of the skull as a result of telescoping, the lack of bony connection between the inner ear and skull renders the odontocete inner ear isolated from the possibility of sound reception via bone conduction and limits the number of pathways via which sound can enter into the auditory bulla (McCormick et al. 1970; Oelschläger 1986). While odontocetes possess three middle ear ossicles similar to land based mammals, little is known about whether or not they function in the same manner as terrestrials mammals. Odontocete ossicles are complex, very dense, and likely stiff (Nummela et al. 1999b). Instead of being connected to the tympanic membrane, the malleus is connected via a bony ridge to the thin lateral wall of the bony tympanic bulla. It is hypothesized that this thin bony wall serves an analogous function to the tympanic membrane in terrestrial mammals (Hemilä et al. 1999; Nummela et al. 1999a). The inner ear, housed in the periodic bulla, consists of the greatly reduced vestibular system and cochlea which is arranged in the same fundamental way as all mammalian inner ears. Yet, all elements of the organ of Corti (the organ of hearing) are larger and more densely packed than other mammals. The ratio of inner hair cells to spiral ganglion cells (the supporting cells that connect the hair cells to the auditory nerve) is greatly increased in odontocetes versus humans. The fibers of the auditory, or VIII, nerve, show increased thickness and are more numerous than in most terrestrial mammals (Ketten 2000). Finally, odontocete brains show hypertrophy of the auditory areas which is largely responsible for their generally increased brain size (Oelschlager and Kemp, 1998).

Coinciding with changes to the gross anatomy of the hearing apparatus, the pathway by which sounds travel to the odontocete inner ear differ from terrestrial animals as well. First proposed by Norris (1968), it is a widely accepted hypothesis that fat pads found in the lower jaw of odontocetes act as an acoustic window for channeling sound to the inner ear. Since then, multiple studies have provided supporting evidence for the mandibular hearing hypothesis (e.g. Bullock et al. 1968; McCormick et al. 1970, 1980; Norris and Harvey 1974; Brill et al. 1988; Brill and Harder 1991; Møhl et al. 1999; Nachtigall et al. 2008). Evidence has also been found for additional, frequency dependent pathways around the auditory meatus (Popov et al. 2008) and gullar region along the ventral neck (Cranford et al. 2008; Mooney et al. 2015; Popov et al. 2016), leading to a hypothesis for multichannel sound reception in odontocetes (Popov and Supin 1990b; Popov et al. 1992a, 2008, Ketten 1994, 2000)

In addition to anatomical adaptation for sound reception in water, odontocetes also exhibit acute mechanistic and perceptual auditory capabilities. These include auditory sensitivity across a broad range of frequencies, high auditory temporal resolution, keen sensitivity to inter-aural time and intensity differences, and the ability to localize small spatial differences in sound source locations. Audiograms have been measured from 17 species of odontocete, which generally exhibit functional sensitivity from low frequencies of below 1 kHz to above 150 kHz in some species (Johnson 1966; Pacini and Nachtigall 2016), giving them the broadest hearing range of any mammalian group (Ketten 1992). The auditory temporal resolution has be described in 9 species thus far, which all have shown the ability to follow acoustic stimuli that are temporally modulated at rates of up to and exceeding 1500 Hz in some species (e.g. Mooney et al. 2011; Linnenschmidt et al. 2013). Odontocetes also have also been shown to be able to discriminate differences in the location of a sound source as small as 2.1° when listening to pure tone acoustic signals (Renaud and Popper 1975). When listening to a sound source that produced broadband clicks, the bottlenose dolphin showed an even more impressive ability to discriminate differences in the source location as small as 0.7º and 0.9º in the vertical and horizontal planes, respectively (Renaud and Popper 1975). It is still not well understood how odontocetes accomplish this feat. Experiments have revealed that a bottlenose dolphin is capable of discriminating inter-aural time and intensity difference thresholds below 7 µs and 1 dB, respectively (Moore et al. 1995), suggesting that binaural cues are utilized in a similar manner to many terrestrial mammal species (Supin and Popov 1993; Moore et al. 1995).

1.3 Odontocete echolocation

The previously described auditory adaptations all play key roles in allowing odontocetes to successfully use echolocation extensively in their aquatic environment for forging, spatial orientation and navigation. All odontocetes studied to date have been shown to echolocate. While the ability has not been demonstrated empirically in all species, pulsed, echolocation-like signals have been recorded from the vast majority of species in the wild. It is generally accepted that all species have the capability to echolocate. Odontocete echolocation clicks that have been observed fall into three general categories: short broadband high-frequency (BBHF) clicks, narrowband high-frequency (NBHF) clicks, and frequency modulated (FM) upsweeps (Fenton et al. 2014). Although broadband, the echolocation clicks of sperm whales are concentrated at much lower frequencies than other odontocetes (Goold and Jones 1995; Møhl et al. 2000) and thus do not fall into any of the three general categories. NBHF clicks are produced by a limited number of smaller odontocete species such as the harbor porpoise (*Phocoena phocoena*), Commerson's dolphin (*Cephalorhynchus commersonii*), Hector's dolphin (*Cephalorhynchus hectori*), Dall's porpoise (*Phocoenoides dalli*), and pygmy sperm whale (*Kogia breviceps*). Beaked whales are the only odontocetes known to produce FM clicks, which has been documented in eight different beaked whale species (Baumann-Pickering et al. 2013). The majority of odontocete species produce BBHF clicks.

Echolocation in odontocetes requires highly specialized features for the production and transmission of acoustic signals. Typical odontocete echolocation signals are short, ultrasonic sounds generated with specialized tissues located within the enlarged nasal complex (Ridgway et al. 1980; Mackay and Liaw 1981; Cranford 1992; Cranford et al. 1996; Aroyan et al. 2000). The produced click is directed out the front of the melon in a directional beam. Multiple structures in the head are responsible for creating this high directivity. Directly posterior to the sound generators in the odonotocete head are air sacs overlaying the concave skull (Cranford et al. 1996). These sacs act as acoustic reflectors for the generated sounds and redirect acoustic energy anteriorly towards the melon (Aroyan et al. 1992). The composition and layering of acoustic fats within the melon further collimate the sound towards the anterior forehead and also act as an impedance matching device for sound traveling into the water (Norris and Harvey 1974; Litchfield and Greenberg 1974). Furthermore, the melon is surrounded by a collection of muscles and tendons (Mead 1975; Heyning 1989; Cranford et al. 1996; Huggenberger et al. 2009), which have been suggested to have the ability to change the directional properties of the emitted sonar beam (Kloepper et al. 2012a; Cranford et al. 2014; Jensen et al. 2015).

The echolocation systems of all species studied to date show acute capabilities for acoustically detecting and discriminating between different targets. Target detection is of the most basic and important capability for a biosonar system. Experiments with trained bottlenose dolphins (*Tursiops truncatus*) and a false killer whale (*Pseudorca crassidens*) in Kaneohe Bay, Hawaii, have shown that these species are capable of detecting small metal spheres up to at least 113 meters away (Au and Snyder 1980; Murchison 1980; Thomas and Turl 1980). Bottlenose dolphins are able to detect targets in the presence of acoustic reverberation (Titov 1972; Murchison 1980; Au and Turl 1983; Turl 1991). This capability is also evident in wild bottlenose dolphins and Atlantic spotted dolphins (*Stenella frontalis*), which have been observed to use echolocation to detect prey buried in the sand of the sea floor (Herzing 1996; Rossbach and Herzing 1997). Additionally, experiments with captive animals have shown that multiple odontocete species are capable of numerous levels of discrimination between different targets, including targets at different ranges (Murchison 1980), targets of different material composition (Evans and Powell 1967; Evans 1973; Au and Hammer Jr 1980; Schusterman et al. 1980; Turl et al. 1991), targets of different shapes (Bagdonas et al. 1970; Nachtigall et al. 1980), and cylindrical targets of different wall thickness (Titov 1972; Au and Pawloski 1992).

1.4 Rationale and research goals

The vast majority of what is known about the hearing and echolocation capabilities of odontocetes comes from a limited number of species: the bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*), harbor porpoise (*Phocoena phocoena*), and beluga (*Delphinapterus leucas*). This is largely due to the fact that such research requires the cooperation of trained individuals in a captive experimental setting, and these species are the most common odontocetes found in captivity around the world. Aspects of hearing and echolocation in additional species have increasingly been collected opportunistically from individuals that have stranded and been rehabilitated, often representing species for which little to no data exist. While such research has revealed that there are many similarities between the acoustic systems of odontocetes in general, there are likewise differences in both sound reception and transmission between species. However, due to the low sample size of individuals and species studied, it is difficult to connect these differences to any specific attribute of the animal's biology such as echolocation signal characteristics, head morphology, or differences in ecology.

Links between acoustic systems and anatomy are essential for understanding the evolutionary processes that shaped these systems (Stebbins and Sommers 1992) and can elucidate ecological factors that influenced the morphology of acoustic structures (Branstetter and Mercado III 2006). Comparative analysis of functional morphology and acoustic systems of echolocating bat species has provided a wealth of knowledge concerning the evolution of echolocation in bats and the selection pressures that shaped it (Bruns et al. 1989; Obrist et al. 1993; Fuzessery 1996; Bogdanowicz et al. 1999; Fenton and Bogdanowicz 2002; Huihua et al. 2003; Jones and Teeling 2006; Jones and Holderied 2007). Conversely, in-depth comparative analysis of acoustic systems in odontocetes is difficult due to the limited number of species and individuals studied. Analysis of unique structures and acoustic systems in previously undescribed species is essential for more powerful comparative analysis.

The goal of the following dissertation research was to opportunistically describe basic characteristics of the hearing and echolocation systems in odontocete species that have been little studied to date and that exhibit a broad range of acoustic, morphological, and ecological characteristics. Specifically, this research aimed to:

1) describe the auditory temporal resolution of four different stranded odontocete species.
2) describe characteristics of acoustic reception and directional hearing in a Risso's dolphin (*Grampus griseus*)
3) describe the spatial transmission beam characteristics of a Risso's dolphin.

1.5 General overview of study species

A. Risso's dolphin (Grampus griseus)

The Risso's dolphin is a medium sized delphinid that is found along deep ocean canyons and continental shelves in both temperate and tropical water (Leatherwood et al. 1980). They usually travel in pods of up to 50 individuals and are often seen interacting with other cetacean species. Information on the life history and reproductive behavior for this species is relatively limited. Individuals are thought to become sexually mature between 8 and 12 years of age, and adults can live to be at least up to 35 years old (Amano and Miyazaki 2004). Analyses of stomach contents from stranded individuals suggest these animals feed primarily on oceanic and neritic squid (Clarke and Pascoe 1985; Cockcroft et al. 1993; Blanco et al. 2006), which are found at depths of 600-800 m (Quetglas et al. 2000). This indicates that Risso's dolphins are deep divers capable of foraging at those depths, although no study on diving behavior has yet been done. A unique morphological feature common to all individual *Grampus* is a visually clear bifurcation in the anterior face of the melon (Leatherwood et al. 1983). This anatomical feature is not present in any other odontocete species, and its function is unknown. The hearing and echolocation systems of *G. griseus* remain little studied in controlled experimental settings compared to other species such as the bottlenose dolphin, beluga whale, false killer whale, and harbor porpoise. Audiograms (Nachtigall et al. 1995, 2005), auditory temporal resolution (Mooney et al. 2006), and hearing pathways (Mooney et al. 2015) have been investigated in a few individuals.

B. Spinner dolphin (Stenella longirostris)

Spinner dolphins (*Stenella longirostris*) are small delphinid odontocetes that are generally found in pantropical, pelagic waters, in large pods that can exceed 1000 individuals (Perrin et al. 2005). Adults reach up to 2.35 m in length, and are generally characterized by dark to lighter shades of grey on the dorsal and ventral sides, respectively, which fade to a white ventral surface (Perrin 2009). They possess a notably long and slender beak that leads to a sloping melon that only slightly protrudes on the forehead, similar in form to common bottlenose dolphins. Their common name derives from their common acrobatic jumping behavior wherein an animal can spin multiple times in quick succession, although the function of this spinning behavior is not fully understood. This species exhibits predictable behavioral patterns by cooperatively feeding at night on small individual mesopelagic prey in open ocean water (Fitch and Brownell Jr. 1968; Norris and Dohl 1980; Perrin et al. 1999) and then resting in shallow, sheltered bays during the daytime (Norris and Dohl 1980). Despite the fact that they are found around in the world in all tropical and subtropical waters and also commonly encountered in the wild by humans, little is known about their hearing and echolocation systems. Audiograms have been collected from two stranded individuals (Pacini et al. 2016). Echolocation characteristics and behavior have also been documented from field recordings with free ranging animals (Lammers et al. 2004a; Schotten et al. 2004)

C. Pygmy killer whale (Feresa attenuata)

The pygmy killer whale (*Feresa attenuata*) is a delphinid odontocete that has been recorded in both tropical and subtropical waters throughout the world. In physical appearance, they are a medium to small sized, reaching average adult lengths of 2.31 m, with a dark grey to black skin coloration. They lack a protruding beak commonly found in dolphins (Donahue and Perryman 2009). While no studies have been conducted on feeding behavior, analysis of stomach contents from stranded individuals and fisheries-bycatch indicate small squid and fish consist of at least part of their diet (Mignucci-Giannoni et al. 2000). Echolocation signals have been recorded from some free-ranging individuals in the wild (Madsen et al. 2004a), and the audiogram has been measured in two individuals (Montie et al. 2011). In general, much of their biology and behavior is unknown, and they are one of the least studied small cetacean species.

D. Long-finned pilot whale (Globicephala melas)

The long-finned pilot whale is one of two existing pilot whale species, the other being the short-finned pilot whale (*Globicephala macrorhynchus*). Pilot whales are medium sized odontocetes that can reach up to 6 meters in length. Generally black in color, they possess a very small or indiscernible beak as well as a large, bulbous melon. These animals are deep-diving odontocetes (Baird et al. 2002; Heide-Jorgensen et al. 2002) that are found in both pelagic and nearshore waters in tropical, subtropical, and temperate environments, depending on the species. *G. melas* generally inhabit cold temperate waters of the North Atlantic and Southern Ocean. Consistent with their deep-diving behavior, pilot whales feed primarily on oceanic squid, and to a lesser extent, fish (Gannon et al. 1997). Behaviorally, they are a social species, occurring in pods of between 20-90 individuals in size and are often seen interacting with other species in mixed aggregations (Olson 2009). Only a single audiogram has been described for *G. melas* (Pacini et al. 2010), and echolocation clicks have been described from recordings of free-ranging individuals (Eskesen et al. 2011).

E. Blainville's beaked whale (Mesoplodon densirostris)

Beaked whales are a cryptic group of deep-diving pelagic odontocetes belonging to the family Ziphiidae. Due to their deep diving behavior, they spend only short amounts of time at the surface to breathe. Thus it is very difficult to locate and collect data on their behavior. Although increased effort has been undertaken in recent years to better understand the biology, behavior, and distribution of these animals (Cox et al. 2006), relatively little is known about the 22 species of beaked whale, including Blainville's beaked whale.

In general, beaked whales are documented deep divers, capable of diving down to depths exceeding 2000 meters to search for prey (Johnson et al. 2004; Zimmer et al. 2005; Tyack et al. 2006; Arranz et al. 2011) which consists primarily of squid and some fish species (Ohizumi et al. 2003). In appearance, they are medium to large sized odontocetes, with individuals ranging in size from 3 to 13 meters in length depending on the species. They exhibit pronounced rostrums that blend smoothly into an unpronounced melon. The echolocation behavior of multiple species has been documented using suction cup archival tags and passive acoustic monitoring (Johnson et al. 2004, 2006; Zimmer et al. 2005; Arranz et al. 2011; Aguilar de Soto et al. 2012). They exhibit elements of stereotyped echolocation behavior while foraging, which includes a silent decent down to around 300 m, a search phase during continued descent where the emit regular clicks, and a quiet ascent phase (Johnson et al. 2004).

Recordings from tagged individuals reveal that Blainville's beaked whales (*Mesoplodon densirostris*) produce both frequency modulated and non-frequency modulated echolocation signals (Johnson et al. 2006). Audiograms have also been collected from one individual of this particular species (Pacini et al. 2011), as well as individuals of one other beaked whale species, the Gervais beaked whale (*Mesoplodon europeus;* Cook et al. 2006; Finneran et al. 2009).

CHAPTER 2

MODULATION RATE TRANSFER FUNCTIONS IN FOUR SPECIES OF STRANDED ODONTOCETE: THE SPINNER DOLPHIN (*STENELLA LONGIROSTRIS*), PYGMY KILLER WHALE (*FERESA ATTENUATA*), LONG-FINNED PILOT WHALE (G*LOBICEPHALA MELAS*), AND BLAINVILLE'S BEAKED WHALE (*MESOPLODON DENSIROSTRIS*).

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2.1 Abstract

Odontocete marine mammals explore the environment by rapidly producing echolocation signals and listening for the corresponding echoes which likewise return at very rapid rates. Temporal characteristics of the echoes provide important information that is processed by the odontocete auditory system, thus it is important that the auditory system have a high temporal resolution to effectively process and extract relevant information from such rapid acoustic signals. Although auditory temporal resolution has only been measured for a small number of odontocete species, all species studied so far show the ability to follow acoustic stimuli modulated at very high frequencies. Using auditory evoked potential methodology, this study measured the modulation rate transfer functions of individuals from four different odontocete species that had previously stranded and been rehabilitated. Similar to other studied species, the individuals all showed the ability to process acoustic stimuli at modulation rates up to or exceeding 1250 Hz, supporting the hypothesis that high temporal resolution is conserved throughout the diverse range of odontocete species. Comparison of the MRTFs between odontocetes of different echolocation characteristics suggests that auditory temporal resolution is not related to echolocation signal type.

