

Functional Analyses of Whale Ears: Adaptations for Underwater Hearing

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Abstract - The echolocation ability of several dolphin species is well documented, but little is known about hearing characteristics of most marine mammals. This paper describes the major features of the peripheral auditory system in both large and small whales and presents a three-dimensional morphometric analysis of the inner ear in 12 species. Correlation analyses of inner ear morphometry vs. hearing characteristics in terrestrial and aquatic species for which audiograms are available were applied to dolphin and whale data to derive estimates of hearing ranges of larger, non-captive whales.

INTRODUCTION

Like all animals, whales (Order Cetacea) must locate food sources, navigate through their environment, and find mates. Unlike most mammals, they are obligate aquatics; i.e., they are so highly adapted to water they are unable to move, reproduce, or feed on land. All functions are accomplished in water, a dense, perpetually dim environment. It is not surprising that sound is the fundamental sensory and communication channel for whales, nor that whale ears are highly developed. Cetaceans evolved from terrestrial carnivores equipped with conventional land mammal ears [1], and evolution in the auditory system paralleled those of the rest of the body, shifting from an air-adapted system to one that transduces water-borne sound.

The term "whale" covers over 76 diverse species that range 1 to 40 meters in length and inhabit virtually every aquatic niche, from fresh water to bathypelagic [2]. The majority (suborder Odontoceti - toothed dolphins and whales, 65 species) are highly efficient echolocating predators. Odontocete echolocation signals range as high as 200 kHz, and performance as a function of noise is 6 to 8 dB lower than expected from an ideal receiver [3, 4]. The second suborder, the Mysticeti (baleen whales, 11 species) are all pelagic omnivores, some of which produce infrasonic signals that may be used for long-range communication or navigation. Substantial differences in the sounds produced by odontocetes vs. mysticetes imply radical differences in their hearing abilities, and therefore in their auditory anatomy.

As a group, whales therefore have two important aspects for hearing research: 1) the only mammalian ears fully adapted to underwater hearing; and 2) the broadest acoustic range of any known mammal group. Most whales cannot be investigated with conventional audiometric techniques.

A comparative anatomy approach was chosen because 1) peripheral auditory structures are important determinants of hearing capacities, 2) anatomical correlates of frequency ranges are well documented, and 3) adequately preserved middle and inner ears are available for most cetaceans [5, 6, 7]. Combining anatomical data with three-dimensional structural analyses to the middle and inner ear provided first level approximations of hearing ranges for non-captive species. Equivalent analyses of ears from animals with known hearing curves were used as controls for the models.

METHODS

Fifty-nine ears from 12 whale and dolphin species were examined with light microscopy and radiography. All specimens were screened with computerized tomography (CT and MRI). Computerized tomography has several advantages for this research: rapid, non-invasive "dissection" of large specimens, undisturbed views of *in situ* tissue relationships, high resolution sectional images, and numerical matrix data base for quantitative analyses, segmentation, and three-dimensional visualization. Intact heads and temporal bones were scanned on a Siemens DR3 or Spiral Plus CT using an ultra-high resolution protocol with 1 millimeter slice reconstruction and in-plane resolution of 65 $\mu\text{m}/\text{pixel}$. One millimeter MRI scans of whole animals were obtained with a Siemens Magnetom. After scanning, ears were extracted, fixed in buffered formalin, decalcified in a modified Schmorl's solution or EDTA, embedded in paraffin or celloidin, sectioned at 20 μm , and stained with hematoxylin and eosin. Fiducials were obtained with micro-drills (30 μm - 100 μm diameter) and biotic implants; e.g., skate cartilage. Unstained sections were archived in ethanol. Cochlear canal anatomy was digitized from every fifth section (80 μm intervals). The contour data were stored as Cartesian matrices from which surface areas and volumes were calculated. Three-dimensional visualizations of the inner ear were performed on Macintosh and Quadra platforms. The SAS statistical package was used for univariate and multivariate analyses of cochlear measurements. Left and right bullae were treated as individuals. Statistical analyses were performed on both raw data and on values normalized by animal length for interspecific comparisons.

