

# Chapter 4

## Ontogenetic Development of Sound Communication in Fishes

Friedrich Ladich

**Abstract** Investigating the potential ability of juvenile fishes to communicate acoustically requires analysing the development of vocalization and hearing. To date, the ontogeny of both processes has been examined in three non-related species, namely the croaking gourami *Trichopsis vittata* (family Osphronemidae, order Perciformes), the squeaker catfish *Synodontis schoutedeni* (family Mochokidae, order Siluriformes) and the Lusitanian toadfish *Halobatrachus didactylus* (family Batrachoididae, order Batrachoidiformes). Juveniles of all three species vocalized during agonistic behaviour and showed similar changes in sound characteristics despite possessing different sonic mechanisms. With growth, dominant frequencies decreased, whereas sound pressure levels, pulse periods and sound duration (except in the toadfish) increased. Generally, hearing sensitivities improved during development, but differences were observed between species. Croaking gouramis of all stages responded to sounds up to 5 kHz. Auditory sensitivity increased in the high frequency range and the best hearing frequency shifted from 2.5 to 1.5 kHz. In the squeaker catfish, hearing abilities increased up to 2 kHz but showed a decrease at 5 and 6 kHz. The Lusitanian toadfish showed the smallest changes of all three species: the best hearing sensitivity was found at 50 Hz in all stages and hearing improved only at some frequencies. A comparison between audiograms and sound spectra within same-sized fish of the respective species revealed that the main energies of sounds were concentrated within the most sensitive frequencies. The comparison also showed that early-stage gouramis and toadfish probably cannot detect conspecific sounds due to low sound levels and high hearing thresholds. Only the catfish is able to communicate acoustically at all stages of development, most likely due to its Weberian apparatus.

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F. Ladich (✉)

Department of Behavioural Biology, University of Vienna, Althanstrasse 14,  
1090 Vienna, Austria

e-mail: [friedrich.ladich@univie.ac.at](mailto:friedrich.ladich@univie.ac.at)

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## 4.1 Introduction

The ontogenetic development of acoustic communication in fishes is poorly known. Analysing its ontogenetic development requires investigating—in parallel—the development of sound production and sound detection. Emission of sounds per se does not give evidence for acoustic communication because it does not show that the mostly faint sounds of early stages are detectable for conspecifics. Such evidence can be provided either by correlating sound energies at particular frequencies to auditory sensitivities or by showing unequivocal behavioural responses to sounds in the absence of visual stimuli. Despite a lack of information on the communicative value of sound production, numerous species from non-related taxa are known to vocalize in early (pre-reproductive) stages (Schneider 1964; Henglmüller and Ladich 1998; Amorim and Hawkins 2005; Kéver et al. 2012). This was typically observed during agonistic interactions such as fights over feeding items or feeding places.

In contrast to the development of sound production, all fish seem to hear from the earliest stages on. Several authors investigated the ontogenetic development of auditory sensitivities (Popper 1971; Iwashita et al. 1999; Wright et al. 2011; Webb et al. 2012; Lu and DeSmidt 2013; for reviews see Ladich and Fay 2013; Ladich 2014). This has been done in species possessing accessory hearing structures such as otophysines and anabantoids as well as in species lacking peripheral specializations for hearing. Developmental trends described in these studies are diverse and to some degree contradictory. In some species, auditory sensitivity did not change during ontogeny (zebrafish *Danio rerio*, Zeddies and Fay 2005; round goby *Neogobius melanostomus*, Belanger et al. 2010, midshipman *Porichthys notatus*, Sisneros and Bass 2005; Alderks and Sisneros 2011; spotfin butterflyfish *Chaetodon ocellatus*, Webb et al. 2012), and in some the absolute sensitivity did not change but the hearing bandwidth expanded (zebra fish *Danio rerio*, Higgs et al. 2001, 2003; American shad *Alosa sapidissima*, Higgs et al. 2004). Some species showed an increased sensitivity at particular frequencies (bicolour damselfish *Stegastes partitus*, Kenyon 1996), or an increase at lower frequencies together with a decrease at higher ones (e.g. croaking gourami *Trichopsis vittata*, Wysocki and Ladich 2001; squeaker catfish *Synodontis schoutedeni*, Lechner et al. 2010). Others exhibited a change in sensitivity and in hearing bandwidth (African bullhead catfish *Lophiobagrus cyclurus*, Lechner et al. 2011). Finally, a decrease during growth was reported in sergeant major damselfish *Abudefduf saxatilis* by Egner and Mann (2005).

This chapter reviews studies in which the ontogenetic development of sound production and auditory sensitivity were investigated and both processes correlated to each other to determine when sound communication starts. So far no study has used sound playback techniques to investigate the development of acoustic communication in fish. Communication is defined as a process in which a sender sends out a signal in order to influence the behaviour of a receiver for its (the sender's) advantage (Myrberg 1981; Bradbury and Vehrencamp 1998, 2011; Ladich et al. 2006).

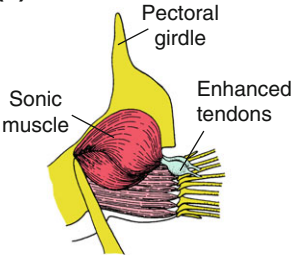
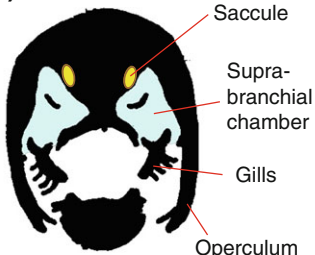
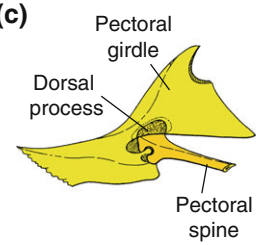
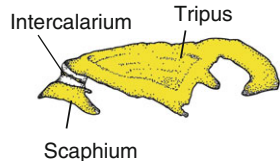
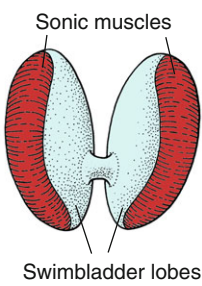
This does not rule out mutual benefit but implies that a receiver detects and responds to a signal. While it is often rather straightforward to prove signal detection and assign a communicative function to territory advertisement signals during playback experiments in which a receiver approaches a sound source (McGregor 1992; Myrberg et al. 1986; McKibben and Bass 1998), such an assignment is quite difficult during agonistic behaviour. During agonistic interactions, opponents typically send out visual signals together with acoustic stimuli (and perhaps olfactory and vibrational signals). Assigning a function to aggressive sounds has seldom been successful in adult fish and less so in the course of an ontogenetic study (for reviews see Ladich 1997; Ladich and Myrberg 2006).

