

Diversity in ambient noise in European freshwater habitats: Noise levels, spectral profiles, and impact on fishes

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The detectability of acoustic signals depends on the hearing abilities of receivers and the prevailing ambient noise in a given habitat. Ambient noise is inherent in all terrestrial and aquatic habitats and has the potential to severely mask relevant acoustic signals. In order to assess the detectability of sounds to fishes, the linear equivalent sound pressure levels (L_{Leq}) of twelve European freshwater habitats were measured and spectra of the ambient noise recordings analyzed. Stagnant habitats such as lakes and backwaters are quiet, with noise levels below 100 dB re 1 μ Pa (L_{Leq}) under no-wind conditions. Typically, most environmental noise is concentrated in the lower frequency range below 500 Hz. Noise levels in fast-flowing waters were typically above 110 dB and peaked at 135 dB (Danube River in a free-flowing area). Contrary to stagnant habitats, high amounts of sound energy were present in the high frequency range above 1 kHz, leaving a low-energy “noise window” below 1 kHz. Comparisons between the habitat noise types presented here and prior data on auditory masking indicate that fishes with enhanced hearing abilities are only moderately masked in stagnant, quiet habitats, whereas they would be considerably masked in fast-flowing habitats. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2713661]

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I. INTRODUCTION

In the aquatic environment, sound is a key signal carrier because it is not attenuated as fast as light or chemical substances, and can be propagated over long distances (Hawkins and Myrberg, 1983; Bradbury and Vehrencamp, 1998; Mann, 2006). This makes sound an important carrier of information for fish and for other aquatic vertebrates. Exploitation of biotic and abiotic acoustic cues may be vital for detecting predators, prey, mates, and competitors but also for acoustic orientation, i.e., detecting coastlines, torrents, wind, and water currents.

The detectability of relevant signals will be strongly affected not only by the hearing abilities of the receiver but also by the environment. Physical properties of the environment such as depth, bottom structure, vegetation, and temperature and salinity clines lead to surface and bottom reflections, causing complex multiple sound propagation paths and therefore often considerable signal distortion and limitation of the propagation distance (Gerald, 1971; Fine and Lenhardt, 1983; Crawford *et al.*, 1997; Mann and Lobel, 1997; Ladich and Bass, 2003).

Another limitation in signal detectability is the presence of an ambient background noise floor inherent in every habitat—aquatic or terrestrial. Such noise emanates from biotic (sounds from animals) and abiotic (i.e., wind, precipitation, surf) sources. Urick (1983) defined underwater ambient noise in a strict sense as the residual noise background in the absence of individual identifiable sources that may be considered the natural noise environment. However, it is often

difficult to identify specific noise sources due to a lack of knowledge about the biotic or abiotic noise components. We therefore apply the term “habitat or ambient noise” throughout this paper. Habitat in an ecological sense is defined as the place where a particular species lives and grows, i.e., the environment that influences a species’ population. Hence, the broad term habitat or ambient noise covers every surrounding noise floor with which an animal is confronted in its natural environment. This noise is likely to vary in level, as well as in spectral composition, between different aquatic ecosystems depending on abiotic and biotic factors; originally, it did not include clearly recognizable anthropogenic sources such as noise emanating from shipping.

This ambient noise can impair the detection of a relevant sound, a phenomenon termed masking (Fletcher, 1940). The masking effect, i.e., the amount by which a signal must be louder in order to still be detected in the presence of background noise of a given level, has been demonstrated to largely depend on the overall hearing sensitivity of a particular fish species (Tavolga, 1967; Champman, 1973; Wysocki and Ladich, 2005). Recently, the masking effect of habitat noise has been studied in several freshwater species (Amoser and Ladich, 2005; Scholz and Ladich, 2006). Amoser and Ladich (2005) showed that hearing-sensitive fish such as carp are only moderately masked by quiet habitat noise levels of standing waters, whereas they are highly affected by stream and river noise, in whose presence acoustic signals must be up to 50 dB louder in their best hearing range (0.5–1.0 kHz) than in the quiet habitats to be detectable. In contrast, the hearing thresholds of perch (a species with much poorer hearing sensitivity than carp) were only slightly affected by the highest habitat noise levels presented. Scholz and Ladich (2006) demonstrated that the topmouth minnow (*Pseudorasbora parva*) can easily intercept feeding sounds

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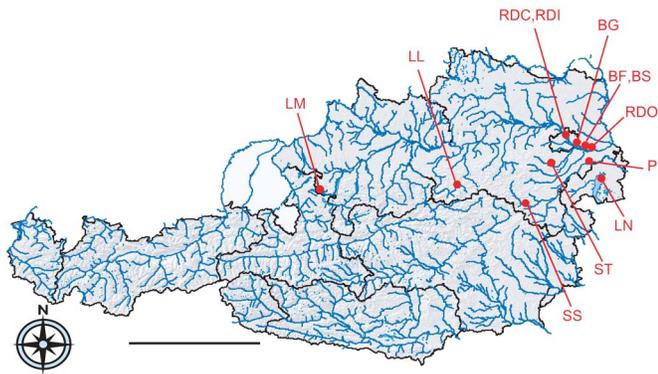


FIG. 1. (Color online) Overview of the study sites. In alphabetical order: BF: Backwater Fadenbach; BG: Backwater Gänsehaufen Traverse; BS: Backwater Schönauer Traverse; LL: Lake Lunz; LM: Lake Mondsee; LN: Lake Neusiedl; P: pond; RDC: Danube Channel; RDI: Danube River at Danube Island; RDO: Danube River at Orth; SS: Schwarza stream; ST: Triesting stream. Bar indicates 120 km. Map of Austria from the Austrian Federal Ministry of Agriculture, Forestry, Environment and Water Management© BMLFUW 1998-2004.

of conspecifics over distances of several dozen centimeters in one of its typical stagnant habitats (a shallow lake), an ability which would be considerably impaired in louder habitats such as creeks or streams.