Because underwater measures of auditory sensitivity are available for very few whales, peak spectra of emitted sounds were used for preliminary acoustic categorizations of animals in this study (Table 1). Vocalizations generally have the same peak spectra as the average hearing curve for that species [8]. Based on the frequency of maximum en-

ergy in a typical echolocation click, there are two ultrasonic odontocete groups: Type I with peak spectra above 100 kHz and Type II with peak spectra below 80 kHz. These acoustic divisions coincide with habitat and societal differences [9]: Type I odontocetes are solitary, inshore species; Type II are predominantly near shore or shelf species that form large, complex social pods. All mysticetes are preliminarily classed as Type M until more broad band recordings become available. The available data indicate baleen vocalizations are in the sonic to infrasonic range (peak spectra 12 Hz to 3 kHz), and are categorized as moans (0.4 to 40 seconds, fundamental <200 Hz), calls (bursts or pulses; peak <1 kHz), and songs, with complex phrasing and spectra [10, 11, 12].

RESULTS

A. Temporal Bone

There are three essential parts to the mammalian auditory periphery: 1) an outer ear which captures sound, 2) a middle ear which filters and amplifies sounds, and 3) the inner ear (cochlea) which is a band-pass filter and mechano-chemical transducer of sound into neural impulses. Although whale ears clearly follow the land mammal blueprint, they have gross and microscopic aquatic related adaptations at all auditory system levels.

Four outer ear adaptations are common to all cetaceans: there are no pinnae, no air-filled external canals, no encapsulated pneumatized areas, and exceptionally dense temporal bones with no direct, fused bony connections to the skull.

In part, these are locomotory and diving related: pinnae provide drag, and air-filled, thin-walled chambers would be a liability in rapid, repeated dives. These adaptations are, however, most extreme in echolocating species, where they subserve an acoustic function. In odontocetes the external ear canals are completely occluded by wax and debris, ending in a blind pouch that does not contact the middle ear. The temporal bones are suspended by ligaments in a peribullar sinus filled with a spongy mucosa. This ligament-mucosa complex isolates the ear from bony sound conduction and aligns the middle ear cavity with two specialized fatty channels. One relatively narrow channel runs anteriorly from the temporal bone to the mid-line of the lower jaw (Fig. 1). Anatomical and behavioral studies [9, 13, 15, 16, 18] suggest this discrete fatty tube is a low impedance channel for ultrasonic signals. Recent MRI data show that a second broader, laterally directed, funnel-shaped channel also aligns with the middle ear. This channel may act as a parallel low frequency conduit (Fig. 1) [17]. Like odontocetes, mysticetes have occluded external canals, but explicit tissue channels to the ear have not been identified. Both soft and hard tissue paths need to be investigated in mysticetes because baleen ears are not fully decoupled from the skull. In all non-echolocating whales, posterior and medial bony flanges wedge the ear against the skull and the middle ear capsule abuts a dense cartilaginous mandibular cap.

TABLE I
CHARACTERISTIC SOUNDS OF TOOTHED AND BALEEN WHALES [8, 9, 10, 11, 12, 13, 14]

Species	Common name	Sound	Frequency Range (kHz)	Frequency at Maximum Energy (kHz)
ODONTOCETI				
Type I <i>Iniua geoffrensis</i> <i>Phocoena phocoena</i>	Boutu Harbour porpoise	Click Pulse	25-200 100-160	95-105 110-150
Type II <i>Delphinus delphis</i>	Common dolphin	Whistle Click	0.2-150 0.2-150	4-9 30-60
<i>Orcinus orca</i> <i>Stenella longirostris</i>	Killer whale long-beaked spinner	Scream Click Whistle	0.25-35 1-160 1-20	12 60 8-12
<i>Tursiops truncatus</i>	bottlenosed dolphin	Click Whistle	0.2-150 2-20	60-80 -
<i>Physeter catodon</i>	sperm whale	Coda	16-30	-
MYSTICETI				
Type M <i>Eschrichtius robustus</i> <i>Balaenoptera musculus</i> <i>Balaenoptera physalus</i> <i>Balaena mysticetus</i> <i>Eubalaena glacialis</i> <i>Megaptera novaeanglia</i>	Grey whale Blue whale Fin whale Bowhead Right whale Humpback	Call Moan Call Call Call Song	- 0.2-0.20 0.16-0.75 0.1-0.580 - 0.05-10.0	1-1.5 0.012 - .018 0.020 0.14 - 0.34† <0.200† <4.0

