COMPARATIVE ANALYSIS OF SWIMBLADDER (DRUMMING) AND PECTORAL (STRIDULATION) SOUNDS IN THREE FAMILIES OF CATFISHES

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ABSTRACT

Among teleosts, only representatives of several tropical catfish families have evolved two sonic organs: pectoral spines for stridulation and swimbladder drumming muscles. Pectoral mechanisms differ in relative size between pimelodids, mochokids and doradids, whereas swimbladder mechanisms exhibit differences in origin and insertion of extrinsic muscles. Differences in vocalization among families were investigated by comparing distress calls in air and underwater. High frequency broad-band pulsed sounds of similar duration were emitted during abduction of pectoral spines in all three families. Adduction sounds were similar to abduction signals in doradids, shorter and of lower sound pressure in mochokids, and totally lacking in pimelodids. Simultaneously or successively with pectoral sounds, low frequency harmonic drumming sounds were produced by representatives of two families. Drumming sounds were of similar intensity as stridulatory sounds in pimelodids, fainter in doradids, and not present in mochokids. Swimbladder sounds were frequency modulated and the fundamental frequency was similar in pimelodids and doradids. The ratio of stridulatory to drumming sound amplitude was higher in air than underwater in both doradids and one of the pimelodids. Also, overall duration of pectoral sounds, compared to swimbladder sounds, was longer in air than underwater in one doradid and pimelodid species. This first comparison of vocalization within one major teleost order demonstrates a wide variation in occurrence, duration, intensity and spectral content of sounds and indicates family- and species-specific as well as context- (receiver-) dependent patterns of vocalization.

Key words: catfishes, distress calls, family-typical vocalization, stridulation, drumming sounds

INTRODUCTION

Vocalization during various social interactions as aggressive behaviour or courtship is well known in fishes (Fine et al. 1977, Myrberg 1981, Ladich in press). The first contexts in which sound production was registered were probably various distress situations, e.g. when fish
were hand-held or caught. Starting with Aristotle (cited after Müller 1857), observations in earlier centuries were mostly limited to distress calls (Müller 1857, Dufossé 1874). Systematic studies on sound-producing abilities of fishes subjected animals to a variety of noxious stimuli and demonstrated that acoustic signals are widespread in teleosts (Fish et al. 1952, Fish and Mowbray 1970). Representatives of several families of catfishes possess two sonic organs (Størnes 1895). Most siluriform species possess an enhanced first pectoral fin ray with a prominent dorsal process, which fits into the bow-like groove in the pectoral girdle (Bridge and Haddon 1889, 1892, Pfeiffer and Eisenberg 1965, Gainer 1967, Schachner and Schaller 1981). Rubbing the ridged process of the pectoral spine against the roof of the bony groove causes a chirping or cracking sound. The second sound-producing apparatus consists of swimbladder drumming muscles, which, however, are absent in several families (Siluridae, Ictaluridae, Lorciariidae, Callichthyidae). Contrary to the uniform pectoral spines, swimbladder mechanisms are very diverse and a family characteristic. In pimelodids, drumming muscles originate from a transverse process of the fourth vertebra and insert ventrally on the swimbladder (Schachner and Schaller 1981, Ladich and Fine 1994). In arinoid families, air bladders are vibrated by thin bony plates, the distal ends of the transverse process of the fourth vertebrae. These distal ends are pointed in arinids (Tavolga 1962) and ovoid in 'doradoids' and are termed 'elastic spring' because of their elasticity. Muscles inserting at the elastic springs originate on the occipital bone (doradoids—Kastberger 1977), the epiotic lamina (arids—Tavolga 1962), or at the epaxial muscles (mochokids—Abu-Gideiri and Nasr 1973, Ladich and Bass 1996). Drumming muscles are furthermore found in auchenoperids (Kastberger 1978), malapterurids and some pangasidiids (Bridge and Haddon 1889). Mahajan (1963) described a dorsal spine stridulatory apparatus in Indian sisorid catfish; it consisted of a modification of the neural spines and the first intercospinous bone of the dorsal fin.

