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## REVIEW ARTICLE

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# Hearing and Acoustic Communication in Cavefishes

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## Abstract

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The constant darkness of caves and other subterranean habitats imposes sensory constraints that offer a unique opportunity to examine how sensory modalities evolve. Adaptations to the underground environment represent replicate natural evolutionary experiments to a similar extreme environment, as many species have evolved similar morphological, physiological, and behavioral adaptations to survive in perpetual darkness and limited resource. Although fish hearing has been studied for over a century and all fish up to date have been shown to be able to hear sounds, hearing in cavefishes has not been well explored. Moreover, despite the diversity of sound-generating mechanisms that have evolved across the Teleostei, acoustic communication was not demonstrated in any cavefish species. Here we review the evidence for hearing in fishes, and particularly in cavefishes. We also discuss our own results in the group Amblyopsids. We chose to study the Amblyopsids because they are a small phylogenetic group with a large portion of its diversity comprised by cavefish, and its phylogeny well understood.

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## Introduction

Fishes are the most diverse vertebrate phyla extant today. Of the approximately 32,000 fish species globally (Nelson, 2006; Eschmeyer, 2012), over 300 have been reported to live in cave and other subterranean habitats, with more than 170 species living exclusively in caves, exhibiting some degree of troglomorphy. Cavefishes exhibit considerable phylogenetic and geographical diversity representing 10 orders and 22 families that occur on every continent but

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Europe and Antarctica (Proudlove, 2006; 2010; Soares & Niemiller, 2013). They represent replicate natural evolutionary experiments to a similar extreme environment, as many species have evolved similar morphological, physiological, and behavioral adaptations to survive in perpetual darkness and resource-limited environments (Poulson, 1963; Niemiller & Poulson, 2010; Soares & Niemiller, 2013). Although cavefishes are among the most well known troglobites, there have been very few comparative studies investigating cavefish ecology and sensory biology. This is likely because many cavefishes occur in habitats that are difficult to access, are in regions with few local resources for researchers; most studies have focused on describing new taxa and resolving systematic relationships. As a result, the literature on cavefish biology is dominated by studies on just a few New World species, particularly the blind Mexican characin *Astyanax*.

Cavefishes are uniquely suited for the comparative study of sensory neurobiology evolution because (i) fish in general are a well-studied group from neurosensory perspectives (von der Emde *et al.*, 2004); (ii) many lineages around the world have independently evolved an obligate, cave-adapted existence allowing for natural replication (Proudlove, 2010; Soares & Niemiller, 2013); (iii) their evolution covers varying timescales from just tens of thousands to several million years; (iv) the directionality of ecological shifts are known (surface to cave) (Culver, 1982) and (v) their evolution can be directly linked to environmental conditions (*e.g.*, absence of light). Much of the interest in cave-adapted species is due to the fascinating suite of morphologies that enable them to survive in caves.

### **Acoustic mechanism and fishes:**

The fact that fish can hear has been known for over a century (Von Frisch, 1938). Fish hearing has been a productive field in biology and despite the great diversity of species; much is understood about how these animals detect sounds underwater. All fish studied to date are able to hear sounds (Fay & Popper, 2000; Kasumyan, 2005). The ability of a fish to detect a sound is usually expressed in terms of some minimum detectable level (threshold) as the level that the fish starts responding to the stimulus and the range of frequencies over which they respond. Behavioral, electrophysiological and anatomical studies all can be used to describe the hearing characteristics of a particular species, although these three approaches sometimes tell different stories. Fish have two sensory systems for detection of water motions: the inner ear (there is no outer or middle ear) and the lateral line system. The ear serves to detect sound up to hundreds or even thousands of Hz depending on the species, whereas the lateral line detects low-frequency sound (*e.g.*, <200 Hz), but is generally considered to be primarily a detector of water motion relative to the body. The fish ear is located lateral to the brainstem and includes semicircular canals and their associated sensory tissues, as well as three otolith organs, the saccule, lagena and utricle. Each of the otolithic end organs has a sensory epithelium (sometimes called a 'macula') in the wall of the membranous chamber. The apical surface of the epithelium is separated from the overlying otolith by a thin otolithic membrane (Dunkelberger *et al.*, 1980; Popper & Lu, 2000) that holds the otolith in place next to the epithelium. The otolithic end organs serve as an inertial system whereby a stimulus, whether it

