Chapter 18
Young Squeaker Catfish Can Already Talk and Listen to Their Conspecifics

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Abstract Numerous fish species are able to produce sounds and communicate acoustically. Nevertheless, hearing and sound production in fishes is poorly understood and the ontogenetic development of acoustic communication has only been studied in a few species. So far the yellow marbled squeaker catfish *Synodontis schoutedeni* is the only species that has been shown to be able to communicate acoustically across generations at all postlarval stages of development. In two further fish species the smallest size groups were not yet able to detect sounds of equal conspecifics. Increasing body size in *S. schoutedeni* correlates with increasing hearing sensitivity for lower frequencies, decreasing hearing sensitivity at higher frequencies, increasing sound pressure level and duration of stridulation sounds, and decreases in stridulation sound dominant frequency. The excellent hearing sensitivities of *S. schoutedeni*, which are characteristic for Otophysi (fish with a Weberian apparatus), is probably the reason for their ability to communicate acoustically in early stages of development.

1 Introduction

The Teleostei, or modern bony fishes, are the most species-rich group of vertebrates. They consist of approximately 30,000 known and extant species (Froese and Pauly 2012), more than of all other vertebrates species combined. Their diversity in matters of morphology and biology exceeds that of all other vertebrates by far and this diversity is also apparent in the different mechanisms for receiving and producing sounds. Fishes have evolved a unique diversity of sound detecting and sound producing mechanisms.

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G. Witzany (ed.), *Biocommunication of Animals*, DOI 10.1007/978-94-007-7414-8_18,

1.1 Hearing in Fishes

Pliny the Elder in the first century AD was probably the first to write about fish hearing (cited after Popper and Casper 2011). In the nineteenth century Retzius showed that there is probably more anatomical variation in the ears across fish species than in all other vertebrate groups (Retzius 1881), but questions of if and how fishes can hear were not answered until many years later. In an experiment with a blinded catfish von Frisch (1923) was the first to prove, that fishes are able to detect sounds and not only just "feel" vibrations.

In contrast to tetrapods fishes do not possess external or middle ears, and without additional structures are likely only able to detect the particle motion component of sounds. Their inner ears have two main functions, they serve the "vestibular" and "auditory" senses, the first responsible for balance, the second for hearing (Popper et al. 2003). Fishes use their lateral line to detect nearby water motion, and can also feel very low frequencies with this organ (Coombs and Montgomery 1999; Slabbekoorn et al. 2010; Higgs and Radford 2013).

To be able to detect the pressure component of sounds, many fish groups have evolved connections between gas filled chambers and the inner ear which transfer sound pressure to the ear. The so called Weberian apparatus of otophysan fishes is the best known of those structures, named after a German scientist who first described it (Weber 1820). A tiny chain of one to four ossicles ("Weberian ossicles"), connected by ligaments, transfers oscillations of the swimbladder in a sound field to the inner ear and thus makes Otophysi sensitive to sound pressure, increasing their hearing sensitivity and broadening the range of sound frequencies they can detect. With more than 8,000 extant species living mainly in freshwater, the four otophysan orders, Cypriniformes (carps and loaches), Characiformes (tetras), Siluriformes (catfishes) and Gymnotiformes (South American knifefishes) comprise about a quarter of all fish species and are the dominant fish group in freshwater worldwide. About half of all freshwater fish species are Otophysi.

Several further fish groups have evolved different ways of coupling gas filled chambers to the inner ear. For example the Mormyridae (elephantfishes) with their otic bulla, the Anabantoidei (labyrinth fishes) with their suprabranchial chamber, and several species of the Holocentridae (squirrelfishes) along with some Clupeidae (herrings) and further taxa, which possess anterior extensions of the swimbladder to the ear (for overviews see e.g. Braun and Grande 2008; Ladich and Popper 2004).

In general, fishes with additional hearing structures were termed "hearing specialists", in contrast to "hearing generalists" or "hearing nonspecialists" without adaptations related to hearing. These groupings however, are inexact and should not be used (Popper and Fay 2011).

In the second half of the twentieth century scientists tested hearing sensitivities of several fish species using mainly behavioural methods. These methods were extremely time consuming and labor intensive. Towards the end of the last century invasive and non-invasive neurophysiological methods, though their results must be interpreted with care (Fay 2011), increasingly began to replace behavioural methods and made measurements of hearing in fishes more rapid and easier.