We do not know if diversity in sonic organs results in differences in vocalization and if sounds are uttered in similar contexts in these families. Abu-Gideiri and Nasr (1973) mentioned that Synodontis schall grunt in various defense and fright situations and that these fish only creak when held. Schachner and Schaller (1981) described drumming sounds during threatening behaviour in the pimelodid Rhamdia sebae and stridulatory sounds during defence behaviour. No adequate observations of vocal behaviour are known from arinids, doradids or representatives of other families. Analyzing previous studies on distress calls which are uttered when fish are caught or hand-held leads to contradictory results. Pfeiffer and Eisenberg (1965) described exclusively pectoral sounds in mochokids and doradids when recorded in air, while Kastberger (1977, 1978) additionally recorded intense drumming sounds in several doradid species underwater.

The aim of this study is to investigate diversity in vocalization between closely related families of one major teleost order and to determine whether differences can be related to morphology of sonic organs. For this purpose distress calls of similar-sized neotropical pimelodid and doradid and African mochokid species were recorded under standardized hand-held conditions. While neotropical pimelodids are regarded as a basal catfish group, neotropical doradids and African mochokids are, despite their geographical separation, closely related (suborder 'doradoids'—Lundberg 1993). Because distress calls are produced in air and water, it was furthermore investigated if a medium- and subsequently receiver- (predator-) dependent influence on sound production exists. Sounds were therefore recorded in both media and a comparative analysis performed.

MATERIALS AND METHODS

Ten to 16 individuals of two species of pimelodid, mochokid and doradid catfishes were investigated (Table 1). The sex of the fish was not determined because animals were mostly immature, and sexing was not possible without sacrificing them.

The fish were kept in 100 to 200 l community tanks which were filtered, planted, and equipped with hiding places. Temperature was kept at 27°C and a 12 h light-dark cycle was maintained.

Fish were measured and weighed after sounds were recorded.

The length of one pectoral spine was determined from the shoulder girdle to its tip. The ratio of the spine length to total body length was calculated for every individual.

Experiments were performed under permission of the Austrian Commission on Experiments in Animals.

| Family, species, number of individuals and size range of fish investigated. |
|-----------------|--------|------------------|------------------|
| **Family**      | **Species** | **Number** | **Body Weight (g)** |
| Pimelodidae     | *Pimelodus blochii* | 12 | 10.3-19.0  |
|                 | *Pimelodus pica* | 16 | 1.1-10.0   |
| Mochokidae      | *Synodontis guineensis* | 10 | 6.7-16.4   |
|                 | *Synodontis schoutedeni* | 10 | 1.7-5.7   |
| Doradidae       | *Aganyx pectinifrons* | 10 | 2.1-4.2    |
|                 | *Platydoras costatus* | 11 | 6.4-18.7   |
Sound recordings in air and under water

In air, fish were held vertically by their dorsal spine (enlarged first dorsal fin ray) at a distance of 5–8 cm from the microphone. Usually fish immediately uttered sounds in this position. Otherwise they were slightly touched at the caudal peduncle. Because pectoral fins were often moved simultaneously, one spine was frequently held in order to obtain individual stridulatory sounds. Calling fish were recorded using a dynamic microphone (AKG 90, frequency range 60–15,000 Hz, sensitivity: 1.9 mV/Pa), a video camera (Sony VX1) and an oscilloscope (Gould 400) in order to determine if sounds were produced during abduction or adduction movements of the pectoral spine. All three signals were recorded simultaneously by a HiFi-S-VHS-video cassette recorder (JVC HRD 4700).

Underwater, fish were recorded in a plastic tank (height 14 cm, diameter 25 cm) whose walls were lined on the inside by acoustically absorbent material (airfilled packing foil) and whose bottom was covered with fine sand. Sounds were recorded using a Brüel & Kjær 8101 hydrophone (frequency range 1–80 kHz ± 2 dB, voltage sensitivity: −184 dB re 1VµPa), a Brüel & Kjær 2804 power supply and a VCR. Fish were held about 5 cm away from the hydrophone in the middle of the tank. All sound recordings took place at temperatures between 25°C and 26°C in a soundproof chamber.

Sound analysis

Sounds were analyzed using S_Tools, the Integrated Workstation for Acoustics, Speech and Signals Processing, developed by the Austrian Academy of Science, Department of Sound Research.

Sounds were defined as follows: One pectoral sound was regarded as the acoustic signal emitted during the movement of the spine in one direction, independently of pulse periods. Thus, abduction (AB-) and adduction (AD-) sounds could be distinguished. Drumming sounds (DS) were usually uninterrupted signals of varying duration.

The following variables were determined from sounds recorded in air, except in cases where a comparison between media was intended (Figure 1):

Duration of sounds (SD): Durations were measured for 10 to 15 AB- and AD-sounds immediately following one another and for all drumming sounds of each individual.