2.2 Introduction

Odontocetes (toothed whales and dolphins) possess highly developed echolocation systems, which require both the effective production of echolocation clicks and also the reception of click echoes. Echolocation clicks are short duration acoustic signals that are produced at variable rates depending on the distance between the dolphin and an echolocation target (e.g. Au 1993; Au and Benoit-Bird 2003). Inter-click intervals can be as low as 1.5-3 ms, corresponding to click rates in some species as high as 300 to above 400 clicks per second (e.g. Lammers et al. 2004; Madsen et al. 2004; Verfuß et al. 2009), which are often associated with the final moments of prey capture. Echoes during such click trains can likewise return to the animal at similarly high rates. Temporal and spectral characteristics of target echoes contain important information about the target that are processed by the odontocete auditory system (Bullock et al. 1968; Au et al. 1988; Au 1993). Thus, it is important that the auditory system have a high temporal resolution to effectively process and extract relevant information from such rapid acoustic signals.

Auditory evoked potentials (AEPs) have been increasingly used to investigate many aspects of the odontocete auditory system, including directional hearing (e.g. Popov and Supin 1988, 1990, 2009, Popov et al. 1992, 2006), hearing pathways (e.g. Mohl et al. 1999; Mooney et al. 2008, 2014, 2015; Popov et al. 2016), audiograms (e.g. Nachtigall et al. 2005, 2007; Yuen et al. 2005; Cook et al. 2006; Finneran et al. 2009), binaural hearing cues (Popov and Supin 1991), and temporal resolution (Supin and Popov 1995a, b; Dolphin et al. 1995; Mooney et al. 2006). Use of AEP methodology is advantageous by allowing research with subjects that have little behavioral training and has proven valuable for measuring auditory characteristics of previously unstudied odontocete species from the wild that have stranded or been rehabilitated (Nachtigall et al. 2005, 2007; Cook et al. 2006; Finneran et al. 2009; Mann et al. 2010; Pacini et al. 2010, 2011, 2016; Schlundt et al. 2011; Montie et al. 2011; Greenhow et al. 2014). When trains of short, tone pip stimuli are presented to a test subject, the individual AEPs generated in response to the stimulus train merge together into a steady state wave called a envelope following response, or EFR. If the stimulus train consists of broadband clicks, the steady state evoked response is called a rate following response, or RFR (Supin et al. 2001). The magnitude of these following responses as a function of the stimulus modulation rate is called a Modulation Rate Transfer Function (MRTF). In mammals, including marine mammals, these functions are generally the shape of a low pass filter, with response magnitudes decreasing and eventually ceasing above a certain modulation frequency as the auditory system can no longer follow the rapid changes of the stimulus envelope. The upper limits of modulation rates that elicit EFRs or RFRs have been used as an estimation of the auditory temporal resolution of test subjects (Supin and Popov 1995b; Popov and Supin 1998).

MRTFs have been described for nine species of odontocete so far, including the Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*; Mooney et al. 2011), harbor porpoise (*Phocoena phocoena*; Linnenschmidt et al. 2013), bottlenose dolphin (*Tursiops truncatus*; Supin and Popov 1995b; Dolphin et al. 1995; Finneran et al. 2007), white beaked dolphin (*Lagenorhynchus albirostris*; Mooney et al. 2009), Risso's dolphin (*Grampus griseus*; Mooney et al. 2006), beluga (*Delphinapterus leucas*; Dolphin et al. 1995; Klishin et al. 2000), false killer whale (*Pseudorca* crassidens; Dolphin et al. 1995), Gervais beaked whale (*Mesoplodon europaeus*; Cook et al. 2006; Finneran et al. 2009), and the killer whale (*Orcinus orca*; Szymanski et al. 1998). While there are some intra and inter-specific differences in MRTF characteristics, all species exhibited the ability to follow acoustic stimuli at modulation rates up to or exceeding 1.2 kHz. Odontocetes exhibit an auditory temporal resolution that is many times greater than non-echolocating mammals, both marine and terrestrial (Mulsow and Reichmuth 2007). Similarly high temporal processing abilities have been found in echolocating bats (Wiegrebe and Schmidt 1996), lending support to the hypothesis that such high temporal resolutions are an adaptation for echolocation (Supin and Popov 1995b). However, it is still unclear to what extent temporal processing differs between odontocete species and how such differences may relate to the hearing ranges, peripheral filter bandwidths, or echolocation characteristics. Data on temporal processing in additional odontocete species may prove valuable to uncovering these relationships.

In the current study, auditory evoked potential methodology was used to measure modulation rate transfer functions in four species of stranded odontocete for which no data on temporal resolution has been documented: a Blainville's beaked whale (*Mesoplodon densirostris*), long-finned pilot whale (*Globicephala melas*), pygmy killer whale (*Feresa attenuata*), and spinner dolphin (*Stenella longirostris*).

2.3 Methods

A. Test subjects and facilities

Hearing measurements were recorded from a single individual of four odontocete species (spinner dolphin, pygmy killer whale, pilot whale, beaked whale) which stranded in four separate events from 2006 to 2014. On August 27th, 2006, a neonate male long-finned pilot whale stranded and was rescued from a beach near Nazare, Portugal. The animal was first treated at the Sociedade Portuguesa de Vida Selvagem facility in Quiaios – Figueira da Foz and was then transferred to the Lisbon Zoo in November 2006 for continued treatment. The animal began to eat solid food after approximately a year of rehabilitation, and was subsequently trained to station horizontally at the surface of the water for auditory evoked potential hearing tests. The audiogram was previously measured and showed good hearing up to 64 kHz (Pacini et al. 2010).

An adult male pygmy killer whale was found stranded near Maalaea Harbor, Maui, on May 22, 2009. The animal weighted 285 kg and was 2.1 m in length. After initial veterinary assessment, the animal was determined to be in poor health and exhibited a very low white blood cell count. Auditory evoked potential measurements were conducted at the stranding site as an additional diagnostic test.

A sub-adult male Blainville's beaked whale stranded near Kihei, Maui on the morning of August 16, 2010. Initial diagnostic tests suggested the animal was suffering from severe immune compromise and renal insufficiency. The animal was subsequently transferred to a rehabilitation pool in Hilo, on the Big Island of Hawaii for treatment and rehabilitation. The whale weighed approximately 800 kg and measured 3.5 m in length. To assist in determining the animal's prospects for rehabilitation, auditory evoked potential hearing measurements were selected as an additional diagnostic test. The audiogram of this individual was previously published by Pacini et al. (2011).

In 2014, a spinner dolphin stranded near Badoc municipality on the west coast of Ilocos Norte province in the Philippines. The animal was initially treated on site for two weeks before being transferred to Ocean Adventures Marine Park, in Subic Bay, the Philippines, for additional treatment and rehabilitation. The animal weighed 38.5 kg and was 1.7 m in length upon arrival at Ocean Adventures, and was treated with antibiotics, fluids, b-complex, vitamin E, and liver support. No ototoxic drugs were administered to the animal. An audiogram of this individual was previous published by Pacini et al. (2016). Auditory temporal resolution measurements were collected on October 8, 2015.

B. Stimulus presentation and evoked response recording

While the general equipment and hardware setup used to conduct the experiments was the same between the separate subjects, different models of instruments were sometimes used. A diagram of the general equipment setup can be seen in Fig. 2.1.

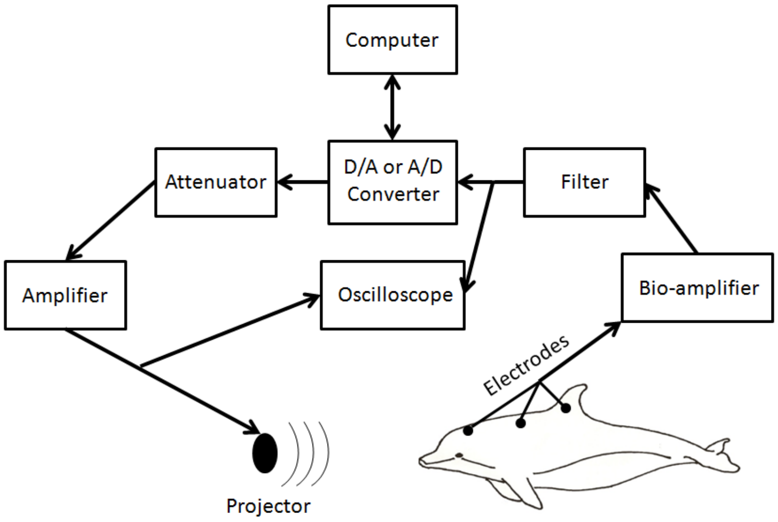

Fig. 2.1 *Diagram of the equipment used to collect electrophysiological data from the four test subjects.*

Acoustic stimuli were digitally generated from a laptop computer using a custom LabView program and sent to a National Instruments PCMCIA-6062E or USB-6251 data acquisition card (Austin, TX, USA). The stimulus level was controlled in 1 dB steps via an attenuator before being amplified by 20 dB and projected to the animal from an underwater transducer. Projected signals were monitored in real time during the experiments on a Tektronix TPS 2014 oscilloscope (Beaverton, OR, USA). During experimentation, the test subjects were in a stationary position with the tops of their heads and backs above the surface of the water. In the case of the beaked whale, pygmy killer whale, and spinner dolphin, the animals were lightly held and supported in the proper position for the tests by training or veterinary staff, while the pilot whale was trained to station in position on its own. A projecting hydrophone was placed 1 meter directly in front of the rostrum of each of the animals at a depth of 30 cm.

Gold plated, 10mm EEG electrodes (Grass, West Warwick, RI, USA) embedded in silicon suction cups were used to record evoked potentials. The active electrode was placed behind the blowhole and the reference electrode was placed on the back towards the dorsal fin. A third, ground electrode was placed on the side of the dorsal fin. Evoked responses were amplified 10,000 times and bandpass filtered by a Grass CP511 bioamplifier. The responses were further filtered with a Krohn-Hite 3384 bandpass filter (Brockton, MA, USA) before being sent to the data acquisition card and recorded on the same computer that produced the stimulus signal. The evoked responses were recorded at a sample rate of 16 kHz over successive 26 ms time windows that were synchronized with the onset generation of the stimulus signal. Between 800 and 1000 AEP recordings were averaged for each stimulus level in order to extract the evoked response from noise and were saved on the computer for offline analysis using MatLab software (Mathworks, Natick, MA).

Broadband clicks, measuring 0.1 ms in duration, were used as an acoustic stimulus, although the spectral emphasis of the clicks differed slightly between subjects. Click spectral power was tailored to the estimated frequencies of best hearing in each animal based on initial probe hearing tests. This resulted in click peak frequencies at 45, 50, 32, and 50 kHz for the spinner dolphin, pygmy killer whale, pilot whale, and beaked whale, respectively. Stimuli were presented within a maximum 20 ms window at different modulation rates ranging from 300 to 1500 Hz.

C. Data analysis

To quantify the magnitude of the EFR response to stimuli presented at each modulation rate, a fast fourier transform (FFT) was performed on the 16 ms section of the recording which contained the evoked response. The magnitude of the response was measured as the value of the spectral peak that corresponded to the frequency of the modulation rate for each trial, which was then plotted according to the modulation frequency to visualize the modulation rate transfer function. Keeping the 20 ms stimulus window constant for all tested modulation rates resulted in a different number of clicks and overall stimulus energy being presented at each rate. To account for this, weighted MRTFs were also generated using two different methods. First, the magnitude of responses for each modulation rate was summed for the fundamental response peak and its harmonics. Second, the response magnitude was calculated from the square root of the sum of squares for the fundamental response peak and its harmonics.

2.4 Results

The number and frequency of modulation rates that were tested differed slightly between the animals, resulting in full MRTFs being collected for the spinner dolphin and pilot while, while partial MRTFs were collected for the beaked whale and pygmy killer whale. Rate following responses were collected at 11 different modulation rates for the spinner dolphin and pilot whale, while the pygmy killer whale and beaked whale were tested at 7 and 8 different rates, respectively. The difference in tested rates was due to the different experimental circumstances between each species. In the case of the pygmy killer whale and beaked whale, the animals had stranded only a few days prior and were under ongoing veterinary care and treatment. At the time of the data collection, the primary purpose of the MRTF tests was to determine suitable modulation frequencies for audiogram measurements. Thus modulation rate tests were conducted opportunistically around the timeline of the more essential veterinary care requirements of the animals. Conversely, the pilot whale and spinner dolphin were successfully rehabilitated prior to the MRTF measurements and were available for a greater number of hearing measurements.

Envelope following responses were elicited and detected from all four of the test subjects and could be seen across a broad range of modulations rates. EFR response waveforms of the spinner dolphin and beaked whale can be seen in Figure 2.2.

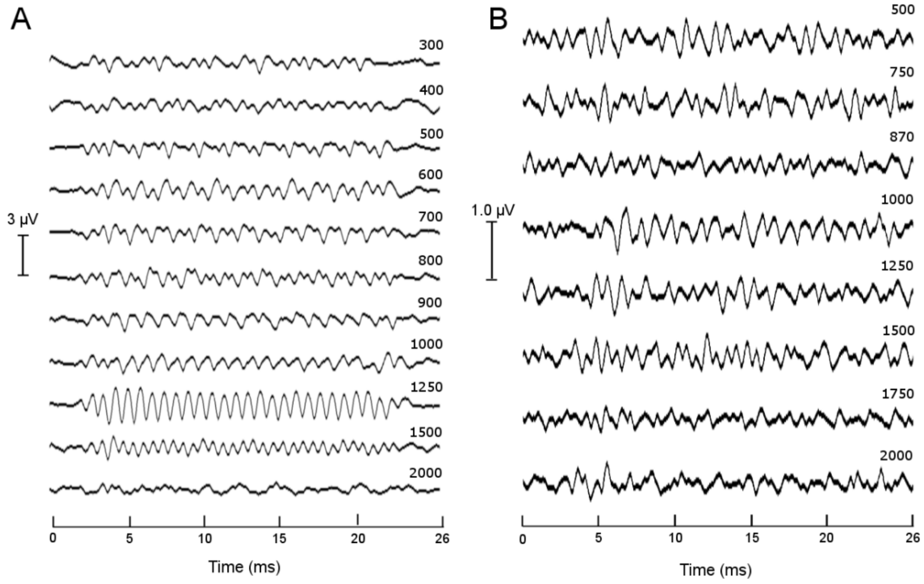

Fig. 2.2 *Rate following response waveforms to different modulation rates presented to the spinner dolphin (A) and Blainville's beaked whale (B).*

Small onset responses can be seen at higher modulation rates in these individuals, although offset responses were not visible. The magnitude of the EFR response was quantitatively determined by calculating an FFT over a 16 ms window of the waveform corresponding to the EFR and the magnitude of the spectral peak was measured at each modulation frequency (Fig. 2.3). Harmonics were clearly observed in FFTs of the EFR waveforms at modulation rates below 1000 Hz. As has been noted in previous studies, the harmonics result from deviations in the EFR waveform from a sine wave (Mooney et al. 2006).

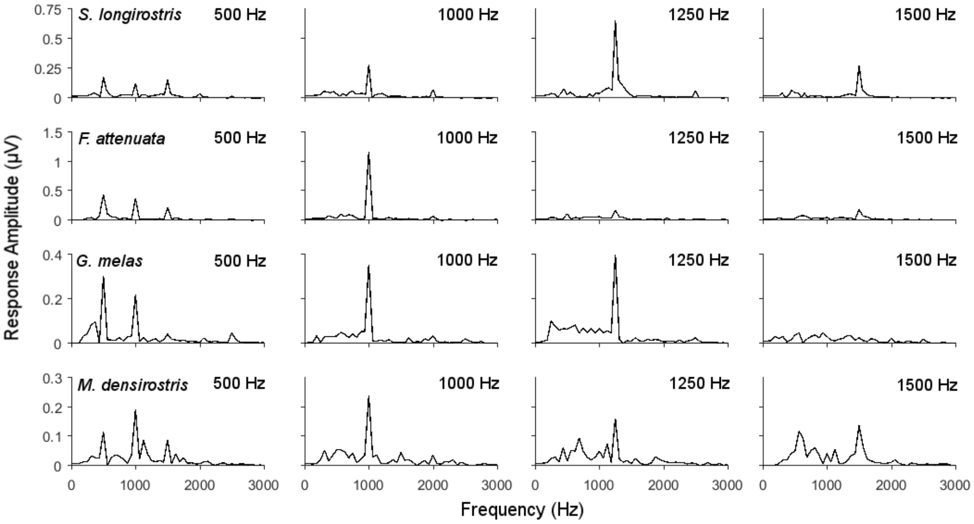

Fig. 2.3 *Fast fourier transform spectra of RFRs at varying modulation rates in the four subject animals. Response magnitudes were determined as the spectral peak corresponding to the frequency of stimulus modulation.*

The MRTFs for each animal all showed a low pass filter shape with clear peaks and notches (Fig. 2.4). The subjects followed modulation rates up to and above 1250 Hz, which was the peak following response for both the spinner dolphin and the pilot whale. Peak following responses for the beaked and pygmy killer whale were found slightly lower at 1000 Hz.

Response magnitudes dropped off rapidly above the peak response frequency in all subjects except the beaked whale. In that individual, response magnitudes appeared to decrease more gradually up to 1500 Hz before falling into the noise floor of the AEP system at 1750 Hz.

