Journal of Fish Biology (2006) **69,** 892–906
doi:10.1111/j.1095-8649.2006.01168.x, available online at http://www.blackwell-synergy.com

Sound production, hearing and possible interception under ambient noise conditions in the topmouth minnow *Pseudorasbora parva*

K. Scholz and F. Ladich*

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

(Received 26 August 2005, Accepted 18 April 2006)

Sounds were produced by the topmouth minnow *Pseudorasbora parva*, a common Eurasian cyprinid, during feeding but not during intraspecific interactions. Feeding sounds were short broadband pulses with main energies between 100 and 800 Hz. They varied in their characteristics (number of single sounds per feeding sequence, sound duration and period, and sound pressure level) depending on the food type (chironomid larvae, *Tubifex* worms and flake food). The loudest sounds were emitted when food was taken up at the water surface, most probably reflecting 'suctorial' feeding. Auditory sensitivities were determined between 100 and 4000 Hz utilizing the auditory evoked potentials recording technique. Under laboratory conditions and in the presence of natural ambient noise recorded in Lake Neusiedl in eastern Austria, best hearing sensitivities were between 300 and 800 Hz (57 dB re 1 μPa *v.* 72 dB in the presence of ambient noise). Threshold-to-noise ratios were positively correlated to the sound frequency. The correlation between sound spectra and auditory thresholds revealed that *P. parva* can detect conspecific sounds up to 40 cm distance under ambient noise conditions. Thus, feeding sounds could serve as an auditory cue for the presence of food during foraging.

Key words: ambient noise; auditory evoked potentials; feeding sounds; masking; sound interception.

INTRODUCTION

The topmouth minnow *Pseudorasbora parva* (Temminck & Schlegel) is a small Eurasian cyprinid, which was introduced from East Asia to Romania and U.S.S.R. in the early 1960s (Bănărescu, 1999) and soon thereafter to other parts of Europe together with the herbivorous grass carp *Ctenopharyngodon idella* (Valenciennes). It then spread to many freshwater habitats all over Central Europe (Bianco, 1988; Ahnelt, 1989). *Pseudorasbora parva* has been reported to produce sounds (Arnold, 1985, 1990), but so far no efforts have been made to investigate the context and characteristics of these sounds and their detectability by conspecifics.

---

*Author to whom correspondence should be addressed. Tel.: + 43 1 4277 54227; fax: + 43 1 4277 9544; email: friedrich.ladich@univie.ac.at

Underwater sound plays an important role for fishes and other aquatic vertebrates because it allows them to acoustically interpret their surroundings and is fundamental for communication. Since sound spreads about five times faster in water and is detectable over longer distances than in air, whereas sight is often restricted in aquatic environments, it is a very efficient carrier of information. Many teleosts produce sounds in various behavioural contexts. For example, sound production in fishes has been observed during agonistic encounters (Myrberg, 1981; Ladich, 1997; Ladich & Myrberg, 2006) or courtship and spawning (Myrberg, 1981; Myrberg & Lugli, 2006).

In these contexts, sounds are emitted by the fishes in order to function as a signal; they result in a change in the behaviour of a receiver, a feature which characterizes communication (Myrberg, 1981; Bradbury & Vehrencamp, 1998).

The acoustic sense is not only important to communicate, but is no doubt also relevant to detect sounds produced unintentionally by conspecifics as well as by predators and potential prey. This action has been termed sound interception or eavesdropping (Myrberg, 1981; Bradbury & Vehrencamp, 1998; Peake, 2005), which means that information sent by one individual reaches another individual for whom it was not intended, but who may reap some benefit. As finding food is a key priority of every individual, it would be advantageous to detect feeding sounds emitted by other fishes because they might be an important cue during foraging through local enhancement (Day *et al.*, 2001).

Sounds produced during feeding have been investigated in several species. Stepanek (1968) reported on the feeding sounds of carp *Cyprinus carpio* L. and Eurasian minnows *Phoxinus phoxinus* (L.), Phillips (1989) investigated those of rainbow trout *Oncorhynchus mykiss* (Walbaum) and Colson *et al.* (1998) examined the clicking sounds produced during feeding by seahorses *Hippocampus* spp. Lagardère & Mallekh (2000) investigated sounds during feeding in turbot *Scophthalmus maximus* (L.), Lobel (2001) described a food grinding sound of the cichlid *Tramitichromis cf. intermedius,* (Trewavas), and Lagardère *et al.* (2004) compared feeding sounds of brown trout *Salmo trutta* L., rainbow trout and turbot.

Any consideration of acoustic communication and interception in animals must bear in mind that every signal or sound has to be detected in the presence of various ambient noise. Such noise is unavoidable in a natural environment and is composed of sounds emanating from different sources. In an aquatic environment, fishes are exposed to abiotic and biotic noise caused by currents, surf, breaking waves, rain, wind or aquatic animals (*e.g.* underwater insects, fishes and frogs) as well as anthropogenic noise. This ambient noise can impair the detection of a relevant signal or sound, a phenomenon called masking: the hearing of one sound is made more difficult in the presence of another one. Masking results in an upward shift of the hearing threshold, as has been demonstrated in several fish species (Buerkle, 1968; Fay, 1974; Amoser & Ladich, 2005; Wysocki & Ladich, 2005). Sound that can be heard by a fish under quiet laboratory conditions is not necessarily detectable under ambient noise conditions. Ambient noise of different freshwater habitats varies in its spectral characteristics and overall sound pressure levels (SPLs) (Lugli *et al.*, 2003; Amoser & Ladich, 2005). The louder the ambient noise, the more difficult it is for a fish to detect a specific sound.

