

Are hearing sensitivities of freshwater fish adapted to the ambient noise in their habitats?

Sonja Amoser* and Friedrich Ladich

University of Vienna, Department of Neurobiology and Behavior, Althanstrasse 14, 1090 Vienna, Austria

*Author for correspondence (e-mail: sonja.amoser@univie.ac.at)

Accepted 26 July 2005

Summary

Several groups of fishes, among them two thirds of all freshwater fishes, have developed hearing specializations that enhance auditory sensitivity and broaden frequency ranges compared with hearing non-specialists (generalists), which lack such adaptations. It has been speculated that the enhanced sensitivities of these so-called hearing specialists have evolved in quiet habitats such as lakes, backwaters of rivers, slowly flowing streams or the deep sea. To test this hypothesis, noise levels and frequency spectra of four different freshwater habitats near Vienna, Austria (Danube River, Triesting stream, Lake Neusiedl, backwaters of the Danube River), were recorded and played back to native fish species while simultaneously measuring their auditory thresholds using the auditory evoked potential (AEP) recording technique. As a representative of hearing specialists, we chose the common carp (*Cyprinus carpio*, Cyprinidae) and for the hearing generalists the European perch (*Perca fluviatilis*,

Percidae). Data show that the carp's hearing is only moderately masked by the quiet habitat noise level of standing waters (mean threshold shift 9 dB) but is heavily affected by stream and river noise by up to 49 dB in its best hearing range (0.5–1.0 kHz). In contrast, the perch's hearing thresholds were only slightly affected (mean up to 12 dB, at 0.1 kHz) by the highest noise levels presented. Our results indicate that hearing abilities of specialists such as carp 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. Hearing in non-specialists such as perch, on the other hand, is only slightly or not at all impaired in all habitats.

Key words: fish, hearing specializations, evolution, masking, ambient noise, auditory evoked potential, freshwater, *Cyprinus carpio*, *Perca fluviatilis*.

Introduction

In the aquatic environment, hearing is an important sense for the survival of an animal. Sound travels faster and is much less attenuated in water than in air, making it the perfect means for communication over long distances (Hawkins and Myrberg, 1983; Rogers and Cox, 1988). By listening to the background noise in an aquatic habitat, an animal can get biotic information about the position of prey or predators, potential mates or competitors, as well as abiotic information about currents, coastlines, torrents, wind, etc. (Popper and Fay, 1993; Lagardère et al., 1994). On the other hand, this ambient noise impairs the detection of signals (Hawkins and Myrberg, 1983; Mann and Lobel, 1997). Studies investigating or mentioning the acoustic characteristics of various aquatic habitats often focus on marine environments (e.g. Wenz, 1962; Cato, 1976; Urick, 1983; McConnell et al., 1992; Samuel et al., 2005), including reefs (Tolimieri et al., 2004; Egner and Mann, 2005). Knowledge about ambient noise spectra of freshwaters (lakes, ponds, rivers) is sparse (Bom, 1969; Boussard, 1981; Lugli and Fine, 2003; Lugli et al., 2003; Amoser et al., 2004).

Teleost fishes have evolved an astonishing diversity in hearing abilities. Hearing non-specialists or generalists such as

salmonids and perches are only able to detect the particle motion component of low frequency sounds (<1 kHz) at relatively high sound intensities. The hearing specialists (e.g. carps, catfishes, mormyrids) detect the pressure component of sounds over a broader frequency range (up to several kHz) at much lower sound intensities. They are able to do so because of accessory hearing structures, which bring an air-filled cavity in close contact with the inner ear (e.g. coupling of the swim bladder *via* the Weberian ossicles to the perilymph of the inner ear in the otophysines; for reviews, see Ladich and Bass, 2003b; Ladich and Popper, 2004).

Over the past decades, knowledge about the hearing abilities of many fish species, both marine and freshwater, has grown. Most of these auditory studies were conducted under various laboratory noise conditions, which sometimes yielded a diversity of audiograms within a single species (Tavolga, 1967; Hawkins, 1981; Fay, 1988). Although appropriate information is lacking, it is possible that many of the published audiograms were masked by relatively high levels of laboratory noise. Despite these shortcomings, the diversity of hearing

sensitivities is well documented, but their functional significance remains largely unknown.

Which selective advantages elicited the evolution of hearing enhancements in fishes? The main driving forces could be acoustic communication, eco-acoustic constraints or a combination of both. It was recently hypothesized that acoustic communication was not a driving force in the evolution of hearing enhancements in fish (Ladich, 1999, 2000). Eco-acoustic constraints seem to be the second factor inducing the ancestors of certain taxa to improve their hearing abilities. Clearly, fish could increase their survival if able to detect faint sounds produced by abiotic sources (wind, surf, etc.) and biotic sources (predators, prey and conspecifics) at larger distances. The evolution of hearing specializations is therefore understandable in quiet habitats such as lakes, slowly flowing waters or the deep sea (Popper, 1980; Deng et al., 2002; Ladich and Bass, 2003a). In addition, in shallow water, sound propagation is limited to frequencies above the cut-off frequency (Rogers and Cox, 1988; Schellart and Popper, 1992; Bass and Clark, 2003; Ladich and Bass, 2003a). Consequently, increasing the distance over which fish are able to detect sounds requires extending their hearing range to frequencies above the cut-off frequency (depending on water depth and bottom sediment, above 1–2.0 kHz; Schellart and Popper, 1992; Ladich and Popper, 2004).

Extending the hearing range to higher frequencies or to lower sound levels would only be advanced by evolution as long as relevant signals are detectable in the presence of the many irrelevant signals or noise that impede their detection. This phenomenon, termed masking (e.g. Fletcher, 1940), has been studied in the laboratory (Tavolga, 1967; Buerkle, 1968, 1969; Fay, 1974; Fay et al., 1978; Wysocki and Ladich, 2005a) but very rarely in the field (Chapman and Hawkins, 1973). Chapman and Hawkins (1973) measured hearing in cod in the sea and observed variations in auditory sensitivities that were related to changes in the ambient sea noise level. Thus, our knowledge of the relationship between ambient noise conditions in various aquatic habitats, the hearing sensitivities of fishes in these habitats, and the question of whether hearing abilities are adapted to these habitats or hearing is masked, is very limited. Furthermore, audiograms measured under laboratory conditions show the maximum sensitivity of the auditory system, but it is generally unknown whether this sensitivity can be utilized in the natural environment in the presence of ambient noise.

We therefore conducted experiments under diverse natural noise conditions in order to test the hypothesis that the enhanced sensitivities of hearing specialists evolved under, and thus are adapted to, low ambient noise levels in certain freshwater habitats (stagnant and slowly flowing inland waters). The questions addressed the following. (1) Are hearing specialists able to fully utilize their excellent hearing abilities under ambient noise conditions? (2) To what degree are hearing sensitivities of specialists such as the carp masked under natural noise conditions? (3) Do different ambient noise conditions influence the auditory sensitivities of hearing generalists such as the perch? The carp *Cyprinus carpio* and

the perch *Perca fluviatilis* were chosen because they are native to Austria, representatives of hearing specialists and hearing non-specialists, and inhabit a range of different habitats (Spindler, 1997; Schabuss and Reckendorfer, 2002).

Materials and methods

Animals

The test subjects were six common carp *Cyprinus carpio* L. [102–142 mm standard length (*SL*), 41–75 g body mass] from a pond near Vienna and six European perch *Perca fluviatilis* L. (90–114 mm *SL*, 13–22 g body mass) from a hatchery at Lake Mondsee (Scharfling, Upper Austria). All animals were kept in planted aquaria, bottom covered with sand and gravel, equipped with half flower pots providing hiding places, filtered by external filters, and maintained under a 12 h:12 h L:D cycle. The fish were fed live *Tubifex* sp., chironomid larvae or commercially prepared flake food (Tetramin, Tetrapond®, Dana Feed®) daily except on weekends. No submerged filters or air stones were used in order to reduce the noise in the holding tanks. Background noise in the holding tanks ranged from 122 to 124 dB (L_{Leq}). All experiments were performed with the permission of the Austrian Commission on Experiments in Animals (GZ 68.210/50-Pr/4/2002 and GZ 66.006/7-BrGT/2004).