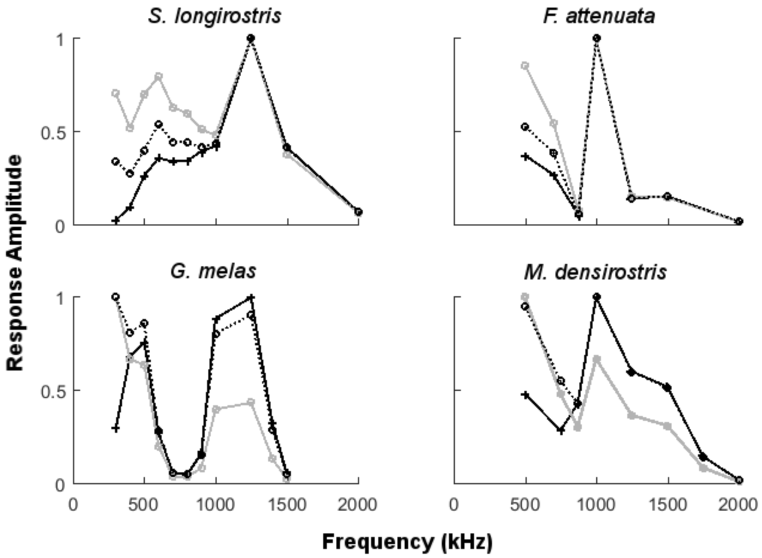

Fig. 2.4 *Normalized fundamental (black lines) and weighted modulation rate transfer functions for the four studied odontocetes. Weighted MRTFs were calculated by taking either the summed magnitude of the fundamental response and its harmonics (dotted lines) or the sum of squares of the fundamental response ad its harmonics (grey lines). Weighted response magnitudes are larger at lower frequencies due to the increased presence of harmonics in the response spectra.*

Weighted MRTFs for each species showed a slightly different shape from non-weighted functions. Differences occurred at lower frequencies, with some weighted response magnitudes even exceeding the non-weighted peak modulation rate magnitudes. As has been documented in other odontocete MRTFs, this difference is due to the fact that harmonics are more present at modulation rates below 1000 Hz which increased the weighted magnitude at those rates (Mooney et al. 2011; Linnenschmidt et al. 2013).

A clear notch was observed between 600-900 Hz in the pilot whale before response magnitudes rose to a secondary peak at 500 Hz. A faint notch was observed in the spinner dolphin MRTF from 700-900 Hz due to a small secondary peak at 600 Hz. In both the spinner dolphin and pilot whale, responses dropped off gradually below the secondary peaks. Modulation rates were not tested below 500 Hz for the beaked and pygmy killer whale, making determination of a secondary peak inconclusive. There was a clear notch below the primary peak in the MRTF for the beaked and pygmy killer whales before the response magnitude began to increase again up to 500 Hz.

The upper cutoff frequency of the MRTF has been defined in previous studies as the modulation frequency that produces a response magnitude -20 dB (or 10%) down from the peak response magnitude (Popov and Supin 1998; Mulsow and Reichmuth 2007). Using the same metric here, upper cutoff frequencies were 2000 Hz for the spinner dolphin, 1750 Hz for the beak whale. The response of the pygmy killer whale at 1500 Hz was slightly above the -20 dB magnitude, suggesting a cutoff frequency of around 1600 Hz. For the pilot whale, the upper cutoff was slightly below 1500 Hz. Although an RFR was not detected above the background noise at this rate, the response magnitude at 1400 Hz represented only an 8 dB decrease in relation to the MRTF peak. Thus, a 1500 Hz cutoff was deemed the most accurate in relation to the -20 dB criteria.

2.5 Discussion

The MRTFs of the four individuals presented here are very similar to other odontocete species, showing a low pass filter shape and detectable RFRs to high modulation rates up to and exceeding 1250 Hz, followed by decreasing response magnitudes at higher rates. It should be noted that due to the differing experimental circumstances in this study that resulted from some of the animals undergoing medical and rehabilitation efforts, the data collected in this study are somewhat limited in the range and number of modulation frequencies tested, resulting in differences in resolution of the MRTFs at both the higher and lower modulation frequencies. Nonetheless, some specific comparisons can be made. Corner frequencies between 1000 and 1250 Hz are generally similar to most other odontocetes, although a corner frequency of 1250 Hz in the spinner dolphin and pilot whale is slightly higher than most other toothed whales (800 Hz: *O. orca*; Szymanski et al. 1998; 1,000 Hz: *G. griseus*; Mooney et al. 2006; 1,000 Hz: *D. leucas*; Klishin et al. 2000; 1,125 Hz: *L. albirostris*; Mooney et al. 2009). The exception to this is the harbor porpoise (*P. phocoena*) which showed a corner frequency of 1400 Hz (Linnenschmidt et al. 2013). The location and magnitudes of peaks and notches in the functions vary somewhat between the species, which is not unexpected given the inter- and intra-specific variation found in other odontocetes. The relative magnitude of these features in the MRTF likely result from response latencies from different locations of anatomical generators of the AEP response (Supin and Popov 1995b; Popov and Supin 1998)

It is widely adopted that the temporal resolution of the auditory system can be characterized from the bandwidth of the MRTF. Estimates of temporal resolution have been calculated using the equation ERD=1/(2*ERB), where ERB is the bandwidth of the MRTF converted to an equivalent rectangular bandwidth, and ERD is the temporal integration function converted to an equivalent rectangular duration (Supin and Popov 1995b). A wider MRTF bandwidth would yield a lower estimated integration time and thus a better temporal resolution. MRTF bandwidths for the pilot whale, pygmy killer whale, Blainville's beaked whale, and spinner dolphin result in estimated temporal integration times of 333, 313, 294, and 250 μs, respectively. Taken together, the MRTF characteristics and estimated auditory integration times indicate that these individuals exhibit very high auditory temporal resolution that is comparable with other studied odontocetes. It also further supports the notion that acute temporal resolution is likely conserved across the diversity of odonocete species.

Despite the increased number of odontocete species for which data is available, it is still difficult to tease apart the extent to which specific biological characteristics may be related to, or influence, auditory temporal processing capabilities. Fine scale comparison between individuals and species is hindered, in part, by methodological differences between studies. However, it is notable that temporal resolution is similarly high between three small odontocetes, including the two porpoise species (*P. phocoena* and *N. phocaenoides*), which use long duration, narrow band high frequency clicks (Mohl and Andersen, 1973, Kamminga 1988), and the spinner dolphin, which produces shorter, broadband clicks (Schotten et al 2004). This similarity provides some indication that auditory temporal processing abilities of different odontocete species may not be related to the specific temporal or spectral characteristics of their outgoing echolocation signals.

Temporal resolution as estimated by MRTFs from a harbor porpoise (Linnenschmidt et al. 2013), bottlenose dolphin (Finneran et al. 2007), and killer whale (Szymanski et al. 1998) appear to be correlated with animal size (Linnenschmidt et al. 2013). Larger animals exhibit a broader MRTF bandwidth, longer estimated integration times, and thus a lower temporal resolution. Despite having published MRTFs, estimated integration times were not stated for six other previously studied species, but can be calculated from either reported MRTF bandwidths (2000 Hz for *N. phocaenoides*, 1475 Hz for *L. albirostris*, 1400 Hz for *D. leucas*; Klishin et al. 2000; Mooney et al. 2009, 2011) or approximated via visual inspection of the MRTFs themselves (1150 Hz for *G. griseus*, 1800 Hz for *M. europeus*, 1500 Hz for *P. crassidens*;

(Dolphin et al. 1995; Cook et al. 2006; Mooney et al. 2006; Finneran et al. 2009). Using body length as a correlate for animal size, the trend between body size and auditory temporal resolution appears to be generally corroborated when estimated integration times and body lengths of studied individuals are pooled between this study and previously published literature (Table 1; Fig. 2.5).

Fine scale comparison between species is hindered by differences in methodology across studies, yet it is nonetheless interesting to speculate if this trend is biologically significant. The ability to localize the position of a sound source is essential for echolocating animals. Mammalian auditory systems utilize a number of cues to determine the direction and location of a sound, including resolution of differences in time of arrival and intensity differences of a sound between the two ears(Heffner and Heffner 1992). While it has been suggested that inter-aural intensity differences (IIDs) operate as the major cue for odontocetes in determining azimuth of sound source locations(Popov and Supin 1991), bottlenose dolphins have experimentally been shown to possess an acute ability to resolve inter-aural time delays (ITDs) as small as 7 µs (Moore et al. 1995). Since the difference in ITD is dependent on the size of the animal's head; an animal with a smaller head is required to resolve a much shorter ITD than an animal with a larger head in order to achieve the same level of ITD acuity (Heffner and Heffner 1992). Thus, perhaps differences in auditory temporal resolution could be related to ITD resolution requirements of the differing head sizes of each species. Alternatively, the temporal and spectral characteristics of biosonar echoes contain important information for the detection and discrimination between desired prey targets (Bullock et al. 1968; Au et al. 1988; Au 1993). Echoes originating from small-bodied

***Table 2.1** List of MRTF cutoff frequencies, estimated integration times, individual body lengths, and adult body lengths for each subject and species.*

Species	MRTF BW (Hz)	Est. IT (µs)	Subject length (m)	Species length (m)
P. phocoena	1900[a]	263[a]	1.43[a]	1.53[b§]
N. phocaenoides asiaeorientalis	2000[c]	250	1.44[c]	1.7[d]
G. griseus	1150[e*]	435	1.47[e]	3.2[f‡]
S. longirostris	2000	250	1.7	1.82[g‡]
F. attenuata	1600	313	2.1	2.31[h†]
L. albirostris	1475[i]	339	2.24[i]	2.75[j‡]
T. truncatus	1750[k]	286	2.24[k]	3.15[l‡]
M. europaeus	1800[m*]	280	3.47[m]	4.35[n†]
G. melas	1500	333	3.5	6[o†]
M. densirostris	1700	294	3.5	4.19[n†]
P. crassidens	1500[p*]	333	3.7[q]	5.5[r§]
D. leucas	1400[s]	357	3.7[s]	4.5[t‡]
O. orca	1200[u*]	417	5.5[u]	8.35[v§]

Key: BW is bandwidth of the MRTF and IT is the estimated integration time.

Sources: [a]Linnenschmidt et al. 2013; [b]Bjørge and Tolley 2009; [c]Mooney et al. 2011; [d]Amano 2009; [e]Mooney et al. 2006; [f]Chen et al. 2011; [g]Perrin 2009; [h]Donahue and Perryman 2009; [i]Mooney et al. 2009; [j]Kinze 2009; [k]Finneran et al. 2007; [l]Wells and Scott 2009; [m]Finneran et al. 2009; [n]NMFS 2016; [o]Olson 2009; [p]Dolphin et al. 1995; [q]Au et al. 1995; [r]Baird 2009; [s]Klishin et al. 2000; [t]O'corry-Crowe 2009; [u]Szymanski et al. 1998; [v]Ford 2009

* MRTF upper cutoff frequencies visually approximated from published data

† mean adult length

‡ median of adult length range

§ median of adult male/female length maximums

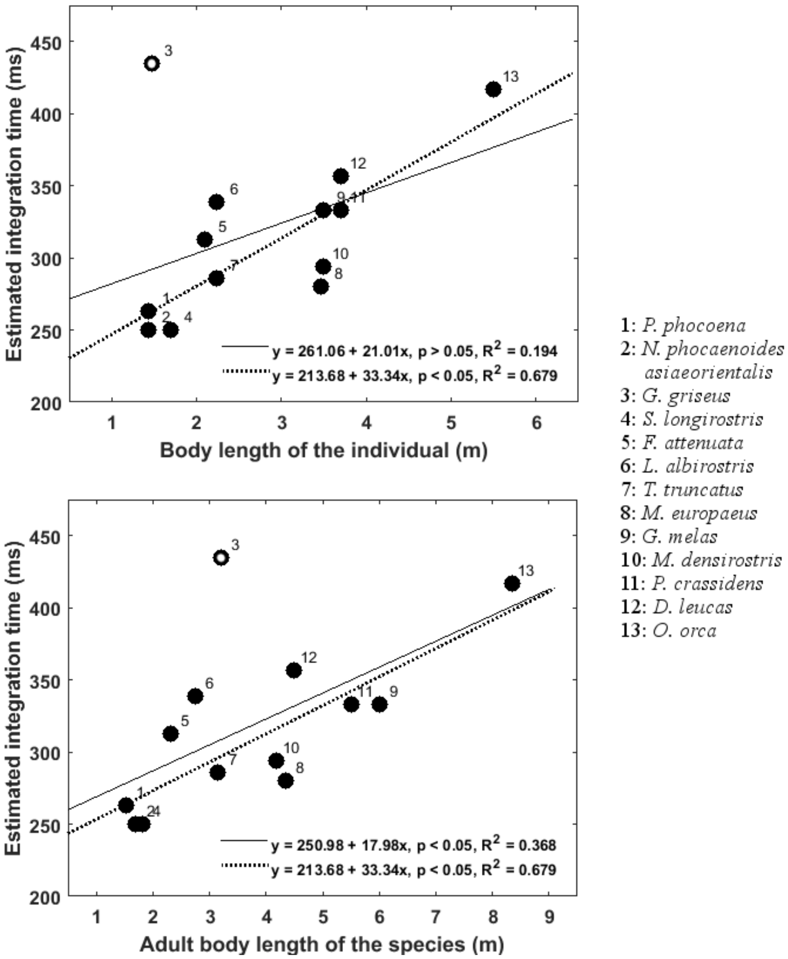

Fig. 2.5 *Comparison of MRTF estimated auditory integration times and body lengths of studied individuals (top) and adult body lengths of each species (bottom). Linear regressions were fitted to data which included all subjects and species (solid line) and also excluded data from the Risso's dolphin (dotted line), which appeared as a noticeable outlier from the trend found with other species (open circle).*

prey items would contain increased fine-scale variation in the echo structure that would need to be identified by a foraging animal that preferred such prey. Thus, perhaps different auditory temporal resolutions across species are related to prey selection and the need to adequately resolve temporal variation in echo structure of preferred prey types and sizes.

However, it is perhaps more likely that the trend it is a byproduct of the electrophysiological methodology. Non-invasive ABR signal amplitudes are influenced by the distances between electrodes and the responding auditory centers of the brain, which generally increase with a subject's size (Supin et al. 2001). Although MRTF estimates of integration times in the bottlenose dolphin (300 µs: Popov and Supin 1998) closely resemble those determined from behavioral experiments (250-300 µs: Moore et al. 1984; Au et al. 1988; Au 1990; Dubrovsky 1990), behavioral experimentation with additional species is needed to corroborate or contradict the same correspondence. Thus the biological significance of the trend between MRTF estimates of auditory temporal resolution and odontocete body size, if any, cannot be concluded from the current data.

The estimated temporal resolution of the small neonate Risso's dolphin (Mooney et al. 2006) appears as an interesting outlier compared the data from other species. While the animal was a stranded individual and its exact age was unknown, its small size and the presence of fetal folds indicate it was likely no more than a few months old. This dolphin was of a similar size (1.47 m) to the spinner dolphin (1.7 m), harbor porpoise (1.43 m), and Yangtze finless porpoise (1.44), yet showed an upper cutoff frequency at 1100 Hz, lower than the similar sized odontocetes by 900 Hz and lower than much larger individuals and species such as the killer whale and false killer whale (Table 2.1). The relatively poor temporal resolution of that Risso's individual thus cannot be attributed to size differences. Yet, as the neonate Risso's is the only individual of the species for which this data is currently available, it is difficult to conclude if the comparatively poor temporal resolution is characteristic of the species or perhaps is influenced by the animal's young age. While auditory temporal acuity in humans and rats is comparably poor during infancy and improves into adulthood (Dean et al. 1990; Werner et al. 1992; Trehub et al. 1995; Trehub and Henderson 1996; Friedman et al. 2004), there is some evidence to alternatively support the former of these possibilities in the case of the neonate Risso's dolphin. The first ontogenetic measurements of basic hearing capabilities and ABRs of an odontocete have recently been described in harbor porpoise calves, which exhibit fully developed hearing within a day after birth (Wahlberg et al. 2017). Due to the importance of hearing for odontocete survival, it is likely that other odontocete species likewise exhibit precocious hearing development (Wahlberg et al. 2017). Furthermore, similar relative latencies between individual ABR waves in the neonate (Mooney et al. 2006) and an adult Risso's dolphin indicate that the neonate Risso's also had fully functional hearing (Wahlberg et al. 2017). However, since there are no MRTF measurements across life stages, the ontogeny of odontocete auditory temporal resolution requires additional exploration, and it remains an open question if the comparably poor auditory temporal resolution of the neonate Risso's dolphin is characteristic of the species.

2.6 Conclusion

The modulation rate transfer functions were measured from four stranded odontocetes by recording auditory evoked potentials in response to temporally modulated stimuli. The individuals all showed the ability to process acoustic stimuli at high modulation rates, indicating auditory temporal resolution similar to other studied odontocetes and supporting the idea that high temporal resolution is conserved throughout the diverse range of odontocete species. Comparison of the MRTFs between odontocetes of different body sizes and echolocation characteristics suggests that auditory temporal resolution is not related to echolocation signal type. MRTF estimates of temporal resolution are correlated with animal body size, although further experimentation is required to elucidate the possible causes and significance of this relationship in terms of each species biology and auditory processing.