## 4.2 Diversity in the Ontogeny of Sound Production and Hearing

Acoustic communication including sound production and detection has been investigated in three non-related species belonging to three different orders of teleosts. These are the croaking gourami *T. vittata* (order Perciformes, family Osphronemidae), the Lusitanian toadfish *H. didactylus* (order Batrachoidiformes, family Batrachoididae) and the squeaker catfish *S. schoutedeni* (order Siluriformes, family Mochokidae) (Henglmüller and Ladich 1999; Wysocki and Ladich 2001; Vasconcelos and Ladich 2008; Lechner et al. 2010). These three species differ considerably in their sound-generating mechanisms, their inner ears and auditory peripheries and subsequently in the development of vocalizations, auditory sensitivities and their abilities to detect sounds of similar-sized conspecifics.

### 4.2.1 Sound-Generating Organs and Auditory Periphery

*Trichopsis vittata*, *S. schoutedeni* and *H. didactylus* produce sounds by fundamentally different mechanisms, illustrating the large diversity in sound-generating (sonic) organs in bony fishes (for reviews see Ladich and Fine 2006 and Chap. 3 by Fine and Parmentier). Croaking gouramis produce pulsed sounds by plucking two enhanced pectoral fin tendons over bony elevations of fin rays when beating their pectoral fins (Fig. 4.1a). Catfish produce broadband stridulation sounds by rubbing the dorsal process at the base of their pectoral spine in a groove of the shoulder girdle when abducting and adducting spines (Fig. 4.1c). Toadfish produce low-frequency drumming sounds when rapidly contracting swim bladder muscles (Fig. 4.1e). Again, the auditory periphery differs widely between the investigated species. Labyrinth fishes (suborder Anabantoidei) possess an air-breathing organ

Species	Sonic organ	Auditory periphery
<i>Trichopsis vittata</i>	(a) 	(b) 
<i>Synodontis schoutedeni</i>	(c) 	(d) 
<i>Halobatrachus didactylus</i>	(e) 	(f) No hearing specialization

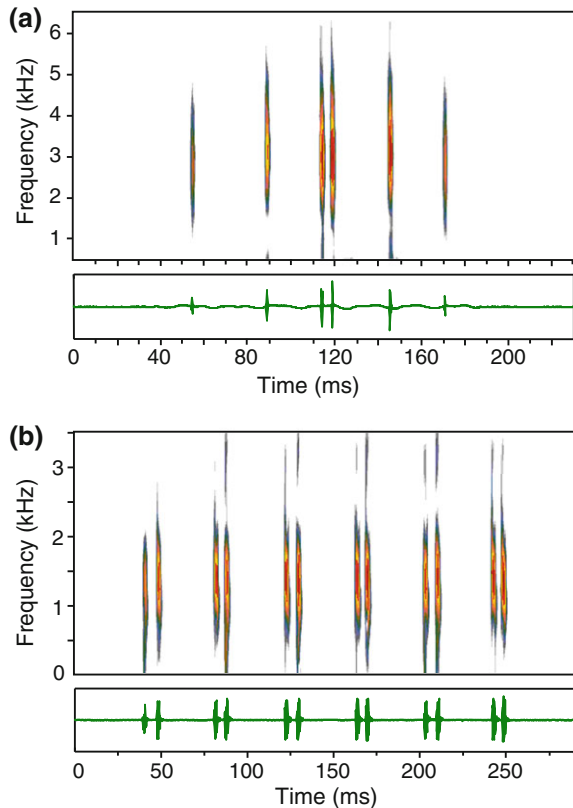
**Fig. 4.1** Overview of sound-generating mechanisms and accessory hearing structures in *Trichopsis vittata*, *Synodontis schoutedeni* and *Halobatrachus didactylus*. **a** Illustrates the tendon plucking mechanism in *T. vittata*, **c** the pectoral stridulatory apparatus in catfish and **e** drumming (sonic) muscles in *H. didactylus*. **b** Cross section through the head of labyrinth fish (perciform family Osphronemidae) showing the close connection between the air-breathing supra-branchial chamber and the inner ear (saccule). **d** Weberian ossicles of the catfish *S. schoutedeni* connecting the swim bladder acoustically to the inner ear. **f** Toadfish lack accessory hearing structures. **a** and **c** Modified after Ladich (1991), **b** modified after Vierke (1978) and **d** modified after Lechner et al. (2010). Drawings in (a), (c) and (e) by H.C. Grillitsch

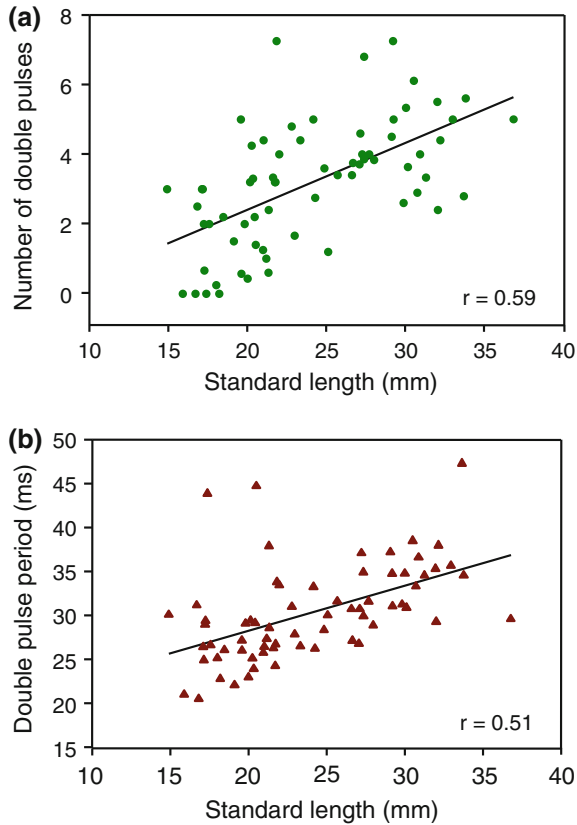
dorsally of the gills, which enhances their hearing sensitivity (Fig. 4.1b) (Schneider 1941; Yan 1998). The squeaker catfish has three Weberian ossicles that transmit swim bladder vibrations to the inner ear (Fig. 4.1d). Finally, toadfish lack any peripheral auditory structures for hearing enhancement.