Besides the acoustical characteristics of the habitat, detectability of sounds depends on the hearing ability of the fish. Fishes possess quite diverse hearing capacities. Hearing non-specialists (generalists) can detect low frequency sounds (<1 kHz) at relatively high sound intensities, whereas hearing specialists have evolved a variety of accessory hearing structures to enhance their ability to detect low intensity sounds in a broader frequency range (Hawkins & Myrberg, 1983; Ladich & Popper, 2004). Minnows such as *P. parva* are otophysines, a group of specialists in which a chain of Weberian ossicles connect the swimbladder to the inner ear and thus improve hearing ability (Ladich & Popper, 2004). Wysocki & Ladich (2005) and Amoser & Ladich (2005) demonstrated that the hearing ability of specialists is affected more by noise than that of non-specialists. Therefore, the absolute hearing threshold is less important than the ability of an individual to detect a relevant signal against background noise.

This study investigated the sound characteristics and the behavioural contexts (*e.g.* social interactions and foraging) in which *P. parva* produces sounds. For this purpose, sounds were recorded in agonistic contexts and during uptake of different food items. In order to analyse a possible signal function, whether these sounds are detectable under natural ambient noise conditions was examined. Auditory sensitivity was measured under quiet laboratory conditions as well as in the presence of noise from a habitat in which these fish commonly occur. Masked hearing curves were then correlated to sound spectra to analyse the detectability of sounds. Additionally, they were played back to the fish to investigate whether fish intercept sounds.

MATERIALS AND METHODS

ANIMALS

Eighteen topmouth minnows (2·09–4·78 g body mass and 53–72·5 mm standard length, L_S) were obtained from a local pet supplier. They were kept in glass aquaria (70 × 50 × 40 cm) whose floors were covered with sand and which were equipped with several underwater plants and half flower pots as hiding places. The water was filtered by external filters; the water temperature ranged from 19 to 23° C. The fish were kept at a 12L:12D cycle and were each fed 0·05–0·1 g of commercially prepared food flakes (Tetramin®), live *Tubifex* sp. or live red chironomid larvae (bloodworms) five times a week. It was not possible to sex fish due to a lack of sexual dimorphism. Auditory 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).

SOUND RECORDINGS

All experiments were performed in a test tank (50 × 27·5 × 30 cm, water depth 20 cm) whose bottom was covered with sand. The walls of the aquarium were lined on the inside, except for the front glass, with air-filled packing wrap in order to reduce resonances and reflections. The water temperature was maintained at 22·0° C, range ±1·5° C. The sounds and behaviour were recorded on HiFi S-VHS video-tapes using a hydrophone (Brüel & Kjær 8106, sensitivity −174 dB re 1 V per μPa) positioned near the centre of the aquarium and a video camera (Sony CCD-VX1E) positioned behind a curtain. Both the hydrophone and the video camera were connected to a HiFi S-VHS video cassette recorder (JVC HRD 4700 EG), so that HiFi audio and S-video signals were both stored synchronously on the tapes. The hydrophone was fed by a microphone power supply (Brüel & Kjær 2804).

Intraspecific interactions as well as feeding behaviour were investigated. To determine whether sounds were produced in an agonistic context, the test tank was separated by a non-transparent plastic sheet. One fish was put in each half and left there for at least 3 h to habituate. Then the separating plate was removed and the behaviour recorded for 30 min. Thirteen fish were paired randomly in 20 agonistic experiments.

To investigate foraging behaviour and to record feeding sounds, 18 fish were consecutively fed commercially prepared flake food (Tetramin®; diameter 3–10 mm), live red chironomid larvae (bloodworms; 8–15 mm long and diameter 0·7–1·0 mm) and live *Tubifex* sp. worms (5–14 mm long and diameter 0·5–0·7 mm) in random order. The following food type was given 1 min after the previous food was entirely eaten: *c.* 0·05–0·1 g of flakes, worms and larvae were fed per individual. Flake food was usually taken up at the water surface, whereas live food was consumed under water. The recordings lasted as long as the fish fed (10–45 min).

SOUND ANALYSIS

The recorded sounds were analysed using S_TOOLS-STx 2.17, a sound analysing software developed by the Acoustics Research Institute (Austrian Academy of Sciences, Vienna), with a sampling rate of 44·1 kHz. The number of sounds per feeding sequence, the sound duration, sound period (duration from the beginning of a sound to the beginning of the following sound) as well as dominant frequencies were determined. If a sound consisted of single pulses, the number of pulses and pulse periods were registered.

SOUND PRESSURE LEVEL MEASUREMENTS

The SPLs (RMS Fast, linear weighting) were measured in parallel with the sound recordings using a second hydrophone (Brüel & Kjær 8101; −184 dB re 1 V per μPa) and a microphone power supply (Brüel & Kjær 2804) connected to a sound level meter (Brüel & Kjær Mediator 2238). The hydrophone was placed 5 cm apart from the first one. Because of the varying distances of the feeding fish to the hydrophone, the test tank was divided into 32 sectors using a grid applied to the front glass of the aquarium (16 grids with a size of 6 × 5 cm, each divided in a front and a back sector), and the sector in which a sound was produced was noted. In order to compensate for different distances, one typical fish sound was played back at a constant SPL using a small loudspeaker (Fuji 7G06, 8 Ohm, 0·8 W) in each of the 32 sectors and the SPL was noted. The relative SPL difference between the sector nearest the hydrophone (10 cm distance) and the sectors where the fish fed was calculated and added to the SPL values measured while fish emitted sounds. Thus, a distance-independent absolute SPL value could be determined for each sound emission.

Absolute sound power spectra levels for a distance of *c.* 10 cm were calculated according to the methods described in Amoser *et al.* (2004) and Wysocki & Ladich (2005). It was not possible to determine SPLs for the chewing sounds because of their low intensity.