Total sound duration: The total duration of sounds uttered in the first 60 s of sound recordings was measured in order to compare stridulation/drumming-ratios between both media. Only those species and individuals that produced several sounds in air as well as under water were used.

Pulse period (PP): Time interval between the onset of one pulse in a stridulatory sound and the onset of the following one. All pulse periods of at least two AB- and AD-sounds were determined for each individual as long as pulses could be clearly separated.

Peak-to-peak amplitude (PA): In order to determine sound intensity differences between AB- and AD-sounds and between pectoral and swimbladder sounds peak-to-peak voltages of the largest amplitude pulse of a sound were measured. AB/AD—ratios and pectoral/drumming—ratios were calculated.

Dominant frequencies: The main frequencies of stridulatory sounds were measured over whole AD- or AB-sounds using cepstrum-smoothed power spectra. Power spectra were calculated using fast Fourier transform (FFT). The highest peak of the smoothed curve is a better representation of the energy distribution than the highest peak energy of the power spectra. Linear regressions were calculated between body mass and dominant frequencies.

Fundamental frequencies: In drumming sounds the mean frequency of the first harmonic was measured over total sound length. Minimum and maximum frequencies of the fundamental frequency (first harmonic) were determined. The absolute extent of frequency modulation (in Hz) was calculated as the difference between minimum
and maximum frequency within a drumming sound. The correlation between mean fundamental frequency and body weight was calculated for drumming sounds.

Statistical analysis

Statistical analysis used DataDesk (Data Description, NY) for ANOVA and SPSS (SPSS, Inc.) for all other calculations.

A mean of up to ten sounds was calculated for every variable for every individual and used to calculate means of individuals. Analyses of data distributions revealed no dramatic departures from normality for any morphological or acoustical variable. Differences between families were analysed by nested ANOVA (nesting species within families) followed by a LSD post hoc test for pairwise comparison. Differences within families or species were calculated by t-tests. Ratios in peak-to-peak amplitudes (PA) of AB- and AD-sounds (AB/AD sound) and of AB-sounds and drumming sounds (strid./drum.) were calculated. In order to compare differences between both media, stridulation/drumming—ratios were determined for air and water. The stridulation/drumming—ratio was also calculated for total duration of sounds within the first minute of sound recording for two to five individuals of every species. In order to control for microphone-dependent differences between PA—ratios in both media, catfish were additionally recorded in air using the hydrophone. In general, no microphone-dependent influence on PA—ratios was observed.

RESULTS

Pectoral spines and movement

For sound production, doradids moved both pectorals simultaneously, utilized just one fin, or abducted one spine while adducting the other. In both other families, pectoral fins always stridulated simultaneously. Doradids and mochokids emitted sounds during abduction and adduction movement of pectoral fins, pimelodids only during abduction. All fish could move pectoral fins silently or lock spines in an abducted position.

The relative size of pectoral spines clearly differed among all three families (nested ANOVA, F = 25.1, df= 2, 3; p < 0.05). Doradid spines were longest and pimelodid spines were smallest compared to total body length (Figure 2). Within doradids, the fins of _P. costatus_ were relatively longer than those of _A. pectinifrons_ (t = 3.4, df = 19, p < 0.001). In both other families, relative spine length did not differ between species (Pimelodidae: t = 1.05, df = 19, n.s.; Mochokidae: t = 2.02, df = 17, n.s.).

Pectoral sounds

Pectoral stridulation consisted of series of short pulses of 0.6 to 2.4 ms duration. Pulse duration did not differ between families (nested ANOVA, F = 3.09, df = 2, 3, p < 0.05) (Table 2).

The duration of pectoral sounds was movement-dependent (AB versus AD) (Figure 3). Length of AB-sounds did not differ between