† Recordings below 100 Hz are not available

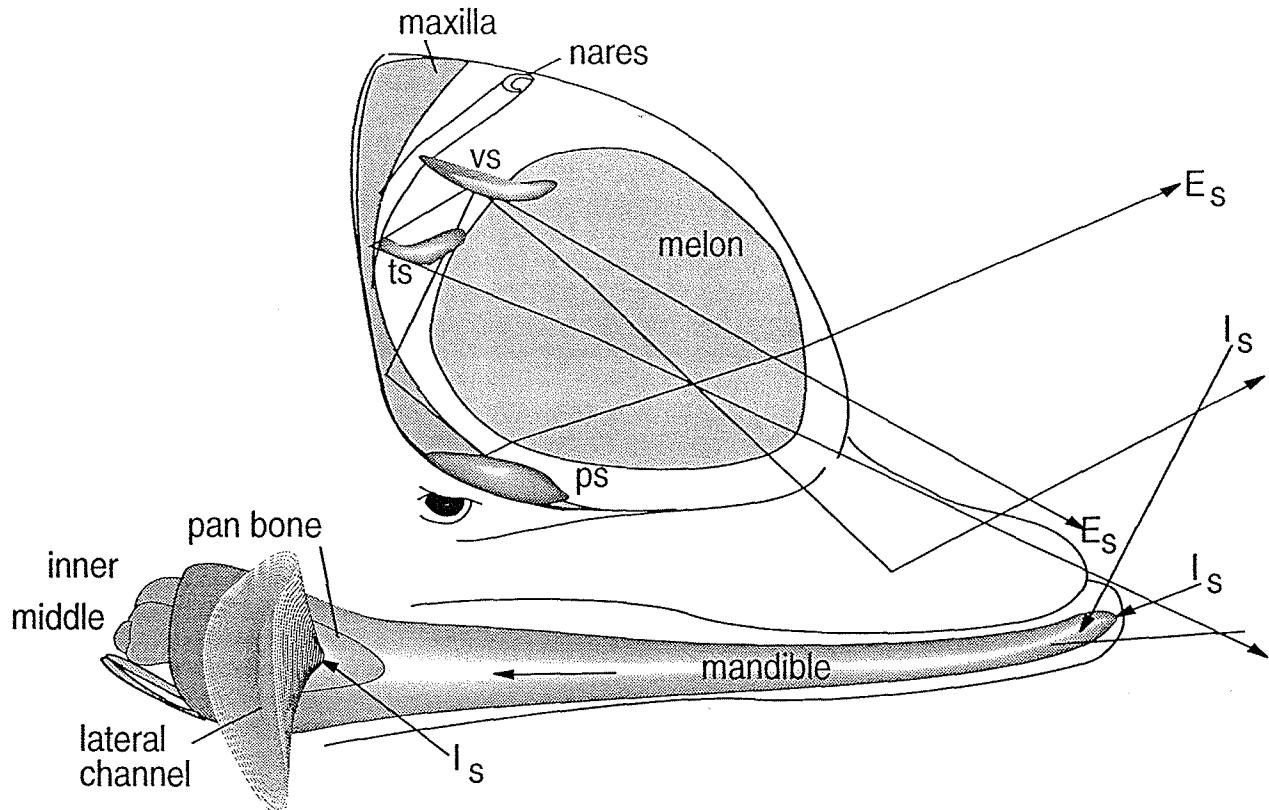


Fig. 1. Hypothetical sound paths for ultrasonic vs. lower frequency signals in the dolphin head. Anteriorly directed ultrasonic signals (E_s) are generated in the vestibular (vs) and tubular (ts) nasal sac diverticulae. Released air is captured by auxiliary sacs and recycled for subsequent sound production. The signals are reflected off the acoustic shield of the telescoped cranium and the premaxillary sac (ps) and focused by multi-layered fats in the melon. Incident sounds (I_s) from anterior targets enter the lower jaw where waxy tissues, rather like acoustic analogues of fiber optic cables, channel the sound to the ear. Mandibular fatty channels can easily accommodate ultrasonic signal from an anterior direction but larger lateral fat channels near the pan bone may provide parallel low frequency input. [Figure copyright D.R. Ketten, 1991, revised 1993. Data compiled from 13, 15, 16, 17, 18.]

