

# Diversity in Hearing in Fishes: Ecoacoustical, Communicative, and Developmental Constraints

Friedrich Ladich

**Keywords** Accessory hearing structures • Ambient noise • Audiometry • Auditory evoked potential • Ecoacoustical constraints Hypothesis • Ontogeny

## 1 Introduction

Fishes have evolved a surprisingly large diversity in hearing sensitivities, which has been known for almost a century. This diversity raises several questions that are dealt with in the course of this chapter. First, what do hearing sensitivities look like in fish and how do they differ between groups? Second, which morphological structures enable some fish to hear better than others? Third, which factors caused fish to develop pronounced differences in ear morphology and hearing abilities? The chapter starts with a short historical overview over the investigation of hearing in fishes and of its diversity.

Early in the 20th century, several investigators, in particular Parker and Von Frisch, demonstrated unambiguously that fish are able to detect sound (e.g., Parker, 1903, 1918; Von Frisch, 1923; Stetter, 1929). It soon became clear that fish species differ widely in the extent to which they react to sounds. Eurasian minnows (*Phoxinus phoxinus*) were sensitive to sound frequencies up to 5 kHz and the brown bullhead catfish (*Ameiurus nebulosus*) even up to 13 kHz (Von Frisch, 1936, 1938; Poggendorf, 1952). In general, the upper frequency limit was found to be much higher in representatives of otophysines, which comprise carps and minnows (Cypriniformes), catfishes (Siluriformes), tetras (Characiformes), and knifefishes (Gymnotiformes), than in non-otophysines, whose “sense of hearing is

---

F. Ladich (✉)

Department of Behavioural Biology, University of Vienna, Althanstrasse 14,  
1090 Vienna, Austria

e-mail: [friedrich.ladich@univie.ac.at](mailto:friedrich.ladich@univie.ac.at)

very poorly developed” (citation from Von Frisch, 1938, p. 10). European perch (*Perca fluviatilis*), mudminnows (*Umbra pygmaea*), brown trout (*Salmo trutta fario*), European eels (*Anguilla anguilla*), common bullhead (*Cottus gobio*), and others did not respond to high-frequency sounds and only to sounds that were much louder.

These differences in hearing sensitivity were then attributed to differences in the connections of the inner ears to gas-filled cavities in the fish’s body. It had been known since Weber’s (1820) work that otophysines possess a series of ossicles connecting the swim bladder to the inner ear. Because of the analogy of these ossicles to the middle ear ossicles in mammals, Weber called them “ossicula auditoria” (auditory ossicles) and named them as in mammals: stapes, incus, and malleus. Currently they are termed scaphium, intercalarium, and tripus because they are not homologous to the mammalian ossicles. Weber (1820) postulated that the swim bladder serves to intensify the sounds that strike the body of the fish and that the ossicles conduct the sound to the ear. After a fierce controversy over the function of the swim bladder and “auditory ossicles” (see Sørensen, 1895), Weber’s theory proved to be correct. Removing the swim bladder in *Phoxinus phoxinus* as well as the tripus in *Ameiurus nebulosus* resulted in decreased hearing abilities (Von Frisch & Stetter, 1932; Poggendorf, 1952).

The fact that fish differ in hearing sensitivities and that this difference can—to various extents—be explained by the connection of the inner ear to air-filled cavities was quite well known in the 1930s (Von Frisch & Stetter, 1932). Numerous subsequent studies in otophysines and non-otophysines with or without such connection supported Weber’s theory and is dealt with in the first section of this chapter.

The functional morphology of this diversity has been successfully investigated over the last 80 years in several taxa and proved to be a quite fruitful field in fish bioacoustics. At the same time, evolutionary questions have seldom been posed and testable hypotheses rarely formulated. Even less often were data provided to support one of these hypotheses. Thus, the evolution of this diversity remains a field of much theoretical consideration and speculation. Did the variety in hearing sensitivity evolve because of ecoacoustical constraints such as different ambient noise situations in different habitats, or was it due to the necessity to detect conspecifics and thus communicate intraspecifically? In the first case, fish would want to glean as much information as possible from the surrounding acoustical environment (auditory scene) including abiotic (wind, waves, currents) and/or biotic sound emanating from animals at the same trophic level (conspecifics, heterospecifics) or different trophic levels (predators or prey) independently of their ability to communicate acoustically. In the latter case, there would be a correlation between hearing sensitivities and sound communication.

The different hypotheses are dealt with in the following sections and their pros and cons discussed in the light of recent data.

## 2 Diversity in Accessory Hearing Structures

The large diversity in hearing sensitivities in fishes can often be explained from a physical point of view by the way inner ears are connected to air-filled chambers within the fish's body. These chambers vibrate in a sound pressure field and may be able to transmit these vibrations to the inner ears (Fig. 1). In the latter case fish are sensitive to sound pressure in addition to particle motion, which all fish are able to detect. This chapter focuses on sound pressure measurements because almost all hearing threshold in fish are given in sound pressure units.

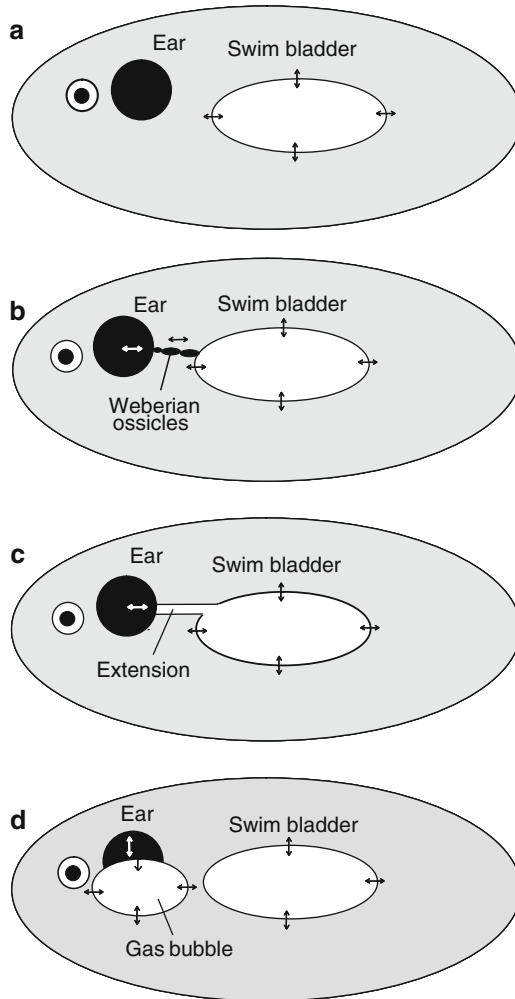
### 2.1 *Otophysines*

#### 2.1.1 Weberian Apparatus

The most widely known of these accessory hearing structures are the Weberian ossicles of otophysines, named “ossicles” because of their similarity to the middle ear ossicles in mammals (Fig. 1b). These “hearing ossicles” are not, however, homologous, because Weberian ossicles derive from anterior vertebrae whereas mammalian auditory ossicles derive from ancestral jaw bones (Romer & Parsons, 1983). Despite different evolutionary origins, both sets of ossicles function in the same way. They transmit oscillations of a membrane (tympanum in mammals, anterior wall of the swim bladder in otophysines) to the perilymphatic canals of the inner ear. Membranes in an acoustic field can move more freely with higher amplitudes when surrounded at least partly by air than membranes completely surrounded by fluids or tissues. Essentially, the swim bladder and other gas-filled cavities are pressure-to-displacement transformers, which transform the sound pressure underwater into membrane motion (Sand & Enger, 1973). The auditory periphery in otophysines and mammals represents an example of convergent evolution. Presumably because of this trait (Weberian ossicles), otophysines became one of the most species-rich taxa among vertebrates, even more numerous than mammals. Today, there are more than 8000 species of otophysines and fewer than 6000 species of mammals (Nelson, 2006).

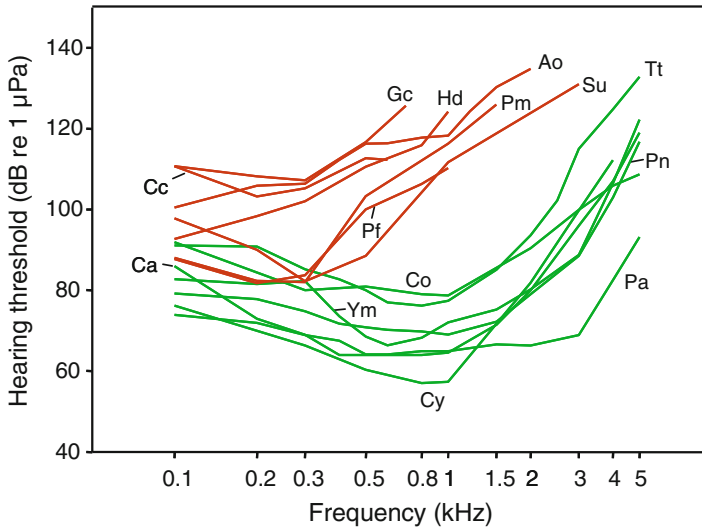
#### 2.1.2 Variation Among Otophysines

Ladich (1999) compared hearing abilities in representatives of seven families of all four otophysine orders and found major differences between species (Fig. 2). All species examined detect tone bursts from 100 Hz to 5 kHz, but audiograms



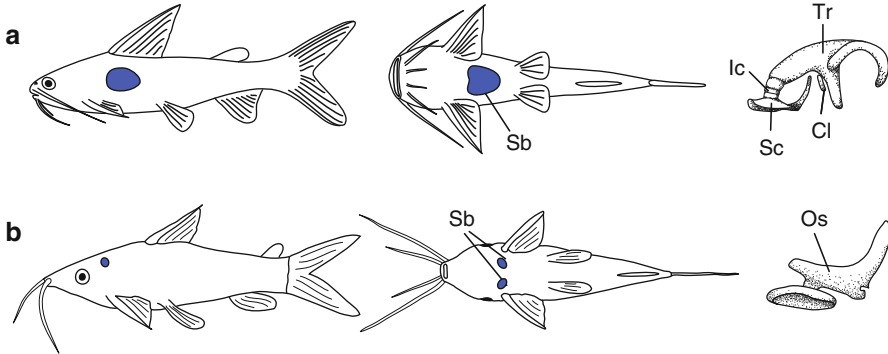
**Fig. 1** Schematic illustration of the relationship between inner ears and air-filled chambers in fishes. (a) Fish without a connection such as toadfish. (b) Otophysines with a series of bony ossicles (Weberian ossicles). (c) Fish possessing an anterior swim bladder extension connecting it to the inner ear such as in the holocentrid *Myripristis kuntee*. (d) Anabantoids (also mormyrids) possessing an air-filled cavity (suprabranchial chamber, tympanic bladder) laterally of the ears. Arrows indicate oscillations of the gas-filled chambers in a sound pressure field and the transmission to the inner ear endolymph. Note, in **A** and **D** there is no connection of the swim bladder to the inner ear and thus oscillations are not transmitted to the inner ear endolymph. (Adapted from Ladich & Popper, 2004, with permission from Springer Science+Business Media)

revealed major differences in auditory sensitivities, especially at higher frequencies (>1 kHz) where thresholds differed by up to 50 dB even within one order (catfishes, Siluriformes). Ladich (1999) argued that this might be due to differences in accessory hearing structures.