Therefore, every speculation on acoustic communication ranges in the field as well as on the detectability of various noise sources must consider the potential masking effects of prevailing ambient noise. While several studies have characterized habitat noise in the marine environment (e.g. Wenz, 1962; Cato, 1976; Urick, 1983; McConnell *et al.*, 1992; Samuel *et al.*, 2005; McDonald *et al.*, 2006), including reefs (Tolimieri *et al.*, 2004; Egner and Mann, 2005), only sparse data are available for freshwater habitats (Bom, 1969; Bousard, 1981; Lugli and Fine, 2003; Lugli *et al.*, 2003; Amoser *et al.*, 2004); especially comparative approaches are lacking.

The present study therefore comparatively describes the sound pressure levels and the spectral composition of ambient noise types in various central European freshwater habitats. Detailed knowledge about the ambient noise in freshwater habitats and about their fish community composition, together with a comparison of the ambient noise types whose effects on fish hearing have already been investigated (Amoser and Ladich, 2005; Scholz and Ladich, 2006), will allow the amount of masking for various fish species to be assessed. This, in turn, will highlight the limitations of fish acoustic orientation and communication.

II. MATERIAL AND METHODS

A. Study sites

Twelve different study sites throughout Austria, which represent the variety of freshwater habitats in Central Europe, were chosen. These comprised stagnant or slowly flowing freshwater habitats (lakes and river backwaters) as well as fast-flowing freshwaters (small streamlets and the large Danube River). Figure 1 provides an overview on the location of the study sites within Austria, and Table I lists further information about the sites.

TABLE I. Geomorphologic information about the study sites. In alphabetical order: BF: Backwater Fadenbach, BG: backwater Gänsehaufen Traverse, BS: Backwater Schönauer Traverse, LL: Lake Lunz; LM: Lake Mondsee; LN: Lake Neusiedl; P: pond; RDC: Danube Channel; RDI: Danube River at Danube Island, RDO: Danube River at Orth; SS: Schwarza stream; ST: Triesting stream; and SL: sea level.

Study site	Geographical position	Altitude (m above SL)	Total depth (m)	Hydrophone depth (m)	Recording date
LM	47.9°N, 13.4°E	481	68	5	3 July
LL	47.9°N, 15.1°E	608	34	1.7	5 June
LN	47.8°N, 16.8°E	115	2	1	4 June
BF	48.1°N, 16.7°E	149	<0.5	0.5	7 July
BS	48.1°N, 16.6°E	153	<1	0.5	4 May
BG	48.2°N, 16.6°E	149	<1	0.4	4 May
P	48.1°N, 17.0°E	163	1.5	0.8	3 April
SS	47.7°N, 15.9°E	457	<0.5	0.4	3 July
ST	48.0°N, 16.1°E	346	<0.5	0.3	4 April
RDC	48.3°N, 16.4°E	149	2	0.5	4 June
RDI	48.3°N, 16.4°E	146	3	0.5	4 June
RDO	48.1°N, 16.7°E	149	2	0.6	4 July

Three different lakes were chosen in order to account for the variety of lakes encountered in Austria. As can be seen in Table I these lakes differ not only in the area they cover [Lake Lunz (LL): 0.7 km²; Lake Mondsee (LM): 14 km²; and Lake Neusiedl [LN]: 321 km²] but also in the total water depth and the altitude.

The backwaters of the Danube River [Fadenbach (BF), Schönauer Traverse (BS), and Gänsehaufen Traverse (BG)] are all part of the Danube Floodplain National Park. The water depth is approximately 0.5 m, but can exceed 1 m during high waters.

The pond (P) is located in Prellenkirchen southeast of Vienna, measures 32 × 22 m with a depth of about 1.8 m and is populated by cyprinids.

The Schwarza (SS) and the Triesting stream (ST) are typical creeks of the Alpine foothills. The bed of the Schwarza contains bedrock (according to the substrate type classification of Yamazaki *et al.*, 2006), making its flow more intermittent, with areas of retained waters (our randomly selected study site was in one such area) and areas where the water can flow freely and fast. Contrary to the Schwarza, the substrate type in the Triesting stream is cobble (65–256 mm) to boulders (>256 mm). At our study site we measured a mean current velocity of 0.5 m/s.

The Austrian part of the Danube River is a mountainous river with a mean slope of 40 cm km⁻¹ and a current velocity of 1–3 m s⁻¹. Its water regime is mainly dominated by the snowmelt in the high Alps; therefore, high water occurs usually from late spring to summer, although precipitation-caused floodings can occur throughout the year. Three different study sites were chosen: one in a free-flowing part [Danube River at Orth (RDO)], the second in a retained part [Danube River at Danube Island (RDI)] of the main river. The last of these study sites was in a now regulated former side-arm of the Danube River flowing through the center of Vienna [Danube Channel (RDC)]. The latter two habitats are affected by human activities (ship and road traffic) but were

included into this study because they are populated by numerous fish species and the fish there have to deal with these modifications of their natural environment.

All recordings were made in spring and early summer of 2003–2005 between 10 a.m. and 2 p.m. (Table I), the main reproductive season of most fish species. The aim of this study was to give a first insight into the variability of ambient noise levels and spectra in various freshwater habitats. We decided to measure at just one site per habitat and concentrate on a wide spectrum of habitats, although by doing this the potential variation within each habitat might be underestimated. However, dealing with this variability would have gone beyond the scope of this study. Three noise types already described in Amoser and Ladich (2005) (the noises of the Danube River at Orth, Triesting stream, and Lake Neusiedl) were included in the present study for comparative purposes; they allow us to estimate the effects of noise in the other habitats on fishes.