Thus, our knowledge of hearing abilities in different fish species has increased enormously in the last decades (Ladich and Fay 2013). Nevertheless, considering the huge number of fish species and their diversity, our ken in fish hearing is still very rudimental.

Fishes without accessory hearing structures are able to detect only lower frequencies up to about 1 or 2 kHz and show high hearing thresholds, while species with accessory hearing structures are able to detect frequencies up to several kHz or even hundreds of kHz in some shads (Mann et al. 1997) and show higher sensitivities; in frequencies below approximately 50 Hz hearing sensitivities converge in all groups, fishes are insensitive to sound pressure in those low frequency ranges and perceive only the particle motion components of sounds (Popper et al. 2003).

1.2 Sound Production in Fishes

Similar to their variety of hearing structures, fishes have evolved a large diversity of sonic organs, and the fact that fishes produce sounds has been well known by humans for ages. Already in the fourth century BC Aristotle described sounds emitted by a number of fish species (cited after the English translation by D'Arcy W. Thompson – Aristotle 1907). Beside accidentally generated sounds produced while swimming, feeding, or breathing, a large number of fish species have evolved different mechanisms to produce sounds for acoustic communication. The most common method of sound production in fishes is oscillating the swimbladder in various ways, either directly by rapid contractions of intrinsic or extrinsic muscles or indirectly with several different bony skeletal elements moved by muscles. The former way of drumming with the swimbladder is well known in many species of the orders Perciformes (perch-like fishes), Gadiformes (cods and relatives), Ophidiiformes, Beryciformes, and Siluriformes (catfishes) (Ladich and Fine 2006; Parmentier and Diogo 2006).

The second widely-used way for sound generation in fishes is the production of stridulatory sounds. Stridulation sounds are produced by rubbing teeth, fin spines or other bony structures against each other (Fine and Ladich 2003), e.g. rubbing the base of the pectoral fin spines within the pectoral girdle or pharyngeal teeth grating.

In some common sound producing groups like gobies and loaches, and also in some cichlids and species of further groups, the sound producing mechanisms are still unidentified (Ladich and Fine 2006; Kasumyan 2008) or have been identified lately as in Pomacentridae, the damselfish family (Parmentier et al. 2007).

1.3 Acoustic Communication

Acoustic communication in fishes has been demonstrated in contexts of agonistic, territorial, courtship and defensive behaviour (Amorim 2006; Ladich and Myrberg 2006; Myrberg and Lugli 2006) and even for species discrimination as shown in nearly related, sympatric elephant fish species (Crawford et al. 1997; Feulner et al. 2009).

Distress calls and disturbance sounds uttered by fishes are well known by fishermen who hear them when handling the catch. Many fish species are able to produce distress sounds when being attacked by predators. The purpose of this kind of fright reaction is not fully understood. No predator has been observed so far releasing its prey because it is uttering distress sounds. It is possible that distress sounds are used to warn conspecifics or even to attract further predators, which could increase the chance for escape (Ladich and Myrberg 2006).

Despite the high variability in sonic organs, the vocal repertoire of fishes is rather limited compared to sounds produced by the larynx or syrinx in tetrapods. Just one to five different types of sounds are normally produced by fishes (Amorim 2006). Nevertheless acoustic communication plays an important role in life of many fish groups.

1.4 Ontogenetic Development of Hearing and Sound Production

Our knowledge of fish hearing is rather scarce, and there are many yet unanswered questions concerning sound production and sound communication in fishes. It is thus not surprising that our understanding of the ontogeny of hearing, sound production and acoustic communication in fishes is even more limited; only few studies have been conducted so far. Concerning the ontogeny of hearing, no consistent trends have been reported. An increase of hearing sensitivities with size has been found in several perciform and batrachoidid species (Kenyon 1996; Iwashita et al. 1999; Wysocki and Ladich 2001; Sisneros and Bass 2005; Vasconcelos and Ladich 2008), but scientists have also discovered no difference in hearing sensitivity between two differently sized groups of goldfish, different size groups of zebrafish and gobies (Popper 1971; Zeddies and Fay 2005; Belanger et al. 2010), a slight decrease of sensitivity at lower frequencies with size in marine perciforms (Egner and Mann 2005; Wright et al. 2011), or only a change in the range of detectable frequencies with varying size in zebrafish (Higgs et al. 2001, 2003). Studies on the ontogeny of hearing in two catfish species of the families Mochokidae and Claroteidae revealed an increase in hearing sensitivity with size in lower frequencies, but a decrease of sensitivity at the highest frequencies tested as soon as the chain of Weberian ossicles was fully developed (Lechner et al. 2010, 2011). A further study showed lower sensitivities at high frequencies in bigger specimens of *Ancistrus ranunculus*, a loricariid catfish species (Lechner and Ladich 2008).