B. Middle Ear

Only a few general observations are available on whale middle ears. All cetacean middle ears are adapted to withstand rapid and extreme pressure changes. One acoustic difficulty for deep-diving mammals is that middle ear resonances are determined by cavity air volume. The dense-walled middle ear cavity in whales is lined with a thick, vascularized epithelium, the corpus cavernosum. It is heavily invested with trigeminal nerve fibers, a sensory-motor nerve which may monitor and pressurize the cavity by adjusting cavernosum fluid content. The task of regulating middle ear volume may also explain exceptionally high trigeminal fiber counts in both mysticetes and odontocetes [19].

Odontocete middle ear structures are comparatively rigid: the eardrum is partially calcified, bony struts attach ossicles to the middle ear cavity wall, and interossicular joints are stiffened with ligaments and a fibrous sheath. In land mammals, similar stiffening elements are found in insectivorous bats. Baleen middle ear cavities are spheroidal and disproportionately large. The cavity is closed laterally by a "glove finger", a complex, thickened tympanum or eardrum that resists inversion or tearing. This hypertrophied tympanic "finger" protrudes laterally from the bulla, and in

some species has a surface area $>4000 \text{ mm}^2$. The ossicles are massive but loosely joined and fully mobile; i.e., a classically low frequency configuration. Although the functionality of the middle ear in whales has been questioned [20] because it is a fluid - fluid coupler, recent CT data show whale middle ears are air-filled *in vivo*. This fact tied with the anatomical complexity and diversity of cetacean middle ear anatomy argues that the ossicular chain has an important role in both echolocating and non-echolocating whale hearing.

C. Inner Ear

As in other mammals, whale inner ears are fluid-filled membranous labyrinths that house two sensory organs: a three-ringed vestibular system (balance) and a spiral cochlea (hearing). The vestibular system is exceptionally small in whales and dolphins, and vestibular innervation is proportionately reduced; i.e., <10% of cetacean VIIth nerve fibers are vestibular, compared to 40% in most mammals. Vestibular down-sizing may be a corollary of fused cervical vertebrae in whales, or alternatively, may be a valuable adaptation that permits animals like spinner dolphins to perform rapid, continuous rotations.

In contrast to the vestibular system, whale cochleae are highly evolved. Earlier studies provide detailed descriptions of odontocete cochlea [13, 14, 21, 22, 25]; therefore, this paper focuses on cytoarchitecture of the cochlear duct and basilar membrane as the chief morphometric correlates of hearing range differences in mammals.

Mammalian basilar membranes are essentially tonotopic resonators built of relatively uniform modules equivalent to the ear's critical bands. The range of the stiffness and mass characteristics of these modules in each ear determines the range of cochlear resonances and therefore the hearing limits of that ear. Because all mammalian basilar membranes have a similar cellular structure, most interspecific differences in stiffness and mass are largely the result of different thickness and width distributions along the membrane. Highest frequencies are encoded in the base of the spiral (basal turn) where the membrane is narrow and stiff. Progressively lower frequencies are encoded as the membrane becomes broader and more pliant apically.

Cetacean basilar membranes are highly differentiated with substantial interspecies differences in length, thickness, and width (Table 2). Width and length [5, 7, 24, 26] have been used independently to estimate frequency ranges for land mammals, but these equations do not predict marine mammal hearing ranges accurately primarily because formulae for terrestrial cochlear length-frequency distributions were based on second order allometric relationships of cochlear length to body size that do not hold for marine mammals. In essence, whales have a fundamentally different ear allometry which cannot be modeled simply as extremes of land

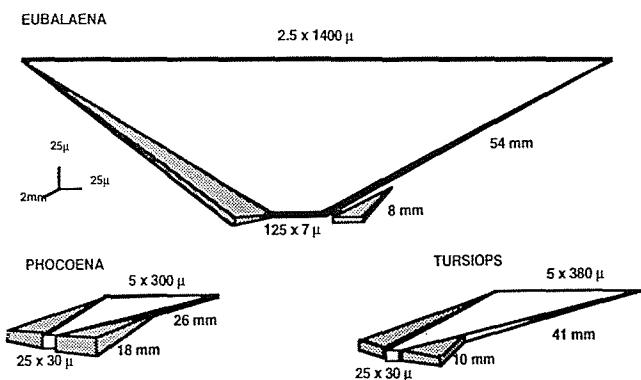


Fig. 2. The basilar membrane and inner and outer spiral laminae (gray) are drawn as orthoscopic projection for representative Type I (*Phocoena*, harbour porpoise), Type II (*Tursiops*, bottlenosed dolphin), and Type M (*Eubalaena*, right whale) species.