PLAYBACKS

In order to determine whether the fish intercept sounds, fish sounds and control sounds were played back to 18 individuals and the behaviour recorded. Before the experiments, the test tank was divided by a non-transparent black plastic foil. An underwater speaker (Fuji 7G06, 8 Ohm, 0·8 W) was placed in the centre of one aquarium partition and the fish in the other so that the fish could not see the speaker (sound source). A typical flake food foraging sound was played back at 117 dB re 1 μPa according to previous SPL measurements. Controls consisted of white noise of similar duration (500 ms) played back at the same SPL. The playbacks consisted of 10 min of silence, 10 test sounds (feeding sounds or white noise) with 5 s intervals between each, and followed again by 10 min of silence. The location of the test subject was determined using a grid of 16 sectors (grid size 6 × 5 cm) applied to the front of the aquarium. The mean distance to the separating plate and to the floor as well as the mean activity (by counting how many of the fields the fish passed in 5 s) were calculated. The position of the test subject was noted every 30 s for the whole test period. One minute before, during and after the playback of the sounds, the position was noted every 5 s.

AUDITORY SENSITIVITY MEASUREMENTS

The auditory sensitivity was measured using the auditory evoked potential (AEP) recording technique. The protocol followed that of Kenyon *et al.* (1998) with modifications of Wysocki & Ladich (2005).

In order to immobilize fish and to minimize myogenic movements during the experiments *c.* 1 μg g^{-1} Flaxedil (gallamine triethiodide; Sigma) was injected intramuscularly. The test subjects were positioned in the centre of a plastic bowl (37 cm diameter, 8 cm water depth, 2 cm layer of fine sand) lined on the inside with acoustically absorbent material (air-filled packing wrap) in order to reduce sound reflections (Fig. 1). Fish 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. The portion of the head above the water surface was covered by a small piece of Kimwipes tissue paper to keep it moist and to ensure proper contact during experiments. A respiration pipette was inserted into each subject's mouth. Respiration was achieved through a simple temperature-controlled (24° C, range ±1° C), gravity-fed water circulation

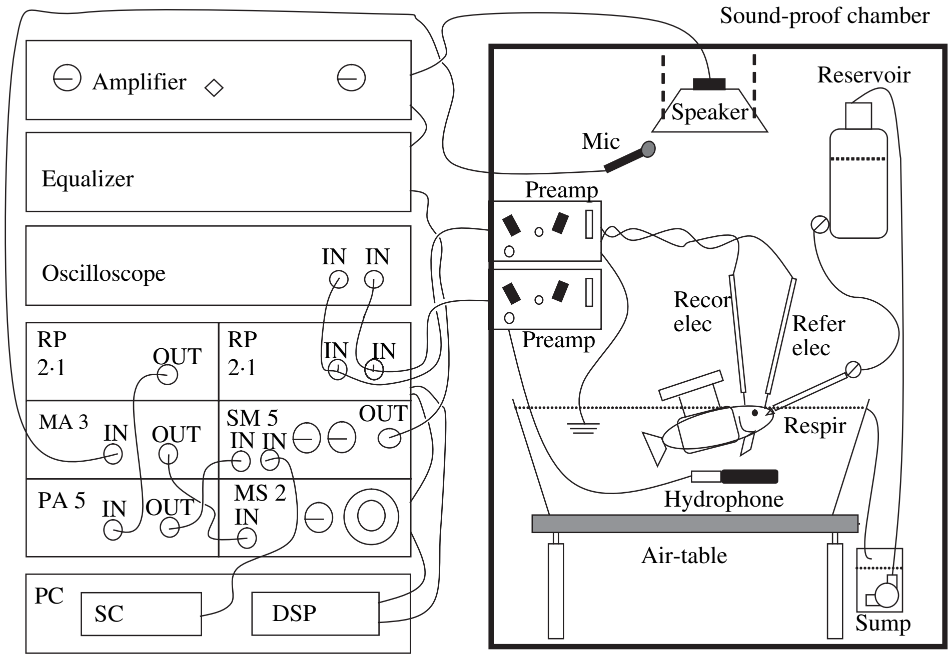

FIG. 1. AEP recording and ambient noise presentation setup modified after Kenyon *et al.* (1998). DSP, digital signal processor; MA 3, microphone amplifier; mic, microphone; MS 2, microphone speaker; PA 5, programmable attenuator; PC, personal computer; preamp, preamplifier; recor elec, recording electrode; refer elec, reference electrode; respir, respiration pipette; RP 2.1, realtime processor; SC, sound card; SM 5, signal mixer.

system. The AEPs were recorded using silver wire electrodes (0·25 mm diameter) pressed firmly against the subject's skin. 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, 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 63-540), 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 × 3·2 × 2·4 m).

Both sound stimuli presentation and AEP waveform recording were accomplished using a Tucker-Davis Technologies (Gainesville, FL, U.S.A.) 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 waveforms were generated using TDT SigGen RP and fed through a power amplifier (Alesis RA 300). A dual-cone speaker (Tannoy System 600, frequency response 50 Hz to 15 kHz ± 3 dB), mounted 1 m above test subjects in the air, was used to present the stimuli during testing.

Sound stimuli consisted of tone bursts presented at a repetition rate of 21 s^{-1}. Hearing thresholds were determined at frequencies of 100, 300, 500, 800, 1000, 2000, 3000 and 4000 Hz presented in random order under normal laboratory conditions. The stimuli were presented at opposite polarities (180° phase shifted) and the corresponding AEPs were averaged by the BioSig RP software in order to eliminate stimulus artefacts. The SPLs of tone-burst stimuli were 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, which was determined by overlaying replicate traces, was considered the threshold. A hydrophone (Brüel & Kjær 8101) was placed near the right side of each fish (1 cm apart) to determine absolute SPLs under water close to the subjects.

In order to measure hearing threshold under natural noise conditions, tone bursts were played back simultaneously with ambient noise recorded in Lake Neusiedl, a typical habitat of *P. parva* in eastern Austria (Wolfram-Wais *et al.*, 1999). Ambient noise was played back at a L-weighted (5 Hz to 20 kHz) equivalent continuous SPL (L_{Leq}) (averaged over 60 s) of 93·0 dB re 1 μPa, range ± 0·4 dB.