The development of sound production in fishes seems to be more consistent; dominant frequencies of sounds decrease with size. This decrease of sound frequency has been found in several perciform, mormyrid, catfish and toadfish species (e.g. Ladich et al. 1992; Myrberg et al. 1993; Lobel and Mann 1995; Connaughton and Taylor 1996; Crawford 1997; Henglmüller and Ladich 1999; Wysocki and Ladich 2001; Amorim and Hawkins 2005; Vasconcelos and Ladich 2008; Parmentier et al. 2009; Colleye et al. 2009, 2011; Lechner et al. 2010; Bertucci et al. 2012), most studies additionally found increases in sound pressure level, total duration, and pulse periods of sounds with size of test specimens.

Hearing and sound production are the key skills for acoustic communication. The ontogenetic development of acoustic communication has only been studied in three fish species so far. While in the croaking gourami *Trichopsis vittata* and in the toadfish *Halobatrachus didactylus* the smallest size groups tested were not yet able to detect sounds of equally sized conspecifics (Wysocki and Ladich 2001; Vasconcelos and Ladich 2008), young squeaker catfish *Synodontis schoutedeni* are capable of hearing sounds produced by their congeners of all size and age groups (Lechner et al. 2010).

2 Ontogeny of Hearing and Sound Production in a Squeaker Catfish

More than 3,000 extant species of catfish (Otophysi, order Siluriformes), belonging to approximately 36 families, are known (Ferraris 2007). Members of the African catfish family Mochokidae are commonly called “squeakers”, because they produce loud stridulation sounds. This is especially true for members of the most species-rich genus, *Synodontis*, which stridulate with their pectoral fin spines. Furthermore, squeaker catfish possess a structure called the “elastic spring apparatus” which enables them to produce drumming sounds with their swimbladder (Sörensen 1895). But drumming sounds in squeakers have been reported rarely; only Abu-Gideiri and Nasr (1973) have reported drumming sounds produced by a mochokid species, *Synodontis schall*.

The yellow marbled squeaker catfish *Synodontis schoutedeni* lives in African Congo river system. It’s a small to medium sized mochokid. Due to its pretty colour pattern (Fig. 18.1), maximum size of little more than 15 cm, and peaceful behaviour, it is quite popular amongst aquarists. Nevertheless, squeaker catfish are extremely hard to breed in captivity (without injection of hormones for artificial stimulation) and the authors of the ontogenetic study were lucky to get young squeakers bread successfully without hormone injection (Drescher 2007).

Synodontis schoutedeni shows excellent hearing abilities due to its chain of three Weberian ossicles and its relatively large swimbladder (Lechner and Ladich 2008) (Fig. 18.2). As a representative of the family Mochokidae it is potentially able to produce communication sounds in two ways, with its pectoral fin spine and its swimbladder (Fig. 18.2); however, drumming sounds could not be recorded in this species.

In the study of ontogeny of acoustic communication in *S. schoutedeni*, specimens from about 22 mm standard length to about 127 mm SL in six size groups from XXS to XL, were tested for their hearing acuities at 11 sound frequencies from 50 Hz to 6 kHz. Stridulation sounds of corresponding size groups, starting from about 28 mm SL in group XXS up to about 127 mm in group XL have been recorded. Hearing measurements were conducted using the non-invasive AEP- (Auditory Evoked Potential) recording technique (according to Kenyon et al. 1998) (also called ABR- (Auditory Brain response) recording technique). Because study specimens are not harmed using this method, specimens could be tested several times

Fig. 18.1 Medium sized specimen of the yellow marbled squeaker catfish *Synodontis schoutedeni* (Picture: André Werner)