mammal cochlea [9]. In whales, cochlear length is correlated strongly with animal size ($0.8 < r < 0.95$), but it is not significantly correlated with frequency, in large part because membrane thickness does not covary with length. A typical odontocete membrane has a square basal cross-section and is rectangular at the apex (Fig. 2). Mysticete membranes have oblong cross-sections throughout the cochlea. Dolphin basilar membrane basal widths are similar to those of bats (35 μm). Baleen basal widths are similar to those in humans (125 μm) but 3X wider than in echolocators. Baleen apical widths are the broadest recorded

TABLE 2.
MEMBRANE AND COCHLEAR SPIRAL MEASUREMENTS

Species	Common name	Cochlear Type	Turns	Membrane Length (mm)	Outer Lamina (mm)	Basal Width (μm)	Apical Thickness (μm)	Basal Diam. (mm)	Axial Height (mm)	Axial Pitch ¹ (mm)	Peak Frequency (kHz)
ODONTOCETI											
<i>Inia geoffrensis</i>	Boutu	I	1.5	38	-	-	-	8.5	2.3	1.5	200
<i>Phocoena phocoena</i>	Harbour porpoise	I	1.5	26	17.6	30/290	25/5	5.6	1.4	1.0	130
<i>Grampus griseus</i>	Risso's dolphin	II	2.5	41	-	40/420	20/5	8.7	5.4	2.1	-
<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	II	2.5	35	8.5	30/360	20/5	8.7	5.3	2.1	40
<i>Stenella attenuata</i>	Spotted dolphin	II	2.5	37	8.4	40/400	20/5	8.6	4.4	1.8	60
<i>Tursiops truncatus</i>	Bottlenosed dolphin	II	2.25	41	10.3	30/380	25/5	9.5	5.0	2.2	70
<i>Physeter catodon</i>	sperm whale	I, II	1.75	54	-	-	-	11.7	3.6	2.0	-
MYSTICETI											
<i>Balaenoptera acutorostrata</i>	Minke	M	2.25	55	-	100/1500	-	12.8	7.5	3.0	-
<i>Balaena mysticetus</i>	Bowhead	M	2.25	61.3	<10	120/1670	7.5/2.5	14.3	8.2	3.4	<0.20
<i>Balaenoptera physalus</i>	Fin whale	M	-	-	-	100/2200	-	-	-	-	0.02
<i>Eubalaena glacialis</i> ²	Right whale	M	2.5	49.5	<8	125/1400	7/2.5	9.7	6	2.4	<0.20
<i>Megaptera novaeangliae</i>	Humpback	M	2.5	54	-	-	-	12.1	7.5	3.0	<4.00

¹ axial height
turns ² neonate

in mammals ($1400 \mu\text{m}$ - $1600 \mu\text{m}$). They are rivaled only by apical membranes of African elephants ($1200 \mu\text{m}$) which hear infrasonics [23]. Based on width alone, odontocete and mysticete basilar membranes are capable of exceptionally wide response ranges.

Previous work on bat, odontocete, and mysticete basilar membrane ratios showed thickness to width ratios are the most significant correlate of frequency ranges. Differences in basal ratios among echolocators are consistent with species differences in peak ultrasonic frequency. The harbour porpoise, a Type I odontocete, has a maximum basal ratio of 0.9 and a peak frequency of 130 kHz; the bottlenosed dolphin (Type II), a ratio of 0.7 and a peak signal of 70 kHz; and the horseshoe bat, a 0.3 basal ratio and a 40 kHz echolocation signal. Mysticete basal ratios (0.1) are equivalent to mid-cochlear ratios of the three echolocators. At the apex, the echolocators ratios (0.01) are 10X higher than the typical mysticete value (0.001).