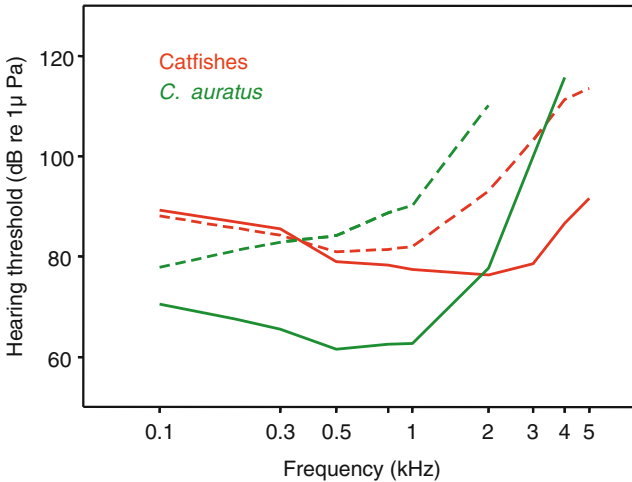


**Fig. 2** Auditory threshold curves for species with accessory hearing structures (*green lines*) and for those species lacking such structures (*dark red lines*). All curves were obtained using the same technique (AEP technique as described by Kenyon et al., 1998). Ao, *Astronotus ocellatus*; Ca, *Carassius auratus*; Cc, *Chromis chromis*; Co, *Corydoras aeneus*; Cy, *Cyprinus carpio*; Gc, *Gobius cruentatus*; Hd, *Halobatrachus didactylus*; Pa, *Platydoras armatulus (costatus)*; Pf, *Perca fluviatilis*; Pm, *Poecilia mexicana*; Pn, *Pygocentrus (Serrasalmus) nattereri*; Su, *Sciaena umbra*; Tt, *Trichogaster trichopterus*; Ym, *Yasuhikotakia (Botia) modesta*. Former genus or species names are given in brackets. In the drum (*Sciaena umbra*), the swim bladder is not connected to the ear, but probably plays a role in hearing. [Audiograms after Kenyon et al. 1998 (Ao, Ca); Ladich & Yan, 1998 (Tt); Ladich, 1999 (Pa, Pn, Ym); Amoser & Ladich, 2005 (Cy, Pf); Vasconcelos et al., 2007 (Hd); Wysocki et al., 2009 (Cc, Gc, Su); Schulz-Mirbach et al., 2010 (Pm); Lechner & Ladich, 2011 (Co)]

The high diversity in the morphology of the swim bladder and Weberian apparatus in otophysines, in particular in catfishes (Bridge & Haddon, 1889), has been well known since the 19th century. Numerous catfish families have large single, nonencapsulated swim bladders. Many other groups have small, paired, and encapsulated swim bladders located to the left and to the right of the vertebral column, directly behind the cranium. Species with single, nonencapsulated air bladders possess one, three, or four ossicles, whereas species with encapsulated bladders possess one or two (Fig. 3) (Lechner & Ladich, 2008). Catfishes with free bladders have significantly better hearing sensitivities above 1 kHz compared to species having tiny encapsulated bladders. The mean differences are 1–3 dB below 1 kHz and up to 25 dB above 1 kHz (Fig. 4). That correlative study suggested that the swim bladder size and number of ossicles positively influence hearing sensitivity.



**Fig. 3** Lateral and ventral view of swim bladders and Weberian ossicles of representatives of catfishes possessing (a) free swim bladders (*Ariopsis seemanni*, family Ariidae) and (b) small paired and encapsulated swim bladders (*Dianema urostriatum*, family Callichthyidae). Ventral views of the Weberian ossicles are on the right. Cl, claustrum; Ic, intercalarium; Os, ossicle; Sb, swim bladder; Sc, scaphium; Tr, tripus. (Adapted after Lechner & Ladich, 2008)



**Fig. 4** Effects of accessory hearing structures in catfishes (order Siluriformes) and the goldfish *C. auratus*. In catfishes the mean hearing threshold of all species with free swimbladders (6 species out of 6 families) (solid red line) and of all species with tiny, paired and bony encapsulated bladders (5 species out of 3 families) (dashed red line) is shown. Note the effect of tripus extirpation in the goldfish: Mean auditory thresholds in intact goldfish (solid green line) and after bilateral tripus extirpation (dashed green line). (*C. auratus* curves reprinted from Ladich & Wysocki, 2003, with permission from Elsevier. Catfish curves after Lechner & Ladich, 2008)

## 2.2 *Non-Otophysines*

Besides Weberian ossicles, several other pathways evolved to connect gas-filled chambers mechanically to the inner ear. Several groups of bony fishes have rostral extensions of the swim bladder that contact the inner ear and improve hearing in a way similar to otophysines (Fig. 1c). The best examples are the extensions in squirrelfishes (family Holocentridae) and cichlids (family Cichlidae). Tavolga and Wodinsky (1963) and Coombs and Popper (1979) showed that squirrelfishes possess extensions of different lengths and that the length is correlated with hearing sensitivity. In the shoulderbar soldierfish (*Myripristis kuntzei*) the rostral extensions are long and directly contact the auditory capsule, which results in the highest sensitivity within this family. Shorter extensions such as in the dusky squirrelfish (*Sargocentron vexillarium*) and the squirrelfish (*Holocentrus adscensionis*), or even missing extensions, reduced the sensitivity accordingly (see also Hawkins, 1993). Schulz-Mirbach et al. (2012) showed that cichlids vary considerably in swim bladder extensions and swim bladder size, which affects auditory sensitivity and the range of frequencies detectable. *Paratilapia polleni* and the orange chromide (*Ectopplus maculatus*) possess anterior swim bladder extensions coming close to the inner ears, which results in significantly higher auditory sensitivities, at 0.5–1 kHz, than in species lacking anterior extensions such as the jewel cichlid (*Hemichromis guttatus*) and the slender lionhead cichlid (*Steatocranus tinanti*). In the latter species the swim bladder is considerably small, which seems to limit the frequency range detectable (highest frequency detectable 0.7 kHz as compared to 3 kHz in all other cichlid species investigated). Further, rostral extensions of the swim bladder were observed in African knifefishes (family Notopteridae), drums or croakers (family Sciaenidae), and numerous other taxa (Coombs & Popper, 1982; Ramcharitar et al., 2006; Braun & Grande, 2008).

Note that such morphological structures are not direct evidence for their acoustical function and do not indicate the manner in which they enhance hearing. Even a lack of accessory hearing structures does not prove the opposite, namely that fish lack enhanced hearing. Myrberg and Spires (1980) demonstrated that Caribbean damselfishes (family Pomacentridae) are sound pressure sensitive and have best hearing at 500 Hz despite lacking swim bladder extensions. Typically, species lacking hearing specializations have best hearing at much lower frequencies.

Sound pressure sensitivity and high-frequency hearing indicates that the swim bladder is involved in hearing, although it is unknown how vibrations are transmitted to the inner ear. Correlations between the inner ear–swim bladder connection and hearing sensitivity within taxa are not always as straightforward as in holocentrids. In sciaenids or drums, more intimate connections between the bladder and the auditory capsule do not result in a higher absolute sensitivity at comparable frequencies, but mainly in a widening of the detectable frequency bandwidth. The common weakfish (*Cynoscion regalis*) has a pair of anterior horns that terminate close to the ear, whereas there are no extensions of the swim bladder in spot *Leiostomus xanthurus*. *C. regalis* detects frequencies up to 2 kHz and

*L. xanthurus* frequencies up to 700 Hz; both species do not differ in absolute sensitivity between 200 and 700 Hz (Ramcharitar et al., 2006).

A special case of swim bladder extensions is found in herrings (family Clupeidae). The extensions widen anteriorly and form auditory bullae—partly gas-filled and partly fluid-filled—that simultaneously contact the utricle of the inner ear and the lateral line (Blaxter et al., 1981). This hearing specialization enables clupeids to detect sounds to greater than 3000 Hz. Representatives of the alosine subfamily even detect ultrasound up to 180 kHz (Wilson et al., 2009) (see the chapter by Narins and Mann in this volume). It has to be pointed out, however, that the absolute hearing sensitivity is much lower in clupeids than in otophysines.

The third major group of accessory hearing structures besides ossicles and bladder extensions are air-filled cavities other than swim bladders that are directly attached to the inner ear (Fig. 1d). Two nonrelated taxa exhibit such structures correlating with enhanced hearing acuity. Elephant-nose fishes (family Mormyridae), weakly electric fishes from tropical Africa, possess small tympanic bladders—gas-filled cranial derivatives of the swim bladder—that are directly attached to the saccule and improve hearing sensitivity up to 3 kHz (Stipetić, 1939; McCormick & Popper, 1984; Fletcher & Crawford, 2001). Labyrinth fishes or gouramis (perciform suborder Anabantoidei) possess suprabranchial organs dorsally of the gills and directly next to the saccules. These chambers are utilized for air breathing but also increase hearing abilities (Schneider, 1941). The paradise fish (*Macropodus opercularis*) and other anabantoids detect sound up to 5 kHz (Ladich & Yan, 1998).

Peripheral specializations for hearing tend to correlate with the inner ear fine structure. The inner ear of fishes consists—besides three semicircular canals—of three end organs, the utricle, saccule, and lagena, each of which is a sac that includes two major structures, the sensory epithelium and the otolith. The sensory epithelium contains sensory hair cells and supporting cells. The otolith consists of calcium carbonate and lies very close to the sensory epithelium (Popper & Fay, 1999). The saccular hair cell bundles form orientation patterns that tend to be similar in species that lack specializations to enhance hearing. In contrast, species having specializations tend to have orientation patterns different from those of the first group (Popper & Schilt, 2008).

### 2.3 Comparison Between Hearing Sensitivities

Figure 2 illustrates auditory sensitivities in 14 species of 13 teleost families as determined using the auditory evoked potential (AEP) recording technique as developed by Kenyon et al. (1998) to eliminate differences potentially caused by different techniques (behavior vs. AEP) or by modifications of the AEP technique (see Section 2.4; for a review see Ladich & Fay, 2013). Species with hearing specializations are compared to those lacking such specializations. All AEP thresholds are given in sound pressure levels (SPLs) relative to 1  $\mu$ Pa as published



by the authors. The fish species lacking known specializations are tentatively put together (dark red lines) although we do not definitively know whether these species are pressure sensitive or not. The brown meager (*Sciaena umbra*) might be pressure sensitive because of its well-developed auditory sensitivity (Wysocki et al., 2009); it, however, lacks even the slightest swim bladder extension. Nevertheless, the comparison reveals clearly that species having morphological specializations for hearing (formerly called hearing specialists) detect a wider frequency range and that they possess, on average, lower auditory thresholds compared with species lacking such specializations (formerly called hearing generalists or nonspecialists). This effect is especially pronounced at frequencies above 500 Hz. Accordingly, auditory sensitivity curves are mainly ramp-shaped in species lacking and U-shaped in species having hearing specializations (Fig. 2).

#### 2.4 *Experimental Evidence of Hearing Enhancements*

The functional significance of accessory hearing structures can be assessed in two different ways. The first is by comparing morphological data (swim bladder to inner ear connection) to auditory sensitivities either in adults of closely related species or by comparing several developmental stages within a species. Such correlative evidence for hearing enhancement was found in adult holocentrids and cichlids (see Section 2.2) and catfishes (see Section 2.1.2) and in different development stages in cyprinids and a bagrid catfish (see Section 5). Conclusions based on such comparisons between species or developmental stages are rather indirect because, as mentioned earlier, there are exceptions to these correlations. The second approach provides direct evidence that a particular morphological structure enhances hearing. It involves eliminating the accessory hearing structure and measuring any decline in sensitivity. Surprisingly, data gained in these elimination experiments varied considerably between species and the methodological approaches used (for AEP studies see Ladich & Fay, 2013). The theoretical assumption is that air-filled chambers improve hearing, in particular at higher frequencies, but this was not always the case.

Several elimination experiments were conducted in otophysines. Investigators either extirpated the largest hearing ossicle or functionally eliminated the swim bladder by removing or deflating it. Poggendorf (1952) extirpated the tripus, the largest of the Weberian ossicles, in *Ameiurus nebulosus* (family Ictaluridae) and observed a largely frequency-independent drop in sensitivity of 36 dB at the lowest (60 Hz) and 42 dB at the highest frequency (6 kHz). Bilateral tripus extirpation in the goldfish (*Carassius auratus*) resulted in a frequency-dependent decline in sensitivity from 7 dB at 100 Hz up to 33 dB at 2 kHz and a narrowing of the detectable frequency range (maximum frequency: 2 kHz vs. 4 kHz) (Fig. 4) (Ladich & Wysocki, 2003). This difference in hearing loss due to tripus extirpation may be caused by different experimental techniques and less so by the use of different species.

Similarly, swim bladder elimination experiments also gave inconsistent results. Frisch and Stetter (1932) (see Section 1) were the first to demonstrate the contribution of swim bladders to hearing. Removing the swim bladder in the European minnow decreased hearing abilities, in particular at higher frequencies. Fay and Popper (1974) calculated that the auditory system of *Carassius auratus* gains sensitivity with increasing frequency due to the impedance transform characteristics of the fish's accessory hearing structures. Swim bladder removal resulted in a sensitivity decline by 20–35 dB, with a smaller drop below 100 Hz. Fay and Popper (1974) argued that this was the case because the fish was motion sensitive at low frequencies and the swim bladder plays little or no role at lower frequencies. Yan et al. (2000) deflated the swim bladder in the goldfish and observed a large loss of sensitivity at low frequencies (55 dB at 300 Hz) and a smaller loss at high frequencies (35 dB at 4000 Hz). In contrast, gas extraction from the swim bladder in the roach (*Rutilus rutilus*, family Cyprinidae) and *Ameiurus nebulosus* resulted in poorer hearing sensitivity at increasing frequencies (Kleerekoper & Roggenkamp, 1959; Laming & Morrow, 1981).