CHAPTER 3

INVESTIGATING AUDITORY THRESHOLDS TO BOTH FAR-FIELD AND LOCALIZED ACOUSTIC STIMULI IN A RISSO'S DOLPHIN (*GRAMPUS GRISEUS*)

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3.1 Abstract

Odontocetes use echolocation as their primary means of foraging and must accurately localize the position of sound in the environment. Multiple aspects of the auditory system can influence sound localization, including the relative sensitivity of the ears, the sound reception pathways, and the directional auditory sensitivity. However, all aspects of the odontocete hearing apparatus have undergone modification. While odontocete hearing asymmetry, sound receiving pathways, and directional sensitivity have been investigated to some degree, the connection and influence between these factors remains unclear and understudied. The current study investigated hearing in a Risso's dolphin (*Grampus griseus*), with the goal of 1) documenting auditory characteristics in this under-studied species, and 2) providing an initial investigation into the relationship between sound reception and far-field directional hearing in an individual odontocete. Auditory evoked potential methods were used to measure directional hearing sensitivities of the dolphin at three different horizontal azimuths, as well as hearing thresholds to acoustic stimuli that were presented via a contact hydrophone attached to the surface of the subject's skin. The contact hydrophone was placed at multiple analogous locations on both the right and lefts sides of the dolphin's head, as well as on multiple points on the melon. The dolphin showed elevated thresholds when jawphone stimuli were presented on the right side of the head. A single area of relatively increased sensitivity was found in the middle of the melon, which may suggest some degree of acoustic reception at this location. Furthermore, the Risso's dolphin exhibited acute, frequency dependent directional hearing, which is similar to other odontocete species that have been studied. However, despite the consistently elevated thresholds to localized stimuli on the right side of the head, far-field thresholds presented from 90 degrees to the right and left of the blowhole were generally symmetric.

3.2 Introduction

Echolocation is used by odontocetes as their primary means of foraging and orientation. The ability to effectively localize the source location of a sound, such as a returning biosonar echo, is thus of the utmost importance for their survival. The few studies that have experimentally investigated sound localization in odontocetes indicate that bottlenose dolphins have very acute acoustic localization and angular discrimination capabilities in both the horizontal and vertical planes (Renaud and Popper 1975; Branstetter et al. 2002).

Sound source localization is dependent, in part, on a subject's directional auditory sensitivity, also called a receiving beam. The directional sensitivity of the odontocte auditory system with respect to sound source location has been investigated in the bottlenose dolphin (*Tursiops* truncatus, Au and Moore 1984; Supin and Popov 1993; Popov et al. 2003, 2006; Popov and Supin 2009a), the beluga whale (*Delphinapterus* leucas, Klishin et al. 2000; Mooney et al. 2008; Popov and Supin 2009a), the harbor porpoise (*Phocoena* phocoena, Kastelein et al. 2005), and the Amazon river dolphin (*Inia* geoffrensis, Popov and Supin 1991). Directional auditory sensitivities for all studied species are generally acute and symmetric in the horizontal plane around the longitudinal axis of the body. Additionally, directional sensitivity narrowed with increasing stimulus frequency across all species tested, relating harmoniously to indications of frequency-specificity of more laterally versus anterior located acoustic receptions pathways (Popov et al. 2008). Yet differences in directional hearing were also apparent, with the receiving beam of the bottlenose dolphin found to be narrower compared to the harbor porpoise and the beluga whale (Popov and Supin 2009a). As of yet, due to the low sample size of individuals and species studied, it is difficult to attribute these differences in directional hearing to any specific attribute of the animal's biology or inter-specific individual variations. Additional measurements of directional auditory sensitivity from both an increased number of individuals and a greater diversity of species would therefore be valuable for future meaningful comparison.

Directional hearing is also partially dependent on the interplay between a number of factors related sound reception, including the shape of the external ears (Coles et al. 1989; Obrist et al. 1993), the location and characteristics of the pathways by which sound is channeled to the inner ear (Popov et al. 2008), and the sensitivity of the inner ears (Plomp 1976). Mammals rely largely on binaural cues to locate a sound source in the horizontal plane, including inter-aural intensity differences and inter-aural time delays (Heffner and Heffner 1992). Both of these cues utilize relative differences in the detection of a sound between each ear. However, with only a single acoustic pathway to each separate inner ear, a loss in of hearing in a single ear can change directional auditory sensitivity, hinder the ability to utilize binaural cues, and thereby hamper localization (Humes et al. 1980; Colburn 1982; Bess et al. 1986; Slattery and Middlebrooks 1994; McPartland et al. 1997; Bosman et al. 2003; Van Wanrooij and Van Opstal 2004, 2007; Wazen et al. 2005; Kumpik et al. 2010; Irving and Moore 2011; Agterberg et al. 2012; Kral et al. 2013; Keating et al. 2013)

Yet, the case is likely more complex with odontocetes. Adaptation to an aquatic environment resulted in the loss of the external pinnae and an open external auditory canal in cetaceans, and odontocete auditory pathways remain poorly understood. First proposed by (Norris 1968), it is a widely accepted hypothesis that the lower jaw of odontocetes acts as an acoustic window for channeling sound to the inner ear. Since then, multiple studies have provided supporting evidence for the mandibular hearing hypothesis (Norris and Harvey 1974; Brill and Harder 1991; Møhl et al. 1999; Mooney et al. 2008, 2014, 2015; Popov et al. 2016). Evidence has also been found for additional pathways around the auditory meatus (Popov et al.

2008) and gullar region along the ventral neck (Cranford et al. 2008; Mooney et al. 2015; Popov et al. 2016). Some pathways may be frequency dependent, with lower frequencies being detected better on the lateral and posterior areas of the head and higher frequencies detected best from the anterior and ventral areas (Popov et al. 2008; Mooney et al. 2014). These results have led to the hypothesis for multichannel sound reception in the head of odontocetes (Popov and Supin 1990b; Popov et al. 1992b, 2008, Ketten 1994, 2000; Mooney et al. 2014). Interestingly, while the melon is widely considered to function solely as an impedance matching device for sounds produced by the animal, there are a few studies that have indicated an area of relatively increased auditory sensitivity on the melon of bottlenose dolphins (Yanagisawa et al. 1966; Møhl et al. 1999) and the upper jaw tip of the false killer whale (Pacini 2011). This has led to speculation that auditory sensitivity above the frontal plane of the head may provide some degree of functional acoustic reception (Pacini 2011; Nachtigall 2016).

However, current understanding of the inter-relationship between factors such as the sensitivity of the ears, the multichannel acoustic receiver hypothesis, and directional sensitivity, is far from complete in odontocetes. The primary aim of this study was to investigate multiple aspects of odontocete auditory reception, specifically those that may have an interconnected influence on directional auditory sensitivity. Using auditory evoked potential (AEP) methods, we investigated aspects of acoustic receiving pathways, possible asymmetry in auditory thresholds of the two ears, and directional auditory sensitivity to far-field stimuli in a captive Risso's dolphin (*Grampus griseus*).

3.3 Methods

A. Test subject

Data were collected from a female Risso's dolphin named Da Hwa, housed in the animal care facilities of Farglory Ocean Park, in Hualien County, Taiwan. The animal was caught from the wild in 2003, but has been at the study site for 12 years and was approximately 18-19 years old at the time of data collection. The dolphin weighed 292 kg and measured 2.93 m in length. Previously, this animal was shown to have hearing sensitivities comparable to those already described for this species (Mooney et al. 2015), which included generally sensitive hearing across the range of frequencies from approximately 10 to 90 kHz (Nachtigall et al. 1995, 2005).

B. Thresholds to broadband click and tone pip stimuli presented via a contact jawphone

The dolphin's auditory thresholds were first measured in response to localized acoustic stimuli that were presented via a "jawphone" transducer, consisting of a Reson 4013 hydrophone (Slangerup, Denmark) encased in a silicon suction cup. A single threshold was collected per experimental session where the animal voluntarily beached itself out of the water in one of two trained methods. Some sessions were conducted in a small pool (5 x 5 x 4 m) with a moveable floor that could be mechanically raised. The dolphin was trained to station in the pool while the floor was raised until its body was completely above the water. Alternatively, data were also collected while the animal voluntarily beached itself on the deck adjacent to the pool. The determination of which situation was used for data collection was based on the training needs of the animal on each given day. In both scenarios, the animal remained out of the water for up to 15 minutes at a time, during which time the dolphin was sprayed with water to keep the skin wet.

Once the dolphin was properly stationed out of the water at the start of an experiment session, the jawphone was attached at one of nine different pre-determined locations around the animal's head (Fig. 3.1). The locations included symmetrical placement at four externally analogous locations on both the right and left sides of the dolphin's head, as well as five spots on the anterior face of the melon and the upper jaw tip. At each location, the jawphone was attached using an electrode gel to prevent the formation of reflective air gaps.

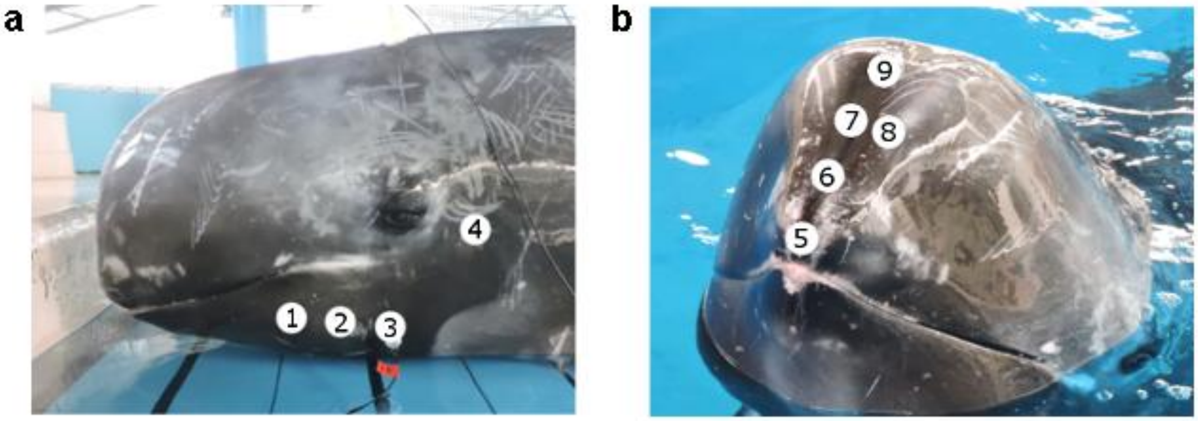

Fig. 3.1 *The jawphone was placed at 9 different locations on the dolphin's lower jaw (a) and melon (b). These locations included the anterior jaw (1), middle jaw (2), posterior jaw (3), external auditory meatus (4), upper jaw tip (5), lower melon valley (6), middle melon valley (7), middle melon ridge (8), and the upper melon valley (9). The jawphone was also placed on the right side of the dolphin's head at spots externally analogous to locations 1-4.*

A total of four different acoustic stimuli were used for the AEP measurements with the jawphone, which included tone pips filled with one of three carrier frequencies: 32, 45 or 60 kHz. The fourth stimulus consisted of a train of broadband clicks, each 0.06 ms in duration with a peak frequency of 50 kHz. Due to time constraints, not all stimuli were tested at each jawphone location. Thresholds to broadband clicks were collected at each of the nine jawphone locations, while thresholds to the frequency-specific tone pip stimuli were collected at only a single location (the anterior jaw, see Fig. 3.1) on both the right and left side of the dolphin's head.

All stimuli were digitally generated from a laptop computer using a custom made LabView program (Austin, TX, USA). Each stimulus consisted of a train of 20 pips modulated at a rate of 1 kHz and presented once every 62.5 milliseconds. Stimuli were then sent to a NI USB-6251 data acquisition card (Austin, TX, USA). The stimulus level was controlled via an attenuator before being amplified by 20 dB and projected from the jawphone. During experiments, the signals were monitored in real time on a oscilloscope. The jawphone stimuli were calibrated in water with a Reson 4032 receiver placed 50 cm apart at a depth of 1 meter. The distance of 50 cm is similar to the estimated distance between the jawphone and the dolphin's ears during experimentation, and has been used for calibration of jawphones in previous study with this animal (Mooney et al. 2015).

C. Directional hearing thresholds to far-field stimuli

The subject's directional hearing sensitivity was explored by measuring evoked responses to stimuli projected from the far-field at three different azimuth angles (-90, 0, and 90 degrees) around the animal's head. Experiments were conducted in the largest of seven interconnected concrete pools that constituted the habitat enclosure at Farglory Park. This experimental pool was approximately rectangular in shape (~104 x 25 m), containing 2500 m^3 of water volume with a maximum depth of 7 m. Due to its size and depth, the pool was considered a relatively free field environment. Hearing measurements were conducted while the dolphin stationed very still at the surface of the water parallel to the center of the pool wall with the top of its head and blowhole above the water (Fig. 3.2). To assist with the animal's stationing behavior, a large 74 by 102 cm foam pad that was 10 cm thick was draped down the side of the wall next to the side of the animal's head. Acoustic measurements in the pool also indicated that the pad reduced acoustic reflections from the nearest wall by approximately 9 dB. The distance between the animal's blowhole and side of the pad was 50 cm. A projecting transducer was positioned 1.5 m away from the animal's blowhole, either directly in front of the animals rostrum (0º azimuth) or to the right side of the blowhole (90º azimuth). To collect hearing measurements with the stimulus presented on the animal's left side, the animal would station in the opposite direction with its head in the same place (-90º azimuth). The animal's head was always kept at the same location in the pool to minimize any possibility of an uneven noise field.

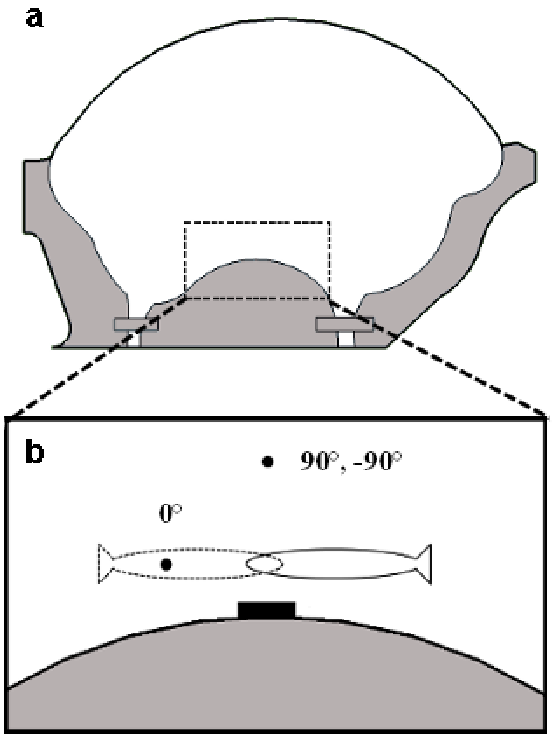

Fig. 3.2 *Diagram of the experimental setup for measurement of directional AEP thresholds to far-field stimuli. Data were collected in the largest pool of the habitat complex (A). The dolphin was trained to station very still at the surface of the water parallel to the pool wall (B). Acoustic stimuli were projected from a hydrophone in front 0° and to the right side 90° of the dolphin's head at a distance of 1.5 meters. To project stimuli on the dolphin's left side (-90°), the dolphin stationed in water facing the opposite direction (dotted outline).*

An experimental session consisted of 7 to 9 trials where the animal was trained to station still at the surface of the water parallel to the pool wall with the top of its head and blowhole above the water. Once the animal was properly stationed, an AEP measurement was started and lasted for approximately 1 minute and 15 seconds per trial. Following completion of a trial, the trainer blew a whistle, signaling the dolphin to break from the station to receive a fish reward. If the animal's body position deviated by more than approximately 5º for longer than 5 seconds during a trial, the trial was aborted and repeated.

A total of four different acoustic stimuli were used for the far-field AEP measurements, which included tone pips filled with one of three carrier frequencies: 16, 32 and 60 kHz. The fourth stimulus consisted of a train of broadband clicks with a center frequency of 50 kHz. All stimulus types were generated from the same computer and equipment described previously for the jawphone hearing measurements, with the exception of the projecting transducer. Far-field stimuli were projected from a Reson 4040 or Reson 4013 hydrophone.

D. Evoked potential measurement and analysis

Evoked potentials were recorded via three gold plated electrodes (Grass, West Warwick, RI, USA) embedded in suction cups that were placed along the dorsal surface of the animal with conductive electrode gel. The active electrode was placed along the midline of the dolphin's back approximately 10 cm behind the blowhole, and the reference electrode was placed on the animal's back between the blowhole and the dorsal fin. A ground electrode was attached to the animal's dorsal fin. Evoked potentials were amplified 10,000X with a Grass CP511 bioamplifier and filtered from .3 to 3 kHz with a KrohnHite 3384 filter (Brockton, MA, USA) before being digitized by the DAQ card at a rate of 16 kHz. A 26 ms evoked response following each stimulus presentation was averaged over 1000 iterations to extract the signal from the background noise. The averaged AEP response was saved to the computer for offline analysis.

The AEP response magnitude at 1 kHz for each stimulus level was then determined via a fast Fourier transform (FFT) on the middle 16 ms section of the recording which contained the evoked response. Response magnitudes at the 1 kHz spectral value were plotted according to their respective received levels (dB SPL re: 1 uPa) and a linear regression was plotted across the data points that contained a detected response (Fig. 3.3). The threshold was taken as the point where the regression line crossed a zero-response magnitude level. Thresholds to stimuli presented on the right and left sides of the head were compared with paired samples T-tests.