Auditory sensitivity measurements

AEP recordings

The auditory evoked potential (AEP) recording protocol followed that developed by Kenyon et al. (1998) and modified by Wysocki and Ladich (2005a,b).

Fishes were mildly immobilized with Flaxedil (gallamine triethiodide; Sigma-Aldrich, Vienna, Austria). The dosage used was $1.07 \pm 0.04 \mu\text{g g}^{-1}$ for *C. carpio* and $1.21 \pm 0.05 \mu\text{g g}^{-1}$ for *P. fluviatilis*. This dosage allowed the fishes to retain slight opercular movements during the experiments but without significant interference of myogenic noise. Test subjects were secured in a bowl-shaped plastic tub (diameter: 33 cm, water depth: 13 cm, 1.5 cm layer of sand) lined on the inside with acoustically absorbent material (air-filled packing wrap) to reduce resonances and reverberations (for details, see Wysocki and Ladich, 2002). Fishes were positioned below the water surface (except for the contacting points of the electrodes, which were maximally 1 mm above the surface) in the centre of the plastic tub. This position was selected because it provided the most convenient way of placing the electrodes and because control experiments yielded no significant difference in hearing thresholds when the fishes were positioned 3 cm below the surface or in this position (Wysocki and Ladich, 2005b). A respiration pipette was inserted into the subject's mouth and respiration was achieved through a simple temperature-controlled ($23 \pm 1^\circ\text{C}$), gravity-fed water system.

The AEPs were recorded using silver wire electrodes (0.25 mm diameter) pressed firmly against the skin. The portion of the head just above the water surface was covered

with a small piece of Kimwipes[®] tissue paper to keep it moist and to ensure proper contact during experiments. The recording electrode was placed in the midline of the skull over the region of the medulla and the reference electrode cranially between the nares. Shielded electrode leads were attached to the differential input of an a.c. preamplifier (Grass P-55, Grass Instruments, West Warwick, RI, USA; gain 100×, high-pass at 30 Hz, low-pass at 1 kHz). A ground electrode was placed in the water near the body of the fish. The plastic tub was positioned on an air table (TMC Micro-g 63Y540, Technical Manufacturing Corporation, Peabody, MA, USA), which rested on a vibration-isolated concrete plate. The entire setup was enclosed in a walk-in soundproof room, which was constructed as a Faraday cage (interior dimensions: 3.2 m×3.2 m×2.4 m).

Both sound stimuli presentation and AEP waveform recording were accomplished using a Tucker-Davis Technologies (TDT, Gainesville, FL, USA) modular rack-mount system (TDT System 3) controlled by a Pentium 4 PC containing a TDT digital processing board and running TDT BioSig RP Software.

Sound stimuli

Sound stimuli waveforms and masking noise were created using TDT SigGen RP software and fed through a power amplifier (Alesis RA 300, Alesis Corporation, Los Angeles, CA, USA). A dual-cone speaker (Wharfedale Pro Twin 8, Huntingdon, UK; frequency response 65 Hz–20 kHz), mounted 1 m above test subjects in the air, was used to present the stimuli during testing.

Sound stimuli consisted of tone bursts that were presented at a repetition rate of 21 per second. Hearing thresholds were determined at the following frequencies: 0.1, 0.3, 0.5, 0.8, 1.0, 2.0, 3.0 and 4.0 kHz for *C. carpio* and 0.1, 0.2, 0.3, 0.5, 0.8 and 1.0 kHz for *P. fluviatilis*. Frequencies were presented in a random order under normal laboratory conditions and in the presence of continuous masking noise. The duration of the sound stimuli increased from two cycles at 0.1 and 0.2 kHz, up to eight cycles at 4 kHz. Rise and fall times were one cycle at 0.1 and 0.2 kHz, and two cycles at all other frequencies. All bursts were gated using a Blackman window.

For each test condition, stimuli were presented at opposite polarities (180° phase shift), and the corresponding AEPs averaged by the Bio-Sig RP software in order to eliminate stimulus artefacts. The sound pressure level (SPL) of the tone bursts was reduced in 4 dB steps until the AEP waveform was no longer apparent. The lowest SPL for which a repeatable AEP trace could be obtained, as determined by overlaying replicate traces, was considered the threshold (Kenyon et al., 1998).

A hydrophone (Brüel & Kjaer 8101, Naerum, Denmark; frequency range: 1 Hz–80 kHz ±2 dB; voltage sensitivity: −184 dB re 1 V μPa^{−1}) was placed close to the right side of the animals (2 cm apart) in order to determine absolute SPL values underwater in close vicinity to the subjects.

Sound pressure is the adequate measure of the degree of

auditory stimulation in pressure-sensitive fishes such as otophysines (Fay and Popper, 1974) in any acoustic field. For technical and comparative reasons, the hearing thresholds of European Perch are also given in SPL values, although hearing generalists detect particle motion of sounds. This is acceptable because our study emphasized the effects of the same defined background noise (noise spectra are given in pressure units) on signal detection in different species using the same experimental setup and on relative threshold shifts within a species rather than absolute thresholds. This approach is valid as long as the displacement field is proportional to the pressure field, because in masking studies the ratio of the tone level to the noise level at nearby frequencies is most important (Wysocki and Ladich, 2005a). Note, however, that those hearing thresholds should not be regarded as absolute values because the exact proportional factor between the two sound parameters remains unknown.

Masking noise

Audiograms were measured under normal laboratory conditions and in the presence of four different habitat noise-types (Lake Neusiedl and backwater of Danube River representing still or slowly flowing waters; Triesting stream and Danube River, representing fast flowing waters, Fig. 1) with different SPL (for sound recording procedure, see L. E. Wysocki, S. Amoser and F. Ladich, unpublished observations).

The four habitat noise types chosen in this study cover the broad range of freshwater habitats in a central European region, in particular around Vienna. They represent snapshots of the ambient noise situation in these waters, as the acoustic characteristics of habitats tend to vary somewhat throughout the year (L. E. Wysocki, S. Amoser and F. Ladich, unpublished observations). Nevertheless, the broad range of both the level and the spectral composition of the ambient noise types chosen fits our purpose to test the hearing abilities of freshwater fish species under very different habitat conditions.

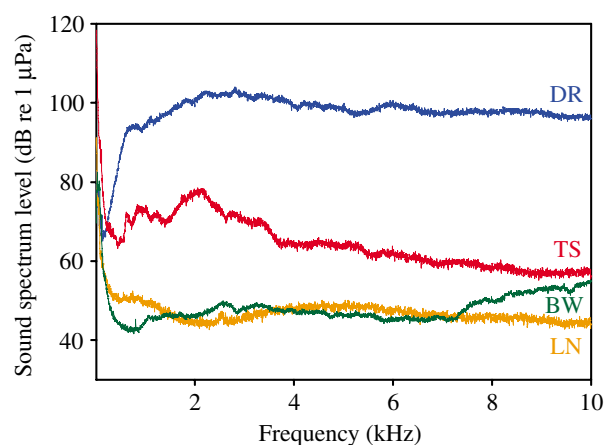


Fig. 1. Sound power spectra of the different ambient noise types recorded in the four habitats and used as masking noise. DR, Danube river; TS, Triesting stream; BW, backwater; LN, Lake Neusiedl. Note the linear frequency axis scaling in this figure and the logarithmic scaling in Figs 2 and 4.