Elimination experiments were also carried out in other taxa. In mormyrids, Yan and Curtsinger (2000) deflated the tympanic ear bladder, whereas Fletcher and Crawford (2001) filled it with physiological saline. Thresholds were elevated maximally at mid-audiogram frequencies (400–800 Hz), with smaller threshold shifts at 100 Hz and 2.4 kHz. In anabantoids, Schneider (1941) showed that the upper hearing range dropped by more than two octaves in the paradise fish (*Macropodus opercularis*, family Osphronemidae) (from 4.5 kHz down to 800 Hz) when the suprabranchial organ was filled with water. Yan (1998), after deflating the organ, found a rather constant decline of hearing sensitivity and no change in the detectable frequency range. The difference in hearing loss when eliminating the suprabranchial chamber in anabantoids is most likely caused by different experimental techniques.

In summary, the effects of accessory hearing structures on auditory sensitivity are not completely understood. Although they clearly enhance hearing by lowering thresholds at particular or at all frequencies, it has not been shown unambiguously that this effect is frequency dependent or that it affects the upper hearing limit. There is strong evidence, however, that the hearing enhancement increases with frequency and that it extends the maximum frequency detectable. This explains why species possessing specializations typically detect a wider range of frequencies than groups without such adaptations (Fig. 2).

## **2.5 Remarks on Comparisons Between Audiograms and Between Noise Spectra**

The main tools for describing hearing abilities in animals are hearing threshold curves or audiograms, which illustrate the lowest SPL at which animals are able to detect sounds at different frequencies. Absolute hearing thresholds given in decibel

values allow a comparison of hearing abilities across different studies, but such comparisons require caution. Comparison of hearing thresholds in goldfish measured in different labs revealed differences of up to 50 dB or more (Fay, 1988; Ladich & Fay, 2013). Hawkins (1981) showed such differences for hearing curves gained by using different behavioral techniques, and Ladich and Wysocki (2009) provided similar data for curves determined by various modifications of the AEP recording technique. It would be interesting to explain the factors behind these differences and to calculate some correction factor for obtaining an ideal audiogram. This, however, is unrealistic because of the many unknown factors potentially influencing results, including animal holding conditions, background noise levels during experiments, different sound fields, calibration errors, and the influence of different threshold definitions. It is therefore advisable (and done throughout this chapter) to compare audiograms gained under similar experimental and acoustic conditions, ideally in the same laboratory.

Comparisons between fish hearing curves are further complicated because fishes detect different acoustical parameters in a sound field. They primarily detect particle motion (in contrast to terrestrial vertebrates, which detect only sound pressure) but may also be able to detect sound pressure if they have air-filled cavities that in some manner transmit their oscillations in a sound field to the inner ear. Because of the lack of particle motion sensors for small fish tanks, almost all hearing sensitivities were described in terms of sound pressure units (dB re 1  $\mu\text{Pa}$ ); the necessary sound pressure hydrophones can easily be purchased from numerous companies. Even if this sensor problem could be overcome, it is technically difficult to determine whether a species is pressure sensitive when it possesses air-filled cavities. Currently, the assumption is that many more species are pressure sensitive than previously thought (Popper & Fay, 2011). This chapter describes and compares audiograms as they have been published, even if this may not be the correct physical parameter for some species.

Similar difficulties can arise when comparing broadband sound/noise pressure levels or spectral levels from different studies. Broadband SPLs typically give the sound energy in the frequency range from 20 Hz to 20 kHz. Sound/noise spectral levels give the sound/noise energy in narrower frequency bands such as octave bands, third-octave bands, 50-Hz bands, or any other bandwidth. Broadband SPLs or spectral levels can be given in absolute decibel or in arbitrary, relative decibel values, either as power spectral levels in decibel values relative to 1  $\mu\text{Pa}$  or as spectral density levels in decibel re 1  $\mu\text{Pa}^2/\text{Hz}$  (see Richardson et al., 1995). In addition, many publications fail to mention the time period over which the noise pressure levels were determined, for example, 1 s, 1 minute, or 1 hour, and so forth. Noise levels determined during short recording periods can be influenced by unwanted noise to a much higher extent than noise levels measured over longer periods. Further, some hydrophones are quite insensitive or “noisy” and are unable to detect low noise levels correctly. This may not be a problem when measuring high noise levels, such as of anthropogenic noise in a marine environment, but it is

certainly problematic in quiet, stagnant freshwater habitats. All of these factors may influence broadband SPLs and subsequently spectral levels within spectral bands and should be considered when comparing sound/noise spectra.

### 3 Diversity and Ecoacoustical Constraints

The notion that hearing sensitivities of fishes (and potentially other animal taxa) are adapted to the acoustical conditions of the waters they inhabit is hereafter called the “ecoacoustical constraints hypothesis.” This hypothesis assumes that hearing thresholds are as low as possible without being masked by the noise in their environment (ambient noise). If the ambient noise varies in aquatic environments, it would inevitably result in the evolutionary selection of a large variety of hearing sensitivities in fishes. Low noise levels would then facilitate the evolution of morphological structures (accessory hearing structures) for hearing enhancement and the detection of low-level sound, whereas high ambient noise levels make accessory hearing structures meaningless. This hypothesis further postulates that improvements of hearing sensitivities evolved independently of the ability to produce sounds for acoustic communication.

According to the ecoacoustical constraints hypothesis, fish optimized their ability to pick up acoustic information emanating from abiotic sources (waterfalls, coastal surf, etc.) and biotic sources such as predators and prey and con- and heterospecifics under all prevailing acoustical conditions. For example, it would certainly be quite important for shoaling cyprinids to hear the feeding noises from con- and heterospecific shoal mates, but this assumption lacks experimental data. Fay (2009) argues that our current understanding of which information fish use out of their soundscape—besides communication sounds—is very limited. Markl (1972) observed that the red piranha [*Pygocentrus (Serrasalmus) nattereri*], a representative of the otophysine order Characiformes, attacked prey producing splashing noise more often than silent prey.

Indirect evidence for the attractiveness of certain underwater sounds for fishes comes from acoustic fishery techniques. As has been documented and exploited by indigenous people all over the world for hundreds of years, the artificial generation of underwater noise attracts fishes (Steinberg, 1957; Wolff, 1966). It is quite unlikely that these sounds are attractive because they resemble communication sounds: fishes attracted are either not vocal or produce sounds in quite different behavioral contexts. Hitting rods on the water surface attracts piranhas in South America as well as cichlids in Lake Tanganyika in Africa. Rattle fishery, known in the Baltic regions since the Medieval period, is based on rattling a plank underwater (Wolff, 1966). This method reportedly caught large numbers of perches. Rattling coconut shells underwater is very attractive for sharks (shark rattle) and was used in the South Seas (Wolff, 1966). It remains to be clarified whether the catch success is based on attracting or startling fishes. More recent experiments indicate that ambient noise may help fish to navigate to suitable settlement habitats. Playback experiments

revealed that pelagic coral reef fish larvae (of the families Trypterigiidae, Pomacentridae, Apogonidae, Gobiidae, Lethrinidae) orient toward loudspeakers playing back reef noise (Tolimieri et al., 2000; Simpson et al., 2008).

Besides orientation to prey items and suitable habitats, predator avoidance seems to be a major selective pressure for the evolution of hearing improvements. Many fish species avoid predators using a C-like startle behavior (C-start) (Canfield & Eaton, 1990; Canfield & Rose, 1996). This escape response is mediated by Mauthner neurons in the spinal cord. Canfield and Eaton (1990) suggested that the sound-pressure-evoked predator evasion coevolved with the addition of hearing to the swim bladder function. Thus, fish with hearing specializations could detect predators earlier and initiate escape responses more effectively. The aforementioned studies point to the importance of hearing for orienting to or away from sounds other than communication sounds (Ladich & Popper, 2004).

Examining the appropriateness of the ecoacoustical hypothesis requires recording ambient noise of habitats and determining their broadband levels. It also calls for demonstrating that a large diversity in ambient noise conditions exists. Finally, it has to be shown that hearing sensitivities of fish are adapted to natural noise conditions. How can this be tested? If fish are adapted to their acoustic environment, then the hearing sensitivity in the presence of ambient noise should be similar to that under quieter conditions. Such quiet conditions are typically given in soundproof rooms. If hearing sensitivities change and thus if thresholds shift up under natural noise conditions, then fish are masked and not well adapted to their natural acoustic environment. The latter result would contradict the ecoacoustical constraints hypothesis.

Additional factors must also be considered. Ambient noise in natural habitats is probably not constant but varies between different location within a species' habitat (microhabitat), varies with different times of the day and seasons, weather conditions (wind, rain, surf, movement of reeds, etc.) and biotic factors (activity of underwater insects, arthropods etc.). To which conditions should fish be adapted? Should fish be adapted to an average noise regime or to the lowest level encountered in their environment, even if these conditions are not always met? Noise levels can also change because of weather conditions such as wind and rain, both in aquatic and terrestrial habitats. One can hear over large distances on a calm day and probably detect many more animals than on a stormy day, when we hear quite badly, owing to the noise emanating from heavily moving vegetation such as trees. It is hypothesized that fish, similar to other animals, are adapted to the lowest noise levels to detect faint sounds of different origin that are important for various reasons (migration, food, prey, predators, communication).

### ***3.1 Diversity in Ambient Noise***

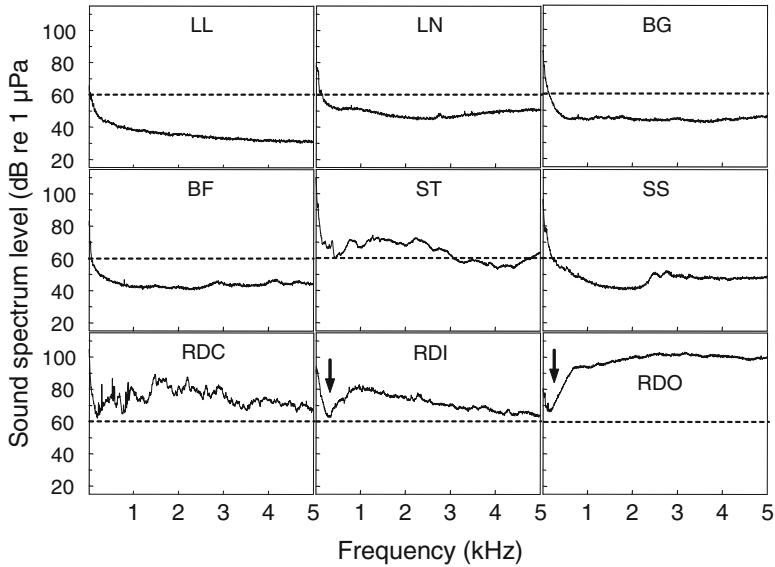
The ambient noise of aquatic habitats has rarely been investigated with regard to the fishes inhabiting these locations. Wenz (1962) and Urlick (1983) estimated and described ambient noise spectra in the ocean and showed a dependence on sea

states, wind speeds, depth, and ship traffic. The general result of these largely theoretical descriptions is that the noise spectrum level increases with sea state, wind speed, and precipitation and that the spectrum level decreases at higher frequencies. Nonetheless, a single set of noise curves for all oceanic habitats is much too rough to analyze meaningfully the differences in noise situations in habitats of marine fishes. Moreover, it does not help our understanding of the evolution of accessory hearing structures in freshwater or deep sea habitats.