B. Noise measurements and recording

Underwater noise was recorded on a DAT recorder (Sony TCD 100) using a hydrophone (Brüel & Kjaer 8101) powered by a power supply (Brüel & Kjaer 2804). Due to the different water depths of the habitats (Table I) it was not possible to position the hydrophone always in the same depth. We managed to place the hydrophone in a depth of 0.3–1 m most of the time, except for the measurements in the lakes (Table I). The minimum recording period was 1 min, but for most recordings this period was expanded to 3 min. Before and after each recording the sound pressure level (SPL) of the ambient noise was measured for a period of 1 min using a sound level meter (Brüel & Kjaer 2238 Mediator), which was connected to one output of the power supply. Thus, it was possible to attribute SPL values to each of the recordings. Two SPL measures were obtained: (1) the instantaneous SPL (L_{LSP} , L-weighted, 5 Hz to 20 kHz, rms fast), to assess the variability of habitat noise levels over time, and (2) the equivalent continuous SPL (L_{Leq}), averaged over 60 s. The L_{Leq} is a measure of the averaged energy in a varying sound field and is commonly used to assess environmental noise (ISO 1996, 2003). During each measurement the L_{LSP} was noted every 5 s, and at the end of the 1 min period we noted the L_{Leq} as well (the B & K Mediator allows parallel reading of four different noise measures), except for Lake Mondsee and the Schwarza stream, where only one L_{Leq} measure was noted before and after, respectively.

C. Sound analysis

For this comparative study, one sound recording of each habitat was chosen. It had to meet certain criteria like time of recording in spring and early summer (April to July, Table I), no anthropogenic noise (i.e., boat noise, road traffic noise) present with the exception of the two habitats, Danube Island and Danube Channel, where no such recordings could be obtained, and good weather conditions (i.e., no rain, no wind, no wind-related waves). The selected sound samples were digitized at a sampling rate of 44.1 kHz, and 60 s samples were analyzed using STX 3.7.4 developed by the Acoustic

Research Institute at the Austrian Academy of Sciences.

First relative noise spectra of the 60 s samples were calculated by fast Fourier transformations using a filter bandwidth of 1 Hz. Absolute spectra were calculated using the L_{Leq} measured immediately before/after the recordings following the algorithm described in Amoser *et al.* (2004) and Wysocki and Ladich (2005).

D. Statistical analysis

L_{LSP} levels between the different study sites were compared using a Kruskal-Wallis test because data were neither normally distributed nor were variances homogeneous. The Mann-Whitney-U-test was used for further pairwise comparisons. Furthermore, the overall difference between stagnant and flowing freshwaters was compared with a T-test using the L_{Leq} measured before and after each noise recording of each habitat noise type. All statistical tests except cross correlations were run using SPSS 12.0

In order to assess similarities in noise spectra between habitats cross correlations from 60 s noise segments of each habitat were calculated using STX 3.7.4. A cross correlation value of 1 indicates a strong correlation, with a plus indicating a positive correlation, i.e., the values of one curve tend to become larger when the values of the other curve become larger, too, and vice versa for negative values. We considered values from 1 to 0.9 as strongly correlated, values from 0.9 to 0.6 as correlated, and values from 0.6 to 0 as weakly correlated or not (Townend, 2002). Furthermore, to assess the effect of habitat noise types on the hearing of fishes, spectral profiles of habitats were compared within their hearing range (20–5000 Hz; Ladich and Popper, 2004) to those habitat noise types whose effects on fish hearing have been described previously (Amoser and Ladich, 2005). Therefore, cross correlations between the newly described noise types and noise types previously described in Amoser and Ladich (2005) were calculated. Since cross correlation coefficients are simply a measure for similarity in shape, i.e., in spectral composition without the absolute noise levels taken into account (Wood *et al.*, 2005), this information needs to be combined with overall absolute sound pressure levels in order to reliably assess potential masking effects of the noise.

III. RESULTS

A. Absolute noise levels

Instantaneous SPLs (L_{LSP}) differed significantly between the various study sites (Kruskal-Wallis: $\chi^2_{11,252}=238.6$, $p \leq 0.001$) (Fig. 2). Subsequent Mann-Whitney-U tests revealed that L_{LSPs} of Lake Mondsee and the backwater Schönauer Traverse [$U=256.0$, $p=0.495$] [Fig. 2(a)], the backwater Gänsehaufen Traverse and the pond [$U=59$, $p=0.436$, Fig. 2(b)] as well as Danube Island and Schwarza [$U=237.5$, $p=0.294$, Fig. 2(c)] did not differ significantly from each other, whereas the levels of all other site combinations were significantly different. The variability within the same study site was lowest at the site with the highest average L_{LSP} values: The difference between maximum and minimum levels measured was only 1 dB at Danube River at Orth (Table II), whereas it was 15 dB at Danube Island and

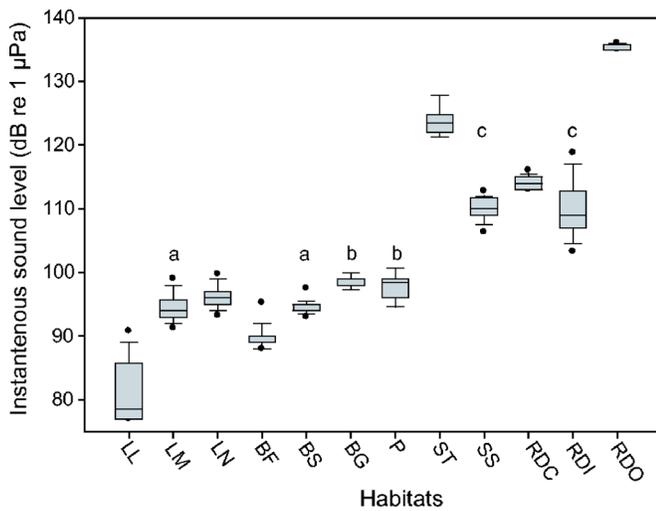


FIG. 2. (Color online) L_{LSP} values (median and quartiles) of the 12 different habitats. Indices indicating values that are not significantly different from each other (Mann-Whitney-U test).

