Animal Signals and Communication 4

Friedrich Ladich *Editor*

Sound Communication in Fishes

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Preface

This book is the first dedicated entirely to *Sound Communication in Fishes*. The topic has frequently been included in other books such as ‘How Animals Communicate’ edited by Sebeok (1977), ‘Hearing and Sound Communication in Fishes’ edited by Tavolga et al. (1981), ‘Behaviour of Teleost Fishes’ edited by Pitcher (1993), ‘Communication in Fishes’ (first volume) edited by Ladich et al. (2006) and ‘Fish Bioacoustics’ edited by Webb et al. (2008). Except for ‘Communication in Fishes’ the number of chapters dealing with sound production and behaviour of fishes was limited to one or two chapters within these books.

What is meant by the term ‘sound communication,’ and what is the content of the present book? Communication per se is an information-transfer process during which a sender generates a signal perceived by a receiver and which results in a change in the behaviour of the receiver for the advantage of the sender (Myrberg 1981; Bradbury and Vehrencamp 1998, 2011). According to this definition communication is only demonstrated when a receiver (be it a conspecific or heterospecific such as a predator) alters its behaviour after detecting a signal. However, we must admit that in the majority of cases and species in which signals in general and sound signals in particular have been described changes in behaviour of receivers have not been reported although there have been several successful playback experiments. Alternatively, we could argue that signals and in particular sound emission per se is evidence for communication because the production of sounds and sound-generating mechanisms would not have evolved without an advantage for the signaler. Sound production can be costly and risky for senders because signals may be intercepted by predators, and the sender may end up in the stomach of the wrong receiver (Myrberg 1981; Tyack 2000). Thus, in the strict sense our knowledge of sound communication in fishes is limited and would never fill up an entire volume. Therefore, this book will deal not only with sounds having a proven signal function but with sounds assumed to have evolved for communication purposes. This is most likely the case with sounds produced by special sound-generating mechanisms and emitted in clearly defined intra- and interspecific behavioural contexts. These sounds are often termed vocalizations to indicate the behavioural context and importance. This definition excludes sounds unintentionally produced during feeding, swimming or exchange of air (e.g. air gulping or air release from swimbladders).

The present book broadens the perspective dealt within the two-volume treatise 'Communication in Fishes' (2006) in which seven chapters were dedicated to sound communication. Chapter 3 by Fine and Parmentier provides an overview and update of our knowledge of sonic organs and their function by concentrating on newly studied taxa such ophidiiformes. It provides a cladogram showing known vocal fish taxa, confirming that sound production evolved independently multiple times in fishes.

Chapter 2 by Bass, Chagnaud and Feng reviews the literature on neuronal control of sound production in fishes. The chapter shows that the large diversity in sound-producing mechanisms is mirrored in the large diversity in sonic/vocal motor nuclei in the hindbrain and the spinal cord. However, the entire vocal pathways up to the mid or forebrain is only investigated in toadfishes, and therefore we need to be cautious when generalizing these data. Many more groups, including taxa lacking swim bladder muscles, need to be studied to determine if sound production is controlled similarly in all vocal fish taxa.

The other chapters review topics which have by my knowledge not previously been dealt with in a comprehensive fashion. Amorim, Fonseca and Vasconcelos analyse in Chap. 1 the degree to which fish sounds are used for choosing mates. So far only a few studies show that female fishes choose mates based on particular sound characteristics. This contrasts with the large number of successful playback studies in other taxa such as insects, frogs and birds.

Ladich reviews two neglected topics, namely sound production in juvenile and female fishes. Typically, investigators concentrate on male vocal behaviour because males are the vocal sex in the majority of reproducing fish species. Males defend territories and attract females to nest sites with vocalizations. Nevertheless, because of the male- and reproduction-centred scientific approach of the majority of studies we miss that females and juveniles also need access to resources such as food throughout the year and that access to limited resources necessarily results in aggressive behaviour and frequently acoustic signalling. Chapters 4 and 5 summarize gaps in our knowledge, attempt to close them and hopefully will stimulate research on juveniles and females.

Lugli directs our attention to the need to study the ecoacoustical conditions in fish habitats (see also Ladich 2013, 2014) in order to understand evolutionary constraints on sound production and communication. In his Chap. 6 he illustrates that fishes communicate acoustically under conditions far from optimal. The majority of vocalizing taxa such as toadfishes, gobies, sculpins, gouramies, holocentrids and damselfishes are substrate breeders and live between rocks, stones, roots, coral reefs and close to hard or soft sandy bottoms, all of which can affect sound spectra and propagation. Many of these substrate breeders inhabit shallow waters, e.g. tidal zones or creeks, which are noisy and quite unsuitable for propagating low-frequency sounds generated via various swim bladder mechanisms. These acoustical conditions subsequently limit acoustic communication to a few metres or even centimetres. Currently, there is no evidence that fishes communicate (respond to sound by showing either positive or negative phonotactic behaviour) beyond 10 m in the field (Mann 2006). Distance restrictions separate fishes from many other vocal animals such as insects, frogs, songbirds and mammals and point to the need for more well-designed playback studies in the field (McGregor 1992).

Finally, in their Chap. 7 Maruska and Sisneros summarize our knowledge of the influence of hormones on acoustic signaling and sound detection in fishes. They report on the hormone-dependent auditory plasticity and vocal production particularly in toadfishes and cichlids and indirectly indicate that our knowledge of endocrinological influences on sound communication is quite limited.

We hope this book will be a useful compendium for professionals as well as students working on animal communication, fish biology, neurobiology and animal behaviour. It should help to stimulate research in this field to close gaps frequently pointed out in the course of this preface.

Friedrich Ladich

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Contents

Chapter 1
Fish Sounds and Mate Choice

M. Clara P. Amorim, Raquel O. Vasconcelos and Paulo J. Fonseca

Abstract Fish acoustic signals associated with mating behaviour are typically low-frequency sounds produced by males when in close proximity to females. However, some species make sounds that serve the function and follow the design of advertisement calls, well known in insects, anurans, and birds. Close-range courtship acoustic signals may be used by females in mate assessment as they contain information of male quality such as size and condition. For example, sound-dominant frequency, amplitude, and fatigue resistance may signal body size whereas pulse period (i.e. muscle contraction rate) and calling activity are related with body condition in some species. Some signal features, such as sound pulse number, may carry multiple messages including size and condition. Playback experiments on mate choice of a restricted number of species suggest that females prefer vocal to silent males and may use sound frequency, amplitude, and mainly calling rate when assessing males. The assessment of males by females becomes more challenging when males engage in choruses or when sounds are otherwise masked by anthropogenic noise but almost nothing is known about how these aspects affect mating decisions and fish reproductive success.

We would like to dedicate this review to Professor Vitor Almada, a person of vision and a landmark in fish behaviour in Portugal.

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1.1 Introduction

Acoustic signals can be regarded as sexual ornaments subject to sexual selection including mate choice (Andersson 1994; Bradbury and Vehrencamp 1998). Male calls play an important role in species recognition and sexual stimulation driving mate attraction and reproductive success in mammals (Charlton et al. 2007), birds (Catchpole and Slater 2008; Nemeth et al. 2012), anurans (Ryan 1985; Gerhardt and Huber 2002), and in insects (Gray 1997; Gerhardt and Huber 2002; Tregenza et al. 2006). Numerous studies on vocal communication of birds, anurans, and insects have shown that acoustic signals convey some aspect of male quality that influences female mating preference, but this has been less investigated in mammals and fish (Charlton et al. 2007; Amorim et al. 2013a). However, fish represent the largest group of vocal vertebrates that rely on acoustic signals during various social interactions (Ladich 2004) and, therefore, are excellent models to study the evolution of vertebrate vocal communication. This taxon is not only highly diverse in species life histories, but also species contain simpler vocal repertoires. In addition, vocal and auditory neural pathways controlling for such behaviour are organised similarly in all vertebrates and evolved from an ancestrally shared brain region already present before the radiation of fishes (Bass et al. 2008).

Despite the many fish species relying on vocal signalling during reproductive activities, studies concerning the role of sounds in mate preferences and mating outcome are scarce. This is probably because such studies can be a daunting task. Difficulties include the inexistence of commercial underwater loudspeakers that can reproduce fish low-frequency pulsed sounds accurately (Fonseca and Maia Alves 2012), hindering the success of playback experiments in most fish species. Fish sounds are usually accompanied by signals of other sensory modalities, such as conspicuous visual displays, making the role of acoustic signals difficult to establish (Amorim et al. 2013b). Also, the lack of adequate motivation by subject fish, which is difficult to evaluate, may limit the response to experimental protocols (Myrberg et al. 1986). In addition, field studies are challenging because of the common visibility restrictions in underwater environments and the depth at which vocal fish live that hinder direct behavioural observation of target species (Zelick et al. 1999).

Despite the difficulties, the number of studies focussing on fish acoustic communication is steadily increasing and a few have started to unravel the function of mating acoustic signals in fish reproduction. Here, we provide an overview of the function of mating signals in fish and discuss possible future avenues in this field of research.

1.2 Acoustic Advertisement

Mate advertising calls are typically produced by males to attract receptive females and may convey information on species and sex identity, sexual motivation, and location (Bradbury and Vehrencamp 1998). The long-distance mate attraction signals are often labelled as advertisement calls (e.g. Tobias et al. 2011) and are common in birds, anurans, and insects (Gerhardt and Huber 2002; Catchpole and Slater 2008). In order to be effective advertisements calls should transmit over long distances (hence loud, low-frequency signals are favoured) and present a high duty cycle (with a long duration and a high repetition rate) to increase the detection distance and the ease of locating the sender. In addition, advertisement signals must contain features that are highly stereotyped within and between individuals to transmit unambiguous information on species identity (Bradbury and Vehrencamp 1998). In contrast, courtship signals that are exchanged during close-proximity interactions leading to mating should follow a different design as they convey information for mate assessment and mating synchronisation. Hence, courtship calls usually have a shorter active space (e.g. soft, higher-frequency signals) to decrease the chances of eavesdropping by conspecific mates and predators, and an increased duty cycle that often increases in tempo to signal motivation and to synchronise copulation (Bradbury and Vehrencamp 1998). In addition, courtship calls contain dynamic features that are dependent on mate quality and are therefore relevant in mate assessment (Gerhardt 1991). A mixed-design occurs in species where advertisement signals are made in a competitive mate-attraction context and/or also serve as courtship signals (Bradbury and Vehrencamp 1998). Examples include frogs, whose signals contain both stereotyped and variable parameters used, respectively, in species recognition and mate assessment (Gerhardt 1991).

1.2.1 Detection Distance

Male fish reproductive sounds are typically low frequency and made in close range of females during courtship or sometimes spawning (reviewed in Myrberg and Lugli 2006). In some species, however, males seem to advertise breeding sites with sounds, such as in batrachoidids (Winn 1967; Ibara et al. 1983; Thorson and Fine 2002a; Vasconcelos et al. 2012), pomacentrids (Myrberg et al. 1986), mormyrids (Crawford et al. 1997), and sciaenids (Mok and Gilmore 1983; Connaughton et al. 2000). In batrachoidids (toadfish and midshipman fish), for example, males establish nests under rocks in shallow waters of intertidal and subtidal zones and form choruses to attract females (Winn 1967; Ibara et al. 1983; Jordão et al. 2012). Batrachoidid sounds are loud and low frequency (e.g. 125 dB re: 1 μPa at 1 m, main frequencies below 300 Hz; Barimo and Fine 1998) but detection distances are probably short as absorption coefficients of low-frequency sounds are high in these shallow water environments (Fine and Lenhardt 1983; Bass and Clark 2003; Mann 2006; see Chap. 6). Ibara et al. (1983) carried out playback experiments in 8 m round tanks (0.6–1 m water level) and showed that female plainfin midshipman (*Porichthys notatus*) started accelerating swimming towards the speaker area from approximately 4.5 m. Consistently, Bass and Clark (2003) described that in intertidal areas with rocky-gravel substrate and approximately 5 m deep, natural male plainfin midshipman sounds attenuate to background noise levels within 3 m from

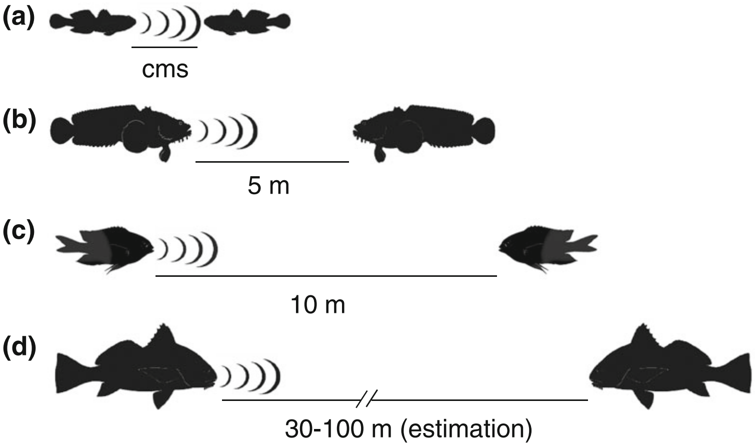

Fig. 1.1 Reported maximum detection/propagation distances of conspecific mating sounds for **a** the common goby *Padogobius bonelli* (Lugli and Fine 2003), **b** the oyster toadfish *Opsanus tau* (Fine and Lenhardt 1983), **c** the bicolor damselfish *Stegastes partitus* (Myrberg et al. 1986), and **d** the black drum *Pogonias cromis* (Locascio and Mann 2011). Detection distances will depend on habitat characteristics (water depth, substrate type, background noise) and auditory abilities of fish species

the nest. Fine and Lenhardt (1983) also found that in natural habitats (of 1 m depth with sandy-silt substrate) played back oyster toadfish (*Opsanus tau*) mating boatwhistles were lost in the background noise within 5 m (Fig. 1.1). Batrachoidids aggregate and form choruses (e.g. Winn 1967; Jordão et al. 2012), probably increasing detection distance, and their mating calls attract gravid females for spawning (Fish 1972; Winn 1972; McKibben and Bass 1998), similarly to advertisement calls of anurans (Gerhardt and Huber 2002).

Likewise, pomacentrids such as the bicolor damselfish (*Stegastes partitus*) advertise their nest sites producing chirps made in association with a conspicuous visual display (signal jumps), which seem to have a larger active space than batrachoidid sounds (e.g. Myrberg et al. 1986). Bicolor damselfish males form relative dense colonies and females need to travel 3 to over 8 m distance from their feeding territories to mate (Myrberg et al. 1986; Knapp and Warner 1991). Myrberg et al. (1986) have shown that chirps played back near conches could attract females from approximately 10 m away showing that male sounds are used to locate conspecific breeding males (Fig. 1.1). In playback studies with pomacentrid and batrachoidid species (Fish 1972; Winn 1972; Ibara et al. 1983; Myrberg et al. 1986; McKibben and Bass 1998), phonotaxis was elicited by playback alone with no additional stimuli, confirming the advertisement function of their calls.

One of the few examples of considerable long-distance advertisement calls in fish is assumed (but not proven by playback experiments) in sciaenids. Sciaenid males produce calls (drums) during the reproduction period in large vocal aggregations to attract females with which to spawn (Mok and Gilmore 1983;

Connaughton et al. 2000). For example, black drums (*Pogonias cromis*) have been estimated to be able to communicate within 30–100 m (Fig. 1.1), the distance limited by the background noise in the estuary and not by auditory sensitivity (Locascio and Mann 2011).

1.2.2 Duty Cycle

Fish advertisement calls also present a high duty cycle (Fig. 1.2). Batrachoidids produce sustained advertisement calls (boatwhistles and hums) with maximum rates of 10 min^{-1} (oyster toadfish; Fine et al. 1977) to 20–30 min^{-1} (Lusitanian toadfish, *Halobatrachus didactylus*; Amorim et al. 2010; Vasconcelos et al. 2012) for a few hours. The higher duty cycles observed in batrachoidids (*H. didactylus*) are comparable to those of some anurans and insects (Fig. 1.2) although the latter generally call at much higher rates (Gerhardt and Huber 2002). For example, the spring peeper *Pseudacris crucifer* call at a

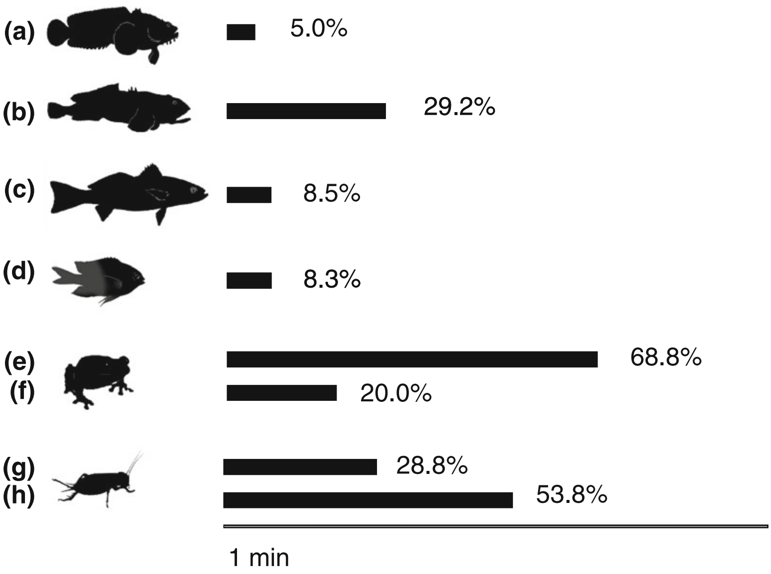

Fig. 1.2 Comparison of advertisement call duty cycles in fish and other taxa. *Black bars* represent the percentage of advertisement sound ('on time') per minute. 'On time' was calculated by multiplying sound duration by call rate. Maximum sustained call rates were used for fish whereas average population values were used in the remaining examples. The following call durations (ms)/call rates (sound min^{-1}) were considered: 300/10 for **a** *Opsanus tau* (Fine et al. 1977; Barimo and Fine 1998); 700/25 for **b** *Halobatrachus didactylus* (Amorim and Vasconcelos 2008; Amorim et al. 2010; Vasconcelos et al. 2012); 255/20 for **c** *Cynoscion regalis* (Connaughton and Taylor 1996; Connaughton et al. 2000); 200/25 for **d** *Stegastes partitus* (Myrberg et al. 1978); 550/21 for **e** *Hyla versicolor* (Wells and Taigen 1986); 160/75 for **f** *Pseudacris crucifer* (Zimmitti 1999); 100/173 for **g** *Gryllus lineaticeps* (Wagner and Reiser 2000); 87/370 for **h** *Cicada orni* (Fonseca 1991)

rate of 75 calls min^{-1} during the hours of maximum chorus activity (Zimmitti 1999), and the variable field crickets *Gryllus lineaticeps* show average calling song rates of 173 calls min^{-1} (Wagner and Reiser 2000). Because the average call duration is lower in *P. crucifer* and *G. lineaticeps* (160 and 100 ms, respectively; Zimmitti 1999; Wagner and Reiser 2000) than in *H. didactylus* (700 ms: Amorim and Vasconcelos 2008; Amorim et al. 2010) duty cycles are comparable in these species (but see Fig. 1.2e). Batrachoidid calls also vary from 300 ms (oyster toadfish; Barimo and Fine 1998) to continuous hums that last for minutes to an hour or more (plainfin midshipman; Ibara et al. 1983), which in combination with a sustained high calling rate can result in a very high duty cycle. Comparable calling rates can also be found in other fish species (Fig. 1.2). The sciaenid *Cynoscion regalis* calls at average rates of 20 calls min^{-1} that can be maintained for at least 2 h (Connaughton and Taylor 1996), whereas damselfishes (*Stegastes* spp.) chirp around 25 times per min during active courtship (Myrberg et al. 1978).

As expected, the calling rate of fish advertisement calls is lower than during courtship and higher than in agonistic interactions. For example, the calling rate of oyster toadfish males increases when females approach the male's nest (Fish 1972). On the other hand, Lusitanian toadfish males defend their nests from other male intruders with single to short sequences of boatwhistles, contrasting with the long sequences of advertising boatwhistles emitted to attract females (Vasconcelos et al. 2010).

1.2.3 Stereotypy

In the aforementioned examples, such as in toadfish choruses or sciaenid spawning aggregations, fish emit advertisement calls in a competitive mate-attraction context and/or during courtship (e.g. Fish 1972; Mok and Gilmore 1983). As expected, these fishes' calls include both highly stereotyped species-specific features and dynamic characteristics relevant to mate assessment (Gerhardt 1991; Bradbury and Vehrencamp 1998). For example, toadfishes and midshipman fish advertisement calls (boatwhistles and hums) share a common tonal structure but show clear interspecific differences in sound duration, fundamental frequency, waveform pattern, amplitude modulation and general structure (presence of additional 'notes'; Amorim 2006; Rice and Bass 2009). Part of these characteristics can also show some plasticity potentially relevant for individual assessment within a male chorus. For instance, sound duration and calling rate are modulated by the level of acoustic competition in the Lusitanian and in the Gulf (*Opsanus beta*) toadfishes (Thorson and Fine 2002a; Amorim et al. 2011). For example, in the Gulf toadfish, chorusing activity increases after sunset and males tend to increase calling rate while decreasing call duration (Fig. 1.3). In addition, calling rate and also pulse period (i.e. sonic muscle contraction period) are related to male body condition (lipid reserves) in the Lusitanian toadfish (Amorim et al. 2010) and calling activity is used at least in mate choice (Vasconcelos et al. 2012).

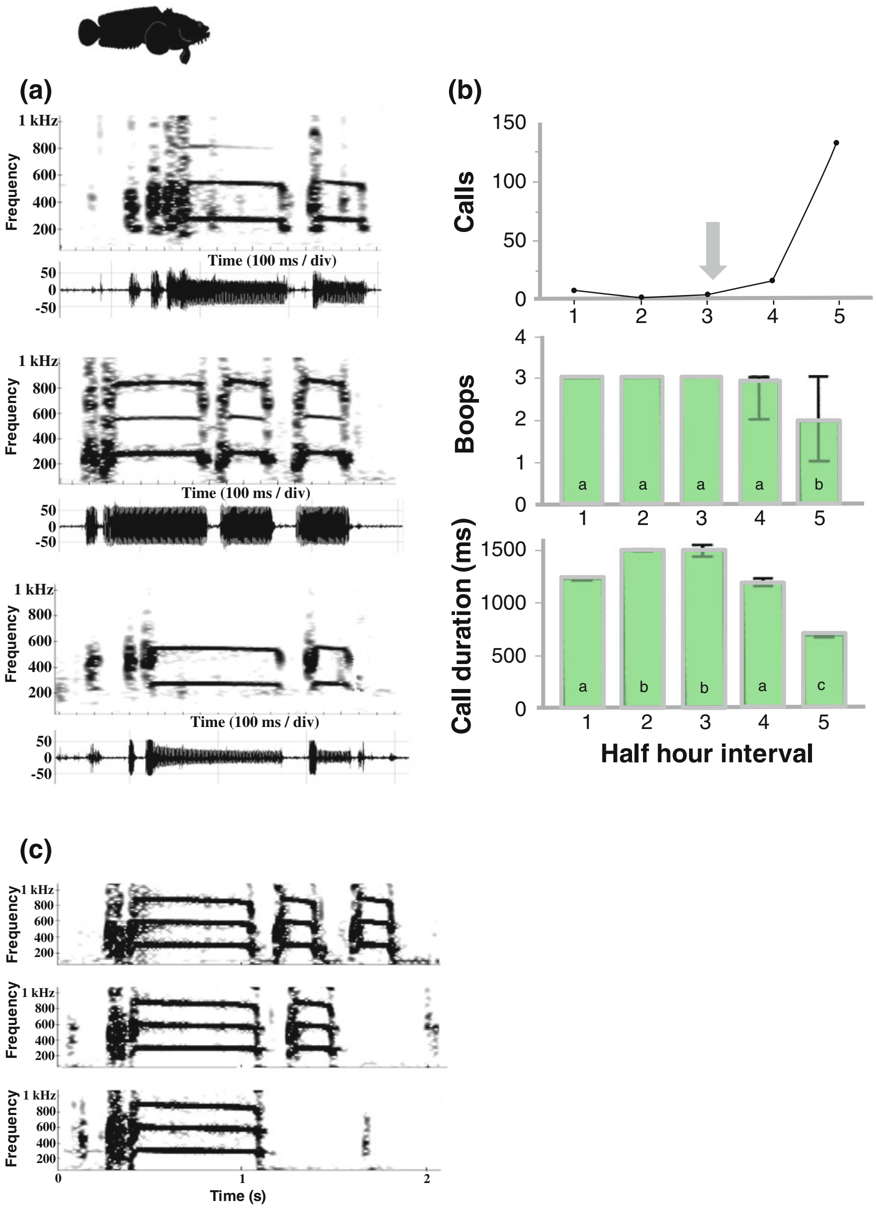

Fig. 1.3 The boatwhistles of *Opsanus beta* are typically made of one or more initial grunts followed by a variable number of tonal boop notes (1–5). **a** Sonograms and oscilllograms of *O. beta* boatwhistles depict individual differences in the number of boop notes and other boatwhistle characteristics. **b** After sunset (depicted by an *arrow*) chorusing activity increases and males tend to increase calling rate while decreasing call duration (different *letters* denote pairwise significant differences). **c** Calls are mainly shortened by producing fewer boop notes. (Adapted after Thorson and Fine 2002a.)

Similar examples can be found in the mormyrids of the genus *Pollimyrus,* the weakly electric fishes. These African fishes breed in murky lakes and rivers and make elaborate species-specific acoustic displays during female attraction that differ in the sequence of mating sounds which include grunts, moans, and growls (Crawford et al. 1997; Lamml and Kramer 2006). *Pollimyrus adspersus* generates prolonged moan–grunt sequences often terminated by a long growl, *P. isidori* emits a single grunt followed by several short moans (Crawford et al. 1997), whereas *P. marianne* and *P. castelnaui* produce a sequence of moans ending in a long-lasting moan superimposed by several grunts (Lamml and Kramer 2006). The acoustic features of a given sound type also differ markedly among species in frequency and temporal parameters (Crawford et al. 1997; Lamml and Kramer 2006). In addition to these more stereotyped features that enable species recognition, weakly electric fish mating sounds also contain dynamic components. For example, in *P. adspersus*, the dominant frequency of grunts is dependent on body mass and males also differ in their ability to produce sustained moans, both features being likely relevant to courtship and mate choice (Crawford et al. 1997).

Pomacentrid chirps of the damselfishes *Stegastes* spp. are no exception to this mixed acoustic design, and different sympatric species can be readily distinguished by the stereotyped number of pulses and pulse interval in the chirps (Myrberg et al. 1978). On the other hand, sound-dominant frequency shows high intraspecific variability as it is size dependent (Myrberg et al. 1986) and, as in many other fish species such as *P. adspersus*, it can be considered an index signal, that is, a signal conditioned by physical or physiological constraints thus revealing honest information (Maynard Smith and Harper 2003).

1.2.4 How Widespread are Advertisement Signals Among Fish?

Fish sounds have traditionally been classified as courtship signals. However, the chirps of pomacentrids and of the remaining given examples clearly fall into the category of advertisement calls inasmuch as they attract mates from relatively large distances (several body lengths), provide information on location of the sender, species identity, sexual identity and motivation, and elicit phonotaxis without additional stimuli. Other fish sounds could also be classified as advertisement calls, such as centrarchids' vocalisations (sunfish, *Lepomis* spp.) that provide further examples of species-specific sounds to attract mates (Gerald 1971). As pomacentrids, these fishes live in mixed-species colonies and are attracted to loudspeakers producing courtship sounds within a 3 m range. The attraction is stronger to conspecific than to heterospecific sounds (Gerald 1971). Goby males emit sounds from their nests to attract mates (e.g. Myrberg and Lugli 2006; Malavasi et al. 2008) but their sounds attenuate into the background noise within centimeters (Fig. 1.1; Lugli and Fine 2003). However, goby mating sounds still provide information on location, gender, and species identity of the sender (Malavasi et al. 2008; Pedroso et al. 2013) and sound playback elicits conspecific attraction (Tavolga 1958; Lugli et al. 1996; Rollo and Higgs 2008).

As many vocal fish live in shallow waters and emit low-frequency sounds with short-range propagation (e.g. Lugli and Fine 2003), perhaps it would be appropriate to extend the terminology of advertisement calls to close-range communication in fish as such signals could have the same function as the song of birds and the calls of insects and anurans.

1.3 Male Sounds and Mate Quality

In addition to calling for mate attraction, males of various fish species vocalise during courtship (reviewed in Myrberg and Lugli 2006). Once females are in close proximity, males will make a series of ritualised behaviours that often include vigorous visual displays and vocalisations, eventually culminating in mating. During these interactions females have the chance to evaluate males and choose the best candidates with which to mate. Choosy females can increase their fitness by either gaining direct benefits (e.g. increased territory quality, increased parental care) or indirect benefits, such as receiving 'good genes' that will enhance the viability and/or increase sexual attractiveness of offspring (Andersson 1994). As such, females prefer male morphological features or behavioural displays that advertise high male quality. In fish, as parental care is exceptionally common and males often need to defend a nest site for successful mating (Gross and Sargent 1985), larger males that are also in good body condition are usually preferred because they have access to better territories, possess larger nests, and can provide better parental care (e.g. Knapp and Kovach 1991; Lehtonen et al. 2007).

1.3.1 Acoustic Indicators of Male Size

How useful are fish courtship sounds in mate evaluation? Several features, as already mentioned, may, for example, be indicators of male body size. Acoustic features that vary with the vocal apparatus dimensions are honest advertisers of the sender size. In species without swimbladders (i.e. a resonant structure associated with sound production) or that produce sounds by contracting sonic muscles at a very high rate (e.g. boatwhistles and hums of batrachoidids; Bass and McKibben 2003) there is no relation between the spectral properties of the sound and male size. However, a negative relation of sound-dominant frequency with size is commonly found in several fish species that make sound pulses at a slow rate

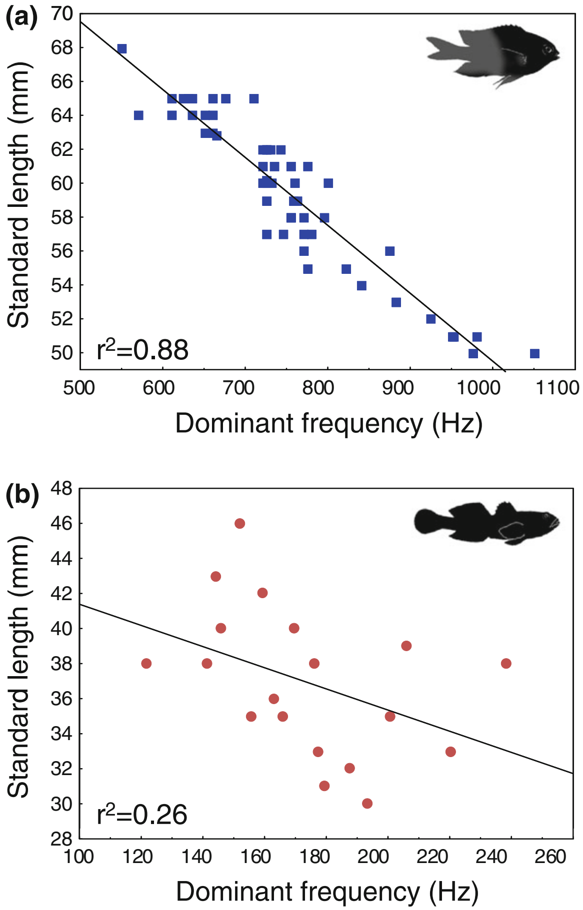

Fig. 1.4 Relation between dominant frequency of mating sounds and male standard length in the bicolor damselfish *Stegastes partitus* (**a**) and in the painted goby *Pomatoschistus pictus* (**b**). Differences in the coefficient of determination (r^2) and in the range of dominant frequencies observed in both species suggest that dominant frequency is a good indicator of male size in *S. partitus* but not in *P. pictus*. r^2 was calculated from raw data in *S. partitus* but from log-transformed data in *P. pictus*. (Adapted after Myrberg et al. 1993 (field data) and Amorim et al. 2013a)

(e.g. Schneider 1964; Myrberg et al. 1965, 1993; Bayoumi 1970; Ladich et al. 1992; Lobel and Mann 1995; Crawford et al. 1997; Connaughton et al. 2000; Amorim et al. 2003; De Jong et al. 2007; Maruska et al. 2012; Amorim et al. 2013a), with some species showing a stronger relation between these two features (e.g. Myrberg et al. 1993) than others (e.g. Amorim et al. 2013a), Fig. 1.4. The strength of this relation will likely depend on the resonant effect of the swimbladder (larger swimbladders resonate at lower frequencies) and on the scaling of sound-producing muscles as larger muscles produce longer twitches and hence sounds with lower frequency (Connaughton et al. 2000).

In fish, there are few studies that have related sound amplitude, namely sound pressure level (SPL), with body size (Wysocki and Ladich 2001; Lindström and Lugli 2000; Connaughton et al. 2000; Vasconcelos and Ladich 2008; Amorim et al. 2013a, b). The existing reports point to a positive relation between these traits, likely also resulting from a scaling effect of the sonic apparatus, namely muscle contraction power. Moreover, there is no report to date on the ability to change sound amplitude in fish, suggesting that it could be a reliable indicator of size. Indeed, Lindström and Lugli (2000) and Amorim et al. (2013a, b) have found that in both the sand goby (*Pomatoschistus minutus*) and the painted goby (*P. pictus*), males show low intramale variability in SPL concurrent with a strong relation between body size and the loudness of mating drums. Both species are small and seem to produce drums of comparable amplitude for a given size; for example, an increase of 1 cm in male standard length is expected to cause an increase in sound amplitude of c. 30 dB if from 3.0 to 4.0 cm, or c. 24 dB from 4.0 to 5.0 cm in both species (note that the relation is exponential) (Lindström and Lugli 2000; Amorim et al. 2013a, b). In contrast, Connaughton et al. (2000) found that in the weakfish *C. regalis*, a change of 11 cm in total length (25–36 cm) causes an increase of c. 10 dB in sound amplitude, suggesting that as with sound frequency, the informative value of certain parameters varies among species. In other taxa, as in insects, anurans, and birds, sound amplitude is known to play an important role in female choice, and although it appears to be unrelated to size it is commonly condition dependent and it can be regulated according to motivation and social context (Wyman et al. 2008; Nemeth et al. 2012).

Other acoustic features such as pulse number (and sound duration) can also be related to and hence informative of body size. For example, Amorim et al. (2013a) observed that in the painted goby *P. pictus* the number of pulses in a courtship drum is a significant predictor of male size but only explains approximately 18 % of the variability in fish length, probably because pulse number also varies with male condition. Likewise, Parmentier et al. (2011) found a relation between the number of pulses and body size in several species of Holocentridae but concluded that this feature is poorly informative as the slope of the relation is weak. The number of pulses in a sound also varies with fish motivation (Myrberg et al. 1965). The increase in pulse number (and pulse rate) in the courtship sounds leading to the spawning embrace of haddock (*Melanogrammus aeglifinus*; Hawkins and Amorim 2000) illustrates that this acoustic feature is motivation dependent and probably carries multiple messages regarding the sender's quality including, size, condition, and motivation.

Fatigue resistance has also been pointed out as an acoustical feature that varies with male size in fish. This feature represents the increase in pulse period during sound production likely caused by fatigue of the sound-producing muscles during pulse emission. Winn and Marshall (1963) noted that in *Holocentrus rufus* (Holocentridae) the pulse period at the start of grunts elicited by human manipulation was fairly constant, whereas at the end of the call the pulse period increased. In this species sound is generated by the repeated contraction of paired bilateral sonic muscles extrinsic to the swimbladder that is dependent on the firing rate of the motor axons innervating the sonic musculature (Gainer et al. 1965). Parmentier et al. (2011) observed the same fatigue pattern in other holocentrid species (genera *Myripristis*, *Sargocentron* and *Neoniphon*) and suggested that resistance to muscle fatigue could be used to assess body size. More recently, Amorim et al. (2013a) have found that fatigue (measured as the ratio between the average pulse period observed at the end and the beginning of the mating drum) was very stereotyped in the painted goby (*P. pictus*) and that it was a good predictor of male size, explaining 45 % of the variability found in this male feature. This increase in resistance to fatigue in larger animals was, however, not found in the congeneric sand goby (*P. minutus*) that make similar drums but with a higher pulse repetition rate than *P. pictus* (Amorim et al. 2013b), suggesting interspecific differences in physiological constraints in sound production.

The aforementioned features can also vary with the animal's physiological state namely in fish species that undergo pronounced seasonal changes in the sonic muscles (e.g. Connaughton et al. 1997; Modesto and Canário 2003; Nguyen et al. 2008). For instance, in the weakfish *C. regalis* sonic muscle hypertrophy associated with the breeding season results in the emission of sounds with lower frequency and higher amplitude (Connaughton et al. 1997).

1.3.2 Acoustic Indicators of Male Condition

Another male feature frequently assessed by females of various animal groups is male condition. In small gobies of the genus *Pomatoschistus* and in the Lusitanian toadfish *H. didactylus*, mating sound duration (higher number of pulses) is positively related with the male condition factor (Fulton condition factor; Amorim et al. 2010, 2013a; Pedroso et al. 2013). In addition, pulse period, which corresponds to the sonic muscle contraction period, is negatively related with body fat reserves in the Lusitanian toadfish (Amorim et al. 2010). In other words, only males with high fat reserves are able to contract sonic muscles in a sustained high rate during the emission of boatwhistles. This acoustic feature shows low intra- and interindividual variability in this species (coefficient of variation <8 %; Amorim and Vasconcelos 2008; Amorim et al. 2011), inasmuch as it is constrained by the central pattern generator in the hindbrain (Bass and Baker 1990; Bass et al. 2008), suggesting that males with higher body lipid levels are advertising their quality to females by sustaining sonic muscle contraction close to their physiological limit.

Perhaps the most striking indicator of male condition is the observed positive relation between calling rate and body lipid reserves in *Pomatoschistus* spp. and in the Lusitanian toadfish *H. didactylus* (Fig. 1.5; Amorim et al. 2010, 2013a; Pedroso et al. 2013). In *Pomatoschistus* the relation between body lipid reserves and calling activity was detected in 20 min periods whereas in *H. didactylus* calling activity was monitored over approximately 2 weeks, suggesting that body energetic reserves are strongly constraining both intense calling bouts and sustained calling activity in these fishes. In *H. didactylus* depletion in body lipid content may also have been due to the limited chances of foraging as males must remain close to secure the nest and to prevent egg predation (Modesto and Canário 2003). Painted goby *P. pictus* males emit both thumps and drums along with visual displays when courting females (Amorim and Neves 2007). Curiously, males of this species that are in better (lipid) condition invest mainly in drumming activity suggesting that drums

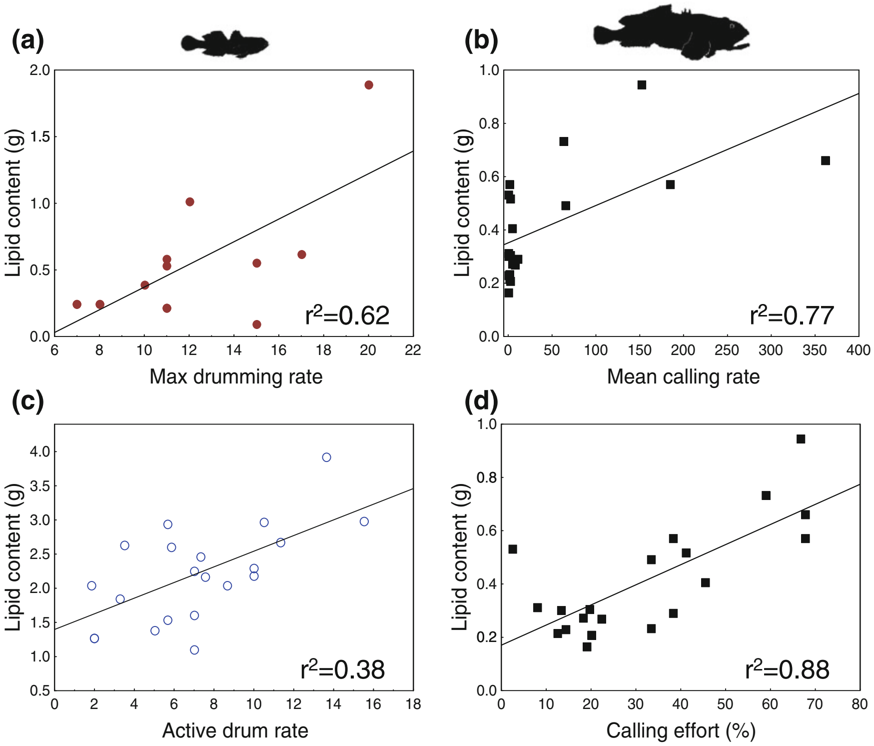

Fig. 1.5 Relation between calling and body lipid content in the gobies *Pomatoschistus pictus* (**a**, *N* = 11), *P. minutus* (**c**, *N* = 20), and the Lusitanian toadfish *Halobatrachus didactylus* (**b**, **d**, *N* = 20) indicating that only males with a higher body condition can sustain a high acoustic activity. Max drumming rate: maximum number of mating sounds produced in a minute in 20 min courtship sessions; Active drumming rate: mean drumming rate (drum min^{-1}) during acoustic activity observed in 20 min courtship sessions; Mean calling rate: mean number of boatwhistles emitted per hour during periods of up to a fortnight; Calling effort: percentage of time (at the hour level) spent calling during periods of up to a fortnight. Lipid content is expressed relative to 100 g of fresh tissue. r^2 concern regressions using lipid content as a dependent variable (**a**, **c**) or as a predictor (**b**, **d**) and refer to log-transformed data in **a**. (Adapted after Amorim et al. 2010, 2013a; Pedroso et al. 2013)

are more costly to produce than thumps or visual displays and are therefore honest signals of male quality (Amorim et al. 2013a). Coincidently, *P. pictus* males that showed high drumming activity tended to successfully mate unlike males that showed a high thumping rate (Amorim et al. 2013a).

In addition to body energetic reserves, Mitchell et al. (2008) have proposed that calling rate may be limited by glycogen depletion in the sonic muscles. Connaughton et al. (1997) observed in the weakfish *C. regalis* a congruent sharp decrease in lipid and glycogen levels in the sonic muscles during the period of maximum sound production at the peak of the breeding season. In contrast, lipid levels of the sonic muscles of *H. didactylus* are not related to calling activity (Amorim et al. 2010).

The above studies lead us to believe that sustained calling (and general courtship) throughout the breeding season is energetically costly, depleting both somatic and sonic muscle reserves, which is sometimes aggravated when associated with nest defence as in gobies and batrachoidids. In addition, conspicuous and sustained calling may accrue extra costs of attracting predators or parasites (Gannon et al. 2005), or conspecific male competitors who can steal fertilisations or take over the nest (Kenyon 1994).

1.4 Testing the Role of Acoustic Signals in Female Mate Choice

Although several studies in fish have shown various acoustic features to be honest signals of male quality there is a paucity of data demonstrating that sounds are used in mate choice (e.g. Aalbers and Drawbridge 2008). The contribution of male sounds to female fish mating decisions has been assessed in several ways including by playback experiments and correlation/regression analyses. Playback experiments are a prime tool to test the role of specific acoustic traits across taxa (McGregor 1992). However, the phonotaxis tests that provide robust bioassays to study call function in frogs can rarely be applied to fish because sounds are usually made within visual contact (Gerhardt and Huber 2002; Sect. 1.2.1). Hence, few playback experiments have been carried out successfully without additional stimuli (Tavolga 1958; Ladich 2004) and others, even when providing additional stimuli, do not manage to elicit clear behavioural responses (reviewed in Myrberg et al. 1986).

1.4.1 Preference for Vocal Males

The first step to demonstrate the relevance of mating sounds is to show that females prefer vocal to silent males. In a classical study Tavolga (1958) has shown that females of the frillfin goby *Bathygobius soporator* neither oriented to visual stimulus of a confined male in a flask nor to a sound source playing back male courtship sounds. However, when both stimuli were presented simultaneously they readily approached the confined male or the transducer. This response was also attained when synthetic sound variants that altered frequency, pulse duration, and pulse repetition rate one at a time, fell within natural ranges (Tavolga 1958). More recently, Myrberg and Stadler (2002) found a similar response pattern in the congeneric notchtongue goby *B. curacao* in which females were only attracted to a conspecific male confined in a bottle when it was accompanied by the playback of courtship sounds. Both studies clearly show that vocal goby *Bathygobius* spp. males are more attractive than silent males.