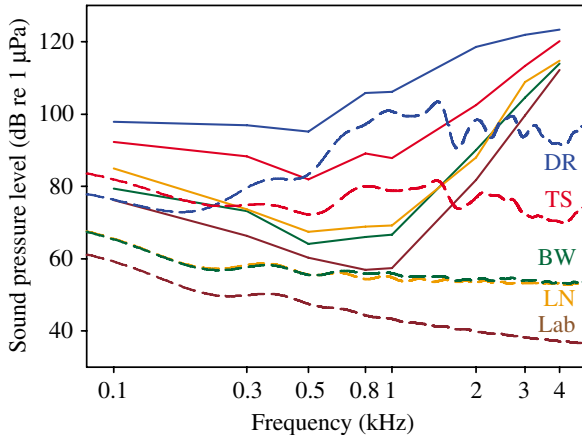


Fig. 2. Mean hearing thresholds of *Cyprinus carpio* (solid lines) under laboratory conditions (baseline) and in the presence of the different ambient noise types. Broken lines show the cepstrum-smoothed sound power spectra of the corresponding noise types (Fig. 1 shows the absolute amplitude spectra). DR, Danube river; TS, Triesting stream; BW, backwater; LN, Lake Neusiedl.

For each habitat noise-type, one representative recording was selected and 30 s were randomly chosen. These sound files were prepared with SigGen RP software, sent to a 30-band equalizer (Alesis MEQ 230, Alesis Corp., Los Angeles, CA, USA) and adjusted to ensure that the noise spectrum was the same in the experimental tub as experienced in the field. The habitat noise was then fed to the second channel and the tone bursts to the first channel of a TDT SM5 signal mixer. Both signals were then fed *via* the Alesis RA 300 amplifier to the loudspeaker and presented simultaneously.

The SPL values of the masking noise were measured at the position of the fish using a Brüel & Kjaer 8101 hydrophone (Brüel & Kjaer, Naerum, Denmark), a 2238 mediator (Brüel & Kjaer), and a 2284 power supply (Brüel & Kjaer) determining the L -weighted (5 Hz–20 kHz) equivalent continuous SPL (L_{Leq}) averaged over 1 min of measuring time. The L_{Leq} is a measure of the averaged energy in a varying sound level and is commonly used to assess environmental noise [ISO 1996; Brüel and Kjaer, Sound and Vibration Measurements, A/S: (2001), *Environmental Noise*; Naerum, Denmark]. The system was calibrated using a Brüel & Kjaer 4229 calibrator.

The L_{Leq} levels of the four different habitat noise types (backwater of the Danube River, Lake Neusiedl, Triesting stream and Danube River) were determined. These levels were the L_{Leq} levels measured in the field for this recording and are representative for these types of freshwater habitats. In addition, background-noise levels in the experimental test tank (hereafter referred to as 'lab-noise') were measured at the position where the fishes were tested. The L_{Leq} level of the lab-noise was 81.5 ± 0.4 dB. After each SPL determination, the ambient noises were recorded using a DAT recorder (Sony TCD D-100, Sony Corporation, Tokyo, Japan), played into a PC, and then analyzed using the acoustic analysis software, S_TOOLS-STx 2.17, developed by the Acoustics Research

Institute at the Austrian Academy of Sciences. Sound power spectra of 1 min recordings were calculated by an FFT analysis using a filter bandwidth of 1 Hz. These spectra were then exported and the relative spectral values were transformed to linear values using the equation:

$$A_i = 10^{(a_i/10)}, \quad (1)$$

where A_i is the linear spectral amplitude value and a_i is the logarithmic spectral amplitude value. From these values, the mean relative root mean square (RMS) was calculated using the equation:

$$e = 10(\log \sum A_i), \quad (2)$$

where e is the mean RMS value calculated from the spectral amplitudes. The mean relative RMS was then equalled to the absolute SPL measured with the Brüel & Kjaer 2238 Mediator, and the relative spectral levels were recalculated into absolute spectral levels.

Statistical analysis

All audiograms obtained in the presence of the different noise types (lab-noise and the four habitat-noises) were compared by two-factor analysis of variance (ANOVA) using a general linear model where one factor was masking noise and the other was frequency. The noise factor alone should indicate overall differences between masking conditions. The noise–frequency combination reveals if there are different tendencies of the noise effects at different frequencies of the audiogram. Bonferroni-adjusted, pairwise multiple comparisons followed every ANOVA to assess specific differences between noise conditions. The P level was set at 0.05 and, taking the Bonferroni correction into account (audiograms: 0.05/5, for five noise types), changes were considered to be significantly different when $P < 0.01$.

In order to make sure that only masked hearing thresholds were considered, auditory thresholds were compared using unpaired t -tests at each frequency separately. After correction for the number of frequencies tested (eight in the carp, six in the perch) the threshold values were only considered to be significantly different when $P < 0.006$ for the carp and $P < 0.008$ for the perch.

Parametric statistical tests were applied because the data were normally distributed and showed homogeneity of variances. All statistical tests were run using SPSS 11.0.

Results

Diversity in habitat noise

The L_{Leq} levels of the four different habitat noise types were 91.5 ± 0.4 dB (backwater), 93 ± 0.4 dB (Lake Neusiedl), 114 ± 0.5 dB (Triesting stream), and 132 ± 0.1 dB (Danube River). Spectral analysis revealed that sound power spectra are rather flat except for low frequencies, where sound energy increased (Fig. 1). The Danube River showed the highest spectral levels among all habitat noise types (about 100 dB re 1 μ Pa) and a major noise window below 500 Hz. The Triesting

stream revealed an energy peak at about 2 kHz (80 dB re 1 μ Pa) and a moderate decline towards higher frequencies. The stagnant habitats showed quite similar, flat sound spectral levels between 40 and 60 dB (Fig. 1).

Hearing under habitat noise conditions

Baseline audiograms (measured under lab-noise conditions) for the carp showed greatest hearing sensitivity at 0.8 kHz and 1.0 kHz (Table 1, Fig. 2), with hearing thresholds lower than 60 dB and a quick decline in sensitivity above 1.0 kHz. Comparing this baseline audiogram with the different masked audiograms by a two-factor ANOVA revealed overall significant differences between audiograms ($F_{4,200}=2049.5$, $P<0.001$) and a significant interaction between noise and

frequency ($F_{28,200}=47.4$, $P<0.001$), yielding different effects of noise at different frequencies of the audiogram. The Bonferroni-adjusted *post-hoc* test strengthens this finding: all audiograms were significantly different from each other.

When playing back noise of the stagnant freshwater habitats, the mean hearing thresholds were elevated by up to 9 dB (backwater) and 12 dB (Lake Neusiedl) (Table 2, Fig. 3). Noise from the two running water habitats had more pronounced effects on auditory sensitivity. In the presence of Triesting stream noise, the mean sensitivity declined by up to 32 dB, whereas it declined by up to 49 dB in the noise from the Danube River (Table 2, Fig. 3). The amount of threshold shift was most pronounced in the range of best hearing (0.5–1.0 kHz), and the amount increased with increasing SPL of the masking noise.