A final factor in cetacean basilar membrane compliance is the amount of membrane stiffening provided by bony laminar support. In land mammals, ossified outer spiral laminae are found in animals with ultrasonic hearing but are absent or reduced in lower frequency animals [26]. Inner

laminae in mysticetes are spongy, fragile structures. Baleen whale outer laminae are narrow spicules that do not contact the basilar membrane. Their broad, thin membranes are supported laterally solely by a flexible spiral ligament, which is consistent with a flaccid low to infrasonic encoder. In all toothed whales, the basilar membrane attaches to a rigid bony outer lamina for some portion of the basal turn (Table 2). The percentage of membrane with outer laminar support correlates directly with peak ultrasonic spectra. In Type I echolocators with peak frequencies above 100 kHz this buttress extends over 60% of the cochlear duct (Table 2; Fig. 2); whereas Type II echolocators (40 to 80 kHz peak frequency) have a bony outer anchor for <30% of the duct. Because Type I and Type II membranes have similar thickness to width ratios for most of their length, more extensive laminar support in the Type I animals is a key component of their ability to detect frequencies >100 kHz.

Schematized three-dimensional cochlear reconstructions illustrate the major features of each cochlear type (Fig. 3). Multivariate analyses of cochlear spiral morphometry show that 91% of the variance amongst species is attributable to the ratio of body size to spiral geometry and that cochlear types and acoustic groups are predicted reliably (0.1% con-

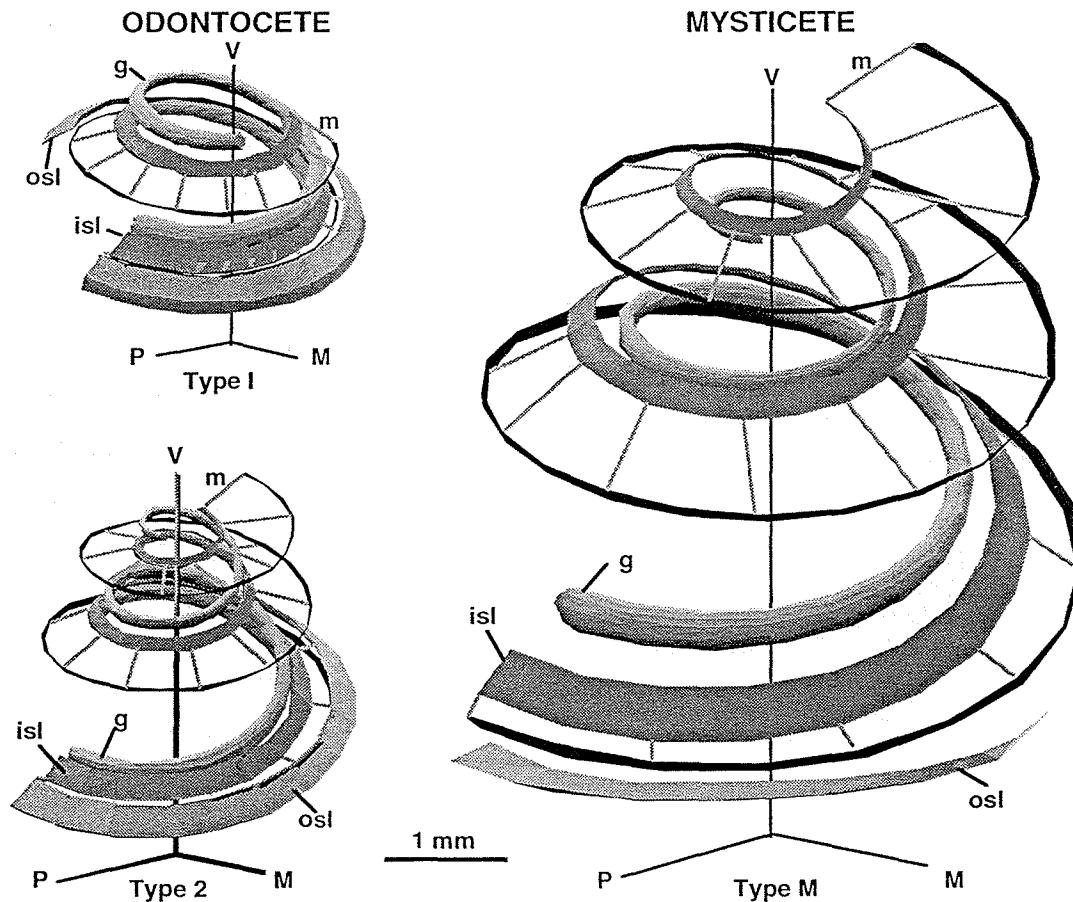


Fig. 3 Basilar membrane and spiral laminae distributions in Cetacea. Three-dimensional schematics summarize major cochlear duct components in Type I, Type II, and Type M inner ears. The cochlea are shown inverted from *in vivo* orientations. (g) spiral ganglion; (isl) inner osseous spiral lamina; (m) basilar membrane; (osl) outer osseous spiral lamina; (l) lateral; (p) posterior; (v) ventral.

