

could be widespread among coastal crab species and of considerable ecological importance for influencing settlement processes in coastal crustaceans.

The use of the binary choice chamber provides a potentially powerful experimental tool for rigorously examining other key aspects of the response of pelagic crustaceans to underwater sound such as measuring acoustic thresholds for different sound frequencies; teasing apart the specific components of underwater sound that elicit behavioural responses; identifying temporal, tidal, and developmental changes in sensory ability and behaviour; and locating acoustic sensory organs with use of localized ablation techniques

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## HEARING IN MARINE CARNIVORES

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### INTRODUCTION

This paper reviews hearing in the marine carnivores: seals *Phocidae*, sea lions and fur seals *Otariidae*, walrus *Odobenidae*, sea otters *Mustelidae*, and polar bears *Ursidae*. The carnivores are unique among marine animals in that they depend on biologically relevant sounds received both in air and underwater for essential activities including

those related to reproduction, foraging, and predator avoidance. Insight into their typical hearing capabilities comes from direct methods, such as electrophysiological and psychoacoustic measurements, and indirect methods, such as studies of sound production, anatomical investigations, behavioural field investigations, and extrapolation from related species. Knowledge about hearing capabilities in marine carnivores can be applied to a broad range of topics including consideration of selective pressures for evolution of aquatic hearing and the potential deleterious effects of anthropogenic noise.

## SUMMARY

Of the five carnivore families that include marine mammals, the pinnipeds (phocids, otariids, and odobenids) include only species that depend on aquatic habitats, whereas the ursid and mustelid families have only a single marine species each. The pinniped lineages began their transition to the marine environment more than 25 million years ago. In contrast, the marine ancestry of sea otters extends only a few million years and the marine ancestry of polar bears only a few hundred thousand years (Berta & Sumich 1999). Thus, the auditory systems of marine carnivores are adapted to varying extents for aquatic function. With respect to anatomy, pinnipeds show several derived features that vary by lineage. These may include reduction or loss of the pinnae, muscular closure of the meatus, cavernous tissue lining the outer and middle ear, enlarged ossicles, and alterations of cochlear structures (Wartzok & Ketten 1999). The ears of otters and polar bears have not been similarly described, although both species appear to show reduction of the pinnae and adaptations for external ear closure during diving.

With regard to auditory function, pinnipeds have been best studied among marine carnivores. Direct measures of underwater hearing sensitivity have been obtained in at least 1 individual for 9 of 33 species. Measures of aerial hearing sensitivity have been obtained for five of these species. In addition to audiograms depicting absolute hearing sensitivity, several other aspects of hearing have been explored in some pinnipeds using psychoacoustic techniques, including effects of depth, sound localization, masking, temporal summation, temporary threshold shift, and permanent threshold shift as a function of aging. A general picture of pinniped hearing is emerging from these studies, suggesting functional hearing groupings based on family relationships (Kastelein et al. 2002; see review in Wartzok & Ketten 1999).

Phocids have an extremely broad range of best hearing sensitivity underwater, with relatively flat audiograms between 1 and 50 kHz. The low-frequency tail of their audiograms has a shallow rise indicating relatively good sensitivity to sounds between

100 Hz and 1 kHz. The high-frequency portion of their audiograms shows a functional upper frequency cutoff around 60 kHz; however, sensitivity to intense sounds above 150 kHz has been documented in some species. The hearing of otariid and odobenid pinnipeds underwater is relatively similar, with the marked exception of a sharp upper frequency cutoff around 30 kHz for the sea lions and fur seals and around 15 kHz for the walrus. In air, the audiograms of pinnipeds appear to be more sharply tuned to midfrequencies, with upper functional limits of sensitivity for phocids and otariids below 30 kHz. Recent aerial hearing thresholds obtained in a quiet testing chamber suggest that some phocid seals may hear sounds below 0 dB re 20  $\mu$ Pa. Comparison of underwater hearing thresholds with aerial thresholds obtained in quiet testing conditions indicates that pinnipeds maintain good sensitivity above and below the surface and that sound detection in the wild is likely to be limited by ambient noise at mid- to low frequencies in both media.

There are no psychoacoustic data addressing hearing sensitivity in sea otters or polar bears in air or water. However, indirect indicators and physiological studies may improve our understanding of sound detection in these species. For example, Nachtigall et al. (2007) recently used electrophysiological techniques to test the aerial hearing of captive polar bears. Results showed functional hearing from at least 1.4 kHz to above 22.5 kHz, with the best sensitivity below that of ambient noise within the testing enclosure. Psychoacoustic studies of aerial hearing sensitivity are ongoing for polar bears, and psychoacoustic, electrophysiological, and anatomical studies are planned for sea otters. The results of these studies may provide much needed insight into the auditory adaptations of these transitional marine carnivores.

Assessment of sound production may inform inferences about species-typical features of sound reception because the frequency range of communicative signals tends to be correlated with regions of best sensitivity in some animals. However, regions of best hearing sensitivity may extend well beyond frequency ranges of vocalizations, and selective pressures acting on hearing sensitivity may include those related to prey detection, predator avoidance, navigation, and the physical and acoustic environment in which the signals are produced and received. For example, most marine carnivores emit mid- to low-frequency sounds in air, whereas their hearing sensitivity extends to ultrasonic frequencies. Underwater, some species are not known to emit sounds at all despite good sensitivity across a wide range of frequencies. In contrast, some aquatic breeding seals have vocal repertoires that may span 10 octaves (Wartzok & Ketten 1999). Furthermore, although hearing may be adaptive for the detection of conspecific, predator, and environmental cues, it is also important to consider that changes in hearing sensitivity may occur not only as

primary adaptations for enhanced signal detection but also as by-products of anatomical and physiological adaptations. For example, anatomical changes to auditory structures that may be related to withstanding pressure effects in diving mammals may have indirect effects on hearing capabilities.

Consideration of hearing capabilities provides important insight into the evolutionary, ecological, and behavioural significance of sound in the lives of animals. Although recent progress has been made in our understanding of sound detection in some marine mammals, a good deal remains to be learned about hearing in marine carnivores. Such knowledge will improve our ability to mitigate the effects of human disturbance in marine coastal habitats.

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## DETECTION OF SOUND BY FISH: A MINIREVIEW

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### INTRODUCTION

This minireview is focused on selected topics of particular relevance regarding effects of anthropogenic noise on fish. Several important aspects of hearing in fish (directional hearing, frequency discrimination, and central processing) are not covered.

### OTOLITH ORGANS ARE ACCELERATION DETECTORS

Soft fish tissue has nearly the same mass density and acoustic