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UNDERWATER EARS AND THE PHYSIOLOGY OF IMPACTS: COMPARATIVE LIABILITY FOR HEARING LOSS IN SEA TURTLES, BIRDS, AND MAMMALS

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INTRODUCTION

The problem of underwater noise is a hydra: manifold, complex, and mutable. It cannot be addressed simply, locally, or with data culled from just one species or region. A recent U.S. Ocean Studies Board panel found anthropogenic noise is doubling per decade, whereas another recent Marine Mammal Commission panel was unable to reach consensus on research and mitigation priorities because of insufficient data. We lack data on noise trends in any marine habitat, and we have audiometric data on fewer than 100 marine species, with even less data on noise-induced threshold shifts. Despite considerable recent research, we are far from understanding the mechanisms and scope of underwater noise impacts. Essentially, we do not know what, where, or how sound is having an impact on any marine organism.

Our knowledge base for larger marine vertebrate hearing is spotty at best. We have behavioural or electrophysiological audiograms for fewer than 22 marine mammal species, all obtained from smaller odontocete and pinniped vertebrates (Nachtigall et al., this volume; Finneran et al., this volume). There has been considerable progress on some noise impacts (e.g., threshold shifts and masking) in captive studies, but conventional audiometric techniques are simply not yet employable with very large marine vertebrates because sheer size creates substantial obstacles on measuring hearing in some species. Virtually nothing is known about the majority of marine mammals and even less about the incidence or aetiologies of hearing loss in wild populations. The data gap is even more acute for basic hearing and hearing loss in sea turtles and sea birds, for which fewer than five species have been tested (Bartol, this volume). However, by combining conventional audiometry from captives with modelling and biomechanical measures of ear tissues, we have obtained a much broader picture of hearing as well as a better understanding of critical features of underwater ears.

This paper summarizes what is known about underwater hearing of sea turtles, sea birds, and marine mammals from auditory system anatomy and modelling and, contextually, what is their relative liability for hearing loss from underwater sound exposures.

APPROACHES

Functional models can fill the broadest gaps in our current knowledge and provide insights into important hearing mechanisms. An important concept in neuroethology is the Umwelt, i.e., an animal's perceived world is a species-specific model constructed of blocks of data that sensory systems capture, which are in turn tuned by evolution. Functional modelling builds on this concept, analyzing sensory system elements in the context of the operational medium. Thus, an important aspect of modelling is that it not only provides sensory ability estimates but also examines the evolutionary habitat-anatomy push-pull.

Major modelling techniques for auditory systems combine biomechanical measures of middle and inner ear stiffness and mass with high-resolution morphometry (see Mountain et al., this volume). Recently, finite element and finite difference models have also been brought to bear on the problem. Much of the data for these techniques derive from another recent development, computerized tomography, which can image simultaneously entire whale heads and the inner ear (Figure 1).

SOUND CONDUCTION

Dolphins and whales lack conventional external ear canals; seal ear canals vary widely in size and patency; and sound-reception mechanisms in seabirds and turtles are poorly understood. Nevertheless, all are believed to hear underwater, and some have better frequency resolution and localization than most land mammals. Computerized tomography reveals well-organized bundles of coherent fatty tissues (Figure 1) connected to the middle ear in all sea mammal, turtle, and sea birds examined. Densities of these fats are similar across all species and are consistent with sound speeds of sea water. Three- dimensional reconstructions of scan data show that in turtles and birds, the fats are single lobes attaching to the tympanum. In seals, the fats align with the external auditory canal. In whales, the fats form one to three distinct lobes along the mandible (see also Yamata et al., this volume). These data suggest that all these taxa evolved in parallel specialized soft tissues as low-impedance sound-channels to the ear.

MIDDLE AND INNER EARS

Marine vertebrates have ears that fundamentally resemble those of their land

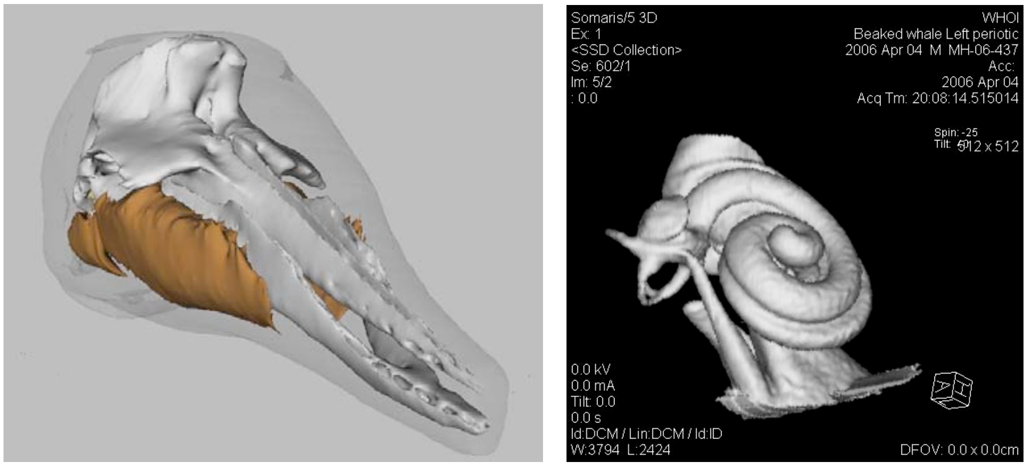

Figure 1. Three-dimensional reconstructions of a beaked whale *(Mesopolodon densirostris)* head showing jaw fats and the skull (left) and its inner ear based on tissue specific CT attenuation values (reprint permission D. Ketten http://csi.whoi.edu).

counterparts but may have broader hearing ranges and better acuity, Odontocetes, like bats, are excellent echolocators, with hearing between 200 Hz and 200 kHz, The upper functional range for mysticetes is predicted to be 20-30 kHz. Most pinnipeds have peak sensitivities between 1 and 20 kHz. Good lower frequency hearing appears to be confined to the largest cetaceans and pinnipeds. No mysticete hearing has been directly tested, but functional models indicate that their hearing extends infrasonical1y, with several species hearing as low as 10-15 Hz. Among pinnipeds tested, only elephant seals have good hearing below 1 kHz. Some pinnipeds may hear adequately in both air and water but are not acute in either.

Like marine mammals, sea turtles are endangered and potentially impacted by human activities. Little is known about their hearing or dependency on sounds. Interestingly, at each life stage, sea turtles have substantial differences in the size, shape, and possibly function of their ears. Currently, their hearing can be broadly summarized as limited to relatively few octaves with best sensitivities near 400-1,000 Hz (see Bartol, this volume).

HEARING LOSS

Although marine ears are impressive, they are not invincible. Some captive animal and postmortem histologic studies suggest that some test animals had substantial preexisting high-frequency hearing loss. We do not know whether these findings represent natural processes or losses exacerbated by anthropogenic underwater sounds.

Virtually all forms of trauma and disease are found in marine mammal ears in all species and age ranges. Ears from older dolphins and seals often have inner ear neuropathy consistent with age-related or presbycusic changes. Damage tends to be more acute in seals, suggesting odontocetes may be less subject to noise-related loss, possibly because their hearing is more sensitive at frequencies higher than are common in ocean ambient noise.

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