<table>
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<tr>
<th>Species</th>
<th>Mean pulse period (ms)</th>
<th>Maximum pulse period (ms)</th>
<th>Pulse length (ms)</th>
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<tr>
<td>AB-sound</td>
<td>AD-sound</td>
<td>AB-sound</td>
<td>AD-sound</td>
</tr>
<tr>
<td>P. blochii</td>
<td>3.56 ± 0.25</td>
<td>—</td>
<td>2.01 ± 0.36</td>
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<tr>
<td>P. pictus</td>
<td>6.32 ± 0.49</td>
<td>—</td>
<td>1.38 ± 0.21</td>
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<tr>
<td>S. eupterus</td>
<td>5.07 ± 0.31</td>
<td>4.03 ± 0.18</td>
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<td>S. schoutedeni</td>
<td>3.68 ± 0.25</td>
<td>3.69 ± 0.55</td>
<td>0.89 ± 0.03</td>
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<tr>
<td>A. pectinifrons</td>
<td>6.52 ± 0.63</td>
<td>7.85 ± 1.65</td>
<td>2.04 ± 0.038</td>
</tr>
<tr>
<td>P. costatus</td>
<td>7.94 ± 0.64</td>
<td>6.32 ± 0.36</td>
<td>1.15 ± 0.027</td>
</tr>
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</table>

families (nested ANOVA, F = 1.64, df = 2, 3, n.s.). Within families, AB-sounds were longer in A. pectinifrons than in P. costatus (t = 4.50, df = 19, p < 0.001), in P. pictus longer than in P. blochii (t = 4.04, df = 22, p < 0.001), but did not differ in machokids (t = 2.13, df = 11, n.s.). The difference between doradids and machokids in duration of AD-sounds is close to significance (nested ANOVA, F = 11.1, df = 1, 2, p = 0.08). Contrary to AB-sounds, AD-sounds did not overlap in duration between doradid and machokid species. The sounds of doradids were always longer than in machokids (Figure 3b). In doradids, AD-sounds were longer in A. pectinifrons than P. costatus (t = 3.43, df = 19, p < 0.01) and within machokids longer in S. eupterus than S. schoutedeni (t = 4.14, df = 11, p < 0.05) (Figure 3b). Within doradid species, AB- and AD-sounds were of similar length, whereas in machokids AB-calls were significantly longer. The sound duration-ratio (AB/AD) was significantly larger in machokids than doradids (nested ANOVA, F = 173.8, df = 1, 2; p < 0.01) (Figure 3).

Total duration of acoustic signals emitted during one abduction and adduction cycle significantly correlated with relative size of pectoral spines (r = 0.807, n = 6, p < 0.05) but not absolute spine length (r = 0.109, n = 6, n.s.) (Figure 4). No correlation existed between sound duration and body size in any species.

Mean pulse period was between 3.56 ms and 7.94 ms in AB-sounds and between 3.69 ms and 7.85 ms in AD-sounds (Table 2). The pulse periods of AB-sounds did not differ between families (nested ANOVA, F = 2.17, df = 2, 3, n.s.), but pulse periods of AD-sounds were longer in doradids than in machokids (nested ANOVA, F = 84.22, df = 1, 2; p < 0.05) (Table 2).

The maximum pulse periods of AB-sounds differed significantly between families (AB-sounds: nested ANOVA: F = 10.99, df = 2, 3, p < 0.05) (Table 2). The pulse period was longer in doradids than in the

Figure 3. Mean duration of pectoral sounds emitted during abduction (AB-sound) and adduction (AD-sound) of pectoral spines. Significance of differences: * p < 0.01, ** p < 0.001. Abbreviations see Figure 2.
Comparing peak-to-peak amplitudes of AB- and AD-sounds reveals significant differences between families (nested ANOVA, F = 37.3, df = 1, 2, p < 0.01). Amplitude ratios (AB/AD-sounds) in mohokids were about twice as high as in doradids (Figure 6). There was no significant difference between amplitude ratios within families (Doradidae: t = 2.08, df = 18, n.s.; Mochokidae: t = 1.17, df = 18, n.s.). Within A. pectinifrons, amplitudes of AB-sounds are significantly larger than of AD-sounds (Wilcoxon-test: Z = -2.24, df = 9, p < 0.05).

The main energy of pectoral sounds was found between 2000 Hz and 3600 Hz. Because of the pulsatile structure of acoustic signals, energies were distributed over a broad frequency range (Figure 5). Negative correlations between body size and dominant frequencies were only found in P. costatus (AB-sounds: r = -0.836, df = 10, p < 0.01; AD-sounds: r = -0.758, df = 10, p < 0.05). There were no differences between families in the main frequencies of either AB-sounds (nested ANOVA, df = 1, 2, F = 8.34, n.s.) or AD-sounds (nested ANOVA, df = 2, 3, F = 7.66, n.s.). Only within S. eupterus did AB-sounds differ from AD-sounds in main frequency components (mean ± SE—AB: 2070 ± 106.4 Hz, AD: 2180 ± 94.5 Hz, t = 3.21, df = 9, p < 0.05).

