

# Acoustic communication and the evolution of hearing in fishes

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Fishes have evolved a diversity of sound-generating organs and acoustic signals of various temporal and spectral content. Additionally, representatives of many teleost families such as otophysines, anabantoids, mormyrids and holocentrids possess accessory structures that enhance hearing abilities by acoustically coupling air-filled cavities to the inner ear.

Contrary to the accessory hearing structures such as Weberian ossicles in otophysines and suprabranchial chambers in anabantoids, sonic organs do not occur in all members of these taxa. Comparison of audiograms among nine representatives of seven otophysan families from four orders revealed major differences in auditory sensitivity, especially at higher frequencies (> 1 kHz) where thresholds differed by up to 50 dB. These differences showed no apparent correspondence to the ability to produce sounds (vocal versus non-vocal species) or to the spectral content of species-specific sounds. In anabantoids, the lowest auditory thresholds were found in the blue gourami *Trichogaster trichopterus*, a species not thought to be vocal. Dominant frequencies of sounds corresponded with optimal hearing bandwidth in two out of three vocalizing species.

Based on these results, it is concluded that the selective pressures involved in the evolution of accessory hearing structures and in the design of vocal signals were other than those serving to optimize acoustic communication.

**Keywords:** evolution; sound-generating mechanisms; hearing specializations

## 1. INTRODUCTION

Fishes, unlike other vertebrates, have evolved a large diversity of sound-generating mechanisms for acoustic communication. These include muscular vibrations of the swim-bladder (characids, searobins, toadfishes, drums) or pectoral girdle (sculpins), pectoral spines rubbing in grooves of the pectoral girdle (catfishes), plucking of enhanced pectoral fin tendons (croaking gouramis) or grinding of pharyngeal teeth (cichlids) (Ladich & Bass 1998). While the former group of mechanisms result in the production of low-frequency (drumming) sounds, activation of the latter group results in the emission of broadband relatively high-pitched sounds. In several vocalizing fish families sonic organs have not been described (pomacentrids, gobiids), and numerous species are not known to be vocal (most cyprinids, knife-fishes). On the other hand, it is suggested that all recent fish species are able to perceive low-frequency sounds, and several groups have developed accessory hearing structures that enhance their hearing ability by allowing detection of high-frequency sounds (> 1 kHz; 'hearing specialists'). These enhanced hearing abilities are primarily based on their having a close connection between an air-filled cavity within the body and the inner ear. Accessory hearing structures are sometimes characteristics of whole taxa such as Weberian ossicles of otophysans, suprabranchial chambers (labyrinths) of anabantoids (labyrinth fishes) or auditory bullae of mormyrids.

To what degree do hearing abilities, and in particular the appearance of accessory hearing structures, correlate with the evolution of sound-generating mechanisms in fishes? Is

acoustic communication a driving force in the evolution of hearing specializations? If the major constraint in the evolution of hearing and sonic organs was the maximization of the effectiveness of intraspecific communication, natural selection would favour the evolution of hearing specializations in vocalizing species and that the main sound energy was generated within the optimal hearing range of a particular species (Ladich 1999).

Cohen & Winn (1967) observed a correlation between the fundamental frequency of sounds and the saccular microphonic response at ca. 150 Hz in the midshipman *Porichthys notatus*, whereas a slight mismatch was observed in the close relative, the oyster toadfish *Opsanus tau* (Fine 1981). In the damselfish, *Eupomacentrus partitus*, the sound energy spectrum matches the audiogram in the region of greatest sensitivity between 500 and 600 Hz (Myrberg & Spires 1980). Stabentheiner (1988) found that the frequency spectrum of typical drumming sounds (barks) covers the range of the best hearing (100–600 Hz) in the piranha *Serrasalminus nattereri*. Schellart & Popper (1992) analysed 15 species of mostly marine teleosts and found a weak correlation between best frequencies of hearing and dominant frequencies of sounds. In a recent study, Ladich & Yan (1998) demonstrated that such a correlation also exists in a single gourami species (*Trichopsis vittata*) producing high-pitched sounds (800 Hz–1.5 kHz). These correlations suggest that sound-producing organs evolved in tandem with hearing abilities and specializations in fishes.