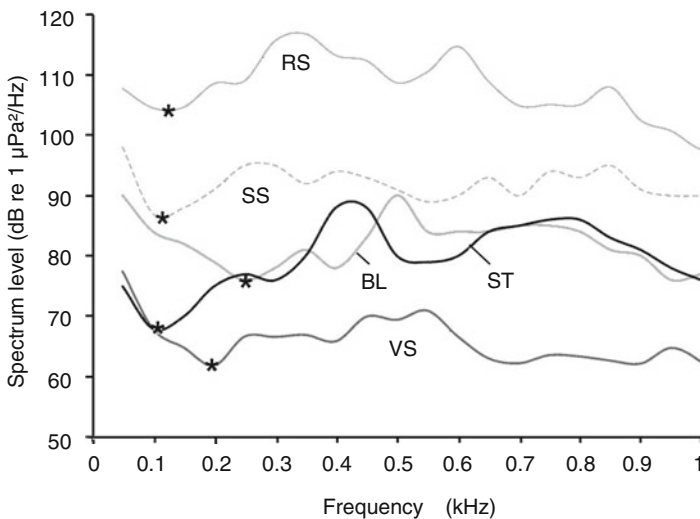
Recently, ambient noise has been recorded in a number of freshwater and marine habitats in central Europe. Wysocki et al. (2007) recorded and analyzed 12 aquatic habitats there (measurements were taken during daylight on a day in spring and early summer), including running waters such as creeks and rivers and quiet standing waters such as lakes and backwaters. The noise levels and spectra differed considerably between these habitats. Standing freshwaters were quiet, with broadband noise levels below 100 dB re 1  $\mu$ Pa (equivalent continuous SPL averaged over a period of 60 s,  $L_{Leq, 1min}$ , root mean square [RMS]) under no-wind conditions. Broadband noise levels in fast-flowing waters were typically above 110 dB and peaked at 135 dB in a free-flowing section of the Danube River. Noise levels ( $L_{Leq, 1min}$ , RMS) differed by more than 50 dB between habitats, making it necessary to consider each habitat separately when looking for masking effects in the field.

The broadband noise level provides a rough estimate of the overall noise situation in a habitat. To determine how fish might be affected in their particular hearing range and how well sounds may propagate, it is important to examine spectral levels in detail. Low levels of spectral noise energy in a limited frequency range, sometimes termed “noise windows,” are far more suitable for sound propagation and sound detection than high levels. Wysocki et al. (2007) showed that most environmental noise in stagnant habitats is concentrated in the lower frequency range below 500 Hz. In fast-flowing waters, high amounts of sound energy were present in the frequency range above 1 kHz, leaving a low-energy “noise window” below 1 kHz (Fig. 5). In addition to sound pressure spectra, there is a need for particle motion spectra to assess fully the ambient noise conditions that fish encounter. Because of the difficulty acquiring appropriate sensors (see Section 2.5), this shortcoming is not easy to overcome.

Differences in broadband and spectral amplitudes of up to 50 dB were described not only for freshwaters in central Europe but also for northern Italy and the Mediterranean. Lugli (2010) investigated the ambient noise profiles between 50 Hz and 1000 Hz at the breeding sites of northern Italian and Mediterranean gobies (family Gobiidae) in stony streams, vegetated springs, brackish lagoons, and sandy as well as rocky shores. Noise spectral levels in the 50- to 500-Hz band differed by more than 40 dB; they were much higher in the brackish/marine habitats (80–115 dB) than in the vegetated spring (60–70 dB re 1 Pa<sup>2</sup>/Hz) and the stream (70–80 dB). Gobies inhabiting the coast, in particular a rocky coast, are exposed to much higher levels of low-frequency masking noise than freshwater gobies (Fig. 6). The noise situation can change over short distances. Ambient noise from a waterfall may attenuate as much as 30 dB between 1 and 2 m, making the acoustical



**Fig. 5** Absolute amplitude spectra of nine habitats within central Europe illustrating the large diversity in ambient noise conditions. BF, Backwater Fadenbach; BG, Backwater Gänsehaufen Traverse; LL, Lake Lunz; LN, Lake Neusiedl; RDC, Danube Channel; RDI, Danube River at Danube Island; RDO, Danube River at Orth; SS, Schwarza stream; ST, Stream Triesting. Arrows indicate potential noise windows. (Adapted from Wysocki et al., 2007. Reprinted with permission from the Acoustical Society of America)



**Fig. 6** Low-frequency spectra (50–1000 Hz) of the ambient noise from five habitats of gobies in northern Italy and the Mediterranean. Asterisks indicate the center frequency of the quiet window of the ambient noise. BL, brackish lagoon; RS, rocky shore; SS, sandy shore; ST, stony stream; VS, vegetated spring. (Adapted after Lugli, 2010, with permission from Springer Science+Business Media)

environment of single fish quite variable (Lugli, 2010). Are these sound pressure spectra representative of the particle motion situation in these goby habitats? Lugli and Fine (2007) showed that the ambient noise spectra are generally similar to particle velocity spectra, including the quiet window at noisy locations, although the energy distribution of velocity spectra is shifted up by 50–100 Hz.

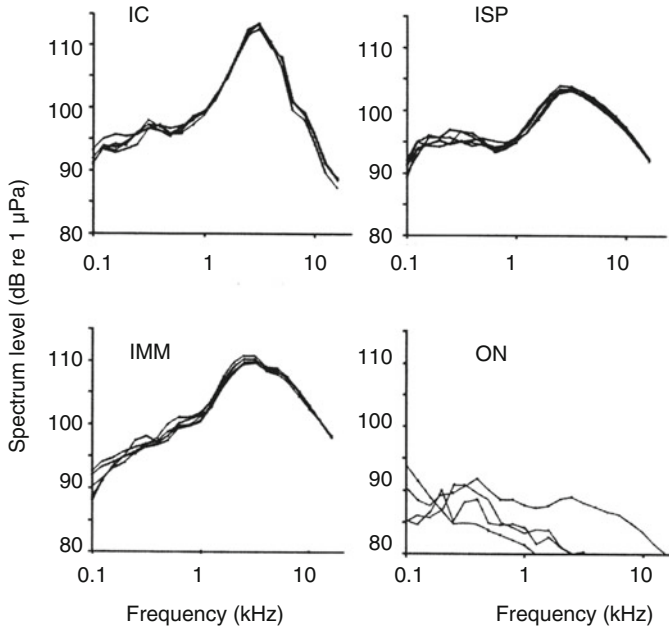
Both comparative studies (Wysocki et al., 2007; Lugli, 2010) thus reveal similar trends. Major differences in spectral levels exist between standing waters such as lakes, backwaters, or pools and rapidly moving waters such as creeks, large streams and rocky shores. These differences amount to 40–50 dB in both geographical regions and illustrate the diversity of soundscapes fish have to deal with.

Additional support for these conclusions comes from a recent study by Speares et al. (2011), who investigated two creeks in Alabama that are inhabited by small darter species (family Percidae). They reported that spectral levels differed between three microhabitats—a run, a riffle and a pool—depending on the water flow velocity. The loudest microhabitat in both streams was the fast-moving riffle. Spectral levels of the riffle were approximately 40–60 dB higher than levels of the other microhabitats in these creeks in the frequency range below 1 kHz. This result agrees with the general observation that large water movements (running water, coastal surf) result in much higher noise levels (Wysocki et al., 2007; Lugli, 2010; see also Tonolla et al., 2009).

Ambient noise profiles of the habitats of marine fish have been characterized several times, but comparative investigations are rare. Several studies of guidance mechanisms for larvae, juveniles, and adult fish described the ambient noise of coral reefs (Tolimieri et al., 2004; Kennedy et al., 2010; Radford et al., 2011). Reef noise is a combination of the sounds produced by various abiotic sources and reef-associated animals. Depending on the reef investigated, different high-energy peaks are caused by vocal fish, crustaceans, and other marine invertebrates. In a comparative study, Kennedy et al. (2010) recorded the ambient noise at 40 reefs of the Las Perlas archipelago in the Gulf of Panama and compared these to offshore sites. Acoustic recordings were taken at each site while the sea was calm. Spectral profiles between different reefs are rather similar, with a peak at around 3 kHz, which was attributed to snapping shrimps. Spectral energies of lower levels between 0.5 and 1 kHz were attributed to damselfish vocalizations (family Pomacentridae). In contrast, offshore recordings were rather quiet and spectral noise levels were about 20–30 dB lower (Fig. 7).

Changes in noise levels and spectra in central Europe were found not only between habitats, but were also reported throughout the year. Amoser and Ladich (2010) observed that changes in broadband SPL were smallest in the river (maximum: 10 dB), whereas higher changes were measured in stagnant habitats and streams (maximum: 31 dB). These local and seasonal changes make the soundscape for fish rather complex, especially when fish migrate between habitats.



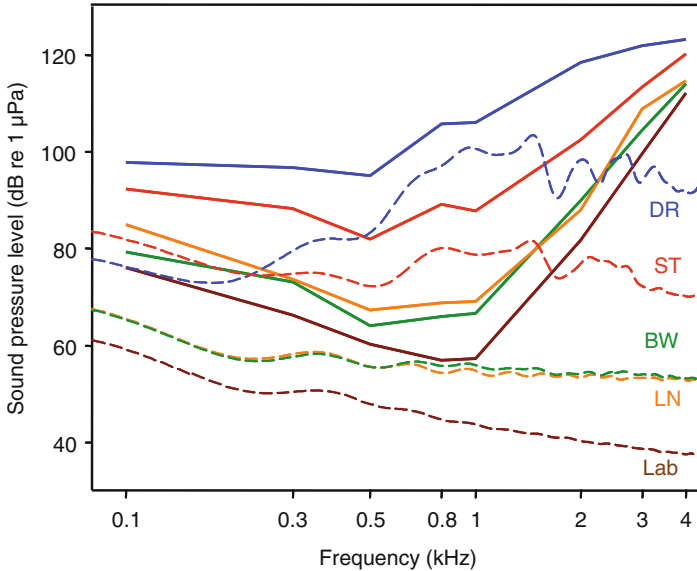


**Fig. 7** Third octave spectra measured at several coral reef sites and at offshore sites in the Las Perlas Archipelago in the Gulf of Panama. Each plot shows five “typical” reef acoustic profiles during the 2-minute recording period. IC, Isla Contadora; IMM, Isla Mongo Mongo; ISP, Isla San Pablo; ON, offshore noise. (Adapted after Kennedy et al., 2010, with permission from Elsevier)

### 3.2 Auditory Adaptation to the Acoustic Environments

The diversity in ambient noise profiles raises the question whether the auditory sensitivities of different fish species are adapted to these ambient noise profiles. The ecoacoustical constraints hypothesis postulates that fish are not masked by the ambient noise in their average habitats, but that they may be masked when they migrate to other habitats or during particular weather conditions or sea states. To test this notion, the hearing sensitivities need to be measured under quiet laboratory and under ambient noise conditions and compared.

The first studies on this topic were carried out in the 1970s. Chapman (1973) and Chapman and Hawkins (1973) determined hearing in the cod *Gadus morhua* and other representatives of the family Gadidae in the field. Fish were tested in a Scottish Loch 15 m below the sea surface and 5 m above the sea bed. Unmasked thresholds were obtained only under calm conditions. The authors showed that any change in the ambient noise level was accompanied by a corresponding decrease in hearing sensitivity in cods. The ratio between hearing threshold and spectral noise level of the environment at a particular frequency was constant and independent of the ambient noise level. In the cod, the ratio increased from 18 dB at 50 Hz to 24 dB



**Fig. 8** Mean hearing thresholds of the carp (*Cyprinus carpio*, solid lines) under laboratory conditions and in the presence of the different freshwater noise types (see also Fig. 1). Broken lines show the spectrum-smoothed noise power spectra of the corresponding noise types. BW, backwater; DR, Danube River; Lab, laboratory noise; LN, Lake Neusiedl; ST, Stream Triesting. (Adapted after Amoser & Ladich, 2005)

at 380 Hz. The different masking effect caused by the changing ambient noise was, further, confirmed when the noise level was raised artificially by transmitting random noise through underwater speakers. Cod, which have an unknown hearing specialization, are able to detect sounds under the quietest conditions encountered in their habitat. Thus cod are adapted to the lowest noise levels encountered in their habitats, which is in accordance with the ecoacoustical hypothesis.

To test the hypothesis further, Amoser and Ladich (2005) measured hearing sensitivities of common European freshwater fishes, the common carp (*Cyprinus carpio*, family Cyprinidae) and the European perch *Perca fluviatilis* (family Percidae) in various parts of their distribution range. They recorded the ambient noise conditions in four different habitats (Danube River, Triesting stream, Lake Neusiedl, backwaters of the Danube River), and played it back to fish while simultaneously measuring their auditory thresholds using the AEP recording technique. *C. carpio*, a species having hearing specializations, is only moderately masked by the quiet habitat noise level of standing waters (mean threshold shift 9 dB), but its sensitivity is heavily affected by river noise (decrease by up to 49 dB) in its best hearing range (0.5–1.0 kHz) (Fig. 8).