12 dB at Lake Lunz, the site with lowest average SPLs (Table II). However, the average difference between maximum and minimum levels measured at the stagnant sites was the same as within fast-flowing waters (6.6 dB).

Continuous SPLs (L_{Leq}) ranged from 79 dB (Lake Lunz) to 135 dB (Danube River) (Table II). Stagnant waters had a L_{Leq} below 100 dB re 1 μ Pa (mean 92.8 ± 1.85 SE) and differed significantly from flowing waters such as creeks and river sites, which were above 110 dB (mean 118.8 ± 3.10 SE) (T-test, $t = -7.59$, $df = 21$, $p < 0.001$). The L_{Leq} values varied to some degree within the same habitat types, e.g., the levels in the seven stagnant habitats (lakes, pond, backwaters) differed by up to 20 dB, the three different study sites at the Danube River (Danube River at Orth, and Danube Channel, and Danube River at Danube Island) differed even more (up to 25 dB), and even within the two creeks (Triesting, Schwarza) there was more than 10 dB variance. Nonetheless, two groups of habitats are apparent: The more quiet stagnant and the noisier fast-flowing habitats.

TABLE II. Continuous (L_{Leq}) and instantaneous (L_{LSP}) noise levels encountered in the 12 freshwater habitats. All values are given in dB re 1 μ Pa. Before: Before noise recording, After: After noise recording.

Study site	L_{Leq}		L_{LSP} ($x \pm SE$)	L_{LSP}	
	Before	After		min	max
LL	80.5	78.6	81.0 ± 0.98	77	91
LM	94.0	^a	94.3 ± 0.40	91	99
LN	97.7	95.7	96.0 ± 0.37	93	100
BF	90.5	88.2	89.5 ± 0.36	88	96
BS	94.7	94.0	94.4 ± 0.21	93	98
BG	98.9	97.8	98.7 ± 0.25	97	100
P	97.1	98.6	98 ± 1.18	96	100
SS	^a	110.4	110.2 ± 0.42	108	113
ST	122.3	123.2	123.6 ± 0.60	121	129
RDC	114.3	114.2	114.3 ± 0.19	113	116
RDI	110.5	113.4	109.6 ± 0.85	103	119
RDO	135.1	135.3	135.3 ± 0.09	135	136

^aNot measured.

B. Spectral profiles

Amplitude spectra of habitat noises differed widely in composition (Fig. 3). All spectra revealed a decline in energy from 20 Hz down to 20 kHz, with a major decline at lowest frequencies. This decline could be very smooth and continuous such as in Lake Lunz or more irregular because of energy peaks such as in the Triesting stream and the Gänsehaufen backwater.

Lakes, backwaters, and the pond showed similar spectral profiles with main energies in the low frequency region followed by a rather steep decline in energy until 100 (backwaters) to 800 Hz (pond), followed by either a continuous, slow decline or a leveling off (BF, P), except for two backwaters which had a region of higher energy between 5.3 and 9.3 kHz (BG), or between 7 and 12 kHz (BS).

The running waters on the other hand showed a different frequency distribution pattern. Again main energies were found in the low frequencies, followed by a rapid decline to a minimum. In contrast to the stagnant waters, spectral levels then increased again, forming an area of lower spectral levels (“noise window”) ranging from 170 to 450 Hz (in the Schwarza stream this window even ranged up to 2 kHz). This noise window was sharpest in the spectra of the Danube River at Orth and Danube River at Danube Island, both being in the main river. In the Danube Channel and the Triesting stream, the energy content was more fluctuating but the presence of such a noise window remained obvious.

In general, the energy in the 200 Hz to 5 kHz range was much higher in the streams and rivers (with the exception of SS) than in the stagnant water bodies.

C. Cross correlations

To assess the masking effect of the ambient noise types, the amplitude spectra of the different habitat noises were cross correlated with each other and with noise types whose effect is already known from Amoser and Ladich (2005): Lake Neusiedl, a backwater of the Danube River, Danube River at Orth and lab noise (Lab) (Table III). The spectral composition of stagnant habitats seems to be more similar in shape than those of fast-flowing habitats with cross correlation coefficients ranging from 0.58 to 0.86 (lakes) and from 0.80 to 0.93 (backwaters). The pond also showed rather high cross correlation coefficients with all other backwaters and the lab noise (Table III). The amplitude spectrum of the quietest habitat, Lake Lunz, was also strongly correlated to the lab noise of Amoser and Ladich (2005) ($r = 0.96$, Table III). In contrast, the correlation coefficients could be very diverse between running waters. Whereas the cross correlation coefficients between the Danube River at Orth and all the other fast-flowing habitats were very low (ranging from -0.67 to 0.13 , Table III), the spectrum of the Triesting was highly correlated to that of the site Danube Island ($r = 0.86$) but not at all correlated to the second creek, the Schwarza ($r = -0.02$).