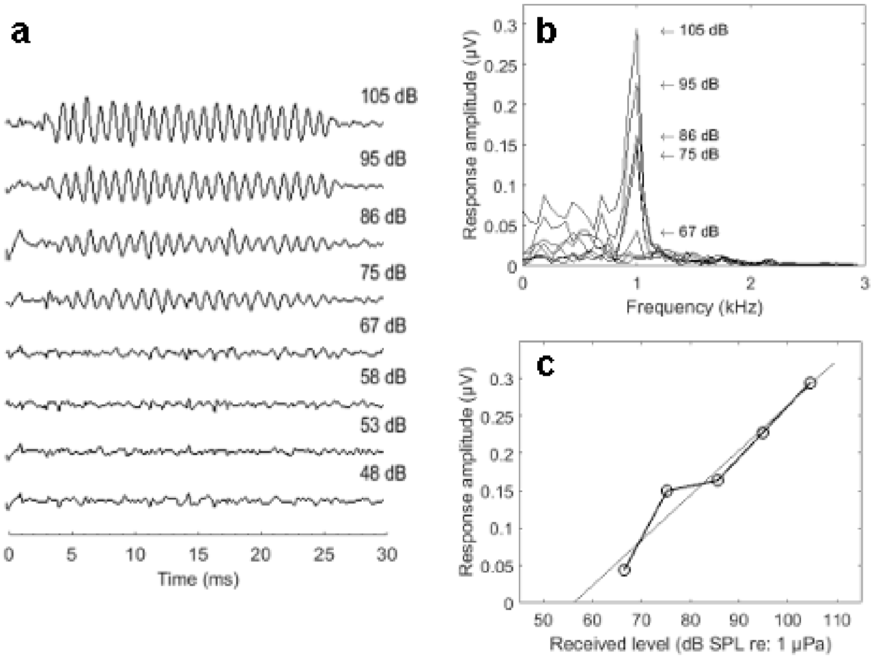

Fig. 3.3 *AEP response measurements to a broadband click stimulus presented from the far-field in front of the Risso's dolphin at a distance of 1.5 meters (A). Fast fourier transforms of the middle 16 ms of the EFR responses (B). EFR response magnitudes at 1 kHz plotted against the received level of the acoustic stimulus, fitted with a linear regression (C). The point where the regression crosses a zero response amplitude is taken as the auditory threshold value.*

3.4 Results

A. Thresholds to broadband click stimuli

Thresholds to broadband click stimuli with the jawphone were measured at three locations along both the right and the left lower jaw of the dolphin, as well as on the right and left meatus. Thresholds were 57, 69, 53, and 76 dB (anterior to posterior positions) on the left side, and 88, 75, 85, and 92 dB on the right side. Thresholds on the right side were consistently elevated in relation to the thresholds at positions on the left side, although the relative threshold difference between the two sides depended on the location (Fig. 3.4). Thresholds differences between analogous right/left locations ranged from 6 to 32 dB, with the maximum difference found at the posterior jaw pad and the minimum difference found at the middle jaw pad. The mean threshold to clicks was 64 (±11) and 85 (±7) dB on the animal's right and left side, which were found to be significantly different via a paired T-test (t(3)=-3.42, p<0.05). Sensitivities to broadband click stimuli at jawphone positions on the upper jaw tip and along the front face of the melon ranged between 75 and 95 dB. The lowest threshold was measured at the middle of the

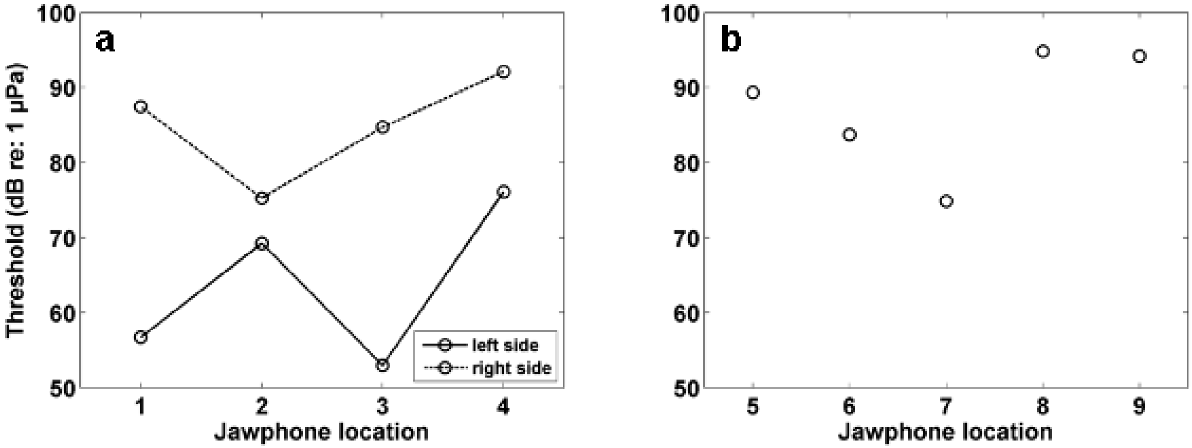

Fig. 3.4 *Threshold measurements to broadband clicks projected via a jawphone transducer at multiple locations on the animals right and left side (A), as well as along the upper jaw tip and anterior face of the melon (B).*

melon groove. Thresholds increased as the stimulus location was moved away from this location. The jawphone locations along the middle of the melon valley were spaced 7 cm apart.

B. Thresholds to tone pip stimuli

Thresholds to frequency specific tone-pip stimuli were measured at a single jawphone position on the anterior mandibular fat pad for each side of the animal's head. Thresholds for each stimulus were consistently lowest when presented on the animal's left mandibular fat pad, although the relative difference between right and left thresholds decreased with decreasing stimulus frequency (Fig. 3.5). There was no threshold difference found for the 32 kHz stimuli, and a difference of 14 dB at 45 kHz. A threshold could not be determined for the 60 kHz stimulus presented on the animal's right anterior jaw. While a small response was detected at 115 dB, increasing the intensity beyond this level caused distortion of stimulus waveform, preventing determination of a threshold. Given that no response was detected at 110 dB, we estimated a

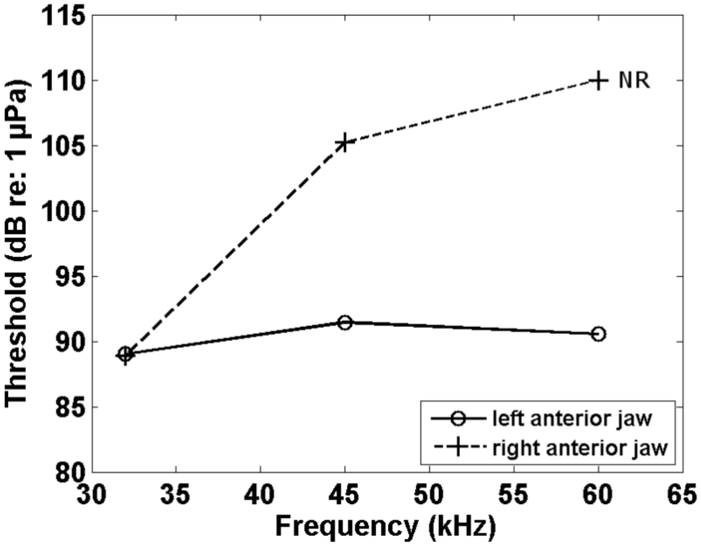

Fig. 3.5 *Auditory thresholds to narrow band tone pip stimuli projected via the jawphone transducer at three carrier frequencies on the right and left anterior jaw. The dolphin showed no response (NR) to the 60 kHz stimulus at 110 dB on the right side.*

right to left difference of 20 dB for this stimulus, which was the maximum threshold difference found to tone pip stimuli at this jawphone location.

C. Directional hearing thresholds to far-field stimuli in the horizontal plane

Relative thresholds were always lowest when presented in front of the animal at an azimuth of 0º and elevated when the sound source location was moved to -90º and 90º (Fig. 3.6). The threshold change was frequency dependent, being greatest for 60 kHz tone pips, and decreasing at lower frequency stimuli. There was no significant difference in thresholds between the right and left source locations (paired t-test; t(3)=-1.1, p=0.35). The relative difference between thresholds at 0° and 90° (averaged between both the -90° and 90° positions) was 11, 23, 28, and 18 dB for the 16 kHz, 32 kHz, 60 kHz, and click stimuli, respectively.

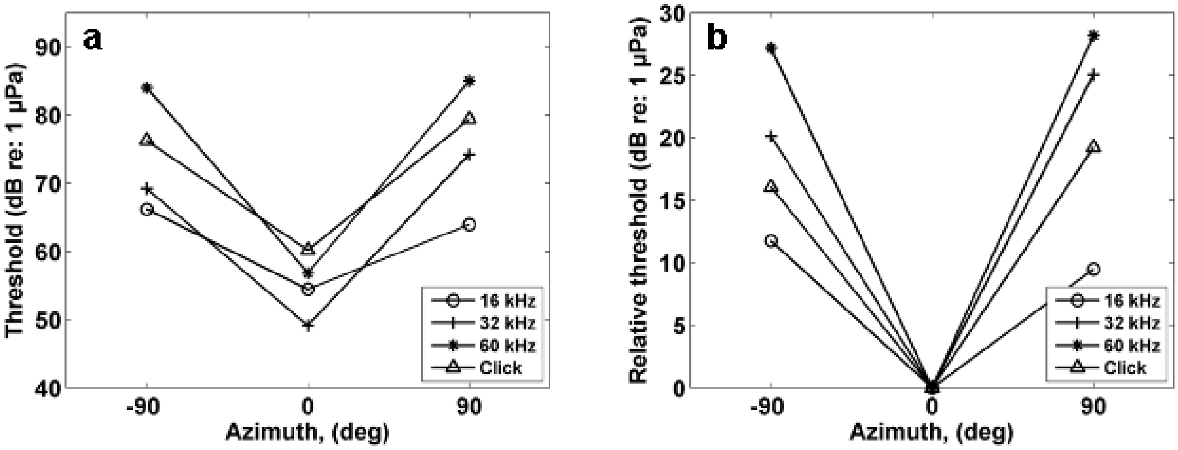

Fig. 3.6 *Directional auditory thresholds to multiple acoustic stimuli projected from the far-field (1.5 m distance) at three different horizontal azimuths around the Risso's dolphins head (left panel). Relative difference between thresholds when the stimulus was presented in the center versus to the left (-90º) and right (90º) of the dolphin (right panel).*

3.5 Discussion

A. Right-left threshold asymmetry

Previous investigation of head related hearing sensitivities in this *G. griseus* individual found a significant difference in auditory thresholds to broadband click stimuli presented at a single location on the animal's right and left mandibular fat pad (Mooney et al. 2015). However, the large head and pan-bone area of the Risso's dolphin, combined with the fact that even small differences in stimulus location between measurements can cause differences in AEP thresholds (Møhl et al. 1999; Popov et al. 2016), leave open the potential that hearing asymmetry determined from only a single location on either side of the animal's head was influenced more by small differences in jawphone location than by actual auditory sensitivity. The auditory sensitivity at multiple analogous left-right locations to broadband clicks found in this study confirm the initial asymmetry found previously, but also indicate that the magnitude of the difference varies across multiple analogous locations, both exceeding and falling short of the 8 dB difference described previously (Mooney et al. 2015).

Frequency-dependent threshold asymmetry was also found between the right and left anterior jaw pad, with the threshold differences increasing for higher frequency stimuli. Although limited to only a few stimulus frequencies at one jawphone location, this result may provide a preliminary indication that Risso's dolphins possess frequency dependent acoustic pathways, of which evidence has been found in other odontocete species (Popov et al. 2008, 2016; Mooney et al. 2014). Additional auditory measurements using more stimuli and at additional analogous right-left locations around the head are needed to further describe frequency and location specific variation in auditory sensitivity of this species.

Much is still unknown about the pathways by which sounds are received by odontocetes, and there is ongoing discussion concerning what extent local acoustic stimulation in the air can be used to characterize hearing processes in these animals. Thus, when interpreting auditory thresholds to localized stimulation with a contact transducer in air, it is difficult to differentiate how much the measured thresholds reflect the actual sensitivity of the inner ears, or alternatively are reflecting differences in acoustic conduction at the stimulated location (Popov et al. 2016). The large variability in thresholds across multiple locations on the same side of the dolphin's head indicates that some of the asymmetry is likely accountable to jawphone location, and while the consistency and magnitude of the threshold elevation across all the right side locations seems to suggest that some level of sensitivity difference is present between the inner ears (at least when using broadband clicks), this cannot be conclusively determined from the present data alone.

Asymmetric hearing thresholds to jawphone stimuli both in the air and in the water have been documented in a few previously published studies, and also attributed to sensitivity differences of the ears. While investigating inter-aural time and intensity difference thresholds, Moore et al. (1995) indicated a 2 to 3 dB difference in sensitivity to jawphone stimuli between the right and left lower jaw of a bottlenose dolphin, with the left side being less sensitive. Using the same animal, Brill et al. (2001) noted that the asymmetric jawphone thresholds were frequency dependent, with the greatest threshold difference occurring at lower frequencies below 5 kHz. The side that exhibited the best sensitivity was also frequency dependent, with the left side being more sensitive from 1-6 kHz, and the right side being more sensitive from 7-9 kHz. Additionally, Houser and Finneran (2006) measured separate audiograms for a population of bottlenose dolphins using a jawphone placed on the pan bone on both sides of the animals' head. Asymmetric thresholds were documented in many of the animals tested, but were not discussed. While the vast majority of studies on odontocete hearing with contact hydrophones have placed the projector on a single side of the animal (Møhl et al. 1999; Mooney et al. 2008, 2014; Popov et al. 2016), the few studies that have placed jawphones on both the right and left sides of an animal's head have all found varying degrees of threshold asymmetry. Thus, this may suggest right-left asymmetrical sound reception is a common occurrence in odontocetes and merits further investigation.

Jawphones have been increasingly used for hearing measurements in both controlled experimental contexts and also in more field-based circumstances with stranded or rehabilitated animals. It has been documented that threshold and audiogram estimates with jawphones are comparable to those measured in the free field (Brill et al. 2001; Finneran and Houser 2006; Houser and Finneran 2006). However, the results of this and other studies suggest that jawphone audiograms for a single individual may vary significantly depending on the side tested, and the specific location along the jaw where the projector is placed. Such possibilities indicate that audiograms collected from new species via the use of a jawphone should be compared with caution, or that audiometric measurements with a jawphone should be separately made with the stimulus presented on both sides of a subjects head.

B. Directional sensitivity to far-field stimuli

There are a number of methodological limitations that should be noted and taken into account when interpreting and comparing the directional auditory thresholds in the current study. First, the availability of test subjects is a consistent limitation for research with whales and dolphins. The current study describes results from only a single individual, and thus may not be characteristic of the species as a whole. Second, the experimental setup was not ideal for collection of directional thresholds due to the acoustic field of the experimental pool, including the proximity of the pool walls, and in particular, the nearest wall on the contra-lateral side of the animal from the stimulus transducer. Such factors are a limiting, but often unavoidable consequence of research in captive pool settings. However, in both cases, it is a reasonable approach to use the current data for cautious interpretation and comparison until additional data become available (Popov and Supin 2009a).

There were a number of steps taken to attempt to minimize possible confounding reflections from the pool walls. First, the minimum distance from the animal to the far walls was 24.5 meters. Stimuli that reflected off this surface would attenuate by 34 dB before returning to the animal's ipsilateral side 32 ms after the stimuli was projected, and thus not overlap or interfere with reception of the primary 20 ms stimulus. While reflections off the pool bottom (6.7 m below the animal) would return in 9 ms and partially overlap with the initial stimulus, their received level would be attenuated by 23 dB. It therefore seems likely that these reflections would have limited influence on an accurate threshold measurement. It is more likely that interfering reflections would arise from the close wall 0.5 m away from the animal on the contra-lateral side of the projecting transducer. A measured absorption of 9 dB by the foam station pad and a distance attenuation of 6.5 dB would result in a total attenuation of reflections from the near wall by an estimated 15.5 dB. It is likely this attenuation is even greater due to shading by the head and body of the animal (Popov and Supin 1991). Therefore, the far-field threshold results in this study are cautiously interpreted as being reflective of the horizontal directional sensitivity of this individual and not impacted by interfering reflections.

Hearing in this individual *G. griseus* exhibited directional dependence in the horizontal plane, with increased auditory thresholds when the sound source was positioned 90° to the left and right side of the animal's head. The change in thresholds was frequency dependent, with higher frequency stimuli showing a greater increase in thresholds at the lateral positions than lower frequencies. Thresholds at 90º on both the right and left sides were also relatively symmetrical. These results suggest the Risso's dolphin generally has an acute, frequency dependent receiving beam across a wide frequency band, similar to that found in other odontocetes such as the bottlenose dolphin (Au and Moore 1984; Popov et al. 2003, 2006; Popov and Supin 2009a), beluga whale (Popov and Supin 2009a), and harbor porpoise (Kastelein et al. 2005). Comparison of the directional thresholds at similar azimuths with the harbor porpoise suggests that the Risso's dolphin possesses a narrower receiving beam. However, the directional threshold results for both the beluga and bottlenose dolphin show significant variability in relative values between these azimuths across multiple studies. As a result, the Risso's dolphin's directional acuity appears both more and less acute than the bottlenose and beluga, depending on which previous study and stimulus is being compared. It is interesting to note that despite the consistent and often large asymmetry in thresholds to click stimuli via the jawphone, the dolphin's far-field sensitivities to clicks at azimuths of ±90º differed by only 3 dB. Unfortunately, since it cannot be concluded that the asymmetric jawphone thresholds signify actual hearing loss, interpretation of these contrasting results is difficult and would be speculative.

C. Auditory sensitivity on the melon

Auditory sensitivity on the odontocete melon is generally not investigated in great detail and is often only measured at a single location, which is commonly different between studies. In most cases, melon thresholds are significantly elevated compared to the mandibular and gullar regions (Møhl et al. 1999; Mooney et al. 2008, 2014), including in a study using the same Risso's dolphin as the one used here (Mooney et al. 2015). However, there are a few documentations of greater sensitivity to sound presented on the melon as well. Yanagisawa et al. (1966) noted two areas of auditory sensitivity on the melon that were nearly equal to the lower jaw. Additionally, Mooney et al. (2014) measured thresholds at a single location on the melon of the Yangtze finless porpoise using multiple stimulus frequencies. They found that the difference between the most sensitive location around the head and the threshold on the melon decreased with increasing stimulus frequency. At 120 kHz, similar to the frequencies found in the species echolocation clicks, the melon was only 11 dB less sensitive that the most sensitive spot on the head.