Drumming sounds

In distress situations drumming sounds were emitted by doradids and pimelodids both underwater and in air. In mohokids no swimbladder sounds were recorded in either media. In contrast to stridulatory sounds, drumming sounds were low frequency harmonic signals built up of single pulses (see oscillograms in Figures 5 and 7). The duration of swimbladder sounds varied between a few ms to 1.5 s. No difference between families was found (nested ANOVA, F = 1.29, df = 1, 2, n.s.), but differences within pimelodids were striking. The mean sound duration in P. pictus was more than ten times longer than in P. blochii (P. pictus: x = 445.6 ± 134.3 ms, P. blochii: x = 40.3 ± 4.47 ms, U-test, U = 8, p < 0.001). In P. costatus and P. blochii, series of short drumming sounds (6–8 ms) were produced. In distress situations swimbladder sounds were usually uttered together with pectoral sounds. They can be produced before, after or simultaneously with pectoral sounds (Figure 5c). Sometimes drumming sounds were emitted without stridulatory signals in pimelodids. In doradids, drumming was frequently recorded after a pair of abduction and adduction sounds of pectoral fins.

Drumming sounds usually possessed 4–5 harmonics and the spacing of harmonics corresponded to the pulse repetition rate (Figure 7a, b). Main energies occurred within the first, second or third harmonic, or occasionally even alternated between two harmonics within a call. Differences in fundamental frequencies between
pimelodids and doradids were close to significance (nested ANOVA: F = 6.9, df = 1, 2, p < 0.05) (Table 3). In both families there is a difference between species (pimelodids: t = 2.27, df = 17, p < 0.05; doradids: t = 2.79, df = 17, p < 0.05). Swimbladder sounds were frequency modulated in both families (Table 3). Sounds began with a frequency increase and were usually modulated downward at the end. The degree of frequency modulation did not differ between families (nested ANOVA: F = 1.8, df = 1, 2, n.s.). Within doradids, however, absolute size of frequency modulation was significantly larger in A. pectinifrons than in P. costatus (t = 3.30, df = 17, p < 0.01). No correlation between body size and mean fundamental frequency existed in either species.

**Intensity comparison of stridulatory and drumming sounds**

In contrast to doradids, drumming sounds of pimelodids could easily be heard in air without amplification. Peak-to-peak ratios of stridulatory
Figure 6. Mean (+ 95% conf. limits) ratios of peak-to-peak amplitudes of AB-sounds and AD-sounds. Abbreviations see Figure 2.

TABLE 3

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Fundamental frequency (Hz)</th>
<th>Frequency modulation (Hz)</th>
</tr>
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<tr>
<td>Pimelodidae</td>
<td><em>P. blochii</em></td>
<td>165.31 ± 2.97</td>
<td>12.85 ± 1.40</td>
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<tr>
<td></td>
<td><em>P. pictus</em></td>
<td>177.14 ± 4.57</td>
<td>14.29 ± 2.31</td>
</tr>
<tr>
<td>Doradidae</td>
<td><em>P. costatus</em></td>
<td>96.15 ± 5.41</td>
<td>18.19 ± 1.76</td>
</tr>
<tr>
<td></td>
<td><em>A. pectinifrons</em></td>
<td>114.12 ± 3.42</td>
<td>28.65 ± 2.55</td>
</tr>
</tbody>
</table>

Note that differences in sonagrams of pimelodid drumming sounds (Figure 6c. versus 7b.) depend on different filter bandwidths.
and drumming sounds were significantly smaller in pimelodids than doradids in both media (air: nested ANOVA: F = 219.27, df = 1, 2, p < 0.01; water: nested ANOVA: F = 84.07, df = 1, 2, p < 0.05 (Figure 8). No differences were found within families.

Comparison of sound production in water and air

The waveforms of sound recorded in air and under water were basically similar. Ratios of peak-to-peak amplitudes of underwater and air stridulatory and drumming sounds differed significantly (Figure 8). In doradids and *P. blochii*, stridulatory sounds were relatively more intense in air than in water compared to drumming sounds (*A. pectinifrons*: t = 5.41, df = 10, p < 0.001; *P. costatus*: t = 6.95, df = 10, p < 0.001; *P. blochii*: t = 3.98, df = 9, p < 0.01). In *P. plicatus* no significant difference was found (t = 2.21, df = 9, n.s.).