### 4.2.2 Croaking Gourami *Trichopsis vittata*

Agonistic behaviour starts on day 11 in croaking gouramis. Pectoral fin beating was first accompanied by sound production on day 57. After day 87, sounds were recorded in the course of all fights (Henglmüller and Ladich 1999). Croaking sounds of *T. vittata* are built up of series of broadband bursts, each one produced by one pectoral fin. Initially, sounds consist of single pulsed bursts indicating that each fin had only one enlarged tendon (Fig. 4.2a). Later, sounds are built up of series of mostly double pulses, which demonstrates that both pectoral tendons are fully developed (Fig. 4.2b).

**Fig. 4.2** Sonograms and oscillograms of croaking sounds of **a** an early stage juvenile (0.11 g) and **b** an adult *T. vittata* (0.8 g). Croaking sounds are built up of series of bursts consisting of single or double pulses. Note different axis ranges in **(a)** and **(b)**. **a** Modified after Wysocki and Ladich (2001). With kind permission from Springer Science and Business Media

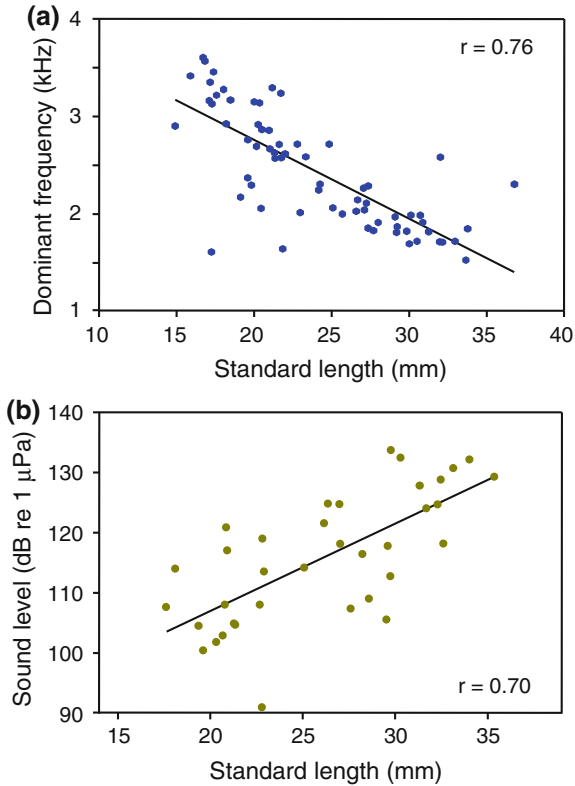




**Fig. 4.3** Correlation between **a** number of double-pulsed bursts and standard length and **b** the burst period of croaking sounds and standard length in *T. vittata*

The increase in the number of double pulses per sound (from 0 up to 7) is accompanied by an increase in the burst period, which results in a longer sound duration as the fish grow (Fig. 4.3a, b) (Henglmüller and Ladich 1999). The dominant frequencies of croaking sounds were always concentrated above 1 kHz. It was negatively correlated with size and decreased from about 3.5 kHz in the smallest fish to about 1.5 kHz in the largest fish investigated (Figs. 4.4a and 4.5a). Vocalizations became louder with growth, which resulted in a significant positive correlation between sound pressure levels and size in *T. vittata* (Figs. 4.4b and 4.5a) (Wysocki and Ladich 2001).

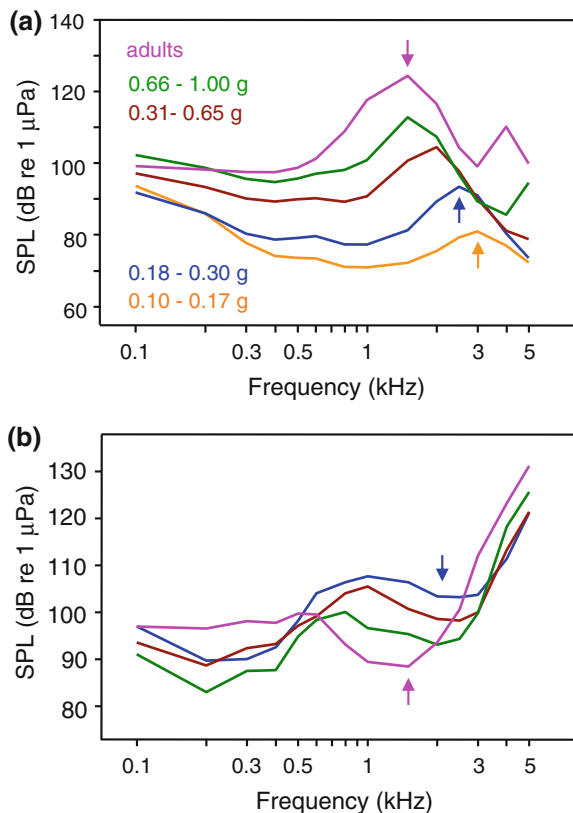
Auditory sensitivity could be obtained from 0.1 up to 5 kHz in all juvenile stages measured. The range of frequencies detectable did not change during growth in *T. vittata*, in contrast to the absolute auditory sensitivity (Fig. 4.5b) (Wysocki and Ladich 2001). Audiograms revealed a low-frequency sensitivity maximum between 0.2 and 0.3 kHz and a high-frequency sensitivity maximum between 1 and 3 kHz.