In the current study, the anterior face of the melon and upper jaw tip of the Risso's dolphin generally showed elevated thresholds compared to the most sensitive locations along the lower jaw. However, there was one location in the middle of the melon groove that exhibited a reduction in threshold by at least 9 dB compared to the surrounding locations. The threshold at this spot was still significantly elevated compared to the animal's left jaw, but it is notable that the sensitive melon threshold was equal to the most sensitive threshold found on the right mandibular fat pad. It may be noteworthy that in Mooney et al. (2014), the location of the contact hydrophone was situated along the middle of the anterior face of the melon, similar to the current study, as opposed to more dorsally oriented positions in most other studies (including Mooney et al. 2015 with the same Risso's dolphin). The sensitivity found here is not high enough to suggest the melon is a primary pathway for received sound, yet it may allow for potentially useful reception of acoustic energy. However, this possibility is difficult to reconcile with the fact that the melon is generally isolated from other auditory structures and there is no clear acoustic pathway to the tympano-periodic complex. Given the unique morphology of the *G. griseus* melon, the possible auditory utility of the melon across odontocete species nonetheless poses an interesting possibility. It has been speculated that a window of auditory sensitivity on the melon could allow odontocetes a greater capacity for sound source localization in the vertical plane

(Nachtigall 2016). Directional sensitivity in the vertical plane could not be tested in the current study but would be a valuable part of future research efforts with this species.

3.6 Conclusion

Auditory evoked potentials were used to investigate auditory thresholds to both localized and far-field acoustic stimuli in a captive Risso's dolphin. Threshold measurements from multiple analogous locations on both the right and left sides of the dolphin's head showed consistent asymmetry, with the animal's hearing being significantly less sensitive on the right side. These results may suggest that either pathways for received sound are asymmetric between the right and left sides of the head, or it may reflect an asymmetry in the auditory sensitivities of the two ears themselves. Additionally, the dolphin showed an area of increased auditory sensitivity in the middle of the melon cleft, which may indicate that the melon provides some degree of auditory reception. Furthermore, the dolphin was found to have acute, frequency-dependent directional hearing that is similar to other described species (Kastelein et al. 2005; Popov et al. 2006; Popov and Supin 2009). In contrast to the right-left threshold asymmetry to jawphone stimuli, the directional hearing measurements showed no significant difference between the right and left sides. The comparison of far-field directional hearing to asymmetric auditory thresholds to contact sound stimuli in this individual provide insight into how these auditory measurements compare to each other and may yield different results. Future research should test directional hearing in *G. griseus* with a greater number of azimuths and stimuli to allow for better comparison. The relationship between asymmetric auditory thresholds and free-field directional hearing remains an interesting topic that deserves further, more extensive investigation.

CHAPTER 4

TRANSMISSION BEAM CHARACTERISTICS OF A RISSO'S DOLPHIN (*GRAMPUS GRISEUS*)

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139, 53-62.

4.1 Abstract

The echolocation system of the Risso's dolphin (*Grampus griseus)* remains poorly studied compared to other odontocete species. In this study, echolocation signals were recorded from a stationary Risso's dolphin with an array of 16 hydrophones and the two-dimensional beam shape was explored using frequency-dependent amplitude plots. Click source parameters were similar to those already described for this species. Centroid frequency of click signals increased with increasing sound pressure level, while the beamwidth decreased with increasing center frequency. Analysis revealed primarily single-lobed, and occasionally vertically dual-lobed, beam shapes. Overall beam directivity was found to be greater than that of the harbor porpoise, bottlenose dolphin, and a false killer whale. The relationship between frequency content, beam directivity, and the estimated size of the sound generating structures for this Risso's deviated from the trend described for other species. These are the first reported measurements of echolocation beam shape and directivity in *G. griseu*s.

4.2 Introduction

Echolocation in odontocetes requires highly specialized features for the production and transmission of acoustic signals. Typical odontocete echolocation signals are short, ultrasonic sounds generated with specialized tissues located within the enlarged nasal complex (Ridgway et al. 1980; Mackay and Liaw 1981; Aroyan et al. 1992, 2000; Cranford et al. 1996; Au et al. 2006; Au and Suthers 2014). The produced "click" is directed out the front of the melon. The highly directional nature of these signals has been investigated in a number of species using hydrophone arrays to measure or estimate transmission beam patterns (for a review, Kloepper 2013). Multiple structures in the head are responsible for creating this high directionality. Directly posterior to the sound generators in the odonotocete head are air sacs overlaying the concave skull (Cranford et al. 1996). These sacs act as acoustic reflectors for the generated sounds, and redirect acoustic energy anteriorly towards the melon (Aroyan et al. 1992). The composition and layering of acoustic fats within the melon further collimate the sound towards the anterior forehead, and also act as an impedance matching device for sound traveling into the water (Norris and Harvey 1974; Litchfield and Greenberg 1974). Furthermore, the melon is surrounded by a collection of muscles and tendons (Mead 1975; Knudsen and Konishi 1979; Heyning 1989; Cranford et al. 1996; Huggenberger et al. 2009), which have been suggested to have the ability to change the directional properties of the emitted sonar beam (Kloepper et al. 2012a; Cranford et al. 2014; Jensen et al. 2015). Some recent studies offer supportive evidence of active focusing during echolocation in a captive false killer whale (Kloepper et al. 2012a, 2015), although the same phenomena was not observed in similar studies with two other odontocete species (*Stenella frontalis*, Jensen et al. 2015; *Phocoena phocoena*, Wisniewska et al. 2015), leaving this topic an active area of discussion.

While it is likely that all odontocetes use homologous structures for the generation and transmission of echolocation signals (Cranford et al. 1996), there are clear differences between species in head morphology, anatomy, and signal design. One species with a visually clear difference in external head morphology is the Risso's dolphin (*Grampus griseus*, Cuvier, 1812), a pelagic species that occurs primarily in temperate and tropical deep waters near continental shelves and submarine canyons (Leatherwood et al. 1980). This species has evolved a vertical indentation, or crease, along the anterior face of the melon (Leatherwood et al. 1983), an anatomical feature not shared by any other odontocete (Fig. 4.1).

Fig. 4.1 *The female Risso's dolphin (Grampus griseus) used in this study, showing the unique melon cleft, a characteristic trait of the species.*

Despite this conspicuous morphological difference and their relative availability in captivity, the Risso's dolphin remains poorly studied, and the function of the melon cleft remains unknown. Given both the established and hypothesized functions of the melon for echolocation (Evans et al. 1964; Norris and Harvey 1974; Litchfield and Greenberg 1974; Malins and

Varanasi 1975), the potential influence of the melon cleft on the outgoing echolocation beam of *G. griseus* is an intriguing question. It was not until relatively recently that the species was empirically shown to echolocate (Philips et al. 2003) and descriptions of the general characteristics of likely on-axis clicks have been obtained from captive (Philips et al. 2003) and wild individuals (Madsen et al. 2004b). It has been speculated that the melon cleft in the Risso's dolphin may be functionally important for echolocation (Nachtigall et al. 1995; Philips et al. 2003). The typically rounded and smooth shape of most odontocete foreheads is thought to be important for the directionality of outgoing echolocation signals (Norris 1968; Litchfield et al. 1979), thus it seems plausible that any influence of the cleft structure may be manifested in the outgoing beam.

Here we report the first beam measurements of an echolocating Risso's dolphin. While the dolphin was echolocating in a stationary location, the signals were recorded using a 16-element hydrophone array, and on-axis characteristics and beam shape were calculated for each click. The Risso's dolphin produced biosonar signals that had acoustic characteristics comparable to those previously recorded for this species. The biosonar beam was predominantly single-lobed, occasionally dual-lobed, and demonstrated greater directionality when compared to beams of similar frequency content reported for the harbor porpoise, bottlenose dolphin, and false killer whale.

4.3 Methods

A. Experimental subject and setup

The experimental subject of this study was a female Risso's dolphin named Da Hwa, housed in the animal care facilities of Fargory Ocean Park, in Hualien County, Taiwan (Fig. 4.1).

The animal was caught from the wild in 2003, but has been cared for at the site of the study for 10 years, and was approximately 17 years old at the time of the experiment. Data were collected on August 13, 2014. At that time, the dolphin weighed 290.5 kg and measured 2.91 m in length. Previously, this animal was shown to have hearing sensitivities comparable to those already described for this species (Mooney et al. 2015), which include generally sensitive hearing across the range of frequencies from approximately 10 to 90 kHz (Nachtigall et al. 1995, 2005). Data were collected in one of the seven interconnected above-ground concrete pools that constituted the habitat enclosure at Farglory Park. This experimental pool was generally rectangular in shape, containing 1520 m^3 of water volume with a maximum depth of 7.2 m. The experimental setup can be seen in Figure 4.2.

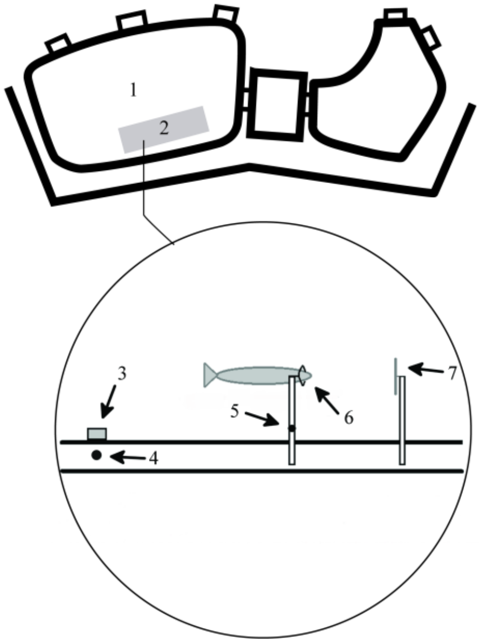

Fig. 4.2 *Experimental setup for recording of echolocation signals. 1 - experimental pool, 2 - location and orientation of the experimental setup within the pool (grey box), 3 - stationing location of animal between trials, 4 - location of trainer, 5 - underwater camera, 6 - station hoop, 7 - recording array.*

Echolocation signals were recorded from the animal when it was stationed horizontally in an underwater hoop parallel to the pool wall. The hoop, made of PVC and rubber tubing, was suspended in the water 1.55 m away from the side of the pool at a depth of 1 m via a wooden plank that extended out above the water perpendicular to the side of the pool. The tip of the animal's rostrum was approximately 15 m away from the perpendicular wall in front of it. In the same manner, the recording array was suspended in the water 2 m in front of the hoop, with the center hydrophone positioned at 1 m depth directly in line with the center of the hoop. To monitor the animal's position during trials, an underwater camera (SCS Enterprises, Montebello, NY, USA) was positioned at a depth of 1 m in the water to the side of the stationing subject at an angle of 90 degrees to the center of the station hoop. This camera was viewed in real time by the trainer as trials were being conducted and also recorded on a laptop.

B. Experimental procedure

The test subject commonly shared pools with bottlenose dolphins also housed at the facility. Prior to the start of an experimental session, the animal was asked to separate into one of the two pools used for data collection. Experiments consisted of multiple trials where the trainer asked the subject to station horizontally in the hoop up to its pectoral fins. Once the animal was properly positioned in the hoop, acoustic recording with the hydrophone array was started and echolocation clicks were collected for up to 60 seconds. Since the animal was not trained for any target detection or discrimination tasks, attempts were often made to stimulate echolocation by dropping a 5 lb scuba weight attached to monofilament line 1 m into the water at varying distances between 2-8 meters behind the array. Clicks were also recorded when the target was not present in the water. Because no detection tasks were being performed, there was no visual obstruction between the subject and the array or target. Trial lengths varied, but typically lasted between approximately 10 and 60 seconds each, after which the trainer blew a whistle, signaling the animal to back out of the hoop and return to the trainer to receive a reward.

C. Data acquisition

Click signals were recorded using an array of 16 Reson 4013 hydrophones (Reson, Slangerup, Denmark) attached to a 1/2 inch PVC frame and arranged in a star shaped pattern (Fig. 4.3).

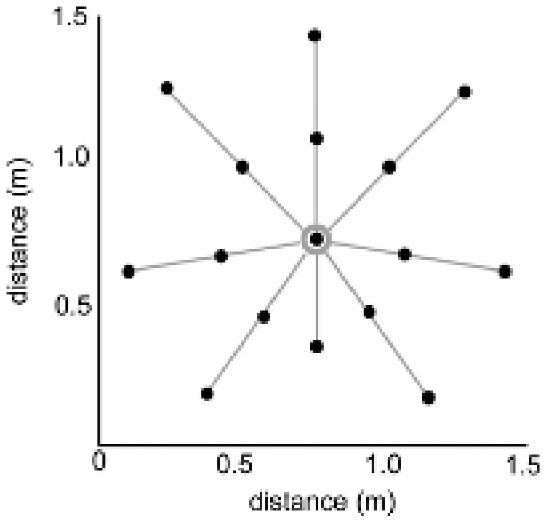

Fig. 4.3 *Diagram of the 16 element hydrophone array, as previously published in Kloepper et al. 2012b. Black circles represent the location of each hydrophone.*

Hydrophones were approximately 25 cm apart, with the full diameter of the array measuring 1.46 m. This configuration has successfully been utilized to investigate echolocation characteristics in a number of previous studies (Ibsen et al. 2012; Kloepper et al. 2012b). The distance between the pool wall and the outmost hydrophones on the near-side of the array was 82 cm. Each hydrophone occupied an independent channel and was amplified by 20 dB with a custom-built sixteen channel amplifier before being sent to two National Instruments DAQmx

PCI-6133 analog to digital (A/D) boards (National Instruments, Austin, TX, USA), where the signals were digitized using a custom LABVIEW (National Instruments, Austin, TX, USA) program at a rate of 500 kHz for offline analysis. Simultaneous recording of a 1000 sample window from all 16 hydrophones was triggered by the central hydrophone, including a 50 sample rolling buffer which allowed the clicks to be recorded in their entirety on all the hydrophones despite the slightly delayed time of arrival on the peripheral hydrophones. The data were then analyzed using custom algorithms written with MATLAB software (Mathworks, Natick, MA, USA). Prior to the experiment, the array was calibrated and demonstrated less than 2 dB variation in sensitivity to received synthetic broadband click signals with a center frequency of 60 kHz projected with a Reson 4040 (Reson, Slangerup, Denmark) transducer.

D. Data analysis

The slightly flexible nature of the PVC station hoop allowed the animal to sometimes push the hoop a few centimeters forward while trying to maintain the proper stationing position. Similarly, the distance that the animal pushed its head into the hoop was also somewhat variable. Both situations resulted in a small measure of variability in the distance between the animal and the receiving array. The structures responsible for sound generation were assumed to be the phonic lips, situated directly underneath the blowhole. Recordings from the underwater hoop camera for each trial were analyzed with Tracker motion analysis software (Brown 2009) to calculate the precise distance the hoop was pushed forward for each click and the distance the animal's sound generating structures were positioned ahead of the hoop. Thus, the precise distance between the animal and the array was measured and this distance was used to determine source level values.

To determine the value of echolocation parameters, first the on-axis echolocation signal was identified as the hydrophone with the highest peak-to-peak voltage value. Signals in which the on-axis click was located on the peripheral array hydrophones were omitted from further analysis. The source level, center frequency, peak frequency and -3 dB bandwidth (as described in Au and Hastings 2008) were calculated from the on-axis clicks using a 200 sample window encompassing the signal, with click energy starting around the sample 50 due to the rolling buffer of the acquisition program.

To determine the full spectrum beam shape, we employed an interpolation method used in prior beam measurement studies (Starkhammar et al. 2011; Kloepper et al. 2012b). The sound pressure levels were first calculated on each hydrophone and then cubically interpolated over a 0.05 m meshgrid superimposed on the array surface. A contour was then constructed representing 3dB less than the peak sound pressure level (SPL) of the click, and the area of the contour was calculated to yield the -3dB beam area. Because the recorded beam was circular (see results and Fig. 4.4), angular beamwidth was calculated using the radius of the beam area and distance measurements between the array and position of the phonic lips obtained from the video analysis.

To determine the frequency dependent beam shape, we used a method similar to Kloepper et al. (2012b). For each individual click, amplitude values from each hydrophone were averaged across 10-kHz bands. These mean amplitude values were estimated via cubic interpolation at the nodes of a 0.05 m square grid superimposed over the array, then normalized to the peak amplitudes across all frequencies. The normalized amplitude values were finally plotted on an approximately 0.7 m^2 two dimensional representation of the array. Classification of the lobe structure of clicks was based on strict criteria for visual inspection of these plots. Clicks were classified as "dual-lobed" if the following criteria were met: 1) two distinct amplitude peaks were present, and were separated by a "valley" of lower energy that was at least 6 dB less than the amplitude of the predominant peak, 2) the secondary peak (i.e. the peak with lower amplitude) was at least 3 dB greater than the amplitude of the valley separating the two peaks, and 3) the amplitude of both peaks was within 12 dB of the peak amplitude of the click.