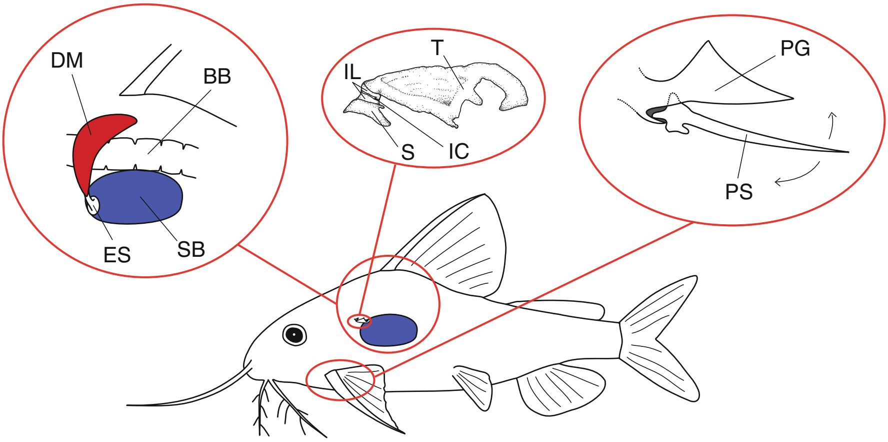

Fig. 18.2 Special adaptations of *Synodontis schoutedeni*. Chain of Weberian ossicles connecting the swimbladder to the inner ear (*center*). Elastic spring apparatus for producing drumming sounds (*left*). Pectoral spine producing stridulation sounds when rubbed in a special groove of the pectoral girdle (*right*). *BB* backbones/vertebrae, *DM* drumming muscle, *ES* elastic spring, *IC* intercalare, *IL* interossicular ligaments, *PG* pectoral girdle, *PS* pectoral spine, *S* scaphium; *SB* swimbladder, *T* tripus

for their hearing acuities during development. The smallest size group XXS consisted of juvenile specimens in postlarval stage. In a study on hearing in the African bullhead catfish *Lophiobagrus cyclurus* (Lechner et al. 2011), even smaller specimens, still in late larval stages with not yet fully developed fins and Weberian ossicles could be tested for hearing. The results in the ontogenetic study of Weberian ossicles and hearing abilities in *L. cyclurus* indicate that a fully developed chain of Weberian ossicles was present in the smallest size group XXS of *S. schoutedeni*, corresponding to the second smallest size group tested in the *Lophiobagrus* study.

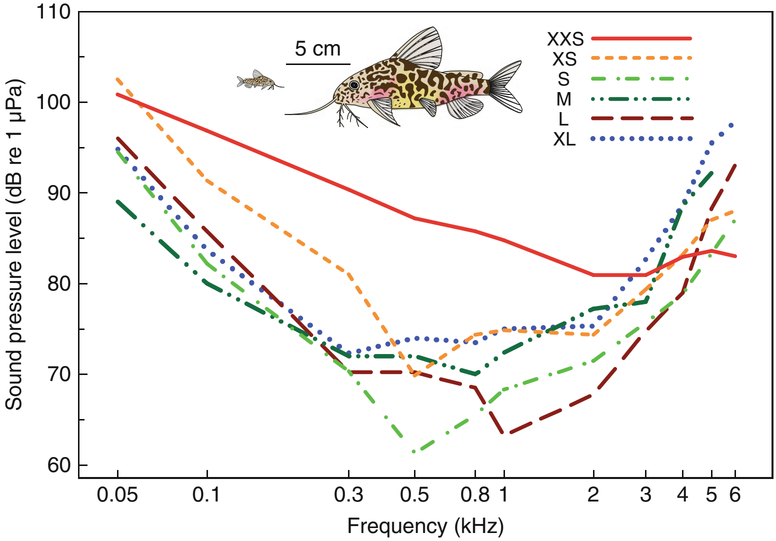

Fig. 18.3 Audiograms (hearing curves) of the six size groups XXS–XL of *Synodontis schoutedeni* tested at 11 frequencies from 50 Hz to 6 kHz. Note the higher hearing thresholds of smaller size groups at lower frequencies and the lower thresholds at the highest frequencies tested. For measures of size groups see text and Lechner et al. 2010 (Modified from Lechner et al. 2010)