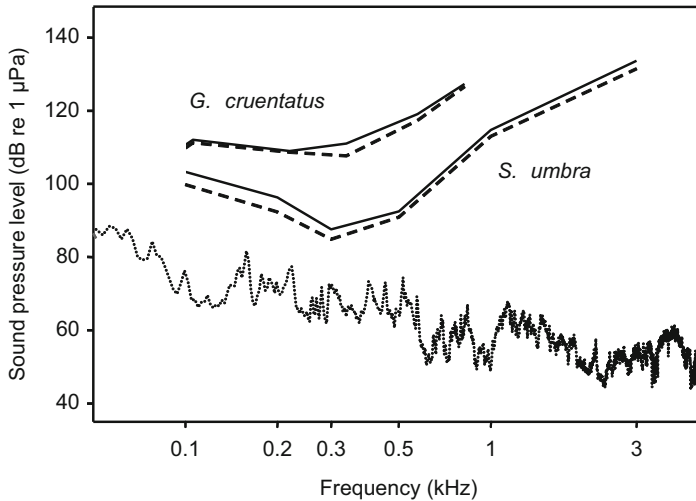
In contrast, the baseline hearing thresholds (lab conditions) of *P. fluviatilis*, a species not known to possess hearing specializations, were much higher and only slightly masked (mean shift up to 12 dB at 0.1 kHz) by the highest noise levels presented.

These results indicated that hearing abilities of otophysines are well adapted to the lowest noise levels encountered in freshwater habitats and that their hearing is considerably masked in some parts of their distribution range, such as a river. The perch, in contrast, is not adapted to low noise levels at all. Does the latter result contradict the ecoacoustical hypothesis or does *P. fluviatilis* prefer more noisy locations within its range?

These data on species having or lacking hearing specializations raise the question whether there is a general trend in the distribution of species according to the noise situations in central European freshwaters. Does diversity in freshwater habitats correlate to the noise levels as described in this study and to the occurrence of particular hearing sensitivities? According to Spindler (1997), Austria is inhabited by 61 fish species belonging to 16 families. Thirty-eight species are otophysines. Within these otophysines, about two thirds (26 species) spend all or part of their life in standing waters such as backwaters of rivers and lakes. Thus, more species—and relatively more otophysines—inhabit quiet waters. In contrast, only 11 of 23 species lacking specializations for hearing (salmonids, percids, cottids, gobiids, and others) live in these habitats. The distribution of species possessing and species lacking specializations in quiet stagnant versus rather noisy freshwater habitats supports, at a local level, the assumption that species having enhanced hearing live in rather quiet habitats, for which their hearing abilities are adapted.

Schellart and Popper (1992) argued that high-frequency hearing might have evolved as a response to the physics of shallow water sound propagation. Low-frequency sound does not propagate in shallow waters owing to a highpass filter effect (Roger & Cox, 1988). Fishes living in shallow waters, as well as other animals that collect acoustic information, must be able to detect higher sound frequencies. Thus the highpass filter effect is an ecoacoustic constraint that may partly explain the evolution of hearing enhancement, in particular at high frequencies. However, it does not explain the detection of low sound levels as is typical for many fishes possessing hearing specializations (Fig. 2).

Are the hearing abilities of marine fish adapted to the ambient noise? Recent studies on nonrelated taxa revealed that fish are well adapted to the ambient noise found during calm sea conditions. In addition to the study on cods by Chapman (1973), investigations on toadfish, on sciaenids or drums, damselfish, and gobies revealed that the hearing sensitivities were only slightly masked by ambient noise. Codarin et al. (2009) observed that the auditory sensitivity of the brown meagre *Sciaena umbra* (family Sciaenidae), the Mediterranean damselfish *Chromis chromis* (family Pomacentridae), and the red-mouthed goby *Gobius cruentatus* (family Gobiidae) changed by less than 3 dB when exposed to the ambient noise recorded in their natural habitat, the Miramare Natural Marine Reserve in the Adriatic Sea (Fig. 9). This effect was independent of the absolute hearing sensitivity of these species. *S. umbra* showed a broader hearing bandwidth (0.1–3 kHz) and lower thresholds than *C. chromis* (0.1–0.6 kHz) or *G. cruentatus* (0.1–0.7 kHz). In addition, Vasconcelos et al. (2007) showed in the Lusitanian toadfish *Halobatrachus didactylus* (family Batrachoididae) that ambient noise from the



**Fig. 9** Mean hearing thresholds of the brown meagre (*Sciaena umbra*) and the red-mouthed goby (*Gobius cruentatus*) under laboratory conditions (dashed lines) and during playback of the ambient noise (solid lines) compared to the sound spectra of the ambient noise (dotted line). (Adapted after Codarin et al., 2009, with permission from Elsevier)

Tagus River estuary in Portugal affected the auditory sensitivity only at low frequencies (50 and 100 Hz) compared to quiet lab conditions. Considerable masking effects were observed at all frequencies tested in these four marine fish families when the noise levels increased artificially, for example, by ship noise.

These data from representatives of five families indicate that their auditory sensitivities are not masked under calm sea conditions. The data, however, do not explain why sensitivities differ between species in the same habitat, as illustrated in *S. umbra* and *G. cruentatus* (difference at 500 Hz: 28 dB) (Fig. 9). This could be due to differences between the microhabitats within the Adriatic Sea, which were not analyzed in detail in the study. More likely, different hearing sensitivities were selected under different ecoacoustical constraints. The family Gobiidae might have evolved under high noise conditions and subsequently some species lost their swim bladders without compromising their hearing sensitivities. Representatives of this immensely successful fish family (approx.. 2000 species according to Nelson, 2006) might not be well adapted to low ambient noise levels encountered in parts of their huge distribution range (Lugli, 2010).

In summary, there is a large diversity in hearing sensitivities in freshwater as well as marine fishes. A high percentage of freshwater species exhibits hearing specializations. Otophysines comprise approximately 8000 of the 12,000 freshwater species (Nelson, 2006). When mormyrids and anabantoids are added to this number, then at least two thirds of all freshwater species possess hearing specializations. No such percentage can be calculated for the 16,000 marine species. A large number of marine fish families possesses rostral swim bladder

extensions but the functional significance of these morphological observations have not been proven in all groups (see table 4.1 in Braun & Grande, 2008). In a few families such as clupeids, holocentrids, sciaenids, pomacentrids, gadids, and gerreids improved hearing was demonstrated physiologically or behaviorally (see Section 2; Parmentier et al., 2011). Interestingly, swim bladder extensions have a limited distribution within many of these marine families (see Section 2). Some holocentrids and sciaenids lack anterior swim bladder extensions and hear poorly, and some clupeids do not detect ultrasound (Hawkins, 1993; Mann et al., 2005). In contrast, not a single otophysine species out of 8000 lacks Weberian ossicles.

The large number of species possessing hearing specializations in freshwaters is probably due to the large number of standing, as well as shallow waters such as lakes and backwaters of rivers where these sensory abilities could have evolved. More direct support for the ecoacoustical hypothesis would be given if a positive correlation between respective ambient noise levels and auditory thresholds would be found in closely related species such as *Myripristis kuntee* and *Adioryx vexillarius*, both belonging to the family Holocentridae but differing in hearing thresholds by about 50 dB.

## 4 Diversity and Acoustic Communication

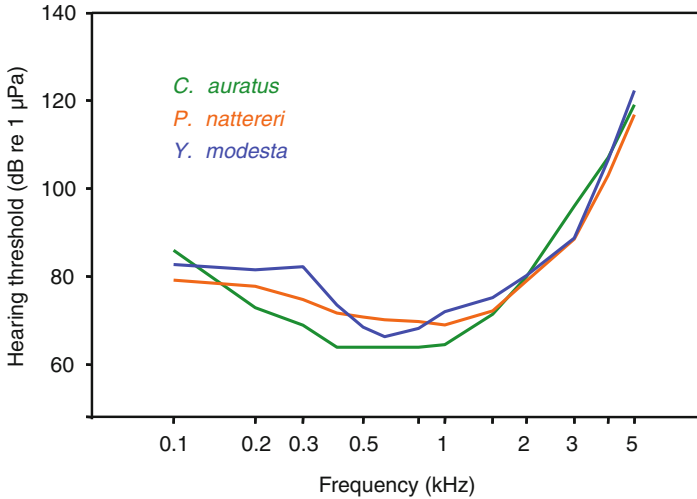
Bony fishes, but not cartilaginous fishes (sharks and rays), possess a large number of sound-generating mechanisms, certainly the largest number among vertebrates (for details see Tavolga, 1971; Ladich & Fine, 2006; Ladich & Bass, 2011). The swim bladder constitutes the most important organ for sound production. It can be vibrated by a large variety of sound-producing (drumming) muscles. Drumming muscles can either be situated in the wall of the swim bladder (intrinsic muscles) such as in toadfishes (family Batrachoididae) or they can originate outside (extrinsic muscles) and insert on the swim bladder, such as in pimelodid catfishes (family Pimelodidae), tigerfishes (family Therapontidae), and squirrelfishes (family Holocentridae). Drumming muscles can vibrate the swim bladder indirectly via broad tendons such as in drums (Sciaenidae) or piranhas (Characidae), or via a bony plate as found in several catfish families such as thorny catfishes (Doradidae). In addition, fishes have evolved several pectoral mechanisms and produce sounds using pectoral fins and girdles. Numerous catfish families (Doradidae, Pimelodidae, Synodontidae) produce sounds by rubbing their pectoral fin spines in a groove of the shoulder girdle. Croaking gouramis (genus *Trichopsis*, family Osphronemidae, Anabantoidei) pluck two enhanced pectoral fin tendons. Sculpins (family Cottidae) vibrate their entire shoulder girdle to emit sounds. Besides pectoral and swim bladder mechanisms, fish can produce sounds in additional ways such as by the pharyngeal apparatus (clownfish, family Pomacentridae). Several modifications of these types of mechanisms exist, and there is some overlap and additional variations, with some species simultaneously possessing two types of mechanisms (Ladich & Fine, 2006; Ladich & Bass, 2011). In several well-known sound

producers, we do not know the sound-producing mechanism at all or in detail, for example, in gobiids, loaches (family Cobitidae), and cichlids (Cichlidae). Finally, many fishes do not produce sounds for acoustic communication purposes, including most members of the cyprinid family (goldfish, carps). This does not exclude that they produce sounds unintentionally as a by-product of feeding, swimming, digging, and so forth. Nevertheless, the latter sounds should be carefully separated from the former communication sounds (often termed vocalizations), whose evolutionary selection pressures resulted in advantages for the sender (Bradbury & Vehrencamp, 1998, 2011).

Swim bladder-generated sounds are typically low-frequency harmonic sounds with main energies between 60 and 300 Hz, whereas pectoral fin stridulatory or plucking sounds are characterized by much higher sound energies at much higher frequencies, often between 1 and 2 kHz. The difference between species in the ability to produce sounds in general and to produce sounds of quite different main frequencies in particular raises several questions with regard to the diversity in hearing sensitivities.

Did fish that evolved (known or unknown) sound-generating mechanisms and produce communication sounds evolve hearing specializations that facilitate acoustic communication? If the detection of communication sounds was the main function of the auditory system, then such a correlative evolution should be observable. This, however, does not seem to be the case. Many well-known sound producers such as toadfish, tigerfish, gobiids, sculpins, triglids, sunfishes (family Centrarchidae), and cichlids lack hearing enhancements. Further, there is no indication that sound production is more widespread in species possessing than species lacking hearing specializations (Ladich, 2000). With few exceptions (*Cyprinella* spp., *Gobio gobio*), most cypriniforms do not vocalize and in no case have sound-generating mechanisms been described (Ladich, 1999). Among anabantoids, which possess a suprabranchial air-breathing chamber, only representatives of 1 out of 19 genera have a well-developed sonic mechanism (*Trichopsis*) and vocalize (Ladich & Yan, 1998). This distribution pattern of sonic organs among fishes with accessory hearing organs indicates once more that sound production and hearing enhancements developed independently of each other. The hearing sensitivities in representatives of three otophysine families with no or different sonic mechanisms are quite similar. The hearing curves of *C. auratus* (family Cyprinidae), the red-finned loach *Yasuhikotakia modesta* (family Cobitidae), and *Pygocentrus nattereri* (family Characidae) reveal best hearing sensitivities between 0.4 and 1 kHz and rather similar hearing curves, independent of the sound-generating mechanism. *C. auratus* is not known to produce sounds, loaches produce knocking sounds by an unknown mechanism, and piranhas possess drumming muscles that vibrate the swim bladder via a broad tendon surrounding it ventrally (Fig. 10) (Ladich, 1999; Ladich & Bass, 2005).