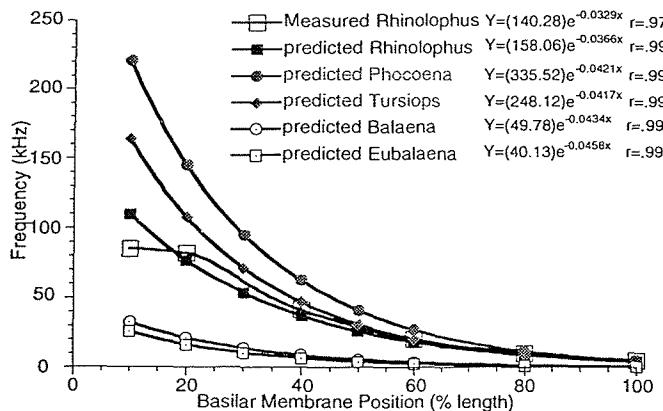


Fig. 4. Frequency vs. cochlear position distributions in the horseshoe bat (*Rhinolophus ferrumequinum*) and 4 whales: harbour porpoise (Type I, *Phocoena phocoena*), bottlenosed dolphin (Type II, *Tursiops truncatus*), bowhead whale (Type M, *Balaena mysticetus*) and right whale (Type M, *Eubalaena glacialis*). Membrane lengths are normalized as percentages of cochlear length. Curves for the bat are based on published data for membrane dimensions (predicted) and electrophysiological recordings (measured) [6]. The predicted curve differs from the measured curve in the basal 10% because data were not available for the foveal region of this bat's membrane.

fidence level) by a composite of basilar membrane ratios, turns, pitch, and basal ratios (Table 2) [9, 21]. This composite is a mathematical descriptor of cochlear length::body size isometry for each whale species; i.e., it is the cetacean analog of the human normalized species size factor derived by Greenwood to predict intracochlear frequency distributions in land mammals [21]. Hearing range estimates for whales are generated by combining basilar membrane morphometric data for each species with stiffness distribution estimates based on cochlear type and outer laminar length. Stiffness gradients for each cochlear type are calculated by modeling basilar membrane segments as simple beams with uniform load partially distributed at one or both ends. These data are then fitted to a species scaled version of the compliance-position function to obtain the species specific equation for mapping frequency against cochlear spiral length [17] (Fig. 4).

CONCLUSIONS

Aquatic influences are most evident in the gross anatomy of whale auditory systems. All whale temporal bones are similarly constructed of exceptionally dense, non-aerated bone. CT and MRI data support the theory that fatty acoustic wave guides are the principal sound paths to the middle ear. Sound reception in baleen whales remains unexplained.

Morphometrically, dolphins and whales have three ear formats which coincide with broad frequency divisions: low to infrasonic Type M mysticetes; upper range ultrasonic Type I odontocetes; and lower range ultrasonic Type II odontocetes. Type I and Type II cochlea are primarily adapted for underwater echolocation, with isolated middle ears and exceptionally stiff basilar membranes. Differences in bat vs. dolphin membrane ratios are proportional to echolocation frequency differences. Given the sound speed

differences of the two media, these data imply dolphins generally use longer wavelengths than bats. Type M ears are clearly adapted for low to infrasonic hearing.

Cetacean ear formats and frequency ranges also coincide with specific habitats and feeding behaviors. Type I spirals were found only in inshore and riverine dolphins, which live in turbid waters and use short wavelength, ultrahigh frequency signals to detect small, nearby objects. Type II formats are common in offshore and pelagic delphinids that use lower sonic-range signals for social communication and lower frequency ultrasonics that are appropriate for resolving larger or more distant objects. Finally, little is known about signal use in mysticetes, but the fact that Type M formats are largely geared to infrasonics may mean baleen whales are capable of very long-range communications or topographic imaging.

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