All size groups of *S. schoutedeni* showed their best hearing abilities between 300 Hz and 1 kHz, with the exception of the smallest group XXS, which had its best frequency at 2 and 3 kHz. Interestingly, specimens of the small size groups showed lower hearing sensitivities than their congeners of larger groups at the lowest frequencies tested, whereas in the highest frequencies tested the results were reversed, the groups of smaller specimens showed better hearing acuity than the groups of the larger ones (Fig. 18.3). At most frequencies tested significant correlations between size and hearing could be found. From 50 Hz to 2 kHz larger catfish showed significantly better hearing, at the highest frequencies tested (5 and 6 kHz) hearing acuity of larger individuals was significantly lower than that of small individuals. At 3 and 4 kHz no correlation between fish size and hearing abilities was found (Lechner et al. 2010).

Specimens of all size groups of *S. schoutedeni* produced stridulation sounds during ab- and adduction (off and towards the body) movement of their pectoral fins (Fig. 18.4). Sounds produced by individuals in the smallest size groups were of significantly lower sound pressure level, shorter duration and shorter pulse period than sounds produced by individuals in larger size groups. Stridulation sounds of individuals in the smallest size groups were more broad band and had higher dominant frequencies, while bigger sized specimens exhibited dominant frequencies that were more pointed and which decreased significantly with size (Figs. 18.4 and 18.5) (Lechner et al. 2010).

Interestingly, all size groups showed their best frequency of hearing in the frequency range with the most energy (dominant frequency) for stridulation sounds produced by their own size groups (Fig. 18.5). Nevertheless, specimens of all size

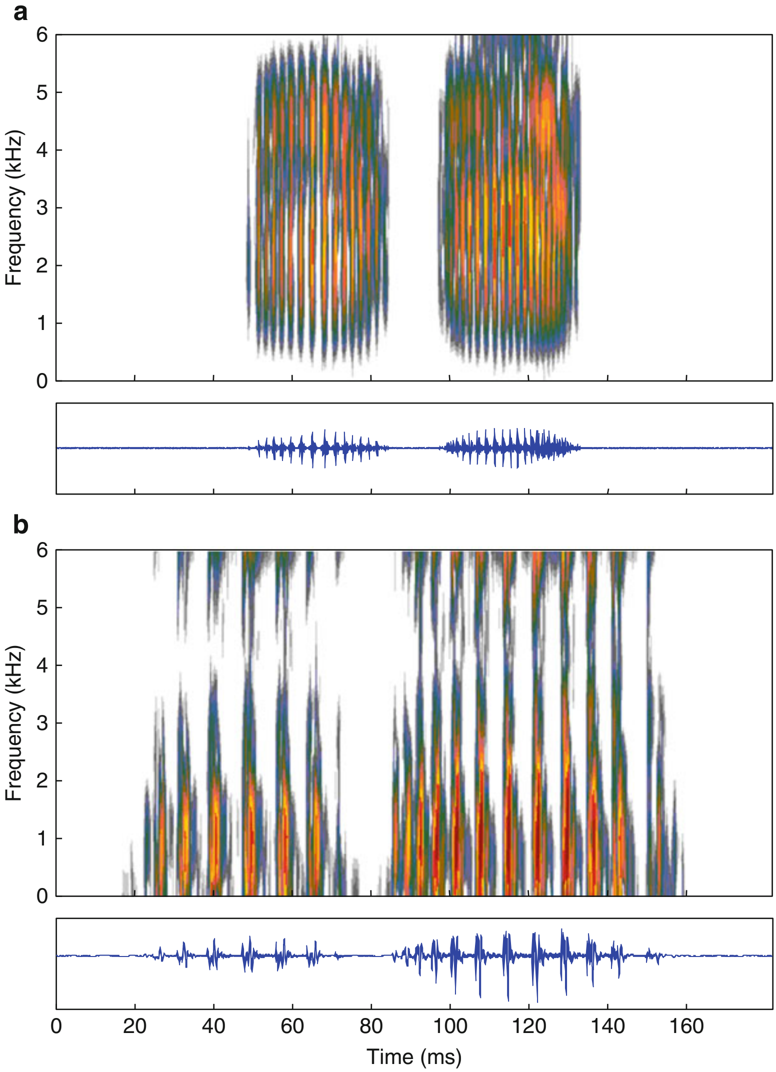

Fig. 18.4 Sonagram (*top*) and oscillogram (*below*) of adduction sounds (*left*) and abduction sounds (*right*) of a specimen of group XXS (**a**) and a specimen of group XL (**b**) of *Synodontis schoutedeni*; 44.1 kHz sampling frequency, 650 Hz (for XXS) and 600 Hz (for XL) filter bandwidth, 75 % overlap, Hanning window (Modified from Lechner et al. 2010)