The ratio (stridulation/drumming) of total duration of acoustic signals uttered in the first minute of sound recordings differed in two species when comparing both media. The doradid *P. costatus* and the pimelodid *P. blochii* emitted significantly more stridulatory sounds than drumming sounds in air compared to the water recordings (mean ± SE stridulation/drumming ratios: *P. costatus*: water = 1.67 ± 0.41, air = 7.43 ± 1.14, Wilcoxon-test, Z = -2.02, n = 5, p < 0.05; *P. blochii*: water = 0.62 ± 0.17, air = 3.72 ± 2.07, Wilcoxon-test, Z = -2.02, n = 5, p < 0.05).

DISCUSSION

Diversity of sounds in fishes has not been investigated in representatives of closely related families or with regard to variation in sonic organs. Comparisons of sound characteristics have been restricted to species of single genera (sunfish: *Lepomis*—Gerald 1971, toadfish: *Opsanus*—Fine et al. 1977, damselfish: *Eupomacentrus*—Spanier 1979, gouramis: *Trichopsis*—Ladich et al. 1992) or one family (cods: Hawkins and Rasmussen 1978). Therefore, differences in vocalization between species are rather small and cannot be related to morphological features. In damselfish (*Eupomacentrus*) and sunfish (*Lepomis*) the sound-producing mechanism was not described. In croaking gouramis (*Trichopsis*), which possess an unique pectoral tendon snapping mechanism, differences in peak-to-peak amplitudes of pulses are mostly due to the differences in the size of the tendons involved (Kraochovi 1978, 1980, Ladich et al. 1992).

Among teleosts, catfish are unique in possessing two sonic organs. There are basic differences in variability of the morphology of both types of organs. Differences in the pectoral sound-producing apparatus are mainly restricted to the relative size of the pectoral spines; doradids have larger spines than mochokids, and pimelodids are even smaller. Swimbladder mechanisms, on the other hand, differ widely in the insertion and origin of muscles as well as vibrating structures.

Pectoral (stridulatory) sounds

Despite differences in the relative size of pectoral spines between families, the duration of sounds emitted during abduction does not differ significantly between doradids, mochokids and pimelodids. The main reasons might be the intra- and interspecific variabilities in velocity of spine movement. On the other hand, duration of AD-sounds is obviously related to spine size. These sounds are much shorter and less intense in mochokids compared to doradids (and to AB-sounds).
and totally lacking in pimelodids. These results suggest that the absolute size of the spine and thus the rubbing dorsal process is not directly responsible for sound duration, but it might influence the pattern of movement during fin adduction. Stridulation in the pimelodid *Rhamdia sebae* is caused by contraction of the dorsal rotator muscle, which turns and presses the ridged dorsal process of the spine against a groove in the shoulder girdle during fin adduction (Schachner 1977, Schachner and Schaller 1981). Although the exact mechanism of sound production is not fully understood in catfish (Fine et al. 1995) the degree to which the spine is pressed against the groove during adduction seems to be the most likely explanation. Obviously, this depends on relative spine size and thus potentially is a family characteristic. It is generally assumed that pulses are produced by single ridges of the spinal process successively contacting the cleithral groove (Fine et al. 1996). Pulse periods should therefore be correlated to distances between ridges and thus spine size as long as spines are moved at similar velocity. Significantly larger maximum pulse periods of *AB-* and *AD*-sounds in doradids compared to all other families indicate larger maximum distances between ridges in doradids.

Pfeiffer and Eisenberg’s (1965) observation that sounds were shorter in mochokids than doradids was not confirmed in this study. Furthermore, they stated that *AD*-sounds are significantly shorter than *AB*-sounds in both families. In the present study, no differences were detected in the duration of *AB-* and *AD*-sounds. The discrepancy between both studies may result from sampling different species, the small number of fish used in the earlier study (1–4 specimens) and the absence of statistic evaluation. Thus, the main difference in stridulatory sounds between mochokids and doradids seems to be the less intense and shorter acoustic signals emitted during adduction by the former.

Only a few data are available for pectoral sounds in other families. Sounds are produced during adduction and adduction of pectoral spines in bunuccephalids (Gainer 1967). Rigley and Muir (1979) mentioned that sounds were produced during both spine movements in *Ictalurus (= Ameiurus) nebulosus*, but Fine et al. (1996) stated that stridulation was typically produced by pectoral fin adduction in *I. punctatus*. Therefore, it remains unclear if there is a family-specific pattern in ictalurids. The duration of sounds obviously does not differ between ictalurids and tropical catfishes investigated in the present paper.