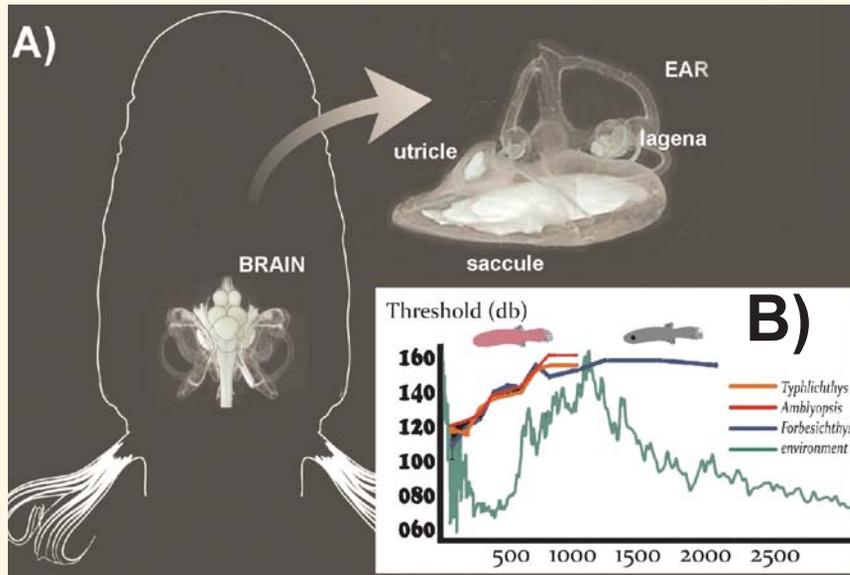
is head motion or sound, causes motion of the fish body relative to the otoliths. Because the otolith is approximately many times denser than the fish body, it moves at a different amplitude and phase than the sensory epithelium. As a result of the direct mechanical contact between the tips of the cilia and the otolith or indirect contact through the otolith membrane, the cilia bend as the otolith moves, opening ion channels and leading to detection of the mechanical signal (reviewed in Popper *et al.*, 2003; Ladich & Popper, 2004).

Sound can be thought of in terms of both particle motion and pressure fluctuations. Sensory hair cells are stimulated by mechanisms that respond to particle motion and are responsible for converting these motions to electrical signals that stimulate the nervous system. Detection of pressure fluctuations depend on a gas-filled bladder that translates these fluctuations into particle motion that can then be transmitted to the ear. Different fish species vary in absolute sensitivity and spectral range of hearing, which relates to an auditory detection continuum based on presence or absence of specially evolved morphological structures that affect the pressure-to-motion transduction. There may also be a direct mechanical connection between the swim bladder and the inner ear through a series of bones (the Weberian apparatus). Generally speaking, most fish hear best within 30-1000 Hz, while species with special adaptations can detect sounds up to 5000 Hz. Some exceptional species are even sensitive to infrasound or ultrasound (Sand *et al.*, 2001; Slabbekoorn *et al.*, 2010; Popper *et al.*, 2004).

Ambient noise will affect a fish's ability to detect biologically relevant signals. Complex arrangement of biological and other ambient sounds can be divided into two major components (Krause, 1987): together, biological environmental sounds can be labeled as “biophony” and describe the sounds created by organisms, while non biological ambient sounds from wind, rain, thunder, etc. can be described as “geophony”. Human generated noises have been labeled as “anthrophony.” Soundscapes constitute an important environmental pressure on the evolution of auditory and acoustic signal systems (Popper & Coombs, 1980). A fish's acoustic environment varies with season, time scale of a day, geography and species composition as well as with more obvious factors such as weather and currents (Schwartz, 1985). Excluding intra-specific acoustic communication, very little is known about how any fish responds to the variety of natural sounds it hears but there is some evidence that fish will have heightened sensitivities at frequencies around a quiet window in background noise (Lugli *et al.*, 2003; Niemiller *et al.*, 2013b).