Two recent two-choice studies have shown that cichlid females preferred to affiliate with males that have been previously associated with courtship sounds than to control males (Verzijden et al. 2010; Maruska et al. 2012). In both studies, sounds and the visual stimulus of the male were presented uncoupled in time putting into evidence a crossmodal function of acoustic signals in courtship. In fact, other studies that assessed the function of fish sounds with playback experiments had already supported the crossmodal function of different sensory modalities in fish communication as animals only responded to conspecific sound playback if pre-exposed to stimuli of other sensory modalities, such as visual or chemical (Tavolga 1956, 1958; Lugli 1997; Lugli et al. 2004). The relevance of the order of sensory stimuli presentation and the degree of temporal displacement has never been studied in fish and needs to be further explored.

Another recent two-choice study has instead approached the relative role of acoustic signals in multimodal communication. Painted gobies gravid females that were exposed to a dichotomous choice of courtship sounds versus a control (silence or white noise) did not show a preference for conspecific sounds (Amorim et al. 2013b). However, when courtship sound playback was associated with visual access (but not chemical) to a conspecific male, females preferred to affiliate with the male associated with sound than with the control male. Notably, female preference was influenced by male visual courtship effort before the start of sound playback (preplayback period) but this effect decreased during playback and disappeared after sounds ceased (postplayback period; Amorim et al. 2013b). These results indicate that courtship sound alone does not seem to affect mate preference in this goby species (as in *Bathygobius* spp.; Tavolga 1958) but when presented in a bimodal context it becomes a salient feature overriding visual information (Fig. 1.6). Different sensory modalities composing multimodal stimuli interplay in complex fashions (Candolin 2003; Bro-Jørgensen 2010) and this interplay needs to be studied if we are to understand the significance of acoustic signals in fish courtship and mating decisions.

1.4.2 Acoustic Features

The previous examples only tackled the relevance of vocalising during courtship interactions but preference is expected towards particular acoustic traits such as dominant frequency or sound duration because they can advertise male quality (see Sects. 1.3.1 and 1.3.2). In a landmark study, Myrberg et al. (1986) carried out a set of playback experiments in the field showing that females of the bicolor damselfish *S. partitus* were preferentially attracted towards sound sources broadcasting natural chirps of lower dominant frequency, characteristic of larger males (see Fig. 1 in Myrberg et al. 1986). As territorial males were removed prior to playbacks, females performed their choices based solely on acoustic information. In these experiments bicolor damselfish females had a choice between the sounds of two males that differed by 4 mm (8 % of standard length) and by 70 Hz (710 vs. 780 Hz) in

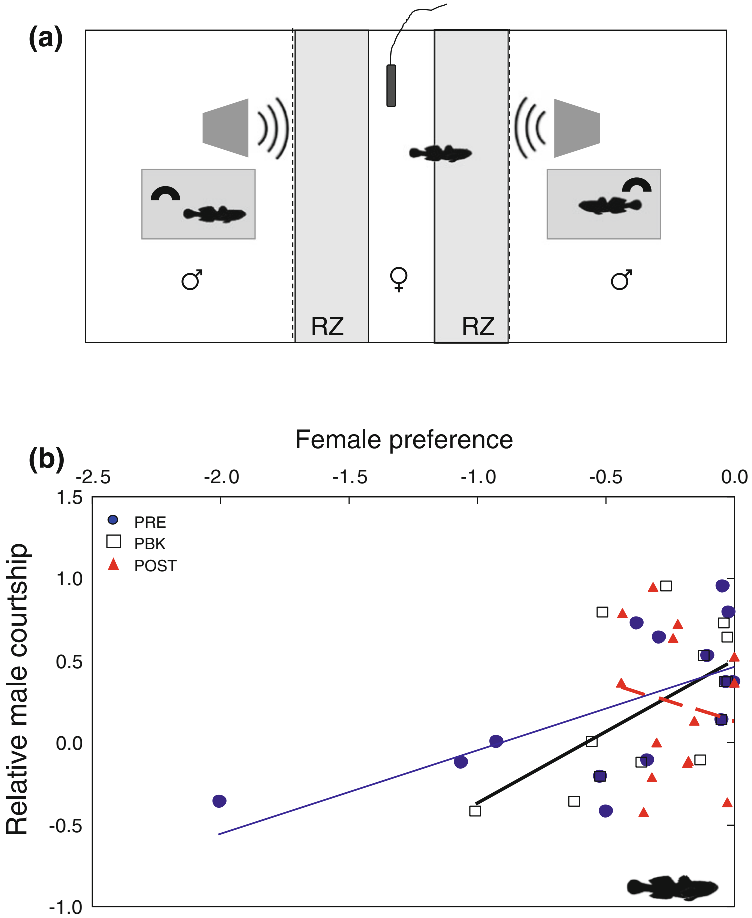

Fig. 1.6 Playback experimental setup used in Amorim et al. (2013b) to assess the role of courtship sounds in mate choice in *Pomatoschistus pictus* (**a**). Female preference for confined males associated with sound playback versus control males (associated with silence or white noise) was measured by the percentage of time the female spent in the sound 'response zone' (RZ) in relation to the total time spent in the two RZs. The experiment consisted in three consecutive 5 min periods of silence (PRE), playback (PBK), and postplayback (POST). Females showed an increase in the percentage of time spent in the sound RZ from PRE to POST periods but male visual courtship activity also influenced female preference. In fact, there was a significant interaction between the relative male courtship (ratio between the mean visual courtship levels of the 'sound' and the 'control' males) and the playback effect (playback period) as depicted in (**b**). In the PRE period (no acoustic stimuli) female preference increased with relative male courtship ($r^2 = 0.40$) but in the PBK period this tendency was weaker ($r^2 = 0.34$). In the POST period, this relationship was reversed and the data showed a large dispersion ($r^2 = 0.02$) indicating that female preference for the sound RZ was unrelated to male visual courtship. Note that the spread of data points in relation to the *x*-axis (female preference for the sound response zone) became smaller and shifted to the right side of the axis (i.e. with larger values) from PRE to POST periods. *Filled circles*, *open squares*, and *filled triangles* refer to PRE, PBK, and POST trial periods, respectively. *Blue fuzzy line*, *solid black line*, and *dashed red line* are tendency lines for the PRE, PBK, and POST trial periods. Female preference and relative male courtship data are log-transformed. (Adapted after Amorim et al. 2013b)

dominant frequency (c. 10 % difference) played back 1.5 m apart. Although this experiment points to the significance of dominant frequency in mate choice in the bicolor damselfish only sounds from two males were used and it is possible that other differences between these two natural pulsed signals, such as in temporal patterns, could have influenced female preference.

Perhaps the only known fish model that shows robust phonotactic response to the playbacks of mating sounds of conspecific males with no additional visual stimulus is the plainfin midshipman *P. notatus*. In a series of playback experiments McKibben and Bass (1998) showed that gravid females quickly approached, touched, and circled underwater loudspeakers playing humlike continuous tones. Playback experiments carried out in concrete tanks showed that female midshipman can distinguish sounds on the basis of their fundamental frequency, intensity, duration, presence of gaps between successive signals, and degree of amplitude modulation (McKibben and Bass 1998, 2001). Although this does not ascertain female preferences it provides the basis for mate choice because choice is probably based on the perception of relative variation of certain parameters within the range of signal recognition (McKibben and Bass 2001). By using two-choice experiments McKibben and Bass (1998) demonstrated female preference for the more intense of two humlike signals differing by 3 dB and for the speaker playing back longer hums with shorter intervals between signals (higher duty cycle; Fig. 1.7). However, in contrast to the results of Myrberg et al. (1986) females did not prefer lower-frequency hums differing by 10 Hz, but they chose the frequency closest to the expected hum frequency at the test temperature. Preference was not detected for

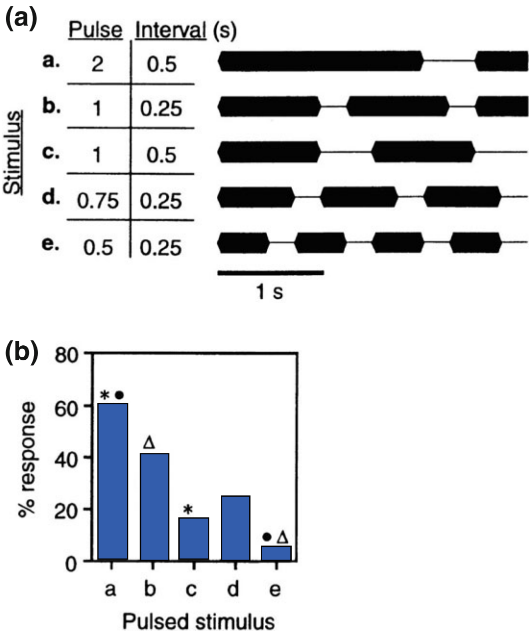

Fig. 1.7 **a** Pulsed stimuli (*a*–*e*) used in playback experiments with *Porichthys notatus* consisted of 90 Hz tones (frequency of mating calls) with the pulse and interval durations indicated. Envelopes are shown at right for 3 s of each stimulus. **b** Percentage of fish that subsequently responded to a continuous tone (responsive fish) that approached each of the five different pulsed stimuli. (Adapted after McKibben and Bass 1998)

pure tones in comparison to tones containing a second harmonic with different relative phases between the first and the second harmonic, suggesting that the harmonics present in natural sounds are not relevant for mate choice (McKibben and Bass 1998).

A few correlative/regression studies have pointed to the importance of calling rate to the male's reproductive success. Mann and Lobel (1995) have passively monitored the sounds made by three damselfish *Dascyllus albisella* males in the field. By continuously recording the sounds of these males these authors found that the maximum calling rate observed in the day prior to spawning was positively correlated with brood size. Although few males were monitored and brood size was assessed visually into brood size classes, the study of Mann and Lobel (1995) suggests that the ability to call at high rates influences mate choice and male fitness. Further, the frequency of the visual behaviour signal jump, which is tightly associated with chirp production (Myrberg et al. 1986), is correlated with male fat reserves and male reproductive success in the bicolor damselfish *S. partitus* (Knapp and Kovach 1991).

1.4.3 Calling Rate

In a recent experiment with the painted goby *P. pictus*, males that succeeded to mate made longer mating drums (higher number of pulses and pulse period) and had higher drumming activity (Amorim et al. 2013a). Although each territorial male was allowed to mate with only one ripe female, and hence females could not choose among several males and could only decide whether to spawn with the available male, the results suggest that painted goby females are choosing males based on their vocal capacity (higher duty cycles) which is tightly linked with body fat reserves (Amorim et al. 2013a). Curiously, neither visual courtship rate nor male size seems to be under mate choice in this species as males that were successful in mating did not differ from unsuccessful males in these traits (Amorim et al. 2013a). As visual courtship is unrelated with fat reserves in *P. pictus* (Amorim et al. 2013a), the above findings suggest that females are choosing males based on condition-dependent traits and go along with the damselfish studies (Knapp and Kovach 1991). It is the male that provides paternal care to the clutches both in painted goby and in damselfish, therefore it is likely that in these species, and in other fish species with paternal care, females prefer high-condition males to maximise their fitness. Consistently, fish males with higher fat reserves enjoy a higher egg-hatching success and females are known to prefer better fathers (e.g. Kvarnemo et al. 1998; Knapp and Kovach 1991; Lindström et al. 2006; Sisneros et al. 2009).

The most compelling study showing that condition-dependent vocal activity determines male mating success in fish with paternal care is the one carried out in nature by Vasconcelos et al. (2012) with the Lusitanian toadfish. Vasconcelos et al. (2012) passively monitored for up to 2 weeks the individual acoustic activity of 56 males that spontaneously occupied artificial concrete nests in an estuarine intertidal area. These authors found that unlike boatwhistle acoustic features (e.g. duration or frequency), the maximum calling rate and the ability to sustain calling (i.e. calling effort: the percentage of time spent calling) were good predictors of the number of eggs received by the male in the nest during the study period (Vasconcelos et al. 2012). Whether the number of eggs obtained by a male in its nest is a reliable proxy of male fitness in this and other fish species remains to be investigated. Also, no study thus far has ascertained that calling activity signals parental quality in fish as observed in other taxa (e.g. Dolby et al. 2005). We can just conclude indirectly from the study by Knapp and Kovach (1991), who demonstrated that the number of courtship dips (dive movements) of male damselfish *S. partitus* are reliable indicators of male parental quality, that courtship calling may indicate parental quality as well. The authors did not record acoustic signals during their investigation but we know from numerous studies that *S. partitus* regularly emits chirp sounds during courtship dips (Myrberg 1972).

1.5 Detecting and Selecting Mates in Aggregations (Chorus)

Many species aggregate during the breeding season. This behaviour may be governed by the need to find appropriate sites for reproduction (Danchin et al. 2001), to reduce predation risks related, for example, to the interception of advertisement signals by predators (Myrberg 1981; Luczkovich et al. 2000) taking advantage of dilution effects (Foster and Treherne 1981), increased vigilance (Boland 2003), or confusion effects (Krakauer 1995), and to enhance mate attraction by increasing loudness and the area covered by the calling fish sounds (McCauley and Cato 2000). The effort and risk for a newcomer to assess a suitable reproduction habitat can be reduced if this habitat is already occupied by breeding conspecifics. Indeed, availability of appropriate nesting sites, food resources, ability for predator detection or defence might have been previously screened by residents, easing the evaluation of such parameters (Doligez et al. 2003). Moreover, for species where mate finding is dependent on acoustic advertisement, the aggregation may reduce the calling effort needed to announce the presence to the opposite sex. Breeding aggregations of vocal breeding fish are widespread and include species where males nest in dense aggregations and provide paternal care to the offspring in the nest (e.g. batrachoidids, centrarchids, and pomacentrids), to species that form leks or spawning aggregations where males only provide gametes to females (e.g. sciaenids and cichlids; Winn 1967; Gerald 1971; Mok and Gilmore 1983; Myrberg et al. 1986; Verzijden et al. 2010).

1.5.1 Choruses and Vocal Interactions

Males that vocalise together in aggregations not only cover a wider ‘vocal area’ for mate attraction, but also extend the duty cycle and enhance output loudness thus increasing the overall sound broadcast. For instance, in the Australian Great Barrier Reef, McCauley and Cato (2000) reported that choruses produced by schools of the grunter *Terapon theraps* spreading over several kilometres, at estimated depths below 30 m, could be heard at 5–8 km out from its centre. *Terapon theraps* sounds are produced in midwater with dominant frequencies above 500 Hz (McCauley and Cato 2000), and thus the wavelength (less than 3 m) is much smaller than the water column depth, enhancing its propagation range (Bass and Clark 2003). However, and as previously mentioned (see Sect. 1.2.1 and Chap. 6), in shallow water reefs or for benthic fish breeding in shallow waters the sounds usually attenuate much faster and may travel only a few metres, but fish should still benefit from an enhanced detection range when engaging in a chorus.

On the other hand, to engage in a chorus will likely entrain some masking of a male’s vocalisations by the background sound cacophony. Masking can, however, be reduced if superposition of sound signals can be avoided by males singing close to each other. Such avoidance is a common strategy found in acoustic interactions in several animals (insects: Gerhardt and Huber 2002; frogs: Dyson and Passmore 1988; Gerhardt and Huber 2002; birds: Todt and Naguib 2000) and probably common in fish. For example, singing Lusitanian toadfish males usually tend to alternate vocalisations with their neighbours (Fig. 1.8). When males of Gulf toadfish *O. beta* increase their calling rate after sunset they make shorter and simpler calls thus avoiding overlapping their calls (Thorson and Fine 2002a; Fine and Thorson 2008). Winn (1967) also found that in the oyster toadfish *O. tau* overlapping is rare but call alternation does not differ from what is expected by chance. Congruently, in the croaking gourami *Trichopsis vittata*, a southeast Asian air breathing labyrinth species (Anabantoidei), opponents always generate sound alternately when engaged in dyadic contexts (Ladich et al. 1992; Ladich 1998) which shows that fish may avoid masking regardless of the social context.

Another strategy found in some sound-signalling animals that tend to synchronise instead of alternate their sounds, is to enhance the detectability of their own signals and the effectiveness for mate attraction by time-shifting the sounds to lead the vocal interactions (precedence effect, insects: Greenfield et al. 1997, 2004; frogs: Dyson and Passmore 1988). This behaviour remains to be recognised in fish. Call synchronisation may also be used in chorusing to disturb and mask the acoustic signals of an opponent (birds: Todt and Naguib 2000). In fish, Thorson and Fine (2002b) observed short agonistic grunts embedded in the mating boatwhistle of a male *O. beta* neighbour and proposed that it is a dominant agonistic display.

Animals may also involuntarily increase the amplitude of their own vocalisations in relation to background noise (Lombard effect, most studied in mammals and birds; e.g. Brumm and Zollinger 2011), which may also be accompanied by a frequency shift. Recently, Holt and Johnstone (2014) observed an increase in sound

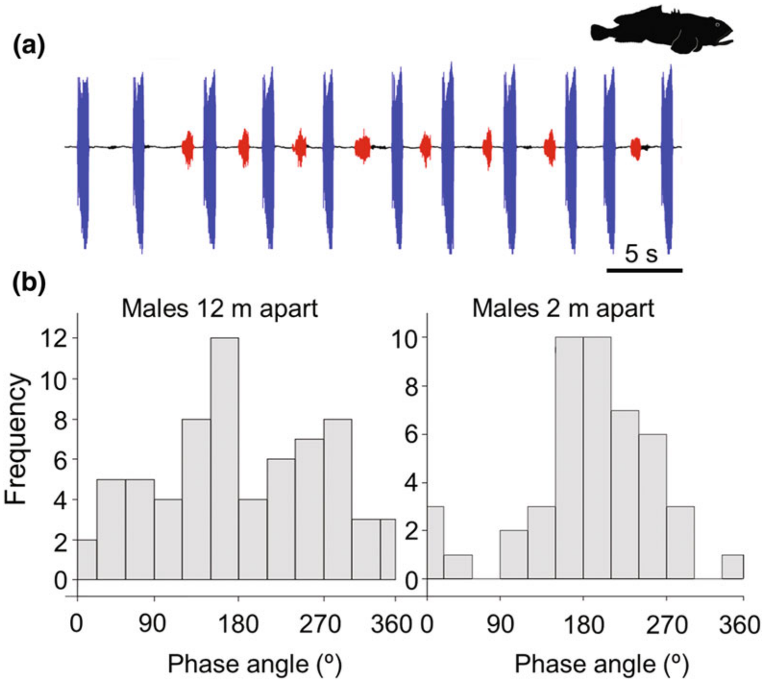

Fig. 1.8 Vocal interactions among neighbour Lusitanian toadfish in a chorus in their natural estuary habitat. **a** Oscillogram depicting boatwhistles of two fish nesting 2 m apart showing alternation of the vocalisations. **b** Phase histograms showing the pattern of vocal interactions between two fish nesting 12 m (*left*) and 2 m apart, respectively. 0° or 360° indicate synchrony and 180° reveals strict alternation with the boatwhistles of one fish occurring in the middle of the interval of the vocalisations of the other male. Vocalisations of close neighbours were entrained in an alternating pattern while the interaction pattern disappeared for larger distances above a few metres

amplitude (Lombard effect) in *Cyprinella venusta* when white noise was played back at a level higher than natural ambient noise. It remains to be shown if the amplitude or frequency of fish sounds change in response to social acoustic interactions, including increased chorus background noise.

Other subtle forms of vocal interactions have been observed in chorusing fish. Males' vocal activity might be adjusted to their neighbours' vocalisation rates, increasing or decreasing their own effort depending on the subject's condition.

Winn (1967) and Fish (1972) showed that in the oyster toadfish, playbacks simulating neighbours calling at a high rate (18 boatwhistle min^{-1}) increased the calling rates of nesting males but boatwhistles played back at a lower rate did not elicit changes in singing behaviour. Jordão et al. (2012) pursued similar experiments with the Lusitanian toadfish and found a more complex pattern of vocal interactions in chorusing males. These authors found that when nesting males were calling at a high rate (typically high-condition males) they adjusted their calling rate to that of their neighbours (i.e. the rate of the playback) but males that were calling at a lower than average rate did not alter their calling rate with the playback. This suggests that there may be several vocal interaction patterns likely dependent on male condition and motivation. Changes in calling rate may further be elicited by territorial intrusions simulated with acoustic playbacks such as found in the Gulf toadfish (Remage-Healey and Bass 2005), suggesting that adjustments in calling rate among neighbouring males mediate not only competition in mate attraction but also direct agonistic interactions.

1.5.2 Detection of Vocalisations in a Chorus

The first constraint for finding a mate would be to discriminate sounds from single males in the complex chorus background. To the best of our knowledge there is only one report of the behaviour of a female entering a chorus. Fish (1972) observed a sudden increase in calling rate by an oyster toadfish male as a female approached and swam to its nest. Recent measurements of the hearing abilities of Lusitanian toadfish, based on the representation in auditory evoked potentials of single boatwhistles embedded in a boatwhistle chorus background, suggest that individuals may discriminate them if the boatwhistle amplitude is 1–2 dB above the level of the chorus. In addition, the amplitude pattern and temporal structure of a boatwhistle could be retrieved by subtracting from the AEP response to a boatwhistle mixed with a chorus the response to the chorus stimulus alone (D. Alves, MCP Amorim, RO Vasconcelos, PJ Fonseca, unpublished data).

Although toadfishes' boatwhistles are relatively short calls (Amorim 2006; Rice and Bass 2009), males of the plainfin midshipman emit continuous hums (for minutes to an hour) with a flat temporal envelope and small interindividual variability in fundamental frequency (Ibara et al. 1983; Brantley and Bass 1994). If males call nearby and differ slightly in their hum's fundamental frequency the acoustic waveforms will interfere to produce acoustic beats characterised by amplitude and phase modulations, resulting from the continual shifting from in to out of phase of the fundamental frequencies (McKibben and Bass 2001). In a single-choice playback experiment with gravid females using two-tone beats (i.e. beats resulting from two humlike tones simulating two neighbouring males), McKibben and Bass (2001) showed that beat stimuli were more attractive as the difference in the frequency of tones decreased and when they were less amplitude modulated, that is, when they best resembled single hums. The preference for single hums in opposition to concurrent hums suggests that females prefer nests with a single humming male (Bass and McKibben 2003) or perhaps males that distance sufficiently from other males to be unequivocally distinguished. Nevertheless, both behavioural and physiological studies have shown that midshipman females have the neural mechanisms required for concurrent signal segregation, that is, the ability to discriminate concurrent humlike signals (e.g. McKibben and Bass 1998; Bodnar et al. 2001). How females discriminate and choose mates within a male chorus still needs to be studied in fish but the high attenuation of fish sounds in shallow waters may ease the female's task, even in species with intense advertising sounds such as batrachoidids (Fine and Lenhardt 1983).

1.6 Hearing Sexy Signals in Today's World

Fishes rely on their mechanosensory systems to interpret crucial information from the acoustic environment, such as the presence of predators, prey, and conspecifics (e.g. Remage-Healey et al. 2006). Indeed, teleosts show an exceptional diversity of structure and function of their sensory systems, such as the auditory system, suggesting that, during the evolutionary process, species acquired different adaptations to assess acoustic information in their highly diverse environments (Braun and Grande 2008).

Animals that communicate with sound must cope with the problem of extracting information under masking background noise. Aquatic habitats comprise sounds generated both by abiotic sources, such as wind and water flow, and biotic sources, such as vocal fish and snapping shrimps and other crustacean sounds. In addition, human-related activities increasingly contribute to aquatic background noise, mostly in coastal areas but also in the open ocean (Andrew et al. 2002; Ross 2005; Tyack 2008). This so-called anthropogenic noise is a growing environmental problem that is expanding in time and space (Slabbekoorn et al. 2012) and is mostly caused by shipping activities, construction work (drilling), seismic surveys, and energy production (hydroelectric power plants or offshore windmills; Richardson et al. 1995; Popper 2003). Most anthropogenic activities generate low-frequency noise under 1 kHz (Richardson and Würsig 1997), matching with the best hearing range (Fay 1988; Ladich and Fay 2013) and spectra of agonistic and mating vocalisations (Ladich and Myrberg 2006; Myrberg and Lugli 2006) of most fish. Figure 1.9 illustrates how the main energy of a ferry-boat noise recorded in the Tagus estuary (Portugal) overlaps with the frequency range of the mate advertising boatwhistles produced by the Lusitanian toadfish (*H. didactylus*).

Animals exposed to continuous masking noise may undergo evolutionary changes to enhance their signals' detectability to conspecifics (e.g. changes in acoustic signal structure; Slabbekoorn and Peet 2003), to make their calls more suitable for auditory reception (e.g. Brumm and Slabbekoorn 2005), or, alternatively, may start relying on different communication channels (e.g. Hödl and Amézquita 2001). Indeed, anthropogenic noise may act as a constraint on acoustic communication systems leading to long-term adaptations.

Fishes exposed to noise may be subject to 'passive effects'; that is, animals suffer an impact but do not actively change their behaviour (Slabbekoorn et al. 2012). These effects include auditory masking and reduction in capability for temporal resolution (Wysocki and Ladich 2005; Vasconcelos et al. 2007; Codarin et al. 2009), temporary hearing loss (Scholik and Yan 2002; Amoser and Ladich 2003; Smith et al. 2003; Popper et al. 2005), endocrinological stress responses (Santulli

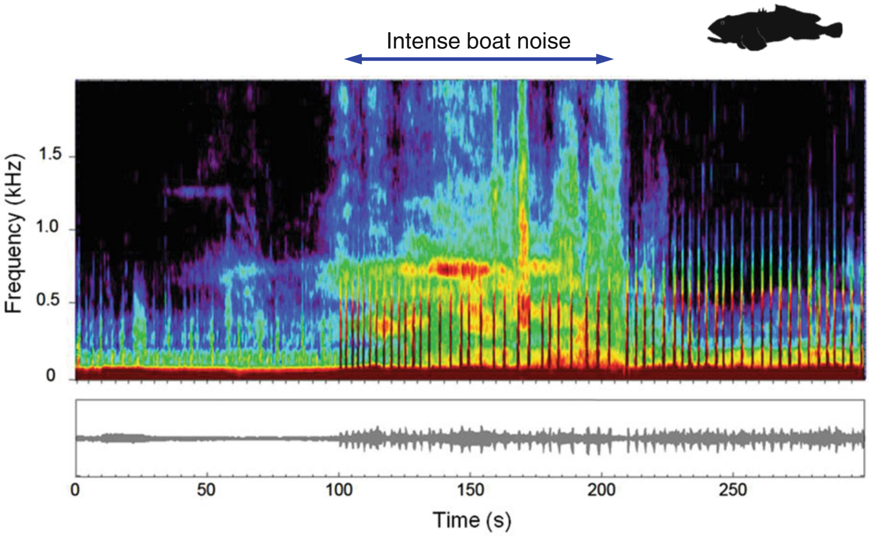

Fig. 1.9 Spectrogram and oscillogram of a representative field recording in an intertidal breeding area of the Lusitanian toadfish in the Tagus river (Portugal) depicting mating boatwhistles (spikes in the oscillogram/spectrogram) made by a chorus of Lusitanian toadfish and the ferry-boat noise with overlapping frequencies. The ferry-boat approached the dock approximately 20 m away from the recording point. Sampling frequency 44.1 kHz, filter bandwidth 40 Hz, Blackman–Harris windows, 50 % overlap

et al. 1999; Sverdrup et al. 1994; Smith et al. 2003; Wysocki et al. 2006), barotrauma injury (Halvorsen et al. 2012), and damage of the inner ear sensory epithelia (Hastings et al. 1996; McCauley et al. 2003). For example, Vasconcelos et al. (2007) reported auditory masking in *H. didactylus* under ferry-boat noise, namely an increase in the auditory thresholds of about 13 dB compared to thresholds obtained under ambient noise conditions. Consequently, the presence of ferry-boat noise may affect vocal communication in this species, because the difference between peak spectral levels of vocalisations and the auditory thresholds decreased considerably. According to Vasconcelos et al. (2007), assuming cylindrical sound spreading in the shallow estuary, gravid females under such noise would not be able to detect vocal nesting males much beyond 2 m.

Similarly, Codarin et al. (2009) described that noise emanating from a cabin-cruiser substantially masked the auditory thresholds within the frequency range where acoustic communication takes place during both agonistic and reproductive contexts in three sympatric species from the Adriatic Sea (*Chromis chromis*, *Sciaena umbra*, and *Gobius cruentatus*). Auditory thresholds increased considerably during boat noise exposure up to 35 dB in *S. umbra*, 20 dB in *C. chromis*, and 10 dB in *G. cruentatus,* as compared to sensitivity under normal ambient noise conditions.

On the other hand, anthropogenic noise may have consequences that involve active responses from fish, such as spatial avoidance, interruption of behaviour, and signal modifications (Slabbekoorn et al. 2012). The active effects (fish responses) have the potential to provide relief on the passive effects, by reducing the level and duration of exposure (Slabbekoorn et al. 2012). Most investigations on behavioural impacts have been conducted within the framework of population assessments for fisheries and environmental impact studies, which mostly concern immediate fish responses to acute noise playbacks (reviewed in Popper and Hastings 2009; Cott et al. 2012). For instance, Jørgensen et al. (2004) reported avoidance responses in the sea capelin (*Mallotus villosus*) to research vessels, namely changes in the distribution depth of dense concentrations on the spawning grounds. Fewtrell and McCauley (2012) reported an increase in the occurrence of alarm responses, such as moving faster in more tightly cohesive groups, in several marine fish species exposed to increasing levels of air gun noise. However, how different anthropogenic noise sources present in nowadays aquatic environments affect fish behaviour, including social and mating activities, and its evolutionary consequences, is still poorly investigated and far from understood. Some studies suggest that in addition to the impact of noise on female detection of mates, masked hearing may also increase escalated aggressiveness as acoustic assessment is impaired (Vasconcelos et al. 2007, 2010).

Finally, in addition to the direct impact on general fish physiology and behaviour, anthropogenic noise may interfere particularly with the transfer of acoustic signal information potentially important for mate choice. Fish vocal communication relies mostly on temporal features of the vocalisations, but also on frequency content and amplitude modulation (see above, Amorim 2006). Anthropogenic noises are extremely variable regarding temporal, frequency, and amplitude patterns, and have the potential to diminish the ability to perceive individual signal differences and, consequently, compromise sexual selection. Moreover, as previously mentioned, most fish species inhabit shallow waters where low-frequency sounds propagate only over short distances and where the frequency composition and temporal patterns are easily altered (Fine and Lenhardt 1983; Mann and Lobel 1997). Additional signal degradation due to man-made noise may impair or restrict acoustic communication with unpredictable consequences for fish welfare, fitness, and evolution.

Studies on the contemporary evolution of fish communication systems are scarce (reviewed in van der Sluijs et al. 2011). Although evolutionary responses have not yet been confirmed, the available studies suggest that environmental changes may impose different selection pressures acting on communication signals. For instance, eutrophication or chemical pollution may influence evolution by weakening sexual selection on male traits in sticklebacks, sand gobies, cichlids, and swordtails (Candolin et al. 2007, Järvenpaä and Lindström 2004; Fisher et al. 2006; Maan et al. 2010). However, little is known of the possible effects of acoustic pollution on fish sexual selection or other processes that might affect evolution.

Further investigation should compare fish populations subjected to different environmental noise conditions, focusing on vocal behaviour, auditory masking, and relative use of different communication channels. Moreover, little is known of how the presence of different background noise conditions (amplitude, spectral components, temporal structure) may affect fine detection of sound features potentially important for mate choice in fish. These are only a few examples of future research directions that may help in understanding how communication systems are evolving in today's acoustic world.

1.7 Concluding Remarks

Fish sounds are commonly emitted in close-range interactions and as part of a more complex multimodal communication system. Acoustic signal information may interplay in a complex way with cues conveyed by signals exploiting other sensory modalities and are also often produced under masking conditions such as in male choruses or under ambient or anthropogenic noise. Present knowledge of the function of fish sounds in mate choice is still scarce but points to the importance of acoustic signals as a source of information on male quality relevant for mate choice. In line with our knowledge from other taxa, it is also becoming clearer that acoustic signals can influence fish reproductive success. The current review stresses the need of further behavioural and physiological work pointing to specific areas of research relevant to clarify the importance of acoustic communication in the reproduction and evolution of fishes.

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Chapter 2
Comparative Neurobiology of Sound Production in Fishes

Andrew H. Bass, Boris P. Chagnaud and Ni Y. Feng

Abstract While studies of sonic mechanisms among vertebrates date back more than 100 years, the past 25 years have witnessed a burgeoning of interest in the bioacoustics and behavioral ecology of sound production among fishes, including in its neural basis. Here, we review the body of comparative literature on the neuroanatomical, neurophysiological, and neuroendocrine mechanisms of sound production/vocalization among fishes. Most studies have focused on teleosts, the most species-rich group of living vertebrates. The past decade alone has witnessed the demonstration of (1) an extensively connected vocal-acoustic network at forebrain, midbrain, and hindbrain levels, (2) distinct neural populations comprising a central pattern generator (CPG) that directly determines the physical attributes of social context-dependent sounds including pulse repetition rate (PRR), fundamental frequency, duration, and amplitude, (3) a highly conserved pattern for the evolutionary developmental origin of vocal CPGs between fishes and tetrapods, (4) shared origins between vocal CPGs that are dedicated to sound production and pectoral appendage motor systems that function in both acoustic signaling and locomotion, and (5) forebrain, midbrain, and hindbrain targets in the vocal-acoustic network for the modulatory actions of steroid hormones and neuropeptides. In sum, the relative simplicity of acoustic signaling in fishes and of the underlying neural circuitry offer both insights into the evolutionary history of sound producing mechanisms among all vertebrates, and practical advantages for investigating adaptations at the cellular and network levels of neural organization that sculpt behavioral phenotypes.

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Abbreviations in Text

11-KT	11-ketotestosterone
AH	Anterior hypothalamus
AR	Androgen receptor
AT	Anterior tuberal hypothalamus
AVT	Arginine vasotocin
CPG	Central pattern generator
ER	Estrogen receptor
Ir	Immunoreactivity
IT	Isotocin
PAG	Midbrain periaqueductal gray
PL	Midbrain paralemniscal tegmentum
POA	Preoptic area
POA-AH	POA Anterior hypothalamus
PRR	Pulse repetition rate
qPCR	Quantitative PCR
VIP	Vasoactive intestinal polypeptide
VMN	Vocal motor nucleus
VPN	Vocal pacemaker nucleus
VPP	Vocal pre-pacemaker nucleus

2.1 Introduction

Acoustic communication is a prominent feature of vertebrate social behavior. Fish and Mowbray's (1970) remarkable volume, *Sounds of Western North Atlantic Fishes*, revealed an astonishingly widespread occurrence of sound production among fishes, and especially among teleost fishes that are the largest group of living vertebrates (Nelson 2006). By way of both spectrograms and oscillograms, Fish and Mowbray documented broad species diversity in spectral and temporal characters, including duration, pulse repetition rate (PRR) and harmonic structure. At about the same time, neurophysiologists were beginning to record from motoneurons in the central nervous system and peripheral nerve roots that activate sound producing (sonic, vocal) muscles (Packard 1960; Skoglund 1961; Pappas and Bennett 1966; Cohen and Winn 1967), while brain stimulation studies began to reveal vocal initiation sites distributed in forebrain, midbrain, and hindbrain regions (Demski and Gerald 1972). Over 40 years later, studies of fishes now draw attention to shared attributes and evolutionary developmental origins of vocal-acoustic behaviors and neural networks across all of the major lineages of vocal vertebrates (Bass and McKibben 2003; Bass et al. 2008; Bass and Chagnaud 2012). Why study the neural basis of sound production in fish? We hope to answer this question in this review, while providing an overview of the current status of research on the neuroanatomy and neurophysiology of central vocal networks in fish.

2.2 Why Study Fish?

Fish provide ideal model systems for investigating the fundamental neural mechanisms of sound production among vertebrates for several reasons. (1) The simplicity of their pulsatile vocalizations that vary within and between species makes them especially amenable to deciphering the neural codes that determine their physical attributes (Fig. 2.1). (2) Sound production typically depends on the actions of a single pair of vocal/sonic muscles whose activity is controlled by a single hindbrain central pattern generator (CPG) (Fig. 2.2). (3) Discrete CPG populations control equally discrete acoustic characters—duration, PRR, and amplitude (Fig. 2.2). (4) The vocal CPG of fishes shares evolutionary developmental origins with the hindbrain vocal CPGs of tetrapods. In sum, the simplicity of vocal mechanisms in fishes leads to a simple translation between neural, mechanical, and behavioral events that inform our understanding of fundamental mechanisms leading to the more complex vocal CPGs and behaviors of tetrapods.

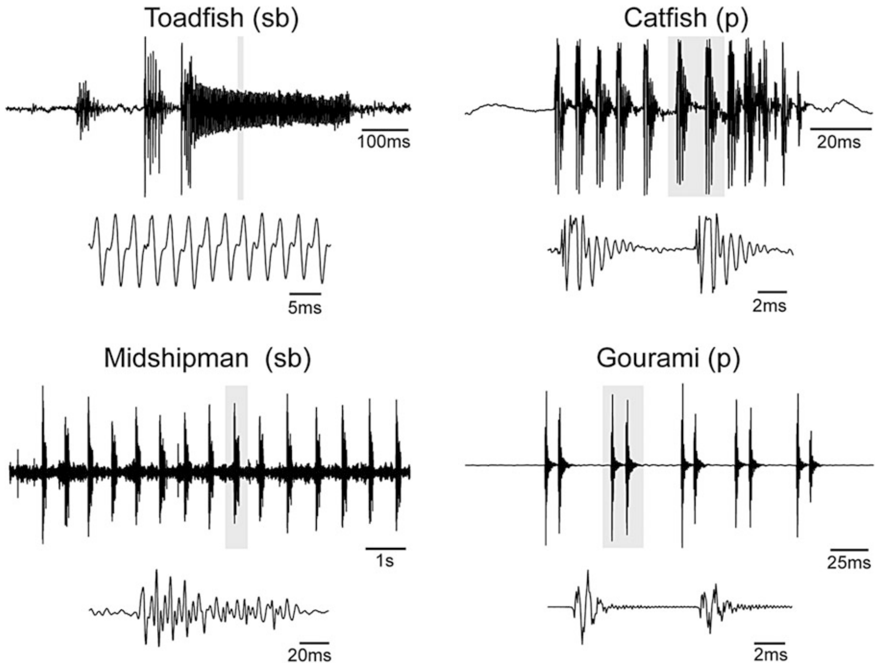


Fig. 2.1 Vocal-acoustic signals in teleost fish. Shown here are representative examples of the pulsatile-like sounds generated by fishes using either vocal swim bladder (*sb*) or pectoral (*p*)-dependent mechanisms. Signals are shown on two time scales for the boatwhistle of the Gulf toadfish (*Opsanus beta*), grunt traingrunt train of the plainfin midshipman (*Porichthys notatus*), grunt of the Raphael catfish (*Platydoras armatulus*) and croak of the croaking gourami (*Trichopsis vittata*). Catfish and gourami records courtesy of F. Ladich

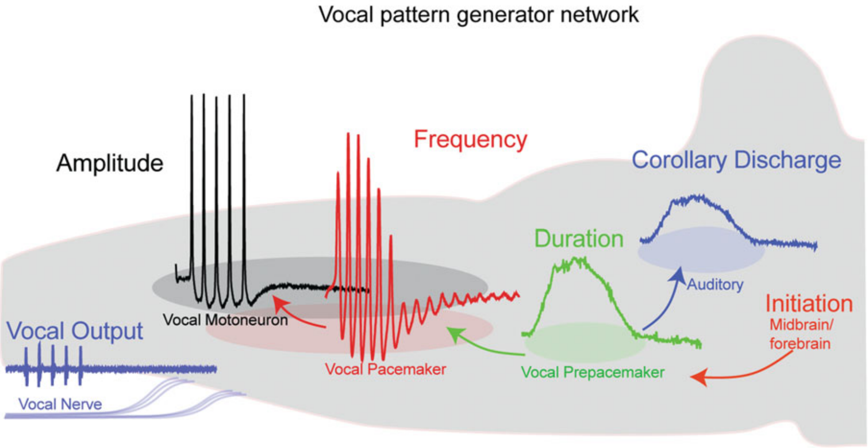


Fig. 2.2 Connectivity and temporal code of hindbrain vocal central pattern generator (CPG). The vocal CPG, depicted here for plainfin midshipman fish (*Porichthys notatus*), is activated by descending input from vocal midbrain regions. The CPG comprises three populations, superimposed here on a background sagittal image of the caudal hindbrain: vocal pre-pacemaker, vocal pacemaker, and vocal motor neurons. Representative intracellular records are shown for each population. The final output of the vocal CPG is carried by vocal nerve activity. The vocal pre-pacemaker nucleus also projects to central auditory nuclei, providing a corollary discharge that informs the auditory system about the duration of natural vocalizations. Modified after (Chagnaud et al. 2011)

The acoustic repertoire of fishes has long attracted the attention of neurobiologists. More than 50 years ago, Packard (1960) demonstrated that individual sound pulses are matched 1:1 with individual nerve spikes that reflect synchronous motoneuron activity (e.g., Chagnaud et al. 2012). Skoglund (1961) and Cohen and Winn (1967) showed for the oyster toadfish *Opsanus tau* and the plainfin Midshipman *Porichthys notatus*, respectively, that simultaneous contraction of a pair of muscles attached to the walls of the Swim bladder leads to the production of one sound pulse, with repetitive muscle contractions directly determining the sound's PRR and total Duration. Cohen and Winn (1967) also drew attention to the hearing abilities of midshipman by providing an audiogram and showing that the saccule was the main organ of hearing. These studies, along with Pappas and Bennett's (1966) description of "swim bladder motoneurons" in the oyster toadfish, set the stage for using fishes as model systems for investigations into the neural mechanisms of vertebrate acoustic communication.

2.3 Vocal-Sonic Neuroanatomy

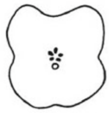
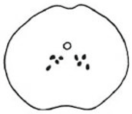
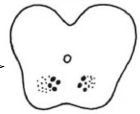
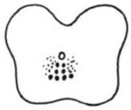
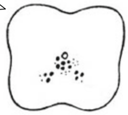
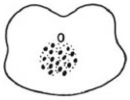
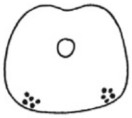
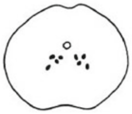
As part of a broader survey of gap junction-mediated electrical coupling in the nervous system, Pappas and Bennett (1966) presented both neurophysiological and ultrastructural evidence for electrical coupling at the level of motoneurons innervating the sonic swim bladder muscles in the oyster toadfish. It was, however, not until the 1980s that the first comprehensive descriptions of the vocal premotor–motor circuit were published, in this case for the closely related plainfin midshipmanmidshipman fish (Bass 1985; Brantley and Bass 1988; Bass and Marchaterre 1989; Bass and Baker 1990). Since that time, our knowledge of patterns of organization of a vocal or sonic motor nucleus, and in some cases pre-motoneurons, has greatly expanded beyond toadfishes as discussed in the next section.

The sounds of fishes are now often referred to as vocalizations and the central network controlling sound production as a vocal circuit to draw attention to their evolutionary relationship to vocal behaviors and neural mechanisms in tetrapods. As when first proposed (Bass et al. 1994), this comparison depends on several key findings. First, the vocalizations of fishes function in social contexts comparable to those of tetrapods, namely mate attraction and aggression. Second, sonic muscles attached to the swim bladder, like sonic muscles of the syrinx and larynx, are dedicated to one behavioral function, sound production. Third, sonic muscles attached to the swim bladder, larynx, and syrinx share developmental origins from occipital somites (Tracy 1959, 1961; Huang et al. 1999; Noden and Francis-West 2006). Fourth, in a range of species, the sonic muscles are innervated by occipital nerve roots, considered homologs of hypoglossal nerve roots that innervate the avian syrinx and parts of the tongue that direct movements for speech in humans (Tavolga 1962; Vicario and Nottebohm 1988; Lieberman 2002; Bass et al. 2008; Ma et al. 2010; Laine and Bailey 2011). As reviewed below, the essential developmental evidence across vertebrate lineages to support comparisons of a hindbrain CPG for patterning the activity of sonic muscles (larynx, syrinx, swim bladder) first became available only during the past few years (Bass et al. 2008). This led to the renaming of the sonic motor nucleus that innervates swim bladder muscles as the vocal motor nucleus, or VMN (Bass et al. 2008), a nomenclature that is followed here and has recently been adopted by studies of the amphibian laryngeal system (Hall et al. 2013).