THRESHOLD-TO-NOISE RATIOS

Threshold-to-noise (T:N) ratios were calculated by subtracting the spectrum level of laboratory noise and ambient noise of Lake Neusiedl from the SPL of the baseline threshold and the masked hearing threshold at the same frequency.

DATA ANALYSIS

Six to 19 sounds were analysed per fish and food type. Means ± S.E. of sound characteristics (number of sounds within a sequence, sound duration, sound period, dominant frequency and SPLs) were calculated for each individual and compared by one-way ANOVA followed by a Bonferroni *post hoc* test. Behavioural data of playback experiments were compared by one-way ANOVAs followed by Bonferroni *post hoc* tests.

Hearing thresholds of the two experimental conditions were compared by two-factor ANOVA using a general linear model where one factor was masking noise and noise condition, and the other was frequency. The noise factor alone should indicate an overall influence of the ambient noise condition, and in combination with the frequency factor if different tendencies exist at different frequencies of the audiogram. To determine if threshold shifts between laboratory and ambient noise condition at each frequency were significant, paired *t*-tests were calculated. The correlation of T:N ratios and frequency was calculated by first-order functions.

Sound spectra of the laboratory noise and ambient noise of Lake Neusiedl were from Amoser & Ladich (2005).

RESULTS

DESCRIPTION OF SOUNDS

Agonistic behaviour started in 11 out of 20 staged dyadic encounters when the non-transparent plastic partition was removed. Eight out of 13 topmouth minnows were involved in aggressive behaviour, which consisted of chasing, circling and tail beating, but no sound production was observed. In contrast, numerous sounds were emitted during feeding.

All feeding sequences consisted of series of broadband sounds, which varied in their number, duration, period and SPL depending on food type. Dominant frequencies of all sounds were between 100 and 800 Hz (Fig. 2).

The food flakes stayed on the water surface, where they were consumed by the fish, while live food sank to the bottom, where it was picked up.

A flake food feeding sequence consisted of one to four feeding strike sounds (mean ± S.E.: 1·9 ± 0·2), with a mean sound duration of 43·7 ms (Fig. 3). While feeding on chironomid larvae and *Tubifex* sp. worms, the fish produced one to three feeding strike sounds during ingestion (mean ± S.E. for chironomid larvae: 1·9 ± 0·2; for *Tubifex* sp. worms: 1·6 ± 0·1), with a mean sound duration of 13·4 and 13·7 ms, respectively. In both cases, a strike sound sequence was followed after *c.* 500 ms by three to 25 food grinding (chewing) sounds (mean ± S.E. for chironomid larvae: 8·7 ± 1·2; for *Tubifex* sp. worms: 6·5 ± 1·4), with mean durations of 34 and 40·2 ms, respectively. Every chewing sound was additionally made up of one to seven single pulses (mean ± S.E. for chironomid larvae: 3·2 ± 0·2; for *Tubifex* sp. worms: 2·6 ± 0·3) with mean pulse periods between 8 and 20 ms (mean ± S.E. for chironomid larvae: 12·6 ± 0·8; for *Tubifex* sp. worms: 16·1 ± 1·5); the single pulse duration was not definable because most of these pulses were superimposed. Food flakes were not chewed (at least not audibly) by the fish.

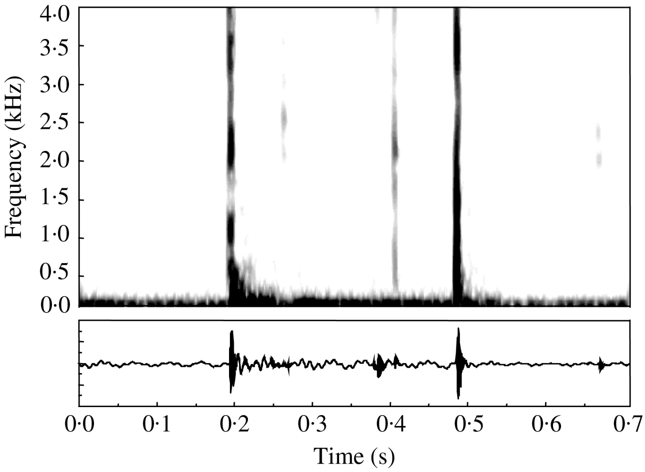

FIG. 2. Sonagram and oscillogram of two flake food feeding strike sounds produced by one fish at the water surface. Sampling rate 44·1 kHz, filter bandwidth 90 Hz, hanning window (filter type), overlap 90%.

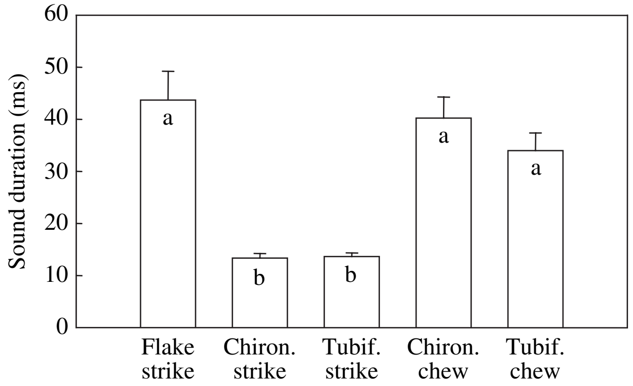

FIG. 3. Mean + S.E. duration of different types of feeding sounds. Significant differences are indicated by different lower case letters. Chiron. strike, chironomid larvae feeding strike sound; Tubif. strike, *Tubifex* sp. feeding strike sound; Chiron. chew, chironomid larvae chewing sound; Tubif. chew, *Tubifex* sp. chewing sound. Number of fish: Flake strike: 16, Chiron strike: 17, Tubif. strike: 16, Chiron. chew: 17, Tubif. chew: 15.