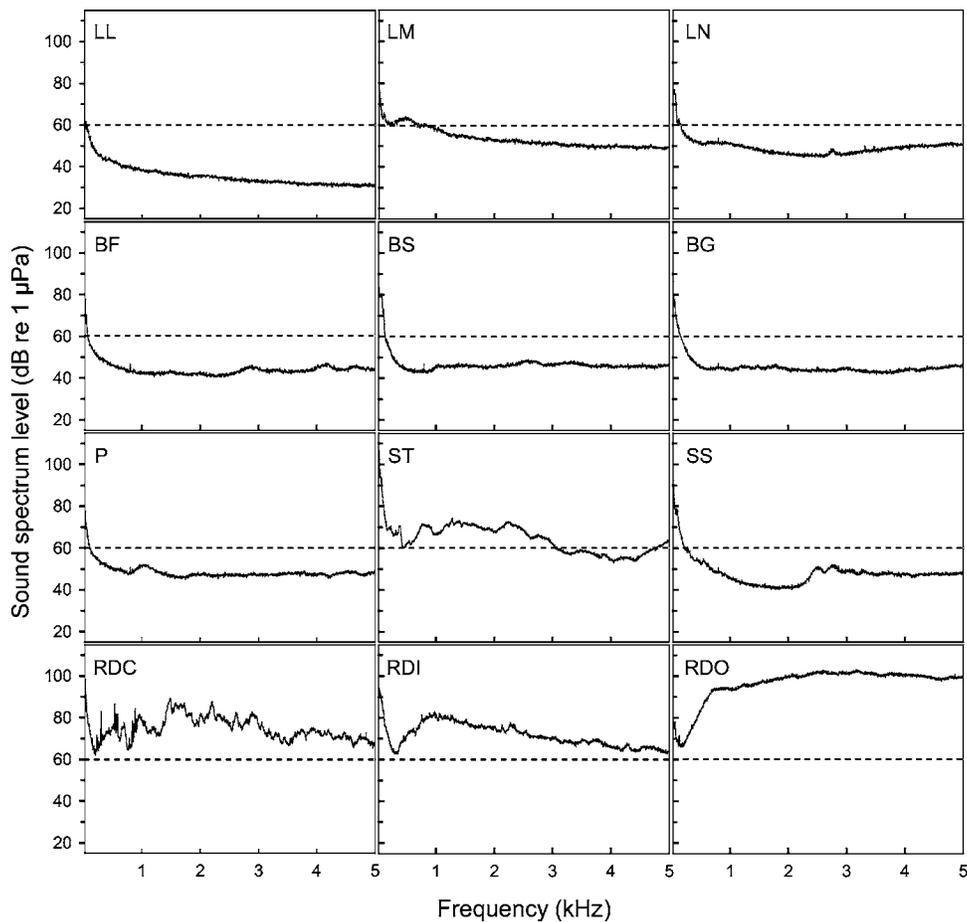


FIG. 3. Amplitude spectra of the 12 habitats. For abbreviations see Fig. 1. Frequency range 20 Hz to 5 kHz, bandwidth 1 Hz, overlap 50%, window: Blackman-Harris.

IV. DISCUSSION

A. Habitat noise levels

In the past decades, interest in the underwater ambient noise in different habitats (mainly in the marine environment) has grown. The diverse studies have applied different methods and measures of noise levels. Therefore, in order to avoid confusion, a short overview of the different values employed is given. The term “overall noise level” usually

refers to broad band (i.e., covering the whole frequency range) root mean square SPLs—rms SPL values—(Richardson *et al.*, 1995). These levels are higher than the spectrum levels, which only render the energy content at particular frequencies or frequency bands. When describing the spectral composition, the given noise levels were either measured in frequency bands of the sound (e.g., 1/3 octave, octave) and expressed as pressure density spectra (unit: dB re

TABLE III. Cross correlation coefficients between the different habitat noises and combined with the corresponding masking noise reported in Amoser and Ladich (2005). For abbreviations see Fig. 1. BW=Backwater noise (in this case not identical to any of the backwater noises of this study). RDO, ST, LN [in italics because the identical noise was used in Amoser and Ladich (2005) and this study], BW and Lab spectra are from Amoser and Ladich (2005). Frequency range: 20 Hz–5 kHz, bandwidth: 1 Hz, 50% overlap, Blackman window. Bold values indicate strongly correlated spectra according to Townend (2002).

	LL	LM	<i>LN</i>	BF	BS	BG	P	SS	<i>ST</i>	RDC	RDI	<i>RDO</i>
LL		0.86	0.73	0.68	0.58	0.63	0.82	0.64	0.58	0.19	0.59	-0.86
LM			0.58	0.37	0.19	0.27	0.64	0.39	0.55	0.17	0.63	-0.72
<i>LN</i>				0.82	0.69	0.77	0.91	0.76	0.21	-0.11	0.27	-0.68
BF					0.83	0.89	0.82	0.85	0.20	0.07	0.12	-0.61
BS						0.93	0.74	0.75	0.28	0.16	0.26	-0.40
BG							0.80	0.80	0.24	0.09	0.21	-0.50
P								0.78	0.32	0.01	0.40	-0.76
SS									-0.02	-0.20	-0.01	-0.67
<i>ST</i>										0.63	0.86	-0.24
RDC											0.53	0.13
RDI												-0.22
BW ^a	0.86	0.65	0.89	0.88	0.80	0.84	0.91	0.83	0.39	0.09	0.39	-0.74
Lab ^a	0.96	0.88	0.75	0.67	0.52	0.59	0.83	0.66	0.50	0.12	0.52	-0.89

^aCross correlation with noise spectra from Amoser and Ladich (2005).

1 $\mu\text{Pa}^2/\text{Hz}$), or given without a correction for filter bandwidth, so-called power spectra (unit: dB re 1 μPa). Unfortunately, very often this information is lacking, complicating direct comparisons between different studies.