2.3.1 Vocal Nerves and Vocal Motor Nucleus

Cranial (occipital) and/or rostral spinal nerve roots innervating sound producing muscle dedicated to this one function have been identified in 12 orders, 20 families and 30 species of teleost fish (reviewed in Ladich and Bass 2005; Onuki and Somiya 2007; Boyle et al. 2013). Innervation varies from occipital only or spinal only to a combination of both. A VMN dedicated to sonic functions has been experimentally demonstrated in 22 species following the labeling of one or more vocal nerve roots with either horseradish peroxidase or a biotin derivative (neurobiotin, biocytin, dextran-biotin) (Table 2.1). Intracellular recording and staining further verifies the position of VMN in three species of Batrachoidiformes (plainfin midshipman; oyster toadfish; and Gulf toadfish, *O. beta*) and one species of Perciformes (northern sea robin, *Prionotus carolinus*) (Pappas and Bennett 1966; Bass and Baker 1990, 1991; Chagnaud et al. 2012; Chagnaud and Bass 2014).

Table 2.1 Vocal motor systems among teleost fishes having swim bladder mechanism

	Sonic organ; innervation	Motoneuron rostro-caudal extent	Motoneuron transverse location	
Cohort Osteoglossomorpha				
Order Osteoglossiformes				
Family Mormyridae				
Brienomyrus sp.[a]	Ex; NI	cM	dors mid	
Cohort Otomorpha				
Order Characiformes				
Family Characidae				
Pygocentrus nattereri[b,c]	Ex; S3-5	rSC	vent cc	
Serrasalmus rhombeus[b]	Ex; S3, 4	rSC	vent cc	
order Siluriformes				
family Ariidae				
Ariopsis felis[d]	Ex; Occ	cM/rSC	vent 4th/cc	
Bagre marinus[d]	Ex; Occ	cM/rSC	vent 4th/cc	
family Doradidae				
Platydoras armatulus[d]	E ; Occ	cM/rSC	vent mid	
family Mochokidae				
Synodontis nigriventris[e]	Ex; Occ, S1	cM/rSC	vent mid	
Synodontis nigromaculatus[e]	Ex; Occ, S1	cM/rSC	vent mid	
family Pimelodidae				
Pimelodus blochii[d,f]	Ex; Occ, S1, 2	cM/rSC	vent mid/4th/cc	
Pimelodus pictus[f]	Ex; Occ, S1, 2	cM/rSC	vent mid/4th/cc	
cohort Euteleosteomorpha				
order Holocentriformes				
family Holocentridae				
Holocentrus rufus[g]	Ex; Occ	cM/rSC	vent lat	
Sargocentron seychellense[g]	Ex; Occ	cM/rSC	vent lat	
Sargocentron xantherythrum[g]	Ex; Occ	cM/rSC	vent lat	
order Beryciformes				
family Monocentridae				
Monocentris japonica[h]	Ex; Occ	cM	vent lat	
order Batrachoidiformes				
family Batrachoididae				
Opsanus tau[i-l]	In; Occ	cM/rSC	vent mid	
Opsanus beta[m]	In; Occ	cM/rSC	vent mid	
Porichthys notatus[a,k n]	In; Occ	cM/rSC	vent mid	
order Perciformes				
family Cottidae				
Leptocottus armatus[a]	PV, Occ*	cM/rSC	vent lat	
Myoxocephalus scorpius	PV, Occ*	cM/rSC	vent lat	
family Scorpaenidae				
Sebastiscus marmoratus[o]	Ex; Occ	cM/rSC	vent lat	
family Triglidae				
Prionotus carolinus[a,k, also p]	In; Occ	cM/rSC	vent lat	
Series Percomorpharia				
family Chaetodontidae				
Hemitaurichthys polylepis[q]	Ex; S1-3	rSC	vent cc	

The *far right column* is line drawings in transverse plane showing location of motoneurons that innervate sonic swim bladder muscles. Symbols: *Filled circles* represent the somata of motoneurons. *Open circle* represents fourth ventricle and/or spinal canal. Abbreviations: *cM* caudal medulla; *dors mid* dorsal to fourth ventricle on midline; *Ex* extrinsic swim bladder muscles;

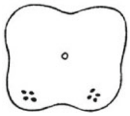
In intrinsic swim bladder muscles; *NI* not identified; *Occ* occipital nerves; *PV* pectoral girdle vibration; *rSC* rostral spinal cord; *S* spinal nerves; *vent cc* ventral to central canal (cc), dorsal and/or lateral to medial longitudinal fasciculus (mlf); *vent 4th/cc* ventral to fourth (4th) ventricle and cc, and lateral to mlf; *vent lat* ventrolateral to mlf within ventral motor column; *vent mid* immediately ventral to 4th ventricle, on midline and dorsal to mlf. References corresponding to superscript alphabets are found below (also see for references on sonic organ). Tables 2.1 and 2.2 adapted from Boyle et al. (2013) and Bass and Ladich (2008). Although Cottidae lack a swim bladder and vibrate the pectoral girdle, they are included in Table 2.1 for developmental and functional reasons (see Sect. 2.3.2 of the text for explanation). See Wiley and Johnson (2010), Betancur-R et al. (2013) and Broughton et al. (2013) for teleost classification in Tables 2.1 and 2.2
[a] Bass (1985); [b] Ladich and Bass (2005); [c] Onuki et al. (2006); [d] Ladich and Bass (1998); [e] Ladich and Bass (1996); [f] Ladich and Fine (1994); [g] Carlson and Bass (2000); [h] Onuki et al. (2010); [i] Bennett and Pappas (1965); [j] Fine et al. (1982); [k] Bass and Baker (1991); [l] Fine and Mosca (1989); [m] Bass and Baker (1997); [n] Bass and Baker (1990); [o] Yoshimoto et al. (1999); [p] Finger and Kalil (1985); [q] Boyle et al. (2013)

As listed in Table 2.1, VMN is positioned along the rostral-caudal axis in the caudal hindbrain medulla and/or the rostral spinal cord in all species so far investigated. VMN location varies within the transverse plane in six discernible patterns (see Table 2.1 for references). (1) A subset of motoneurons at the level of the vagal motor nucleus in the caudal medulla, positioned dorsal to the fourth ventricle and near the midline (dors mid). This pattern has only been identified in weakly electric mormyrid fish. A caveat to this study is that, while it identified neurons connected to musculature of the swim bladder, it was not performed in a highly vocal mormyrid species, namely *Pollimyrus isidori* or *Pollimyrus adspersus* (Crawford et al. 1997). More comprehensive studies should be completed in highly vocal mormyrids. (2) Rostral spinal cord only with motoneurons diffusely spread dorsal and/or lateral to medial longitudinal fasciculus and ventral to central canal (vent cc). (3) Caudal medulla and rostral spinal cord with the motor nucleus positioned ventral to the fourth ventricle and central canal, near the medial longitudinal fasciculus (vent 4th/cc). (4) Caudal medulla and rostral spinal cord with the motor nucleus positioned ventral to the fourth ventricle on the midline and dorsal to the medial longitudinal fasciculus (vent mid). (5) Combination of patterns 2–4 as described above (vent mid/4th/cc). (6) Caudal medulla and rostral spinal cord with the motor nucleus ventrolateral to the medial longitudinal fasciculus, along the ventral surface of the brain and spinal cord (vent lat). Patterns 4 and 6 are the most prevalent.

2.3.2 Sonic-Pectoral Signaling

Swim bladder dependent mechanisms of sound production are the most prevalent so far documented among teleosts (Ladich and Fine 2006; also see Chap. 3). Sonic-pectoral signaling, i.e., using some part of the pectoral girdle or appendage (fin, forelimb, wing) to generate sound, is also well known among fishes (Ladich and

Table 2.2 Vocal motor systems among teleost fishes having pectoral fin mechanism

	Sonic organ; innervation	Motoneuron rostro-caudal extent	Motoneuron transverse location
Cohort Otomorpha			
Order Siluriformes			
Family Mochokidae			
Synodontis nigromaculatus[a]	PS; Occ	cM/rSC	vent lat 
Family Pimelodidae			
Pimelodus blochii[b,c]	PS; Occ, S1, 2	cM/rSC	vent lat
Pimelodus pictus[c]	PS; Occ, S1, 2	cM/rSC	vent lat
cohort Euteleosteomorpha			
order Anabantiformes			
family Osphronemidae	PT; Occ	cM/rSC	vent lat 
Trichopsis vittata[d]			

The *far right column* includes a single line drawing in transverse plane showing location of motoneurons that innervate muscles linked to pectoral spine stridulation (PS) or pectoral tendon plucking (PT) for all species listed. Symbols: *Filled circles* represent the somata of motoneurons. *Open circle* represents fourth ventricle and/or spinal canal. Abbreviations: *cM* caudal medulla; *Occ* occipital nerves; *rSC* rostral spinal cord; *S* spinal nerve; *vent lat* ventrolateral to medial longitudinal fasciculus within ventral motor column. References corresponding to superscript alphabets are found below (also see for references on sonic organ)

[a] Ladich and Bass (1996); [b] Ladich and Bass (1998); [c] Ladich and Fine (1994); [d] Ladich and Fine (1992)

Fine 2006), as it is among birds (Prum 1998; Hingee and Magrath 2009; Miller and Baker 2009; Bostwick et al. 2010; Barske et al. 2011) and mammals (Reynolds 1965; Remedios et al. 2009). As noted in Sect. 2.3, the use of the term vocal for fishes was adopted in reference to systems dedicated to sound production, akin to syringeal and laryngeal systems among tetrapods (Bass et al. 1994). Although sculpin, members of the family Cottidae, lack a swim bladder and depend upon vibration of the pectoral girdle for sound production, their motor system is included in Table 2.1 (vent lat, see pattern 6 described at end of last section) as a VMN for two reasons. First, like the VMN that activates swim bladder muscles, the sonic muscle of sculpin appears to be dedicated to sound production (Barber and Mowbray 1956). Second, the sonic muscle of sculpin shares the same developmental history as the sonic muscles driving swim bladder vibration in the closely related scorpaenids (Hallacher 1974).

Several families of catfishes include species that use both swim bladder and pectoral spine sonic mechanisms (e.g., Mochokidae and Pimelodidae in Table 2.1) (also see Kaatz et al. 2010). Unlike sculpin, pectoral mechanisms in catfishes, and in the croaking gourami (*Trichopsis vittata*) that snap a pair of hypertrophied pectoral tendons during sound production, are multi-functional because of their added involvement in posture, locomotion and defense mechanisms (see Ladich 1989; Ladich and Fine 1992). Catfishes exhibit patterns 3–5 for VMN (Table 2.1) and pattern 6 for pectoral motoneurons (Table 2.2). Gouramis also show pattern 6. We place these pectoral fin systems into a separate Table 2.2 to distinguish them from the dedicated sonic systems listed in Table 2.1. How multi-functional pectoral motoneurons switch between sonic and non-sonic functions remains a fascinating neural CPG puzzle to solve. The central control of other sonic mechanisms that are also likely multi-functional, such as those engaging pharyngeal muscles (e.g., Rice and Lobel 2002; Parmentier et al. 2007), remains to be investigated.

The charting of sonic motoneuron populations in widely divergent groups of teleost fishes that utilize dedicated vocal and/or multi-functional pectoral-sonic provides both a more complete mapping of acoustic signaling systems among vertebrates in general, as well as essential information for guiding future comparative electrophysiological investigations.

2.3.3 Brainstem Vocal Network

Besides identifying VMN location as summarized above, transneuronal transport of anatomical tracers has further recognized vocal premotoneurons in several families of fish. In 1994, Bass and colleagues showed that labeling the vocal nerve of midshipman fish at the level of the swim bladder with either biocytin or neurobiotin led to transneuronal transport and bilateral labeling of the paired VMN as well as an extensive premotor network in the caudal hindbrain. The premotor network included two expansive columns of neurons alongside each VMN that matched the location of neurons identified by Bass and Baker (1990) as pacemaker neurons because their oscillatory-like firing properties appeared to determine VMN's firing rate. Bass et al. (1994) then identified a second premotor nucleus immediately rostral to the VPN–VMN circuit that was designated the ventral medullary nucleus because of its location. Bass et al. (2008) later renamed this nucleus the vocal pre-pacemaker nucleus or VPP, because it directly innervates the VPN–VMN circuit (also see Goodson and Bass 2002; Chagnaud et al. 2011). A subsequent study further identified intra- and intersexual dimorphisms in the size of neurons in the VPP–VPN–VMN network (Bass et al. 1996) that expanded upon earlier observations of differences in VPN and VMN neuron size by Bass and Baker (1990) who also reported intra- and intersexual differences in the firing rate of the VPN–VMN circuit. A third transneuronal study provided an initial mapping of the early development of the VPP–VPN–VMN circuit in larval midshipman fish (Knapp et al. 1999a).

Vocal premotoneurons directly within, adjacent to, or rostral to VMN have also been identified by transneuronal biotin transport in catfish (Mochokidae, Table 2.1) (Ladich and Bass 1996), squirrelfish (Holocentridae, Table 2.1) (Carlson and Bass 2000) and rockfish (Scorpaenidae, Table 2.1) (Yoshimoto et al. 1999). For these groups of fish, as in midshipman and toadfish (Bass et al. 1994, 2008; Chagnaud and Bass 2014), biocytin or neurobiotin labeling also showed connections between the vocal system and the central auditory system, including the octavolateralis efferent nucleus (OEN) that directly innervates the inner ear and lateral line organs. The activity of putative OEN axons projecting to the inner ear and lateral line system was correlated to call duration and frequency (Weeg et al. 2005), as later verified via intracellular OEN recordings (Chagnaud and Bass 2013). VPP neurons were shown to be the predominant source of the vocal-auditory coupling using intracellular recording and single cell staining in midshipman (Chagnaud et al. 2011; Chagnaud and Bass 2013). The identification of a VPP in other species, along with its connection to the OEN, however, awaits comparable studies.

2.4 Evolutionarily Conserved Hindbrain Compartments

2.4.1 Vocal Hindbrain Compartment

Experimental investigations of the early development of the vocal pattern generator network in midshipman and toadfish larvae soon after hatching show that it maps onto the same region of the developing hindbrain as the hindbrain-spinal vocal circuitry in tetrapods (Bass et al. 2008). This mapping was accomplished by using confocal microscopy in combination with labeling of the developing sonic swim bladder muscle and either the spinal cord or other musculature with different wavelength fluorescent dextran-amines and Alexa-biocytin. In this way, vocal neurons could be positioned within the context of well-documented hindbrain landmarks (e.g., reticular formation neurons projecting to the spinal cord, and other cranial and spinal motor neuron populations). The results showed that VMN forms in a segment-like compartment in the caudal hindbrain that extends into the rostral spinal cord (Fig. 2.3a). Transneuronal transport of neurobiotin in progressively older larvae further showed that the premotor VPN and VPP populations formed in the same neural compartment (Fig. 2.3b–d). Given the conserved location of vocal circuitry in the caudal hindbrain and rostral spinal cord among diverse groups of teleosts (Sects. 2.3.1 and 2.3.2, Table 2.1), the developmental phenotype in midshipman and toadfish (batrachoidids) likely extends to these other groups. A comparison to the early development of vocal systems in birds and frogs, along with the available evidence on motoneuron development in mammals and organization of the vocal circuitry in adult mammals, revealed that the VPP–VPN–VMN network in fish developed in the same neural compartment as in tetrapods (Fig. 2.3e) (Bass et al. 2008).

Teleosts, including sonic species, belong to a larger clade of bony vertebrates known as Actinopterygii or ray-finned fishes (Fig. 2.4a, b). So far, all of the neurobiological studies of sound communication in fishes have focused on teleosts. Sound production is, however, also reported for more basal groups of actinopterygians, namely Polypteriformes (bichir; Ladich and Tadler 1988), Acipenseriformes (sturgeon; Johnston and Phillips 2003) and Amiiformes (bowfins; Fülleborn 1894).

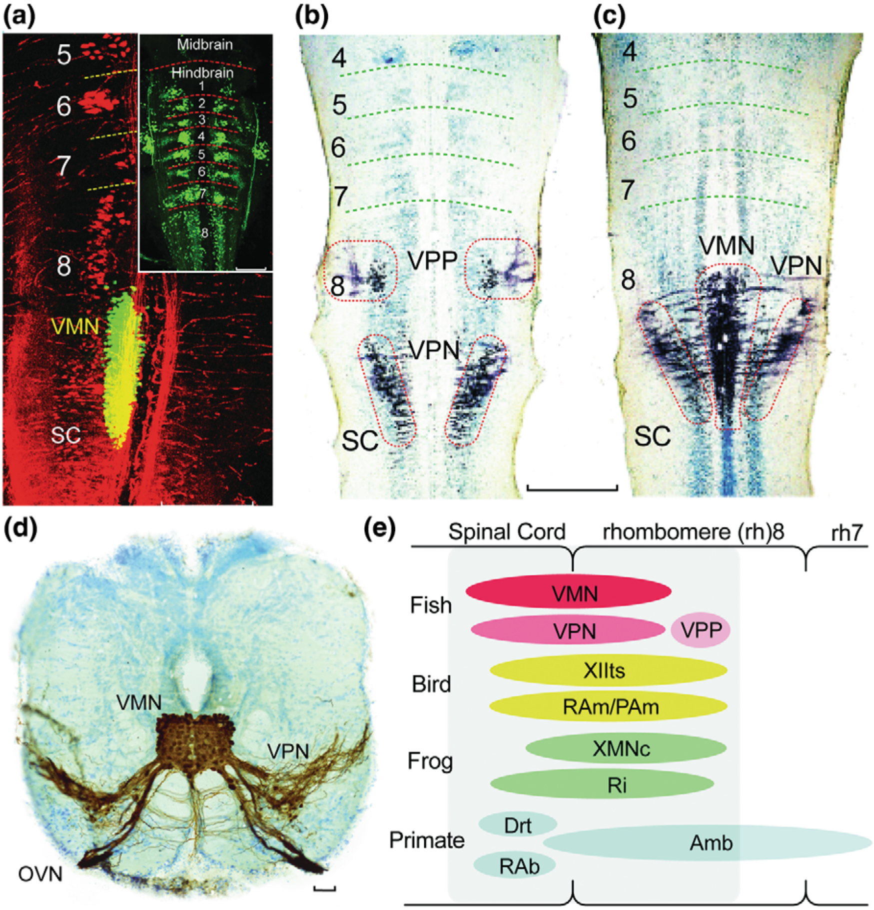


Fig. 2.3 Map of developing hindbrain vocal central pattern generator. The location of the developing vocal motor nucleus (VMN) was mapped onto the embryonic segments of the developing hindbrain known as rhombomeres (rh) and the spinal cord (SC) in larval plainfin midshipman fish (*Porichthys notatus*). **a** Fluorescently labeled neurons are visualized with laser scanning confocal microscopy (*horizontal plane*). Simultaneous visualization of clusters of reticular formation neurons labeled in rh 5–8 via retrograde transport from the spinal cord (Alexa 546 dextran-amine, *red*), and VMN labeled via retrograde transport from the developing vocal muscle (Alexa 488 dextran-amine, *green*). *Yellow* is composite overlap and does not indicate double labeling. *Inset* clusters of reticulo-spinal neurons (Alexa biocytin 488, *green*) in each rh, from 1 to 8. (*Scale bar* 0.2 mm.) **b**, **c** Mapping in *horizontal plane* of vocal pre-pacemaker (VPP), vocal pacemaker (VPN), and VMN neurons (*black*) in Gulf toadfish (*Opsanus beta*) larvae; labeling via transneuronal transport of neurobiotin from developing vocal muscle. Cresyl violet counterstain reveals reticulospinal clusters in rh segments. (*Scale bar* 0.2 mm.) **d** Transverse section in caudal hindbrain of juvenile Gulf toadfish showing extensive transneuronal bilateral labeling with neurobiotin (*brown*) of dendritic and axonal branching of VMN and VPN. VMN axons exit brain via occipital vocal nerve root (OVN; cresyl violet counterstain). (*Scale bar* 100 μm.) **e** Schematic in sagittal plane summarizing relative positions of hindbrain vocal premotor–motor networks in rh8-spinal compartment of several lineages of vocal vertebrates (see Bass et al. 2008 for details). Abbreviations: *Amb*, nucleus ambiguus; *Drt* dorsal reticular nucleus; *PAm* nucleus parambigualis; *RAb* nucleus retroambiguus; *RAm* nucleus retroambigualis; *Ri* inferior reticular formation; *XIIts* tracheosyringeal division of hypoglossal motor nucleus; *XMNc* caudal XMN. From Bass and Chagnaud (2012)

There are also reports of sound production in Dipnoi (lungfish; Thompson 1968) belonging to the Sarcopterygii or lobe-finned fishes, a group basal to tetrapods in the sister clade to Actinopterygii (Fig. 2.4b). While only comprising a small percentage of fishes in general, it remains important to investigate both the biomechanical and neural bases for sound production in these non-teleost lineages of fishes. If the adult and early developmental vocal phenotypes observed so far in teleosts do *not* extend to more basal actinopterygians, we will conclude that the teleost phenotype evolved

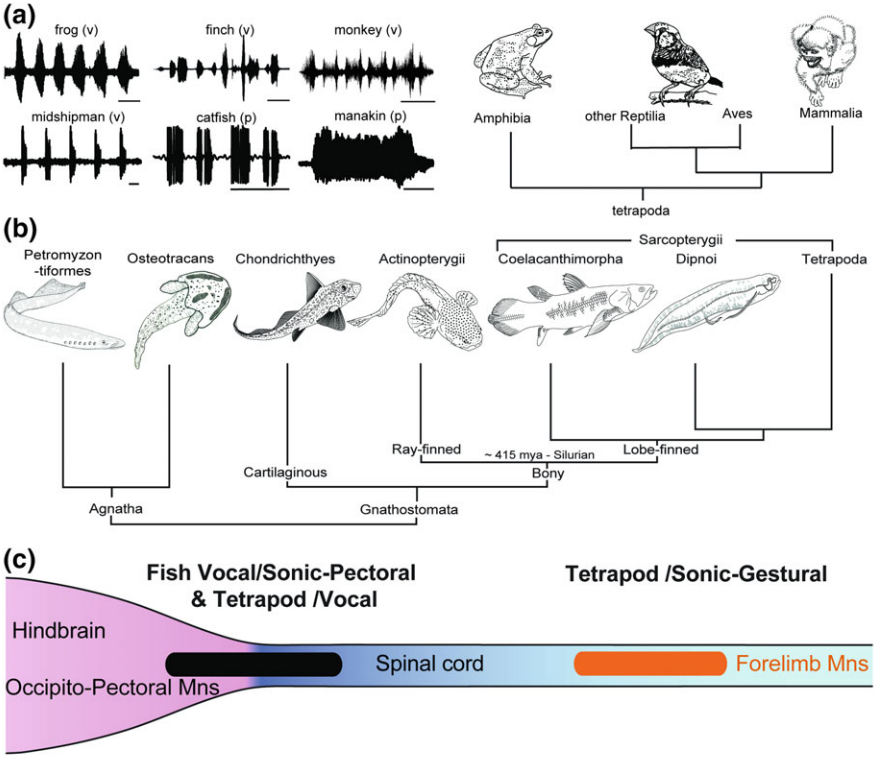


Fig. 2.4 Evolution of vocal–pectoral motor systems in fishes and tetrapods. **a** Waveforms of vocalizations of bullfrog (*Lithobates catesbeiana*, time base 1 s), zebra finch (*Taeniopygia guttata* 250 ms), squirrel monkey (*Saimiri sciureus*, 200 ms), midshipman fish (*Porichthys notatus*, 500 ms), catfish (*Platydoras armatulus*, 250 ms), and club-winged manakin (*Machaeropterus deliciosus*, 100 ms). Vocal (v) and pectoral (p) basis for sound production is shown. **b** Vertebrate cladogram depicting both jawless (agnathan) and jawed (gnathostome) radiations (Osteostracans represent an extinct agnathan group with pectoral fins). **c** Schematic summary in sagittal plane showing location of vocal and sonic-pectoral motoneurons. The occipito-pectoral motor column (*black*) in fishes gives rise to motoneurons innervating muscles of vocal organs dedicated to sound production (e.g., swim bladder) and pectoral fins that can also serve a sonic function. The occipito-pectoral column also gives rise to vocal motoneurons in tetrapods. Forelimb motoneurons (*orange*) that function in both sonic and gestural signaling in tetrapods are located in the spinal cord. (**a**, **b**) From Bass and Chagnaud (2012). (**c**) Modified from Ma et al. (2010)

independently among actinopterygians. If the teleost pattern applies broadly to actinopterygians, but not to lungfish, then the pattern observed in teleosts and/or actinopterygians, in general, versus that observed in tetrapods (Fig. 2.3e) is a case of convergent evolution.

2.4.2 Vocal and Sonic-Pectoral Motor Systems Share Developmental Origins

Bass et al.'s (2008) study of the early development of the vocal system in fish also shows that motoneurons innervating pectoral musculature are located in the same compartment as the developing vocal (swim bladder muscle) circuitry. This finding led to a more comprehensive, phylogenetic analysis of pectoral motoneuron development by Ma et al. (2010). Using similar methods to identify the developing pectoral system in the embryos and larvae of three orders of teleosts—Batrachoidiformes (midshipman), Cypriniformes (zebrafish and goldfish), and Salmoniformes (salmon and trout), Ma et al. (2010) also included a more basal group of fishes, Acipenseriformes (paddlefish), in their investigation. Using a more complete set of developmental landmarks such as molecular marking of the hindbrain-spinal boundary and the location of myotomes, Ma et al. (2010) precisely mapped a pectoral column extending between the caudal hindbrain and rostral spinal cord in all species investigated. Labeling of occipital myotomes at the same stages of development in several species, including midshipman, also delineated the entire extent of the occipital motor column (Fig. 2.5). The results showed overlapping caudal occipital and rostral pectoral columns, including the region where vocal circuitry is located in larval and adult toadfishes (Bass et al. 2008) (Fig. 2.5). This finding led to the conclusion that sonic systems, both vocal and pectoral, share developmental origins in fishes (Bass and Chagnaud 2012) (Fig. 2.4c).

2.5 Vocal Neurophysiology

While sound production among vertebrates has received considerable attention in terms of biomechanics and behavioral context (Bradbury and Vehrencamp 2011), and the location of sonic motoneurons has been mapped in all of the major lineages of vocal vertebrates (Bass et al. 2008), there is an astonishing lack of knowledge of how vocal muscles are patterned by the central nervous system. For tetrapods, this is due, in part, to several factors: (1) The strong coupling of CPGs for respiration and vocalization in birds and mammals makes functional characterization technically difficult due to simultaneous activity of CPGs (exhalation during breathing and vibration of vocal chords; Riede and Goller 2010). (2) The surgical accessibility of the vocal hindbrain in songbirds, the most studied vertebrate lineage in terms of

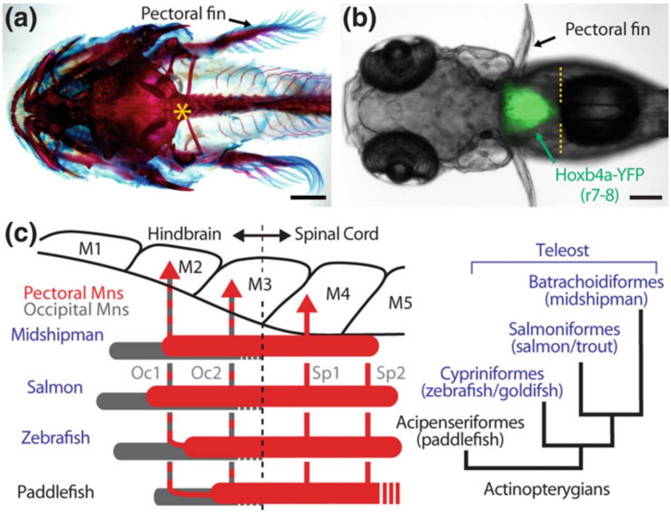


Fig. 2.5 Map of developing pectoral motor column in actinopterygian fish. **a** Dorsal view of juvenile plainfin midshipman fish (*Porichthys notatus*) cleared and stained with *alcian blue* and *alizarin red*; *asterisk* indicates location of craniovertebral junction. **b** Dorsal view showing the boundary between hindbrain rhombomere (r)8 and spinal cord (*yellow* hatching) defined by hoxb4a expression in zebrafish (*Danio rerio*) hoxb4a enhancer trap line. **c** Alignment in sagittal plane of columns of pectoral (*red*) and occipital (*gray*) motoneurons, segmental myotomes ("M"), and occipital (Oc1, Oc2) and spinal (Sp1, Sp2) nerves. Phylogeny of study species is shown to the *right*. Modified from Ma et al. (2010)

vocal production, is limited, thus discouraging neurophysiological recording from hindbrain premotor and motoneuron populations in an intact, in vivo preparation (e.g., Sturdy et al. 2003; Kubke et al. 2005). (3) The complexity of the vocal apparatus in birds and mammals poses significant technical challenges in delineating the neuromuscular patterning of individual syllables and entire vocalizations. The avian syrinx, for example, has several muscles that are controlled independently, thus potentiating the complexity of sequencing muscle contraction patterns (Vicario 1991; During et al. 2013).

Vocal fish lack all of the above complications and thus offer an optimal model to investigate CPG(s) underlying the neuromuscular patterning of vocalization, especially at the hindbrain level. In addition, due to the evolutionary conserved organization of the vocal hindbrain (Bass et al. 2008), functional comparisons to other vocal lineages can be drawn from the organization of vocal fish neuronal patterning. Clearly, the simplicity of vocal structure in fishes (Fig. 2.1) presents limitations in providing explanations for the more complex repertoires of birds and mammals, including answers to the question of fully innate versus partially learned vocalizations. Given the technical challenges of single unit recordings in a freely behaving animal in the aquatic medium (Palmer et al. 2003), this aspect of vocal behavior has remained largely unexplored in vocal fishes, unlike the case for songbirds and primates (e.g., Hage and Jürgens 2006; Goldberg et al. 2012). While the central mechanisms underlying the switching between call types, e.g., advertisement versus agonistic signals, and the patterning of vocalizations that include both amplitude and frequency modulated components such as toadfish boatwhistles (Mosharo and Lobel 2012) (Fig. 2.1) and midshipman growls (Bass et al. 1999) remains to be demonstrated for any vertebrate, fish have already offered significant contributions to our understanding of vocal patterning as reviewed below.

The mechanical decoupling of the vocal and respiratory systems makes vocal fishes an optimal model to study vocal CPGs. This is not to say that the vocal system of fish neither influences, nor is influenced by, other motor systems, including respiration. For instance, Bass and Chagnaud (2012) provide behavioral evidence in midshipman for interactions between vocalization, respiration and pectoral appendage movement (Fig. 2.6). Midshipman fish also inflate their swim bladder during advertisement humming (Fig. 2.7), likely to increase call amplitude

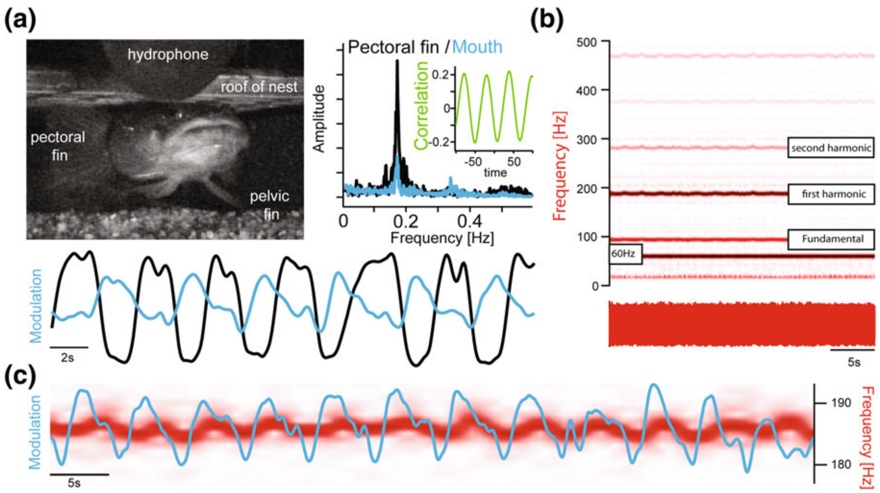


Fig. 2.6 Spatiotemporal patterning of vocal-respiratory-pectoral mechanisms in fish. **a** *Upper left* Photograph from video sequence at night of a type I male plainfin midshipman fish (*Porichthys notatus*) that is producing his advertisement "hum" call while in an artificial nest constructed of elevated ceramic tile in an aquarium (video courtesy of A. Bass and M. Marchaterre, Cornell University). *Lower* Waveforms of modulation rhythm of pectoral fin (*black*) and mouth (*blue*) movement during humming are superimposed to indicate temporal relationship (analyzed by video tracking). *Upper right* Corresponding fast Fourier transforms of pectoral fin and mouth waveforms shows matched modulation frequencies; correlation (*inset*) shows high temporal matching of both rhythms. **b** Sonogram (*upper*) and waveform (*lower*) of hydrophone recording of type I male midshipman hum (dense *bottom trace*) recorded simultaneously with the video in (**a**). The fundamental frequency, first two upper harmonics and 60-Hz band from nearby power line are indicated. **c** Overlay of waveform of mouth waveform (*blue*, approximate breathing rhythm) and modulation hum frequency (*red*, first harmonic) of simultaneous recorded midshipman hum in (**b**). Despite call generation in fishes not requiring airflow over a membrane as in most terrestrial vertebrates, the respiratory and vocal modulations are in phase. From Bass and Chagnaud (2012)

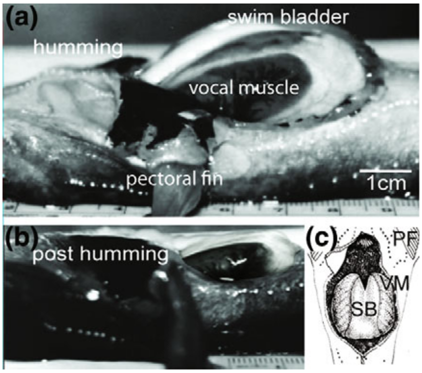


Fig. 2.7 Swim bladder inflation during hum advertisement calling in type I male midshipman (*Porichthys notatus*). *Photomicrographs* showing swim bladder of type I males that were recently humming (**a**) and several hours after humming (**b**). See Genova et al. (2012) for experimental details (**c**). Also shown is *line* drawing of ventral view of type I male swim bladder showing paired vocal muscles (*VM*) attached to the lateral walls of the swim bladder (*SB*); the position of the pectoral fin (*PF*) is also indicated

(Bradbury and Vehrencamp 2011) and perhaps also resonance frequency. Some species of weakly electric fish that employ their electric organ discharge (EOD) for social communication (Hopkins and Bass 1981) are also vocal, using a sonic swim bladder mechanism (Crawford et al. 1986; Crawford and Huang 1999). Pectoral-sonic mechanisms are coupled to swimming/hovering and intraspecific signaling movements when fish such as sculpins, gouramis, and catfish spread their pectoral fins (Ladich 1989; Ladich and Fine 2006). The neurophysiological basis for the coupling between sonic and other motor functions remains to be investigated.

2.5.1 Peripheral Vocal Physiology

Tower (1908) provided a historical overview of physiological observations and theories of how fish produce sound up to the time of his report. In a landmark series of experiments, Tower also provided the first demonstration of the relationship between *sonificus* muscle contraction and sound production in the Squeteague, *Cynoscion regalis*. He also evoked “a perfectly normal grunt” in the northern sea robin, *P. carolinus*, after directly stimulating either the swim bladder nerves and/or muscles in vivo and in the isolated swim bladder. Tavolga (1962) carried out similar experiments in two species of ariid catfishes, the gaff-topsail catfish, *Bagre marinus* and the sea catfish, *Ariopsis* (formerly *Galeichthys*) *felis* as well as Schneider (1964) for the tigerfish, *Therapon jarbua*. Together, these studies showed the close relationship between muscle contraction and sound production.

Barber and Mowbray (1956) showed in the longhorn sculpin, *Myoxocephalus octodecimspinosus*, a 1:1 relationship between individual muscle contractions and sound pulses. The same correlations with the pattern of nerve activity were reported by Packard (1960) and Skoglund (1961) for the pectoral muscles of the southern pigfish, *Congiopodus leucopaecilus* and the swim bladder muscles of the oyster toadfish, respectively. Nerve firing patterns have since been identified in several other distantly related species. Figure 2.8 shows drawings outlining the position of the VMN and bilateral recordings from occipital nerves in representative Batrachoidiformes (plainfin midshipman and oyster toadfish) and Perciformes (the shorthorn sculpin, *Myoxocephalus scorpius* and the northern sea robin). Nerve firing patterns highlight four important behavioral and neural attributes of vocal motor systems in fishes. First, each of the nerve's spike-like compound action potentials directly translates into individual sound pulses (also see beginning of this section). Second, each nerve spike reflects the synchronous firing of VMN neurons (Pappas and Bennett 1966; Chagnaud et al. 2012). Third, the nerves on either side of the midline fire either in (e.g., midshipman, toadfish, sculpin; Fig. 2.8a–c) or out of (e.g., searobin, Fig. 2.8d) phase. Fourth, nerve activity directly determines the PRR and duration of natural sounds (Packard 1960; Skoglund 1961; Cohen and Winn 1967; Connaughton 2004). Fifth, the pattern of nerve activity does not reflect pattern of VMN organization. For example, sea robin and sculpin both display a ventrolateral VMN at the same hindbrain-spinal level (Fig. 2.8) (also see Bass and Baker 1991; Ladich and Bass 1998). However, sculpin, like midshipman and toadfish, display bilateral nerve firing that is in phase, while it is out of phase in sea robins (Fig. 2.8) (see Bass and Baker 1991 for comprehensive study). These firing patterns are consistent with patterns of sonic muscle contraction (Skoglund 1961; Cohen and Winn 1967; Connaughton 2004). The mismatch between a ventrolateral VMN and neurophysiological mechanisms (bilateral synchrony in sculpin, but not in sea robins) extends to peripheral sonic mechanics—pectoral girdle vibration in sculpin which lack a swim bladder (Barber and Mowbray 1956) and vibration of sonic muscles directly attached to the swim bladder in sea robins (Tower 1908; Bass and Andersen 1991) (also see Table 2.1). These findings show at a gross level that underlying neurophysiological patterning cannot be easily predicted from either central anatomy or peripheral mechanics.

2.5.2 *Anatomically Distinct Brain Nuclei Code for Vocal Characters*

As reviewed in Sects. 2.3.1 and 2.3.2, several anatomical studies have identified the neuronal circuitry involved in sonic signaling among fishes. Most of these investigations are limited to the identification of the position and extent of motoneurons with few also identifying pre-motoneuron circuitry (Sect. 2.3.3). Taken together, these studies provide a comparative basis for neurophysiological investigations of vocal pattern generation.

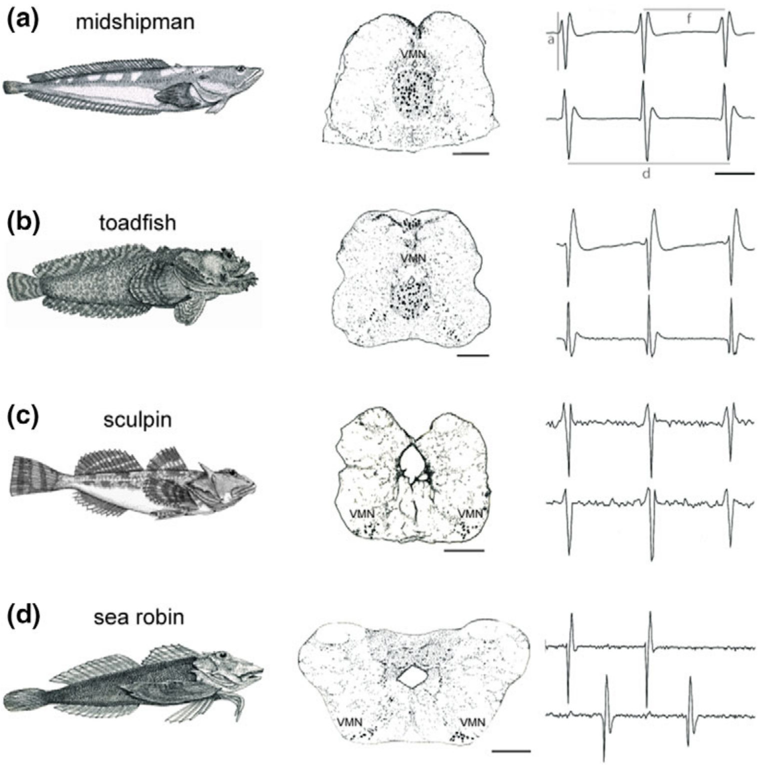


Fig. 2.8 Location of the vocal motor nucleus (VMN) does not predict phase relationship of bilateral vocal nerve firing in fishes. Portrait (*left column*) of fishes using swim bladder mechanisms (plainfin midshipman fish, *Porichthys notatus*; oyster toadfish, *Opsanus tau*; and northern sea robin, *Prionotus carolinus*) and pectoral girdle vibration (shorthorn sculpin, *Myoxocephalus scorpius*) to produce sound. *Line* drawings of transverse sections (*middle column*) of caudal hindbrain depict location of the bilateral VMN (*midline* VMNs are directly apposed to one another). *Bar scales* indicate 500 µm. Vocal nerve records from the *left* and *right* (*right column*) sides of the body demonstrate a synchronous motor volley in midshipman, toadfish, and sculpin, but an asynchronous volley in sea robins. *Bar scale* indicates 5 ms for midshipman and applies to other species. The paired vocal nerve volleys directly determine the duration (d) and PRR/fundamental frequency (f) and amplitude (a) of the vocalization as schematically indicated in the midshipman record

Most of the available cellular neurophysiological data on vocal patterning in fishes originates from studies of toadfishes that include midshipman and species generally referred to as toadfish (Nelson 2006). The success of these studies has relied, in part, on the direct translation between the neural output of the hindbrain vocal CPG, and the physical attributes of the vocal behavior. Hence, the spike-like appearance of vocalizations in fishes directly reflects distinct spike-like events comprising the activity pattern of occipital nerves (Fig. 2.8). The pattern of vocal nerve activity is referred to as a *fictive call* because it directly determines multiple call characters and is produced in the absence of muscle activation in an in vivo neurophysiological preparation.

Demski and Gerald (1972, 1974) and Fine (1979) used electrical stimulation to identify vocally active sites in the hindbrain, midbrain and forebrain of Gulf and oyster toadfishes. These studies provided landmarks for later studies to reliably elicit vocal activity in identified vocal hotspots. Anatomical tract tracing studies in plainfin midshipman and Gulf toadfish revealed an extensive network of connections between vocally active sites from forebrain to hindbrain levels, including what came to be identified as the hindbrain vocal CPG (Bass et al. 1994; Goodson and Bass 2002). These and other (Bass et al. 2000) studies that also revealed extensive connectivity with the central auditory system continue to provide anatomical guideposts for neurophysiological investigations of central vocal mechanisms.

Kittelberger et al. (2006) showed in the plainfin midshipman that vocally active neurons in the periaqueductal gray (PAG), a highly conserved midbrain region integral to vocal function in birds and mammals (see Kingsbury et al. 2011), shared a role with mammalian vocal PAG neurons in the initiation of downstream vocal CPG activity. A PAG role in the direct patterning of either fictive call duration or PRR (equal to fundamental frequency for multi-harmonic sounds in fishes) was lacking, thus leaving hindbrain targets of descending PAG pathways (Goodson and Bass 2002) as candidates for a vocal CPG in fishes. Demski and colleagues proposed that a set of hierarchically organized nuclei determined the duration and frequency of teleost fish/toadfish vocalization (Demski et al. 1973). The model was largely verified in midshipman fish by Bass and colleagues who provided the essential cellular level experiments (Bass and Baker 1990; Goodson and Bass 2000a; Kittelberger et al. 2006). As recently shown by Chagnaud and colleagues (Chagnaud et al. 2011, 2012; Chagnaud and Bass 2014), the VPP and vocal pacemaker nuclei (VPN) discussed earlier code for call duration and fundamental frequency/PRR, respectively. VPP neurons receive PAG input (Kittelberger and Bass 2013) and project to the VPN-VMN region (Chagnaud et al. 2011), acting as a link that gates forebrain/midbrain activation of hindbrain vocal sites (Kittelberger et al. 2006). Pharmacological inactivation experiments demonstrate that decreasing or increasing the activity of VPP neurons leads to an increase or a decrease in fictive call duration, highlighting the importance of this nucleus in determining call duration (Chagnaud et al. 2011). In contrast, VPN neurons exhibit prominent subthreshold oscillations that underlie an oscillatory-like firing, not present in VPP neurons, that directly determines the fundamental frequency/PRR of calls (Fig. 2.2). Pacemaker neurons project to VMN and fire in a 1:1 relationship with motoneurons; each VPN action potential directly precedes VMN action potentials. The duration of VPN-VMN spiking activity strongly correlates with the duration of the VPP long-lasting membrane depolarization from which they receive direct input (Fig. 2.2). Taken together, this evidence is highly supportive of VPN neurons determining the frequency/PRR and VPP the duration of natural vocal activity.