Chewing sounds as well as flake food strike sounds were significantly longer than live food strike sounds (one-way ANOVA, d.f. = 4, 76, $P < 0{\cdot}001$) (Fig. 3). The mean sound periods of *P. parva* feeding sounds ranged between 152·7 ms (*Tubifex* sp. strike) and 303·1 ms (flake food). There were significant differences between the feeding sound types (one-way ANOVA, d.f. = 4, 69, $P < 0{\cdot}001$) (Fig. 4).

Flake food sounds were clearly audible to human listeners at a distance of several metres and were significantly louder than the other two feeding strike sounds by *c.* 6–8 dB (one-way ANOVA, d.f. = 2, 19, $P < 0{\cdot}001$) (Fig. 5).

PLAYBACKS

During the playback of flake food feeding sounds, neither the distance of the 18 topmouth minnows to the sound source (which they could not see) or to the

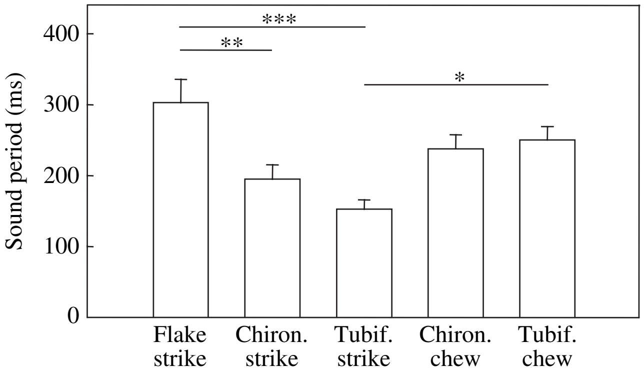

FIG. 4. Mean + S.E. periods of different types of feeding sounds (see Fig. 3). Significant differences are indicated by: *, $P < 0{\cdot}05$; **, $P < 0{\cdot}005$; ***, $P < 0{\cdot}001$ (*n* as in Fig. 3).

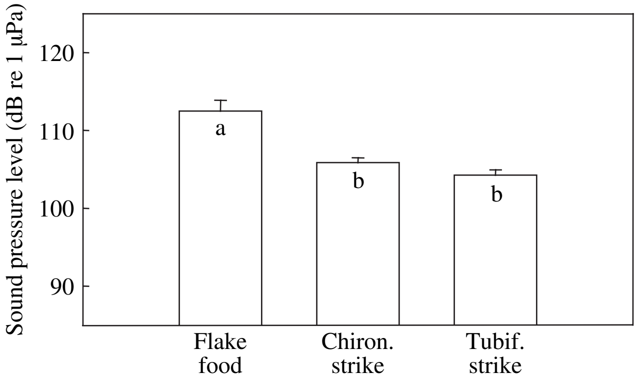

FIG. 5. Mean + S.E. sound pressure levels of different types of feeding strike sounds (see Fig. 3). Significant differences are indicated by different lower case letters. Number of fish: Flake strike: 7, Chiron. strike: 8, Tubif. strike: 7.

water surface, nor the activity, differed significantly before, during and after playback sessions (sound source: one-way ANOVAs, d.f. = 2, 45, $P > 0{\cdot}05$; water surface: d.f. = 2, 45, $P > 0{\cdot}05$; activity: d.f. = 2, 45, $P > 0{\cdot}05$). A similar result was achieved when behaviour was compared before, during and after the playback of white noise control sounds (sound source: one-way ANOVAs, d.f. = 2, 45, $P > 0{\cdot}05$; water surface: d.f. = 2, 45, $P > 0{\cdot}05$; activity: d.f. = 2, 45, $P > 0{\cdot}05$).

AUDITORY SENSITIVITY

Baseline thresholds of eight *P. parva* measured under quiet laboratory conditions showed greatest hearing sensitivity at 500 Hz (Fig. 6), with a mean hearing threshold of 57 dB re 1 μPa. In the presence of natural ambient noise

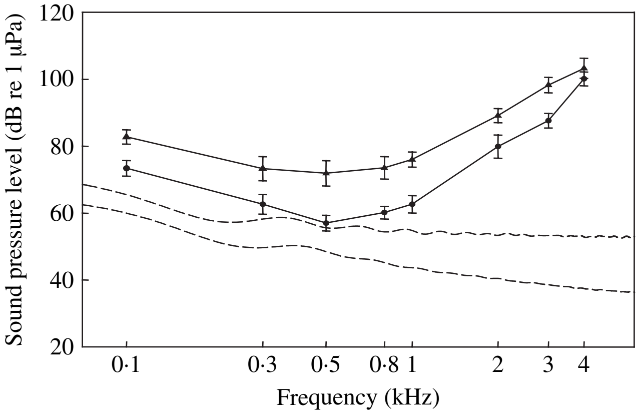

FIG. 6. Mean ±S.E. baseline (lower curve) and masked (upper curve) hearing thresholds of *P. parva*. The dashed lines show the cepstrum-smoothed power spectra of the laboratory noise (lower) and the ambient noise recorded in Lake Neusiedl (upper).

recorded at Lake Neusiedl, the mean hearing thresholds of the test subjects increased by up to 15 dB (mean hearing thresholds at 500 Hz: 71·9 dB). A two-factor ANOVA showed that the whole baseline hearing curve was significantly different from the masked one (two-factor ANOVA, d.f. = 1, 112, $P < 0{\cdot}001$) and that there was a significant interaction between played back noises and frequencies tested (d.f. = 7, 112, $P < 0{\cdot}001$). Additionally, paired *t*-tests revealed significant differences between baseline and masked thresholds at all frequencies (paired *t*-test, d.f. = 7, $P < 0{\cdot}001$ for 100, 300, 500, 800, 1000, 2000 and 3000 Hz; $P < 0{\cdot}05$ for 4000 Hz).