**Fig. 4.4** Correlation between **a** dominant frequencies and standard length and **b** sound pressure level of croaking sounds and standard length in *T. vittata*

In the frequency range 1–3 kHz, where main sound energies were concentrated, auditory sensitivity continuously improved with size, whereas at 4 and 5 kHz an opposite trend was observed. At lower frequencies a similar trend towards improvement was reported, except for adults. The most sensitive frequency in the high-frequency range shifted from 2.5 kHz in juveniles to 1.5 kHz in adults (see arrows in Fig. 4.5b).

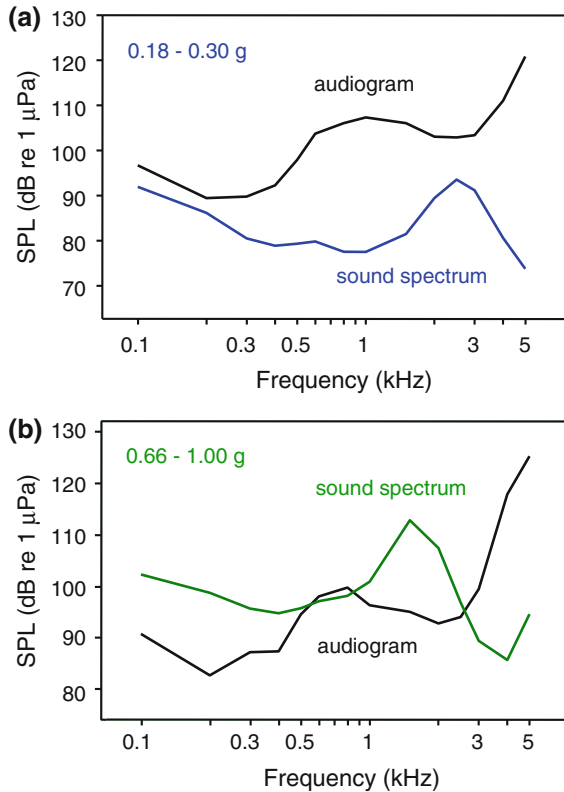
The ability to perceive vocalizations of similar-sized conspecifics during agonistic encounters and thus to communicate acoustically develops continually in *T. vittata*. Smallest juveniles investigated are most likely unable to communicate by sound because sound energies are too low to be detectable at any frequency. This is mainly due to low sound pressure levels and partly due to high hearing thresholds (Fig. 4.6a). When fish grow, sound pressure level and auditory sensitivity increase



**Fig. 4.5** **a** Mean sound spectral levels and **b** mean audiograms of different stages of juvenile and adult *T. vittata*. Arrows indicate shifts in main energies of sounds as well as of the auditory sensitivity maximum to lower frequencies during growth. Note that auditory sensitivity could not be determined in the smallest stage. After Ladich and Yan (1998), Wysocki and Ladich (2001). With kind permission from Springer Science and Business Media

and sound energies become high enough to be detectable (Fig. 4.6b). The high-frequency sensitivity maximum corresponds to the frequency range where main energies of sounds are concentrated (1–3 kHz) (Fig. 4.6b). In general, the results indicate that the auditory sensitivity develops prior to the ability to vocalize and that vocalizations occur prior to the ability to communicate acoustically.



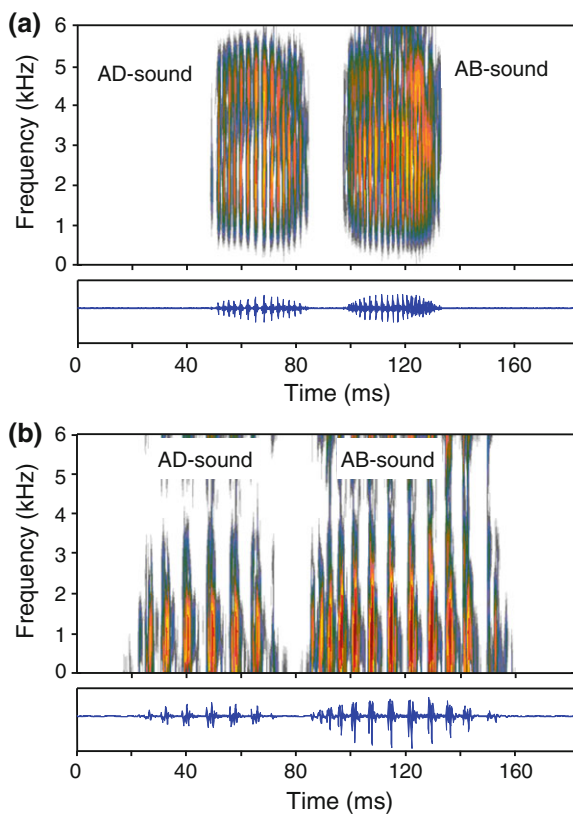


**Fig. 4.6** Comparison of mean audiograms in relation to mean absolute sound power spectra of croaking sounds in the **a** smallest and **b** the largest juvenile size group of *T. vittata* in which auditory sensitivities have been determined. After Wysocki and Ladich (2001). With kind permission from Springer Science and Business Media

### 4.2.3 Squeaker Catfish *Synodontis schoutedeni*

African squeaker catfish *S. schoutedeni* of all stages tested produce stridulation sounds during adduction and abduction of pectoral spines when animals were handled (Fig. 4.7a, b) (Lechner et al. 2010). Main sound characteristics change during growth. Pulse period and subsequently duration of adduction and abductions sound increased with size (Fig. 4.8a, b). This indicates that the distance between ridges as well as the entire dorsal process of the pectoral spine increases with growth.