The overall broadband continuous equivalent habitat noise level in the current study was lowest in Lake Lunz (79 dB L_{Leq}). This Alpine lake is fed and drained by a small creek with slow current and the water exchange rate is very slow. The creek flowing through the lake (“Seebach”) did not contribute a significant amount of background noise in our recording, and its effect is probably more local. In contrast, the highest noise levels were found in the Danube River at Orth (135.3 dB L_{Leq} ; Table II), mainly due to the high current velocities (1–3 m s^{-1}) as well as to the transportation of a larger water body and of cobble or gravel in the river bed. In between these two extremes, there was a great variability of overall noise levels. Nonetheless, the study sites can be separated into two large groups based on their overall broadband noise levels: stagnant habitats with L_{Leq} levels generally below 100 dB, and fast-flowing habitats with L_{Leq} levels above 110 dB.

Interestingly, when examining the variability of instantaneous noise levels (L_{LSP}), the situation is inverse: The noise levels at the noisiest study site (Danube River at Orth) were highly conservative (only a 1 dB variation, Table II), whereas variability in quieter habitats such as Danube Island and Lake Lunz were relatively high (15 and 12 dB, respectively). One possible explanation is that noise levels in the former are at such high levels that additional noise sources barely contribute to the overall level. On the other hand, in quieter habitats even slight changes in the noise environment (e.g., swimming activities of fishes and birds, insect sounds, but also noises of anthropogenic origin) are clearly detectable and thus contribute to the overall noise level.

Whereas data are available for noise levels in the ocean, data on freshwater systems—with which our measurements could be compared—are very sparse and often limited to spectral levels. While noise spectrum levels in the ocean are generally above 100 dB re 1 μPa (Wenz, 1962), the few freshwater data point to spectrum levels mostly below 100 dB re 1 μPa and of a higher variability. Exceptions have been reported. Hawkins and Johnstone (1978) mentioned that noise spectrum levels (1 Hz bands) in the River Dee are 5–10 dB higher than in the sea (Loch Torridon, Scotland). Data on noise levels in different European and one African river showed a high variability: Boussard (1981) measured ambient noise band levels (1/3-octave bands) ranging from 80–100 dB (re 1 μPa) in the River Meuse. Crawford *et al.* (1997) reported spectrum levels of up to 70 dB (1 Hz bands) at low frequencies, with a steady fall-off to about 40 dB above 1 kHz in the background noise of a floodplain of the Niger River (Mali, Africa). Lugli and Fine (2003) observed spectral levels (1 Hz bands) ranging from 70 dB in quiet places to 100 dB in fast-flowing areas. This is very similar to our data on the Danube River: depending on whether measurements were conducted in a retained (Danube River at “Danube Island”) or a free-flowing area (Danube River at Orth), the noise spectrum levels ranged from about 60 to 100 dB (Fig. 2).

Data about noise levels in freshwater lakes, again, are very sparse. In an Italian Lake (Lake Sarzana), Bom (1969) encountered noise spectrum levels of 40–50 dB (octave bands). Nystuen (1986) measured spectral levels ranging from 40–60 dB (1 Hz bands) in Lake Clinton, IL. Amoser *et al.* (2004) observed higher spectral noise levels (1 Hz bands) in an Austrian Alpine lake (Lake Traunsee): about 80 dB at low frequencies and about 60 dB above 5 kHz. This is likely due to the Traun stream, which flows through that lake and contributes to these high levels. Our current data from three other lakes suggest that spectrum levels are below 65 dB at frequencies above 100 Hz and below 50 dB (or even below 35 dB in the case of Lake Lunz) above 5 kHz (Fig. 2).

In general, noise levels in freshwater habitats apparently depend primarily on the hydrology (abiotic sources), most notably the volume and speed of the water flow with cavitations and sediment transportation, whereas biotic sources (such as water insects) can only significantly contribute to the overall noise levels in stagnant or slowly flowing habitats with otherwise low noise levels.

B. Habitat noise spectra

Knowledge of sound spectra composition and the noise sources in specific frequency regions is also better explored in the marine environment. Wenz (1962) and Urick (1983) reported that the ambient noise in the ocean contains high amounts of energy in the low frequency regions (up to several hundred hertz), followed by a rapid decline with increasing frequency. Different noise sources contributed in the former study to different parts of the noise spectrum, e.g., oceanic traffic noise (i.e., the noise from distant shipping) seems to be the characteristic source for 10 Hz to 1 kHz, whereas wind-dependent noise (from spray and bubbles) contributes more to higher frequencies (100 Hz to 10 kHz). Biological noise has been observed at all frequencies from as low as 10 Hz to as high as 10 kHz.

Again, for freshwater habitats, no such general data are available and only a few studies have described the spectral profiles of ambient noise. Rivers commonly have high amounts of energy at low frequencies, sometimes followed by a “noise window” of relatively low noise levels in the 100–300 Hz region (Lugli and Fine, 2003) and a more or less steep rise of energy to about 1–2 kHz. The subsequent gradual decline with increasing frequency is also supported by our data. The Schwarza stream, however, differed by exhibiting a wider noise window (200–2000 Hz). Crawford *et al.* (1997) reported an acoustic window in the noise of the Niger River (Mali, Africa) in the 200–3000 Hz region, followed by high amounts of energies above 4 kHz, most likely of biotic origin (aquatic insects stridulating underwater)—a feature that was not observed in the present study. Apparently, the noise spectra of fast-flowing waters such as the Danube River in Austria, in contrast to the slowly flowing Niger River, are dominated by the water current, including transport of sediment and cavitation. This yields a considerable amount of energy in the high frequency range. Differences between flowing waters could mainly be attributed to differences in current velocity and type of bottom substrate.