Dominant frequencies of pectoral sounds are not correlated to body mass in the species investigated except in *P. costatus*, in which larger fish had lower main frequencies of *AB-* and *AD*-sounds. The lack of correlations in other species might be due to the fact that stridulatory sounds usually consist of broadband pulses, with main energies distributed over a wide frequency range. Significant correlations between body mass and spectral content of sounds have rarely been found and described in fishes, with the exceptions of *Trichopsis viitata*, *T. schalleri* and *T. pumila* (Marshall 1966, Ladich et al. 1992), *Pomacentrus paritus* (Myerberg et al. 1993), *Dascyllus albisella* (Lobel and Mann 1993) and *Ictalurus punctatus* (Fine et al. 1995). Croaks of gouramis and chirps of damselfish are both pulsed sounds, but their sonic mechanisms are obviously different from catfish. The size range of species investigated might influence correlation. Maximum body mass range in damselfish was about 1.45 (Myerberg et al. 1993) and 1.2 (Lobel and Mann 1995), while in *Trichopsis* spp. 1.8, 1.2 and 1.22 respectively. In the doradid *P. costatus*, body weight ranged from 1.29, but two species had larger minimum: maximum size ranges (P. pictus: 1.86; S. schoutedeni: 1.3–1.7), although three species had smaller ones (A. pectinifrons: 1.2–2.08; P. blochii: 1.74; S. eupterus: 1.2–2.45). Regarding the small size differences in croaking gouramis and the fact that catfish species with higher size ranges than *P. costatus* do not show a correlation, the peak frequency/size relationship does not appear to hold for catfish stridulatory sounds in general. This is in contradiction to the fact that all catfish species studied possess both prerequisites for a peak frequency/size relationship: a gas bladder which functions as a resonating “drum” and sounds which clearly possess a defined pulse structure (Myerberg et al. 1993). Because no correlation was found in any out of seven catfish species it is questionable if the above relationship can be generalized for pulsed sounds in fishes.

**Swimbladder (drumming) sounds**

Family-specific differences in the production of low frequency distress calls exist in the catfish studied. Pimelodids produce intense sounds, which could easily be heard several meters away from the tank, whereas doradids sounds were of much lower sound pressure; no swimbladder sounds were emitted by mochokids during this study. The much higher sound pressure levels in pimelodids compared to similar-sized doradids might depend on morphological differences in sound-producing mechanisms between both families. In pimelodids the drumming muscle is inserting ventrally on the swimbladder and covers its ventral part almost totally, whereas in doradids and mochokids a small elastic bony plate (elastic spring) touches the bladder cranially. Thus the percentage of the swimbladder wall which is directly put into vibration is much larger in pimelodids than doradids and might result in higher sound intensity. The fundamental frequency, which corresponds to the pulse repetition rate, seems to be higher in pimelodids (species means: 165 and 177 Hz) than in doradids (96 Hz and 114 Hz). Kastberger (1977, 1978) mentioned that the main
energies of doradid sounds (Ocydoras, Doras, Megalodoras) are concentrated between 60 Hz and 90 Hz except in Acanthodoras, in which fundamental frequencies range up to 250 Hz. In the closely related auchenopterids, Kasberger (1978) described low frequency first harmonics (120 Hz) in Trachycorystes and Tavolga (1962) measured 150 Hz in arid catfish. Schacher and Schaller (1981) observed that the fundamental frequency in the pemelodid Rhamdia sebae is about 200 Hz. Because only a few species have been investigated so far, it is not clear if drumming muscle contraction rates are lower in families with elastic spring mechanisms (doradids, aruids) than in pemelodids. Drumming sounds in both families are usually frequency modulated. Although common in birds and many mammals, frequency modulation of sounds are rarely observed in fishes (Fine et al. 1977). Tavolga (1960) presented sonagrams of arid catfish Bagre marinus and toadfishes Opsanus sp., in which the fundamental frequency changed slightly. Long spawning calls of male haddocks Melanogrammus aeglefinus exhibit distinct frequency modulations (Hawkins and Rasmussen 1978, Hawkins 1986) and the mormyrid Potlomyrus isidori modulate ‘moans’ upward or downward (Crawford et al. 1986). Frequency modulations reflect changes in pulse repetition rates, i.e., the drumming muscle contraction rate. Frequency modulations occur in representatives of non-related teleost families (mormyrids, catfishes, cods and toadfish) and are perhaps due to muscle fatigue or to different levels of excitement. Other studies reveal that changes in fundamental frequencies are highly related to water temperatures (Fine 1978, Brantley and Bass 1994).