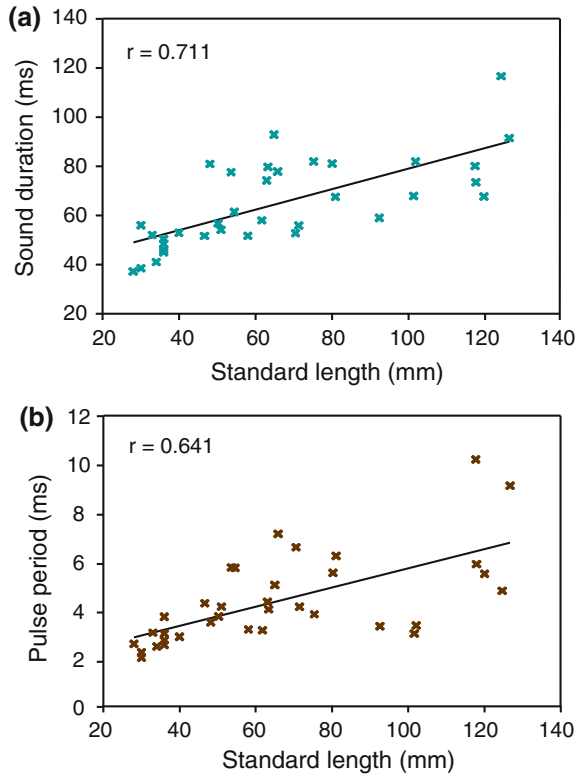
Sound pressure levels of stridulation sounds increased up to a standard length of 58 mm, whereas no further increase was observed in larger-sized *S. schoutedeni* (Fig. 4.9a). The Dominant frequencies of vocalizations decreased with size (Figs. 4.9b and 4.10a).



**Fig. 4.7** Sonograms and oscillograms of stridulation sounds of **a** an early stage juvenile (28–36 mm) and **b** an adult *S. schoutedeni* (group 116–127 mm). An adduction sound (AD-sound) and an abduction sound (AB-sound) is shown in both figures. Note different sound duration, pulse periods and main energies of sounds in **(a)** and **(b)**. Modified after Lechner et al. (2010)

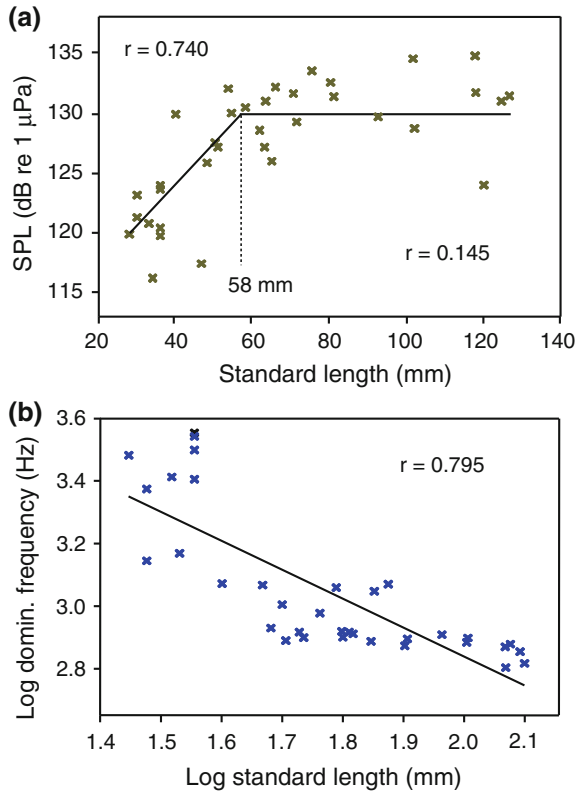
The auditory sensitivity in *S. schoutedeni* revealed different trends. First of all, hearing thresholds between 50 Hz and 6 kHz could be determined in all size stages (Fig. 4.10b). Best hearing abilities were found between 0.3 and 1 kHz except in the smallest group. The latter had their highest sensitivity between 2 and 3 kHz (91 dB re 1  $\mu$ Pa), whereas the largest group showed the lowest threshold at 0.3 kHz (72 dB). In general, larger animals showed better hearing at lower frequencies (50 Hz and 2 kHz) and lower hearing at the highest frequencies (5 and 6 kHz) (Lechner et al. 2010).

Comparison between absolute sound spectra levels and hearing thresholds of different-sized *S. schoutedeni* demonstrated that all size groups showed highest auditory sensitivity where main energies of sounds were concentrated (Fig. 4.11a, b).

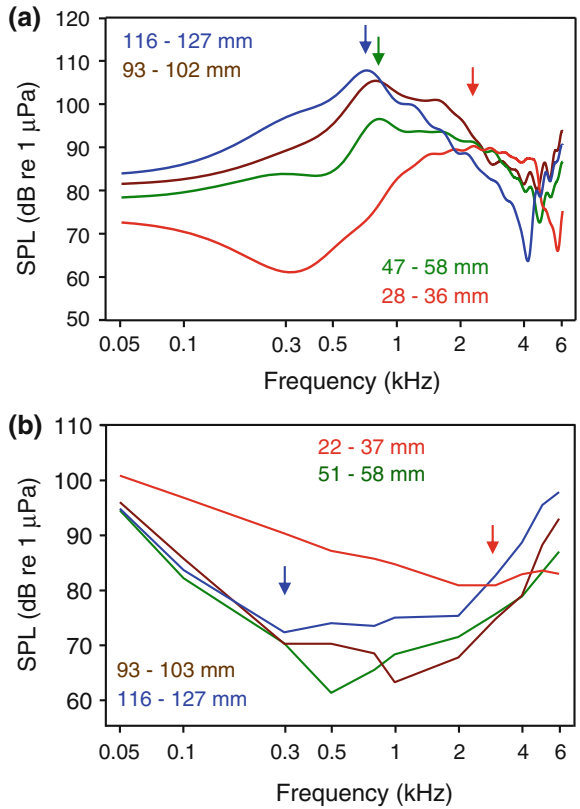


**Fig. 4.8** Correlation between **a** sound duration and standard length and **b** the pulse period of stridulation sounds and standard length in *S. schoutedeni*. Modified after Lechner et al. (2010)