Vocalizations, however, are not characterized by frequency and duration alone, but also by other characters such as amplitude, and modulations of amplitude and/or frequency. The amplitude of midshipman vocalization has been proposed to be directly related to the recruitment pattern of VMN motoneurons (Chagnaud et al. 2012), i.e., motoneurons are recruited in accordance with the size principle, with the smallest ones activated first (Henneman and Mendell 1981). The question remains, however, as to which premotor nucleus determines the number of motoneurons to be recruited at any one time. One potential mechanism could originate from a differential activation of VPP neurons that, besides projecting to VPN, also project to VMN (Chagnaud et al. 2011). This further raises the question as to which brain region determines the differential recruitment of VPP neurons and by which means (e.g., size principle again?). The midbrain PAG would be an excellent candidate due to its role in vocal initiation, but also because of its suggested contribution to shaping vocal duration (Kittelberger et al. 2006). Direct testing of these hypotheses awaits further experimental investigation.

2.5.3 Neuronal Synchrony—An Essential Trait of Vocal Neurophysiology

Few studies have investigated the neurophysiological adaptations of single vocal motoneurons or of the activity pattern of the entire VMN population. As noted earlier, each vocal nerve spike reflects the synchronous firing of VMN neurons, and directly determines the onset of muscle contraction and in turn, the production of one sound pulse. Hence, the vocal nerve motor volley provides a direct readout of natural vocal behavior, providing information about the onset of a call, as well as its frequency, duration, and amplitude (see Fig. 2.8) (Cohen and Winn 1967; Bass and Baker 1991; Remage-Healey and Bass 2004; Remage-Healey et al. 2006; Rubow and Bass 2009; Chagnaud et al. 2012). The firing frequency of the vocal motor volley, which directly translates into natural call PRR/fundamental frequency, increases linearly with increasing temperature across multiple species irrespective of peripheral vocal mechanism, i.e., swim bladder (oyster toadfish, midshipman, sea robin) versus pectoral girdle vibration (sculpin) (Bass and Baker 1991). Together, the available evidence suggests that stable and precise temporal patterning of a high degree of neuronal synchrony is a shared motoneuron character across distantly related groups of vocal fishes (Bass and Baker 1991).

Sonic swim bladder muscles qualify as superfast muscles known to be adapted to generate speed rather than force (Rome et al. 1996; Rome 2006). To do so, these muscles require simultaneous activation of muscle fibers within a brief period of time in order to reach a high PRR. In Gulf toadfish, for instance, full muscle contraction and full muscle relaxation has to occur within a period of 5 ms in order to reach PRRs of 200 Hz at ambient temperatures of 25–30 °C (Demski et al. 1973; also see Rome 2006 for midshipman muscle and Bass and Baker 1991 for temperature dependency). The presence of superfast muscles is, however, not limited to toadfishes. They have also been found in other sonic systems such as in the rattlesnake tail shaker (Rome et al. 1996), the avian syrinx (Elemans et al. 2004, 2008) and the bat larynx (Elemans et al. 2011).

The first neurophysiological studies investigating the properties of a superfast motor system were in the oyster toadfish by Bennett and colleagues (Pappas and Bennett 1966; Bennett et al. 1985) who provided brief descriptions of several key characters contributing to vocal motoneuron synchrony, including gap junctional (electrotonic) coupling, low motoneuronal excitability, and inhibitory input. Pappas and Bennett (1966) showed electrotonic synapses onto swim bladder motoneurons (see Bass and Marchaterre 1989 for midshipman). Antidromic activation of motoneurons and presynaptic afferents via stimulation of the "swim bladder nerves" provided neurophysiological evidence of gap junctional coupling, later supported by anatomical studies showing extensive transneuronal transport of biotin compounds throughout the VPN–VMN circuit (Bass et al. 1994). In-depth studies of these neurophysiological characters were recently completed in midshipman fish by Chagnaud et al. (2012) who also demonstrated the importance of oscillatory excitatory input from vocal pacemaker neurons and a hyperpolarizing conductance that is activated upon network activity in generating an extreme level of synchrony. While each mechanism alone can establish synchronous activity (see Chagnaud et al. 2012 for details), the entire suite of characters contributes to the extreme level of neuronal synchrony controlling superfast muscle vocal systems, comparable to levels observed for electric fish (Bennett 1971). Interestingly, both systems share key neuronal components, including pacemaker circuitry in the same hindbrain compartment (Bass and Baker 1997; Bass and Zakon 2005). We propose similar vocal CPG adaptations in any sonic system where either nerve or EMG recordings, or sound characters themselves, indicate modulation rates of >60 Hz. This would include pectoral-dependent mechanisms in sculpin (Barber and Mowbray 1956; Bass and Baker 1991) and croaking gouramis (Ladich et al. 1992).

While midshipman and other toadfish species provide insights into the cellular mechanisms of vocal CPGs, there is an urgent need for more in-depth comparative studies of other toadfishes and other groups of sound producing fishes to test how widespread the cellular mechanisms so far identified mainly for midshipman can be applied to other species and lineages. Is extreme neuronal synchrony found among other fishes using other sonic mechanisms, e.g., sonic muscles not directly attached to the swim bladder, unlike toadfishes (see Ladich and Fine 2006)? While the dependency of superfast sonic muscle activation on synchronous neuronal activity is perhaps obvious, the question remains whether this synchrony will also be found in sound producing systems that do not apparently utilize superfast muscles given their low PRRs (e.g., damselfish; Lobel and Mann 1995) compared to toadfishes or other superfast motor systems (see above).

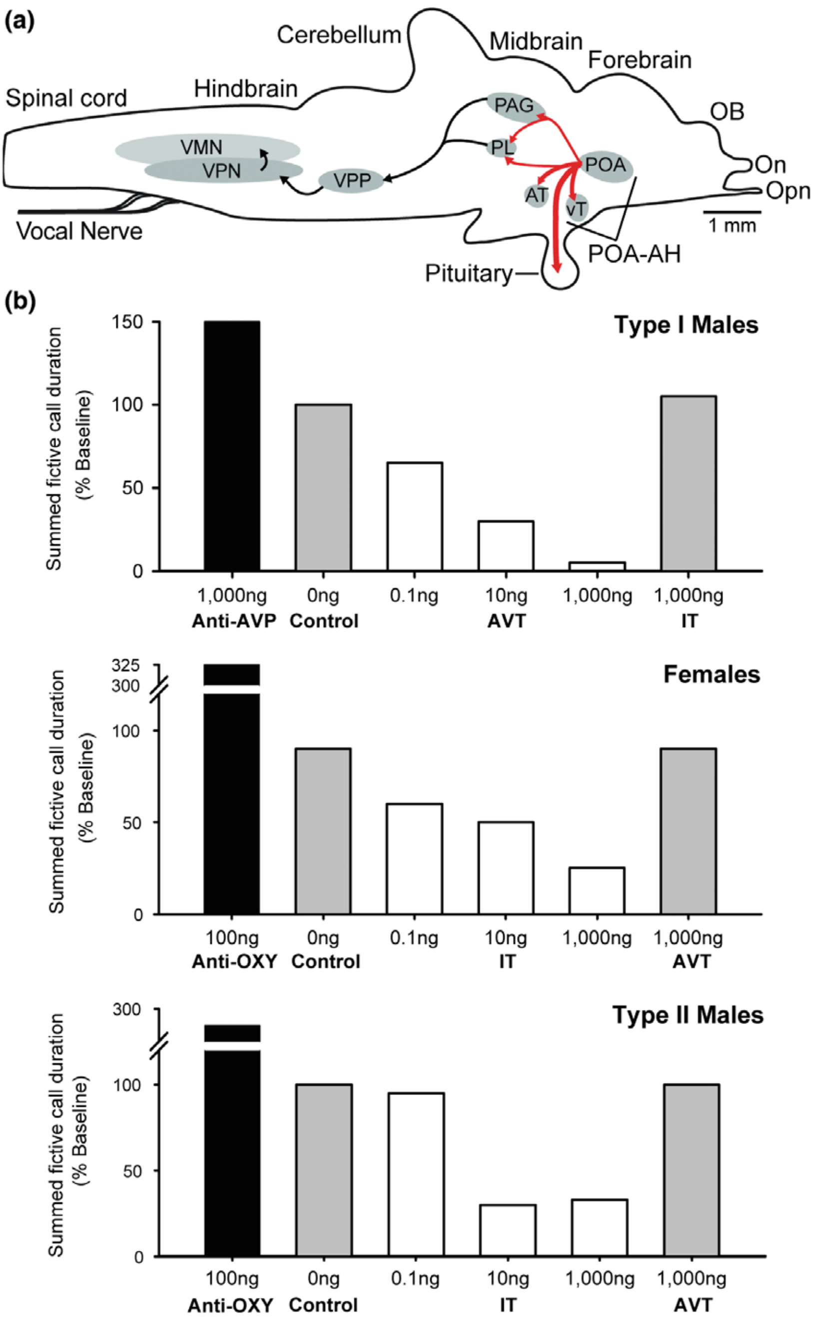
Many aspects of the neural coding of vocal behavior in fishes and among vertebrates in general remain elusive. Besides those noted at the end of the last section, other unanswered questions include: Will a single premotor nucleus be the critical node for switching between call types? What role might hormones, neuromodulators, and inhibitory and excitatory neurotransmitters play in such network level decisions and in the sculpting of call parameters in general? We next consider how hormones might contribute to the diversity of vocal signaling.

2.6 Hormonal Modulation of Vocalization and Central Sites of Action

In many vertebrates, including sonic fish, vocalizations are inextricably tied to the expression of social and reproductive states, and as such are under the influence of hormones and neuropeptides that regulate a host of related behaviors and physiology (Remage-Healey and Bass 2006; Bass and Remage-Healey 2008; Goodson 2008). Much of this is likely related to the seasonal and, in some cases daily, cycles in reproductive related acoustic communication. Among the hormones shown to modulate vocal mechanisms in fish are steroids such as androgens, estrogens, and glucocorticoids, as well as neuropeptides such as vasoactive intestinal polypeptide (VIP), arginine-vasotocin (AVT; the non-mammalian homolog to arginine-vasopressin (AVP)), and isotocin (IT; the non-mammalian homolog to oxytocin) (Goodson and Bass 2000a, b, c; Remage-Healey and Bass 2004; Remage-Healey et al. 2006). AVT is the ancestral nonapeptide in vertebrates that gave rise to closely related nonapeptides such as IT, and is found in all non-mammalian vertebrates examined to date (Bentley 1998). Several studies in midshipman fish have found divergent hormone profiles and sensitivity to specific hormone types between the sexes as well as between two male morphs exhibiting alternative reproductive strategies and vocal repertoires (Brantley et al. 1993a; Goodson and Bass 2000a; Sisneros et al. 2004a; Remage-Healey and Bass 2007; Arterbery et al. 2010a). These alternative male morphs include type I males that defend nests and acoustically court females, and type II males that sneak fertilization from type I males by aligning with females in morphology and behavior (Brantley and Bass 1994). Here, we review the effects of AVT-like peptides and steroids on the vocal behavior and neurophysiology of toadfishes, their neuroanatomical sites of action, and differences found between and within the sexes therein.

2.6.1 *Neuropeptide Regulation of Vocal Motor Output*

Modulation of vocal output by nonapeptides of the AVT family is widespread among vertebrates such as fish (Goodson and Bass 2000a, c), amphibians (Diakow 1978; Marler et al. 1995; Tito et al. 1999; Trainor et al. 2003), and birds (Voorhuis et al. 1991; Maney et al. 1997; Goodson 2008). The two main nonapeptides produced by the teleost preoptic area (POA) are AVT and IT (Bentley 1998; Goodson 2008). While all vertebrates produce vasotocin-like peptides in the POA-anterior hypothalamus (AH), the teleost brain produces AVT and IT almost exclusively within the parvocellular and magnocellular nuclei of the POA-AH, making vocal teleosts like toadfishes an ideal model for understanding vasotocin-like peptidergic regulation of vocal behavior in a fundamental and well-conserved neural circuit (Fig. 2.9a) (Goodson and Bass 2002; Goodson 2008).


(a)
Cerebellum
Midbrain
Forebrain
Spinal cord
Hindbrain
OB
VMN
VPN
VPP
PAG
PL
POA
AT
vT
On
Opn
1 mm
Vocal Nerve
POA-AH
Pituitary
(b)
Type I Males
Summed fictive call duration (% Baseline)
150
100
50
0
1,000ng Anti-AVP
0ng Control
0.1ng
10ng AVT
1,000ng
1,000ng IT
Females
325
300
100
50
0
100ng Anti-OXY
0ng Control
0.1ng
10ng IT
1,000ng
1,000ng AVT
Type II Males
300
100
50
0
100ng Anti-OXY
0ng Control
0.1ng
10ng IT
1,000ng
1,000ng AVT

◀**Fig. 2.9** Arginine vasotocin neural expression and regulation of vocal central pattern generator output. **a** Simplified representation of AVT pathways (*red arrows*) mapped onto a sagittal view of the plainfin midshipman (*Porichthys notatus*) vocal network (*black arrows*) based on immunocytochemistry (Goodson and Bass 2000c). *Arrow thickness* denotes projection density. AVT-immunoreactive (AVT-ir) pathways originate almost exclusively from the preoptic area (POA) and innervate vocally active brain sites in the POA, anterior tuberal nucleus (AT), ventral tuberal hypothalamus (vT), paralemniscal midbrain tegmentum (PL), and midbrain periaqueductal gray (PAG). Other abbreviations: *OB* olfactory bulb; *On* olfactory nerve; *Opn* optic nerve; *POA-AH* pre-optic area-anterior hypothalamus; *VMN* vocal motor nucleus; *VPN* vocal pacemaker nucleus; *VPP* vocal pre-pacemaker. **b** Vocal motor output of the midshipman in responses to POA-anterior hypothalamus stimulation 10 min after delivery of AVT, isotocin (IT), or their respective mammalian antagonists (Anti-AVP; Anti-OXY). *Top panel*, type I males; *middle panel*, females; *bottom panel*, type II males. Total fictive call duration of type I males is inhibited in a dose-dependent manner by AVT, disinhibited by anti-AVP, and not affected by IT. By contrast, fictive calls of females and type II males are not affected by AVT, but inhibited by IT and disinhibited by anti-OXY. Adapted from Goodson and Bass (2000a)

In the midshipman vocal network, the in vivo fictive call preparation in combination with central or peripheral delivery of hormones and/or their receptor antagonists has been an effective and essential tool for investigating hormone action. Delivery of AVT into, and subsequent electrical stimulation of, the POA-AH of midshipman type I males induced a dose-dependent decrease in fictive call duration and number of elicited calls, while delivery of an AVP V_{1a} receptor antagonist significantly increased call duration but not the number of calls elicited (Fig. 2.9b) (Goodson and Bass 2000a). When AVT is delivered to vocally active sites in the paralemniscal midbrain tegmentum (PL), the number of fictive calls evoked was significantly decreased and the latency of fictive call onset after stimulation was increased, while fictive call duration was not significantly affected (Goodson and Bass 2000c). Thus, in type I males, AVT inhibits vocal network excitability at both forebrain and midbrain levels, but seems to act in the forebrain to inhibit both call duration and initiation and in the midbrain to inhibit only call initiation.

Despite the conservation in amino acid sequence (AVT and AVP differ in only one amino acid) and expression within the POA-AH, the vasotocin family of nonapeptides are evolutionarily labile in that their effects are often sex-, morph-, and species-dependent (Goodson 2008; Bass and Grober 2009). A good example can be found in their differential modulation of vocal output between and within the sexes of midshipman (Fig. 2.9b). As discussed above, AVT is effective in decreasing vocal output in the nest-guarding and highly vocal type I male morph. However, AVT has negligible effects on vocal output in females or type II males (Fig. 2.9b), the alternative male morph that steals spawning from type I males and shows female-typical behaviors and morphology (Brantley and Bass 1994). Instead, IT injection in the POA-AH of females and type II males exerts dose-dependent inhibition of vocal output, while an oxytocin antagonist facilitated vocal output (Fig. 2.9b) (Goodson and Bass 2000a). These results suggest that in species with alternative reproductive tactics such as the midshipman, vasotocin-like peptides are dissociated from gonadal sex and align instead with phenotypic sex.

Placing neurophysiological results within a neuroanatomical framework (Fig. 2.9a) provides a more comprehensive view of nonapeptide action within vocal neural networks, and is made possible by immunocytochemistry studies in midshipman (Goodson and Bass 2000c; Goodson et al. 2003). Based on AVT injection studies reviewed above, projections from AVT-immunoreactive (AVT-ir) neurons in the POA to anterior (AT) hypothalamic areas (Fig. 2.9a) could be important for modulating call duration, while the AVT-ir pathway from the POA to the PAG and nearby PL (Fig. 2.9a) (Goodson and Bass 2000c) likely plays a crucial role in gating vocal initiation, since AVT injections into PL only affect call initiation and not duration (Goodson and Bass 2000c). The importance of the PAG in gating vocal output was highlighted by single unit recordings in the PAG that correlated PAG neuronal firing with call initiation. Furthermore, no fictive calls could be evoked from the POA-AH when the PAG was pharmacologically inactivated (Kittelberger et al. 2006). Thus, AVT terminals originating from the POA could be influencing call initiation via the PAG and adjacent midbrain regions.

Although females and type II males diverged from type I males in nonapeptide sensitivity (see above), no qualitative sex or morph differences in AVT or IT neuroanatomical distribution were observed (Goodson et al. 2003). Like AVT, IT-ir somata were found in the POA and projected to vocal regions in the hypothalamus and midbrain (see above). At hindbrain levels, both AVT-ir and IT-ir terminals could be found within the vicinity of the vocal CPG, especially within the vocal pacemaker region (Goodson and Bass 2000c; Goodson et al. 2003). Since no sex or morph differences were observed in AVT or IT distributions, the differential effects of these peptides on vocal motor output could be mediated by sex- or morph-specific expression of AVT or IT receptors within individual vocal nuclei, which remain to be characterized in midshipman.

2.6.2 *Sex Steroid Hormone Regulation of Vocal Behavior and Neurophysiology*

To our knowledge, the first report of hormone effects on sound production in fish were qualitative observations for the satinfin shiner, *Cyprinella analostana* (formerly *Notropis analostanus*), where testosterone injections led to increased sound production over a period of 5–10 days (Winn and Stout 1960). Since then, more comprehensive studies have shown that steroids exert rapid and robust effects on vocal behavior and the output of the underlying vocal network (Remage-Healey and Bass 2004, 2005, 2007; Remage-Healey et al. 2006).

The classic model of steroid action is the regulation of gene transcription by binding to intracellular cytosolic receptors, forming a steroid-receptor complex that translocates into the nucleus and binds to steroid-specific DNA response elements (Lösel and Wehling 2003). The resulting genomic response could take from longer than 30 min to days (e.g., as suggested for satinfin shiner), whereas rapid, nongenomic steroid effects occur on the order of seconds–minutes and may involve activation of non-classical membrane receptors in addition to classical intracellular receptors that lead to changes in secondary messenger pathways (Lösel and Wehling 2003). From the field to the laboratory, investigations in vocal teleosts have cemented the role of steroid hormones in regulating vertebrate vocal-acoustic communication over dynamic time scales, from seasonal changes in reproductive states to rapid changes in context- and stimulus-driven vocalization (see Table 2.3 for summary).

11-ketotestosterone (11-KT) is the main circulating androgen found in many male teleosts (Bentley 1998), including in type I males of the plainfin midshipman (*P. notatus*) and the Lusitanian toadfish (*Halobatrachus didactylus*), as well as in male oyster toadfish (Brantley et al. 1993b; Genova et al. 2012; Knapp et al. 1999b; Modesto and Canário 2003; Fine et al. 2004; Sisneros et al. 2004b; Maruska et al. 2009). By contrast, testosterone, which is the main circulating androgen in female teleosts, is predominant in both type II male and female midshipman and Lusitanian toadfish (Brantley et al. 1993b; Modesto and Canário 2003; Sisneros et al. 2004a). Circulating 11-KT levels peak during the pre-nesting and nesting season in the summer, coinciding with peak levels of acoustic courtship and spawning activity (Modesto and Canário 2003; Sisneros et al. 2004b). Several field studies in the plainfin midshipman strongly implicated androgens in facilitating vocal behavior in individually identified fish by showing significant correlations between plasma 11-KT levels and advertisement calling activity (Genova et al. 2012), including over rapid time-scales (within 5 min) in response to acoustic playback challenge (Remage-Healey and Bass 2005). A causal relationship linking androgens to increased vocalization was established by field studies in the Gulf toadfish, where exogenous food delivery of 11-KT rapidly increased the rate of natural calling behavior within 10–20 min (Remage-Healey et al. 2006). Complementing field behavioral studies, in vivo neurophysiological investigations in type I male midshipman and male Gulf toadfish (this species exhibits no evidence of alternative male morphs) showed that systemic injections of 11-KT, but not testosterone, rapidly elevated the duration of the vocal pattern generator output within 5 min, an effect that lasted for at least 2 h (Remage-Healey and Bass 2004; Remage-Healey et al. 2006). Thus, 11-KT is the main androgenic steroid that rapidly facilitates male vocal behavior, likely by exerting non-genomic actions via classical intracellular receptors, which was supported by receptor-specific antagonist treatments during fictive calling (Remage-Healey and Bass 2004). Steroid actions are presumably taking place within specific vocal nuclei that express androgen receptors (ARs) (see Fig. 2.10a) (Forlano et al. 2010), though effects of focal steroid injections directly into vocal nuclei remain to be investigated.

In the Gulf toadfish, field experiments showed that cortisol levels were elevated in experimental males who began vocalizing after two days of being placed among a natural population of calling males (Remage-Healey and Bass 2005). Unlike 11-KT, cortisol levels did not rapidly elevate in response to acoustic playbacks of tones resembling natural toadfish boatwhistle calls (Remage-Healey and Bass 2005). Food delivery of cortisol to naturally vocalizing toadfish also did not rapidly

Table 2.3 Summary of steroid hormone profiles and effects of hormone injection on vocal behavior and central pattern generator output (measured in fictive call duration)

Ref	Species	Measured parameter	11-KT	T	E2	Cort
1	*Cyprinella analostana,* formerly *Notropis analostanus*	Number of sounds	N.M.	↑ In ♂ 5–10 days post-injection	N.M.	N.M.
2	*Porichthys notatus*	Plasma levels	**Higher** in hummers than non-hummers	**Equal** between hummers and non-hummers	N.M.	N.M.
3	*Opsanus beta*	Plasma levels	↑ In calling population ↑ After playback	N.M.	N.M.	↑ In calling population ✖ After playback
4	*Opsanus beta*	Natural call rate and fictive call duration	↑ Natural call rate and ↑ fictive call duration in ♂	✖ Fictive call duration in ♂ and ♀	✖ Fictive call duration in ♂ and ♀	↑ Fictive call duration in ♂ and ♀
5	*Porichthys notatus*	Fictive call duration	↑ In I♂	✖ In I♂	↑ In I♂	↑ In I♂
6	*Porichthys notatus*	Fictive call duration	✖ In II♂ and ♀	↑ In II♂ and ♀	↑ In II♂ and ♀	↓ In II♂ and ♀

I♂, II♂, ♀ respectively represent type I males, type II males, and female midshipman (*Porichthys notatus*)
↑, ✖, ↓ respectively denote an observed increase, no change, and decrease in measured parameter
Abbreviations: *11-KT* 11-Ketotestosterone; *T* testosterone; *E2* 17β-estradiol; *Cort* cortisol; *N.M.* not measured
Ref references; (1) Winn and Stout (1960); (2) Genova et al. (2012); (3) Remage-Healey and Bass (2005); (4) Remage-Healey and Bass (2006); (5) Remage-Healey and Bass (2004); (6) Remage-Healey and Bass (2007)

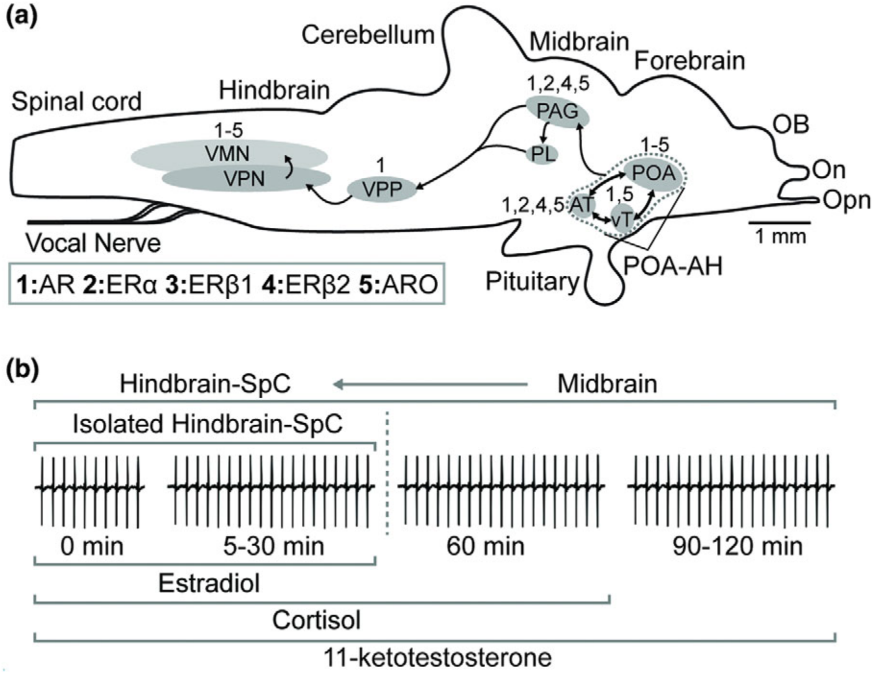


Fig. 2.10 Steroid sensitivity of vocal pattern generator. **a** Steroid receptors and aromatase (ARO) localization mapped onto the descending vocal network based on studies in plainfin midshipman (*Porichthys notatus*). Abbreviations: *AR* androgen receptor; *AT* anterior tuberal nucleus; *ER* estrogen receptor; *OB* olfactory bulb; *On* olfactory nerve; *Opn* optic nerve; *PAG* periaqueductal gray; *POA-AH* preoptic area-anterior hypothalamus; *VMN* vocal motor nucleus; *VPN* vocal pacemaker nucleus; *VPP* vocal pre-pacemaker; *vT* ventral tuberal hypothalamus. Numbers within or apposing each nucleus indicate localization of corresponding receptors or aromatase. Note that "1–5" indicate the presence of all receptors and aromatase, whereas *1*, *5* indicate the presence of only ARβ and aromatase. *Dotted lines* enclose the reciprocally connected vocal nuclei within the POA-AH. **b** Summary for type I male midshipman fish of rapid steroid hormone action on the spike-like vocal nerve motor volley, or fictive call, that is the output of vocal central pattern generator activity; adapted from (Remage-Healey and Bass 2006). The isolated hindbrain-spinal cord (SpC) is sufficient for responding to rapid stimulatory actions of steroids only up to 30 min. Intact descending midbrain input is necessary for sustained effects of steroids lasting up to 2 h. Depicted on the bottom is temporal specificity of estradiol-, cortisol-, and 11-ketotestosterone-induced increases in fictive call duration that directly determines natural call duration; each nerve spike corresponds to a single sound pulse

increase call rate, unlike what was observed for 11-KT (Remage-Healey et al. 2006). Playback experiments using foraging sounds of Atlantic bottlenose dolphins, major predators of soniferous fish including toadfish, led to decreases in call rate within 5 min by toadfish housed in enclosures in their natural habitat, while increasing their plasma cortisol levels (Remage-Healey et al. 2006). Although this study suggested a negative correlation between cortisol and natural call rate, exogenous cortisol delivered to Gulf toadfish did not change their call rate

(Remage-Healey et al. 2006). These field results would lead to predictions that either cortisol has no direct effect on natural vocal behavior or that it inhibits calling specifically in the presence of sonic predators.

Results from in vivo neurophysiology experiments, however, strongly support a regulatory role for cortisol at the vocal neural circuit level. Peripheral intramuscular cortisol injections induced a rapid increase in fictive call duration within 5 min that lasted at least 2 h in both male and female Gulf toadfish (Remage-Healey et al. 2006). Similarly, neurophysiology experiments in type I male midshipman showed that intramuscular injections of cortisol rapidly increased fictive call duration within 5 min, which lasted for 60 min, an effect blocked by the glucocorticoid receptor antagonist mifepistone (Remage-Healey and Bass 2004). In summary, although strong evidence supports cortisol action within vocal neural circuitry, a direct demonstration of consequences for vocal behavior is still lacking.

Similar to nonapeptides, steroid action on the vocal neural network in midshipman is sex- and male morph-specific (Remage-Healey and Bass 2007). In contrast to the stimulatory action of cortisol on the type I male vocal circuit, intramuscular injections of cortisol in type II male and female midshipman rapidly inhibited fictive call duration, which also lasted from 5 to 60 min (Remage-Healey and Bass 2007). Male morph-specific patterns in the abundance of corticosteroid receptors and steroid synthetic enzymes in different brain regions could mediate observed differences in neurophysiology, although such receptors have yet to be localized to specific parts of the central vocal network (Arterbery et al. 2010a, b).

As mentioned earlier, 11-KT, but not its androgenic precursor, testosterone, stimulated the output of the vocal circuitry in type I male midshipman (Remage-Healey and Bass 2004). In type II males and females, the opposite is true, where testosterone rapidly increased vocal motor output and 11-KT had no effects (Remage-Healey and Bass 2007). Testosterone's rapid action in type II males and females only lasted for 45 and 30 min, respectively, consistent with testosterone being 10 times less potent than 11-KT in activating teleost ARs (Bentley 1998), though other factors could have accounted for sex and morph differences in androgen sensitivity. Although type II male neuroendocrine sensitivity profiles align mostly with females instead of type I males, sex-specific divergence between type II males and females was discovered by the use of cyproterone acetate, an AR blocker, and fadrozole, an inhibitor for aromatase, the enzyme that converts testosterone into estradiol (Remage-Healey and Bass 2007). In these experiments, pre-injection of cyproterone acetate blocked the ability of testosterone to increase fictive call duration in type II males but not in females. By contrast, pre-injections of fadrozole blocked testosterone's ability to increase call duration in females but not in type II males. These results suggest that in type II males, testosterone acts through ARs to increase vocal output, whereas in females, testosterone is converted into estradiol, which presumably acts through estrogen receptors (ER) (Fig. 2.10a) to increase vocal output.

Estradiol injections rapidly increased fictive call duration in both sexes and male morphs of midshipman (Remage-Healey and Bass 2004, 2007), but were not effective in either male or female Gulf toadfish (Remage-Healey et al. 2006).

Furthermore, while testosterone induced rapid increases in fictive call duration in type II male and female midshipman (Remage-Healey and Bass 2007), it was ineffective in female Gulf toadfish (Remage-Healey et al. 2006). In fact, the only steroid tested that exerted rapid effects on female Gulf toadfish fictive vocalization was cortisol (Remage-Healey et al. 2006). These differences reveal striking species divergence in steroid hormone regulation of vocal neural networks.

Interestingly, when the descending midbrain input to the hindbrain vocal pattern generator was severed in type I male midshipman, the effects of 11-KT and cortisol on fictive call duration did not last more than 30 min, compared to 2 h (11-KT) and 45 min (cortisol) in intact preparations (Fig. 2.10b) (Remage-Healey and Bass 2004). In male Gulf toadfish, a similar reduction in the duration of call potentiation resulting from 11-KT and cortisol was observed when descending midbrain input into the hindbrain vocal pattern generator was severed (Remage-Healey et al. 2006). These results suggest that steroid action within forebrain and midbrain vocal acoustic centers mediate sustained stimulation of vocal behavior, while steroid action within the hindbrain alone is sufficient to elicit rapid increases in vocalization (Remage-Healey and Bass 2004).

In summary, complementary field and neurophysiological studies in toadfishes demonstrate steroid regulation of dynamic social behaviors that fluctuate on the minute-by-minute time scale, and neurophysiological studies have uncovered both sex- and male morph-specific steroid sensitivities of the midshipman vocal network (Table 2.3) (Remage-Healey et al. 2006). The ability to monitor changes in natural vocal behavior in the field together with the highly accessible and predictive readout of the vocal neural network makes toadfishes an ideal model for studying hormone regulation of vocal behavior at various levels of analyses.

2.6.3 Central Sites of Steroidogenesis and Hormone Action

2.6.3.1 Aromatase

All steroids are derived from cholesterol and converted by steroidogenic enzymes to bioactive or inactive metabolites (Bentley 1998; Adkins-Regan 2005). The brain itself contains all the necessary enzymes to locally synthesize steroids in addition to being capable of responding to and processing circulating steroids derived from the gonad or the adrenal gland (Baulieu and Robel 1990; Forlano et al. 2006; Saldahna and Schlinger 2008). One of the steroidogenic enzymes that has received the most attention with respect to regulating reproductive and courtship behavior is aromatase, which converts aromatizeable androgens such as testosterone into estrogens (Adkins-Regan 2005). Since estrogens cannot be converted back to androgens, aromatase levels in the brain regulate the local ratio of testosterone and estrogens to modulate steroid-dependent behaviors (Adkins-Regan 2005; Remage-Healey et al. 2008). It is important though to note that the more potent androgens, such as 11-KT in teleosts and 5α-dihydrotestosterone in other tetrapods, cannot be aromatized and thus cannot be shunted from exerting androgen action (Bentley 1998; Adkins-Regan 2005). Neuroanatomical studies in midshipman have localized steroid receptor messenger RNA (mRNA) and protein expression as well as the estrogen synthetic enzyme aromatase within forebrain, midbrain, and hindbrain regions controlling vocal behavior. Figure 2.10a summarizes steroid receptor expression within the midshipman vocal network.

The teleost brain has a remarkably high level of aromatase activity when compared to other taxa (Callard et al. 1990; Forlano et al. 2001, 2006). In plainfin midshipman, studies that quantified enzymatic conversion of radioactive ligand found that the forebrain had higher aromatase activity compared to midbrain and hindbrain (Schlinger et al. 1999). Furthermore, aromatase activity in the hindbrain region containing the vocal pattern generator of females and type II males was significantly higher than in type I males (Schlinger et al. 1999). Type II male hindbrain had higher aromatase activity than type I males even after castration, indicating that the male morph difference in aromatase activity was not dependent on circulating gonadal testosterone (Schlinger et al. 1999). These sex and morph differences were later confirmed by quantitative PCR (qPCR) of midshipman aromatase in isolated hindbrain tissues with the VMN removed (Fig. 2.11) (Fergus and Bass 2013). These results suggest that differences in constitutive hindbrain aromatase activity could prevent testosterone from masculinizing the vocal pattern generator in females and type II males.

Neuroanatomical distribution patterns within the midshipman vocal network were extensively characterized by in situ hybridization using midshipman-specific aromatase mRNA probes, and immunocytochemistry using midshipman-specific aromatase antibodies (Forlano et al. 2001). Overall aromatase immunoreactivity (ir) confirmed brain region differences in aromatase activity summarized above. Aromatase containing cells were identified as glial and not neuronal (Forlano et al. 2001).

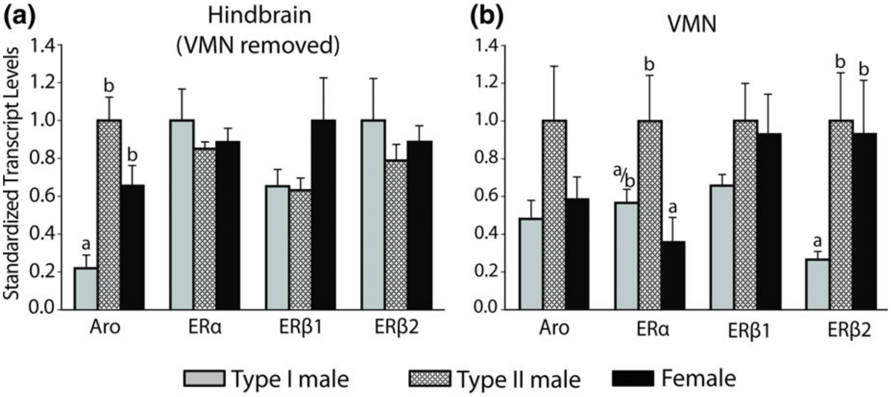


Fig. 2.11 Sex and morph differences in hindbrain estrogen sensitivity. Sex- and male morph-specific mRNA expression profiles of aromatase (*Aro*) and estrogen receptor (*ER*) subtypes, quantified by real-time PCR, for vocal motor nucleus (*VMN*) dissected in toto and for surrounding hindbrain region without VMN. Taken from Fergus and Bass (2013)

Aromatase-ir and mRNA expression were abundant throughout the vocal network, including the forebrain POA, midbrain PAG and hindbrain VMN (Forlano et al. 2001). Dense aromatase-ir containing glial cells around the dorsolateral margin of VMN extended their processes throughout the nucleus in a radial-like pattern. Thus, aromatase is found within every major node of the midshipman vocal control network, likely providing sources of locally converted estradiol, which was shown to rapidly increase fictive call duration (Table 2.3; Fig. 2.10b) (Remage-Healey and Bass 2004, 2007).

2.6.3.2 Androgen and Estrogen Receptors

Two isoforms of AR (ARα and ARβ) have been characterized in teleost fish that are sensitive to both 11-KT and testosterone (Sperry and Thomas 1999, 2000; Ogino et al. 2009). Compared to ARα, teleost ARβ shows higher sequence identity to tetrapod ARs and therefore likely resembles the ancestral AR in function (Sperry and Thomas 1999, 2000; Ogino et al. 2009; reviewed in Forlano et al. 2010). Midshipman ARβ mRNA was highly expressed in the POA, AT and ventral tuberal nuclei, sites that evoke fictive calls when electrically stimulated (Goodson and Bass 2000a, c; Kittelberger et al. 2006; Forlano et al. 2010). ARβ mRNA was also found in midbrain vocal-acoustic regions, such as the PAG, as well as in hindbrain vocal pattern generator, including the VPP and VMN (Forlano et al. 2010). An early report in the oyster toadfish using steroid autoradiography reported a sparse distribution of ARs in the medulla at the level of VMN, including a region that likely corresponds to VPP (Fine et al. 1996). It is unclear if ARα and ARβ receptor subtypes exhibit divergent localization or expression patterns in the midshipman brain, as have been shown in other teleosts (Harbott et al. 2007). Furthermore, what accounts for the differential sensitivity of the vocal network of male morphs and sexes to 11-KT versus testosterone is also not clearly understood. We know from studies in the peripheral vocal muscle that ARα mRNA expression is elevated in type I males who were actively humming at the time of tissue collection compared to males who were not, whereas ARβ was higher in non-humming type I males (Genova et al. 2012). Perhaps then, divergent sex- or morph-specific AR subtype profiles in vocal nuclei could account for differences in neural androgen sensitivity.

Several ER, including ERα, ERβ1, and ERβ2 have been sequenced and localized to vocal control regions in the midshipman brain (Fig. 2.10a) (Forlano et al. 2005; Fergus and Bass 2013). Strikingly, all three ERs are strongly expressed in the POA, previously shown to express aromatase (see above; Forlano et al. 2001, 2005; Fergus and Bass 2013). In the hypothalamus, ERβ2 showed robust expression in vocally active AT (Goodson and Bass 2000a; Fergus and Bass 2013). At midbrain levels, only ERβ2 was distributed within the PAG. In the hindbrain vocal pattern generator, ERα, ERβ1, and ERβ2 were all strongly expressed within VMN neurons (Forlano et al. 2005; Fergus and Bass 2013). Interestingly, females and type II males showed stronger staining for ERβ2 in VMN neurons compared with type I males, which was verified by qPCR using the isolated VMN (Fig. 2.11) (Fergus and

Bass 2013). These qPCR studies also revealed a significant elevation of ERα within type II male VMN compared to female VMN (Fig. 2.11). These sex and morph differences in ER expression were specific to the VMN, as qPCR of ER expression in surrounding hindbrain tissue did not show any significant differences (Fig. 2.11).

Taken together, the brain of toadfishes can be characterized as an exquisitely sensitive endocrine organ that directs the expression of adaptive vocal behavior under a variety of social and environmental contexts, including territorial defense, mate attraction, and predator avoidance.

2.6.4 Hormone Regulation of Daily Rhythms in Vocal Behavior

Midshipman courtship vocalization follows dramatic daily and seasonal rhythms, occurring at night during the summer breeding season (Brantley and Bass 1994; McIver et al. 2014). The daily nocturnal peak in vocal activity is similar to that observed for other toadfish species and sonic fish (Locascio and Mann 2008; Rice and Bass 2009). In vivo physiological studies show that the duration of type I male fictive calls increases and threshold levels decrease in midshipman tested during the summer at night (Rubow and Bass 2009). This nocturnal-dependent increase in vocal excitability is abolished in fish held under 5 days of constant light, and is substantially increased in fish held under constant darkness (Rubow and Bass 2009). Although we have accumulated strong evidence for the rapid modulation of fish vocal behavior by steroids and neuropeptides, the hormone control of rhythmic vocal behavior over the daily cycle has not been well studied.

Since the vertebrate time-keeping hormone melatonin shows elevated levels at night that is abolished under constant light (Falcón et al. 2010), we recently tested whether changes in vocal excitability under constant photo-regimes are melatonin-dependent in type I male midshipman (Feng and Bass 2014). Melatonin implants in fish held under 5 days of constant light decreased fictive call threshold and increased fictive call duration, effectively rescuing the decreased vocal excitability seen in control animals. However, pilot studies did not show a rapid effect of melatonin on the order of minutes–hours, suggesting that melatonin's actions on increasing vocal network excitability may depend on its interaction with other effectors, such as the steroid hormones and/or neuropeptides discussed above. It remains to be shown that melatonin receptors are expressed in vocal brain regions as seen in songbirds (Gahr and Kosar 1996; Bentley and Ball 2000; Jansen et al. 2005) and whether receptor expression levels change across the day. Future work also needs to test whether fish vocalizations are under endogenous circadian control by recording vocal behavior under constant photo-regimes, which has recently been demonstrated in a songbird (Wang et al. 2012). Thus, although we have some evidence for a melatonin-sensitive vocal network, the cascade of cellular events leading to daily and seasonally rhythmic vocal behaviors remain to be defined.

2.7 Future Directions

Fishes have become a prime model system to understand not only the neuronal patterning of vocalizations, but also the modulation of vocal behavior. However, most of these studies have so far been performed in only one group of fishes, toadfishes. There is an urgent need for comparative neurophysiological data at the level of vocal nerve output and of premotor and motor circuitry. We need to know whether the mechanisms of vocal pattern generation found in toadfishes hold true for other fish species using the same or a different vocal apparatus. While we now know how simple sounds such as grunts are patterned, we are still lacking any data demonstrating how CPGs pattern calling sequences like grunt trains or repetitive boatwhistles. We also need to better understand how vocal CPGs interact with other CPGs, especially given the proposal that vocal-pectoral appendage and vocal-respiratory coupling in fishes may be the evolutionary antecedent of vocal-gestural and vocal-respiratory coupling exploited among tetrapods during the course of vertebrate evolution (Bass and Chagnaud 2012). To best elucidate these and related questions, novel recording systems to acquire physiological data in freely behaving animals, like those being pioneered in birds and mammals, are essential.

Although we have strong evidence for steroid and neuropeptide regulation of fish vocal behavior over rapid timescales, how hormones regulate daily rhythms in vocal behavior is still unknown. Specifically, are fish vocalizations under endogenous circadian control and is the time-keeping hormone melatonin involved? Finally, investigations of other neuromodulators, such as dopamine and serotonin, are needed to paint a more complete picture of hormone regulation of vocal behavior and underlying vocal motor networks.

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Chapter 3
Mechanisms of Fish Sound Production

Michael L. Fine and Eric Parmentier

Abstract Fishes have evolved multiple mechanisms for sound production, many of which utilize sonic muscles that vibrate the swimbladder or the rubbing of bony elements. Sonic muscles are among the fastest muscles in vertebrates and typically drive the swimbladder to produce one sound cycle per contraction. These muscles may be extrinsic, typically extending from the head to the swimbladder, or intrinsic, likely a more-derived condition, in which muscles attach exclusively to the bladder wall. Recently discovered in Ophidiiform fishes, slow muscles stretch the swimbladder and associated tendons, allowing sound production by rebound (cock and release). In glaucosomatids, fast muscles produce a weak sound followed by a louder one, again produced by rebound, which may reflect an intermediate in the evolution of slow to superfast sonic muscles. Historically, the swimbladder has been modeled as an underwater resonant bubble. We provide evidence for an alternative hypothesis, namely that bladder sounds are driven as a forced rather than a resonant response, thus accounting for broad tuning, rapid damping, and directionality of fish sounds. Cases of sounds that damp slowly, an indication of resonance, are associated with tendons or bones that continue to vibrate and hence drive multiple cycles of swimbladder sound. Stridulation sounds, best studied in catfishes and damselfishes, are produced, respectively, as a series of quick jerks causing rubbing of a ribbed process against a rough surface or rapid jaw closing mediated by a specialized tendon. A cladogram of sonic fishes suggests that fish sound production has arisen independently multiple times.