Bom (1969) and Nystuen (1986) described very similar noise curves for lakes (Lake Sarzana, Italy, and Lake Clinton, IL., respectively), with high amounts of energy in low frequencies, followed by a rapid decline to higher frequencies and a more gradual decline above 10 kHz. We also observed the highest levels in the low-frequency region, followed by a fast decline, but only up to 1 kHz. Thereafter, the noise spectra remained relatively stable with only a gradual decline toward higher frequencies (Fig. 2). Bom (1969) and Nystuen (1986) also reported that these spectra depended highly on the weather conditions, especially rain. As we tried to measure under considerably good weather conditions, this can only be speculated for our data, but we expect the noise levels in Lake Neusiedl to be rather susceptible for wind-related noise due to its shallow water depth and large surface area.

The 6 to 12 kHz region of higher energy observed in two of the backwaters was due to aquatic insects. Aiken (1982) described spontaneous calls of a waterboatman (*Palmacorixa nana*, Corixidae), with dominant frequencies ranging from 5 to 8 kHz and Crawford *et al.* (1997) described for the Niger River that insect sounds considerably added to the noise floor above 4 kHz.

C. Effects of ambient noise on sound detection in fishes

While most studies on fish hearing have been performed under relatively quiet lab conditions, field studies in the sea (Loch Torridon, Scotland) showed that the hearing thresholds of four gadiform species (haddock *Melanogrammus aeglefinus*, pollack *Pollachius pollachius*, ling *Molva molva*, and cod *Gadus morhua*) were masked by the ambient noise (Champman, 1973; Champman and Hawkins, 1973). Several lab experiments (i.e., Fay, 1974; Amoser and Ladich, 2005; Wysocki and Ladich, 2005; Scholz and Ladich, 2006) have shown that the masking effect depends not only on level and type of noise but also on the overall hearing sensitivity of a given fish species.

In order to estimate the effect of the ambient noise encountered in the different habitats of this study, we correlated their amplitude spectra with those of habitat noise types analyzed by Amoser and Ladich (2005), whose effects on hearing are already known (Table III) with the assumption that highly correlated noise spectra in combination with comparable noise levels should have similar effects on hearing thresholds. Accordingly, we conclude that hearing thresholds measured under quiet lab conditions will only be reached in the quietest habitats such as Lake Lunz in fishes with enhanced hearing sensitivities (usually referred to as “hearing specialists,” i.e., carps, minnows, catfishes) and that they will be moderately masked (by not more than 12 dB in their best hearing range) in the other stagnant habitats (lakes, backwaters, and pond). In contrast, they would be masked by up to 50 dB in the free-flowing areas of the Danube River, by 32 dB in creeks such as the Triesting, and by roughly 20 dB in slower-flowing parts of the Danube River such as in the Danube Channel and at the Danube Island. It is difficult to estimate auditory sensitivities in other creeks such as the Schwarza because its sound composition differed consider-

ably from the Triesting stream, but the prevailing noise levels indicate that cyprinids are probably also significantly masked in this habitat. Perciforms (many prefer flowing habitats) would barely be masked in creeks (by maximally 9 dB) and even in the free-flowing Danube River at Orth (by only 13 dB).

Even though we recorded from only one site per habitat and there is certainly a variation within each habitat with regard to absolute levels and spectral composition in dependence on recording site and depth, season, or weather conditions, it is possible to draw the following general conclusions: (1) Absolute SPLs are clearly different between stagnant and fast-flowing habitats and (2) sound spectra from randomly selected sites per habitat are clearly correlated between similar habitat types while barely so between habitats with different limnological characteristics. Based on the observed differences in ambient noise level and composition, we conclude that improved absolute hearing sensitivity—as has been evolved in all cyprinids and catfishes by the development of an accessory peripheral auditory structure (the Weberian apparatus)—only represents a significant advantage compared to hearing nonspecialists (e.g., most perciforms) in quiet, standing waters. This advantage is limited in fast-flowing waters due to the high masking effects of the ambient noise.

One solution for optimizing intraspecific communication in a loud environment is to use acoustic “niches” which has been analyzed in three freshwater species living in quite different habitats. The African mormyrid *Pollimyrus isidori* in the Niger River as well as the European gobies *Padogobius martensii* and *Gobius nigricans* in the Italian Rivers Serchio and Stirone emit sounds with peak frequencies falling in the low frequency band of low ambient noise levels (“noise window”) (Crawford *et al.*, 1997; Lugli and Fine, 2003). Our study confirmed that variable noise windows—regions of lower spectral energy in the low frequency range—seem to be a common feature in fast-flowing habitats, providing an acoustic niche for interception or communication. The extent to which such niches are utilized for intraspecific communication in the habitats analyzed in the present study is unknown. Three species from unrelated taxa are known to vocalize in these habitats: The marmoreal goby *Proterorhinus marmoratus* (Gobiidae; Ladich and Kratochvil, 1989), the sculpin *Cottus gobio* (Cottidae; Ladich, 1989), and the gudgeon *Gobio gobio* (Cyprinidae; Ladich, 1988). While the goby inhabits stagnant waters such as Danube River backwaters, the cyprinid and especially the sculpin prefer flowing waters such as the Triesting stream. The hearing specialist *G. gobio* will be masked in running waters, which is unlikely the case in the hearing generalist *C. gobio*.

In summary, noise levels as well as spectral composition are highly diverse in the various freshwater habitat types. Water currents, and the accompanying sediment transportation, are apparently the main cause of elevated noise levels in fast-flowing water systems; these specific hydrological and geological factors are probably also responsible for the relatively high variation of the spectral components of the habitat noise. In contrast, the sound spectra of stagnant water bodies are much more similar to each other, simplifying es-

timates of potential auditory sensitivity of autochthonous fish based on comparisons with previous studies. These data show that the environment significantly constrains the efficiency of a sensory system such as the auditory system, with enhanced auditory abilities presenting an advantage only in stagnant habitats with low noise levels. This provides additional evidence for the evolution of enhanced hearing capabilities in quiet freshwater habitats, as has been hypothesized in earlier studies (Schellart and Popper, 1992; Amoser and Ladich, 2005; Ladich and Popper, 2004).