Table 1. Hearing threshold values of *C. carpio* and *P. fluviatilis* measured under the different background noise conditions

Fish	Frequency (kHz)	Hearing threshold (dB re 1 μ Pa)				
		Lab-noise	BW	LN	TS	DR
<i>C. carpio</i>	0.1	76.2 \pm 0.65	79.3 \pm 0.61	85.0 \pm 0.45	92.3 \pm 0.95	97.8 \pm 0.87
	0.3	66.3 \pm 0.99	73.2 \pm 0.31	73.7 \pm 1.45	88.3 \pm 1.38	96.8 \pm 1.30
	0.5	60.3 \pm 0.49	64.2 \pm 0.54	67.3 \pm 0.80	82.0 \pm 0.86	95.2 \pm 2.70
	0.8	57.0 \pm 0.45	66.0 \pm 0.68	68.8 \pm 0.65	89.2 \pm 0.91	105.8 \pm 0.48
	1.0	57.3 \pm 0.61	66.7 \pm 0.67	69.2 \pm 0.65	87.8 \pm 0.83	106.2 \pm 0.54
	2.0	81.8 \pm 0.54	90.0 \pm 0.68	88.0 \pm 0.86	102.5 \pm 1.18	118.5 \pm 0.96
	3.0	99.7 \pm 0.71	104.5 \pm 1.12	108.8 \pm 0.54	113.3 \pm 0.56	122.0 \pm 1.00
	4.0	112.2 \pm 0.65	114.0 \pm 0.52	114.7 \pm 0.33	120.2 \pm 0.91	123.3 \pm 0.76
<i>P. fluviatilis</i>	0.1	87.7 \pm 0.42	89.5 \pm 0.34	93.8 \pm 0.65	96.5 \pm 0.86	100.2 \pm 0.87
	0.2	81.7 \pm 0.56	88.2 \pm 1.49	86.2 \pm 0.95	88.2 \pm 1.49	92.7 \pm 1.28
	0.3	83.7 \pm 0.30	88.0 \pm 1.07	87.8 \pm 0.98	87.5 \pm 1.18	91.2 \pm 0.91
	0.5	100.0 \pm 0.37	100.7 \pm 0.71	104.2 \pm 0.91	102.0 \pm 1.10	105.2 \pm 0.79
	0.8	106.3 \pm 0.80	112.7 \pm 1.12	111.5 \pm 0.96	111.3 \pm 0.67	114.8 \pm 0.79
	1.0	110.2 \pm 0.87	114.0 \pm 0.63	112.0 \pm 1.03	116.5 \pm 1.43	118.7 \pm 0.99

Lab-noise, baseline audiogram; BW, backwater; DR, Danube River; LN, Lake Neusiedl; TS, Triesting stream. Values are means \pm S.E.M. ($N=6$).

Table 2. Threshold shift for *C. carpio* and *P. fluviatilis* with the baseline audiogram as reference level

Fish	Frequency (kHz)	Threshold shift (dB)			
		BW	LN	TS	DR
<i>C. carpio</i>	0.1	3.2 \pm 1.05	8.8 \pm 0.95	16.2 \pm 0.87	21.7 \pm 1.50
	0.3	6.8 \pm 0.87	7.3 \pm 1.31	22.0 \pm 1.24	30.5 \pm 1.23
	0.5	3.8 \pm 0.75	7.0 \pm 1.15	21.7 \pm 0.71	34.8 \pm 1.08
	0.8	9.0 \pm 0.52	11.8 \pm 0.60	32.2 \pm 1.05	48.8 \pm 0.79
	1.0	9.3 \pm 0.80	11.8 \pm 1.05	30.5 \pm 1.18	48.8 \pm 0.48
	2.0	8.2 \pm 0.95	6.2 \pm 1.11	20.7 \pm 1.61	36.7 \pm 0.80
	3.0	4.8 \pm 0.79	9.2 \pm 0.79	13.7 \pm 0.95	22.3 \pm 0.80
	4.0	1.8 \pm 0.98	2.5 \pm 0.81	8.0 \pm 0.77	11.2 \pm 0.79
<i>P. fluviatilis</i>	0.1	1.8 \pm 0.48	7.2 \pm 1.25	8.8 \pm 0.60	12.5 \pm 0.99
	0.2	6.5 \pm 1.26	4.7 \pm 1.17	6.5 \pm 1.50	11.0 \pm 1.48
	0.3	4.3 \pm 1.12	4.5 \pm 1.18	4.5 \pm 1.20	7.5 \pm 1.06
	0.5	0.0 \pm 1.00	4.0 \pm 0.89	2.0 \pm 1.06	5.2 \pm 0.75
	0.8	6.3 \pm 1.05	5.0 \pm 0.97	5.0 \pm 1.24	8.5 \pm 1.23
	1.0	3.8 \pm 0.48	1.8 \pm 1.17	6.3 \pm 1.63	8.5 \pm 1.57

BW, backwater; DR, Danube River; LN, Lake Neusiedl; TS, Triesting stream. Values are means \pm S.E.M. ($N=6$).

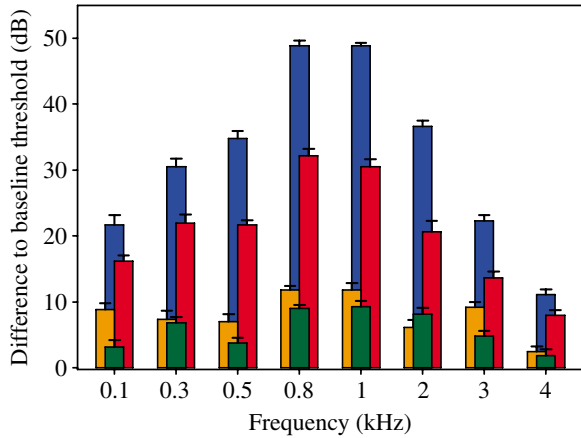


Fig. 3. Differences in hearing thresholds between the baseline audiogram of *C. carpio* and the masked audiograms. Values are means \pm S.E.M. ($N=6$). Colours indicate the differences for the respective habitats according to Fig. 1. Blue, Danube river; red, Triesting stream; green, backwater; orange, Lake Neusiedl.

The perch was much less sensitive than the carp, with hearing thresholds above 80 dB re 1 μ Pa (Table 1, Fig. 4) throughout the audiogram. The best threshold values were found in the frequency range 0.1–0.3 kHz (Table 1). Applying the different masking noise types had slight, and in some cases significant, effects on the hearing thresholds. Comparing the baseline with the masked audiograms by a two-factor ANOVA revealed significant overall differences between hearing curves gained during the presentation of all habitat noises ($F_{4,150}=66.243$, $P<0.001$) and a significant interaction between noises and frequencies tested ($F_{20,150}=3.189$, $P<0.001$). Bonferroni-adjusted *post-hoc* testing revealed that all habitat noise audiograms were significantly different from the baseline curve. However, no significant differences were found between the two stagnant habitats (backwater, Lake Neusiedl) and

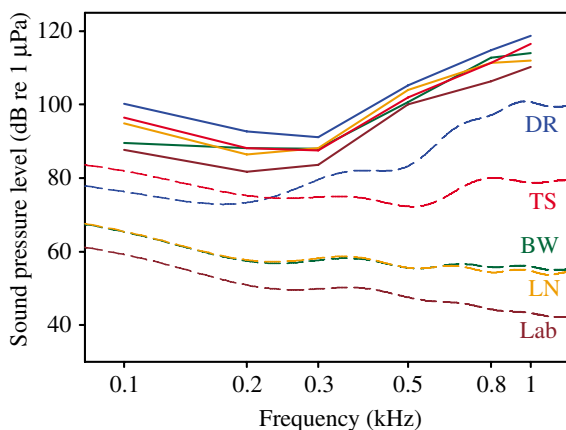


Fig. 4. Mean hearing thresholds of *Perca fluviatilis* (solid lines) under laboratory conditions (baseline) and in the presence of the different ambient noise types. Broken lines show the cepstrum-smoothed sound power spectra of the corresponding habitat noise (Fig. 1 shows the absolute amplitude spectra). DR, Danube river; TS, Triesting stream; BW, backwater; LN, Lake Neusiedl.

between them and the Triesting stream. Mean hearing thresholds were maximally elevated by 12.5 dB at 0.2 kHz for the Danube River-noise (Table 2, Fig. 5).

Threshold-to-noise ratios

Signal-to-noise ratios at threshold (hereafter referred to as threshold-to-noise ratios, T/N) were calculated by subtracting the spectrum level of the masking noise (in a 1 Hz band) from the SPL at hearing threshold at this particular frequency. This was done for all masked hearing thresholds in the two species, that is, for all values that were significantly different from baseline values. The T/N ratios for the four habitat-noise types were significantly different from each other.