Given the variable environment in which the recordings were made, care was taken to remove all potentially confounding acoustic signals from the final dataset. While the test subject was the only animal present in the experimental pool during data collection, the pools were interconnected via swimming channels with metal barred gates as a barrier. This prevented complete acoustic separation between the test animal and the bottlenose dolphins in adjacent pools. Occasionally, clicks from the bottlenose dolphins in the side pools (see Fig. 4.2) could trigger the array recording through the gates. Such recordings were easily identified and removed from the analysis dataset via time-of-arrival differences of individual clicks at each hydrophone. Additionally, some recordings on the array would be triggered by a Risso's dolphin click but would also contain a recording of a bottlenose click within the 1000 sample recording window. Visual analysis of all waveforms was performed to determine if the bottlenose clicks were within the 200 sample analysis window surrounding the Risso's click. If so, they were subsequently omitted from the final dataset. At the same time, any other significant spurious acoustic energy that occurred within the recording window was also identified, usually in the form of returning echoes from either the animal's ensonification of the target or likely reflection off the perpendicular wall in front of it. If such reflections occurred within the 200 sample analysis window, the click was removed from the dataset. Furthermore, clicks were only included in the final analysis if the center hydrophone was within the -3dB beam area contour. These conservative criteria were used to ensure that the -3dB beam area was represented in its entirety on the array.

To characterize the directivity of the dolphin's signals, we calculated the Directivity Index (DI), a measure of the directional property of a reception or transmission beam that is proportional to the size of the acoustic transducer (Urick 1983). We assumed the sound generator to be modeled as a circular piston in a baffle (Au 1993), and that the radius of that piston transducer is much greater than the wavelength of the projected sound. The angular beamwidth of a circular piston is given by the following equation from Au and Hastings (2008):

$$\theta \ = \ \sin^{-1}(\frac{0.509}{d/\lambda}) \tag{1}$$

If the angular beamwidth (2θ) and wavelength (λ) of the transmitted sound are known, the diameter (*d*), and thus the area (*A*) of the circular transducer can be calculated by rearranging Eq. (1) into

$$A = \ \pi\left(\frac{0.509\lambda}{2\sin(\theta)}\right)^2 \tag{2}$$

Using the measured -3dB angular beamwidth (2θ) and center frequency wavelength (λ) of the transmitted sound, we first calculated the area of the hypothetical piston with Eq. (2). Then, using the calculated area, the DI was determined with the following equation:

$$DI = 10\log\,(\frac{4\pi A}{\lambda^2}) \tag{3}$$

Regression analysis was conducted to compare the relationship of the calculated acoustic features of all clicks, and an unpaired t-test was conducted to compare acoustic features between single and dual-lobed signals. All statistics were conducted using SPSS v.22 (IBM, Armonk, NY, USA).

4.4 Results

A data set of 1190 echolocation clicks were recorded and considered for analysis. After our selection process (see methods), the final dataset consisted of 656 clicks. The mean distance between the animal's blowhole and the array was 1.71 m, which was used for all range dependent calculations. The on-axis waveform, spectra, and full-spectrum beam shape of a typical click are represented in Figure 4.4.

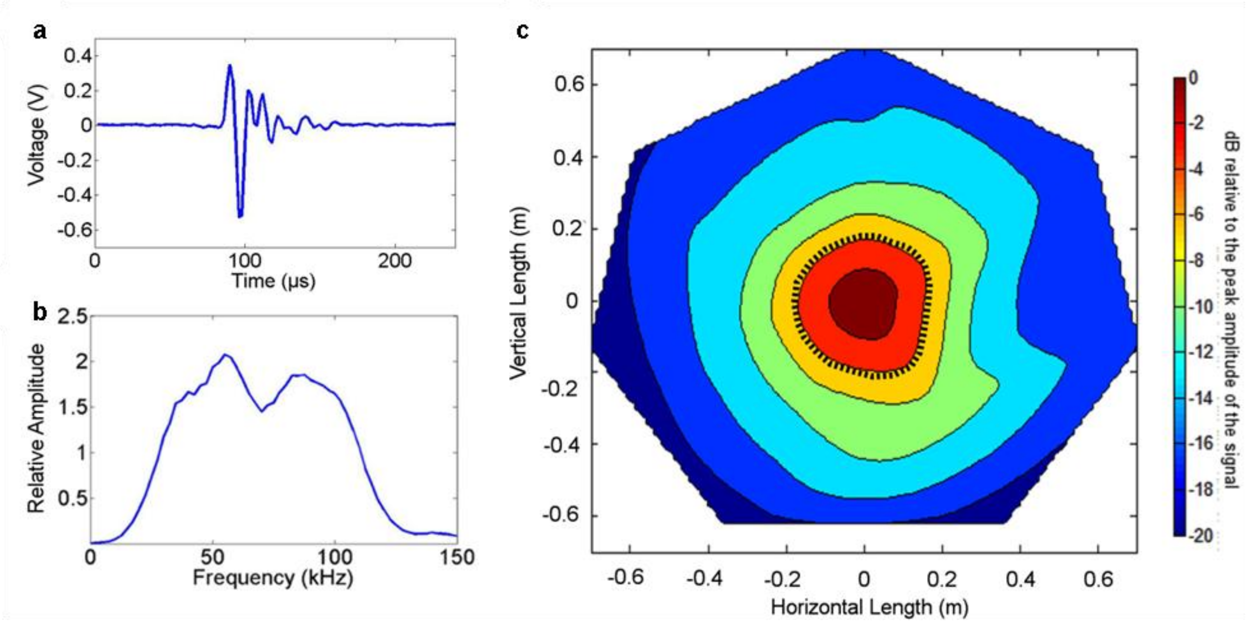

Fig. 4.4 *Waveform (a) and spectrum (b) of a typical on-axis click produced by the Risso's dolphin in this experiment. Click durations were approximately 80 µs long. (c) The full-spectrum beam shape of the same click. The dotted line encircles the -3dB beam area (0.035* m^2*).*

On-axis echolocation signals were produced at peak-to-peak levels ranging between 171 and 216 dB SPL re: 1µPa (mean: 192 ± 9). Mean and standard deviation values for centroid frequency, peak frequency, and -3 dB bandwidth were 61 ± 8, 53 ± 12, and 38 ± 15 kHz, respectively. Peak frequencies showed a bimodal distribution, with separate groupings centered around 38 and 60 kHz. The -3 dB beam areas for all clicks were circular in shape, with a mean area of 0.055 ± 0.024 m^2.

There was a significant positive linear relationship ($R^2 = 0.32$, $p < 0.01$) between center frequency (CF) and source level (SL, Fig. 4.5A) of the echolocation clicks, with $SL = 150.72 + 0.67(CF)$. There was a significant negative linear relationship ($R^2 = 0.55$, $p < 0.01$) between CF and beam area (BA, Fig. 4.5B), with $BA = 0.16 - 0.002(CF)$. There was a significant, albeit weak ($R^2 = 0.18$, $p < 0.01$) positive linear relationship between CF and -3dB bandwidth (BW, Fig. 4.5C), with $BW = -12.23 + 0.82(CF)$.

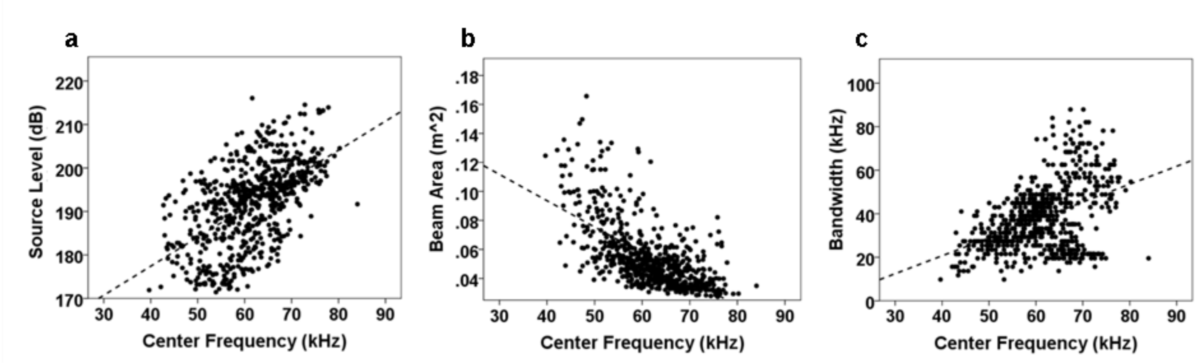

Fig. 4.5 *Relation between center frequency and acoustic features of signals. a) Change in source level (dB re: 1µPa) with center frequency. There was a significant positive linear relationship ($R^2 = 0.32$, $p < 0.01$) between center frequency and source level; b) Change in beam area with center frequency. There was a significant negative linear relationship ($R^2 = 0.47$, $p < 0.01$) between center frequency and beam area; c) Change in -3dB bandwidth with center frequency.*

Echolocation clicks with smaller beam areas demonstrated on-axis click spectra with higher overall amplitudes and more energy at higher frequencies than signals with wider beam areas. In addition to varying the click spectra, the dolphin demonstrated flexibility in the overall beam size within a trial. Over just a few clicks, the dolphin changed its beam area nearly three-fold with no clear pattern in beam area modification. Across all trials, there was no correlation ($R^2 = 0.02$) between click number and beam area, indicating the dolphin varied its beam area unpredictably throughout a trial. This is not unexpected given that the animal was not performing a trained echolocation task.

The frequency dependent beam shapes of a typical click can be seen in Figure 4.6A. The majority (98.2%) of clicks were relatively symmetrical and circular in shape, exhibiting energy in a single primary lobe both for the full-spectrum beam (Fig. 4.4C) and for a frequency-dependent beam separated into 10 kHz bins (Fig. 4.6A), with a narrowing at higher frequencies. However, a small subset (1.8%) of clicks exhibited a vertically oriented dual lobe structure that was frequency dependent (Fig. 4.6B).

For these signals, the dual-lobed structure appeared consistently within the 60-100 kHz frequency band. There was a significant difference in peak frequency (PF) and bandwidth (BW) between the single lobed and dual-lobed conditions; (PF: $t(656) = 2.75$, $p < 0.01$; BW: $t(656) = 2.65$, $p < 0.01$). The dual-lobed signals demonstrated higher peak frequencies and wider bandwidths than the single-lobed signals. There was no significant difference in source level, center frequency, or beam area between the two beam types ($p > 0.05$).

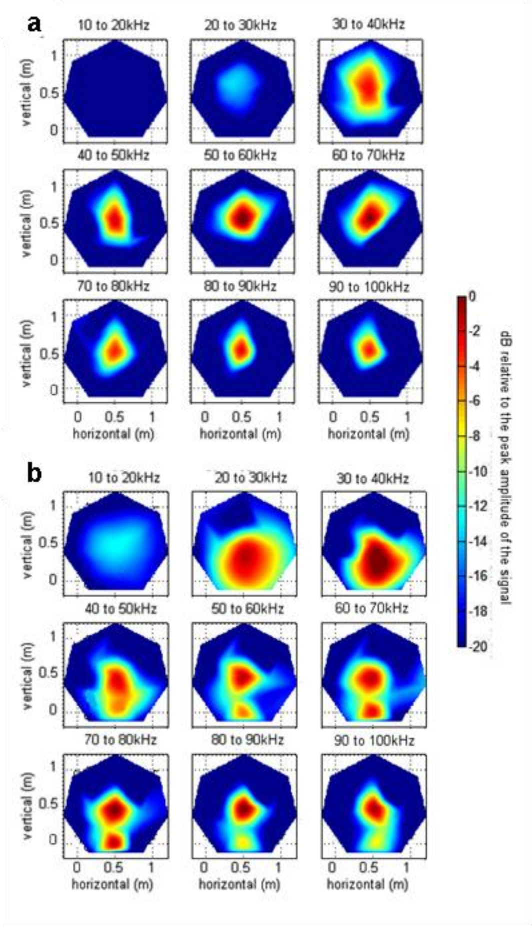

Fig. 4.6 *Frequency dependent amplitude plots of two separate clicks exhibiting (a) single-lobed and (b) vertically oriented dual-lobed beam shape. The spectrum of each click as recorded across the hydrophones is binned into 10 kHz groups and overlaid across spatial representations of the recording array. The two separate lobes in (b) are separated by approximately 13.2°.*

The average -3 dB angular beamwidth for all clicks was 8.7 degrees. The resulting mean radius of the hypothetical circular piston was 13 cm (see Eq. 1 and 2 in methods), with a minimum of 9 cm. This is more than three times greater than the 2.4 cm wavelength of the CF, making a calculation of the DI from Eq. (2) valid. Using the CF, radius values, and distance between the phonic lips and array, a directivity index was calculated for each recorded echolocation click. The mean DI was 26.6 dB (± 1.5 SD) for this Risso's dolphin, ranging between 21.7 and 30.0 dB. Angular beamwidth narrowed and the DI increased as CF of the

Risso's echolocation clicks increased (Fig. 4.6), generally following the principles of linear acoustics in which higher frequencies create more directional beams than lower frequencies. However, the relationship between CF and DI in the Risso's dolphin showed a significantly logarithmic relationship (Fig. 4.7, $R^2 = 0.5$, $p<0.01$), with $DI = -7.11 + 8.21 * \log(CF)$, with the directivity of clicks appearing to level off at higher CF values.

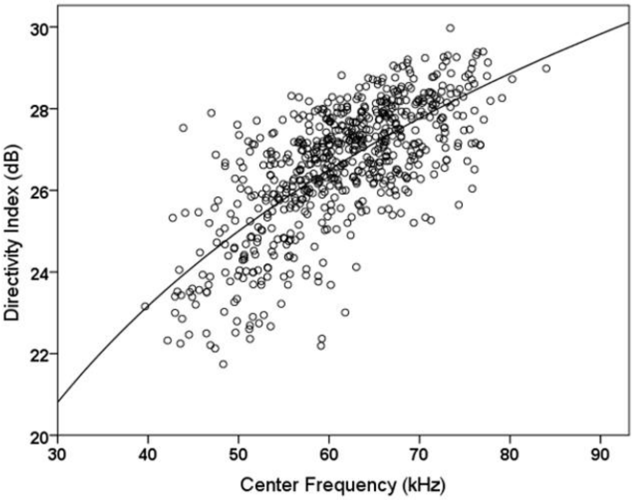

Fig. 4.7 *Change in directionality index (DI) of Risso's echolocation clicks according to centroid frequency (CF), fit with a logarithmic regression (*CF^2*,* $p < 0.01$*,* $R^2 = 0.5$*).*

4.5 Discussion

In this study, we recorded and analyzed the echolocation clicks of a stationary Risso's dolphin with an array of 16 hydrophones. These results demonstrate the first reporting of controlled, conclusive on-axis echolocation clicks and beam characteristics from a Risso's dolphin. Echolocation clicks have previously been recorded from both captive and free-ranging Risso's dolphins (Philips et al. 2003; Madsen et al. 2004b), although the on-axis nature of the echolocation signals was assumed in both these studies and not directly controlled for. The mean, maximum, and minimum values for SL, CF, peak frequency, and -3dB bandwidth reported here fall closely in line with those reported previously, which further supports the assumption of Philips et al. and Madsen et al. that they recorded on-axis echolocation signals. While our mean SL and centroid frequency were lower than the recorded free ranging individuals by 30 dB and 14 kHz, respectively, such differences are not unexpected since odontocetes have been shown to produce higher SPLs in open water environments versus closed tank environments in captivity (Au 1993).

Despite the strong similarity of on-axis acoustic parameters measured here with the previously studied captive individual and free-ranging animals, it is important to note that the beam measurements were collected from only a single individual and may not be representative of the entire species. There is demonstrated variability of click spectral properties and beamwidth between multiple individuals within a species (Houser et al. 1999), and individuals also change their outgoing signals according to the task being performed (Au et al. 1985; Houser et al. 1999; Philips et al. 2003; Kloepper et al. 2012a; Wisniewska et al. 2015). In this study, the test subject was not performing a trained echolocation task and therefore comparison of the Risso's in this study to other species should be made with caution. However, these are the first beam measurements taken of a Risso's dolphin and it is nonetheless valuable to make comparisons with the data that are available, as has been done in previously published studies on the beam characteristics of individuals of other odontocete species (Au et al. 1995, 1999; Rasmussen et al. 2004).

The Risso's produced a small subset of echolocation signals that exhibited a dual-lobed structure (Fig. 4.6). This dual-lobed characteristic has been reported for other odontocete species (Starkhammar et al. 2011; Kloepper et al. 2012b) and with bats, another group of echolocating mammals (Ghose et al. 2007). Although the exact mechanism for producing these dual-lobed signals is unknown, it is thought that this dual-lobe structure might aid in signal processing during echolocation. The dual-lobed signals produced by this individual Risso's dolphin have higher peak frequencies and wider - 3 dB bandwidths than the single-lobed signals. This suggests that the dual-lobed nature of these signals may be generated internally, since the frequency characteristics of signals are thought to be driven by properties of the soft tissue structure generating echolocation clicks (Cranford et al. 2014). However, since the Risso's was not performing a trained echolocation task and the dual lobed occurrences were rare, their biological relevance cannot be determined from this study.

The mean angular beamwidth of 8.7 degrees for this Risso's dolphin is narrower than that recorded for the harbor porpoise (16.5º, from Au et al. 1999; 13º and 11º in the horizontal and vertical plane, respectively, from Koblitz et al. 2012) and bottlenose dolphin (10º, from Au 1993), but wider than that of the beluga (6.5º, Au et al. 1987). It is also similar to that of the false killer whale, which was found to have a 9.7º and 6.2º angular beamwidths in the vertical and horizontal planes, respectively (Au et al. 1995). The directionality of a sound is influenced by the frequency content of the emitted sound, therefore complicating any comparison of the DI between different species. Nonetheless, comparisons can be made if the appropriate signals are considered. While the Risso's dolphin produces clicks with mean centroid frequencies almost one octave lower than those of trained bottlenose or belugas (Madsen et al. 2004b), there are a subset of Risso's clicks that exhibit centroid frequencies between 70-85 kHz (N=94, 14% of total), which bear the closest resemblance to the overall spectral content of clicks from the other species. A mean DI of 28.0 dB for this subset of clicks further indicates the Risso's dolphin in this study has a narrower echolocation beam than that reported for a harbor porpoise (22 dB, Au et al. 1999; 24 dB, Koblitz et al. 2012) and a bottlenose dolphin (26 dB, Au 1993), a similar beam to that of a false killer whale (28.5 dB, Au et al. 1995), but a wider beam than a beluga (32.1 dB, Au et al. 1987).