groups were able to hear the sounds produced by all other size groups. Specimens of group XXS were therefore able to detect sounds produced by their own group as well as the (louder) sounds produced by the bigger groups. In addition, specimens of the largest group XL could not only hear sounds produced by congeners of similar size, but could also hear those produced by catfish of the smallest size group XXS (Fig. 18.6) (Lechner et al. 2010). This means that acoustic communication with stridulation sounds is possible between all generations of *Synodontis schoutedeni*.

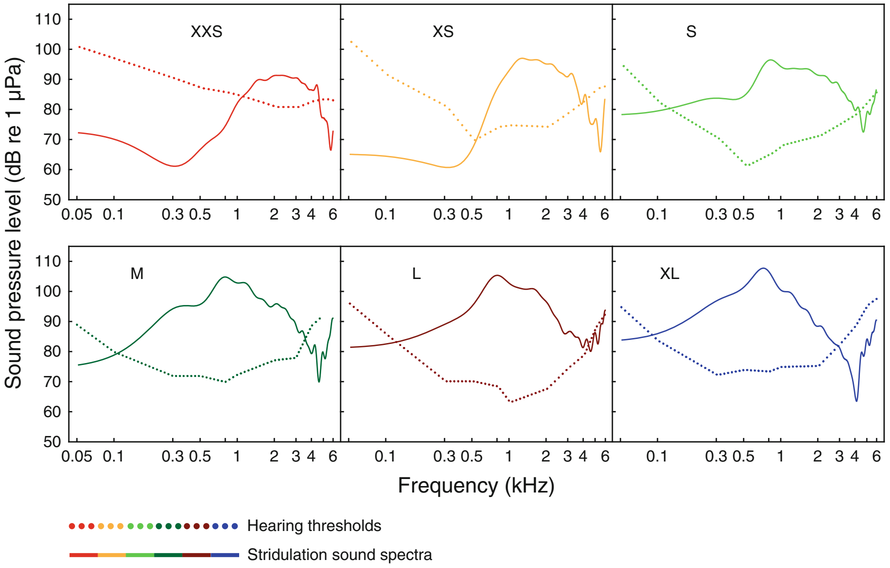

Fig. 18.5 Smoothed sound power spectra of stridulatory sounds (calculated for a distance of 5 cm from the recording hydrophone) of the six size groups compared to their auditory thresholds. For measures of sizegroups see text and Lechner et al. 2010 (Modified from Lechner et al. 2010)