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3.1 Introduction

Fishes produce sounds in courtship, spawning, agonistic behavior, competitive feeding, and when disturbed. Unlike homologous sonic mechanisms in birds and mammals (syrinx and larynx, respectively), fish sonic mechanisms appear to have evolved independently (see below). Consequently, they show the widest range of sound production apparatuses among vertebrates (Ladich and Fine 2006). The mechanisms are so diverse that authors have not defined a simple classification. The two major mechanisms of sound production involve exciting the swimbladder with a variety of specialized sonic muscles and the stridulation of bones. Sonic muscles may be intrinsic or extrinsic. Extrinsic muscles are present in numerous fishes and typically originate on various bones on the skull (but also epineurals, ribs, pectoral girdles, and vertebral bodies) and insert on the swimbladder or on a bone or tendon connected to the swimbladder. Intrinsic muscles, likely a more-derived condition, attach exclusively to the bladder wall and do not have typical origins or insertions. Summaries of gross anatomy of sonic muscle variation in various fishes have been described elsewhere (Ladich and Fine 2006).

This chapter will focus on the functional morphology of fish sound production, the relationship of morphology, physiology, and behavior, concentrating on swimbladder and stridulatory mechanisms. Our goal is when possible to put this information into an evolutionary context, which is a stretch since sounds, muscles, and swimbladders leave no fossil record although a fossilized catfish pectoral spine has been described (Hubbs and Hibbard 1951). Some of the issues discussed are intimately related to sister fields (hearing, passive, and active acoustics), and these fields will be discussed briefly as necessary. Fish sound production has been reviewed a number of times (Fish and Mowbray 1970; Tavolga 1971b; Fish 1972; Demski et al. 1973; Fine et al. 1977a; Hawkins 1993; Zelick et al. 1999; Ladich and Fine 2006; Parmentier and Diogo 2006; Rosenthal and Lobel 2006; Kasumyan 2008; Lobel et al. 2010) calling into question the need for another review. However, the basic model of swimbladder acoustics, the underwater resonant bubble, which had assumed doctrinal status, is being challenged, and there has been new work on a variety of species. This review will attempt to present summaries and opinions about the state of the field and will not attempt to be encyclopedic since references are available in other reviews. It is also intended as an introduction for new investigators to explain fish sound analysis.

3.2 Water as an Acoustic Medium

Because of its compressibility, water is often considered superior to air for acoustic communication: the speed of sound in water (*ca* 1,500 m/s) is close to five times faster than in air, and sound can travel for long distances underwater, in some cases hundreds or even thousands of miles when collimated into the SOFAR

(Sound Fixing and Ranging) channel that hinders vertical spreading (Munk 1974). Olfactory communication is restricted to fish in close proximity or requires a receiver to be downstream in a current. With an obvious exception of tropical shallow water coral reefs that are well lit, many freshwater and marine habitats have turbid water restricting visual propagation, and most of the deep ocean is dark except for bioluminescence. Long-distance propagation of sound is sometimes heralded as the ideal modality for underwater communication, and whale sounds are commonly recorded in deep ocean (Au and Hastings 2008). This notion, however, faces several related problems when applied to fishes. Seemingly all fishes hear (Ladich 2014), but most species do not produce sounds for social communication and are not considered sonic in this review. We note, however, that an ever expanding list of families of sonic fishes has been compiled (Lobel et al. 2010). There are sonic and nonsonic teleosts in a variety of habitats including various freshwater bodies, estuaries, and diverse oceanic habitats. Environmental or other conditions that would select for sonic muscles or for their loss are unexplored although sonic fishes are often associated with territoriality and substrate breeding (Marshall 1967; Ladich and Myrberg 2006).

Based on anatomical data, i.e., the presence of sonic swimbladder muscles, only a small number of families (mostly ophidiids, macrourids, and possibly morids) produce sound in the deep ocean where it would be of maximal advantage (Marshall 1962) due to the absence of surface light and low population densities. Although whale sounds are commonly recorded in deep water, fish sounds have not been demonstrated conclusively (Mann and Jarvis 2004; Wall et al. 2012, 2013, 2014) below some hundreds of meters. Quite likely, sounds are important for courtship and reproduction in deep water, but it is unlikely that females are homing in on male callers from great distances. The problem of recording and identifying particular callers is compounded by the need to use light to identify the calling fish since a bright light is an alien stimulus in dark waters. Recording sounds, identifying the caller's identity and the role sound production will be a daunting task even with automated underwater vehicles and long-term underwater installations. Negative data should not be taken to indicate that fish sounds are unimportant in the dark deep waters of the world's oceans.

Even in shallow often turbid water, identification of the species of calling fish can be a problem, and investigators have been fooled by an unseen cusk-eel in a pen until the call was recently identified (Mann et al. 1997; Sprague et al. 2000). Therefore it is mandatory to record captive fish. Holding fish often, but not always, evokes sound production and can confirm species identity although sounds can be changed by small containers (Akamatsu et al. 2002; Parmentier et al. 2014) or if recorded in air (Fine et al. 2004). Trawling for callers or finding identified eggs following a chorus can also serve for identification although vigilance is required. In some cases, it is possible to see or feel movement when the fish produces a sound, but this is not always true. For instance, pomacentrids make courtship dips, cichlids change colors, and head movements have been seen in cottids and gobies. In most cases, even if the species emitting sound is clearly identified, the caller will not be visible underwater, and therefore only a small amount of work has been done on sound pressure levels of fishes in the field (Barimo and Fine 1998; Locascio and Mann 2005; Mann et al. 2009). One way around this problem is using multi-hydrophone arrays to localize callers (Locascio and Mann 2011). Source levels require calibrated measurements of fish at a known distance (typically 1 m), and the distance between the caller and the hydrophone is usually unknown.

Similarly, the acoustical Umwelt (the boundaries of the perceptual world) of fishes is typically unknown largely because of the difficulties of working underwater. The midshipmen *Porichthys notatus*, a west coast toadfish, has been attracted to speakers over short distances (McKibben and Bass 1998), and calling of different toadfish has been manipulated by playbacks from a nearby speaker (Winn 1967, 1972; Fish 1972; Jordão et al. 2012). Gulf toadfish (*Opsanus beta*) have responded to short distance playbacks of dolphin sounds by elevating cortisol levels (Remage-Healey et al. 2006). Many species, particularly sciaenids call in choruses (Lagardère and Mariani 2006; Ramcharitar et al. 2006), but there is little evidence of fish actually communicating over long distances. Silver perch sounds have been detected at several hundred meters under ideal conditions (Sprague et al. 2000), but considering background vocalizations, they believe communication is likely to occur over several meters. Females may know the positions of established choruses, and no one has demonstrated whether they use sound to localize a chorus, to identify nearby spawning partners, to be stimulated into final spawning readiness or some combination of all three.

Most known sound production occurs in relatively shallow water. At extremely shallow depths, the long wavelengths of low-frequency underwater sound suffer rapid attenuation and restrict communication to short distances (Fine and Lenhardt 1983; Mann and Lobel 1997; Mann 2006). For example, a 100 Hz sound will have a wavelength of ca 15 m (the speed of sound divided by the frequency) and will not propagate in water less than several meters in depth: the wavelength divided by four (Urick 1975). In an extreme case, sounds of a small goby in a rock-lined stream several 10s of centimeters deep, attenuation can be as much as 30 dB in half a meter (Lugli and Fine 2003; Lugli et al. 2003; Lugli 2008, 2010). In addition to water depth, acoustic communication is limited by ambient (or more recently man-made) noise (Ladich 2013).

3.3 Sound Parameters

Three major tools for describing fish sounds are sonagrams, an output of frequency against time; oscillograms, which depict amplitude against time (Fig. 3.1); and frequency spectra, which show amplitude against frequency and indicate dominant frequencies within a sound. These outputs are available on various software programs. Most fish sounds are a series of short-duration pulses and therefore present as vertical lines (a wide frequency band with a short duration) on a sonagram. A smaller number of species produce tonal sounds by a continuous series of muscle contractions, and these present as a series of horizontal lines at the muscle

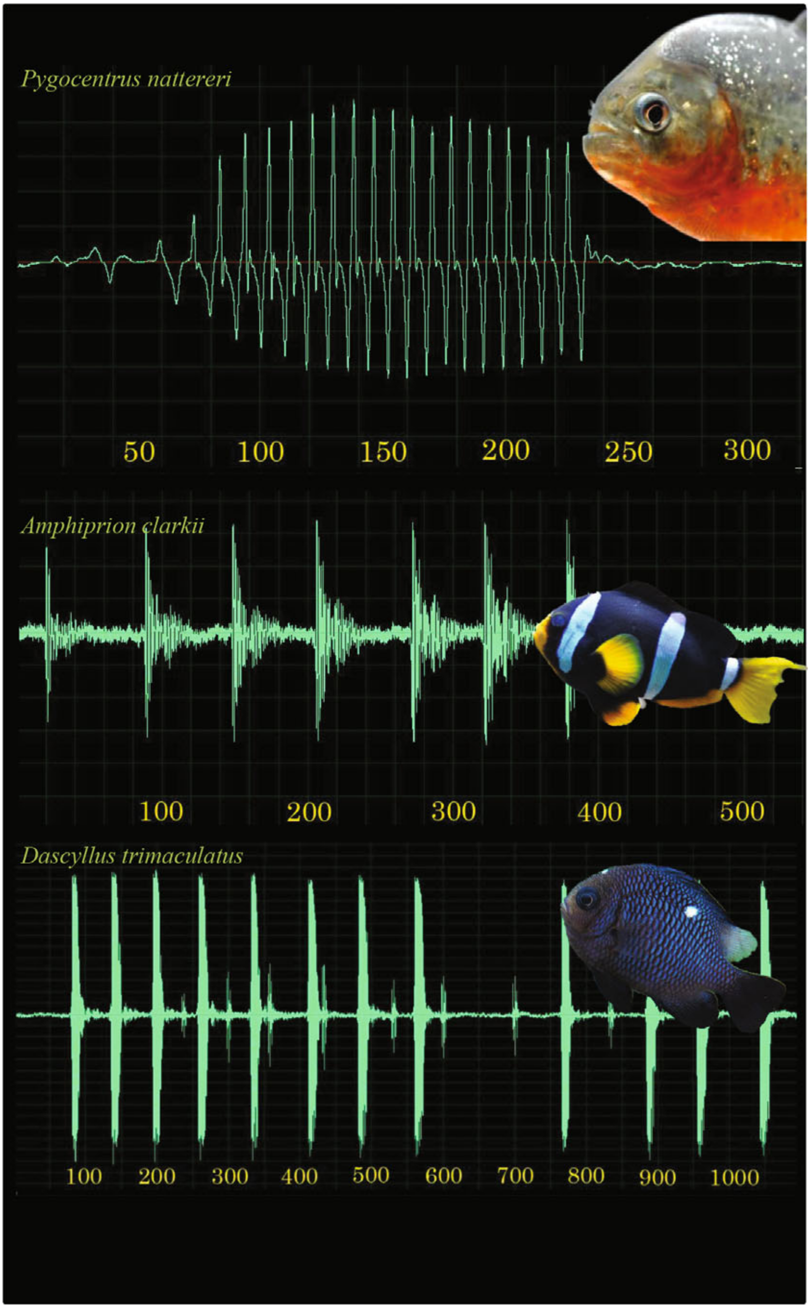

Fig. 3.1 Oscillograms (Voltage against time) of representative sounds for a piranah (*Pygocentrus*), two pomacentrid damselfish (*Amphiprion* and *Dascyllus*), a toadfish (*Opsanus*), a cusk-eel (*Ophidion*), and a butterfly fish (*Heniochus*). The piranah and toadfish sounds are tonal and the others consist of a series of pulses with various attenuation patterns

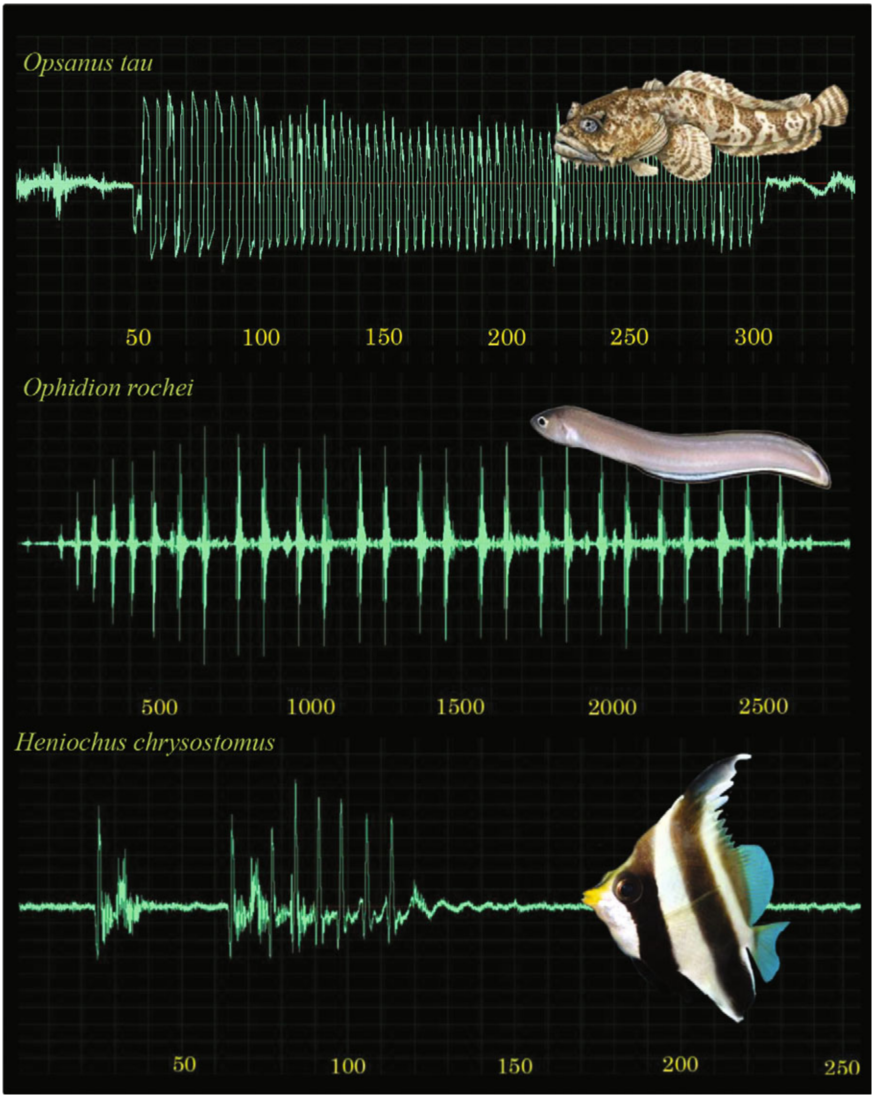

Fig. 3.1 (continued)

contraction rate, e.g., the fundamental frequency and at harmonic multiples of the fundamental frequency (see below). Caution is necessary since a rapid series of pulses can appear tonal on a sonagram, if using narrow-band filter widths (Watkins 1967), and potentially misrepresent the sound. This problem can be important in sounds of some sciaenids, which can include a rapid series of pulses that are better resolved in oscillograms. Generally, both outputs are presented in published papers, and it is important to present oscillograms at various time scales, i.e., a train of pulses often taking a number of seconds, several pulses showing the sound envelope and finally individual pulses using a millisecond scale that illustrates the pulse waveform. We stress the pulse waveform, which is not always presented, is important in understanding sound generation. The intrapulse period τ, the time to complete one cycle of a waveform, is inversely related to frequency ($f = 1/\tau$ or 1,000 ms divided by the intrapulse period). For instance, a fundamental frequency of 100 Hz would come from a waveform that repeats every 10 ms. Note that the interval between pulses can be used to calculate a pulse period (the time between one pulse and the next, which is not the same as the intrapulse period).

Since many fish sounds include a series of pulses, one can measure the duration and number of pulses in the series, pulse period (time between the start of one pulse and the next), the related pulse repetition rate (number of pulses per time within a unit), interpulse interval (the silent period between pulses), pulse duration and the frequency or power spectrum (an output of the amplitude, typically in dB, against frequency). Winn categorized sounds as fixed- and variable-interval (Winn et al. 1964), and variation in interval between pulses should also be considered when presenting pulse repetition rate. In squirrelfish, for instance, the time between the penultimate and final pulse is longer than preceding intervals (Winn and Marshall 1963; Parmentier et al. 2011a).

Sound spectra are calculated by a fast-Fourier transform or FFT, and biologists can usually use them successfully without getting into trouble. There are a number of different filter algorithms (windows) for spectra, Hanning (properly Hann) being one of the most common. These different algorithms usually produce similar spectra, and there is no definitive one used universally.

In a continuous tonal sound, the fundamental frequency would equate to the muscle contraction rate, i.e., a toadfish boatwhistle with a 200 Hz fundamental frequency would be caused by 200 contractions a second and would have energy at multiples of 200 Hz (harmonics). The fundamental frequency is often the one with the greatest energy, but it need not be present, particularly in shallow water where it could be filtered out (Fine and Lenhardt 1983). A sound with 400 and 600 Hz bands (the missing fundamental) would be caused by 200 Hz contractions and would be heard as 200 Hz by the human ear. Fish bioacousticians often measure the peak or dominant frequency, the band with the greatest energy, but some caution should be used here. Fish sounds are usually not sharply tuned (see below), and the difference in amplitude of different peaks can be slight (a dB or two) so that 400 Hz might be the peak in one sound and 600 Hz in another. Peak frequency, therefore, has the potential to add spurious variability to a data set and may not always be particularly meaningful. This does not mean that the parameter is not important, but it may be helpful to present the actual power spectrum in papers although this is often not done. It is also useful to present the spectrum of the background noise since this information helps clarify which parts of the signal are above background levels and therefore may convey information. Peak frequencies are meaningful when they are compared to the main auditory sensitivities of a particular species (see Chap. 4 this volume).

Sharpness of tuning can be measured by a quality factor Q, which is the peak frequency divided by the bandwidth 3 dB down (Fine et al. 2001, 2004; Connaughton 2004; Parmentier et al. 2006b), and a low Q indicates that the swimbladder is not sharply tuned (see discussion on the underwater bubble below). Additionally, sounds with greater amplitude will excite a swimbladder to emit higher modes of vibration. Therefore, the highest frequency of a signal may not be of great importance and in some cases may be above the fish's upper range of hearing. On the other hand, harmonics allow redundancy so that if one frequency does not propagate sufficiently, other bands may transmit the message (Fine and Lenhardt 1983; Sisneros et al. 2004).

3.4 Statistical Issues

Recording sounds of unseen fish presents additional statistical problems in call description. Ideally, one records and analyzes a number of sounds from an individual, averages them, and treats the average as an *N* of 1. This is not typically possible in field recordings. Toadfish are unusual in this regard since they will enter and call from shelters, and it is possible to record individuals (Gray and Winn 1961; Winn 1972; Thorson and Fine 2002a; Amorim and Vasconcelos 2008; Amorim et al. 2009, 2010). Although sounds of individuals can sometimes be identified in choruses by differences in frequency spectra and amplitude (Thorson and Fine 2002b; Amorim and Vasconcelos 2008), this is clearly not the norm. Presenting averages from field recordings of sounds from an unknown number of fish likely involves some degree of pseudoreplication, i.e., measuring the height of a person five times and calling it an *N* of 5. In a classic example that ignored this problem, Fine measured fundamental frequency and duration of 20 field-recorded boatwhistles from weekly recordings in Delaware, Virginia, and South Carolina, USA (Fine 1978a, b) and demonstrated convincing temperature, seasonal, and geographical variation in these parameters. However, the number of recorded fish, albeit from multiple individuals, was undetermined and clearly fewer than one boatwhistle from 20 individuals. We argue that the rigors of statistical purity, while ideal, should be relaxed in field recordings since valuable information can be obtained with imperfect data. However, when the calling individual can be identified, multiple sounds from individuals should be averaged into a single data point.

Although species identification is critical, passive acoustics tends to pay less attention to parameters of sounds from individual fishes. The biggest problem in this field is the ease of obtaining hours of data but the huge amount of time required to quantify sound production and the difficulty to identify the species. One can spend hours analyzing seconds of a recording, and this will always be a challenge for the field. David Mann and colleagues have developed algorithms that quantify signal amplitude levels in specific frequency bands characteristic of a caller. These have been used successfully to establish daily calling periodicity with *Cynoscion* species (Locascio and Mann 2005; Luczkovich et al. 1999) and black drum (Locascio and Mann 2011) and can only be used with the appropriate windowing characteristics for a given species. These algorithms are probably not sensitive enough to separate mixed choruses of fishes and snapping shrimp. These algorithms avoid statistical problems by presenting population data for circadian and seasonal periodicity, but they are not yet suitable for describing sound parameters of individual fishes. Of course, individual sounds from such recordings can be analyzed to demonstrate acoustical signatures.

3.5 Tank Recordings

Sounds from small fishes (cichlids, minnows, gobies, darters, etc.) are often recorded in small tanks, which can distort sound spectra and amplitude. Sounds can be reflected back out of phase from the tank boundary and cancel sound energy. In a completely closed plexiglass respirometer, electrically stimulated toadfish sounds could be heard outside the shelter but were almost completely canceled within (Amorim et al. 2002). Additionally, tank resonance can excite frequencies not present in the natural call. Akamatsu et al. examined these problems in detail and provide a simple formula for calculating tank resonant frequency (Akamatsu et al. 2002). They conclude that tank recordings can be useful when the hydrophone is close to the fish and frequencies are below the tank's resonant frequency. Additionally, one should be careful to reduce pump and electrical noise (50 Hz in Europe and 60 Hz in the US), and be alert to sounds caused by fishes hitting the tank wall or the hydrophone.

Fish disturbance calls have been recorded in air to escape the problems of small-tank acoustics (Waybright et al. 1990; Connaughton et al. 1997; Fine 1997), and physiological work that exposes the swimbladder and muscles to electrical stimulation cannot always be done underwater—or completely underwater (Connaughton et al. 1997; Fine et al. 2001). In order to directly compare the effects of the two media, sounds were recorded from individual Atlantic croakers *Micropogonias undulatus* both in air and underwater in a large shallow boat harbor (Fine et al. 2004). The change in loading had no effect on peak frequency in either media and sounds looked similar on sonograms unless compared side by side. Although still broadly tuned, spectra of recordings in water were more peaked (higher Q) and required an extra cycle to attenuate compared to recordings from the same fish in air. We suggest that sounds in air more or less approximate the same sound in shallow water, and with appropriate caution can be useful. Additionally, catfish sounds have been recorded in both media (Ladich 1997; Knight and Ladich 2014).

3.6 The Swimbladder as a Sonic Organ

The primary function of the swimbladder is buoyancy control, and a typical teleost with a bladder is neutrally buoyant, i.e., zero weight in water (Alexander 1966). However, some benthic fishes may have a relatively smaller volume of gas in the bladder and still gain lift although they are somewhat negatively buoyant as in the oyster toadfish (Fine et al. 1995). Negative buoyancy can be an advantageous and help fish maintain position on the bottom. Since swimbladders function in buoyancy, as an oxygen reservoir, and in many cases in hearing and sound production, their morphology is shaped by multiple selection pressures that can be difficult to interpret. Catfishes of the families Loricariidae and Callichthyidae (e.g., *Ancistrus ranunculus, Corydoras sodalis, Dianema urostriatum, Hemiodontichthys acipenserinus, Hypoptopoma thoracatum*) have reduced bladders encased in bone that decrease auditory sensitivity above 1 kHz (Lechner and Ladich 2008). Gas in the swimbladder is an exaptation that can be co-opted into a sound-producing organ or an accessory auditory structure, and there is no conflict between buoyancy and acoustic functions (Fine et al. 1995).

3.7 The Resonant Bubble

Classically, the swimbladder has been modeled as a pulsating underwater bubble (Harris 1964; van Bergeijk 1964), an omnidirectional, resonant monopole that is vibrated by incident sound and then radiates near-field vibrations to the ears. The resonant frequency of an underwater bubble is given by the following equation (Weston 1967):

$$F = \frac{1}{2\pi R}\sqrt{\frac{3\gamma P^2}{\rho}}$$

where F is resonant frequency calculated for an underwater bubble; R, swimbladder radius (cm); γ, ratio of specific heats (=1.4); P, pressure (atmospheric pressure + hydrostatic pressure); ρ, water density. This model does not consider the swimbladder wall. The resonant bubble model, ingrained in the marrow of fish bioacousticians for well over 50 years, conflicts with numerous aspects of fish biology:

- Sonic muscles attached to swimbladders are among the fastest muscles in vertebrates; yet, a resonant structure like a crystal goblet or bell does not require extreme speed to excite it into resonance.
- Resonant frequency of an underwater bubble increases with depth (hydrostatic pressure) and decreases with bladder radius. Bladder and sonic muscle size

increase with fish growth and could create mismatches between communicating individuals.

- Most fish sounds have a wide rather than a tuned frequency spectrum, and target-strength studies of fishes in an underwater sound field demonstrate a lower Q (i.e., broader tuning) than an underwater bubble.
- A resonant bubble will continue to oscillate after sound termination and would interfere with temporal coding of fish sounds (Winn 1964), most of which are of short duration and pulsed.
- Resonance will compromise the time fidelity of an auditory system whether used for communication or not, i.e., except for reflections in echolocation, it is not advantageous to hear a sound after it has ended.
- Sonic swimbladders have a number of interesting shapes (i.e., heart shaped in toadfish) or diverticula (e.g., in herrings, thorny catfishes, cichlids, and numerous sciaenids), which is not logical for an omnidirectional source.

Although numerous underwater studies have demonstrated that swimbladders have a lower Q and damp more rapidly than a free bubble (Weston 1967; Batzler and Pickwell 1970; McCartney and Stubbs 1970; Sand and Hawkins 1973), this difference has typically been ignored and explained away as a consequence of damping by surrounding fish tissue rather than a property of the bladder. One notable exception, a study by Feuillade and Nero modeled the fish acoustically assuming the bladder cavity acts as an underwater bubble, the bladder wall as rubber, and the surrounding fish tissue as viscoelastic (Feuillade and Nero 1998). Their model attempted to explain changes in frequency of target returns from cod in a Norwegian fjord (Sand and Hawkins 1973). After utilizing extensive math, considerably beyond the grasp of most biologists, they, unfortunately, had to resort to parameter fitting to make their model conform to the data. Most swimbladders have a cylindrical shape that tapers posteriorly, and one boundary-element model has utilized shape as a variable (Francis and Foote 2003) rather than assuming a prolate spheroid although Weston (1967) demonstrated that bladder shape, unless extremely elongate, should have a minor effect on natural frequency. The decay waveform of weakfish sounds following sonic muscle contraction has also been used in an acoustic model (Sprague 2000). Clearly there is much to understand about the acoustic behavior of swimbladders. However, the concept of the pulsating resonant bubble has been the dominant paradigm since the 1960s and is still the default belief of many investigators.

In many cases investigators have assumed that the resonant properties of swimbladders can magnify sounds produced elsewhere in the body, but to our knowledge this has not been demonstrated except in cases of direct contact between the structure and the bladder. Fine et al. recorded hand-held disturbance calls from juvenile channel catfish both before and after removal of air with a hypodermic needle (Fine et al. 1997). Following this manipulation, both the sound amplitude and power spectrum of the calls did not change, suggesting that the swimbladder did not affect sound production. Note, however, that removing gas from toadfish (Tavolga 1964), cichlid (Longrie et al. 2009) and damselfish swimbladders

(Colleye et al. 2012) decreases sound amplitude, indicating the importance of gas in the bladder to amplify and radiate movement of sonic muscles but not necessarily supporting the logic of a resonant structure.

3.8 Swimbladder Damping and Tuning

The resonant bubble model posits a sharply tuned vibration with gradual exponential damping and predicts that larger fish with bigger bladders will have lower peak frequencies. The argument of surrounding tissue damping the swimbladder is not supported by physiological work in the toadfish in which the body cavity was opened to expose the swimbladder (Fine et al. 2001, 2009). In toadfish, the damping coefficient averaged 0.37, and values between 0.1 and 0.5 are equivalent to automobile shock absorbers—a device to prevent resonance. The frequency spectra are flat rather than peaked, and peak frequencies do not correlate with fish size. Although recordings of Atlantic croaker in water are more sharply tuned with higher Qs in water than in air (Fine et al. 2004), the Q values are considerably lower than predicted by the bubble model. Although peak frequency decreases with fish size in weakfish, lower frequencies have been interpreted as a the scaling effect (Connaughton et al. 1997, 2002): bigger fish with longer muscles will take more time to complete a muscle twitch, resulting in a longer period in the acoustic waveform and therefore a lower dominant frequency. Similarly colder temperatures, not part of the bubble equation, will decrease muscle twitch time and result in lower frequency sounds (see also Connaughton et al. 1997; Feher et al. 1998; Papes and Ladich 2011).

Amplitude decay in a resonant structure like a tuning fork will maintain a constant frequency, i.e., waveform period. However, sound periods from fish calls often increase after the final muscle contraction. This type of response is illustrated in the long-duration advertisement call of a black drum produced by multiple muscle contractions (Locascio and Mann 2011) in which later sound cycles have longer periods than earlier ones (Fig. 3.2). This phenomenon is likely explained by muscle fatigue resulting in longer contraction and relaxation times and clearly indicates that frequency is not being driven by bladder resonance.

3.9 The Swimbladder as an Omnidirectional Radiator

The underwater bubble model assumes a monopole that radiates sound omnidirectionally, but some sonic swimbladders have interesting shapes, diverticula, internal septa, and muscle investments that could impart a directional pattern to sound radiation. The swimbladder of the oyster toadfish is heart shaped (Fig. 3.3), and the sonic muscles extend from the most rostral point on the swimbladder, around the sides and meet at the posterior midline of the bladder. Additionally, the

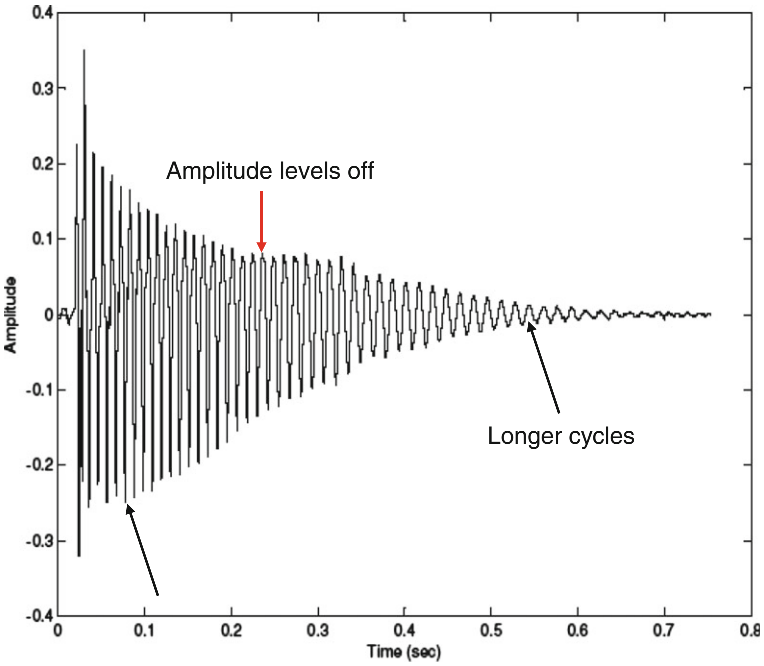

Fig. 3.2 Oscillogram of the advertisement call of the *black* drum *Pogonias cromis* modified from Locascio and Mann (2011). The *red arrow* above the waveform indicates that the amplitude levels off, which should not occur during exponential decay. The two *black arrows* below demonstrate that cycle duration increases during the call indicating muscle fatigue and slower contractions

confluence of the two anterior projections is stiff and without muscles. Barimo and Fine tested the hypothesis that the swimbladder is adapted to avoid stimulating the saccular otoliths that are several centimeters forward of the bladder (Barimo and Fine 1998). They therefore predicted a directional sound field that parallels bladder shape. Sound amplitude decreased ca 1 dB drop from 0° to about 45° and then increased to 180°; sounds were several dB greater behind than in front of the fish at a distance of 1 m. The sonic muscles of the toadfish are arranged in onion-like lamellar sheets so that muscle fibers assume a circular shape, and fibers attach to the bladder wall at both ends (Fine et al. 1990, 1993; Hirsch et al. 1998). As circular muscles, their contractions push the bladder sides inward, increasing internal pressure, which pushes the ventral bladder outward (Skoglund 1961; Fine et al. 2001). This quadrupole motion is inefficient because gas is being shunted in opposite directions, contrary to the pulsating bubble in which all surfaces would be exerting an equivalent force on the medium. Slow motions of the bladder fail to produce audible sound (Fine et al. 2001, 2009), thereby explaining the need for superfast muscles. Although utilizing a quadrupole motion, acoustically the bladder is a mixed source with monopole, dipole, and quadrupole components, and the monopole component would be responsible for most of the sound radiation.

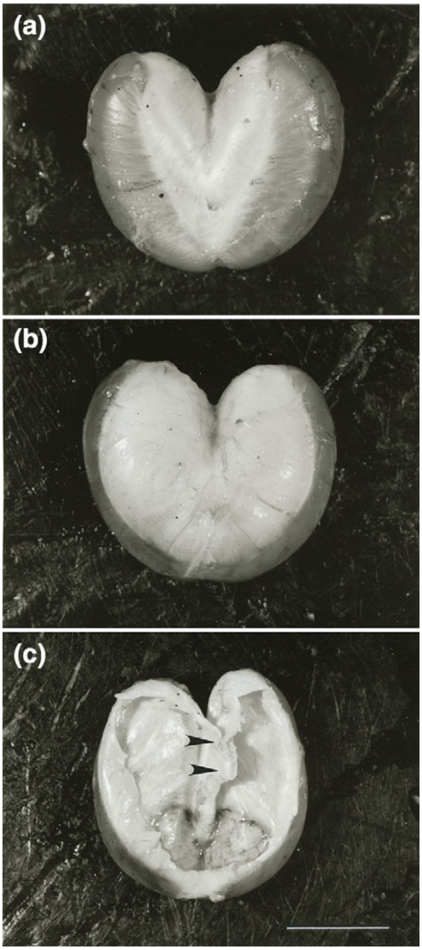

Fig. 3.3 Photographs of the swimbladder of the oyster toadfish *Opsanus tau* from Barimo and Fine (1998). **a** Dorsal view. **b** Ventral view. **c** Ventral view exposing the internal structure of the bladder. Note that the muscles are closer to the midline on the dorsal than the ventral surface and that sonic muscles connect behind the bladder but do not invest the bladder's anterior-medial surface. At the confluence of the two anterior chambers there is an internal column (*arrows*) that supports the bladder and is hypothesized to damp vibrations

The sea catfish *Ariopsis felis* may use sound for echolocation, which would require a forward-directed sound (Tavolga 1971a, 1976). Tavolga found that sound amplitude decreased about 7 dB behind the fish, consistent with sonic muscles vibrating the anterior portion of the swimbladder via the bony elastic spring (Tavolga 1977). Thus the sea catfish and the oyster toadfish have directional propagation that peaks in opposite directions, relating to different patterns of muscle attachment and contraction.

In the Atlantic croaker (see Fig. 1.7 in Ladich and Fine 2006), the sonic muscles originate on a tendon on the ventral midline, follow the inner contour of the hypaxial muscles and insert on an aponeurosis that attaches to the dorsal surface of the mid to posterior bladder. Contraction of these muscles should pull the dorsolateral surfaces of the swimbladder inward and downward, increasing internal pressure. This pressure likely expands the anterior portion of the bladder, which is not covered by muscles or aponeurosis. Thus the anterior and posterior ends of the swimbadder likely vibrate with different patterns and phases making a complex source, which has yet to be investigated.

Typically, sound amplitude is determined by volume velocity (Bradbury and Vehrencamp 1998) of a speaker or a bladder, i.e., louder sounds will be caused by more rapid movement of a larger surface. Many swimbladders taper posteriorly: we note that fishes as different as the fawn cusk-eel (Fine et al. 2007) and the Atlantic croaker (Fine unpublished observation) terminate in a heavy protruding point (duck tail). We hypothesize that due to the small surface area and thickness of the duck tail, the caudalmost part of the bladder will not radiate sound efficiently and will likely reflect internal pressure forward thus contributing to vibration amplitude in the anterior bladder. Additionally, males of some ophidiid fishes have thick protruding "donuts" near the posterior bladder that are lined internally with a thin membrane (Courtenay 1971; Casadevall et al. 1996; Parmentier et al. 2010b) that could function as a pressure release surface.

Swimbladders typically have a single chamber, but there is incredible variability in shape and multiple chambers can occur (Birindelli et al. 2009). The swimbladder in the oyster toadfish has a thin septum containing a sphincter that separates anterior and posterior parts of the organ (Fänge and Wittenberg 1958), and Tracy indicated that this partitioning separated gas secreting and reabsorbing parts of the bladder (Tracy 1911). Based on the physiology of toadfish sound production (Skoglund 1961; Fine et al. 2001), it is unlikely to affect sound production although it has not been tested experimentally. Many ostariophysine fishes have two or even three chambers, and we suggest that all chambers contribute to buoyancy but divisions likely indicate acoustic specializations. Note differences in the channel catfish *Ictalurus punctatus* and the blue catfish *Ictalurus furcatus,* which have, respectively, one and two chambers despite being in the same genus (Miano et al. 2013). Piranhas and other characids (Ladich and Bass 2005) have a large anterior and a smaller posterior chamber. The anterior chamber is the major radiator, and the posterior chamber makes little contribution to sound production (Millot et al. 2011). The batrachoidid *B. trispinosus* has a bilaterally divided swimbladder, forming two separate bladders, which are responsible for the individual production of acoustic beats as reported in some tetrapods (Rice and Bass 2009). In summary, there are many swimbladder adaptations that have not been studied functionally and much we do not understand.

3.10 Swimbladder as an Auditory Organ

Historically, the swimbladder was seen as an accessory auditory organ that transduces acoustic pressure into vibrations (creation of particle motion) that stimulate the otolith organs directly. Fishes were classically divided into auditory generalist and specialist species (Popper and Fay 2011). Generalists have spaces between the swimbladder and the ears, are relatively insensitive (high auditory thresholds) and respond to low frequencies. Specialists have direct connections to the ears such as Weberian ossicles (Weber 1913), rostral swimbladder diverticula (Coombs and Popper 1979; Ramcharitar et al. 2006; Parmentier et al. 2011a, b, c; Schulz-Mirbach et al. 2013) that terminate in close proximity to the ears, or anterior bladders in mormyrids and suprabranchial chambers in gouramis (Yan 1998; Yan et al. 2000; Fletcher and Crawford 2001). Specialists hear higher frequencies and have lower thresholds than generalists. Recently, Popper and Fay argued against these terms, correctly noting that boundary between specialists and generalists is imprecise, and the term generalist is not suitably descriptive (Popper and Fay 2011). The future of these terms is unclear because despite their weakness, they valuably, if imperfectly, succeed in separating two ends of a continuum. In the toadfish, blue gourami, and a goby, deflating the bladder has no effect on hearing (Yan 1998; Yan et al. 2000). However, under the same conditions, bladder deflation or extirpation of auditory ossicles in goldfish, an auditory specialist, increased thresholds by up to 50 dB (Yan et al. 2000; Ladich and Wysocki 2003). Therefore, excitation of a “generalist” swimbladder, without a direct connection to the ears, did not produce vibrations of sufficient amplitude to stimulate the ears.

This issue brings up an interesting paradox given that swimbladders are responsible for most of fish target strength. How can sonar stimulate returns from fishes that may be hundreds of meters distant, but vibrations do not travel several centimeters between the swimbladder and the ears unless there are specific connections? The probable answer is that most nonspecialized fish hear low frequencies (typically below 1 kHz) and most sonars utilize much higher frequencies (up to 430 kHz) with small wavelengths that will be scattered by the bladder. Longer wavelengths of low-frequency sounds fail to “see” the bladder and pass through the fish with minimal interaction. Thus it appears that bladder resonance does not serve a hearing function in unspecialized fishes that hear low-frequency sound. Note that the acoustic impedance of animal tissue (ρc or the density times the speed of sound) is similar to that of water (Urick 1975), and it does not provide a discontinuity to sound. This phenomenon was demonstrated in a biological context by recording sounds of carapid fish in and outside of their sea cucumber hosts (Parmentier et al. 2006a). Sound amplitude was similar in both contexts indicating no measureable effect by passing through the sea cucumber integument.

Several studies indicate that fishes without a connection between the swimbladder and ears can detect sound pressure [e.g. pomacentrids (Myrberg and Spires 1980), cods (Sand and Hawkins 1973) and midshipman (Coffin et al. 2014)], suggesting species differences in the ability to detect pressure. However, these studies do not rule out the possibility of an unknown conducting pathway between the bladder and the ears (see treatment of pomacentrid sound production below) requiring further work to settle this question.

3.11 The Forced Response and Swimbladder Sounds

The alternative to the resonant bubble is the forced-response model (Fine 2012), which posits that swimbladder sounds damp rapidly, exhibit directionality, and their frequency spectrum is dictated by contraction dynamics of superfast sonic muscles. This contention is supported by recent work (Fine et al. 2001; Connaughton 2004; Millot et al. 2011; Parmentier et al. 2011a, b, c). A faster-contracting muscle will produce a higher frequency sound. The resonant frequency of the gas inside the bladder (the internal underwater bubble) does not appear to be of major importance in dictating frequency because damping prevents the expression of resonance. At the very least, one should not use bladder resonance to explain frequency and size changes without direct evidence. The gas is important in radiating muscle contractions, and deflation of the toadfish swimbladder decreases sound amplitude (Tavolga 1964) but not fundamental frequency, which is determined as a forced response (Skoglund 1961; Fine et al. 2001).

3.12 The Forced Response, Sound Frequency, and Size Effects

In some instances, larger individuals produce swimbladder sounds with lower peak frequencies, which have been interpreted as bladder resonance since resonant frequency would decrease with bladder size. However, what was a simple story is unraveling, and there are alternate interpretations and variation between various mechanisms within different groups of fishes (see discussion below).

3.13 Fast Intrinsic Muscles

Intrinsic muscles attach completely to large areas of the swimbladder (Parmentier and Diogo 2006) and are classic examples of superfast muscles (Skoglund 1961; Rome et al. 1996; Fine et al. 2001) in various toadfishes (Tower 1908; Rice and Bass 2009) and sea robins (Connaughton 2004). Intrinsic muscles are capable of producing short-duration pulsed-type sounds with a small number of contractions, but they are generally associated with production of long-duration tonal notes. Tonal sounds require each subsequent muscle contraction to occur before the previous muscle twitch (the relaxation component) is complete. In such fishes, the fundamental frequency may not change with fish size since muscle contraction rate determines the fundamental frequency (Skoglund 1961; Fine et al. 2001), i.e., one sound cycle for each contraction. Although fundamental frequency varies with temperature and seasonally (Fine 1978a, b), choruses of toadfish, comprised of different-sized fish, can have fundamental frequencies varying over as little as

10 Hz (Fine 1978a, b). Similarly, the fundamental frequency of the toadfish grunt does not vary with fish size (Waybright et al. 1990). In small Lusitanian toadfish *Halobatrachus didactylus*, a European species, the sound spectrum of fishes <7 cm is concentrated at the third and fourth harmonics (420–570 Hz) whereas bigger fish have most energy at the fundamental frequency at about 110 Hz (Vasconcelos and Ladich 2008; see Chap. 4 this volume). This difference likely reflects the relationship between the swimbladder size and the wavelength of sound it produces. The small bladders of young fish will be more effective in coupling higher frequencies into water. Such a difference is unlikely to reflect differences in sonic muscle physiology or the sonic mechanism and certainly not bladder resonance.

During a sustained contraction, the sonic muscle contraction rate can decrease slightly causing a slight frequency modulation of the fundamental frequency. In the sea robin, the two intrinsic muscles contract alternately, doubling the fundamental frequency of evoked sounds (Connaughton 2004).

3.14 Extrinsic Muscles

There are numerous arrangements of extrinsic muscles, which generally have their origins on various bones on the skull although that is not invariant (Ladich and Fine 2006). Extrinsic muscles connect to the swimbladder or to other modified bones, such as ribs, epineurals, the pectoral girdle, or tendons that attach to the bladder. In cases in which the bladder connects directly to a large area of the swimbladder, as in pimelodid catfishes (Ladich and Fine 2006), the mechanism of sound generation appears similar to that of intrinsic muscles, i.e., one muscle twitch pulls on the bladder and then relaxes, producing a back and forth bladder movement and one forced cycle of sound generation, i.e., a fast mechanism. We will also discuss recently discovered sonic mechanisms with a slow muscle and a glaucosomatid fish that makes sounds using a slow-type system although activated by a fast muscle, which may represent an intermediate condition in the evolution of fast sonic muscles. Subsequent sections will discuss sonic systems that utilize other body muscles that vibrate the swimbladder although they are not directly connected to it, and finally a parallel system that appears to produce sounds by rapidly vibrating the pectoral radials. As stated previously (Ladich and Fine 2006), there is no clear way of simply classifying all these systems because of numerous convergences.