THRESHOLD-TO-NOISE RATIOS

The mean ± S.E. T:N ratios ranged from 3·97 ± 0·82 at 500 Hz to 64·97 ± 0·74 at 4000 Hz for the baseline thresholds and from 14·74 ± 1·28 at 300 Hz to 49·77 ± 1·06 at 4000 Hz for the masked thresholds. The T:N ratios were significantly correlated to the frequencies tested (Fig. 7).

SOUND DETECTABILITY

A correlation between the feeding sound spectra (calculated for a distance of 10 cm) and the hearing thresholds at ambient noise conditions (Fig. 8) showed that the food flake feeding sound energies were above the threshold in the frequency range between 100 and 1000 Hz, whereas the insect larvae and *Tubifex* sp. feeding were only detectable between 100 and 800 Hz and between 100 and 500 Hz, respectively (Fig. 8).

DISCUSSION

SOUNDS

The topmouth minnow produces numerous sounds while feeding, whereas no vocalization was recorded during interspecific interactions, in particular in

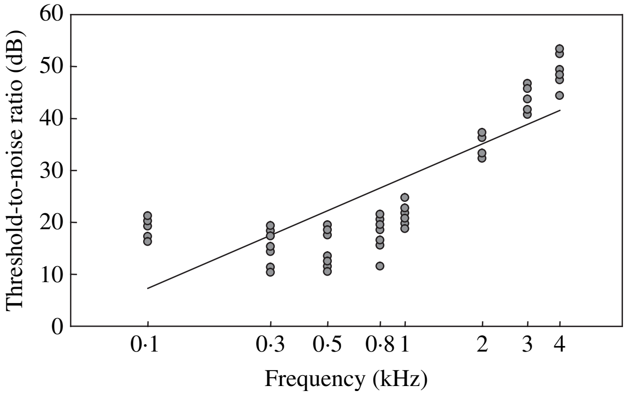

FIG. 7. Threshold-to-noise ratios for hearing thresholds under natural ambient noise conditions. The curve was fitted by $y = 21{\cdot}38x + 28{\cdot}67$ ($r = 0{\cdot}81$, $P < 0{\cdot}001$).

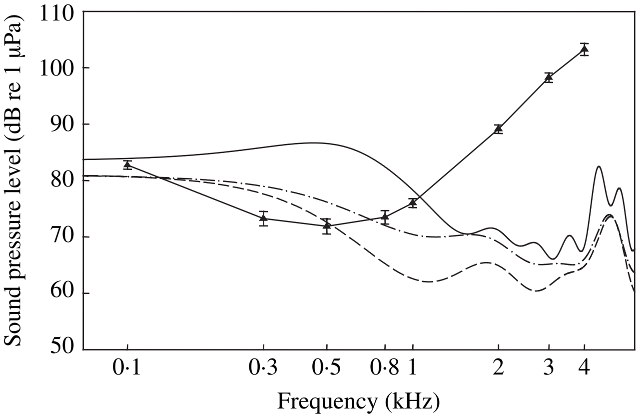

FIG. 8. Mean ± S.E. hearing thresholds (▲) under ambient noise conditions and sound spectra of flake food feeding sound (—), chironomid larvae feeding sound (-··-) and *Tubifex* sp. feeding sound (--).

agonistic contexts. The fish showed no courtship or spawning behaviour during experiments, so it remains uncertain if they produce sounds in a reproductive context.

All feeding strike sounds in this study were recorded during the initial stage of the feeding sequence. In cyprinids like *P. parva*, 'suction' feeding is the most common way of taking up prey during strikes: a negative pressure is generated in the buccal cavity by a rapid opening of the mouth and, due to the negative pressure, the food item is 'sucked' in (Jobling, 1995), which could cause the strike sound. The pulsed chewing sounds occurred after food intake during food grinding. One chewing sound matches one movement of the jaw, but the single pulses might be produced by individual teeth (Jobling, 1995).

The feeding sound types differed in certain sound characteristics such as duration, period and sound level, according to the food item and depending on the place where it was eaten. *Tubifex* sp. worms and red chironomid larvae were ingested under water and chewed, while food flakes were taken from the water surface and swallowed without audible chewing. Flake food feeding was significantly louder than all other sound types. One explanation is that, during 'suctorial' feeding at the water surface, air is ingested together with the food item, thus breaking through the surface tension. Therefore it is assumed that the typical sounds of topmouth minnow described in the literature (Arnold, 1985, 1990) were 'suctorial' feeding sounds emitted at the water surface.

For topmouth minnows, these loud clicking sounds could indicate that food items are taken up by conspecifics at the water surface. Intercepting these feeding sounds and localizing the sound source could be a major advantage for foraging fishes (local enhancement; Day *et al.*, 2001). Interception, *i.e.* the detection of sounds that disadvantage the sender (Myrberg, 1981), is a neglected acoustical phenomenon. Sound interception was probably a major selective force in the evolution of Weberian ossicles and thus in enhancing the auditory sensitivities in otophysines (Ladich, 1999, 2000; Ladich & Popper, 2004). The detection of sounds unintentionally produced by conspecifics, predators and prey is crucial even in species not known to communicate acoustically, such most cypriniforms (Ladich, 1999, 2000). A prerequisite for the evolution of Weberian ossicles would be low ambient noise levels. Indeed, Amoser & Ladich (2005) demonstrated that cyprinids can fully utilize their excellent hearing sensitivity in 'quiet' fresh water such as backwaters of rivers and lakes, but that their hearing is highly masked in certain habitats such as running waters.

Lasting *c.* 13–14 ms, strike sounds of *P. parva* when feeding on *Tubifex* sp. worms and red chironomid larvae are similar in duration to those of seahorses (Colson *et al.*, 1998), which lasted 5–20 ms, although the proposed sound-producing mechanism is different. Feeding sounds of turbot, produced when food pellets are sucked into a fish's mouth, are somewhat shorter (*c.* 5 ms; Lagardère & Mallekh, 2000).