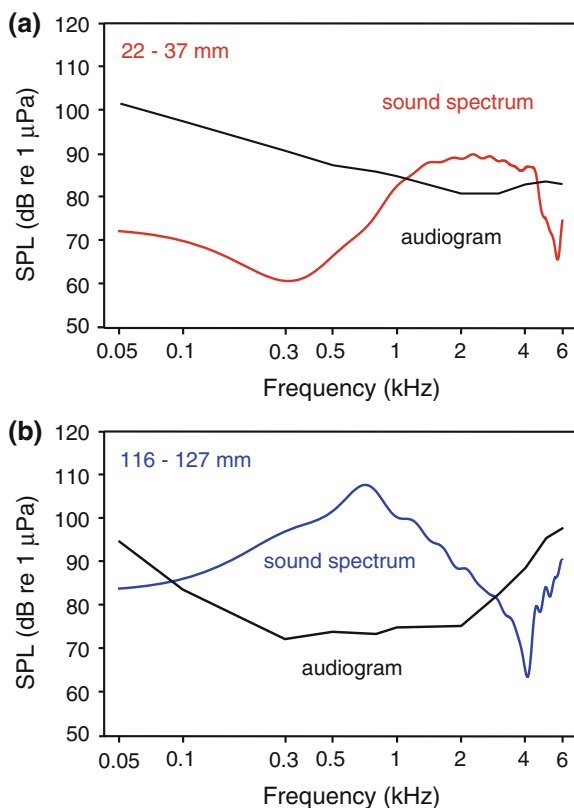
Furthermore, all size stages were able to detect sounds of same-sized fish. Due to their high auditory sensitivity, squeaker catfish are probably able to communicate acoustically at distances of 3–10 cm. This contrasts with the findings in the croaking gourami, where the smallest size group is probably unable to hear sounds of similar-sized conspecifics.



**Fig. 4.9** Correlation between **a** sound pressure level and standard length and between **b** dominant frequencies of stridulation sounds and standard length in the catfish *S. schoutedeni*. Note that the sound pressure level is correlated to standard length up to 58 mm SL (*left r-value*). **a** modified after Lechner et al. (2010)



**Fig. 4.10** **a** Mean sound spectra levels and **b** mean audiograms of different stages of juvenile and adult catfish *S. schoutedeni*. Sound pressure levels were measured at a distance of 5 cm. *Arrows* indicate shifts in main energies of sounds as well as in the auditory sensitivity maximum to lower frequencies during growth. Note differences between stages in **(a)** and **(b)**. Modified after Lechner et al. (2010)

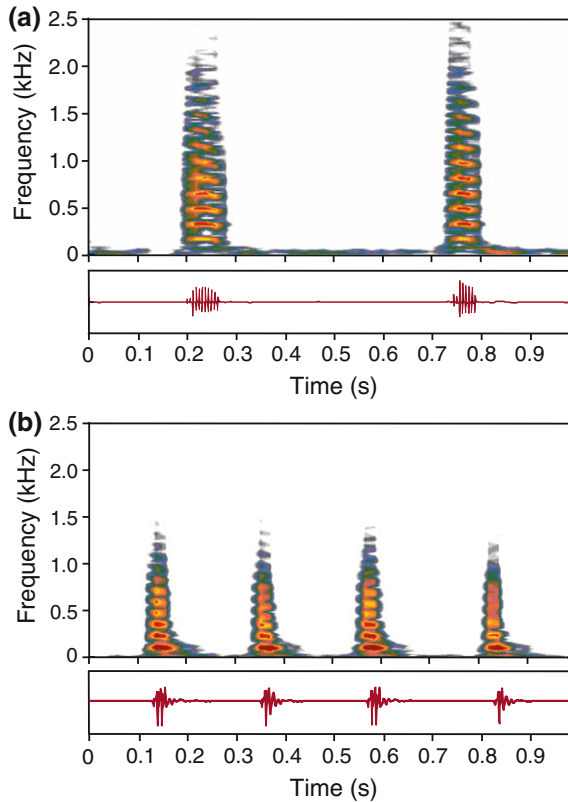


**Fig. 4.11** Comparison of mean audiograms in relation to mean absolute sound spectra levels of stridulation sounds in **a** the smallest and **b** the largest size group investigated in the catfish *S. schoutedeni*. Modified after Lechner et al. (2010)

#### 4.2.4 Lusitanian Toadfish *Halobatrachus didactylus*

Lusitanian toadfish exhibit aggressive behaviour at early stages of development, in particular when defending their shelters and when feeding. Sounds were recorded in all groups tested and started immediately when fish were handled (Vasconcelos and Ladich 2008). In the smallest size group ranging from 28 to 38 mm, not all individuals vocalized, in contrast to larger groups. In the smallest and the second group (54–66 mm), acoustic signals consisted of single grunts, whereas larger fish produced grunts in series (Fig. 4.12a, b). The total duration of single grunts decreased even though the pulse period within grunts increased. This is mainly due to the decrease in the number of pulses within grunt sounds (Fig. 4.13a).

Sound pressure levels increase with growth from approximately 110 dB up to 140 dB measured at a distance of 10 cm (Figs. 4.14 and 4.15a). The energy content of sounds also changes during development (Fig. 4.15a). Grunt sounds are built up