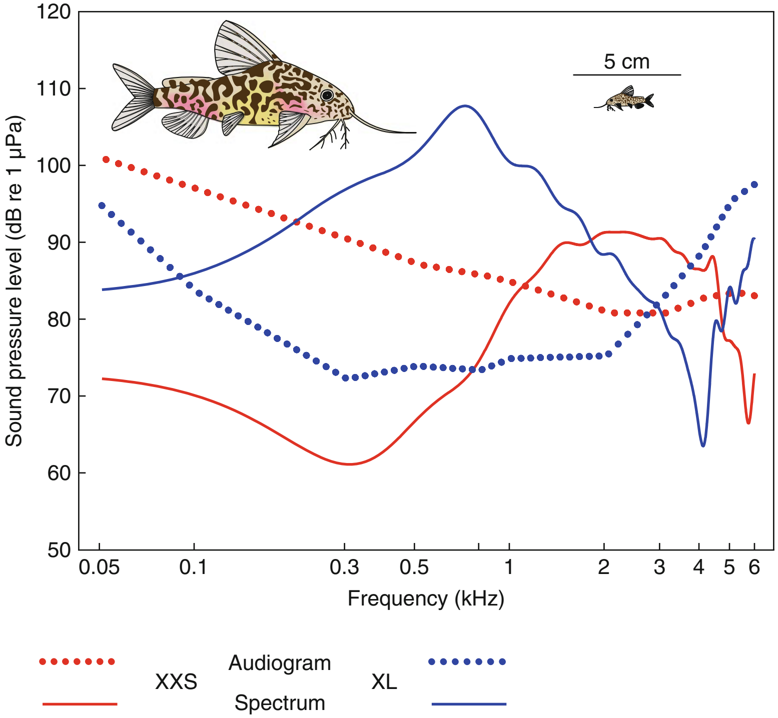

Fig. 18.6 Smoothed sound power spectra of stridulatory sounds of group XXS and group XL (calculated for a distance of 5 cm from the recording hydrophone) compared to their hearing thresholds. Note that both groups are able to detect sounds produced by specimens of their own size group as well as sounds produced by the other sizegroup

3 Conclusions

Different forms of communication are fundamental to animal behaviour. Most vertebrates can interact using visual, acoustical, chemical, and tactile modalities, and some groups can even use electrical signals (Kramer 1990; Moller 2006; Bradbury and Vehrencamp 2011). While acoustic communication is well studied and understood in birds, mammals, frogs, and many sound producing invertebrate species (Gerhardt and Huber 2002; Narins et al. 2007; Bradbury and Vehrencamp 2011), it never grabbed the attention of scientists to a similar extent in fishes. This is probably based on the difficulty for us land living vertebrates to hear underwater sounds (Hawkins 1993). Studies of underwater sounds require greater effort and are more difficult to carry out than similar studies in air (Hopp et al. 1998). Nevertheless, water is full of sounds and noise produced by animals and abiotic sources (Slabbekoorn et al. 2010). The acoustic sceneries of biotopes have considerable influence on their inhabitants, both on land and underwater. To understand and consider these bioacoustics influences, it is necessary to know, what and how participating creatures hear and talk. But our understanding of hearing and acoustic communication in fishes is currently rudimentary.

If an animal produces sounds in a specific context, it is of course of high interest for the sender that receivers are able to hear those acoustic signals. Human generated noise, or “underwater noise pollution”, deriving e.g. from shipping, recreational activities, sonar, or industrial activities (e.g. pile driving, seismic air guns), highly affects fishes and aquatic life (see e.g. Popper and Hastings 2009a, b; Slabbekoorn et al. 2010 for overviews). A very nice example of the influence of anthropogenic noise can be found in toadfish, whose intraspecific acoustic communication is impeded by the noise of ferry boats in their habitat (Vasconcelos et al. 2007).

Because hearing abilities vary greatly between different fish groups and species (Fay 1988; Ladich and Fay 2013), general statements about the effect of different kinds of noise on fishes are nearly impossible. More studies covering a broader range of the variety of hearing abilities in fishes are indispensable to improve our understanding in fish hearing. We know that different fish groups show best hearing in very different frequency ranges and also use sounds of variable frequency ranges for acoustic communication.

The study of the squeaker catfish *Synodontis schoutedeni* is an excellent example of fishes producing sounds in their “best frequencies” of hearing (or showing best hearing abilities in the dominant frequency range of their own sounds?). This is even evident at different developmental stages with stage dependent best hearing frequencies and sound characteristics (Fig. 18.5). At least some fish groups thus seem to adapt their hearing to frequencies of communication sounds (or vice versa), or even adapt communication sound frequencies to their natural habitats. This has been shown in many tetrapod species (e.g. Ryan and Brenowitz 1985; Slabbekoorn and Peet 2003) and also in fishes (e.g. Lugli 2010).

Propagation of low frequency sounds over long distances in shallow waters is rather shallow (Myrberg 1981; Mann 2006), but the majority of acoustically communicating fish species lives in rather shallow waters and many of them utter sounds of low frequencies. Thus acoustic communication is probably used over short distances in those species. The main frequencies of fish stridulation sounds are mostly in the low kHz range. This would allow communication in shallow water over larger distances than with swimbladder drumming sounds. The main frequencies of fish drums are in much lower frequency ranges and thus cannot propagate over longer distances at least in shallow waters (see e.g. Amorim 2006; Ladich and Fine 2006 for reviews and main frequencies of the sounds of vocalizing fish groups). This supports the hypothesis that stridulation sounds in catfishes are being used as alarm calls and drumming sounds are being used for nearby communication.