The feeding sounds of carps are 75 ms long, with intervals of similar duration. Those of Eurasian minnows are shorter (Stepanek, 1968) and resemble, with a duration of 25 ms, feeding strike sounds of *P. parva* although the intervals are much shorter (20 ms). This, however, might reflect the different food types studied. According to Stepanek (1968), different food items are the main reason for variances in feeding sounds. Sounds made by rainbow trouts during feeding last up to one second and most of the signal energy is <8 kHz (Phillips, 1989; Lagardère *et al.*, 2004). The characteristics of food grinding sounds in *T. cf. intermedius*, with a mean duration of 8·6 ms and a mean interval of 8·2 ms (Lobel, 2001), conform to single pulses of chewing sounds in *P. parva* in the present study.

PLAYBACKS

No significant reaction to the playback of feeding sounds was observed, although some fish showed startle responses to feeding sounds or white noise or both. One explanation for the lack of a consistent reaction of all fish may be the lack of additional olfactory or visual cues, *i.e.* no sound-producing fish was in sight. Phillips (1989) reported that rainbow trout reacted to feeding sounds only when the test subjects had visual contact with their feeding conspecifics.

AUDITORY SENSITIVITY AND SOUND DETECTION

The audiograms of *P. parva* show that this species is a relatively sensitive hearing specialist. Their sensitivity is similar to those of other cyprinids (Tavolga, 1974; Ladich, 1999; Ladich & Popper, 2004; Wysocki & Ladich, 2005), with best hearing in the range of 300–800 Hz. The correlation of the feeding sound spectrum to the masked auditory thresholds shows that feeding sounds can be detected by the fish under ambient noise conditions up to a distance of 0·4 m, assuming that signal energy attenuates *c.* 6 dB with doubling distance. The Austrian Lake Neusiedl is a typical habitat of *P. parva* (Wolfram-Wais *et al.*, 1999). It has a spectrum noise level of *c.* 60 dB re 1 μPa at the best hearing sensitivity of the topmouth minnow and, being a stagnant water, is quieter than flowing fresh water (Amoser & Ladich, 2005). In noisier habitats, feeding sounds would be more difficult to detect and only possible at shorter distances. Since *P. parva* prefers stagnant and slowly flowing waters (Bănărescu, 1999), it can probably fully utilize its highly developed hearing sensitivity. The present study shows that the topmouth minnow detected lower-intensity sounds under low ambient noise levels. Therefore it is assumed that they can detect 'suctorial' feeding sounds over greater distances under lower ambient noise levels. On the other hand, detectability could be reduced in the presence of recreational activities (*e.g.* boating, surfing and swimming in Lake Neusiedl), although this is restricted to daytime hours and the warmer season. Even then, areas of anthropogenic noise pollution may be avoided by the fish. Boussard (1981) demonstrated that roach *Rutilus rutilus* (L.) and rudd *Scardinius erythrophthalmus* (L.) flee when boats approach.

The present data show that the T:N ratios are lowest in the range of the best hearing sensitivity (300–800 Hz); the regression shows that the ratios are positively correlated to the particular frequency, which matches prior findings in otophysines and perciforms (Fay, 1974; Amoser & Ladich, 2005; Wysocki & Ladich, 2005).

Pseudorasbora parva produces surface feeding sounds, which are significantly louder than in other cyprinids. These sounds may be an intraspecific signal or an unintentional cue. A possible signal function could be to drive off competitors, as Amorim & Hawkins (2000) suggested for streaked gurnard *Trigloporus lastoviza* (Bonnaterre) and Amorim *et al.* (2004) for grey gurnard *Eutrigla gurnardus* (L.). Conversely, such sounds might attract conspecifics, minimizing the risk of predation, for example, by water birds that prey on fishes (Pitcher & Parrish, 1993). If the 'suctorial'' sound production is accidental, it could also be intercepted (overheard) easily by conspecifics searching for suitable food items such as insects trapped on the water surface. The current findings lead to the conclusion that the topmouth minnow is a non-vocalizing cyprinid, which may potentially utilize its excellent hearing sensitivity in sound interception.

The authors would like to thank S. Amoser and L. E. Wysocki for providing recordings and spectra of laboratory noise as well as ambient noises of Lake Neusiedl. Furthermore, we want to thank M. Stachowitsch for professional scientific English proofreading. This study was supported by the Austrian Science Fund (FWF grants No. 15873 and 17263 to F. L.).

References

Ahnelt, H. (1989). Zum Vorkommen des asiatischen Gründlings *Pseudorasbora parva* (Pisces: Cyprinidae) in Ost-Österreich. *Österreichs Fischerei* **42,** 164–168.

Amorim, M. C. P. & Hawkins, A. D. (2000). Growling for food: acoustic emissions during competitive feeding of the streaked gurnard. *Journal of Fish Biology* **57,** 895–907. doi: 10.1006/jfbi.2000.1356

Amorim, M. C. P., Stratoudakis, Y. & Hawkins, A. D. (2004). Sound production during competitive feeding in the grey gurnard. *Journal of Fish Biology* **64,** 182–194. doi: 0.1111/j.1095-8649.2004.00443.x

Amoser, S. & Ladich, F. (2005). Are hearing sensitivities of freshwater fish adapted to the ambient noise in their habitats? *Journal of Experimental Biology* **208,** 3533–3542.

Amoser, S., Wysocki, L. E. & Ladich, F. (2004). Noise emission during the first powerboat race in an Alpine lake and potential impact on fish communities. *Journal of the Acoustical Society of America* **116,** 3789–3797.

Arnold, A. (1985). *Pseudorasbora parva* (Schlegel 1842) nun auch in der DDR! *Zeitschrift für die Binnenfischerei in der DDR* **32,** 182–183.

Arnold, A. (1990). *Eingebürgerte Fischarten*. Wittenberg Lutherstadt: A. Ziemsen Verlag.