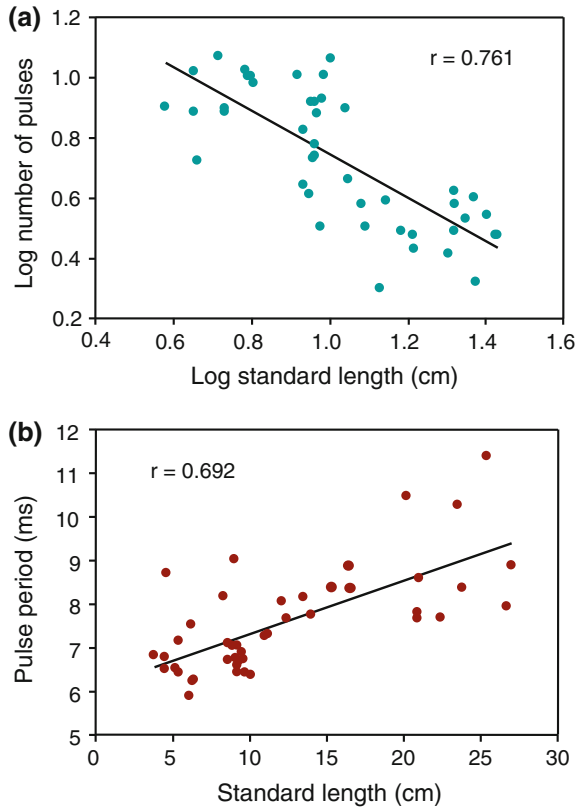


**Fig. 4.12** Sonograms and oscillograms of grunt calls emitted by **a** an early stage juvenile (6.1 cm SL) and **b** a representative of the largest group (28.5 cm SL) of *H. didactylus*. **a** shows two single grunts and **b** part of a grunt train. Note the shorter grunt duration and lower dominant frequency in (b). Modified after Vasconcelos and Ladich (2008)

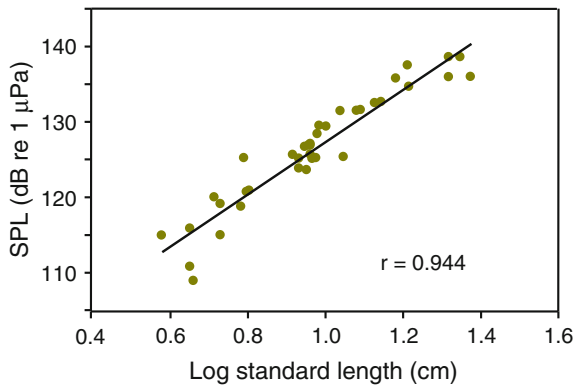
of several harmonics and main energies are found in different harmonics in different groups. While in the smallest group main energies are concentrated in the third and fourth harmonic, this gradually changes as fish grew. In the largest group, main energies are found in first harmonic (= fundamental frequency) (Fig. 4.15a).

In contrast to sound spectra, hearing abilities changed only slightly during growth. All size groups revealed best hearing at 50 Hz and a decrease in sensitivity towards higher frequencies (Fig. 4.15b). All audiograms are ramp-like, which indicates that toadfish lack hearing specializations. The smaller groups detect sounds up to 800 Hz, whereas larger fish hear up to 1 kHz. Moreover, smaller fish have slightly lower sensitivities at particular frequencies (100 Hz, 800 Hz, 1 kHz).

Comparison between sound power spectra and audiograms within the same size group showed that the agonistic vocalizations are clearly detectable in the largest groups. Sound energies of the first and second harmonics are considerably above hearing thresholds at their most sensitive frequencies below 300 Hz (Fig. 4.16b).

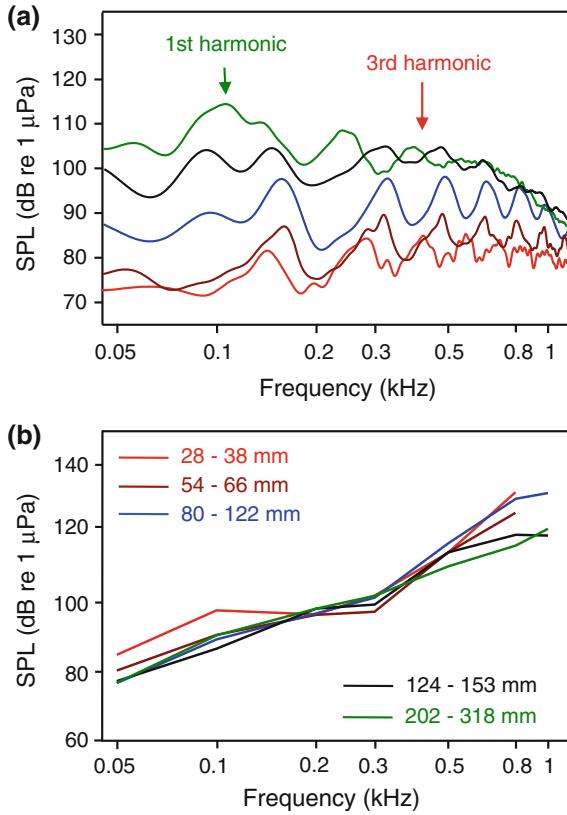


**Fig. 4.13** Correlation between **a** number of pulses within a grunt sound and standard length and **b** the pulse period and standard length in the toadfish *H. didactylus*. Modified after Vasconcelos and Ladich (2008)



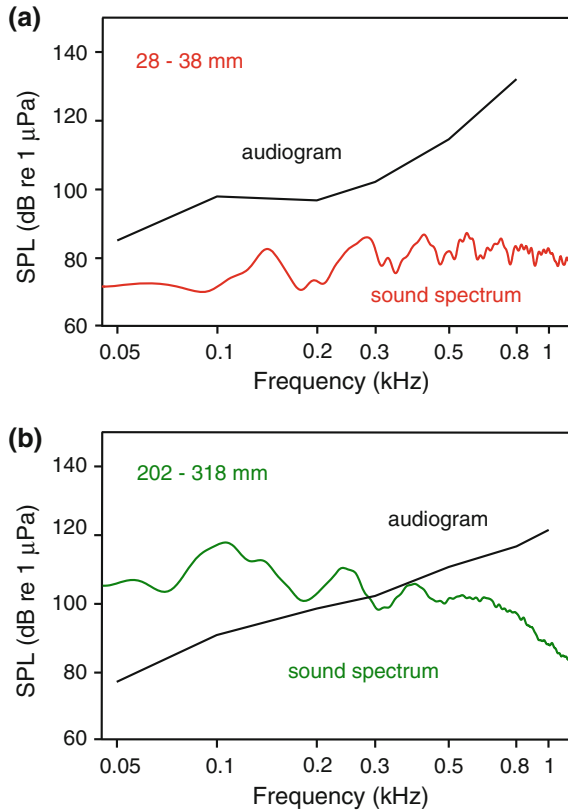
**Fig. 4.14** Correlation between sound pressure level and standard length in the toadfish *H. didactylus*. Modified after Vasconcelos and Ladich (2008)