In contrast to the croaking gourami *Trichopsis vittata* and the Lusitanian toadfish *Halobatrachus didactylus* (Wysocki and Ladich 2001; Vasconcelos and Ladich 2008), the squeaker catfish *Synodontis schoutedeni* is able to detect conspecific sounds in early stages of development (Lechner et al. 2010). Comparing hearing abilities of squeaker catfish, croaking gouramis and Lusitanian toadfish, shows that the catfish has much better hearing acuity at most frequencies (Ladich and Yan 1998; Wysocki and Ladich 2001; Vasconcelos et al. 2007; Vasconcelos and Ladich 2008; Lechner and Ladich 2008; Lechner et al. 2010). This ability to communicate acoustically at very small size stages is probably based on the excellent hearing abilities of *S. schoutedeni* and high sound pressure levels of the stridulation sounds produced by the smallest size groups. But this is the first and so far only evidence showing that the ability to communicate acoustically is present in very young specimens. However, this is probably more a matter of very few studies conducted in this field so far than of exceptional abilities in this species. Similar studies in further vocative fish species with excellent hearing acuities would probably bring similar results. Stridulation sounds of squeaker catfish are fright reactions which are probably used to warn conspecifics of predation. Alarm calls are useful for specimens of all size groups. In contrary toadfish sounds are territorial and advertising calls; croaking gouramis use their sounds in territorial fights which are typical for adults (nevertheless, already small size stages show this territorial behaviour). The meaning of those sounds is different, maybe this is a reason for squeaker catfish to be able to detect their alarm sounds already at very young stages. It is neither necessary nor useful for toadfish and gouramis to detect conspecific agonistic and advertisement calls as very young fish.

But why do smaller specimens of *S. schoutedeni* hear better at higher frequencies than larger congeners? This is a question still to be answered. Significantly better hearing of the smaller specimens at the highest frequencies tested has been shown in *S. schoutedeni* and the African bullhead *Lophiobagrus cyclurus* (Lechner et al. 2010, 2011). Comparing hearing abilities of the pimelodid catfish *Pimelodus pictus* used in three studies (Ladich 1999; Amoser and Ladich 2003; Wysocki et al. 2009) indicates similar trends – the smallest specimens tested by Wysocki et al. (2009) showed lower hearing thresholds at the highest frequencies tested than the largest fish tested by Ladich (1999); and data of hearing in gouramis (Ladich and Yan 1998; Wysocki and Ladich 2001) also show a slight trend of better high frequency hearing in smaller specimens. The biological significance of this fact has still to be found.

Both groups, catfishes and gouramis, use air-filled cavities to aid their hearing, catfish the swimbladder and gouramis their suprabranchial chamber. The physical properties of swimbladder and connective tissues vary over the course of development, and are thus also likely to exhibit variable response properties to sound energy. This could be one reason for those findings. The interestingly congruence of best hearing and sound production frequency in all generations of *S. schoutedeni* maybe is a hint for its biological relevance.

Only one single study so far has shown, that there are fish species which are able to communicate acoustically across all generations. These new and surprising results in the study on ontogeny of sound production and hearing in the mochokid catfish *Synodontis schoutedeni* (Lechner et al. 2010) provide further evidence for many new findings researchers probably will discover in the future in the so far poorly studied field of fish hearing and sound production. The class of bony fishes is highly diverse both in anatomy and biology and so are the capabilities in hearing and sound production of the approximately 30,000 species of teleosts. General statements in fish bioacoustics are nearly impossible. Fishes are an important food source for men in all parts of the world and bioconservation and fisheries management are fields of the highest interest. So far only little attention has been drawn to factors such as "noise pollution" and fish-bioacoustics. But today, authorities and scientists more and more realize their importance. We can expect numerous new studies in these so far poorly understood fields of fish hearing, sound production and communication and probably many of those studies will bring findings as new and surprising as those of the study of the squeaker *Synodontis schoutedeni* did.

Acknowledgements I am grateful to Tanja Schulz-Mirbach and Daniel Bowling for helpful comments and suggestions on the manuscript and to André Werner for the photography of *Synodontis schoutedeni*.

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