Bănărescu, P. M. (1999). *Pseudorasbora parva* (Temminck et Schlegel 1846). In *The Freshwater Fishes of Europe*, Vol. 5, Part 1 (Bănărescu, P.M., ed.), pp. 207–224. Wiebelsheim: AULA-Verlag.

Bianco, P. G. (1988). Occurrence of the Asiatic gobionid *Pseudorasbora parva* (Temminck and Schlegel) in south-eastern Europe. *Journal of Fish Biology* **32,** 973–974.

Boussard, A. (1981). The reactions of roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) to noises produced by high speed boating. In *Proceedings of the 2nd British Freshwater Fishes Conference*, pp. 188–200. Liverpool: University of Liverpool.

Bradbury, J. W. & Vehrencamp, S. L. (1998). *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates Inc.

Buerkle, U. (1968). Relation of pure tone thresholds to background noise level in the Atlantic cod (*Gadus morhua*). *Journal of the Fisheries Research Board of Canada* **25,** 1155–1160.

Colson, D. J., Patek, S. N., Brainerd, E. L. & Lewis, S. M. (1998). Sound production during feeding in *Hippocampus* seahorses (Syngnathidae). *Environmental Biology of Fishes* **51,** 221–229.

Day, R. L., MacDonald, T., Brown, C., Laland, K. N. & Reader, S. M. (2001). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour* **62,** 917–925. doi: 10.1006/anbe.2001.1820

Fay, R. R. (1974). Masking of tones by noise for the goldfish (*Carassius auratus*). *Journal of Comparative and Physiological Psychology* **87,** 708–716.

Hawkins, A. D. & Myrberg, A. A. (1983). Hearing and sound communication under water. In *Bioacoustics, a Comparative Approach* (Lewis, B., ed.), pp. 373–378. London: Academic Press.

Jobling, M. (1995). *Environmental Biology of Fishes*. London: Chapman & Hall.

Kenyon, T. N., Ladich, F. & Yan, H. Y. (1998). A comparative study of hearing ability in fishes: the auditory brainstem response approach. *Journal of Comparative Physiology A* **182,** 307–318.

Ladich, F. (1997). Agonistic behavior and significance of sounds in vocalizing fish. *Marine and Freshwater Behaviour and Physiology* **29,** 87–108.

Ladich, F. (1999). Did auditory sensitivity and vocalization evolve independently in otophysan fishes? *Brain, Behavior and Evolution* **53,** 288–304.

Ladich, F. (2000). Acoustic communication and the evolution of hearing in fishes. *Philosophical Transactions of the Royal Society London B* **355,** 1285–1288.

Ladich, F. & Myrberg, A. A. (2006). Agonistic behaviour and acoustic communication. In *Communication in Fishes*, Vol. 1 (Ladich, F., Collin, S. P., Moller, P. & Kapoor, B. G., eds), pp. 121–148. Enfield, NH: Science Publishers.

Ladich, F. & Popper, A. N. (2004). Parallel evolution in fish hearing organs. In *Evolution of the Vertebrate Auditory System* (Manley, G. A., Popper, A. N. & Fay, R. R., eds), pp. 95–127. New York: Springer.

Lagardère, J. P. & Mallekh, R. (2000). Feeding sounds of turbot (*Scophthalmus maximus*) and their potential use in the control of food supply in aquaculture. I. Spectrum analysis of the feeding sounds. *Aquaculture* **189,** 251–258.

Lagardère, J. P., Mallekh, R. & Mariani, A. (2004). Acoustic characteristics of two feeding modes used by brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*) and turbot (*Scophthalmus maximus*). *Aquaculture* **240,** 607–614.

Lobel, P. S. (2001). Acoustic behaviour of cichlid fishes. *Journal of Aquariculture and Aquatic Sciences* **9,** 167–186.

Lugli, M., Yan, H. Y. & Fine, M. L. (2003). Acoustic communication in two freshwater gobies: the relationship between ambient noise, hearing thresholds and sound spectrum. *Journal of Comparative Physiology A* **189,** 309–320.

Myrberg, A. A. (1981). Sound communication and interception in fishes. In *Hearing and Sound Communication in Fishes* (Tavolga, W. N., Popper, A. N. & Fay, R. R., eds), pp. 395–425. New York: Springer.

Myrberg, A. A. & Lugli, M. (2006). Reproductive behavior and acoustical interactions. In *Communication in Fishes*, Vol. 1 (Ladich, F., Collin, S. P., Moller, P. & Kapoor, B. G., eds), pp. 149–176. Enfield, NH: Science Publishers.

Peake, T. M. (2005). Eavesdropping in communication networks. In *Animal Communication Networks* (McGregor, P. K., ed.), pp. 13–37. Cambridge: University Press.

Phillips, M. J. (1989). The feeding sounds of rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* **35,** 589–592.

Pitcher, T. J. & Parrish, J. K. (1993). Functions of shoaling behaviour in teleosts. In *The Behaviour of Teleost Fishes* (Pitcher, T. J., ed.), pp. 363–439. London: Chapman & Hall.

Stepanek, M. (1968). Beiträge zur Bioakustik der Binnengewässer. II. Freßgeräusche von Karpfen und Elritzen. *Archiv für Hydrobiologie* **33,** 423–430.

Tavolga, W. N. (1974). Signal/noise ratio and the critical band in fishes. *Journal of the Acoustical Society of America* **55,** 1323–1333.

Wolfram-Wais, A., Wolfram, G., Auer, B., Mikschi, E. & Hain, A. (1999). Feeding habits of two introduced fish species (*Lepomis gibbosus, Pseudorasbora parva*) in Neusiedler See (Austria) with special reference to chironomid larvae (Diptera: Chironomidae). *Hydrobiologia* **408/409,** 123–129.

Wysocki, L. E. & Ladich, F. (2005). Hearing in fishes under noise conditions. *Journal of the Association for the Research in Otolaryngology* **6,** 28–36.