The development of hearing enhancements is thus clearly not related to the presence or absence of sound-generating mechanisms in fishes. However, does the maximum auditory sensitivity of taxa with sonic organs correlate to the sound frequencies, and would that explain part of the diversity, at least in vocalizing



**Fig. 10** Comparison of mean hearing thresholds of the goldfish (*Carassius auratus*, (Cyprinidae), the red-finned loach *Yasuhikotakia modesta* (Cobitidae), and the red piranha *Pygocentrus nattereri* (Characidae). (Adapted after Ladich, 1999, with permission from S. Karger AG)

species? Several studies demonstrate that this is the case. The main energies of sounds correlate with main auditory sensitivities in the damselfish *Stegastes* spp. (500 Hz) and green damselfish *Abudefduf abdominalis* (90–300 Hz), the croaking gourami *Trichopsis vittata* (1500 Hz) and in toadfish *Halobatrachus didactylus* (100 Hz) (Ladich & Yan, 1998; Maruska et al., 2007; Vasconcelos et al., 2007). In contrast, a detailed study in otophysines investigating representatives of seven families of all four orders revealed that differences in hearing sensitivities showed no apparent correspondence to the spectral content of species-specific sounds. In particular, fishes emitting both low- and high-frequency sounds, such as pimelodid and doradid catfishes, did not possess two corresponding auditory sensitivity maxima (Ladich, 1999).

In summary, there is no consistent evidence that hearing enhancement and sound production coevolved in fishes. Thus, acoustic communication was not the main driving factor in the evolution of the diversity in hearing (Ladich, 2000). Well-known sound-producing groups such as toadfishes or gobies compensate their low hearing sensitivities in two ways to facilitate communication—either by increasing sound levels or by communicating over short distances. In fact, field measurements by Lugli and Fine (2003) on courtship sound transmission in the freshwater goby *Padogobius bonelli* (formerly *P. martensii*) showed that the communication distances are less than half a meter. The low amplitude of goby sounds (90–120 dB at 5–10 cm) are below the noise level at a location 50–60 cm from the source, even under quiet conditions. Close-distance communication is widespread among all fish taxa. *Trichopsis vittata*, for example, typically communicates at distances of 5–10 cm during aggressive and reproductive behavior (Ladich, 2007).

## 5 Ontogenetic Diversity of Auditory Sensitivity

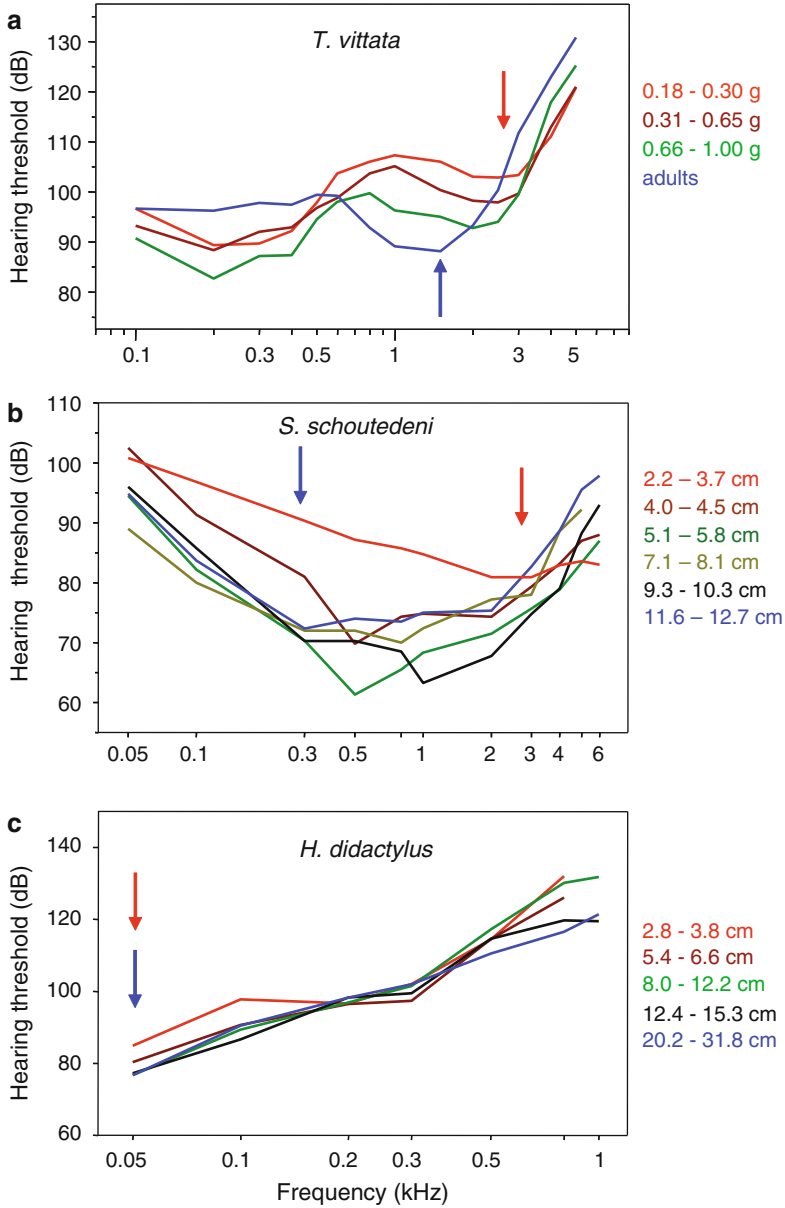
The diversity in hearing in fish becomes even more complicated when including ontogenetic development. Several studies showed changes in hearing sensitivities in the course of ontogenetic development. However, no uniform pattern has emerged on what these changes look like or whether they occur at all.

Developmental changes vary considerably between species in both non-otophysine and otophysine fishes. In perciforms, the largest fish order, four out of approximately 150 families have been studied using different techniques. Kenyon (1996) described the ontogenetic development in the bicolour damselfish (*Stegastes partitus*, Pomacentridae) and found a large increase in sensitivity with size. At 500 Hz, sensitivity increased from 130 dB re 1  $\mu$ Pa in 12–14 mm stages to 76 dB re 1  $\mu$ Pa in adults. The most sensitive frequency (500 Hz) and the detectable frequency range did not change; hearing curves were flatter in the early stages and V-shaped in adults. Such an increase of more than 50 dB within 100 days of development is rare in fish. While Kenyon (1996) observed similar hearing improvements (40 dB at 500 Hz) in the congeneric *Stegastes variabilis*, Egner and Mann (2005) observed the opposite trend in the sergeant major damselfish (*Abudefduf saxatilis*), another representative of this teleost family. The most sensitive frequency was found to be 100 Hz and the sensitivity decreased with growth by 10–20 dB. The authors argued that this difference could be because *Abudefduf saxatilis* is less vocal than *Stegastes partitus* and that different techniques were utilized (heart rate conditioning vs. AEP technique). In the red seabream (*Pagrus major*, family Sparidae), Iwashita et al. (1999) observed an improvement in sensitivity at 100–200 Hz of about 20 dB but not at other frequencies. In *Trichopsis vittata* (family Osphronemidae), Wysocki and Ladich (2001) found that the absolute sensitivity improved by 14 dB in the high-frequency range (0.8–3 kHz) where the main energies of croaking sounds were concentrated and that the most sensitive frequency shifted from 2.5 kHz to 1.5 kHz (Fig. 11a). This shift corresponds with the shift in the main energies of sounds.

In the round goby (*Neogobius melanostomus*, Gobiidae) and in the spotfin butterflyfish (*Chaetodon ocellatus*, family Chaetodontidae) no differences in hearing abilities between different size stages were found (Belanger et al., 2010; Webb et al., 2012). Thus, within the teleost order Perciformes, hearing sensitivity changes during ontogeny from an improvement by more than 50 dB in one damselfish, to no change in a gobiid and a butterflyfish to a sensitivity decrease of 10–20 dB in another damselfish species. Some of this difference may be due to different measurement techniques, but accessory hearing structures may be the main explanation. Some damselfish utilize their swim bladder for hearing and gouramis use their suprabranchial chamber, whereas some gobiids lack swim bladders.

In an ontogenetic study on marine fish larvae where only stages between 9 and 28 mm were investigated, Wright et al. (2011) found an improvement in auditory





**Fig. 11** Mean hearing threshold of different developmental stages of (a) the croaking gourami (*Trichopsis vittata*), (b) the squeaker catfish *Synodontis schoutedeni*, and (c) the Lusitanian toadfish (*Halobatrachus didactylus*). All thresholds were determined by the AEP technique (Kenyon et al., 1998). Arrows indicate the most sensitive frequency of the smallest juveniles and the largest stage (adults). In (a) the most sensitive frequency above 1 kHz is indicated in the smallest juveniles, because the dominant frequency of croaking sounds is found above 1 kHz. (a adapted after Wysocki & Ladich, 2001, with permission from Springer Science+Business Media)

sensitivity in four of five perciform species: the giant trevally *Caranx ignobilis* (family Carangidae), the orange spotted grouper *Epinephelus coioides* (family Serranidae), the fourfinger threadfin *Eleutheronema tetradactylum* (family Polynemidae), and the Australian bass *Macquaria novemaculeata* (family Percichthyidae) but not in the brown marbled grouper *Epinephelus fuscoguttatus* (family Serranidae).

Among otophysines the ontogenetic development has been investigated in 3 out of more than 40 families, namely in cyprinids and in two catfish families. Again, results are contradictory, despite their common accessory hearing structures (Weberian ossicles). Popper (1971) found no differences in hearing capabilities in 5 cm and 10 cm goldfish. Popper's results can probably be explained by the fact that the major improvements in hearing take place in stages smaller than 20 mm and that his specimens were much larger. Nevertheless, that study showed that larger fish, which have larger inner ear sensory maculae and thus more hair cells, do not necessarily hear better. In the zebrafish *Danio rerio* (Cyprinidae), much earlier stages have been investigated. Higgs et al. (2003) showed that the development of Weberian ossicles affected the bandwidth of detectable frequencies rather than absolute thresholds. The youngest *D. rerio* (10 mm total length) detected sounds up to 200 Hz, while older *D. rerio* (40 mm total length) detected frequencies up to 4 kHz. In contrast, Lechner et al. (2010, 2011) found that hearing sensitivities changed at all frequencies in both catfish species investigated. In the squeaker catfish (*Synodontis schoutedeni*, family Mochokidae) and the African bullhead catfish (*Lophiobagrus cyclurus*, family Bagridae), auditory sensitivities improved at lower frequencies (0.05–1 kHz) but were worse at higher frequencies (4–6 kHz). Except for the smallest stages of *L. cyclurus*, which detected frequencies up to 2–3 kHz, no change in the detectable frequency range was observed in catfishes (Fig. 11b). In the later stages, sensitivity increased by about 40 dB, which raises the question how such an improvement could be explained. Anatomical investigations using  $\mu$ CT and other techniques revealed that Weberian ossicle (intercalarium) and interossicular ligaments were not developed in the youngest group of *L. cyclurus* (Lechner et al., 2011).

Besides perciforms and otophysines, ontogenetic development has been investigated in two more nonrelated taxa—in two toadfish species (family Batrachoididae) and one herring species (family Clupeidae). Toadfishes are lacking hearing specializations, which seems to be reflected in small or no ontogenetic changes at all. In Lusitanian toadfish (*H. didactylus*), hearing abilities change only slightly during growth. The best hearing was below 300 Hz in all stages. Only the smallest toadfish group revealed lower hearing sensitivity at the best frequency (100 Hz). Moreover, at higher frequencies (i.e., 800 and 1000 Hz), younger fish demonstrated either the absence of auditory response or lower sensitivity (Fig. 11c) (Vasconcelos & Ladich, 2008).

Sisneros and Bass (2005) investigated the response properties of individual primary auditory afferents in the plainfin midshipman (*Porichthys notatus*) and showed that the best hearing range was between 60 and 200 Hz in small juveniles, large juveniles, and adults. Similar to the Lusitanian toadfish, the most sensitive frequencies did not change during ontogeny. The auditory sensitivity improved at

the most sensitive frequency by approximately 10 dB from small to large juveniles, but no difference was found between large juveniles and adults. Alderks and Sisneros (2011) found only small differences in the maximum detectable frequency, in that larger fish had a higher probability of detecting frequencies above 400 Hz. Higgs et al. (2004) investigated ultrasound detection in the American shad (*Alosa sapidissima*) and found that the response to ultrasound apparently improved during ontogeny. Fish smaller than 30 mm responded only to 90-kHz tones whereas fish 30–100 mm in size responded to frequencies from 40 to 120 kHz. No significant difference in thresholds was found.