However, several points contradict this assumption. Morphologically similar sonic organs such as swim-bladder

muscles and subsequently low-frequency drumming sounds evolved in hearing specialists (catfishes, characids, mormyrids) as well as non-specialists (toadfishes, triglids). In addition, hearing sensitivities of non-vocal species have to be included in these considerations. In order to analyse the correlated evolution of sound-generating and -detecting organs in more detail, two groups were investigated that possess a variety of sound-generating mechanisms: otophysan and anabantoid fishes. Otophysines are characterized by having Weberian ossicles, which facilitate sound transmission from the swimbladder to the inner ear. Although some otophysans are not known to be vocal, several representatives emit low-frequency drumming as well as knocking sounds or broad-band stridulatory sounds. Representatives of some catfish families (doradids, pimelodids) even possess two sonic organs (Ladich 1999). Anabantoids, perciforms from South-east Asia, possess an air-filled chamber located dorsal to the gills (suprabranchial chamber) that is used for air breathing; it enhances the hearing performance of these fishes due to its close contact to the saccule. Anabantoids occasionally produce stridulatory sounds that are variably associated with social behaviour, but only representatives of the genus *Trichopsis* (croaking gouramis) have developed a unique pectoral sound-producing mechanism and regularly emit sounds during agonistic behaviour (Ladich & Yan 1998).

To determine if enhanced hearing abilities evolved for facilitation of acoustic communication or alternate functions such as detection of predators or prey, two questions need to be answered: (i) Do hearing abilities differ between closely related species that use different channels (acoustic versus non-acoustic) for communication? (ii) Do auditory sensitivities match the differences in main energies of sounds produced in species investigated?

## 2. MATERIAL AND METHODS

Vocal and non-vocal species were chosen in order to determine whether the former possess lower hearing thresholds.

Auditory sensitivity was investigated using the auditory brainstem response (ABR) recording technique, an electrophysiological, non-invasive far-field recording of auditory evoked potentials (Ladich & Yan 1998). Tone bursts were presented at frequencies of 100, 200, 300, 400, 500, 600, 800, 1000, 1500, 2000, 3000, 4000 and 5000 Hz and the lowest sound pressure level determined for which a repeatable ABR trace could be obtained. The ABR technique is a suitable method for comparing the auditory sensitivity among representatives of a large taxon because it allows measurements under identical acoustic conditions, independent of limitations of training different species. Spectra of sounds emitted during intraspecific behaviour or in distress situations were analysed by measuring the amplitudes of frequencies used in the audiogram determination.

Among otophysans, representatives of seven families from four orders were chosen according to their ability to produce a wide range of different sounds. Among anabantoids five species from four genera were investigated (table 1).

## 3. RESULTS AND DISCUSSION

All 14 species examined were sensitive to high-frequency sounds (100 Hz–5 kHz), but the shapes of curves differed

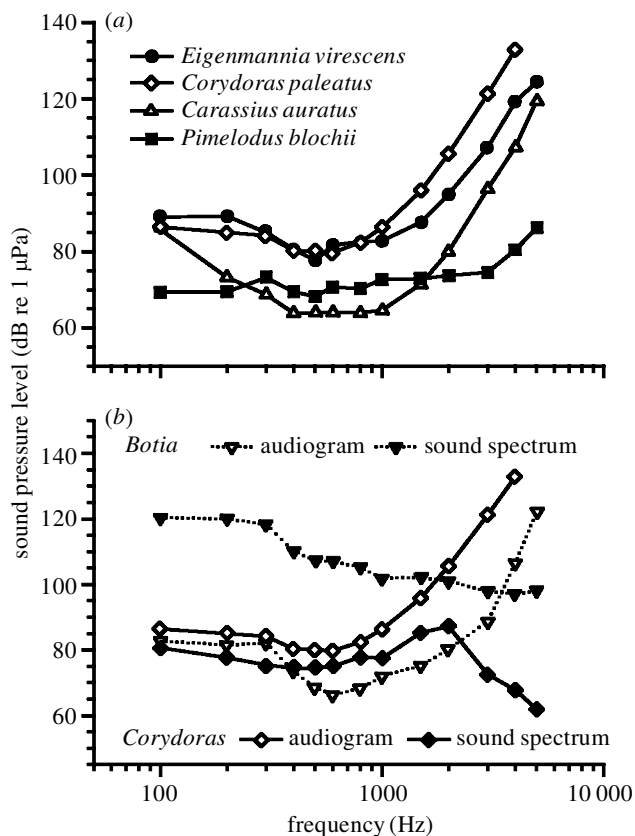


Figure 1. (a) ABR audiograms of four otophysans investigated. (b) Audiograms of the loach *Botia modesta* and the catfish *Corydoras paleatus* in relation to spectral and intensity characteristics of sounds.

between both groups. In otophysans, audiograms were U-shaped or almost flat with maximum sensitivities between 400 Hz and 1.5 kHz. Anabantoids, on the other hand, possessed a pronounced high-frequency hearing maximum between 800 Hz and 1.5 kHz. Audiograms revealed major differences within both groups (otophysans and anabantoids) despite their hearing specialization. Among otophysans, auditory sensitivities differed especially at higher frequencies (> 1 kHz). While the hearing thresholds differed maximally by 30 dB from 100 Hz to 1 kHz, this difference increased rapidly to more than 50 dB at 4 kHz. However, no clear difference between otophysan taxa could be observed (figure 1a,b). Differences in auditory thresholds were found between representatives of different orders (*Carassius* and *Eigenmannia*; catfishes and *Eigenmannia*) as well as within one order (Siluriformes: *Pimelodus* and *Corydoras*) (figure 1a). In addition, there were no clear differences in hearing ability between vocal and non-vocal species. Among cypriniforms the overall difference between the non-vocal cyprinid *Carassius* and the sound-producing cobitid *Botia*, as well as between *Carassius* and the sound-generating characiform *Serrasalmus*, was not significant (Ladich 1999).