### Acoustic mechanism in cavefishes:

Hearing studies of cavefishes have been few, despite the fact that there should be strong selection to enhance non-visual sensory modalities. Greater sound sensitivity and extended frequency range in subterranean habitats may be adaptive for various reasons, such as to detect the environment, prey, predators or conspecifics. In 1970, Popper examined differences in hearing in the Mexican tetra *Astyanax mexicanus* (family Characidae), which has two ecomorphs: a cave-adapted form found in several caves and a surface-adapted form. He found no behavioral differences in hearing sensitivities between cave and surface forms, and both



A) Diagram of location of ears in relationship to the brain in fishes. B) Auditory thresholds of amblyopsid fishes. Values are means. The surface fish *Forbesichthys* (blue) reaches up to 2kHz while the cave fish *Typhlichthys subterraneus*(1) and *Amblyopsis spelaea*(2) are limited to 1kHz. Fast Fourier Transformation (FFT, green line) of sound recorded in a Drowned Rat Cave pool. The pool was carved in rockbed by a small stream. The recording was made 0.5 m deep and approximately 1 meter from a small waterfall. The ceiling of the cave was also dripping onto the pool.

forms had a minimum threshold at 1000 Hz. More recently, Schulz-Mirbach *et al.* (2008) examined the anatomy of ears of the Atlantic Molly (*Poecilia mexicana*) and found that there are noticeable morphological differences between the hearing organs of cave and surface forms of these fishes. However, hearing thresholds are similar between the two forms with lowest thresholds between 200 and 300 Hz (Schulz-Mirbach *et al.*, 2010), as measured by electrophysiology (auditory evoked potentials).

Our own studies examined differences in hearing between related cave and surface fishes (Niemiller *et al.*, 2013b) of the North American family Amblyopsidae. We examined the surface-dwelling species *Forbesichthys agassizii* and two related cave-dwelling species, *Typhlichthys subterraneus* and *Amblyopsis spelaea*. These three species share a most recent common ancestor dating to 8.6 Mya (Niemiller *et al.*, 2013a). *Forbesichthys* and *Amblyopsis* are sister groups diverging 5.7 Mya (Niemiller *et al.*, 2013a,c). We used auditory evoked potentials to show that all three species have similar hearing thresholds below 800 Hz. Unexpectedly however, the two cave species were not able to hear above 800 Hz, whereas surface-dwelling *F. agassizii* how responses up to 2 kHz. We also noted differences in morphology. *T. subterraneus* and *A. spelaea* had significantly lower hair cell densities compared to surface *F. agassizii*. The reduction in hair cell density suggests peripheral involvement in high-frequency hearing loss in the cave species. Loss of high frequency hearing in *Typhlichthys* and *Amblyopsis* represents the first report of regressive evolution of hearing in a subterranean organism.

In addition to testing these amblyopsid cavefishes, we characterized aquatic environmental sound profiles in caves and surface habitats inhabited by each amblyopsid cavefish and the surface fish (Niemiller *et al.*, 2013b). Audio recordings from native cave habitats revealed that ripples in cave streams and water droplets dripping from the ceiling create loud high-frequency background noise generally above 800 Hz. We therefore hypothesized that cave amblyopsids may have lost hearing at high frequencies in response to living in loud acoustic cave environments. It remains to be determined what factors contribute most to high background noise levels in aquatic cave habitats and the evolutionary mechanisms (*i.e.*, neutral loss or selection) behind auditory regression.

Acoustic communication plays an important role in intra-specific communication in many groups of fishes (reviewed in Ladich & Myrberg, 2006; Myrberg & Lugli, 2006). Acoustic communication may be important in some cavefish species that are no longer able to communicate visually (Schulz-Mirbach *et al.*, 2010). Fishes have evolved a multiplicity of sound-generating organs, including a vibrating swim bladder and pectoral girdle by rapidly contracting muscles or rubbing bony components against each other (stridulation) (Ladich, 2004). While swim bladders produce low-frequency (<500 Hz) sounds, stridulation generates broadband sounds with frequencies up to a few kHz. However, little is known about acoustic communication in cavefishes because of the difficulties of observing fish in subterranean habitats. Acoustic communication has yet to be demonstrated in any cavefish species despite the diversity of sound-generating mechanisms that have evolved across the Teleostei, including several clades that contain cavefishes (Ladich, 2000). Acoustic communication has been investigated in the poeciliid *Poecilia mexicana* but evidence is not yet conclusive (Schulz-Mirbach *et al.*, 2008; 2010; 2011). Several fish species use their swim bladder to produce sound, including some deep-sea fishes. For example, males of some ophidiiform fishes produce sound with sexually dimorphic sets of antagonistic sonic muscles (Mann *et al.*, 1997; Nguyen *et al.*, 2008). Ophidiiform fishes are the dominant group of benthic deep-sea fishes in tropical and subtropical regions (Nielsen *et al.*, 1999) and eight species of ophidiiforms are known from caves; thus this group represents good candidates to examine acoustic communication in cavefishes.

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