In summary, hearing ability changes during ontogenetic development in almost all fishes investigated. The ontogenetic change typically includes an improvement in absolute sensitivity and sometimes an extension of the detectable frequency range. Absolute sensitivity either increased slightly (toadfishes) or considerably (*Stegastes* spp.) during ontogeny, or increased only at particular frequencies (*P. major*) or not at all (*A. sapidissima*, *N. melanostomus*)—or even decreased (*A. saxatilis*). An increase at lower frequencies and a decrease in sensitivity at higher frequencies were documented in *T. vittata*, *S. schoutedeni*, and *L. cyclurus*. An extension of the frequency range was observed in species lacking or possessing specialization for hearing—in *H. didactylus*, *P. notatus*, *A. sapidissima*, *L. cyclurus*, *D. rerio*—but the degree of extension varied considerably between taxa. Differences between taxa in the course of the ontogeny of hearing could reflect different developmental constraints (acoustic communication, accessory hearing structures, inner ear anatomy), different developmental stages investigated or different techniques used to measure auditory sensitivities or a combination of these factors.

Several studies showed that juvenile fish of different size vocalize during agonistic encounters (Henglmüller & Ladich, 1999; Wysocki & Ladich, 2001; Vasconcelos & Ladich, 2008; Lechner et al., 2010). Sound characteristics change during ontogenetic development. In general, sounds become louder and longer and dominant frequencies decrease. Does the hearing sensitivity develop in accordance with sound characteristics to facilitate acoustic communication in early stages and can the diversity during ontogenetic development be explained by the factor communication? In *T. vittata*, *S. schoutedeni*, and *H. didactylus*, dominant frequencies of sounds decrease in parallel to the decrease in the most sensitive frequencies; this is not the case in *H. didactylus*, where the most sensitive frequency remains constant. This correspondence does not necessarily explain the diversity during ontogenetic development. Comparisons between audiograms and absolute sound spectra in *T. vittata* and *H. didactylus* within the same-sized fish revealed that smaller juveniles would barely be able to detect agonistic vocalizations owing to the low SPLs of vocalizations (Wysocki & Ladich, 2001; Vasconcelos and Ladich, 2008; Lechner et al., 2010). Thus, acoustic communication is not facilitated during ontogenetic development and does not explain the change in the diversity.

## 6 Summary

Fishes of different taxa evolved a large diversity of hearing sensitivities as well as changes during ontogenetic development. This diversity is linked mainly to differences in the way the inner ear is connected to gas-filled cavities such as the swim bladder. A close connection between both (ear and gas-filled cavity) results in higher auditory sensitivity or an expansion of the detectable frequency range or in both. Why do auditory sensitivities in fish differ so much? Hearing enhancements might be related to the detection of vocalizations of conspecifics and facilitation of acoustic communication. However, a comparison of hearing abilities in fish with and without accessory hearing structures does not support this notion. Fish utilize sounds for acoustic communication independently of their hearing abilities. Ecoacoustical constraints are a more likely explanation for the diversity in hearing sensitivities. Low ambient noise levels most likely facilitated the evolution of accessory hearing structures, allowing fish to detect various abiotic and biotic sound sources such as con- and heterospecifics, including predators and prey items. Only few studies, however, measured hearing sensitivities in the presence of ambient noise from the habitat of particular fish species and analyzed the detectability of sounds crucial for survival. Many more studies are necessary to get a clear picture as to why fish evolved such a diversity in hearing abilities. In particular we need ambient noise measurements in habitats where closely related species occur which differ widely in hearing sensitivities such as holocentrids, catfishes, or cichlids. If the ecoacoustical constraints hypothesis is right then habitats should differ in the ambient noise regime according to the fish's hearing sensitivities.

The second major question is linked to the latter one. If the fish ear is adapted to the ambient noise then the question raises to which sound sources do fish listen to in their natural environment? This is particularly interesting in species that do not vocalize. What kind of sounds do predators, prey items, con- and heterospecifics or even abiotic noise sources emit? At which distances do fish detect these sound sources and how do they react? Answering these questions calls for many more sound recordings in the immediate vicinity of fish and for analysis and subsequently playbacks of these sounds, particularly in the field. Currently, we still do not know what well-known nonvocal fish such as carps are actually listening to in the field.

**Acknowledgments** The author was supported by the Austrian Science Fund (FWF grant 22319).

## References

- Alderks, P. W., & Sisneros, J. A. (2011). Ontogeny of auditory saccular sensitivity in the plainfin midshipman fish, *Porichthys notatus*. *Journal of Comparative Physiology A*, 197, 387–398.
- Amoser, S., & Ladich, F. (2005). Are hearing sensitivities of freshwater fish adapted to the ambient noise in their habitats? *Journal of Experimental Biology*, 208, 3533–3542.

- Amoser, S., & Ladich, F. (2010). Year-round variability of ambient noise in temperate freshwater habitats and its implications for fishes. *Aquatic Sciences*, 72, 371–378.
- Belanger, A. J., Bobeica, I., & Higgs, D. M. (2010). The effect of stimulus type and background noise on hearing abilities of the round goby *Neogobius melanostomus*. *Journal of Fish Biology*, 77, 1488–1504.
- Blaxter, J. H. S., Denton, E. J., & Gray, J. A. B. (1981). Acousticolateralis system in clupeid fishes. In W. N. Tavolga, A. N. Popper & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 39–56). New York: Springer.
- Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer.
- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*. 2nd edition. Sunderland, MA: Sinauer.
- Braun, C. B., & Grande, T. (2008). Evolution of peripheral mechanisms for the enhancement of sound reception. In J. F. Webb, A. N. Popper & R. R. Fay (Eds.), *Fish bioacoustics* (pp. 99–144). New York: Springer.
- Bridge, T. W., & Haddon, A. C. (1889). Contribution to the anatomy of fishes. I. The airbladder and Weberian ossicles in the Siluridae. *Proceedings of the Royal Society London*, 46, 209–227.
- Canfield, J. G., & Eaton, R. C. (1990). Swimbladder acoustic pressure transduction initiates Mauthner-mediated escape. *Nature*, 347, 760–762.
- Canfield, J. G., & Rose, G. J. (1996). Hierarchical sensory guidance of Mauthner-mediated escape response in goldfish (*Carassius auratus*) and cichlids (*Haplochromis burtoni*). *Brain, Behavior and Evolution*, 48, 137–156.
- Chapman, C. J. (1973). Field studies of hearing in teleost fish. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 24, 371–390.
- Chapman, C. J., & Hawkins, A. D. (1973). A field study of hearing in the cod, *Gadus morhua* L. *Journal of Comparative Physiology A*, 85, 147–167.
- Codarin, A., Wysocki, L. E., Ladich, F., & Picciulin, M. (2009). Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy). *Marine Pollution Bulletin*, 58, 1880–1887.
- Coombs, S., & Popper, A. N. (1979). Hearing differences among Hawaiian squirrelfish (family Holocentridae) related to differences in the peripheral auditory system. *Journal of Comparative Physiology*, 132, 203–207.
- Coombs, S., & Popper, A. N. (1982). Structure and function of the auditory system in the clown knifefish *Notopterus chitala*. *Journal of Experimental Biology*, 97, 225–239.
- Egner, S. A., & Mann, D. A. (2005). Auditory sensitivity of sergeant major damselfish *Abudefduf saxatilis* from post-settlement juvenile to adult. *Marine Ecology Progress Series*, 285, 213–222.
- Fay, R. R. (1988). *Hearing in vertebrates: A psychophysics databook*. Winnetka, IL: Hill-Fay Associates.
- Fay, R. R. (2009). Soundscapes and the sense of hearing in fishes. *Integrative Zoology*, 4, 26–32.
- Fay, R. R., & Popper, A. N. (1974). Acoustic stimulation of the ear of the goldfish (*Carassius auratus*). *Journal of Experimental Biology*, 61, 243–260.
- Fletcher, L. B., & Crawford, J. D. (2001). Acoustic detection by sound-producing fishes (Mormyridae): The role of gas-filled tympanic bladders. *Journal of Experimental Biology*, 204, 175–183.
- Hawkins, A. D. (1981). The hearing abilities of fish. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 109–133). New York: Springer.
- Hawkins, A. D. (1993). Underwater sound and fish behaviour. In T. J. Pitcher (Ed.), *Behaviour of teleost fishes* (pp. 129–169). London: Chapman and Hall.
- Henglmüller, S. M., & Ladich, F. (1999). Development of agonistic behaviour and vocalization in croaking gourami. *Journal of Fish Biology*, 54, 380–395.
- Higgs, D. M., Rollo, A. K., Souza, M. J., & Popper, A. N. (2003). Development of form and function in peripheral auditory structures of the zebrafish (*Danio rerio*). *Journal of the Acoustical Society of America*, 113, 1145–1154.

- Higgs, D. M., Plachta, D. T. T., Rollo, A. K., Singheiser, M., Hastings, M. C., & Popper, A.N. (2004). Development of ultrasound detection in American shad (*Alosa sapidissima*). *Journal of Experimental Biology*, 207, 155–163.
- Iwashita, A., Sakamoto, M., Kojima, T., Watanabe, Y., & Soeda, H. (1999). Growth effects on the auditory threshold of red sea bream. *Nippon Suisan Gakkaishi*, 65, 833–838.
- Kennedy, E. V., Holderied, M. W., Mair, J. M., Guzman, H. M., & Simpson, S. D. (2010). Spatial patterns in reef-generated noise relate to habitats and communities: Evidence from a Panamanian case study. *Journal of Experimental Marine Biology and Ecology*, 395, 85–92.
- Kenyon, T. N. (1996). Ontogenetic changes in the auditory sensitivity of damselfishes (Pomacentridae). *Journal of Comparative Physiology*, 179, 553–561.
- Kenyon, T. N., Ladich, F., & Yan, H. Y. (1998). A comparative study of hearing ability in fishes: The auditory brainstem response approach. *Journal of Comparative Physiology A*, 182, 307–318.
- Kleerekoper, H., & Roggenkamp, P. A. (1959). An experimental study on the effect of the swimbladder on hearing sensitivity in *Ameiurus nebulosus* (Lesueur). *Canadian Journal of Zoology*, 37, 1–8.
- Ladich, F. (1999). Did auditory sensitivity and vocalization evolve independently in otophysan fishes? *Brain, Behaviour and Evolution*, 53, 288–304.
- Ladich, F. (2000). Acoustic communication and the evolution of hearing in fishes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 355, 1285–1288.
- Ladich, F. (2007). Females whisper briefly during sex: Context- and sex-specific differences in sounds made by croaking gouramis. *Animal Behaviour*, 73, 379–387.
- Ladich, F., & Yan, H. Y. (1998). Correlation between auditory sensitivity and vocalization in anabantoid fishes. *Journal of Comparative Physiology A*, 182, 737–746.
- Ladich, F., & Wysocki, L. E. (2003). How does tripus extirpation affect auditory sensitivity in goldfish? *Hearing Research*, 182, 119–129.
- Ladich, F., & Popper, A. N. (2004). Parallel evolution in fish hearing organs. In G. Manley, R. R. Fay, & A. N. Popper (Eds.), *Evolution of the vertebrate auditory system* (pp. 95–127). New York: Springer.
- Ladich, F., & Bass, A.H. (2005). Sonic motor pathways in piranhas with a reassessment of phylogenetic patterns of sonic mechanisms among teleosts. *Brain, Behavior and Evolution*, 66, 167–176.
- Ladich, F., & Fine, M. L. (2006). Sound-generating mechanisms in fishes: A unique diversity in vertebrates. In F. Ladich, S. P. Collin, P. Moller, & B. G. Kapoor (Eds.), *Communication in fishes* (pp. 3–43). Enfield, NH: Science Publishers.
- Ladich, F., & Wysocki, L. E. (2009). Does speaker presentation affect auditory evoked potential thresholds in goldfish? *Comparative Biochemistry and Physiology A*, 154, 341–346.
- Ladich, F., & Bass, A. H. (2011). Vocal behavior of fishes: Anatomy and physiology. In A. P. Farrell (Ed.), *Encyclopedia of fish physiology: From genome to environment* (Vol. 1, pp. 321–329). San Diego: Academic Press.
- Ladich, F., & Fay, R. R. (2013). Auditory evoked potential audiometry in fish. *Reviews in Fish Biology and Fisheries*, 23, 317–364.
- Laming, P. R., & Morrow, G. (1981). The contribution of the swimbladder to audition in the roach (*Rutilus rutilus*). *Comparative Biochemistry and Physiology A*, 69, 537–541.
- Lechner, W., & Ladich, F. (2008). Size matters: Diversity in swimbladders and Weberian ossicles affects hearing in catfishes. *Journal of Experimental Biology*, 211, 1681–1689.
- Lechner, W., & Ladich, F. (2011). How do albino fish hear? *Journal of Zoology*, 283, 186–192.
- Lechner, W., Wysocki, L. E., & Ladich, F. (2010). Ontogenetic development of auditory sensitivity and sound production in the squeaker catfish *Synodontis schoutedeni*. *BMC Biology*, 8, 10.
- Lechner, W., Heiss, E., Schwaha, T., Glösmann, M., & Ladich, F. (2011). Ontogenetic development of Weberian ossicles and hearing abilities in the African bullhead catfish. *Plos One* 6/4, e18511.