In the carp, the mean T/N ratios of all habitats increased with increasing frequency from 13.1 ± 0.95 to 49.1 ± 0.91 (Fig. 6A). In contrast, in the perch, the mean T/N ratios of only three out of four habitat-noise types increased with increasing frequency from 17.7 ± 0.73 dB to 60.3 ± 0.63 dB (backwater), while the ratios for Danube-noise showed no such trend (Fig. 6B).

Discussion

Diversity in habitat noise

Ambient noise is the ubiquitous acoustic background consisting of abiotic (wind, waves, rain, surf) and biotic (animal vocalizations, feeding sounds) sources (Hawkins and Myrberg, 1983). Urick (1983) defined ambient noise more strictly as the environment itself, which is part of the noise background and not due to some identifiable, localized source of noise. When comparing the various ambient noise levels, one has to keep in mind that different values are often given. Spectrum levels render the energy distribution at particular frequencies. Power spectra do not include a correction for filter bandwidth and units are dB re 1 μ Pa, whereas pressure density spectra levels render the energy distribution in narrow bands of the sound (e.g. 1 Hz, 1/3 octave) and the units are dB re

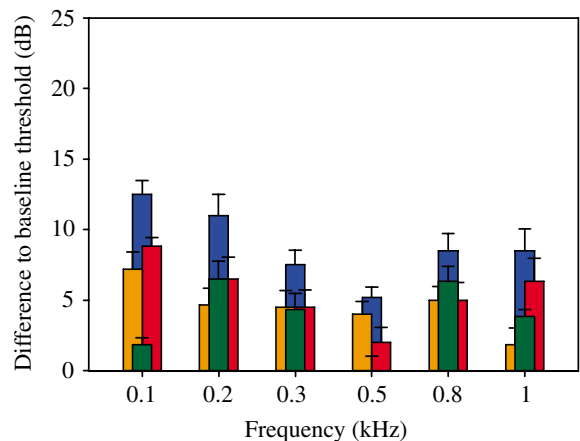


Fig. 5. Differences hearing thresholds between the baseline audiogram of *P. fluviatilis* and the masked audiograms. Values are means \pm S.E.M. ($N=6$). Colours indicate the differences for the respective habitats according to Fig. 4. Blue, Danube river; red, Triesting stream; green, backwater; orange, Lake Neusiedl.

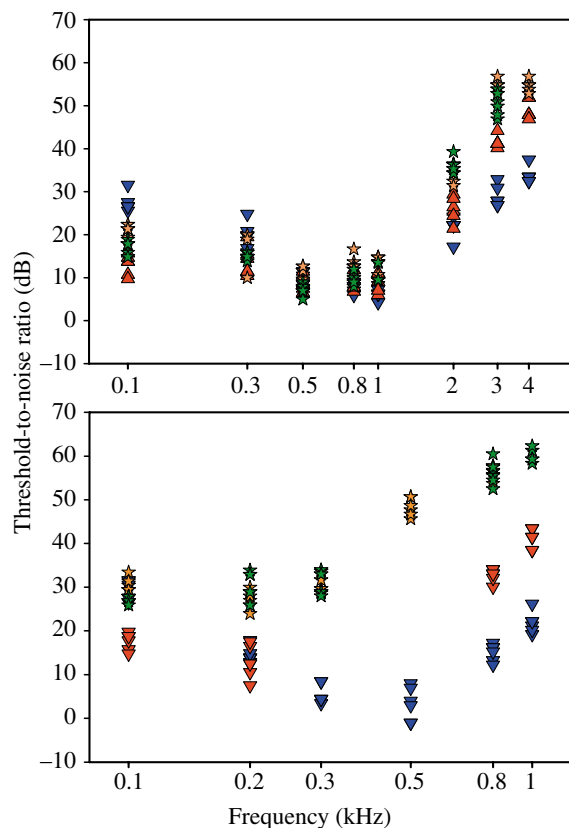


Fig. 6. Threshold-to-noise ratios for masked thresholds of (A) *C. carpio* (T/N-ratio = signal frequency \times 0.0093 + 9.14, $r=0.789$, $P<0.001$) and (B) *P. fluviatilis* (T/N-ratio = signal frequency \times 0.0214 + 20.128, $r=0.456$, $P<0.001$). Colours indicate the T/N ratios for the respective habitats according to Fig. 1.

$1 \mu\text{Pa}^2/\text{Hz}$. Root mean square sound pressure levels (RMS SPL values), on the other hand, are the energy over the whole frequency range measured (Richardson et al., 1995). Therefore, spectrum levels tend to be lower than RMS levels. Unfortunately, this information is not always given.

Our knowledge of natural ambient noise characteristics in freshwater as well as marine habitats is very limited and comparative studies are totally lacking. One of the pioneering works on marine noise was conducted in the early 1960s by Wenz (1962), who showed that the overall noise spectrum levels are above 100 dB re $1 \mu\text{Pa}$ and consist of a high amount at low frequency noise (up to several hundred Hz), which declines rapidly with increasing frequency. Sources contributing to the ambient noise spectra include seismic events, water turbulences, wind noise and surface waves, animal sounds, precipitation and human activities. The ambient noise levels in the deep-water areas are relatively constant, the main sources being wind force and sea state. In coastal waters and bays, ambient noise levels are highly variable due to a variety of different sources; they differ not only from place to place, but also from time to time (Wenz, 1962; Cato, 1976; Urick, 1983; McConnell et al., 1992; Greene, 1995). One of the noisiest habitats in the ocean is coral reefs, with surf waves

crashing against the reefs as the principal abiotic, and intermittent click-sounds from snapping shrimps as the principal biotic source of ambient noise. Mean spectral levels there are between 95 and 110 dB re $1 \mu\text{Pa}$ (Tolimieri et al., 2000, 2004; Egner and Mann, 2005).

In contrast, very little data is available on background noise in freshwater habitats (Boussard, 1981; Crawford et al., 1997; Lugli and Fine, 2003; Amoser et al., 2004). Hawkins and Johnstone (1978) reported the highest noise levels in the River Dee as being 75 dB (spectrum level, 1 Hz bands). Generally, they observed 5–10 dB higher levels in the river compared to the sea (Loch Torridon, Scotland). Boussard (1981) observed ambient noise levels of 80–100 dB re $1 \mu\text{Pa}$ (1/3-octave bands) in the River Meuse, Belgium. Lugli and Fine (2003) presented data on the ambient noise of two Italian rivers (Stirone stream, River Serchio) and reported spectrum levels ranging from below 70 dB at quiet places, up to 100 dB in fast-flowing areas of the rivers. Although the authors used a different frequency bandwidth from ours, the spectrum levels of the Triesting stream (Fig. 2) are similar. Lugli and Fine (2003) described the shape of the river's ambient noise as being relatively high in low frequencies, with a fall-off to the higher frequencies; we also observed this pattern in the Triesting stream (Fig. 2). Crawford et al. (1997) reported spectrum levels of up to 70 dB (1 Hz band) at low frequencies, dropping steadily to about 40 dB above 1 kHz in the background noise of a flood plain of the Niger River (Mali, Africa). There is very limited data available on ambient noise levels in freshwater lakes. Bom (1969) reported levels of 40 to 50 dB (spectrum level in octave bands) in an Italian lake (Lake Sarzana), and Nystuen (1986) reported ambient noise levels ranging from 40 to 60 dB (spectral level, 1 Hz band). Amoser et al. (2004), on the other hand, observed relatively high noise levels in an Alpine lake (Lake Traunsee, Austria) of more than 80 dB (1 Hz band). The values decreased steadily to about 60 dB at 5 kHz, presumably due to the Traun stream, which flows rapidly through this lake.