Among labyrinth fishes, auditory sensitivities differed especially in the range between 400 Hz and 1 kHz. Again, this difference does not reflect the occurrence of sound production in an intraspecific context. The non-vocal blue gourami *Trichogaster trichopterus* differed from vocalizing species by having absolute auditory thresholds

Table 1. Frequency ranges containing the lowest hearing thresholds (audiogram) and the main energies of sounds (sound spectra)

(Minimum and maximum frequency were determined as those frequencies used during experiments where hearing sensitivity decreased by 10 dB in relation to the frequency of the maximum hearing sensitivity and where amplitudes within sound spectra dropped by 10 dB relative to the dominant frequency of sounds. Two sound spectra ranges are given in species producing two types of sounds.)

order (O), suborder (SO), family (F), genus and species	frequency range audiogram (Hz)	frequency range sound spectra (Hz)
O: Cypriniformes		
F: Cyprinidae		
<i>Carassius auratus</i>	200–2000	—
<i>Botia modesta</i>	300–2000	100–400
O: Characiformes		
F: Characidae		
<i>Serrasalmus nattereri</i>	100–2000	100–600
O: Siluriformes		
F: Doradidae		
<i>Platydoras costatus</i>	100–4000	100–300, 100–4000
<i>Agamyxis pectinifrons</i>	100–3000	100–400, 100–5000
F: Pimelodidae		
<i>Pimelodus blochii</i>	100–4000	100–800, 100–4000
<i>Pimelodus pictus</i>	300–400	100–800, 800–5000
F: Callichthyidae		
<i>Corydoras paleatus</i>	100–1500	600–3000
O: Gymnotiformes		
F: Sternopygidae		
<i>Eigenmannia virescens</i>	200–1500	—
O: Perciformes		
SO: Anabantoidei		
F: Belontiidae		
<i>Trichopsis vittata</i>	600–2500	800–2500
<i>Trichopsis pumila</i>	100–2500	1000–4000
<i>Colisa lalia</i>	100–2500	400–1600
<i>Macropodus opercularis</i>	100–2000	—
<i>Trichogaster trichopterus</i>	300–2000	—

22–25 dB below those of *Trichopsis* or *Colisa* (Ladich & Yan 1998).

In otophysans, the major portions of acoustic signals were in the frequency range 100–400 Hz (swim-bladder drumming sounds, knocking sounds) and of 1–3 kHz (stridulatory sounds) (table 1). Sound spectra of pectoral stridulatory sounds of catfishes match the flat hearing curves, except for *Corydoras*. In this callichthyid species a clear mismatch was observed between its poor hearing ability above 1 kHz and the main energy of sounds, which were concentrated between 1 and 2 kHz (figure 1b). None of the species producing acoustic signals with dominant frequencies below 400 Hz (*Botia*, *Serrasalmus*, *Platydoras*, *Pimelodus*) possessed a pronounced low-frequency sensitivity maximum (figure 1b). Fishes emitting both

low- and high-frequency sounds, such as pimelodid and doradid catfishes, did not possess two corresponding sensitivity maxima.

In anabantoid fishes, the main energies of the high-pitched sounds correspond with the best-hearing bandwidth in *Trichopsis vittata* (1–2 kHz) and *Colisa lalia* (800 Hz–1 kHz). In the pygmy gourami *Trichopsis pumila* dominant frequencies of sounds were found above 1.5 kHz and thus do not match the lowest threshold, which was below 1.5 kHz (table 1).

An analysis of these recent findings in otophysans and anabantoids reveals that differences exist in hearing sensitivity among representatives of both taxa. These differences, obviously, do not correspond to the importance of acoustic communication in certain representatives of these groups. Non-vocal species, such as the goldfish and the blue gourami, were found among the most sensitive species in both groups of hearing specialists. In addition, poor hearing abilities occur in vocal and non-vocal forms (*Corydoras* and *Eigenmannia*). Therefore, it is assumed that differences in hearing curves reflect differences in accessory hearing structures most likely caused by other selective pressures. In labyrinth fishes these are thought to be caused by the resonant frequency of different-sized suprabranchial chambers, the air-breathing cavities close to the inner ear (Ladich & Yan 1998).