3.14.1 Fast Extrinsic Muscles

3.14.1.1 Catfishes

There are different arrangements of sonic muscles in various catfish families (Kaatz and Stewart 1997, 2012; Fine and Ladich 2003; Ladich and Fine 2006; Parmentier and Diogo 2006) and some families (for instance the North American ictalurids) do not possess swimbladder muscles. In the pimelodids, muscles attach directly to large expanses of the rostroventral surface of the bladder, but there are other cases in which the sonic muscle inserts on variously derived elastic spring mechanisms, the Springfederapparat or Ramus Műlleri, a modified rib, that attaches to the bladder (Sörensen 1895; Chardon 1968; Ladich and Bass 1996). The muscle pulls the bladder forward directly or through the spring mechanism. Sound production is due to the pull and rebound from the stretched bladder and the spring mechanism. Catfishes make a variety of sounds, and some appear to have multiple cycles per unit (Kaatz and Stewart 2012). Although undetermined, multiple cycles likely result from vibrations of the elastic spring apparatus that causes the bladder to oscillate repeatedly, and it is possible that the elastic spring mechanism precluded the evolution of intrinsic muscles in this group.

3.14.1.2 Piranhas

Sonic muscles in piranhas originate on the vertebral column (Markl 1971) or second rib (Ladich and Bass 2005) and insert on a broad tendon that surrounds the ventral surface of the anterior chamber of the swimbladder. The fish uses fast muscles (Kastberger 1981a, b) to produce two swimbladder sounds: a single pulse during circling and fighting behavior associated with food competition and a multicycle harmonic bark produced during frontal displays (Millot et al. 2011). Most of the vibration comes from the anterior chamber, and the posterior chamber is not a major contributor to sound production. The peak of the sound occurs during maximal swimbladder velocity, and the sound damps rapidly after the final muscle contraction. Millot et al. (2011) note the similarity in sound generation between piranhas and unrelated toadfish (Fine et al. 2001, 2009), despite major differences in sonic muscle morphology and connectivity with the swimbladder. Interestingly, muscles contract more rapidly after the initial part of the bark, which would be controlled by more rapid commands from motor neurons.

3.14.1.3 Squirrelfish

Sounds have been recorded from several squirrelfish genera under natural and hand-held conditions (Winn and Marshall 1963; Winn et al. 1964; Salmon 1967; Horch and Salmon 1973). Parmentier et al. (2011) recorded sounds and described the sonic system in different species of *Neoniphon, Sargocentron, Holocentrus,* and *Myripristis*. In all species, sonic muscle contraction leads to a rostral displacement of the proximal end of the first ribs and of the anterior swimbladder. The displacement is brief because of the numerous ligaments between the vertebrae and the ribs, and the abrupt arrest in displacement likely contributes to the short pulses of the call. The skeletal components likely oscillate for several cycles in *Neoniphon, Sargocentron,* and *Holocentrus*, which drive the swimbladder to produce three-cycle pulses. *Myripristis,* however, produces a single cycle for each pulse, and the skeletal mechanism for quicker damping is unclear. In *Myripristis,* the muscles and sonic ligament insert only on the ribs of the third vertebra whereas they insert on ribs of third, fourth, and fifth vertebrae in other species.

3.14.1.4 Sciaenids

Sciaenids are important commercial and recreational species whose choruses have been studied on at least five continents. They form concentrated mating aggregations at night and have been the major subject of passive acoustics studies (Guest and Lasswell 1978; Mok and Gilmore 1983; Connaughton and Taylor 1995; Mok et al. 2009; Tellechea et al. 2010a, b; Miles et al. 2012; Picculin et al. 2012; Borie et al. 2014). At least during the mating season, males will produce disturbance calls when held, which aids in identification. A typical sciaenid such as the weakfish has sonic muscles that originate on a small tendon on the ventral midline and follow the inner contour of the hypaxial trunk muscles to insert on an aponeurosis (flattened tendon) attached to the dorsal surface of the bladder (Ono and Poss 1982; Connaughton et al. 1997; Lagardère and Mariani 2006; Parmentier et al. 2014). The muscles form during puberty and grow down from the aponeurosis to the ventral origin (Hill et al. 1987). Muscles continue to grow, and therefore larger fish produce sounds with greater amplitude and lower peak frequency (Connaughton et al. 1997; Tellechea et al. 2010a, b). Sonic muscles also undergo a seasonal cycle so that their muscles hypertrophy during the mating season (Connaughton et al. 1997; Borie et al. 2014). Although it may appear that these muscles split off from the hypaxial musculature, their development makes their affinity unclear. Electromyograms (EMGs) of weakfish *Cynoscion regalis* sonic muscles demonstrated one action potential per sound pulse (Connaughton et al. 1997), and typical sciaenid sounds consist of a series of pulses that rapidly damp (Sprague 2000). The peak frequency of their sounds is determined largely by the cycle period with the greatest amplitude (Connaughton et al. 1997).

3.14.2 Slow Extrinsic Swimbladder Muscles

Parmentier et al. (2006b) demonstrated that a carapid fish, which produces sounds from the cloacal cavity of a sea cucumber, uses slow muscles. In *Carapus* species, (Parmentier et al. 2008a, b), the muscles travel from the orbital region of the skull to the rostrodorsal swimbladder. In *Carapus mourlani*, *C. acus,* and *C. boraborensis*, the muscle ends on a hooked tendon that is held in place by two swimbladder tubercles. In *C. homei* and *E. gracilis*, the muscle inserts directly on the swimbladder (Parmentier et al. 2008a, b). Just caudal to the insertion is a swimbladder fenestra, a stretchable band without the heavy tunica externa that covers the rest of the bladder (Parmentier et al. 2003a, b). Caudal to the fenestra, the swimbladder is firmly fastened to the vertebral column, which restricts its movement during muscle contraction. Finally, a modified epineural rib, the swimbladder plate, attaches to the bladder surrounding the lateral edges of the fenestra. Contraction of the sonic muscles stretches the swimbladder fenestra until the insertions pop off the tubercles, and the anterior bladder snaps back generating a sound pulse. The recoiling bladder appears to set the swimbladder plate into resonance, which in turn causes multiple cycles of swimbladder vibration.

The sonic muscle requires 490 ms for a twitch, compared to 10 ms in the oyster toadfish (Skoglund 1961; Fine et al. 2001), and the muscle exhibits an unfused tetanic contraction at about 10 Hz (Parmentier et al. 2006a, b, c). Thus there is one slow muscle contraction for each sound pulse and a resonant response appears to be driven by a bone, the swimbladder plate, rather than the swimbladder. With slow muscles, each muscle contraction generates a pulse but not the frequency within a pulse. Moreover, differences in the way the sonic muscles contact the swimbladder can allow the production of different kinds of sounds (Parmentier et al. 2008a, b). Although there are a few shallow water species, most cusk-eels are found in deep water over the continental slope. The complex anatomy of several species has been described, (Courtenay 1971; Howes 1992; Fine et al. 2007; Nguyen et al. 2008), but the sounds of deep species have not been recorded. Moreover, there are a number of sexually dimorphic components of the sonic system, suggesting sounds are important in courtship. Within the subfamily Ophidiinae, sounds have been recorded from two species: *Ophidion marginatum* (Mann et al. 1997; Sprague and Luczkovich 2001) and *Ophidion rochei* (Parmentier et al. 2010b; Kéver et al. 2012b, 2014). Calls from the striped cusk-eel *Ophidium marginatum* have peak frequencies above 1 kHz (Mann et al. 1997; Sprague and Luczkovich 2001), which should be impossible using conventional fast swimbladder muscles since twitches would have to occur in less than 1 ms, faster than any known direct muscle. There are insect flight muscles that contract at such high rates, but they are indirect muscles working with wing resonance in small insects, i.e., there are multiple contractions for each nerve volley (Josephson 2006).

In males of *Ophidion rochei* and *O. barbatum,* the sonic apparatus includes three pairs of extrinsic sonic muscles that act directly or indirectly on the swimbladder (Parmentier et al. 2006, 2010a; Kéver et al. 2012a) (Fig. 3.4). The dorsal sonic muscle inserts on the first neural arch, referred to as the neural rocker because it is modified to pivot in the rostrocaudal plane, toward and away from the cranium (Fine et al. 2007; Parmentier et al. 2010a). The intermediate sonic muscle inserts directly on the first pair of epineurals which attach to the neural rocker and connect by ligaments to the swimbladder. The ventral sonic muscles insert on the rocker bone, a bean-shaped skeletal structure that grows out of the anterior surface of the swimbladder (Parmentier et al. 2008a, b).

As in *Carapus* species, calls would result from a release mechanism that utilizes three steps. The contraction of the dorsal muscle first pulls the epineural, epineural ligament, and the rocker bone backward, placing them under tension. Second, contraction of the ventral muscle pulls the rocker bone forward, while the dorsal muscle remains contracted. Third, ventral muscle relaxation combined with the

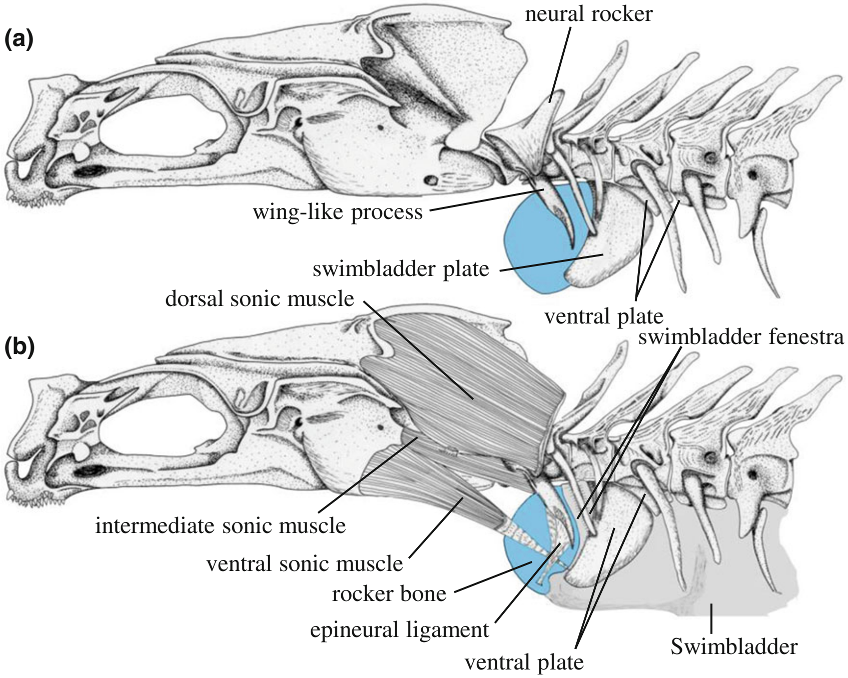

Fig. 3.4 Drawing of the skeleton, swimbladder, and sonic muscles of a representative ophidiid fish

tension on the dorsal muscle causes the rapid backward movement of the rocker bone and the rebound of the swimbladder (Parmentier et al. 2010b).

Sounds of a male *Ophidion rochei* differ from those of juveniles and females and reflect major shifts in male anatomy during puberty (Kéver et al. 2012b, 2014). Female sounds are harmonic and have a short intrapulse period (3.7 ms) (see Chap. 5 this volume). In fact, oscillograms are typical of fish sounds produced by high-speed muscles (Skoglund 1961; Cohen and Winn 1967; Fine et al. 2001; Millot et al. 2011). Female sounds have a fundamental frequency of about 250 Hz, suggesting rapid contraction rate of sonic muscle (Kéver et al. 2012b). These systems need to be evaluated physiologically.

3.14.3 Intermediate Condition with Fast Extrinsic Muscles

The pearl perch *Glaucosoma buergeri* is an advanced perciform not closely related to Ophidiiform fishes. It has a number of characteristics of fishes with slow muscles including rostral sonic muscles that extend from the head to the dorsal and rostral edge of the swimbladder, a swimbladder fenestra, and a firm vertebral attachment of the caudal bladder behind the fenestra (Mok et al. 2011) (Fig. 3.5). The sonic

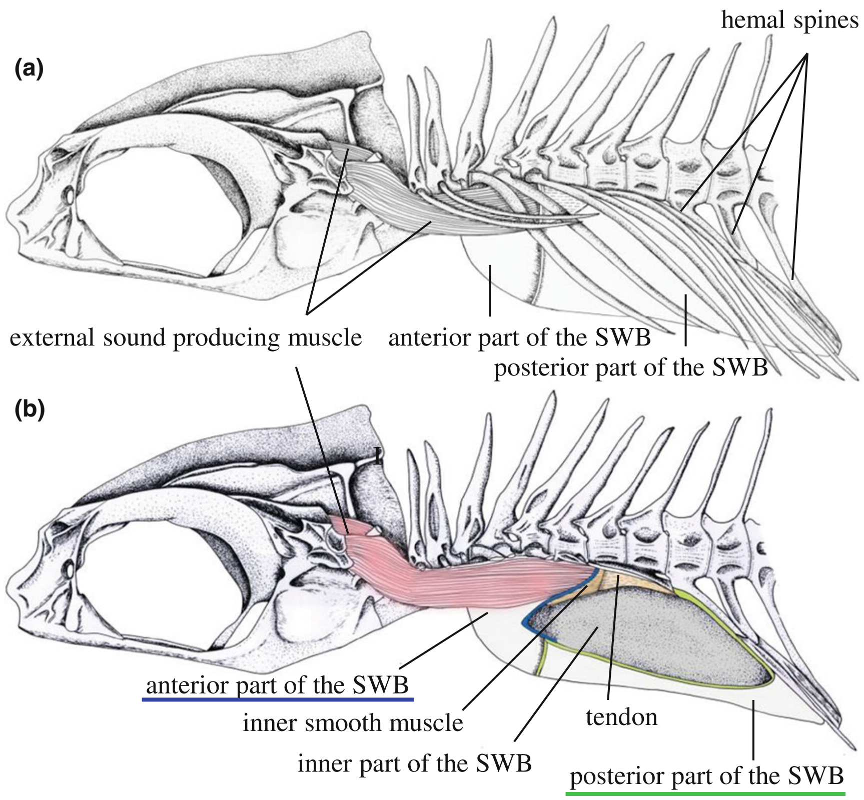

Fig. 3.5 Drawing of the skeleton, swimbladder, and sonic muscles of a glaucosomatid fish. Parallels between the glaucosomatid and the ophidiid in Fig. 3.4 include muscles attached to the dorsal anterior swimbladder, a swimbladder fenestra, and a rigid coupling of the posterior swimbladder to the vertebral column

system includes a tendon from the ninth vertebra that ends in a smooth muscle attached to the underside of the dorsal tunica externa of the swimbladder. The tendon acts as an antagonist to the head sonic muscles. Pulling on the skeletal sonic muscles stretches the anterior swimbladder and places the caudal tendon-smooth muscle combination under strain, which causes the swimbladder to snap back once the muscle twitch is released. The fish produces a two-part pulse: pulse part 1 (PP1) is a low amplitude component followed by pulse part 2 a high amplitude component (Fig. 3.6). However, the waveform of PP1 has a period of 4.2 ms, indicative of a superfast muscle, but the high-amplitude PP2 would be caused by rebound of the stretched tendon pulling the bladder back to a resting state. Thus, we have an intermediate condition with a fast muscle that operates primarily by rebound of a stretched bladder and tendons, a slow cock and release mechanism. Removal of the tendon and an increase in the size of the head muscle could represent a sequence in the evolution of typical sonic systems driven by extrinsic muscles.

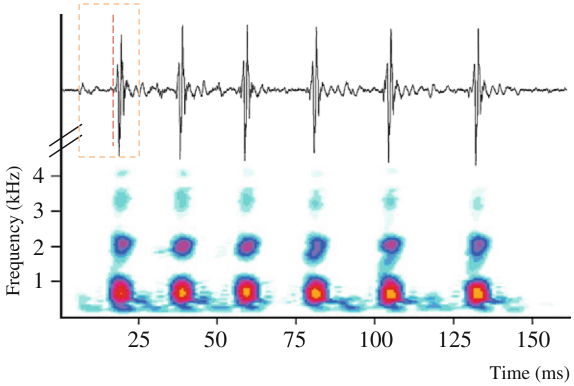

Fig. 3.6 Oscillogram and sonogram of a series of sound pulses evoked by touching the abdomen of the pearl perch *Glaucosoma buergeri*. The box in the oscillogram designates the first pulse, and the vertical *dashed line* separates pulse parts 1 and 2. From Mok et al. (2011)

3.15 Muscles that Vibrate the Swimbladder Although not Directly Attached

3.15.1 Cichlids

Longrie et al. found that sound production in a cichlid, the black tilapia *Oreochromis niloticus* occurs by contraction of a horizontal band of muscle, the *vesica longitudinalis* (Longrie et al. 2009). Contraction, stimulated electrically, causes backward movement of the pectoral and pelvic girdles and forward movement of the anal fin. Individual fibers have an oblique orientation that would displace the rib cage, which is intimately connected to the lateral surface of the bladder. Spontaneous sounds have been separated into an initial high-frequency phase and a second and longer low-frequency phase that occurs after body movement stops (Longrie et al. 2009). Bladder deflation alters the amplitude of the sounds but has little effect on the frequency spectrum indicating that it does not depend on bladder resonance, and thereby implicates rib movement as driving bladder vibrations. An eraser placed in the mouth prevented contact of pharyngeal teeth ruling them out as the cause of the sounds in this species but not necessarily in other cichlids.

3.15.2 Butterflyfish (Chaetodontidae)

There is considerable variation in sonic mechanisms in the family Chaetodontidae (Tricas et al. 2006; Boyle and Tricas 2010, 2011). The pennant butterflyfish *Heniochus chrysostomus* has an unusual sonic system with a series of paired superior oblique muscles (Parmentier et al. 2011a, b, c). A superficial and a deep muscle originate on the occipital region of the skull and insert on the rostral surface of the third rib. There is also a massive series of six muscles that form a band connecting ribs 3 through 9. Close to the medial surface, these ribs are also connected by a series of tendons. The swimbladder is united with the medial surface of the ribs, and thus muscle contraction will stimulate bladder vibration. The fish produces both isolated and trains of pulses with a fundamental frequency between 130 and 180 Hz. Sound pulses have a complex waveform with one relatively slow high amplitude cycle, a series of higher frequency oscillations that increase in amplitude without a change in frequency, and continue to oscillate for a number of cycles. The fundamental frequency does not vary with fish size, yet vibrations continue with a relatively constant period suggesting resonance. Our interpretation of the waveform is that the initial muscle twitch, which extends the third rib forward and compresses the remaining ribs, excites the ribs and tendons to resonance, driving multiple cycles of swimbladder oscillation. The coral reef Pyramid Butterflyfish *Hemitaurichthys polylepis* has a similar process of sound production. However, Boyle et al. (2013) provide new insights. *Hemitaurichthys polylepis* also produces rapid pulse train sounds with extrinsic high-speed swimbladder muscles (Boyle et al. 2013) that also cause a rapid buckling of the tissues lateral to the anterior swimbladder (Boyle and Tricas 2010).

Experiments with Forcepsfish (*Forcipiger flavissimus*) demonstrate a dramatically different kinematic pattern associated with sound emission (Boyle and Tricas 2011). Electromyograms indicate many unsynchronized muscle action potentials during activity, and no synchronous activity of anterior hypaxial musculature was observed during sound emission (Boyle and Tricas 2011). Thus, sonic motor kinematics in Forcepsfish likely involves diverse motor nuclei with muscles innervated by multiple nerves.

3.16 Slam Mechanism that Excites the Swimbladder Indirectly

3.16.1 Damselfish (Pomacentridae)

Numerous pomacentrids produce series of pulses in male courtship that have been shown to carry species-specific information (Myrberg et al. 1978, 1993; Parmentier et al. 2009; Colleye et al. 2011). Larger individuals produce lower frequencies and a pulse waveform with a slow exponential decay, suggesting swimbladder resonance and potentially refuting the forced-response model (Lobel and Mann 1995; Colleye et al. 2009, 2011). Parmentier et al. (2007) found sound pulses are produced using a stretched tendon that causes the jaw to snap in the clown fish *Amphiprion clarkii*. Further study on the sonic mechanism (Colleye et al. 2012) indicates the importance of the bladder as the sound radiator since filling its lumen with saline decreases pulse duration, raises the dominant frequency and complicates the attenuation pattern. However, the dominant frequency of natural sounds was lower than predicted by the resonant bubble equation. When regressed against fish standard length, the dominant frequency regression lines for the predicted and observed frequencies had similar slopes suggesting another resonant structure drives swimbladder vibrations. The fish's ribs press into the bladder and striking them with a piezoelectric hammer induces a waveform similar to that of natural sounds (Colleye et al. 2012). Decreasing frequency in larger fish therefore suggests that longer and more massive ribs oscillate at a lower natural frequency and are therefore drive lower dominant frequencies. The component of the pathway that conducts vibrations from the jaw slam to the ribs is not yet understood.

In summary, there are fish swimbladder sounds that damp quickly, and others that continue to oscillate for several cycles after muscle contraction ends. Historically, such slow-damping sounds would be ascribed to swimbladder resonance. However, multiple oscillations occur in sonic systems with bones and tendons that continue to drive the swimbladder. At this point it appears that the structure of the bladder wall and not damping by surrounding fish tissue is responsible for rapid swimbladder damping and that in general swimbladder sound production is consistent with the forced-response model.

3.17 Sounds with Muscles Not Associated with a Swimbladder

3.17.1 Sculpins and Gobies

Barber and Mowbray described tonal sounds of the longhorn sculpin *Myxocephalus octodecimspinous* produced by a series of continuous contractions of the cranioclavicula muscle, which moves the pectoral girdle (Barber and Mowbray 1956). Gobies can produce pulsed sounds, tonal sounds, and complex sounds with both components, and there are species with and without a swimbladder (Lugli et al. 1995; Malavasi et al. 2008). As in the sculpin, the fast levator pectoralis muscle, which originates on the skull and inserts on the dorsal tip of the cleithrum, fires one action potential per sound cycle. The left and right muscles contract in relative synchrony, and the enlarged pectoral radials are the likely sound radiators (Parmentier et al. 2013). Thus this mechanism works similarly to muscles that drive the swimbladder directly although with a different radiator since the sculpin and this goby do not have a swimbladder. Parmentier et al. (2013) note that both sculpins and gobies are demersal species that, although not closely related, share similar pectoral morphologies. The sonic mechanism in these species likely represents another case of convergent evolution. The sound system in darters (Johnston and Johnson 2000a, b; Speares and Johnston 2011) and blennies (De Jong et al. 2007) is not yet clarified, but similar pectoral vibrations might be a good candidate.

3.18 Sonic Muscle Structure, Biochemistry, and Physiology

In order to produce the rapid contractions necessary to excite swimbladder sounds, sonic fibers have a number of convergent morphological and biochemical adaptations for speed (Fawcett and Revel 1961; Bass and Marchaterre 1989; Fine et al. 1993; Loesser et al. 1997). Similarities in fiber ultrastructure between sonic muscles of the toadfish (occipital innervation) and the weakfish (true and segmental spinal innervation) are striking and support convergent evolution. Morphological, physiological, and biochemical features of sonic muscles appear to facilitate high contraction rates. Complementing the mitochondria arrangement, multiple capillaries surround fibers providing exchange of oxygen and other metabolites (Lewis et al. 2003).

Superfast muscles are endowed with general physiological traits which are generally common to all fibers of that type (Rome and Lindstedt 1998; Rome et al. 1999; Young and Rome 2001; Rome 2006). However, all superfast fibers should not be seen as identical because not enough information is available to determine adaptations that occur in all of these muscles and ones that are species-specific (Tikunov and Rome 2009). For instance, sonic fibers in *Opsanus tau* and *O. beta* commonly contract two to three times faster than in Type I *Poricthys notatus*, which produces long-duration (multi-minute) calls.

Excluding the small volume devoted to metabolic fuels (lipid and glycogen), myofibrils, sarcoplasmic reticulum (SR), and mitochondria comprise approximately 100 % of muscle fiber volume (Rome and Lindstedt 1998). Myofibril volume determines the contraction force, SR determines the contraction rate, and the mitochondria permit sustained performance (fatigue resistance). The volume of the three contributes to a zero-sum game, i.e., functional specializations are attributable to shifts in the proportions of these structures (Lindstedt et al. 1998; Rome and Linstedt 1998). Superfast muscles in toadfish have the fastest known calcium spike in a vertebrate muscle (Rome et al. 1996), rapid cross-bridge detachment (Rome et al. 1999), huge activator stores of calcium (Somlyo et al. 1977; Feher et al. 1998), multiple innervation of muscle fibers (Gainer 1969; Hirsch et al. 1998), and modified parvalbumins (Hamoir et al. 1980). In the toadfish, which produces long-duration boatwhistle calls, an expanded SR increases calcium capacity so that the muscle can keep contracting despite surprisingly slow reuptake of calcium (Feher et al. 1998). Remaining calcium can be returned to the SR between boatwhistle calls, and specialized parvalbumin will bind calcium released from troponin until it can be resequestered in the SR. However, concentration of foot protein (part of the functional calcium-release channel at the SR-T-tubule junction) is higher in the sonic muscle than in other skeletal muscles (Appelt et al. 1991). In terms of mechanical function, morphology of superfast fibers and locomotory fibers are mutually exclusive. Locomotory fibers of the toadfish are too slow to drive sound production, which requires high frequencies. Conversely at the low frequencies used for locomotion, superfast fibers cannot generate sufficient mechanical power for locomotory movement.

Coincident with an expanded SR, myofibril and mitochondria volume are reduced in the oyster toadfish (Appelt et al. 1991). The small volume of mitochondria, about 4 % of fiber volume in males (Appelt et al. 1991) decreases fatigue resistance (Mitchell et al. 2008); therefore, the muscle can contract rapidly but for short periods. Boatwhistles are emitted intermittently requiring contractions for only several seconds per minute even when calling at a rapid rate. In fact, toadfish spend most of their time in silence (Fine et al. 1977a, b; Thorson and Fine 2002a; Jordão et al. 2012). Not surprisingly, oxygen consumption for muscle contraction is negligible on a whole animal basis (Amorim et al. 2002). In marked contrast, Type I male midshipman have banks of mitochondria at the fiber periphery, and they can produce courtship hums continuously for many minutes (Bass and Marchaterre 1989). However, the midshipman contracts its muscles at approximately half the speed of the oyster toadfish, again a caution that not all superfast muscles are equivalent. Like the midshipman, rattlesnake shaker muscle is also much slower than in the toadfish (Schaeffer et al. 1996).

3.18.1 Morphology

Fibers and myofibrils of fast-twitch teleost sonic muscles have a smaller diameter than in trunk muscles (Evans 1973; Ono and Poss 1982; Fine et al. 1990, 1993; Connaughton et al. 1997; Loesser et al. 1997; Parmentier et al. 2003b, 2014; Boyle et al. 2013). Sonic muscle fibers, generally but not always, have a central core of sarcoplasm (Fine et al. 1993; Ladich 2001) surrounded by a radially arranged contractile cylinder consisting of alternating ribbons of SR and myofibrils (Fawcett and Revel 1961; Eichelberg 1976; Ono and Poss 1982; Fine and Pennypacker 1988; Bass and Marchaterre 1989; Appelt et al. 1991; Brantley et al. 1993; Fine et al. 1993; Connaughton et al. 1997; Loesser et al. 1997; Ladich 2001). The fiber periphery contains a large sarcoplasmic band beneath the sarcolemma (Hamoir et al. 1980; Hamoir and Focant 1981; Feher et al. 1998; Parmentier et al. 2013).

Mitochondria are located in the central core and beneath the sarcolemma (Eichelberg 1977; Bass and Marchaterre 1989; Fine et al. 1993; Parmentier et al. 2013); typically, they are not present in the contractile cylinder. Thus fiber morphology appears to be a trade-off: the intimate association of the SR and myofibrils minimizes the distance that calcium has to shuttle from the SR to the myofibrils and back. However, the absence of mitochondria in the contractile cylinder means that the energy-producing and energy-utilizing portions of the fiber are separated, which could hinder muscle performance. Fine et al. (1993) provided evidence that the distance between outer and core mitochondria is limiting and noted that large fibers tend to differentiate multiple sarcoplasmic cores and to fragment nonmitotically into smaller fibers. The presence of mitochondria at both ends of well-spaced stacks of thin planar myofibrils serves to minimize the diffusion time of ATP into the contractile tube (Lewis et al. 2003). However, a central core is not present in all fish sonic muscles and is lacking in for example *Pimelodus pictus, Carapus acus, Hemitaurichthys polylepis* and *Gobius paganellus* (Ladich 2001; Parmentier et al. 2003b, 2013; Boyle et al. 2013). In some of these fishes, there are a small number of mitochondria in the center of the fiber, which could be an incipient core that has not fully differentiated.

Triads, consisting of the transverse or t-tubule and two surrounding sarcoplasmic cisternae are usually found at the Z-line in fishes with white fibers (Akster 1981; Luther et al. 1995). Triads are also found at the Z-line in sonic muscles in weakfish *Cynoscion regalis* (Ono and Poss 1982), tigerfish *Terapon jarbua* (Eichelberg 1976), catfishes *Pimelodus* and *Platydoras* (Ladich 2001) and the butterflyfish *Hemitaurichthys polylepis* (Boyle et al. 2013). The transverse tubule in toadfish *Opsanus tau* (Fawcett and Revel 1961; Loesser et al. 1997), midshipman *Porichthys notatus* (Bass and Marchaterre 1989), and tigerfish *Therapon jarbua* (Eichelberg 1976) is located at the A-I junction, as in mammals. They are at the level of both the Z-line and A/I junctions in the primary sound-producing muscles of the carapid *Carapus acus* (Parmentier et al. 2003b). Triads at the level of A/I junction are closer to the myosin myofibrils and should decrease diffusion time.

3.18.2 Metabolism

For a muscle to contract and relax rapidly, calcium, the trigger for muscle contraction, must enter and be removed from the myoplasm rapidly. Myosin cross-bridges must attach to actin and generate force shortly after calcium levels rise, and bridges must quickly detach to stop generating force as levels fall (Rome and Lindstedt 1998). Multiple sonic muscle characteristics appear to be adaptations for speed because the high surface: volume ratio minimizes travel distance and seemingly facilitates fast flow of metabolites, oxygen, and calcium (Eichelberg 1976; Fine et al. 1990; Feher et al. 1998). Similar to fibers of other high endurance muscles (Schaeffer et al. 1996), the banks of mitochondria under the sarcolemma in male Porichthys type I sonic muscle fibers (Bass and Marchaterre 1989) reflects its high oxidative capacity (Walsh et al. 1995). However, typical sonic fibers have a lower volume of mitochondria although it is higher than in white trunk muscle.

Details on the metabolic machinery that powers the remarkable contractile abilities of sonic muscle are far from complete (Walsh et al. 1995). Skeletal muscles are usually divided into three broad types: slow oxidative (SO), fast oxidative glycolytic (FOG) and fast glycolytic (FG), which is more meaningful than the classic division of red or white muscles (Johnston et al. 1974; Patterson et al. 1975; Korneliussen et al. 1978; Hamoir and Focant 1981; Meyer-Rochow et al. 1994; Devincenti et al. 2000). SO muscles (red or Type I histochemically) have slow-type ATPase (acid stable), abundant mitochondria, and high activity of oxidative enzymes such as succinic dehydrogenase. FG muscles (white or Type IIb histochemically) have fast-type ATPase (alkali stable), few mitochondria, use primarily glycogen for anaerobic metabolism (Moyes et al. 1989, 1992), and are associated with rapid or burst motion in fishes. These muscles fatigue rapidly with use (Akster and Osse 1978; Johnston 1981; te Kronnie et al. 1983).

In phylogenetically distant fishes with intrinsic (*Opsanus tau*, Batrachoidiformes) or extrinsic muscles (*Terapon jarbua,* Perciformes; *Cynoscion regalis*, Perciformes; *Carapus acus,* Ophidiiformes), sonic muscles consist of FOG fibers (Type IIa histochemically): they will be considerably faster (fast type ATPase), less powerful than typical fast white muscle, and have more mitochondria and aerobic enzymes (Walsh et al. 1987; Fine and Pennypacker 1988; Chen et al. 1998; Parmentier et al. 2003b). These findings have been demonstrated in only a few species and additional work is required for generalizations to all sonic muscles. For instance, *Carapus acus* muscles are relatively slow, tetanizing above 10 Hz (Parmentier et al. 2006b). Yet its sonic fibers, as in *Opsanus tau*, have more glycogen and mitochondria than in white trunk muscles and possess high alkali-stable ATPase activity (Parmentier et al. 2003b).

3.18.3 Parvalbumins

Parvalbumins are polymorphic, low-molecular-mass calcium-binding proteins. They are particularly abundant in the white fast-contracting muscles of amphibians and fishes, where they function as a calcium shuttle between the cytoplasm and the SR. Parvalbumin isoforms and myofibrillar proteins differ between fish larvae and adults (Focant et al. 1992, 2003; Crockford and Johnston 1993; Huriaux et al. 2003), providing different contractile properties. They are considered responsible for calcium accumulation in the cytoplasm during muscle activity and may promote faster muscle relaxation (Gerday 1982; Klug et al. 1988; Appelt et al. 1991). The parvalbumin content is more elevated in high-speed sonic than in white muscle of the oyster toadfish *Opsanus tau* (Hamoir et al. 1980; Appelt et al. 1991; Tikunov and Rome 2009). Because of the relationship between the PA content and muscle relaxation speed, high PA levels are likely necessary for fast contraction and relaxation in muscles (Chiu et al. 2013). Parvalbumin would permit the muscle to have a superfast Ca^{2+} transient with only a relatively modest SR–Ca^{2+} pumping rate (Feher et al. 1998; Rome 2006). However, there is no significant difference between the sonic and white muscles in the midshipman (*Porichthys notatus*) and in the toadfish *Allenbatrachus grunniens*. Likely different parvalbumin isoforms found in fishes may be related to different Ca^{2+} binding abilities and make different contributions to muscle movement (Walsh et al. 1995; Chiu et al. 2013).

3.19 Stridulation Mechanisms

Stridulatory mechanisms are based on friction of skeletal elements such as teeth, fin rays, and vertebrae (Burkenroad 1931; Tavolga 1971b). Characteristically, stridulation sounds are rasps and creaks, often composed of a series of rapidly produced and irregular transient pulses, containing a wide range of frequencies (Hawkins 1993).

They contain considerably higher frequencies than present in swimbladder sounds (Ladich 1997) and are likely to exhibit greater variation in temporal parameters. In South American catfishes, for instance, such sounds are sufficiently different that they have been described with onomatopoeic names, which suggests sounds may be species-specific (Kaatz et al. 2010). However, the comparison of six species of *Synodontis* showed that acoustic parameters varied considerably, and it was not possible to determine the specificity of sounds because of overlap in sonic data (Parmentier et al. 2010b). We caution that different investigators may hear and describe the same sound differently, which can lead to confusion.

Unfortunately, in many fishes without obvious distinct sound-producing elements, the sonic mechanism has been attributed to sounds from the pharyngeal jaw and a resonating effect of the swimbladder without explicit evidence. In some cases, no special adaptation for sound generation has been described nor has tooth movement been examined during sound generation (Ladich and Fine 2006). These assumptions likely stem from a study on the white grunt *Haemulon plumieri* in which the upper and lower pharyngeal teeth grate against each other (Burkenroad 1930). The author noted that the swimbladder acts as a “resonator” because the character of the sound became “dry” and lost its grunt-like quality after the swimbladder deflation. The notion of swimbladder amplification clearly meshed with popular conception of the structure as a resonant bubble, which has been treated extensively in this review. Obviously, this work should be repeated with modern physiological and acoustic tools. A recent study using X-ray videos has conclusively demonstrated sound pulses generated by rubbing pharyngeal teeth in the French grunt *Haemulon flavolineatum* (Bertucci et al. 2014).

Feeding sounds have been investigated in several species and generally correspond to pulsed chewing sounds that occur during food grinding and manipulation by teeth of the pharyngeal jaws (Lobel 2001; Lagardère et al. 2004; Scholz and Ladich 2006). We are uncertain if these sounds function in communication because nonspecialized morphological structures are involved and behavioral studies are lacking. However, the detection of sounds unintentionally produced by conspecifics, predators and prey is crucial even in species not known to communicate acoustically. The interception and localization of these feeding sounds could be a major advantage for foraging fishes (Scholz and Ladich 2006), but a disadvantage for the sender (Myrberg 1981).

Feeding sounds can represent early stages in the process of ritualization in which an adaptation can evolve for communication. For instance, aggressive sounds emitted by the clownfish *Amphiprion clarkii* (Pomacentridae) result from teeth collision after rapid mouth closing (Parmentier et al. 2007). This fast jaw slam is induced by the cerato-mandibular (c-md) ligament, an apomorphic trait of pomacentrids that joins the hyoid bar to the medial side of the mandible (Stiassny 1981). Opening the mouth puts the ligament under tension causing the rapid jaw slam. The male pomacentrid *Dascyllus flavicaudus* produces pulsed sounds during different behaviors, and similarity between these sounds implies the same mechanism, i.e., the c-md ligament. A pulse produced during fighting involves a single jaw slam. Biting may have been the origin of the sound display because fighting sounds usually occur before aggressive behavior with biting (Parmentier et al. 2010a). Olivier et al. (submitted) nicely demonstrated the relationship between sound production and feeding movements. High-speed video has been used in *Amphiprion clarkii* to compare sound production with movements of the head, the jaws, and the hyoid apparatus in different feeding modes (sucking of plankton and biting of prey). The kinematic pattern of jaw slamming is the same in sound production and biting but different in sucking. Moreover, ablation of the c-md ligament prevents both sound production and biting movements. Interestingly, the piranha *Pygocentrus nattereri* also produces jaw-snapping sounds when it bites a conspecific (Millot et al. 2011), and their biting sounds are quite different from sounds generated by fast-contracting swimbladder muscles (Kastberger 1981a; Ladich and Bass 2005).

Another stridulatory mechanisms related to feeding has been found in seahorses, which produce rapid clicking sounds resembling a finger-snap (Gill 1905; Fish 1953) in a variety of contexts—feeding, courtship, and copulation (Fish and Mowbray 1970; Oliveira et al. 2014). The frequency distribution of sounds recorded from *Hippocampus hudsonius* range from 50 to 4,800 Hz although the most intense energy band varies between 400 and 800 Hz (Fish 1954). The feeding click ranges from 2.7 to 3.4 kHz in *H. zostera* and between 2.0 and 2.4 kHz in *H. erectus*. Descriptions of head morphology, analysis of high-speed video and surgical manipulations indicate that stridulatory sounds are produced during head movement by a bony articulation between the supraoccipital ridge of the neurocranium and the grooved anterior margin of the coronet (= the bony crown of the seahorse). The use of sounds in the different behavioral contexts may derive from feeding behavior (Colson et al. 1998).

A second stridulatory mechanism utilizes catfish pectoral spines (Sörensen 1895; Schachner and Schaller 1981; Fine and Ladich 2003). The spine can be abducted, bound, and locked as a predator defense against gape-limited predators (Alexander 1981). In the channel catfish, the armored pectoral spine decreases attack by predators in community situations and increases survival after attack (Bosher et al. 2006; Sismour et al. 2013). An erect spine more than doubles the width of juvenile Channel catfish (Sismour et al. 2013) and can cause additional difficulties in swallowing and potential injury (Fine et al. 2011). Spines are reduced in size during domestication and their development appears to be controlled by selection pressures (Fine et al. 2014). We suspect that morphological changes (apomorphic dorsal, anterior, and ventral processes on the spine base) that allow for binding and locking of the spine occurred before the evolution of ridges on the dorsal process necessary for sound production.

Stridulatory sounds can be produced during abduction and adduction of spines in bagrids, mochokids, doradids, and aspredinids and during abduction only in ariids, pimelodids, callichthyids, and loricariids and ictalurids (Fine et al. 1996; Ladich 1997; Heyd and Pfeiffer 2000). Pulses produced by the left and right spine tend to alternate, and channel catfish tend to favor one spine (right or left-handed) although both spines are used (Fine et al. 1996). Stridulation in doradids, pimelodids and mochokids are pulsatile, with durations ranging from 25 to 100 ms and energy concentrated between 2 and 3.6 kHz (Ladich 1997). Sounds are produced by friction of the base of the first pectoral spine within a channel in the pectoral girdle (Fine et al. 1997; Heyd and Pfeiffer 2000; Vance 2000). The dorsal process on the proximal end of the pectoral spine contains microscopic bony ridges (Tavernse and Aloulou-Tiki 1974; Schachner and Schaller 1981; Fine et al. 1997; Parmentier et al. 2010c), and silent species lack the ridges or edge knobs on the dorsal process (Kaatz et al. 2010).

In *Ictalurus punctatus*, stridulation sounds are produced when ridges on the ventrolateral surface of the dorsal process of the pectoral spine contact the spinal fossa of the ventrolateral wall of the cleithrum. Sweep movements of the pectoral spine produce a number of discrete pulses with varying waveforms (Fine et al. 1996, 1997, 1999; Vance 2000). These pulses are created by the ridges as they rub against the rough surface of the spinal fossa of the cleithrum. The channel catfish work initially assumed a cricket-type mechanism in which individual pulses would be caused by collisions of individual ridges with features on the cleithrum, i.e., a finger nail over a succession of teeth of a plastic comb. However, the cleithrum, though rough was surprisingly featureless. Intervals between pulses indicated insufficient time for a ridge to make contact, lift up before recontacting the cleithrum. In other words, the mechanism of pulse production was unclear but was not caused by contact of a single ridge. Further investigation on mochokids using high-speed photography (500–1,250 frames per second) clarified the mechanism. Pectoral sweeps (abduction and adduction) are not continuous but are made of a series of distinct movements designated "jerks." The analogy for sound production would be a brake shoe pressing against a wheel. In this mechanism, pulses are produced during the movements would be produced by multiple ridges simultaneously rubbing against the cleithrum (Parmentier et al. 2010b).

In the catfish *Sisor rhabdophorus,* a dorsal fin stridulating mechanism is based on rubbing of a radial or pterygophore on an interspinous bone having file-like ridges (Mahajan 1963; de Pinna 1996). This mechanism is not known in other catfish families.

Three species of croaking gouramis of the genus *Trichopsis* provide a final example of a well-studied pectoral mechanism (Kratochvil 1978; Ladich et al. 1992). Rather than bone against bone, the pectoral fin has two hypertrophied tendons that rub against other fin rays producing a double-pulsed sound. Ablation of the tendons stops sound production, which returns upon regeneration of the tendons (Kratochvil 1985). This mechanism is not known in other labyrinth fishes (family Osprhronemidae).

3.20 Evolution of Sound Production

Although there are numerous families of sonic fishes, sound production does not occur in most fish families. The most complete enumeration of sonic fishes comes from a table in Lobel et al. (2010). In some families (catfishes, toadfishes, gadids, sciaenids, holocentrids, pomacentrids, and carapids) all or almost all species have the ability although a few species of catfish and sciaenids have mute species that have secondarily lost the ability. Conversely, minnows (cyprinids) are mostly mute, but a couple of species produce socially relevant sounds (Winn and Stout 1960; Stout 1963; Ladich 1988; Johnston and Johnson 2000a, b; Johnston and Vives 2003). Overall, a cladogram of sound producers (Fig. 3.7) indicates the ability has arisen sporadically, suggesting independent and convergent evolution. Independent evolution accounts for disparate mechanisms such as stridulation and sounds produced by sonic swimbladder muscles vibration.

We have placed vocal species on a newly derived phylogenetic tree (Betancur et al. 2013) that clearly shows the ability to produce sound has developed in many taxa (Fig. 3.7). The tree was derived from 19 nuclear and one mitochondrial gene and reflects major reorganization of teleost groups, many with new names that may be surprising to scientists who have not stayed current in fish systematics. Families indicated as sonic in the figure may have representatives that do not produce sounds and others that have not been examined. In the Gobiidae, for example, with more than 1,500 species, sounds have been recorded in only 21 species from 10 genera. One small goby has lost the ability to produce sounds (Gkenas et al. 2010) and the status of planktonic species is unknown (Lugli personal communication). We should bear in mind that negative data are unlikely to be published. In the Euacanthomorphata, sonic species are actually found in all taxa but the Scombriformes. Additionally to the broad taxonomic categories in Fig. 3.7, below are some details for different groups:

- In the Gobiomarpharia, sounds were recorded only in Gobiidae.
- In the Syngnathiformes, sounds were found in Centriscidae, Dactylopteridae, Syngnathidae, Mullidae, and Cephalacanthidae.
- In the Anabantomorphariae, sounds were only studied in the Osphronemidae.
- In the Carangimorphariae, vocal species were found in Carangidae and Sphyraenidae.
- In the Ovalentariae, acoustic species belong to Cichlidae, Cyprinodontidae, Hemiramphidae, Pomacentridae, and Blenniidae.