In summary, ambient noise levels reported for oceanic habitats tend to be considerably higher than those in stagnant freshwater habitats. Marine spectral noise levels are generally at about 100 dB re $1 \mu\text{Pa}$ even in low sea state conditions, whereas the values in Lake Neusiedl and the backwaters of the Danube River are generally below 60 dB. Some freshwater habitats (rivers, streams) are apparently as noisy as marine environments (mean spectral levels in the Danube River at about 100 dB and in the Triesting stream up to 80 dB).

Effects of habitat noise on hearing sensitivity

Ambient noise ultimately determines the detectability of all stimuli impinging on an animal (Fay, 1974). In dealing with the evolution of hearing capabilities, it is crucial to know how an animal copes with the problem of differentiating relevant acoustic events (signals) from the background noise. This problem cannot be solved simply by enhancing the auditory sensitivity since this would affect both signals and noise detection (Fay et al., 1978).

In the present study we were able to show that the carp *C.*

carpio, a hearing specialist, can exploit its excellent hearing abilities in the two stagnant habitats' noise (backwaters of Danube River and Lake Neusiedl). Here, its hearing thresholds were only slightly masked (compared to the baseline audiogram obtained under quiet lab-noise conditions). In contrast, the carp was considerably masked at stream-noise levels and to an even higher degree in the Danube River-noise. On the other hand, various noise types did not affect the hearing sensitivity in the perch *P. fluviatilis*, a hearing non-specialist. The perch was only slightly masked even in the Danube River-noise. This is consistent with prior results where hearing sensitivity was measured in the presence of white noise (Fay, 1974; Wysocki and Ladich, 2005a). Several studies (Tavolga, 1967; Buerkle, 1968; Chapman and Hawkins, 1973; Enger, 1973; Fay, 1974) showed that masking effects are an approximately linear function of noise level, i.e. an increase of the background noise by 10 dB elevated the hearing thresholds by 10 dB. This is supported by a recent study in which hearing sensitivities of two hearing specialists (the goldfish *Carassius auratus* and the catfish *Platydoras costatus*) and a hearing generalist (the sunfish *Lepomis gibbosus*) were measured in the presence of white noise utilizing the non-invasive AEP recording technique (Wysocki and Ladich, 2005a). Auditory thresholds increased almost linearly with white noise level in the hearing specialists, whereas the hearing generalist was only slightly affected by the higher white noise level applied (spectral level approx. 95 dB). The increase was linear for the most sensitive frequencies but not for the upper and lower ends of the fish's hearing ranges. This corresponds to our results in the otophysine *C. carpio*: a 50 dB increase of noise level (lab-noise vs Danube River-noise) led to an almost 50 dB threshold shift (in the frequency range of 0.8–1.0 kHz, Fig. 4). Similar to Wysocki and Ladich (2005a), we observed that the mean hearing thresholds of the European Perch were only slightly elevated by the highest noise level applied (Danube River-noise, spectral level on average 100 dB).

In our study the masking effect was most pronounced in the range of best hearing (i.e. 0.5–1.0 kHz in the carp and 0.2–0.3 kHz in the perch), which was also reported in the cod *Gadus morhua* by Buerkle (1968) and Chapman and Hawkins (1973). This effect was more pronounced in the hearing specialist, the carp, indicating that interspecific differences in masking effects are due to differences in baseline auditory sensitivity. The masking effect was most pronounced in the most sensitive frequency range, which may explain why we observed significant interactions between noise and frequency, yielding different trends of noise effects at different frequencies.

Threshold-to-noise ratios

The so-called threshold-to-noise ratio (T/N ratio) is very important for understanding the influence of ambient noise on the detection of relevant signals and ultimately on acoustic communication. It is a quantitative measure of the amount of masking (Chapman and Hawkins, 1973; Wysocki and Ladich, 2005a), indicating the required level of a signal above the ambient noise in order to be heard.

T/N ratios (in older studies also called signal-to-noise ratios) have been obtained in several fish species (Buerkle, 1968; Fay, 1974; Tavolga, 1974; Hawkins and Chapman, 1975; Fay and Coombs, 1983; Wysocki and Ladich, 2005a). They generally increase with frequency, ranging from 14 to 25 dB for hearing specialists and 16 to 36 dB for hearing generalists. In the present study, the T/N ratio increased over a wider range (6–55 dB in the carp and 6–60 dB in the perch). This cannot be explained by the overall noise levels applied because Wysocki and Ladich (2005a) used white noise at 130 dB, which resembles our highest overall noise level (Danube River-noise: 135 dB). Perhaps noise type can explain the difference. Wysocki and Ladich (2005a) played back white noise with a flat frequency spectrum, whereas we used natural ambient noise; the latter fluctuates with time and in its power content over the frequency range.

The ability to segregate important cues from a mixture of biotic and abiotic sound sources in the environment is a common feature within vertebrates (auditory stream segregation; Bregman, 1990). This is achieved by detecting either the temporal or the spectral characteristics of sounds, or both, as shown in the goldfish (Fay, 1998). Thus, auditory stream segregation could be a major selective force in the evolution of hearing specializations.

Evolutionary considerations

Our results strongly support the hypothesis that the excellent hearing abilities of hearing specialists such as otophysines evolved in quiet habitats such as backwaters, lakes, slowly flowing waters, or perhaps in the deep sea for some marine fish (Popper, 1980; Deng et al., 2002; Ladich and Bass, 2003a). Only in such habitats can hearing specialists utilize their excellent hearing sensitivities. To further increase an animal's probability of survival it would be advantageous to increase the range over which the acoustic environment, consisting of various biotic (sounds from other aquatic animals) and abiotic (wind, waves, precipitation) sources, can be detected. The importance of abiotic sound for fish is widely unknown. Lagardere et al. (1994) did, however, show that sole *Solea solea* used wind-produced noise for orientation, and Tolimieri et al. (2004) demonstrated that pomacentrid larvae orient to ambient reef sound in binary choice experiments.

In shallow waters where low frequencies do not propagate, broadening one's hearing bandwidth (above the cut-off frequency) and increasing the sensitivity may have been a major selective advantage and would have enabled fish to detect a broad range of sound sources (Popper and Fay, 1997; Ladich and Popper, 2004). Connecting the inner ear to gas-filled cavities (e.g. the swim bladder) enabled fish to detect pressure waves emanating from striking predators. Canfield and Eaton (1990) and Eaton et al. (1995) demonstrated that sudden pressure changes initiate Mauthner-mediated escape responses in specialists contrary to non-specialists; this most likely increased survival rates in predator attack situations.

Besides helping to detect pressure waves and non-communicative sounds, the enhancement of hearing

capabilities could serve in intraspecific acoustic communication. Some studies investigating potential correlations between hearing sensitivities and the spectral composition of sound did indeed find such correlations (Myrberg and Spires, 1980; Stabentheiner, 1988; Schellart and Popper, 1992; Ladich and Yan, 1998). If, on the other hand, maximizing the effectiveness of acoustic communication was a major constraint in the evolution of hearing, then hearing specializations should primarily be found in vocalizing species (Ladich, 1999). However, the ability to produce sounds and communicate acoustically is not confined to hearing specialists. In both otophysans and anabantoids, sound-generating mechanisms and acoustic communication are not a common feature of all members (Ladich, 2000). For example, among the otophysans, cypriniforms are thought to be the most primitive group, but only a few species within this group are known to be vocal (Stout, 1963; Ladich, 1988; Johnston and Johnson, 2000). Specialized sonic organs like swim bladder drumming muscles evolved later, and only in related groups (Ladich and Bass, 2003a; Ladich and Popper, 2004) such as characids and catfishes. In anabantoids the situation is quite similar. In addition, hearing sensitivity curves do not always match the frequency spectra of communication sounds (Ladich, 1999). Therefore, it is unlikely that acoustic communication was the major force behind the evolution of hearing specializations in fish.