The beam pattern data for a false killer whale published by Au et al. (1995) includes multiple DIs calculated for different groups of echolocation clicks, allowing for closer comparison with the Risso's in our study. In the Au et al. study, signals were categorized into 4 groups according to spectral shape and frequency emphasis, with a mean CF and DI calculated for each group. Comparison of DI values between the Risso's clicks and false killer whale click groups reveals that the DI of the Risso's tended to be higher than the false killer whale when CF is taken into account (Fig. 4.8). The difference between the individuals appears to be greater at the lower and mid CFs (~40-70 kHz) than higher ones (>70 kHz).

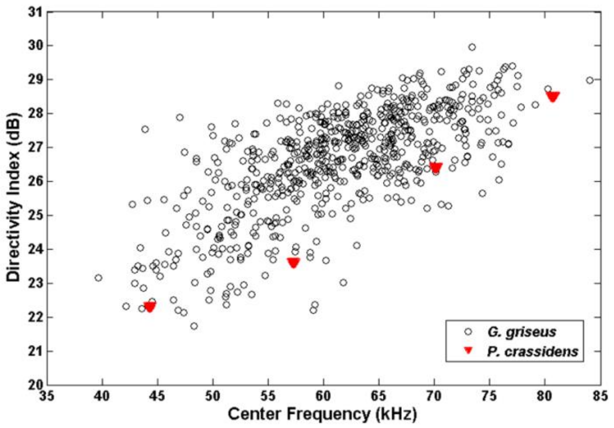

Fig. 4.8 *Comparison of directionality index (DI) according to centroid frequency for the Risso's dolphin and false killer whale. DI values for the false killer whale came from Au et al. (1995).*

Given the experimental differences in data collection between the Risso's and false killer whale, it cannot be concluded here if the differences in DI between the two are task or species related. However, it is reasonable that a generally increased directionality of lower frequency signals could be valuable for effective performance of the Risso's biosonar. Risso's dolphins occur primarily in temperate and tropical deep waters near continental shelves and submarine canyons (Leatherwood et al. 1980), and are thought to feed almost exclusively on neritic and oceanic squid as indicated by analysis of stomach contents from stranded individuals (Clarke and Pascoe 1985; Cockcroft et al. 1993; Blanco et al. 2006). While only one study has documented the diving behavior of a single, rehabilitated individual (Wells et al. 2009), the species' capability to dive deeply in search of prey is further corroborated by passive acoustic recordings on receivers at depths of 800 m in the Mediterranean (Giorli et al. 2015). The increased directionality of the Risso's outgoing beam at lower frequencies, combined with reduced attenuation of lower frequencies through a medium, would result in an improvement in the overall detection range of a biosonar system; an adaptation that is likely advantageous for an animal foraging in deeper, open ocean waters.

In addition to being influenced by frequency, the DI parameter is also proportional to the size of a transducer (Urick 1983). If a circular piston transducer with a larger area produces the same beam pattern at the same frequency as a transducer with a smaller area, the larger transducer would have a higher directivity index. Thus, perhaps difference in DI between the *G. griseus* and *P. crassidens* individuals may be explained by a difference in size of the sound generating structures. Au et al. (1999) made a comparison of DI to the head diameter of four species of odontocete, using head diameter as a likely relative indicator of the size of the animal's sound generators, and found there was a strong correlation between DI and head diameter divided by the wavelength of the peak frequency (d/λ) of the animal's click signals. The head circumference of the Risso's used in this study was 120 cm at the position of the blowhole, with a corresponding diameter of 38.2 cm. Coincidentally, these are the same head measurements as those reported for the false killer by Au et al. (1999). Like the above DI comparison between species, it is important to make comparisons based on clicks with the most similar spectral emphasis. The subset of Risso's echolocation clicks that most closely resembled the clicks for other species (i.e. the 14% of clicks with the highest CF values), exhibited a mean peak frequency of 63.4 kHz, with a corresponding wavelength of 0.023 m. The same analysis of Au et al. (1999) applied to this Risso's dolphin resulted in a d/λ parameter value of 16.6 cm/Hz. Plotting these values for the Risso's dolphin alongside those for the additional species originally published by Au shows that the directional beam characteristics of this Risso's do not fit well into the relationship reported for other species (Fig. 4.9). Despite producing peak frequencies lower than the other species by more than 50 kHz, the Risso's beam was surprisingly directional even when accounting for the large head size.

The Risso's deviation from the trend seen in other species cannot be attributed to click frequency content nor the size of the head (and thus the presumably related size of the sound generating structures), suggesting it may be due to influences from anatomical structures responsible for the directional transmission of echolocation clicks into the environment. Such structures are thought to be homologous in odontocete species (Cranford et al. 1996), and include the skull, air sacs, and melon (Aroyan et al. 1992; Cranford et al. 2014). Definitive attribution to one of these specific structures is not possible with the data available. However, as the unique melon cleft is arguably the most conspicuous difference in head morphology of the Risso's and its function remains unknown, it is interesting to speculate on the cleft as a possible factor influencing this deviation.

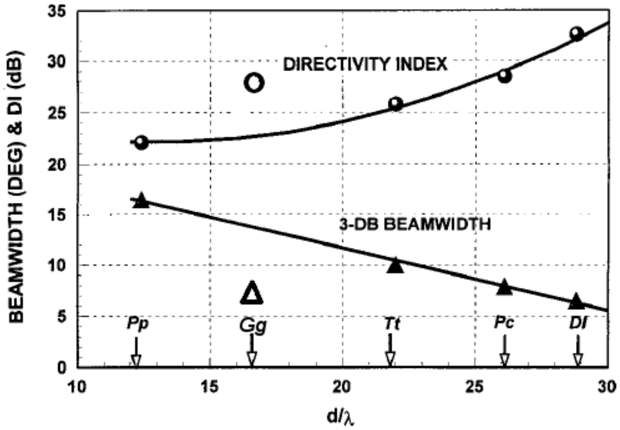

Fig. 4.9 *Plot originally published by Au. et al., (1999) of the relationship between directivity index, - 3 dB angular beamwidth, head circumference, and wavelength of peak frequencies for four odontocete species (Pp - harbor porpoise, Phocoena phocoena; Tt - bottlenose dolphin, Tursiops truncatus; Pc - false killer whale, Pseudorca crassidens; Dl - beluga whale, Delphinapterus leucas). The results of that study showed a strong correlation between the parameters in the four previously studies species. The same data for the Risso's dolphin was collected in this study, and has been added to the original plot for comparison (Gg - Grampus griseus). The relationship between the four parameters in the Risso's dolphin does not fit well with the relationships described in other species. It should be noted that recent studies have found the transmission beam of a second harbor porpoise individual to be narrower than that recorded by Au et al. (1999), with a DI of 24 dB (Koblitz et al. 2012), however since no data on head circumference or click peak frequencies was simultaneously presented, it cannot be included in the current comparison.*

The shape of the melon likely has an influence on the directional formation of signals in most odontocete species (Litchfield and Greenberg 1974; Mckenna et al. 2012), and it has been speculated that the unique external morphology of the *G. griseus* melon is important for the echolocation of the species (Nachtigall et al. 1995; Philips et al. 2003). It seems plausible that the cleft structure may influence some aspect of the outgoing beam, including the directionality of the signal. Multiple studies have documented the lipid topography inside the odontocete melon, which shows a low-density, slower sound speed core surrounded by a gradient of higher density, faster sound speed layers towards the outer regions of the acoustic fats and tissue near the seawater interface. The variable sound velocities as a result of this layering are thought to significantly assist in the refractive collimation of the directional acoustic beam (Litchfield et al. 1979), which has been corroborated by studies using finite element modeling methods (Cranford et al. 2014). The magnitude of this refraction would also be influenced by the angle at which the generated sound waves hit the interfaces between the layers, including the tissue-seawater interface (i.e. forehead shape). The increased amount of surface curvature of the Risso's melon created by the raised ridges would result in different angles of incidence of projected echolocation clicks than the smoothly rounded melon shapes of most odontocetes, which may be one mechanism by which the cleft could increase the directionality of the outgoing beam. Furthermore, the magnitude of this potentially increased refractive collimation may also be frequency dependent due to the spatial location of the thickened ridges lateral to the midline of the melon. However, no conclusions can be made about these hypotheses from this study alone. More controlled investigations with a greater number of individuals of the species are required to further address these possibilities.

4.6 Conclusions

Echolocation signals were recorded with an array of hydrophones from a captive Risso's dolphin (*Grampus griseus*) that was trained to station in an underwater hoop. On-axis signal characteristics were investigated from the hydrophone with the highest peak-to-peak voltage, and beam characteristics were explored using both broadband and frequency dependent amplitude plots of click signals. These data show that the overall two dimensional shape of the beam in *G. griseus* is similar to that reported for the bottlenose dolphin and false killer whale. The relationship between signal frequency content, directionality, and estimated size of the sound generating structures in the Risso's individual does not fit well with the same relationship trend described for individuals of other species. This Risso's showed an increased directionality at lower frequencies when the signal frequency content and estimated size of the sound generating structures were considered, which suggests the influence from anatomical structures responsible for the directional transmission of echolocation clicks into the environment such as the skull, air sacs, or melon.

Chapter 5

CONCLUSION

5.1 Summary

Odontocetes are considered to be acoustic specialists, which extensively utilize sound to forage, navigate, and communicate with conspecifics. Yet, while there are approximately 76 species of odontocete (Committee on taxonomy 2014), there are little to no data available on hearing or echolocation characteristics from the vast majority of them. The specific goal of this dissertation research was to investigate and describe basic characteristics of hearing and echolocation in under-studied odontocete species. The results presented here provide the first descriptions of auditory temporal resolution in four species (the spinner dolphin, pygmy killer whale, long-finned pilot whale, and Blainville's beaked whale), a comparison of far-field directional hearing and auditory pathways in the Risso's dolphin, and also the first description of the transmission beam in the same individual of this species.

In the second chapter, the modulation rate transfer functions were measured from four stranded odontocetes by recording auditory evoked potentials in response to temporally modulated stimuli. The individuals all showed the ability to process stimuli at high modulation rates up to and exceeding 1250 Hz. These data indicate auditory temporal resolution similar to other studied odontocete species and support the hypothesis that high temporal resolution is conserved throughout the diverse range of odontocete species (Mooney et al. 2009). Comparison of the MRTFs between odontocetes of different echolocation characteristics suggests that auditory temporal resolution is not related to echolocation signal type. However, there is a general trend indicating that animals with smaller body sizes show better auditory temporal resolution as estimated from their MRTF.

The results of the third chapter expand upon the work of previous researchers and provide a more detailed characterization of asymmetric auditory thresholds in the Risso's dolphin, as well as auditory reception along the unique morphology of the Risso's dolphin melon. The Risso's dolphin shows an area of increased auditory sensitivity in the middle of the melon cleft, which may indicate that the melon provides some degree of auditory reception. Additionally, auditory threshold measurements from multiple analogous locations on both the right and left sides of the dolphin's head showed consistent asymmetry, with the animal's hearing being significantly elevated on the right side. These results may suggest that either pathways for received sound are asymmetric between the right and left sides of the head, or it may reflect an asymmetry in the auditory sensitivities of the two ears themselves. Furthermore, this research resulted in the first description of directional hearing in this species, constituting only the fifth odontocete species for which directional hearing measurements are available. The Risso's dolphin was found to have acute, frequency-dependent directional hearing that is similar to other described species (Kastelein et al. 2005; Popov et al. 2006; Popov and Supin 2009). The comparison free-field directional hearing to asymmetric auditory thresholds to contact sound stimuli in one individual provided the first insight into how these auditory measurements compare to each other and may yield different results.

The results of the fourth chapter provide the first description of the echolocation transmission beam of a Risso's dolphin. Echolocation signals were recorded with an array of hydrophones from a captive individual that was trained to station in an underwater hoop. On-axis signal characteristics were investigated from the hydrophone with the highest peak-to-peak voltage, and beam characteristics were explored using both broadband and frequency dependent amplitude plots of click signals. The overall two dimensional shape of the beam is similar to that reported for the bottlenose dolphin and false killer whale, although the relationship between signal frequency content, directionality, and estimated size of the sound generating structures in the Risso's individual does not fit well with the same relationship trend described for individuals of other species (Au et al. 1999). Compared to the false killer whale (Au et al. 1995), the Risso's showed an increased directionality at lower frequencies when the signal frequency content and estimated size of the sound generating structures were considered, which suggests the potential influence from anatomical structures responsible for the directional transmission of echolocation clicks into the environment such as the skull, air sacs, or melon. As a deep diver foraging in open ocean water, this increased directionality is likely advantageous for individuals of the species by increasing the detection range of their biosonar system.

Fundamental aspects of echolocation and hearing remain largely unexplored in most odontocete species due to the fact that such research can only be conducted with animals under direct human care and often requires extensive training and resource investment for research specific tasks. Such requirements have largely limited most complex auditory research to the few species that are trained and cared for at scientific institutions. The availability of different species is a common limitation when doing research with marine mammals in controlled experimental settings. This research highlights the value of supporting and partnering with public display and rehabilitation facilities which care for and train a much greater diversity of marine mammal species than are found in research institutions. Such collaborative efforts provide an invaluable opportunity to increase basic knowledge of acoustic systems in additional odontocetes and provide for more powerful comparative analysis across species.

5.2 Future research

The results presented here also yield new research questions that should receive additional investigation. The apparent correlation between animal size and auditory temporal resolution requires further exploration to elucidate the possible causes of this relationship and whether or not it represents a biologically significant trend in odontocete audition. Currently, it cannot be ruled out that the trend is an epiphenomenon related to the use of non-invasive AEP methods across subjects with a large gradient in body size. To exclude this possibility, auditory temporal integration times should also be estimated via behavioral experiments with trained individuals of the same species. Such experiments would both test the assumption that MRTF estimates of auditory integration time match those of behavioral paradigms in species' beside the bottlenose dolphin and also indicate if the trend between body size and MRTF estimates of auditory temporal resolution is simply an artifact of the electrophysiological methodology. Additionally, while auditory temporal resolution has now been investigated in 13 odontoctes, this represents a small fraction of the total number of extant species. Attempts should also be made to opportunistically measure auditory temporal resolution in additional odontocetes, which could allow for comparison of temporal acuity in relation to ecological factors such as prey choice, habitat, diving behavior, or foraging strategies.

The auditory temporal resolution of the small, neonate Risso's dolphin (Mooney et al. 2006) constitutes a noticeable deviation from the trend described here. The relatively poor resolution found in this individual cannot be attributed to a disparity in body size. It is possible that the poor temporal acuity in this individual may be due to its very young age. While there is evidence that neonate odontocetes exhibit precocious hearing (Wahlberg et al. 2017), the development of auditory temporal resolution has not been measured directly. It is suggested that

MRTFs should be collected from an adult Risso's dolphin for comparison, and future efforts should be made to measure MRTFs from individual odontocetes at different life stages.

Current understanding of odontocete sound reception is still incomplete. The asymmetry to contact acoustic stimuli found in the Risso's dolphin here as well as multiple other odontocetes may suggest that asymmetry in auditory pathways is likely more pervasive in these animals than previously considered. It has been hypothesized that there are multiple, frequency dependent pathways by which sound is channeled to the odontocete ear (Popov and Supin 1990b; Ketten 1992, 2000, Popov et al. 1992b, 2008; Mooney et al. 2014). Asymmetric, frequency dependent acoustic pathways on either side of an animal's head perhaps confer some benefit towards signal processing and localization of sound. However, most studies of odontocete auditory pathways test only a single side of an individual's head. Future research of odontocete auditory pathways should thus investigate the possibility of frequency and site-specific asymmetry between the right and left sides of a test subject's head, and attempt to tie these characteristics to signal processing and localization abilities.

These same experiments should also extend to the possibility of auditory reception on the melon. Multiple documentation of areas of increased auditory receptivity along the anterior face of the melon beg the question: does sound reception via the melon represent a functionally significant acoustic pathway? It has been postulated that a window auditory sensitivity along the melon could play some role in the directional localization of received acoustic signals (Nachtigall 2016). This question could be approached by measuring minimum audible angles in a trained a captive individual under two experimental contexts: one where acoustic signals incident on subject's melon cleft are blocked by neoprene and a second context where the subject's melon cleft is uncovered. Such an method has previously been used to investigate auditory reception in the bottlenose dolphins (Brill and Harder 1991).

This future research direction is particularly intriguing when considering the potential function of the unique morphology of Risso's dolphin melon. If the melon does represent a functional pathway for received sound, then perhaps the raised ridges, which create the bifurcated melon shape and appear to exhibit poorer sensitivity than the melon valley, shade or attenuate sounds laterally incident on the dolphin's head. Such a mechanism could potentially increase the magnitude of binaural cues available to the dolphin, and improve sound localization acuity. However, due to the importance of the melon for effective transmission of sound into the environment, it has been more commonly hypothesized that the melon groove of the Risso's dolphin plays some role in the acoustic systems of the species (Nachtigall et al. 1995). The transmission beam of the individual studied here showed no clear difference in shape from those found in other odontocetes, but did show increased directivity than would be expected by the size of the animal and the characteristics of its outgoing echolocation clicks. Finite Element Modeling is one method that could assist in determining if the melon groove plays a part in shaping the transmission beam pattern. Finite element modeling could also be paired with anatomical investigations of the tissues in the melon cleft, which would provide information about the tissues' possible acoustic properties.

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