The Percomopharia is a huge taxon that now includes many orders and families (Fig. 3.7) with numerous sonic species, including the Serranidae, Percidae, Scorpaenidae, Sebastidae, Triglidae, Gasterosteidae, Cottidae, Caesionidae, Apistidae, Tetrarogidae, and Synanceiidae.

Note that detailed treatment of sonic clades that utilize different mechanisms such as stridulation (independently evolved using pharyngeal teeth, pectoral spines, or neck vertebrae), sonic muscles that are intrinsic and extrinsic but have occipital spinal or true spinal innervation, which may utilize different nerve roots would require an entire monograph. Further complications arise since some catfishes have both swimbladder and stridulation mechanisms. Thus the lumped cladogram we present obscures much of the variation of a number of ad hoc independently derived adaptations. On the other hand, some but not all extrinsic and intrinsic swimbladder muscles could be homologous and represent different stages of evolution as in the pearl perch (slow mechanism excited with a fast muscle) or the black drum

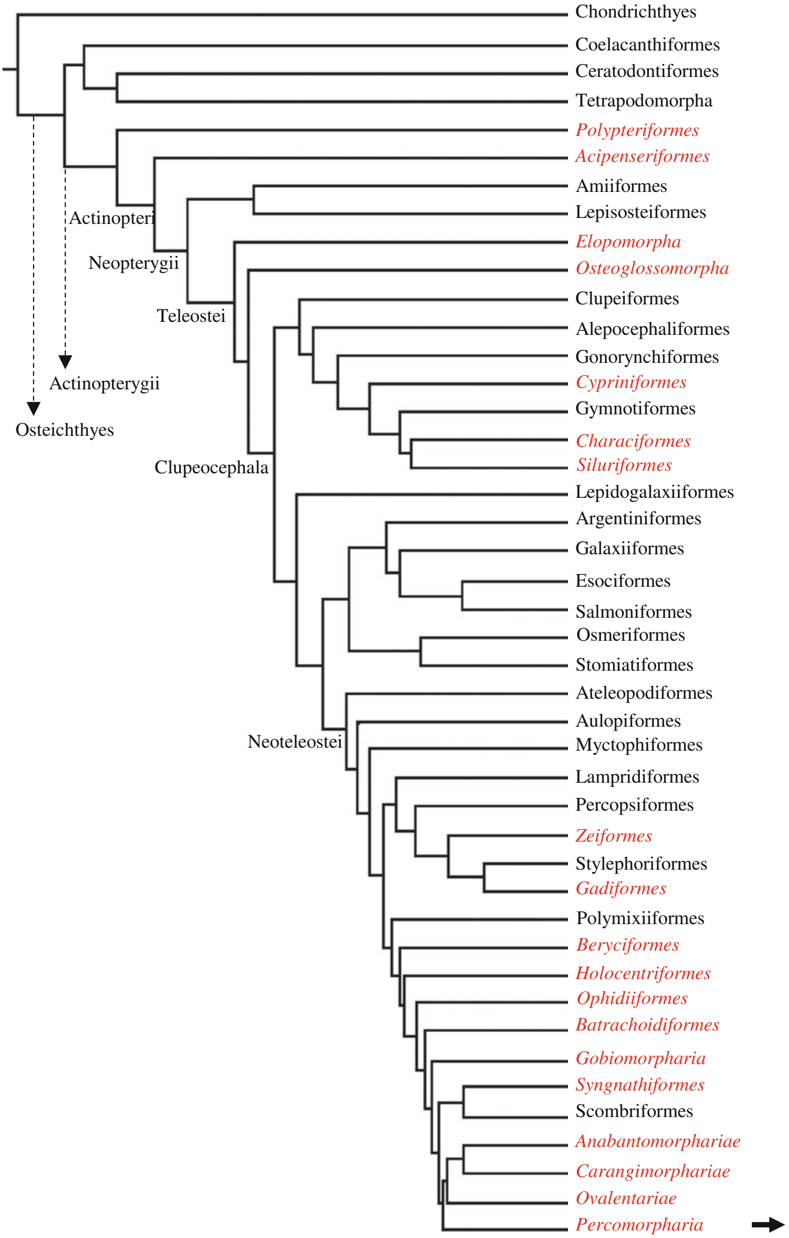

Fig. 3.7 Cladogram indicating groups of fishes that include sound producers (in *red* and italicized). The cladogram indicates that sound production has developed independently in multiple clades suggesting convergent evolution. Due to space considerations, the cladogram lumps diverse mechanisms including swimbladder muscles innervated by occipital spinal and true spinal nerves, slow and fast muscles, diverse stridulation and pectoral mechanisms, and cases in which the sonic mechanism is unknown. A cladogram that considered these different types of sound production separately would be much more fragmented. A couple of basal groups produce sounds, but there is no indication that they provide a homologous basis for sound production in more derived groups

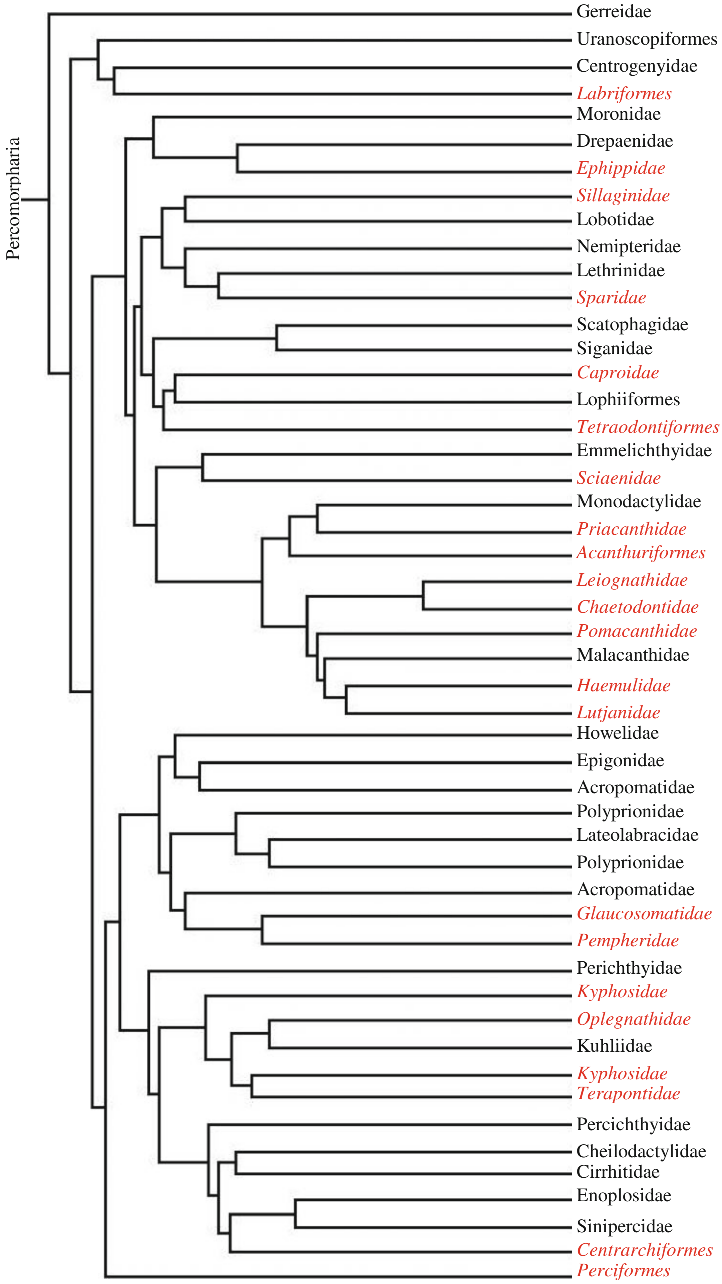

Fig. 3.7 (continued)

(intrinsic muscles compared to the extrinsic muscles in most sciaenids). We note that a list of the various origins of sonic muscles from the head has never been attempted. It would be a complex subject since muscle origins as well as insertions can migrate, complicating the determination of homologies.

Swimbladder sonic mechanisms can be divided into ones stimulated by occipital spinal nerve roots and ones driven by a series of segmental true spinal nerves (sciaenids, pinecone fish, pollack, and piranhas) (Vance et al. 2002; Onuki and Somiya 2007), indicating that motor neurons in the two situations have different embryonic origins (see Chap. 2 this volume). Spinal and occipital spinal systems are clearly not homologous and have arisen independently. For the occipital sonic swimbladder nerve cases, the SMN was originally demonstrated by electrical brain stimulation (Demski and Gerald 1972, 1974) and retrograde transport in toadfish (Fine et al. 1982). The toadfish SMN is a long midline column just beneath the fourth ventricle and central canal and above the medial longitudinal fasciculus (Demski and Gerald 1972; Fine 1982; Fine et al. 1984; Bass 1985; see Chap. 2 this volume for more modern references). Later Ladich and Fine (1994) demonstrated that the SMN in pimelodid catfish was strikingly similar in appearance and position to the SMN in toadfish although toadfish and catfish are in separate radiations that are distantly related. Additionally, *Pimelodus* has an intermediate occipital-spinal pattern, indicating that motor neurons in the two situations have different embryonic origins (see Chap. 2 this volume). In more advanced perciform teleosts, the SMN migrates to a more lateral position typical of the mammalian hypoglossal nucleus (Finger and Kalil 1985; Yoshimoto et al. 1999; Carlson and Bass 2000). Note Boyle et al. (2013) recently demonstrated sonic neurons in a lateral position exiting through occipital nerve roots in a butterflyfish although they appear to innervate hypaxial sonic muscles.

Bass and colleagues have written a series of high profile papers (Bass et al. 2008; Chagnaud et al. 2011, 2012; Bass and Chagnaud 2012) demonstrating that the sonic motor nucleus, likely a hypoglossal homolog, differentiates in rhombomere 8 in fishes and other vertebrate classes; they make a strong case that the SMN is homologous with vocal motor nuclei in amphibians, birds, and mammals. However, although fishes possess occipital nerves, only a small number of adult species have been demonstrated with a putative hypoglossal nucleus, and in those cases it has been associated with sonic swimbladder muscles. The fish cladogram suggests independent evolution (homoplasy) (Boyle et al. 2013), but Bass and colleagues consider a vocal motor nucleus a basal vertebrate character. Butler and Saidel (2000), describing the sporadic distribution of the fish nucleus rostrolateralis in fish brains, define the term "syngeny," or generative homology, as the relationship of a given character in different taxa that is produced by shared generative pathways. Presuming that all fishes have an embryonic hypoglossal (Gilland and Baker 1993), which in most cases likely degenerates embryonically (apoptosis) would solve this potential contradiction. Furthermore, it would suggest that all fishes are preadapted to produce sounds, likely with a swimbladder. Reasons why a hypoglossal would degenerate or be maintained in a species are unclear, but the problem could likely be studied in zebrafish by demonstrating an embryonic hypoglossal nucleus and providing appropriate growth factors for its maintenance. Note that sexual dimorphism in rat penis muscles is determined by cell death in females and exposure to the appropriate androgens spares the spinal nucleus and muscles (Breedlove and Arnold 1980). In conclusion, although fishes may have embryonic similarities that may preadapt them to be sound producers (syngeny), it is likely more profitable to consider most of the myriad of fish sound production mechanisms to be independently evolved.

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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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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

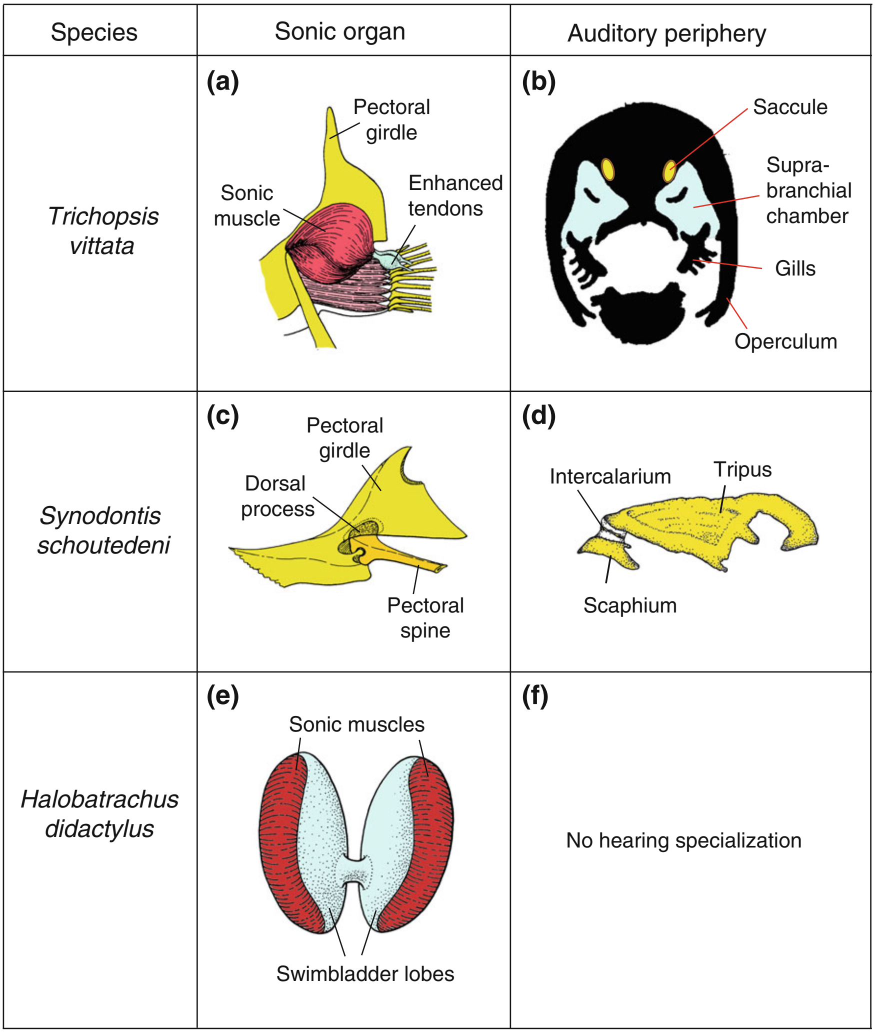

Fig. 4.1 Overview of sound-generating mechanisms and accessory hearing structures in *Trichopsis vittata*, *Synodontis schoutedeni* and *Halobatrachus didactylus*. **a** Illustrates the tendon plucking mechanism in *T. vittata*, **c** the pectoral stridulatory apparatus in catfish and **e** drumming (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 suprabranchial 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).

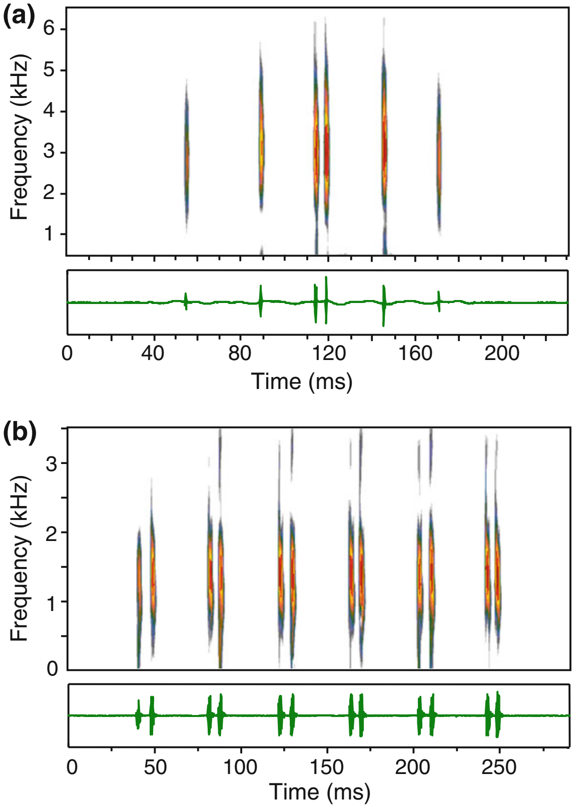

Fig. 4.2 Sonograms and oscillograms of croaking sounds of **a** an early stage juvenile (0.11 g) and **b** an adult *T. vittata* (0.8 g). Croaking sounds are built up of series of bursts consisting of single or double pulses. Note different axis ranges in (**a**) and (**b**). **a** Modified after Wysocki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

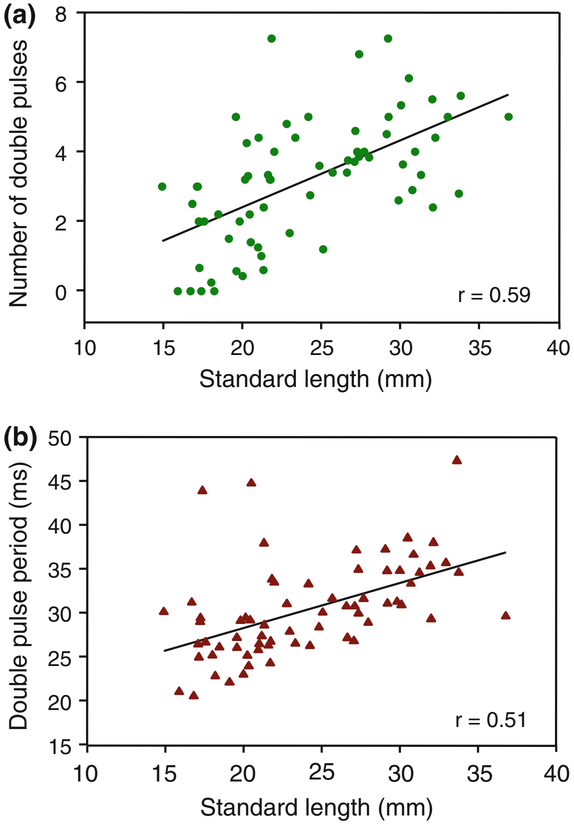

Fig. 4.3 Correlation between **a** number of double-pulsed bursts and standard length and **b** the burst period of croaking sounds and standard length in *T. vittata*

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.

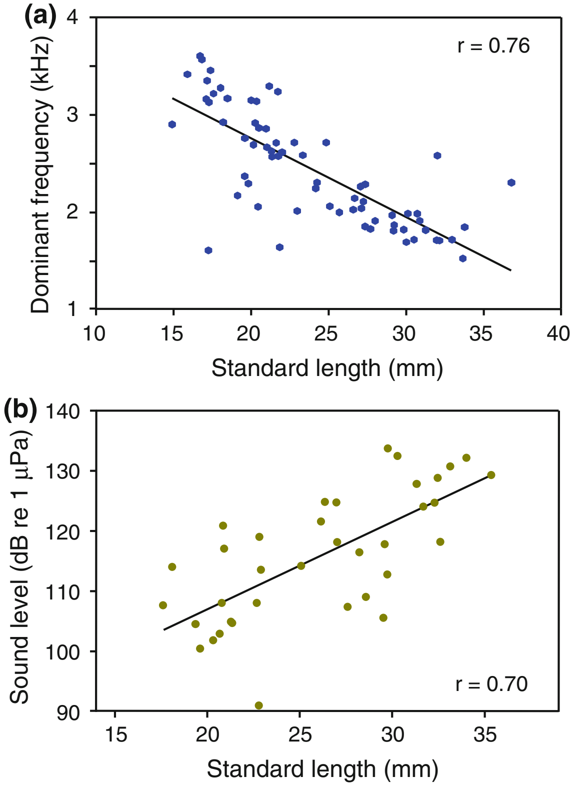

Fig. 4.4 Correlation between **a** dominant frequencies and standard length and **b** sound pressure level of croaking sounds and standard length in *T. vittata*

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

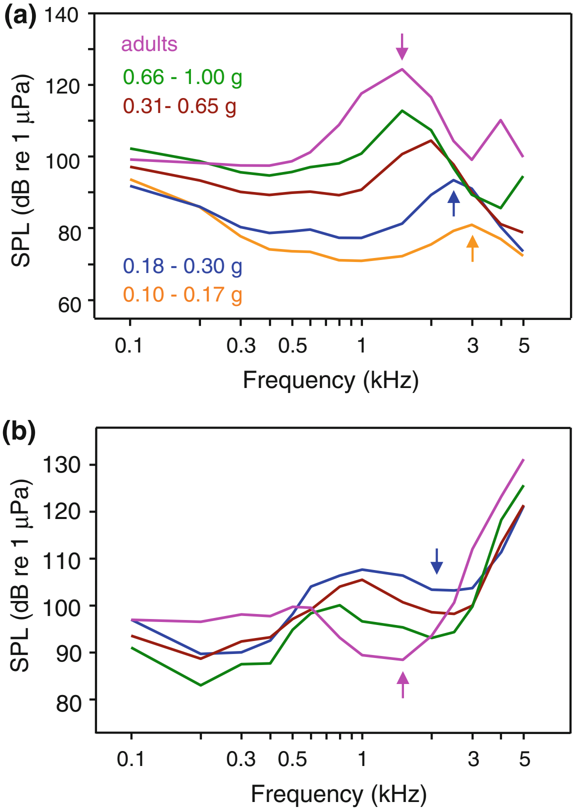

Fig. 4.5 **a** Mean sound spectral levels and **b** mean audiograms of different stages of juvenile and adult *T. vittata*. *Arrows* indicate shifts in main energies of sounds as well as of the auditory sensitivity maximum to lower frequencies during growth. Note that auditory sensitivity could not be 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.

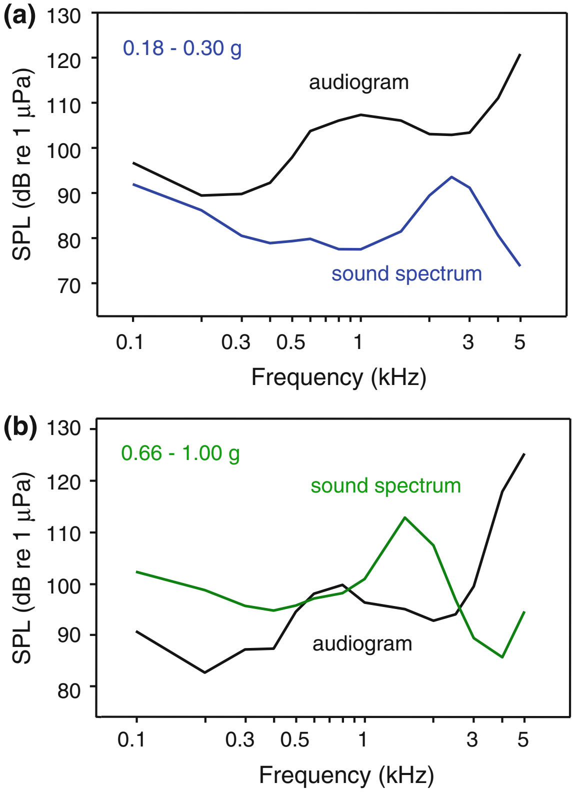

Fig. 4.6 Comparison of mean audiograms in relation to mean absolute sound power spectra of croaking sounds in the **a** smallest and **b** the largest juvenile size group of *T. vittata* in which auditory sensitivities have been determined. After Wysocki and Ladich (2001). With kind permission from Springer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

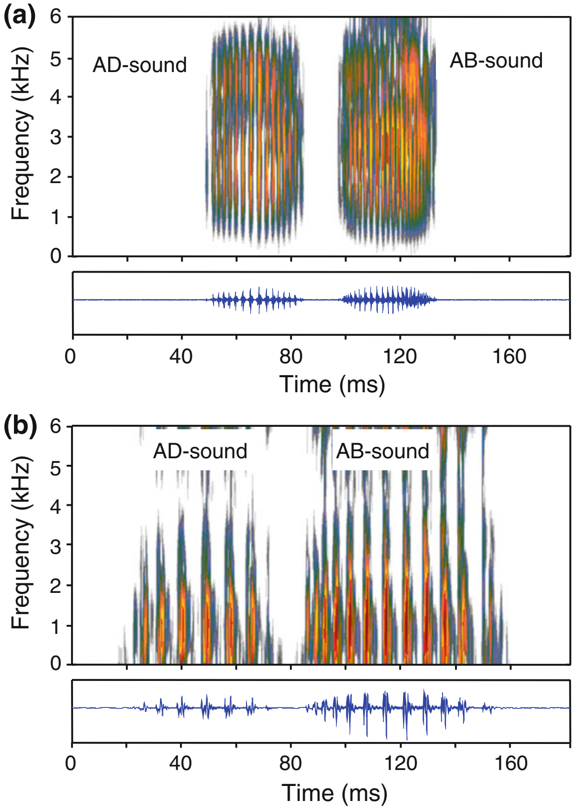

Fig. 4.7 Sonograms and oscillograms of stridulation sounds of **a** an early stage juvenile (28–36 mm) and **b** an adult *S. schoutedeni* (group 116–127 mm). An adduction sound (AD-sound) and an abduction sound (AB-sound) is shown in both figures. Note different sound duration, pulse periods and main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

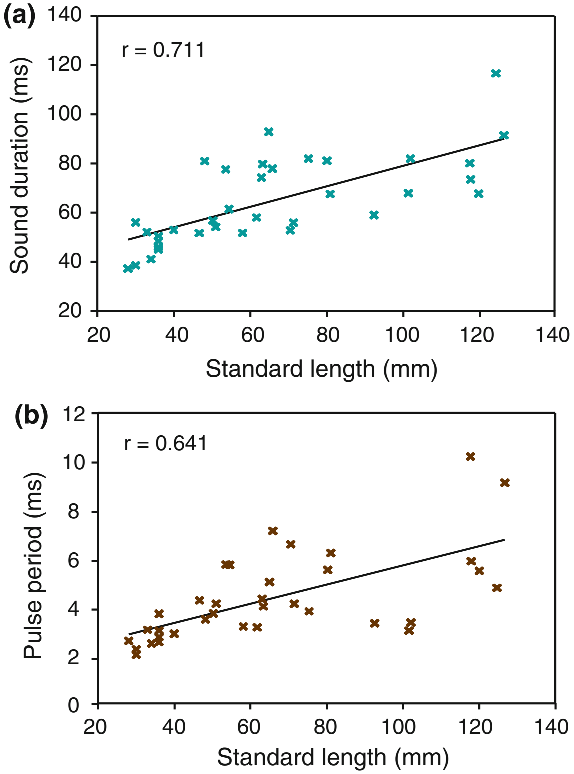

Fig. 4.8 Correlation between **a** sound duration and standard length and **b** the pulse period of stridulation sounds and standard length in *S. schoutedeni.* Modified after Lechner et al. (2010)

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.

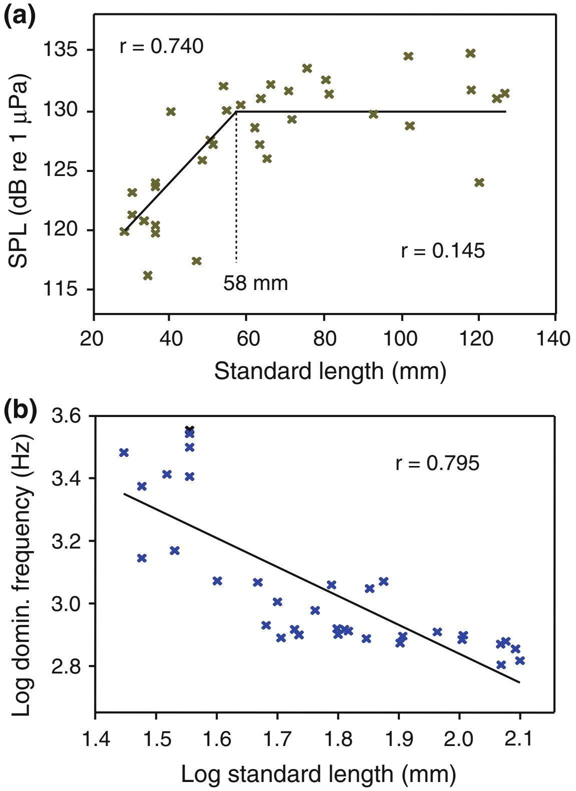

Fig. 4.9 Correlation between **a** sound pressure level and standard length and between **b** dominant frequencies of stridulation sounds and standard length in the catfish *S. schoutedeni.* Note that the sound pressure level is correlated to standard length up to 58 mm SL (*left r-value*). **a** modified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

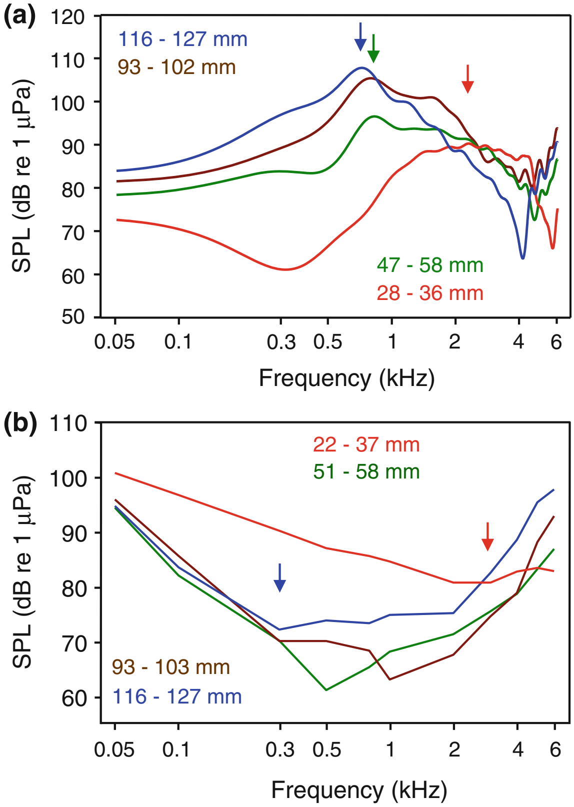

Fig. 4.10 **a** Mean sound spectra levels and **b** mean audiograms of different stages of juvenile and adult catfish *S. schoutedeni.* Sound pressure levels were measured at a distance of 5 cm. *Arrows* indicate shifts in main energies of sounds as well as in the auditory sensitivity maximum to lower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

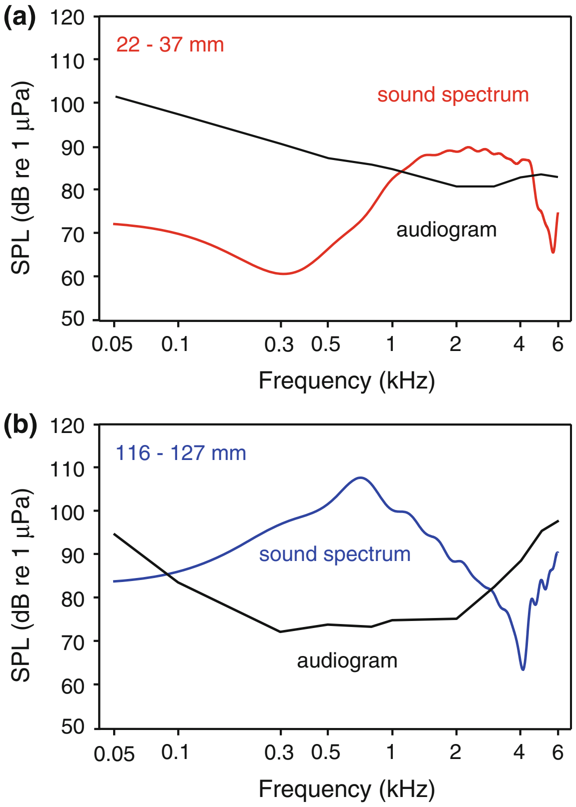

Fig. 4.11 Comparison of mean audiograms in relation to mean absolute sound spectra levels of stridulation sounds in **a** the smallest and **b** the largest size group investigated in the catfish *S. schoutedeni*. Modified after Lechner et al. (2010)

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

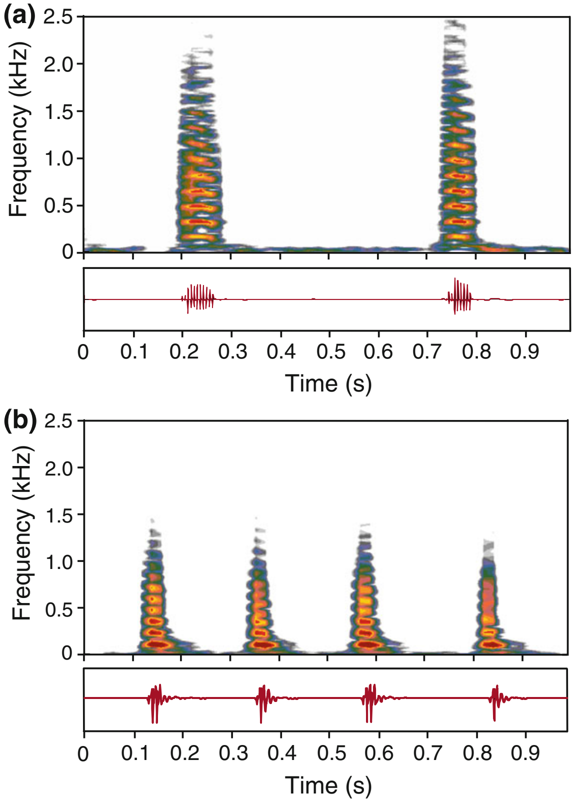

Fig. 4.12 Sonograms and oscillograms of grunt calls emitted by **a** an early stage juvenile (6.1 cm SL) and **b** a representative of the largest group (28.5 cm SL) of *H. didactylus*. **a** shows two single grunts and **b** part of a grunt train. Note the shorter grunt duration and lower dominant frequency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

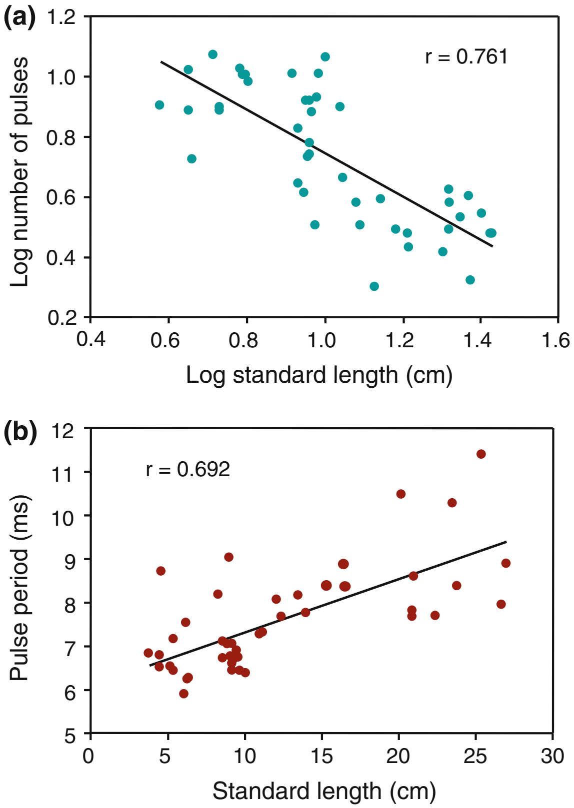

Fig. 4.13 Correlation between **a** number of pulses within a grunt sound and standard length and **b** the pulse period and standard length in the toadfish *H. didactylus*. Modified after Vasconcelos and Ladich (2008)

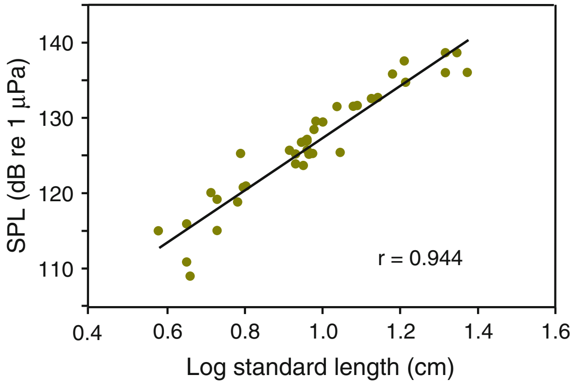

Fig. 4.14 Correlation between sound pressure level and standard length in the toadfish *H. didactylus*. Modified after Vasconcelos and Ladich (2008)

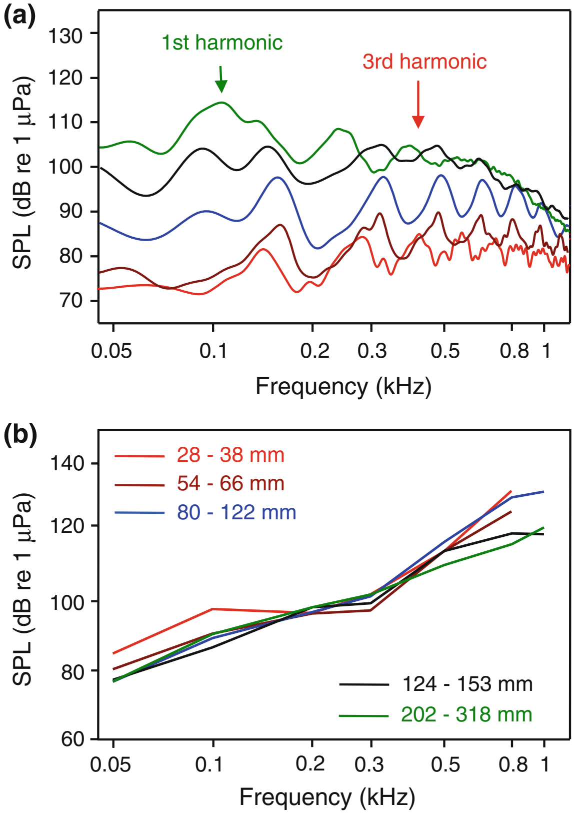

Fig. 4.15 **a** Mean sound spectra levels of grunt sounds and **b** mean audiograms of different stages of juvenile toadfish *H. didactylus*. *Arrows* indicate shifts in main energies of sounds during growth. Modified after Vasconcelos and Ladich (2008)

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).

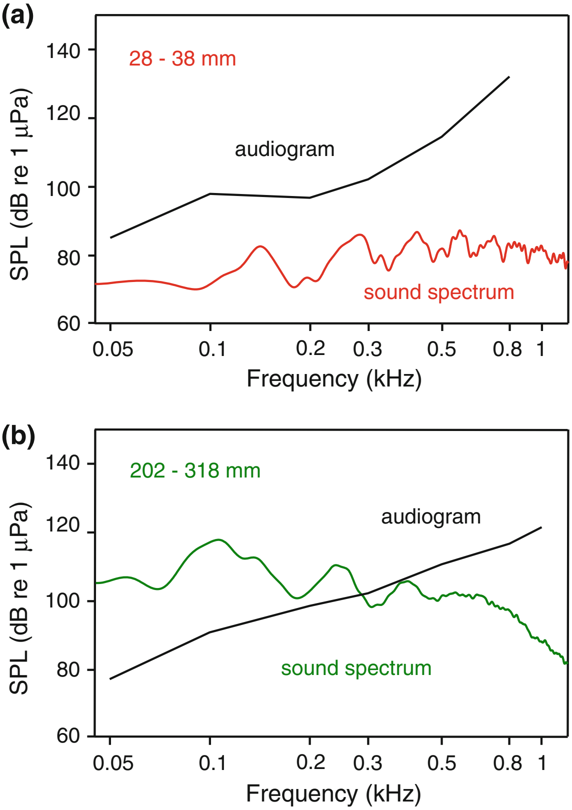

Fig. 4.16 Comparison of mean audiograms in relation to mean absolute sound power spectra of grunt sounds in **a** the smallest and **b** the largest size group investigated in the toadfish *H. didactylus*. Modified after Vasconcelos and Ladich (2008)

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—*Metriaclima 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.

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Chapter 5
Acoustic Signalling in Female Fish

Friedrich Ladich

Abstract Sound production in female fish has only seldom been mentioned, which is in contrast to the vast literature on male sound production. This lack of information is surprising because sound-generating mechanisms are present in females of (almost) all vocal species. Typically, female sonic organs are smaller than those of the males, for example in batrachoidids or callichthyids. Moreover, female sonic muscles do not hypertrophy during the reproductive season, such as they do in male gadids and sciaenids. The sexual dimorphism in sonic organs indicates that males are more active sound producers than females. In most species, males emit advertisement and mating sounds. The exceptions are one osphronemid species in which only females vocalise prior to spawning, and seahorses in which both sexes produce courtship sounds. At the same time, agonistic behaviour and aggressive sounds are rather similar in males and females, indicating that both sexes defend feeding and breeding sites. In numerous cichlids, females are even the more aggressive sex while defending their brood. This resembles the situation in hermaphroditic clownfish, in which females are the larger sex and primarily defend their host sea anemones. Sounds have very rarely been recorded under standardised conditions in both sexes, and sound characteristics have therefore seldom been analysed and compared in detail. Female agonistic sounds may differ in frequency and sound level from male sounds, reflecting differences in body and sonic organ size between sexes. Furthermore, sex-specific differences in pulse length and number of pulses have been described. Differences between female mating and female agonistic sounds have been described in one species. Overall, the assumption is that sex-specific differences in acoustic signalling during agonistic behaviour are minor in vocal species. These differences seem to depend on morphological differences. Furthermore, a more detailed analysis of reproductive behaviour in fish is expected to show more teleost species in which females are vocal during courtship and spawning.

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5.1 Introduction

Representatives of numerous fish families produce sounds during agonistic behaviour, courtship and spawning (reviewed in Amorim 2006; Ladich and Myrberg 2006; Myrberg and Lugli 2006). Most of these descriptive studies did not distinguish between sexes (Schneider 1964a; Pfeiffer and Eisenberg 1965; Fish and Mowbray 1970; Ladich 1988, 1997). In those species in which sexes have been investigated separately, the majority of studies described sound production in males. This partly reflects the fact that investigators concentrated on reproductive behaviour, whereby males advertise their nest sites, reproductive readiness etc. more frequently via visual and acoustic signals than females (Myrberg et al. 1986; Hawkins 1993; McKibben et al. 1998, Hawkins and Amorim 2000; see chapter by Amorim et al. in this volume). Interestingly, studies on agonistic behaviour often revealed that both sexes vocalise and that differences in behaviour and sound characteristics are small (Myrberg et al. 1965; Ladich 1990, 2007; Lagardere et al. 2005). Nevertheless, detailed analyses of female sound production and sound characteristics have seldom been provided.

This striking difference in research effort on female and male sound production during agonistic and reproductive behaviour is certainly due to differences in the life history and acoustic signalling between sexes (resulting in less or even no vocalisations in females). It also reflects a male-biased and territory as well as reproduction-biased research approach: investigators did not pay similar attention to females in different contexts. Only few studies focused on male and female sound production under similar conditions, analysing and comparing sound characteristics (Lagardere et al. 2005; Ladich 2007; Oliveira et al. 2014). Often male and female sounds were described very generally, without statistical analyses. Moreover, sounds were seldom recorded under standardised conditions, e.g. same-sex versus mixed-sex agonistic encounters, making it difficult to describe and compare the behavioural contexts during which sounds were produced.

The aim of this chapter is to review the status quo of our knowledge on sound production in female fish. It starts with an overview on sex-specific differences in sound-generating structures, followed by outlining differences in acoustic behaviour and in sound characteristics. Differences between sexes are described systematically in all orders and families for which data are available.

5.2 Sexual Dimorphism in Sonic Organs

The sexual dimorphism of sound-generating (sonic) mechanisms has been described in several taxa in detail. This was particularly the case in cods (family Gadidae), cusk-eels (family Ophidiidae), toadfishes (family Batrachoididae), labyrinth fishes (family Osphronemidae) and croakers (family Sciaenidae).

Among Gadiformes, sexual dimorphism of drumming muscles (but of no other structures) has been described in several species of the families Gadidae and of Merluciidae. In the haddock *Melanogrammus aeglefinus* (formerly *Gadus aeglefinus*), drumming muscles are entirely embedded in the ventral wall of the swim bladder. Templeman and Hodder (1958) observed that sonic muscles of mature male haddock are larger than those of females and that male muscles are twice as large during the pre-spawning and spawning period in May and June. No seasonal variation in muscle size is known from female haddock. The Atlantic cod *Gadus morhua* (formerly *G. callarias*) has three pairs of drumming muscles which originate dorsally at vertebral parapophyses and insert ventrally on the swim bladder wall. Nordeide et al. (2008) observed in cods kept in net pens that drumming muscle mass is similar in both sexes several months prior to spawning. Rowe and Hutchings (2004, 2006) reported that male drumming muscles were larger than female muscles and that they undergo an annual cycle of hypertrophy during the spawning period, followed by a post-spawning atrophy. Results gained in closely related merluciids support the data on gadids. The hake *Merluccius merluccius* (family Merluciidae) has paired drumming muscles located at the anterior wall of the swim bladder close to its ventral wall. There is no consistent difference in weight between immature males and all stages of females. Muscles enlarge as the males become sexually mature, an effect not observed in females (Groison et al. 2011).