**Fig. 4.15** **a** Mean sound spectra levels of grunt sounds and **b** mean audiograms of different stages of juvenile toadfish *H. didactylus*. Arrows indicate shifts in main energies of sounds during growth. Modified after Vasconcelos and Ladich (2008)

In the smallest juveniles, however, main sound energies are lower than in larger groups and are also present above 400 Hz, where hearing sensitivity is very low (Fig. 4.16a). The conclusion is that smallest juveniles will be unable to communicate acoustically with same-sized conspecifics or be able to do so at only very short distances. Acoustic communication develops gradually in the toadfish *H. didactylus*. This is mainly because the sound levels of grunt sounds are very low in the beginning and less so because of major improvements in hearing sensitivity during growth. Although Vasconcelos and Ladich (2008) determined only sound pressure levels in their ontogenetic study, the authors assume that that conclusion also holds for particle acceleration levels (for a discussion see Ladich and Fay 2013).



**Fig. 4.16** Comparison of mean audiograms in relation to mean absolute sound power spectra of grunt sounds in **a** the smallest and **b** the largest size group investigated in the toadfish *H. didactylus*. Modified after Vasconcelos and Ladich (2008)

### 4.3 Summary and Conclusions

The onset of acoustic communication is still poorly investigated in fishes. Competition for resources such as food (and places) and predator defence are no doubt the main elements in the life of animals at all stages (Schneider 1964; Henglmüller and Ladich 1999; Amorim and Hawkins 2005; Bertucci et al. 2012). Such competition often results in aggressive behaviour, which probably always includes visual threat signals and frequently acoustic signals. Due to a major lack of data, we cannot assess the percentage of fish that starts vocalizing in early stages of development. Data from representatives of non-related taxa such as siluriforms (Mochokidae—*S. schoutedeni*), scorpaeniforms (Triglidae—*E. gurnardus*), batrachoidiforms (Batrachoididae—*H. didactylus*) and perciforms (Osphronemidae—*T. vittata*; Cichlidae—*Metriaclicma zebra*) indicate that acoustic signalling during agonistic behaviour is

widespread in bony fishes. Nonetheless, it needs to be added that some vocal fish taxa do not compete aggressively during early stages of development and thus do not communicate acoustically. In these taxa, sound production and acoustic communication may start abruptly at the onset of the reproductive phase in their lives. Lack of sound production in pre-reproductive phases, however, is difficult to prove as long as these stages have not yet been investigated carefully. Researchers tend to neglect juvenile stages, although they may be very interesting in this context.

The papers reviewed in this chapter underline that sound production in early stages of development does not provide evidence that fish communicate acoustically. Proving that fish communicate by sound according to the definition given above requires showing that receivers react to acoustic signals independently of other types of signals. As long as this has not been demonstrated by complicated playback experiments in several ontogenetic stages, we must rely on other data. One approach is to compare absolute sound spectra for particular communication distances with hearing curves; this has been done in three studies so far. This comparison between sound production and detection allows us to assess whether sounds are detectable in different stages of development. Current results gained in three non-related taxa indicate that the development of acoustic communication is quite diverse between taxa. This is due to different trends and processes during development.

Trends in the development of sound production are more homogeneous than trends in the development of auditory sensitivities among those taxa in which both processes have been investigated. Sound production is linked to the growth of sound-generating organs and of animals in general. These morphological changes result in an increase in sound duration, pulse periods, pulse numbers and in sound pressure levels, but a decrease in the main frequencies of sounds. The only exception from these trends is that the duration of toadfish grunts becomes shorter with growth. This, however, may be because larger toadfish produce series of grunts (more grunts per time) than smaller toadfish. The common trends in the development of sound characteristics are interesting considering that sounds are produced in completely different ways. The croaking gourami produces sounds by plucking enhanced pectoral fin tendons, the squeaker catfish by rubbing pectoral spines in the shoulder girdle and the Lusitanian toadfish by contracting intrinsic swim bladder muscles. Besides changes in the main frequencies of sounds, the most important common process is the increase in sound intensity due to the increase in sound-generating structures such as muscle mass, fin ray sizes and swim bladder volumes.

Common trends are less clear in the ontogenetic development of auditory sensitivities. This may reflect the large diversity in the auditory structures involved in hearing. In the croaking gourami, hearing is improved by an air-breathing chamber located laterally of the inner ears, in the squeaker catfish by an ossicular connection to the swim bladder, whereas toadfish lack any peripheral structure for hearing improvement. Absolute sensitivity in the gourami and the catfish increases and the most sensitive frequency decreases where the main energies of vocalizations are concentrated. No such trends are found in the Lusitanian toadfish. Absolute

sensitivity increases only slightly at the lowest frequencies in the toadfish, and the most sensitive frequency does not change at all. Similarly, Alderks and Sisneros (2011) showed that there were no differences in the saccular tuning profiles in small juveniles, large juveniles and adults of the midshipman *P. notatus*, and that the ability to detect higher frequency sounds increases with size.

Based on these data it can be concluded that pre-reproductive stages of all species investigated can communicate acoustically. This is because the frequency range where main energies of sounds are concentrated correlate with the frequency range of highest auditory sensitivity. Nonetheless, there are major differences between species in the onset of acoustic communication. In the croaking gourami and the Lusitanian toadfish, the results suggest that sound detection develops prior to the ability to generate sounds and that acoustic communication might be absent in earliest developmental stages because of low hearing sensitivities and low sound levels. This contrasts with the ontogenetic development of the squeaker catfish, a species which possesses the highest auditory sensitivity due to its Weberian apparatus and in which all stages are potentially able to detect sounds of similar-sized conspecifics. Thus, the development of intraspecific acoustic communication differs between bony fish species mainly because of differences in the development of their hearing abilities. This development does not necessarily depend on the presence or absence of peripheral hearing structures. The croaking gourami and the squeaker catfish differ although both utilize air-filled cavities for hearing enhancement. This calls for detailed analyses in order to determine whether agonistic behaviour potentially involves sound communication besides visual threat displays.

## References

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