- Lugli, M. (2010). Sound of shallow water fishes pitch within the quiet window of the habitat noise. *Journal of Comparative Physiology A*, 196, 439–451.
- Lugli, M., & Fine, M. L. (2003). Acoustic communication in two freshwater gobies: ambient noise and short-range propagation in shallow streams. *Journal of the Acoustical Society of America*, 114, 512–521.
- Lugli, M., & Fine, M. L. (2007). Stream ambient noise, spectrum and propagation of sounds in goby *Padogobius martensii*: sound pressure and particle velocity. *Journal of the Acoustical Society of America*, 122, 2881–2892.
- Mann, D. A., Popper, A. N., & Wilson, B. (2005). Pacific herring hearing: Does not include ultrasound. *Biological Letters*, 1, 158–161.
- Markl, H. (1972). Aggression und Beuteverhalten bei Piranhas (Serrasalmiinae, Characidae). *Zeitschrift für Tierpsychologie*, 30, 190–216.
- Maruska, K. P., Boyle, K. S., Dewan, L. R., & Tricas, T. G. (2007). Sound production and spectral hearing sensitivity in the Hawaiian sergeant damselfish, *Abudefduf abdominalis*. *Journal of Experimental Biology*, 210, 3990–4000.
- McCormick, C. A., & Popper, A. N. (1984). Auditory sensitivity and psychophysical tuning curves in the elephantnose fish, *Gnathonemus petersii*. *Journal of Comparative Physiology A*, 155, 753–761.
- Myrberg, A. A., & Spires, J. Y. (1980). Hearing in damselfishes: An analysis of signal detection among closely related species. *Journal of Comparative Physiology A*, 140, 135–144.
- Nelson, J. S. (2006). *Fishes of the world* (3rd ed). New York: John Wiley & Sons.
- Parker, G. H. (1903). Hearing and allied senses in fishes. *Bulletin of the United States Fish Commission*, 1902, 45–64.
- Parker, G. H. (1918). A critical survey of the sense of hearing in fishes. *Proceedings of the American Philosophical Society*, 57(2), 69–98.
- Parmentier, E., Mann, K., & Mann, D. (2011). Hearing and morphological specializations of the mojarra (*Eucinostomus argenteus*). *The Journal of Experimental Biology*, 214, 2697–2701.
- Poggendorf, D. (1952). Die absolute Hörschwelle des Zwergwelses (*Amiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparates der Ostariophysen. *Zeitschrift für vergleichende Physiologie*, 34, 222–257.
- Popper, A. N. (1971). The effects of size on auditory capacities of the goldfish. *Journal of Auditory Research*, 11, 239–247.
- Popper, A. N., & Fay, R. R. (1999). The auditory periphery in fishes. In R. R. Fay & A. N. Popper (Eds.), *Comparative hearing: Fish and amphibians* (pp. 43–100). New York: Springer.
- Popper, A. N., & Schilt, C. R. (2008). Hearing and acoustic behavior: Basic and applied considerations. In J. F. Webb, R. R. Fay, & A. N. Popper (Eds.), *Fish bioacoustics* (pp. 17–48). New York: Springer.
- Popper, A. N., & Fay R. R. (2011). Rethinking sound detection by fishes. *Hearing Research*, 273, 25–36.
- Radford, C. A., Stanley, J. A., Simpson, S. D., & Jeffs, A. G. (2011). Juvenile coral reef fish use sound to locate habitats. *Coral Reefs*, 30, 295–305.
- Ramcharitar, J. U., Higgs, D. M., & Popper, A. N. (2006). Audition in sciaenid fishes with different swim bladder-inner ear configurations. *Journal of the Acoustical Society of America*, 119, 439–443.
- Richardson, W. J., Greene, C. R., Malme, C. J., & Thomson, D. H. (1995). *Marine mammals and noise*. San Diego: Academic Press.
- Rogers, P. H., & Cox, H. (1988). Underwater sound as a biological stimulus. In J. Atema, R. R. Fay, A. N. Popper, & W. N. Tavolga (Eds.), *Sensory biology of aquatic animals* (pp. 131–149). New York: Springer.
- Romer, A. S., & Parsons, T. S. (1983). *Vergleichende Anatomie der Wirbeltiere*. Hamburg: Paul Parey.
- Sand, O., & Enger, P. S. (1973). Evidence for an auditory function of the swimbladder in the cod. *Journal of Experimental Biology*, 59, 405–414.

- Schellart, N. A. M., & Popper, A. N. (1992). Functional aspects of the evolution of the auditory system of actinopterygian fish. In D. E. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 295–322). New York: Springer.
- Schneider, H. (1941). Die Bedeutung der Atemhöhle der Labyrinthfische für ihr Hörvermögen. *Zeitschrift für Vergleichende Physiologie*, 29, 172–194.
- Schulz-Mirbach, T., Ladich, F., Riesch, F., & Plath, M. (2010). Otolith morphology and hearing abilities in cave- and surface-dwelling ecotypes of the Atlantic molly, *Poecilia mexicana* (Teleostei: Poeciliidae). *Hearing Research*, 267, 137–148.
- Schulz-Mirbach, T., Metscher, B., & Ladich, F. (2012). Relationship between swim bladder morphology and hearing abilities: A case study on Asian and African cichlids. *PLoS ONE* 7, e42292.
- Simpson, S. D., Meekan, M. G., Jeffs, A., Montgomery, J. C., & McCauley, R. D. (2008). Settlement-stage coral reef fish prefer the higher frequency invertebrate-generated audible component of reef noise. *Animal Behaviour*, 75, 1861–1868.
- Sisneros, J. A., & Bass, A. H. (2005). Ontogenetic changes in the response properties of individual, primary auditory afferents in the vocal plainfin midshipman *Porichthys notatus*. *Journal of Experimental Biology*, 208, 3121–3131.
- Sörensen, W. (1895). Are the extrinsic muscles of the air-bladder in some Siluroidea and the “elastic spring” apparatus of others subordinate to the voluntary production of sounds? II. What is, according to our present knowledge, the function of the Weberian ossicles? *Journal of Anatomy and Physiology*, 399–423.
- Speares, P., Holt, D., & Johnston, C. (2011). The relationship between ambient noise and dominant frequency of vocalization in two species of darters (Percidae: *Etheostoma*). *Environmental Biology of Fishes*, 90, 103–110.
- Spindler, T. (1997). Fischfauna in Österreich. Ökologie – Gefährdung – Bioindikation – Fischerei – Gesetzgebung (Fishfauna of Austria. Ecology – Endangerment – Bioindication – Fisheries – Legislation) Vienna. *Umweltbundesamt Monographien [Federal Environment Agency Monographs]*, 87, 140 pp.
- Steinberg, R. (1957). Unterwassergeräusche und Fischerei. *Protokolle zur Fischereitechnik*, 4, 216–249.
- Stetter, H. (1929). Untersuchungen über den Gehörsinn der Fische, besonders von *Phoxinus laevis* L. und *Amiurus nebulosus* Raf. *Zeitschrift für Vergleichende Physiologie*, 339–477.
- Stipetić, E. (1939). Über das Gehörorgan der Mormyriden. *Zeitschrift für Vergleichende Physiologie*, 26, 740–752.
- Tavolga, W. N. (1971). Sound production and detection. In W. S. Hoar & D. J. Randall (Eds.), *Fish physiology*, Vol. 5: *Sensory systems and electric organs* (pp. 135–205). New York: Academic Press.
- Tavolga, W. N., & Wodinsky, J. (1963). Auditory capacities in fishes. Pure tone thresholds in nine species of marine teleosts. *Bulletin of the American Museum of Natural History*, 126 (Article 2), 177–240.
- Tolimieri, N., Haine, O., Jeffs, A., McCauley, R., & Montgomery, J. (2004). Directional orientation of pomacentrid larvae to ambient reef sound. *Coral Reefs*, 23, 184–191.
- Tolimieri, N., Jeffs, A., & Montgomery, J. C. (2000). Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Marine Ecology Progress Series* 207, 219–224.
- Tonolla, D., Lorang, M. S., Heutschi, K., & Tockner, K. (2009). A flume experiment to examine underwater sound generation by flowing water. *Aquatic Sciences*, 71, 449–462.
- Urick, R. J. (1983). The noise background of the sea: Ambient noise. In *Principles of underwater sound* (pp. 202–236). Los Altos, CA: Peninsula Publishing.
- Vasconcelos, R. O., & Ladich, F. (2008). Development of vocalization, auditory sensitivity and acoustic communication in the Lusitanian toadfish *Halobatrachus didactylus*. *Journal of Experimental Biology*, 211, 502–509.
- Vasconcelos, R. O., Amorim, M. C. P., & Ladich, F. (2007). Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. *Journal of Experimental Biology*, 210, 2104–2112.



- Von Frisch, K. (1923). Ein Zwergwels, der kommt, wenn man ihm pfeift. *Biologisches Zentralblatt*, 439–446.
- Von Frisch, K. (1936). Über den Gehörsinn der Fische. *Biological Reviews*, 210–246.
- Von Frisch, K. (1938). The sense of hearing in fish. *Nature*, 141, 8–11.
- Von Frisch, K., & Stetter, H. (1932). Untersuchungen über den Sitz des Gehörsinnes bei der Elritze. *Zeitschrift für Vergleichende Physiologie*, 687–801.
- Webb, J. F., Walsh, R. M., Casper, B. M., Mann, D. A., Kelly, N., & Cicchino, N. (2012). Development of the ear, hearing capabilities and laterophysic connection in the spotfin butterflyfish (*Chaetodon ocellatus*). *Environmental Biology of Fishes*, 95, 275–290.
- Weber, E. H. (1820). *De aure et auditu hominis et animalium. Part I. De aure animalium aquatilium*. Lipsiae: Apud Gerhardum Fleischerum.
- Wenz, G. M. (1962). Acoustic ambient noise in the ocean: Spectra and sources. *Journal of the Acoustical Society of America*, 34, 1936–1956.
- Wilson, M., Montie, E. W., Mann, K. A., & Mann, D. A. (2009). Ultrasound detection in the gulf menhaden requires gas-filled bullae and an intact lateral line. *Journal of Experimental Biology*, 212, 3422–3427.
- Wolff, D. L. (1966). Akustische Untersuchungen zur Klapperfischerei und verwandter Methoden. *Zeitschrift für Fischerei und deren Hilfswissenschaften*, 14, 277–315.
- Wright, K. J., Higgs, D. M., & Leis, J. M. (2011). Ontogenetic and interspecific variation in hearing ability in marine fish larvae. *Marine Ecology Progress Series*, 424, 1–13.
- Wysocki, L. E., & Ladich, F. (2001). The ontogenetic development of auditory sensitivity, vocalization and acoustic communication in the labyrinth fish *Trichopsis vittata*. *Journal of Comparative Physiology A*, 187, 177–187.
- Wysocki, L. E., Amoser, S., & Ladich, F. (2007). Diversity in ambient noise in European freshwater habitats: Noise levels, spectral profiles, and impact on fishes. *Journal of the Acoustical Society of America*, 121, 2559–2566.
- Wysocki, L. E., Codarin, A., Ladich, F., & Picciulin, M. (2009). Sound pressure and particle acceleration audiograms in three marine fish species from the Adriatic Sea. *Journal of the Acoustical Society of America*, 126, 2100–2107.
- Yan, H. Y. (1998). Auditory role of the suprabranchial chamber in gourami fish. *Journal of Comparative Physiology A*, 183, 325–333.
- Yan, H. Y., & Curtsinger, W. S. (2000). The otic gasbladder as an ancillary structure in a mormyrid fish. *Journal of Comparative Physiology A*, 186, 595–600.
- Yan, H. Y., Fine, M. L., Horn, H. S., & Colon, W. E. (2000). Variability in the role of the gasbladder in fish audition. *Journal of Comparative Physiology A*, 186, 435–445.