As found in both otophysans and anabantoids, sound-generating mechanisms and acoustic communication is not a common feature of all members of other taxa. Hawkins & Myrberg (1983) mentioned mute species among gadids and pomacentrids, groups of fishes that are known to contain large numbers of sound-producing species. Also, within mormyrids only a small number of species seem to be vocal and their hearing curves resemble each other (J. D. Crawford, personal communication). Therefore, recent findings provide evidence that the development of sound-producing (sonic) mechanisms did not seem to selectively improve hearing abilities in species using the acoustic channel for communication.

Comparison of whole audiograms and total spectra of sounds in vocalizing members of otophysans and anabantoids produces contradictory findings. A clear match between dominant frequency of sounds and best-hearing bandwidth in a limited frequency range was only found in one species, the croaking gourami *Trichopsis vittata* (1–2 kHz) (Ladich & Yan 1998). None of the species emitting low-frequency sounds possesses a pronounced low-frequency hearing sensitivity. Broad-band stridulatory sounds and their flat energy distribution correspond with flat hearing curves in doradids and pimelodids; however, a mismatch was observed in the callichthyid catfish. The lack of a match does not necessarily imply that fishes cannot detect conspecific calls or that acoustic communication is limited. Sound pressure levels of emitted acoustic signals, communication distances and environmental conditions have to be considered. Acoustic signals can easily be recognized by species emitting high-amplitude sounds such as the loach *Botia* (40 dB above threshold), despite the fact that dominant frequencies of sounds are outside the best auditory sensitivity (figure 1b). But even in species where sound pressure levels are maximally 15 dB above hearing thresholds, as in *Agamyxis*, sounds are detectable because species investigated communicate at distances of a few centimetres.

However, a concentration of sound energies in a frequency region with low auditory sensitivity might endanger intraspecific communication by increasing the risk of interception by predators or conspecifics.

In summary, when comparing hearing curves of vocalizing and non-vocalizing species as well as audiograms of species emitting drumming sounds to those producing stridulatory sounds or knocking sounds, no clear relationship can be found between sound spectra and auditory sensitivity. Therefore, acoustic communication does not seem to be the major force for the evolution of hearing specializations in fishes. This idea is supported by evidence that numerous sound producers are hearing generalists such as toadfishes, sculpins, triglids, cods, gobiids, pomacentrids and sunfishes.

Is the generation of certain sound types related to particular hearing abilities? The development of low-frequency swim-bladder sounds is clearly not limited to certain hearing abilities, environmental or systematic constraints. Drumming sounds are generated by hearing specialists such as catfishes, characids and mormyrids as well as by numerous hearing generalists such as cods, triglids, toadfishes and drums (Ladich 1999). Additional observations point to the fact that different selective pressures resulted in the evolution of hearing and hearing specializations on the one hand, and sound-generating mechanisms and vocalizations on the other hand. As hearing specializations are often characteristics of whole taxa whereas sonic organs appear in a limited number of species within these taxa, it is assumed that the former evolved much earlier. This idea is corroborated by a phylogenetic analysis of the sound-producing organs within otophysans. Cypriniformes are the most primitive group among otophysans with Characiphysi (Characiformes and Siluriphysi) being its sister group. Interestingly, only a few representatives of the large order of Cypriniformes are known to be vocal and in no case was there a sonic/vocal organ described. This indicates that sound-generating structures are less specialized within Cypriniformes. Highly specialized sonic organs such as swim-bladder drumming muscles only evolved in its sister group Characiphysi. Many characids as well as numerous catfish families possess extrinsic swim-bladder muscles. Phylogenetic analysis revealed that the Weberian apparatus is a main feature of all otophysans while sound production evolved occasionally in Cypriniformes and on a regular basis in Characiphysi.

Which environmental constraints have caused the ancestors of certain fishes to improve their hearing abilities? It appears that hearing specializations mostly occur in quiet environments such as lakes, slowly flowing waters and the deep sea, and only occasionally in turbulent and

noisy habitats such as coasts and reefs (holocentrids). Additionally, most sound energy that propagates in shallow freshwater habitats is of higher frequency (Schellart & Popper 1992). Lowering the auditory thresholds and extending the frequency range would improve the chance of survival during attacks by predators and/or enable better prey detection. Predator avoidance through development of hearing may largely explain the evolution of ultrasonic hearing in numerous nocturnally flying insects and perhaps some fishes. Clupeids are sensitive to ultrasound and responded to echolocating pulses of dolphins in playback experiments by startle behaviour (Mann *et al.* 1997; A. N. Popper, personal communication).

Based on these results it appears that the major selective pressures involved in the evolution of hearing specializations could be predator avoidance and/or prey detection in quiet freshwater habitats and less so the optimization of acoustic communication.

I thank Allen Mensinger, Art Popper and one anonymous reviewer for critically reading this manuscript. Research was supported by the Austrian Science Fund (FWF grant no. 10295 and 12411).

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