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- Aiken, R. B. (1982). "Sound production and mating in a waterboatman, *Palmacorixa nana* (Heteroptera: Corixidae)," *Anim. Behav.* **30**, 54–61.
- Amoser, S., and Ladich, F. (2005). "Are hearing sensitivities of freshwater fish adapted to the ambient noise in their habitats?," *J. Exp. Biol.* **208**, 3533–3542.
- 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.
- 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," *Proceedings of the second British Freshwater Fisheries Conference*, pp. 188–200.
- Bradbury, J. W., and Vehrencamp, S. L. (1998). *Principles of Animal Communication* (Sinauer, Sunderland, MA).
- Cato, D. H. (1976). "Ambient sea noise in waters near Australia," *J. Acoust. Soc. Am.* **60**, 320–328.
- Chapman, C. J. (1973). "Field studies of hearing in teleost fishes," *Helgoländer wissenschaftliche Meeresuntersuchungen* **24**, 371–390.
- 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.
- 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.
- Egner, S. A., and Mann, D. A. (2005). "Auditory sensitivity of sergeant major damselfish *Abudefduf saxatilis* from post-settlement juvenile to adult," *Mar. Ecol.: Prog. Ser.* **285**, 213–222.
- Fay, R. R. (1974). "Masking of tones by noise for the goldfish," *J. Comp. Physiol. Psychol.* **87**, 708–716.
- Fine, M. L., and Lenhardt, M. L. (1983). "Shallow water propagation of the toadfish mating call," *Comp. Biochem. Physiol. A* **76**, 225–231.
- Fletcher, H. (1940). "Auditory patterns," *Rev. Mod. Phys.* **12**, 47–65.
- Gerald, J. W. (1971). "Sound production in six species of sunfish (Centrarchidae)," *Evolution* (Lawrence, Kans.) **25**, 75–87.
- Hawkins, A. D., and Johnstone, A. D. F. (1978). "The hearing of the Atlantic Salmon, *Salmon 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*, edited by B. Lewis (Academic, London), pp. 347–405.
- ISO 1996 (2003). "Acoustics: Description, measurement and assessment of environmental noise," International Organization for Standardization.
- 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. (1989). "Sound production by the river bullhead *Cottus gobio* L. (Cottidae, Teleostei)," *J. Fish Biol.* **35**, 531–538.
- Ladich, F., and Bass, A. H. (2003). "Underwater sound generation and acoustic reception in fishes with some notes on frogs," in *Sensory Processing in Aquatic Environments*, edited by S. P. Collin and N. J. Marshall (Springer, New York), pp. 173–193.
- Ladich, F., and Kratochvil, H. (1989). "Sound production by the marmoreale goby, *Protherorhinus marmoratus* (Pallas) (Gobiidae, Teleostei)," *Zoologische Jahrbücher. Abteilung für allgemeine Zoologie und Physiologie der Tiere* **93**, 501–504.
- Ladich, F., and Popper, A. N. (2004). "Parallel evolution in fish hearing organs," in *Evolution of the Vertebrate Auditory System*, edited by G. A. Manley, A. N. Popper, and R. R. Fay (Springer, New York), pp. 95–127.
- 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. (2006). "Propagation of fish sounds," in *Communication in Fishes*, edited by F. Ladich, S. P. Collin, P. Moller, and B. G. Kapoor, Vol. 1 (Science Publishers, Enfield, NH), pp. 107–120.
- 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.
- McDonald, M. A., Hildebrand, J. A., and Wiggins, S. M. (2006). "Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California," *J. Acoust. Soc. Am.* **120**, 171–178.
- Nystuen, J. A. (1986). "Rainfall measurements using underwater ambient noise," *J. Acoust. Soc. Am.* **79**, 972–981.
- Richardson, W. J., Greene, C. R., Malme, C. J., and Thomson, D. H. (1995). *Marine Mammals and Noise* (Academic, San Diego).
- 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.
- 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*, edited by D. E. Webster, R. R. Fay, and A. N. Popper (Springer, New York), pp. 295–322.
- Scholz, K., and Ladich, F. (2006). "Sound production, hearing and possible interception under ambient noise conditions in the topmouth minnow *Pseudorasbora parva*," *J. Fish Biol.* **69**, 692–906.
- Tavolga, W. N. (1967). "Masked auditory thresholds in teleost fishes," in *Marine Bio-Acoustics*, edited by W. N. Tavolga (Pergamon, Oxford, UK), pp. 233–245.
- 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.
- Townend, J. (2002). *Practical statistics for environmental and biological scientists* (Wiley, Chichester, UK), pp. 132–134.
- Urick, R. J. (1983). "The noise background of the sea: ambient noise level," in *Principles of Underwater Sound*, edited by R. J. Urick (Peninsula, Los Altos, CA), pp. 202–236.
- Wenz, G. M. (1962). "Acoustic ambient noise in the ocean: spectra and sources," *J. Acoust. Soc. Am.* **34**, 1936–1956.
- Wood, J. D., McCowan, B., Langbauer, W. R., Jr., Viljoen, J. J., and Hart, L. A. (2005). "Classification of African elephant *Loxodonta africana* rumbles using acoustic parameters and cluster analysis," *Bioacoustics* **15**, 143–161.
- Wysocki, L. E., and Ladich, F. (2005). "Hearing in fishes under noise conditions," *J. Assoc. Res. Otolaryngol.* **6**, 28–36.
- Yamazaki, Y., Haramoto, S., and Fukasawa, T. (2006). "Habitat uses of freshwater fishes on the scale of reach system provided in small streams," *Environmental Biology of Fishes* **75**, 333–341.