Which environmental constraints may have led to enhanced hearing capabilities in fishes? Hearing specializations are rare in marine habitats. The most remarkable exception is marine squirrelfishes (holocentrids), in particular representatives of the subfamily Myripristinae, which have hearing sensitivities similar to carps (best sensitivity at about 50 dB re 1 μ Pa), and to a lesser degree the genus *Audioryx* (Coombs and Popper, 1979; for a comparison between *Cyprinus* and *Myripristis*, see Hawkins and Myrberg, 1983). To our knowledge, no behavioural or eco-acoustic explanation has been forwarded for this highly evolved hearing sensitivity in marine *Myripristis* sp. or for the great diversity in sensitivity among squirrelfishes. We hypothesize that different genera live under different ambient noise conditions. Only a few otophysines inhabited brackish or marine waters. Popper and Tavalga (1981) showed that the sea catfish *Ariopsis (Arius) felis* is only able to detect sound in a narrow frequency range from 50 to 1000 Hz, which is rather unusual compared with most catfish species (Ladich and Bass, 2003b). These few examples are in contrast to several thousand freshwater fish species possessing hearing specializations and thus excellent hearing abilities. About two thirds of all freshwater species (6600 out of 10 000 species, according to Nelson, 1994) are thought to be hearing specialists, including catfishes, cypriniforms, characiforms, knife fishes (Fay, 1988; Ladich, 1999), labyrinth fishes (Ladich and Yan, 1998) and mormyrids (Fletcher and Crawford, 2001). On the other hand, numerous non-specialists found in freshwaters, such as perciforms (percids, gobiids) or scorpaeniforms (sculpins), derive from marine habitats. According to Nelson (1994), most perciforms are marine shore fishes.

Does a correlation exist between the diversity in freshwater habitat noise levels as described in our study and the occurrence of particular hearing sensitivities on a more local level in Central Europe? According to Spindler (1997), Austria is inhabited by 61 autochthonous fish species belonging to 16 families. Thirty-three species belong to the family Cyprinidae and a total of 38 species to otophysines, all representing hearing specialists. 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 (eurytopic, stagnophilic and rheophilic type B species). Thus, more species – and relatively more hearing specialists – inhabit quiet waters (binomial-test). On the other hand, only 11 out of 23 species of hearing generalists (salmonids, percids, cottids, gobiids and others) live in these habitats. The distribution of hearing generalists and specialists in rather noisy vs quiet stagnant freshwater habitats supports, at a local level, the assumption that hearing specialists live in rather quiet habitats, for which their hearing ability is adapted.

Combining these global and local data, it can be argued that the evolution of hearing specializations was facilitated by low ambient noise levels. This evolution was most likely forced by the necessity to detect abiotic noise, avoid approaching predators and detect prey, and to a much lesser degree, by acoustic communication.

We would like to thank Lidia Eva Wysocki for her help during sound recording in the field and for critically reading the manuscript. Furthermore, we want to thank Michael Stachowitsch for professional scientific English proofreading. This study was supported by the Austrian Science Fund (FWF Grants Nos 15783 and 17263 to F.L.).

References

- Amoser, S., Wysocki, L. E. and Ladich, F. (2004). Noise emission during the first powerboat race in an Alpine lake and potential impact on fish communities. *J. Acoust. Soc. Am.* **116**, 3789-3797.
- Bass, A. H. and Clark, C. W. (2003). The physical acoustics of underwater sound communication. In *Acoustic Communication* (ed. A. M. Simmons, A. N. Popper and R. R. Fay), pp. 15-64. New York: Springer.
- Bom, N. (1969). Effect of rain on underwater noise level. *J. Acoust. Soc. Am.* **45**, 150-156.
- Boussard, A. (1981). The reactions of roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) to noises produced by high speed boating. *Proc. 2nd Brit. Freshw. Fish. Conf.* 188-200.
- Bregman, A. S. (1990). *Auditory Scene Analysis. The Perceptual Organisation of Sound*. Cambridge, MA: MIT Press.
- Buerkle, U. (1968). Relation of pure tone thresholds to background noise level in the Atlantic Cod (*Gadus morhua*). *J. Fish. Res. Bd Canada* **25**, 1155-1160.
- Buerkle, U. (1969). Auditory masking and the critical band in Atlantic Cod (*Gadus morhua*). *J. Fish. Res. Bd Canada* **26**, 1113-1119.
- Canfield, J. G. and Eaton, R. C. (1990). Swimbladder acoustic pressure transduction initiates Mauthner-mediated escape. *Nature* **347**, 760-762.
- Cato, D. H. (1976). Ambient sea noise in waters near Australia. *J. Acoust. Soc. Am.* **60**, 320-328.
- Chapman, C. J. and Hawkins, A. D. (1973). A field study of hearing in the cod, *Gadus morhua* L. *J. Comp. Physiol.* **85**, 147-167.
- Coombs, S. and Popper, A. N. (1979). Hearing differences among Hawaiian squirrelfish (family Holocentridae) related to differences in the peripheral auditory system. *J. Comp. Physiol.* **132**, 203-207.
- Crawford, J. D., Jacob, P. and Bénech, V. (1997). Sound production and reproductive ecology of strongly acoustic fish in Africa: *Pollimyrus isidori*, Mormyridae. *Behaviour* **134**, 677-725.