No drumming sounds are emitted in S. euperus and S. schoutedeni. Abu-Gideiri and Nasr (1973), however, described deep grunts produced by protractor muscles of the swimbladder in several distress situations in S. schall. This species emits grunts when trapped, held by forceps, and as a response to tactile stimuli. On the other hand, Pfeiffer and Eisenberg (1965) only recorded stridulatory sounds in distress situations in mohokids and doradids. Their result might be due to the low intensity of drumming sounds (as in Platydoras and Agamyxus) or their absence as in the mohokids investigated in this study. Audible sounds in S. schall (Abu-Gideiri and Nasr 1973) and Doras spp. (Sorensen 1895, Kasberger 1978) may be related to the larger size (up to 1 kg) compared with the fishes investigated by Pfeiffer and Eisenberg (1965) and in the present study.

**Comparison between different media**

The results presented here and observations in aruids (Tavolga 1962), ictalurids (Fine et al. 1995), bunocephalids (Gainer 1967), as well as in loricariids, doradids and pangasiids (pers. obs.) clearly demonstrate that catfishes regularly emit distress calls when caught or hand-held. No data indicate that this behaviour depends on age or sex of fish. Although direct evidence that distress calls in fish deter predators in fish or warn conspecifics is lacking (Myrberg 1981, Ladich, in press), vocalizations are likely used to warn predators underwater and in air. Forbes (1989) demonstrated that ictalurid catfish with locking spines are an injury risk during digestion for birds predators and therefore less frequently taken than perciforms. Neotropical catfishes frequently live in shallow waters, e.g., during migration or ‘dry’ seasons when water levels fall (Lowe-McConnell 1987). Therefore, broad band cracking noise (1000–4000 Hz) might be an effective warning signal due to the best hearing sensitivities of non-oscine bird predators, e.g., herons (Dooling 1982). The high energy contents of pectoral sounds are well above the hearing abilities of many fish predators, e.g., cichlids, and can only be perceived by hearing specialists such as ostariophysines (Hawkins and Myrberg 1983, Fay 1988). Therefore, two different types of acoustic signals—low frequency sounds against aquatic piscivores and high frequency sounds against aerial predators—might be advantageous. Catfishes with two sonic organs should primarily utter high intensity drumming sounds under water. A medium-dependent difference in the ratio of peak-to-peak amplitudes between both types of sounds was observed independent of the particular recording equipment. In three out of four species (A. pectinifrons, P. costatus, P. blochii) the drumming sounds (compared with stridulations) were of significantly higher level underwater than in air. The total duration of vocalization emitted at the beginning of a recording session showed that the doradid P. costatus and the pemelodid P. blochii produce significantly more stridulatory sounds than drumming sounds in air.

Pfeiffer and Eisenberg (1965) only registered pectoral sounds in doradids in air, while Kasberger (1977) described intense drumming signals in several doradid genera when hand-held in water.

Although no detailed information is available, there are some indications that catfishes utilize different organs in different intraspecific contexts: *Synodontis* grunts (= drumming sound) in fright situations, when fleeing from a conspecific or during courtship, but creaks (= stridulations) when held (Abu-Gideiri and Nasr, 1973). The pemelodid *Rhamdia* emits drumming sounds during threatening and stridulates during defense behaviour (Schacher 1977, Schacher and Schaller 1981). These observations corroborate the assumption of situation-dependent (different receivers or behavioural context) utilization of sound-producing mechanisms in catfish.
Conclusion

This first extensive comparison of sound production within a teleost order indicates a family-, species- as well as context-specific diversity in occurrence, duration, amplitude and spectral content of sounds. The results suggest that different factors (morphology, motivation) influence sound parameters. For example, the lack of differences between families in the duration of sounds emitted during abdication of fins is based on a high variability which is certainly due to motivational factors. The total duration of pectoral sounds (AB + AD-sounds) on the other hand is highly correlated to morphological structures, especially relative size of pectoral spines. Differences in relative intensity and amount of sounds produced in air and underwater indicate that catfishs can utilize different frequency ranges when conveying messages for different receivers or in different social contexts.

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