- Deng, X., Wanger, H. J. and Popper, A. N. (2002). Messages from the bottom of the Atlantic Ocean: comparative studies of anatomy and ultrastructure of the inner ears of several gadiform deep-sea fishes. *Abst. Assn. Res. Otolaryngol.* **25**, 101.
- Eaton, R. C., Canfield, J. G. and Guzik, A. L. (1995). Left-right discrimination of sound onset by the Mauthner system. *Brain Behav. Evol.* **146**, 165-179.
- Egner, S. A. and Mann, D. A. (2005). Auditory sensitivity of sergeant major damselfish *Abudefduf saxatilis* from post-settlement juvenile to adult. *Mar. Ecol.-Progr. Ser.* **285**, 213-222.
- Enger, P. S. (1973). Masking of auditory responses in the medulla oblongata of goldfish. *J. Exp. Biol.* **59**, 415-424.
- Fay, R. R. (1974). Masking of tones by noise for the goldfish. *J. Comp. Physiol. Psychol.* **87**, 708-716.
- Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook*. Winnetka, IL: Hill-Fay Associates.
- Fay, R. R. (1998). Auditory stream segregation in goldfish (*Carassius auratus*). *Hear. Res.* **120**, 69-76.
- Fay, R. R. and Coombs, S. (1983). Neural mechanisms in sound detection and temporal summation. *Hear. Res.* **10**, 69-92.
- Fay, R. R. and Popper, A. N. (1974). Acoustic stimulation of the ear of the goldfish (*Carassius auratus*). *J. Exp. Biol.* **61**, 243-260.
- Fay, R. R., Ahroon, W. A. and Orawski, A. A. (1978). Auditory masking patterns in the goldfish (*Carassius auratus*): Psychophysical tuning curves. *J. Exp. Biol.* **74**, 83-100.
- Fletcher, H. (1940). Auditory patterns. *Rev. Mod. Phys.* **12**, 47-65.
- Fletcher, L. B. and Crawford, J. D. (2001). Acoustic detection by sound-producing fishes (Mormyridae): the role of gas-filled tympanic bladders. *J. Exp. Biol.* **204**, 175-183.
- Greene, C. R., Jr (1995). Ambient noise. In *Marine Mammals and Noise* (ed. W. J. Richardson, C. R. Greene, Jr, C. I. Malme and D. H. Thomson), pp. 87-100. London: Academic Press.
- Hawkins, A. D. (1981). The hearing abilities of fish. In *Hearing and Sound Communication in Fishes* (ed. W. N. Tavolga, A. N. Popper and R. R. Fay), pp. 109-133. New York: Springer.
- Hawkins, A. D. and Chapman, C. J. (1975). Masked auditory thresholds in the cod, *Gadus morhua*. *J. Comp. Physiol.* **103**, 209-226.
- Hawkins, A. D. and Johnstone, A. D. F. (1978). The hearing of the Atlantic Salmon, *Salmo salar*. *J. Fish Biol.* **13**, 655-673.
- Hawkins, A. D. and Myrberg, A. A., Jr (1983). Hearing and sound communication under water. In *Bioacoustics, a Comparative Approach* (ed. B. Lewis), pp. 347-405. London: Academic Press.
- Johnston, C. E. and Johnson, D. L. (2000). Sound production in *Pimephales notatus* (Rafinesque) (Cyprinidae). *Copeia* **2000**, 567-571.
- Kenyon, T. N., Ladich, F. and Yan, H. Y. (1998). A comparative study of hearing ability in fishes: the auditory brainstem response approach. *J. Comp. Physiol. A.* **182**, 307-318.
- Ladich, F. (1988). Sound production by the gudgeon, *Gobio gobio* L.; a common European freshwater fish (Cyprinidae, Teleostei). *J. Fish Biol.* **32**, 707-715.
- Ladich, F. (1999). Did auditory sensitivity and vocalization evolve independently in otophysan fishes? *Brain Behav. Evol.* **53**, 288-304.
- Ladich, F. (2000). Acoustic communication and the evolution of hearing in fishes. *Phil. Trans. R. Soc. Lond. B* **355**, 1285-1288.
- Ladich, F. and Bass, A. H. (2003a). Underwater sound generation and acoustic reception in fishes with some notes on frogs. In *Sensory Processing in Aquatic Environments* (ed. S. P. Collin and N. J. Marshall), pp. 173-193. New York: Springer.
- Ladich, F. and Bass, A. H. (2003b). Audition. In *Catfishes*, Vol 2 (ed. G. Arratia, B. G. Kapoor, M. Chardon and R. Diogo), pp. 701-730. Enfield, NH: Science Publishers.
- Ladich, F. and Popper, A. N. (2004). Parallel evolution in fish hearing organs. In *Evolution of the Vertebrate Auditory System* (ed. G. Manley, A. N. Popper and R. R. Fay), pp. 95-127. New York: Springer.
- Ladich, F. and Yan, H. Y. (1998). Correlation between auditory sensitivity and vocalization in anabantoid fishes. *J. Comp. Physiol. A* **182**, 737-746.
- Lagardère, J. P., Bégout, M. L., Lafaye, J. Y. and Villotte, J. P. (1994). Influence of wind-produced noise on orientation in the sole (*Solea solea*). *Can. J. Fish. Aquat. Sci.* **51**, 1258-1264.
- Lugli, M. and Fine, M. L. (2003). Acoustic communication in two freshwater gobies: Ambient noise and short-range propagation in shallow streams. *J. Acoust. Soc. Am.* **114**, 512-521.
- Lugli, M., Yan, H. Y. and Fine, M. L. (2003). Acoustic communication in two freshwater gobies: the relationship between ambient noise, hearing thresholds and sound spectrum. *J. Comp. Physiol. A.* **189**, 309-320.
- Mann, D. A. and Lobel, P. S. (1997). Propagation of damselfish (Pomacentridae) courtship sounds. *J. Acoust. Soc. Am.* **101**, 3783-3791.
- McConnell, S. O., Schilt, M. P. and Dworski, J. G. (1992). Ambient noise measurements from 100 Hz to 80 kHz in an Alaskan fjord. *J. Acoust. Soc. Am.* **91**, 1990-2003.
- Myrberg, A. A. and Spires, J. Y. (1980). Hearing in damselfishes: an analysis of signal detection among closely related species. *J. Comp. Physiol. A* **140**, 135-144.
- Nelson, J. S. (1994). *Fishes of the World*. New York: John Wiley and Sons.
- Nystuen, J. A. (1986). Rainfall measurements using underwater ambient noise. *J. Acoust. Soc. Am.* **79**, 972-981.
- Popper, A. N. (1980). Scanning electron microscopic studies of the sacculus and lagena in several deep-sea fishes. *Am. J. Anat.* **157**, 115-136.
- Popper, A. N. and Fay, R. R. (1993). Sound detection and processing by fish: critical review and major research questions. *Brain Behav. Evol.* **41**, 14-38.
- Popper, A. N. and Fay, R. R. (1997). Evolution of the ear and hearing: issues and questions. *Brain, Behav. Evol.* **50**, 213-221.
- Popper, A. N. and Tavolga, W. N. (1981). Structure and function of the ear in the marine catfish, *Arius felis*. *J. Comp. Physiol.* **144**, 27-34.
- Richardson, W. J. and Greene, C. R. (1995). Measurement procedures. In *Marine Mammals and Noise* (ed. W. J. Richardson, C. R. Greene, C. I. Malme and D. H. Thomson), pp. 33-58. London: Academic Press.
- Rogers, P. H. and Cox, M. (1988). Underwater sound as a biological stimulus. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 131-149. New York: Springer.
- Samuel, Y., Morreale, S. J., Clark, C. W., Greene, C. H. and Richmond, M. E. (2005). Underwater, low-frequency noise in a coastal sea turtle habitat. *J. Acoust. Soc. Am.* **117**, 1465-1472.
- Schabuss, M. and Reckendorfer, W. (2002). Die Hydrologie als Schlüsselparameter für die Verteilung der Adult- und Jungfischfauna im Altarmsystem der Unteren Lobau. [Hydrology as a key factor for the dispersal of adult and juvenile fishes in the backwater system of the Lower Lobau.] Vienna: Nationalpark Donauauen GmbH, 27p.
- Schellart, N. A. M. and Popper, A. N. (1992). Functional aspects of the evolution of the auditory system of actinopterygian fish. In *The Evolutionary Biology of Hearing* (ed. D. E. Webster, R. R. Fay and A. N. Popper), pp. 295-322. New York: Springer.
- 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**, 140p.
- Stabentheiner, A. (1988). Correlations between hearing and sound production in piranhas. *J. Comp. Physiol. A* **162**, 67-76.
- Stout, J. F. (1963). The significance of sound production during the reproductive behaviour of *Notropis analostanus* (Family Cyprinidae). *Anim. Behav.* **11**, 83-92.
- Tavolga, W. N. (1967). Masked auditory thresholds in teleost fishes. In *Marine Bioacoustics*, Vol. 2 (ed. W. N. Tavolga), pp. 233-245. Oxford: Pergamon Press.
- Tavolga, W. N. (1974). Signal/noise ratio and the critical band in fishes. *J. Acoust. Soc. Am.* **55**, 1323-1333.
- Tolimieri, N., Jeffs, A. and Montgomery, J. C. (2000). Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Mar. Ecol. Prog. Ser.* **207**, 219-224.
- Tolimieri, N., Haine, O., Jeffs, A., McCauley, R. D. and Montgomery, J. C. (2004). Directional orientation of pomacentrid larvae to ambient reef sound. *Coral Reefs* **23**, 184-191.
- Urlick, R. J. (1983). The noise background of the sea: ambient noise level. In *Principles of Underwater Sound* (ed. R. J. Urlick), pp. 202-236. Los Altos, California: Peninsula Publishing.
- Wenz, G. M. (1962). Acoustic ambient noise in the ocean: spectra and sources. *J. Acoust. Soc. Am.* **34**, 1936-1956.
- Wysocki, L. E. and Ladich, F. (2002). Ontogeny of hearing and sound production in fishes. *Bioacoustics* **12**, 183-185.
- Wysocki, L. E. and Ladich, F. (2005a). Hearing in fishes under noise conditions. *J. Assn. Res. Otolaryngol.* **6**, 28-36.
- Wysocki, L. E. and Ladich, F. (2005b). Effects of noise exposure on click detection and the temporal resolution ability of the goldfish auditory system. *Hear. Res.* **201**, 27-36.