The sonic apparatus of representatives of the family Ophidiidae (cusk-eels, order Ophidiiformes) is much more complex than in cods and differs widely between sexes. For example, a male striped cusk-eel *Ophidion marginatum* (formerly *Rissola marginata*) can easily be distinguished from females by the presence of a hump on the head. The hump is produced by a dorsal enlargement of the skull and attachment of dorsal sonic muscles which are part of the sound-producing mechanism. Males have larger drumming muscles, ossicular structures (supraoccipital crest, neural arches of first vertebra) onto which sonic muscles insert and a rocker bone on the swim bladder which is lacking in females (Courtenay 1971; Kéver et al. 2012).

In toadfishes (family Batrachoididae), drumming muscles differ between sexes and even male reproductive morphs. Fine et al. (1990) observed in the oyster toadfish *Opsanus tau* that the swim bladder and attached sonic muscles increased in size throughout life and were between 20 and 44 % larger in males than in females (adjusted mean weights of sonic muscles: 3.67 g versus 2.55 g). This was paralleled by a major difference in the number of muscle fibres (adjusted means: 307,000 in males versus 209,000 in females). The midshipman *Porichthys notatus* is characterised by two different male morphs: nest-owning type I males which advertise their nest sites vocally by humming, and non-vocal and sneaking type II males. Type I males possess 25-fold larger sonic muscles than other adults and, adjusted for body size, approximately sixfold larger muscles (Fig. 5.1). Furthermore, type I males have approximately four to fivefold more fibres in each sonic muscle than type II males or females (Fig. 5.1) (Bass 1992; Brantley et al. 1993).

Within the order Perciformes, sexual dimorphism in sound-generating mechanisms has been described in the family Osphronemidae (suborder Anabantoidei,

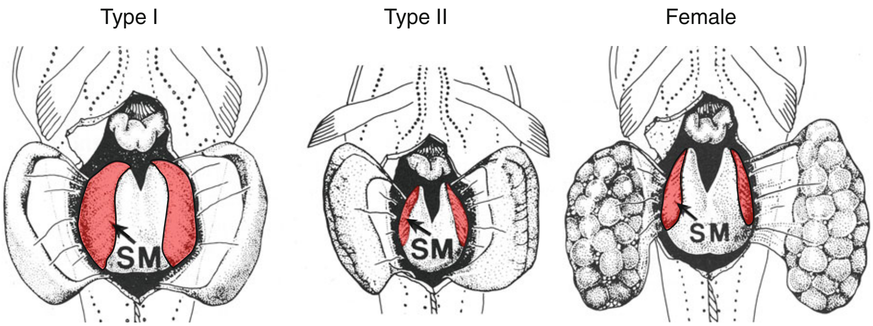


Fig. 5.1 Inter- and intrasexual dimorphism of swim bladders and sonic muscles (SM) in the midshipman *Porichthys notatus*. Ventral views illustrate differences in size of swim bladders and sonic muscles in type I males, type II males and females. Gonads are deflected outside the body cavity. Modified from Bass (1992), with permission from Elsevier

labyrinth fishes or gouramis) as well as in the family Sciaenidae (croakers or drums). Within gouramis, Sexual dimorphism of the sound-generating mechanism is known in two out of three species of the genus *Trichopsis* spp. (croaking gouramis). The mechanism consists of enlarged pectoral fin muscles which stretch enhanced fin tendons and snap them over specialised pectoral fin rays. Alternate beating of pectoral fins produces pulsed croaking sounds (Kratochvil 1978). This mechanism is expressed only within the genus *Trichopsis* but not in related genera such as *Betta* (Siamese fighting fishes) or *Macropodus* (paradise fishes) (Kratochvil 1985). The morphology of the sonic apparatus differs between sexes and species. In the croaking gourami *T. vittata* (formerly *T. vittatus*) the sonic mechanism is approximately one third smaller in females than in males (Fig. 5.2). In the pygmy gourami *T. pumila*, male sonic muscles are much larger than in females, which do not produce sound (Fig. 5.2). Thus, a large diversity in sexual dimorphisms is present even within one genus of teleosts.

A large diversity of sexual dimorphisms of sonic muscles has been described in the family Sciaenidae. In this group, drumming muscles generally originate on the body wall lateral to the swim bladder and insert on a broad tendon which attaches to the swim bladder dorsally (see Chap. 3). Sonic muscles are either present only in males or in both sexes, in the latter case growing larger in males. Takemura et al. (1978) stated that in the Japanese marine drums koichi *Nibea albiflora* and shiroguchi *Argyrosomus argentatus*, drumming muscles of males are thicker. Similarly, Ueng et al. (2007) reported that male Japanese croaker *Argyrosomus japonicus* males have thicker, heavier and longer sonic muscles than females. Studies on Atlantic species confirm these results and partly reveal even more pronounced sexual dimorphisms within this teleost family. The adjusted weight of sonic muscles of the Atlantic croaker *Micropogonias undulatus* was 1.92 % in males and 1.4 % in females. In contrast to all species mentioned above, sonic muscles were present only in males of the spot *Leiostomus xanthurus* and the weakfish *Cynoscion regalis* (Hill et al. 1987). In male weakfish, sonic muscles

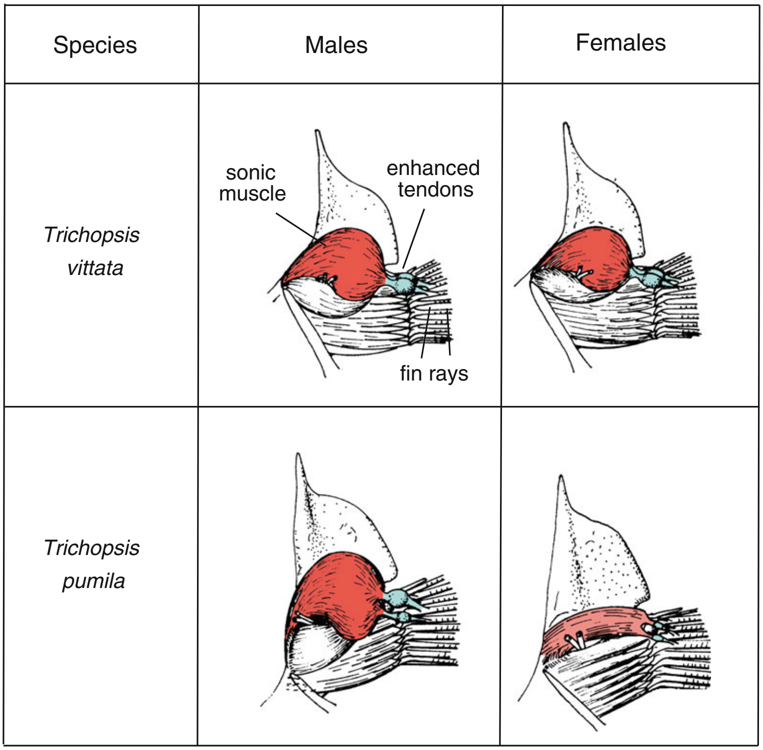


Fig. 5.2 Sexual dimorphism of sound-generating mechanisms in anabantoids. Shown are two species of the genus *Trichopsis*, the croaking gourami *T. vittata* and the pygmy gourami *T. pumila* (family Osphronemidae). Note differences in sonic muscle size (*red*) and enhanced tendons (*blue*) size between sexes and species. Modified after Kratochvil (1985)

hypertrophy in the spawning season and atrophy afterward (Connaughton et al. 2002). This hypertrophy is the result of increasing muscle thickness caused by elevated androgen levels, which are triggered by photoperiod and temperature (Connaughton and Taylor 1995).

Within otophysines, a taxon characterised by having Weberian ossicles to enhance hearing, sound-generating mechanisms have been described in two out of four orders, namely the Siluriformes (catfishes) and the Characiformes (tetras). Numerous catfish families produce sounds using a pectoral mechanism. Rubbing a process of the base of the pectoral spine (first enhanced fin ray) in a groove of the shoulder girdle emits pulsed sounds (for a review see Fine and Ladich 2003). Sexual differences in the pectoral mechanisms have been described in the family Callichthyidae (armoured catfishes). Males of the peppered corydoras *Corydoras paleatus* and of *Megalechis thoracata* have larger pectoral spines than females (Pruzsinszky and Ladich 1998; Hadjiaghai and Ladich 2015).

The difference in the morphology of sonic organs between sexes in numerous fish species indicates two different trends, namely that both sexes are able to produce sounds in numerous taxa and that males will probably be the more active sound producers. The latter is based on the observation that male sound-producing mechanisms are larger and may even hypertrophy seasonally.

5.3 Sex-Specific Differences in Acoustic Signalling

Sex-specific differences in acoustic behaviour and vocalisations are described here following the systematics by Nelson (2006). A lack of knowledge about female vocalisations in a species does not prove unequivocally that only males are vocal and females mute. Most studies failed to examine female sound production at all or did not do so in a systematic manner, i.e. under comparable experimental designs. Therefore, differences between sexes in acoustic signalling need to be interpreted cautiously.

5.3.1 Gadiformes

Within the order Gadiformes or cods, sounds have frequently been described in representatives of the family Gadidae (Brawn 1961; Hawkins and Rasmussen 1978; Almada et al. 1996; Hawkins and Amorim 2000) but not in other families, although sound-generating mechanisms are known in the family Merluciidae.

Several studies investigated sound production in cod *Gadus morhua* and determined that, for most of the year, both sexes produced grunting sounds (Brawn 1961). Brawn (1961) mentioned that grunting sounds were produced by male fish during aggressive encounters with other males and ‘unripe females’, and also as part of the courtship behaviour directed towards ripe females. Hawkins and Rasmussen (1978) wrote that grunts were produced during defensive and aggressive behaviour by cod of both sexes. Those authors differentiated between escape sounds after an encounter with an aggressive cod, startle sounds when confronted with an artificial stimulus and aggressive sounds. They did not find any difference in calls produced by the cod in different contexts.

In contrast, the haddock *Melanogrammus aeglifinus* produces a range of sounds that are unusual within the family Gadidae (Hawkins and Rasmussen 1978; Hawkins 1993; Hawkins and Amorim 2000). Both male and females produce short sequences of repeated ‘knocks’ during agonistic encounters (Hawkins and Amorim 2000). Males produce series of slowly repeated knocks towards males and series of fast knocks which merge into humming towards females, both of which continued throughout the mating embrace. Females remain silent during spawning and between spawning bouts. No sex-specific difference in characteristics of grunts or knocks has been mentioned in any of these studies. Thus, differences between sexes occur exclusively during reproductive behaviour, whereby males are very vocal and females do not signal acoustically at all. This behavioural observation is supported by the sexual dimorphism of the sonic muscles (see above), indicating that females may choose males based on their vocal output and sound characteristics.

Sound production has not been described in the closely related sea hakes (family Merluciidae). Sea hakes possess sexually dimorphic sonic muscles (Groison et al. 2011). It is assumed that sound production will be similar to other members of the family Gadidae, namely that both sexes emit sound in agonistic contexts and that males become more vocal during the spawning period.

5.3.2 Ophidiiformes

Within the order Ophidiiformes or cusk-eels, sound production is known in the family Ophidiidae (cusk-eels) and in the family Carapidae (pearlfish). Sex-specific descriptions of sound characteristics are available for representatives of both families (Lagardere et al. 2005; Parmentier and Vandewalle 2005; Kever et al. 2012).

The cusk-eel *Ophidion rochei* produces sounds consisting of series of pulses differing considerably between sexes in duration, pulse number, pulse length, pulse periods and main frequencies (Kever et al. 2012). According to Kever et al. (2012), males emit much longer calls (3.5–4 s) than females (18–20 ms). Pulse duration is 12.4 ms in single and 16 ms in multi-pulsed sounds in males in captivity, but only 0.7 ms in females, with pulse numbers ranging from 2 to 13. The spectral characteristics of female sounds strongly suggest that they are harmonic, in contrast to males. The fundamental frequency of female sounds was at 246–249 Hz, and additional second and third harmonics were found. In males, main energies were located at 541 and 885 Hz in captivity and 191 and 355 Hz in the field. Despite these detailed description of sex-specific differences in sound characteristics, the behavioural contexts in which males or females produced the sounds remains unknown.

Several species of carapids have symbiotic relationships with marine invertebrates such as sea cucumbers. Sounds were regularly recorded when one individual entered a host that was already occupied (Lagardere et al. 2005). In the pinhead pearlfish *Carapus boraborensis*, sounds consisted of series of pulses whose pulse length and periods allowed sex distinction. Those authors interpreted pearlfish sound production as serving in communication between con- and heterospecifics. Such acoustic signalling was no doubt part of agonistic interactions within hosts, although behavioural observations were not reported. In males, the sound duration ranged from 3 to 5 s and in females from 3 to 15 s. Sounds consisted of a series of 10–28 pulses in males and 16–83 pulses in females. Pulses lasted on average for 83 ms in male and 136 ms in females, with a period of 181 ms in the former and 212 ms in the latter (Fig. 5.3). Pulse periods allowed discrimination between sexes. The frequencies of these sounds varied between 55 and 800 Hz, with a main

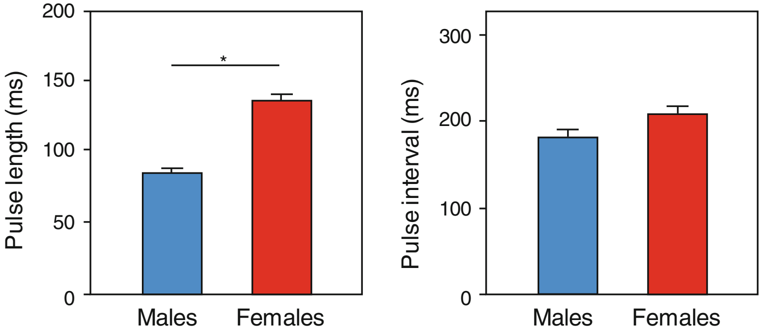


Fig. 5.3 Sound characteristics in male and female pinhead pearlfish *Carapus boraborensis*. The *asterisk* indicates a significant difference in pulse length between sexes. Redrawn after Lagardere et al. (2005). With permission from Wiley

frequency of 204 Hz in both sexes (Lagardere et al. 2005). Mature female pinhead pearlfish are larger than males and it is possible that sex-specific differences in some sound characteristics are based on differences in body size.

5.3.3 Batrachoididae

Among batrachoidids or toadfishes, both sexes obviously produce agonistic grunts, but only males emit tonal courtship sounds (boatwhistles or hums) by rapidly contracting their intrinsic sonic muscles (for a review see Amorim 2006; Ladich and Bass 2011). In the oyster toadfish *Opsanus tau*, a vocal fish species frequently chosen for acoustic studies, next to nothing is known about female acoustic signalling. It was frequently mentioned that females produce grunts in agonistic contexts, but no details have been published so far (Fish 1954; Gray and Winn 1961; Maruska and Mensinger 2009).

The plainfin midshipman *Porichthys notatus* is known for having two male reproductive morphs (type I and type II) which differ considerably in size and acoustic signalling (Brantley and Bass 1994). Type I males maintain nests and produce long-duration hums to attract gravid females, whereas type II males are sexual parasites of nest-building type I males and do not vocalise during spawning. Both male morphs and females produce short duration grunts, most likely in an agonistic context. The behavioural context has only been described in nest-holding type I males. They emitted grunts or sequences of grunts together with open-mouth threats. Brantley and Bass (1994) did not observe agonistic interactions during sound production in type II males and females directly and thus assumed that grunts were emitted similarly to type I males during agonistic encounters.

Sound characteristics of grunts differ somewhat between male morphs and females. Brantley and Bass (1994) reported that grunts were 50–200 ms in duration in type I males and that duration differed significantly between type II males (143 ms) and females (230 ms). The fundamental frequency of grunts depended on temperature but less so on the reproductive morph or on sex. In type I males, the fundamental frequency was 104 Hz at 14 °C (according to the regression equations) and 131 Hz at 20 °C, while in females and type II males it was 100 Hz at 14 °C and 141 Hz at 20 °C (Brantley and Bass 1994). No amplitude measurements are given but it was observed that the sounds were of low amplitude in females and type II males.

5.3.4 Otophysines

Otophysines are well known for their Weberian auditory ossicles, which enhance their auditory sensitivity and thus might facilitate acoustic communication (Ladich 1999, 2014). Representatives of three out of four orders (Cypriniformes, Siluriformes and Characiformes) vocalise in various contexts, mostly during agonistic interactions. Sex-specific differences have either not been described or are limited to the observation that males are the vocal sex. In studies on cypriniforms, sexes could not be distinguished (Valinski and Rigley 1981; Ladich 1988; Raffinger and Ladich 2008) or sound production was described solely in males. According to Stout (1975), only males of the satinfin shiner *Cyprinella analostana* (formerly *Notropis analostanus*; family Cyprinidae) emit knocking sounds during agonistic encounters and purring sounds during courtship. This difference between sexes could either be due to a complete absence of acoustic signals in females or because females were not specifically investigated. A comparison of sonic organs between sexes is not possible within cypriniforms (>3,000 species) because sound-generating mechanisms have never been described convincingly in this order. Delco (1960) claimed that only females produce sounds in *Cyprinella lutrensis* and *C. venusta* (formerly *Notropis lutrensis* and *N. venustus*). Stout (1975), based on his own investigation in the genus *Cyprinella*, argued that Delco's observations were unconvincing because he presented no evidence as to how he determined which sex made the sound.

Among siluriformes (catfishes), vocalising was seldom described during social behaviour. Most studies investigated the production of distress sounds when fish were hand-held; in this otophysine order, sexes were typically indistinguishable (Pfeiffer and Eisenberg 1965; Ladich 1997). Armoured catfishes (family Callichthyidae) seem to be one exception. Males of the armoured catfish *Corydoras paleatus* emitted trains of pectoral stridulation sounds during courtship and during dyadic encounters but did not behave aggressively towards each other (Pruzsinzsky and Ladich 1998). No sounds could be recorded in females and juveniles during social interactions. In contrast to social interactions, both sexes and juveniles emitted single sounds in distress situations when hand-held. Nonetheless, differences in sound characteristics between sexes were small and were mainly based on body size (Table 5.1). In this species, the sound duration was positively correlated to relative length of the pectoral spine, and the dominant frequency was negatively correlated with body mass (Fig. 5.4). As females are larger than males, the

Table 5.1 Means (±S.E.) of distress sound characteristics in *Corydoras paleatus*

Sound characteristic	Males	Females	Juveniles
Sound duration (ms)	19.9 ± 1.4[a]	15.7 ± 1.3	13.6 ± 1.0
Number of pulses	8.0 ± 0.6	7.5 ± 0.9	7.9 ± 0.8
Pulse period (ms)	2.6 ± 0.2	2.7 ± 1.4	2.1 ± 0.7
Dominant frequency (Hz)	1,466 ± 36[b]	1,235 ± 44	4,082 ± 20

Superscripts indicate significant differences between groups

[a] Males and juveniles differ significantly in sound duration

[b] Both sexes and juveniles differ significantly in dominant frequency. From Pruzsinszky and Ladich (1998)

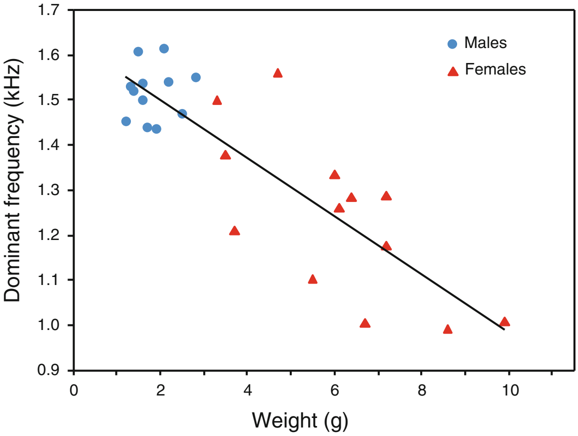


Fig. 5.4 Correlation between body weight and dominant frequency of stridulation sounds in male and female *Corydoras paleatus*. Regression equation: frequency = 1631 – 64.7 * weight. Modified after Pruzsinszky and Ladich (1998). With kind permission from Springer Science and Business Media

dominant frequency was significantly lower in females (Table 5.1). Vocalising behaviour differs considerably within the callichthyid family. In contrast to *C. paleatus*, both sexes of *M. thoracata* vocalise during agonistic encounters. Males produced low-frequency harmonic barks at longer distances and thumps at close distances, whereas females emitted broadband pulsed crackles at close distance. Female aggressive sounds were significantly shorter than those of males and had a higher dominant frequency (Hadjiaghai and Ladich 2015).

5.3.5 Scorpaeniformes

Within the order Scorpaeniformes (mail-checked fishes), sound production is known in several families, in particular in the families Scorpaenidae (rockfishes),

Table 5.2 Number of single-knock sounds (first number) and growls (second number) emitted by two males and a female *Cottus gobio* in each of the four aquarium tanks during 18 h of observation. After Ladich (1989)

	Tank 1	Tank 2	Tank 3	Tank 4	Total
Large male	523/53	555/24	399/32	1,209/3	2,798
Small male	387/41	460/29	251/102	123/41	1,434
Female	46/46	0/0	25/0	46/3	166

Triglidae (searobins and gurnards) and Cottidae (sculpins). Sexes have not been distinguished in studies on sound production in scorpaenids and triglids, which indicates that both sexes behave similarly and vocalise during agonistic encounters, in particular when foraging for food (Miyagawa and Takemura 1986; Amorim and Hawkins 2000; Amorim et al. 2004a, b).

In contrast, sound production during agonistic encounters has been described in detail in male and female river bullhead *Cottus gobio* (Cottidae) (Ladich 1989). Both sexes produce single-knocking sounds or trains of knocks termed growls, with main energies located between 50 and 500 Hz, when defending their territories. Sculpins behaved aggressively throughout the year at different temperatures and light conditions. The ability to produce sounds did not differ between sexes but males emitted significantly more sounds (Ladich 1989) (Table 5.2). The main reason for the different vocalising activity between sexes was the size difference. Females were smaller than males and typically unable to defend territories successfully (Ladich 1990). The number of sounds produced was significantly correlated to the number of encounters won (Fig. 5.5). If females were larger than males, they could also defend a territory successfully and threaten away intruding males (Ladich 1990).

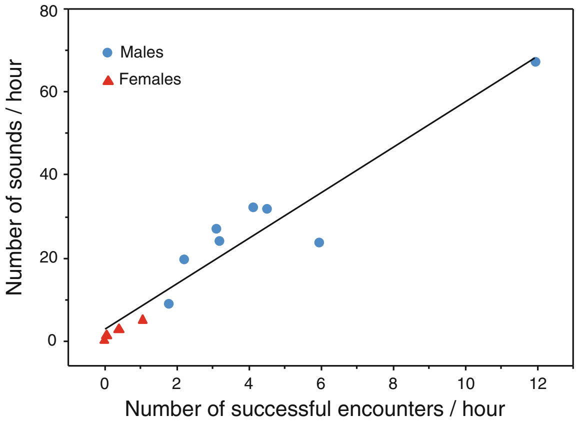


Fig. 5.5 Correlation between number of sounds emitted per hour and number of encounters won per hour in male and female *Cottus gobio*. Regression equation: number of sounds emitted = 2.89 +5.48 * number of won encounters. Modified after Ladich (1990). With permission from Wiley

5.3.6 Perciformes

Within the most species-rich fish order Perciformes (perches), numerous families are known to possess sound-generating mechanisms and produce sounds in various contexts. Well-known sound producers are found within the families Serranidae (sea basses), Sciaenidae (drums or croakers), Terapontidae (tiger perches), Centrarchidae (sunfishes), Cichlidae (cichlids), Pomacentridae (damselfishes), Gobiidae (gobies) and Osphronemidae (gouramis) (for reviews see Ladich and Myrberg 2006 and Myrberg and Lugli 2006). The most detailed description of sex-specific differences in acoustic signalling is given for osphronemids.

5.3.6.1 Serranidae—Sea Basses

Within serranids, sound production has been described by Lobel (1992) in the butter hamlet *Hypoplectrus unicolor*. *H. unicolor* is a simultaneous hermaphrodite and each individual of a pair alternates sex roles during matings. Each sex role produces a particular sound type. Before mating, the individual which spawned as a male emitted a courtship call. It consisted of a series of pulses with an overall duration of 0.2–1.2 s and a dominant frequency of 500 Hz. The individual releasing the eggs and thus mated as a 'female' produced a bipartite sound. The first part was a short frequency modulated tonal sweep (600–200 Hz) and the second part a long-duration broadband noise (350–1,600 Hz). No further details on the differences in sound characteristics were given.

5.3.6.2 Sciaenidae—Drums or Croakers

In sciaenids, different degrees of sexual dimorphism in swim bladder drumming muscles in particular during the breeding season indicate that males are more vocal than females in the reproductive context. Nonetheless, the presence of sonic muscles in females of several drum species indicates that they produce sounds too, although the behaviuoral context is less clear in this family. Takemura et al. (1978) mentioned differences in fundamental frequencies of male and female sounds in two species of Japanese drums. The fundamental frequencies were higher in males of the Koichi *Nibea albiflora* (males 668 Hz, females 334 Hz) as well as in the Shiroguchi *Pennahia argentata* (formerly *Argyrosomus argentatus*) (males 457 Hz, females 267 Hz).

A detailed analysis and comparison of male and female sounds is given by Ueng et al. (2007) for the Japanese croaker *Argyrosomus japonicus* A. japonicus. produced pre-spawning advertisement calls which could be recorded from males and females in single-sex groups and spawning calls during actual spawning. Ueng et al. (2007) stated that both sexes emitted advertisement calls before and longer calls during spawning together with regular croaks. Males seemed to be vocally

Table 5.3 Mean (±S.D.) characteristics of advertisement calls emitted by male and female *Argyrosomus japonicus* in single-sex groups during the spawning season

Call characteristics	Males	Females	Significance
Duration (ms)	231 ± 65	316 ± 62	*
Number of pulses/call	10.5 ± 3.0	15 ± 3.2	*
Pulse length (ms)	13 ± 2	10 ± 1	*
Pulse interval (ms)	11 ± 1	14 ± 1	*
Dominant frequency (Hz)	686 ± 203	587 ± 190	*

Asterisk indicates significant differences between sexes. * $p < 0.01$. From Ueng et al. (2007)

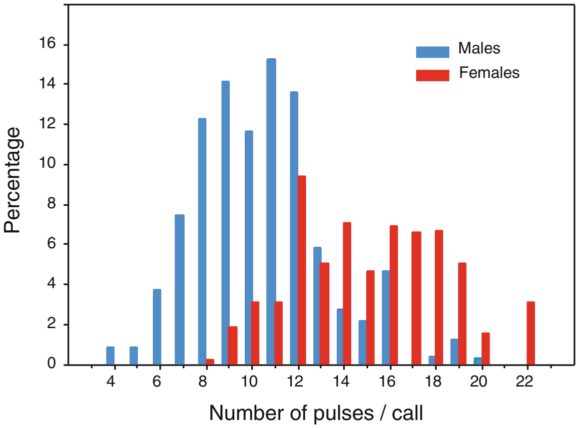


Fig. 5.6 Sex-specific differences in sound characteristics in the sciaenid *Argyrosomus japonicus*. Comparison of the percentage and the number of pulses per advertisement call is shown. Calls were recorded in two single-sex tanks. Modified after Ueng et al. (2007)

more active under pre-spawning conditions. All characteristics of male and female advertisement calls differ from each other significantly. Female sounds are longer, have a higher number of pulses, a longer pulse-interval, a shorter pulse duration and a higher dominant frequency (Table 5.3; Fig. 5.6). Differences in advertisement sound characteristics were not due to size because sexes did not differ in body length. Ueng et al. (2007) argued that, according to Sprague (2000), thinner female sonic muscles should generate a weaker tension, which may be related to the lower frequency of sounds, independent of body size.

Japanese croakers seem to be the only fish species in which both sexes produce advertisement and spawning calls during reproductive behaviour. However, observations on the courtship behaviour of males and females are not detailed enough to definitively support this notion. In particular it remains to be clarified whether chasing observed by the authors cannot be regarded as agonistic behaviour and whether vocalisations are not uttered (partly) in agonistic contexts. Ueng et al. (2007) discuss that additional experiments are necessary to determine if spawning calls are emitted by one or both sexes.

5.3.6.3 Cichlidae—Cichlids

Sound production has been described in numerous cichlid species but, in contrast to sciaenids, sound-generating mechanisms are largely unknown and no sexual dimorphism has been mentioned in any species so far (see Chap. 3). Analyses of sound production within this family reveal a rather uniform pattern of the vocalising behaviour (Amorim 2006). In general, both sexes or just one sex produce sounds during aggressive interactions such as territory or brood defence. Only males emit sounds during courtship.

Myrberg et al. (1965) reported that both sexes of the juwelfish *Hemichromis bimaculatus* emit pulsed 'br-r-r' sounds in agonistic contexts (around 35 pulses/s, dominant frequency 400 Hz). Females produce far more sounds than males during the parental period before attacking, in particular when confronting conspecific intruders. Sound production increased during egg incubation, peaked during development of larvae and decreased when young became free-swimming. The female also vocalised during courtship while aggressively 'holding ground' against the male after he had attempted to bite or ram her. Male *H. bimaculatus* emitted br-r-r sounds during aggressive situations in early courtship and during the parental period and 'thump' sounds during the early stages of fights with conspecific males. No sounds were heard from the species during non-aggressive courtship, spawning or fanning eggs or taking care for the young. Interestingly, Myrberg et al. (1965) observed that male convict cichlids *Amatitlania nigrofasciata* (formerly *Cichlasoma nigrofasciata*) never produced sounds during fights. Sounds were most often recorded when a female was 'holding ground' while being attacked by a male. Br-r-r sounds were similar to *H. bimaculatus* but of higher frequency (480 Hz) and lower pulse repetition rate (20 per second). No sounds were heard during courtship and there was no evidence that males produced sounds. Similarly, parents of the freshwater angelfish *Pterophyllum scalare* defended their broods against conspecific intruders emitting 'tzz-tzz' sounds. The sex of the vocaliser could not be determined in the study by Myrberg et al. (1965). Similarly, Schwarz (1980) reported that in the flier cichlid *Archocentrus centrarchus* (formerly *Cichlasoma centrarchus*) that both sexes produced sound during the breeding cycle but all sounds were aggressive in context. The absence of courtship sounds in earlier studies contradicts subsequent studies which frequently showed that males of several cichlid species emit sounds during courtship. It remains to be analysed if this discrepancy is based on differences between genera or is due to different interpretations of agonistic and courtship behaviour (Amorim et al. 2003, 2004a, b; Simoes et al. 2008; Maruska et al. 2012).

In contrast to the potential difference in male behaviour, vocal behaviour in females is rather constant. All studies on females showed them to be very vocal during aggressive behaviour, in particular after spawning and when defending their brood; they did not, however, vocalise during courtship. Simoes et al. (2008) analysed courtship in males and agonistic sounds in both sexes of the zebra mbuna *Maylandia zebra* (formerly *Pseudotropheus zebra*). Sounds were generally produced during agonistic quivers in male–male and female–female encounters. Male

Table 5.4 Mean (±S.D.) characteristics of sounds emitted by male and female *Maylandia zebra* during male–male and female–female agonistic interactions

Sound characteristics	Males	Females	Significance
Duration (ms)	960 ± 295	524 ± 153	*
Number of pulses/sound	8.7 ± 3.48	4.9 ± 0.99	*
Mean pulse period (ms)	125.7 ± 23.91	123.8 ± 27.06	*
Peak frequency 1 (Hz)	138.0 ± 14.97	143.1 ± 6.72	ns
Peak frequency 2 (Hz)	462.9 ± 35.40	480.2 ± 29.14	ns

* $p < 0.01$. After Simoes et al. (2008)

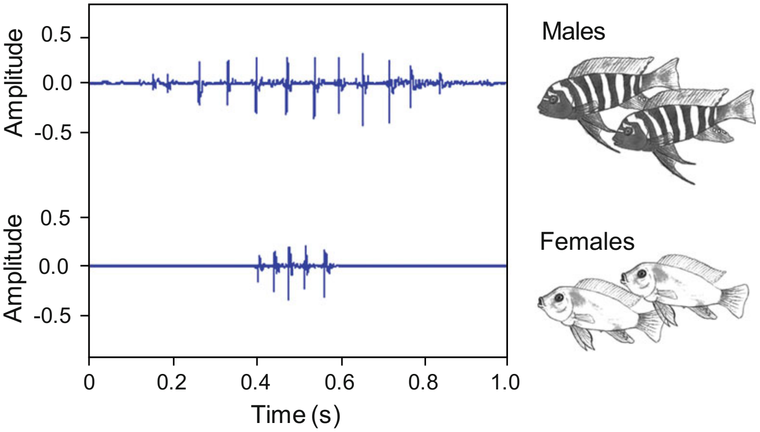


Fig. 5.7 Oscillograms of sounds produced by male and female *Maylandia zebra* during intrasexual agonistic quivering behaviour. Modified after Simoes et al. (2008). Reprinted with permission from the Acoustical Society of America

and female sounds differed in all temporal characteristics but not in the spectral content (Table 5.4). Male sounds were longer due to the higher number of pulses (Fig. 5.7). Courting male sounds showed shorter pulse periods than agonistic sounds of both sexes.

5.3.6.4 Gobiidae—Gobies

Within the large and ubiquitous family Gobiidae, comprising approximately 2,000 species, vocalisations are known in approximately two dozen species. In general, sound production has been described in males during courtship and mating (Lugli et al. 1997). Nevertheless, sounds are also emitted during agonistic encounters, but this behaviour has seldom been investigated. In a few cases, females were briefly mentioned as producing sounds during agonistic interactions. Kinzer (1960) noted sound production in the female *Gobius niger* (formerly *Gobius jozo*) and Ladich and Kratochvil (1989) in the tubenose goby *Proterorhinus marmoratus*. Male *P. marmoratus* emitted short (240–260 ms) harmonic sounds with fundamental frequencies between 70–130 Hz. Female sounds were detectable but could not be analysed due to their low levels. Protasov et al. (1965) mentioned that males of round goby *Neogobius melanostomus* produced the low-frequency courtship sounds and females in contrast high-frequency squeaking sounds. No further details on female sounds are available in any of these studies.

5.3.6.5 Pomacentridae—Damselfishes

Pomacentrids are perhaps the most important fish family in terms of the diversity of behavioural data gained in the field. Besides others, Myrberg and colleagues investigated female mate choice based on male sound characteristics (Myrberg et al. 1986), and individual recognition (Myrberg et al. 1985) and species recognition based on temporal patterns of acoustic signals (Myrberg and Spires 1972). Nevertheless, all sounds described and played back in the genus *Stegastes* were recorded from males. Myrberg (1972) mentioned in his monography on the bicolor damselfish *Stegastes partitus* (formerly *Eupomacentrus partitus*) that pop sounds are produced by both sexes. Similarly, Maruska et al. (2007) reported that only males of the Hawaiian sergeant damselfish *Abudefduf abdominalis* produced sounds during aggression, nest preparation and courtship.

Several studies analysed agonistic behaviour and vocalisations in clownfish (genus *Amphiprion*). While investigators described the existence of several sound types, the sexes were not distinguished in any study (Schneider 1964a; Chen and Mok 1988; Amorim 1996). Schneider (1964a) observed that both the yellowtail clownfish *Amphiprion clarkii* (formerly *A. xanthurus*) and the saddleback clownfish *A. polymnus* produced three different sounds types when fighting for anemones. Clownfish attacks were accompanied by 'fighting sounds' and 'threatening sounds', while the attacked individual often responded by producing 'shaking sounds'. Similarly, Chen and Mok (1988) described aggressive sounds in *A. clarkii* and in the tomato clownfish *A. frenatus*. As clownfish are protandrous hermaphrodites and the larger sex typically defends anemones, it can be assumed that mainly female clownfish vocalise during nest defence. In fact, Moyer (1980) observed that resident female *A. clarkii* attacked intruders with aggressive staccato rattling. Nevertheless, it would be interesting to determine the extent to which female and male clownfish vocalise and differ in their acoustic signals.

Only Mann and Lobel (1998) described sound production in males and females of damselfish. They observed that both sexes of the domino damselfish *Dascyllus albisella* made aggressive sounds. Less surprisingly, only male *D. albisella* emitted sounds during courtship behaviour.

5.3.6.6 Osphronemidae—Gouramis

The most comprehensive description of sex-specific differences in vocal behaviour is found in the osphronemid genus *Trichopsis*. Both sexes of the croaking gourami *T. vittata* and of the three stripe gourami *T. schalleri* produced croaking sounds during agonistic encounters (Marshall 1966; Ladich et al. 1992; Schleinzer 1992; Ladich 2007). Females of the pygmy gourami *T. pumila* seldomly emitted sounds, most likely because of their less-developed sonic apparatus compared to those of congenerics (Kratochvil 1985) (see Fig. 5.2).

Ladich (2007) investigated sound production during agonistic and mating behaviour in *T. vittata*. Agonistic behaviour and the sounds produced are similar in both sexes, probably reflecting their similar sound-generating apparatus (Kratochvil 1985) (see Fig. 5.2). Agonistic interactions between two males, two females (or a male and a female) consisted of spreading the unpaired fins and vigorous head-to-tail circling (Fig. 5.8a). This behaviour was generally accompanied by the alternate production of croaking sounds, recognisable by rapid pectoral fin beating. No obvious difference could be discerned between sexes in this lateral displaying behaviour. During this stage of the conflict, the opponents did not physically contact each other. Mating behaviour started after a male built a bubble nest under a floating plant. Females approached a male, adopted a vertical head-up position and started to undulate their body while rapidly beating their pectoral fins, thereby producing a purring sound (Fig. 5.8b). This behaviour was followed by spawning, during which the male wrapped his body tightly around the female, turning her on her back while she released eggs. Only females vocalised during pre-spawning behaviour (Ladich 2007).

All sounds produced by croaking gouramis were built up of a series of bursts consisting of either one or two pulses (Fig. 5.9a, b). Agonistic sounds consisted of approximately five, mostly long double-pulse bursts, whereas female mating sounds had fewer bursts and a higher percentage of single-pulsed bursts (Fig. 5.10) (Ladich 2007). The time between the onset of two consecutive bursts, the burst period, was 5 ms longer in female agonistic sounds than in female pre-spawning sounds, whereas the agonistic sounds burst period did not differ from that in males. The mean dominant frequency was lower in male croaking sounds than in female mating sounds but did not differ between female sound types (Fig. 5.11a). The sound intensity was sex- and context-dependent. Male agonistic sounds were loudest, whereas the female purring sound had the lowest sound pressure level (Fig. 5.11b). The differences between dominant frequencies and sound pressure levels were not due to differences in size. Neither body weight nor standard length differed between sexes (Ladich 2007).

In summary, *T. vittata* shows no or only minor differences between sexes in the duration, temporal patterns and spectral content of acoustic signals produced in the agonistic context. Only sound levels were higher in males, probably due to their larger sonic muscles and tendons. *T. vittata* is apparently the only known fish species in which females produce sounds during courtship and mating, making it unique among fishes. Differences in acoustic characteristics between contexts

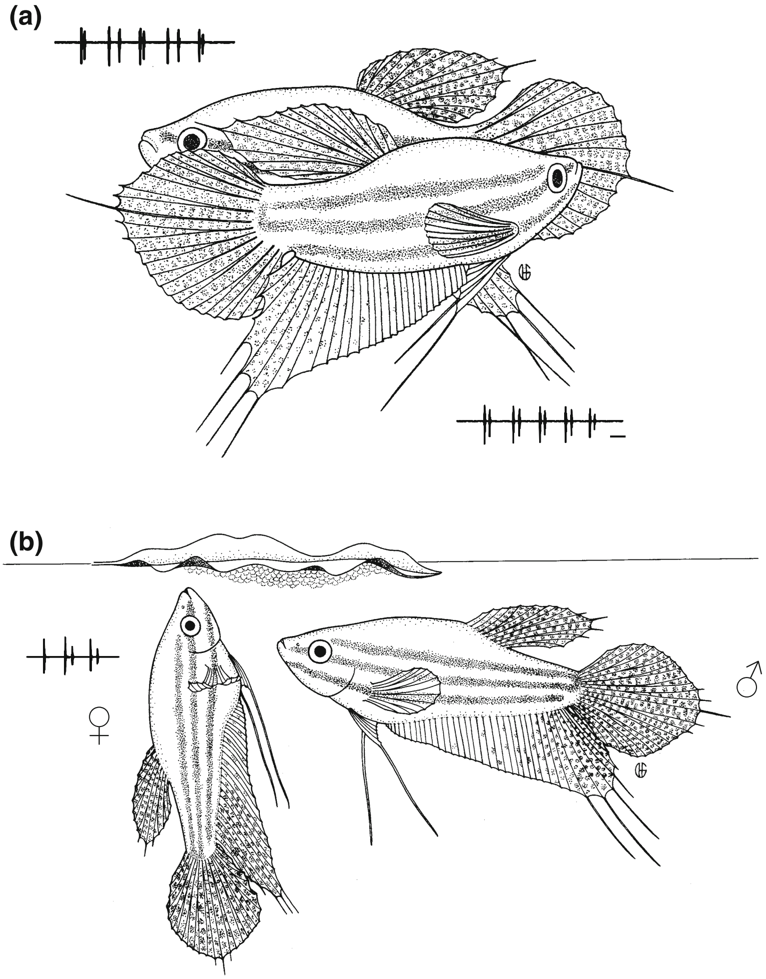


Fig. 5.8 Agonistic and reproductive behaviour in *Trichopsis vittata*. **a** Lateral displaying by two fighting males. Inserts show oscillograms of croaking sounds produced by both opponents alternately. From Ladich (2004). **b** Mating behaviour: the female (*left*) assumes a vertical head-up position and generates purring sounds while the male (*right*) hovers in a horizontal position beneath its bubble nest. The insert shows an oscillogram of purring sounds. From Ladich (2007). With permission from Elsevier

indicate that different receivers are being addressed. Loud and long agonistic sounds may help assess the fighting ability of territory owners and thus help to avoid escalation of fights. In contrast, short, less conspicuous pre-spawning signals of lower amplitude should avoid interception by conspecifics and help to synchronise the spawning activity (Ladich 2007). A parallel development of two different sound types was observed in the damselfish *S. partitus*, except that both

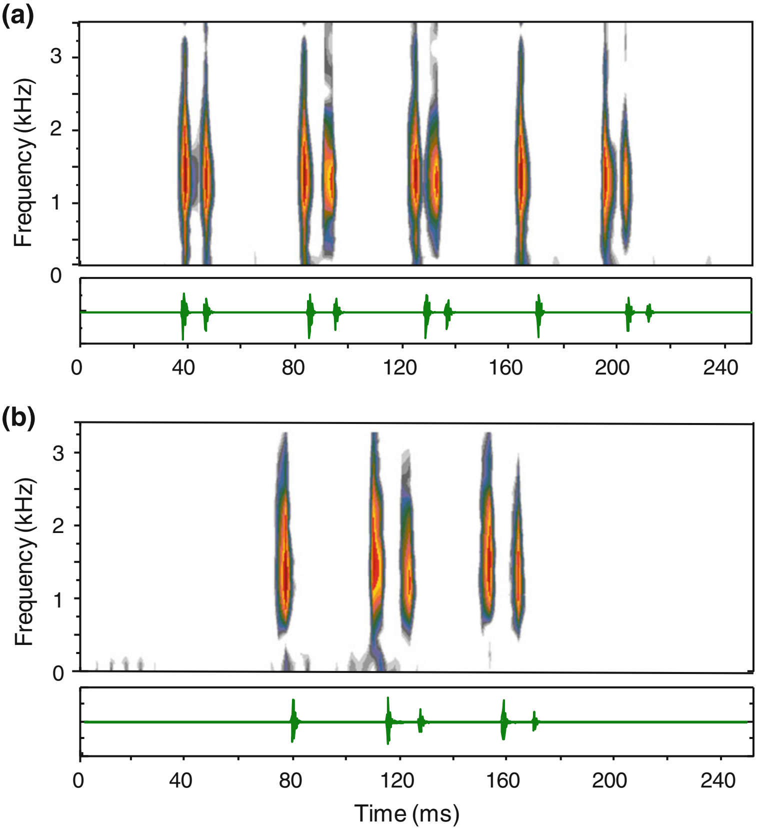


Fig. 5.9 Sonogram and oscillogram of **a** a croaking sound and **b** a purring sound. The croaking sound consists of five (four long, double-pulsed and one single-pulsed burst) and the purring sound of three bursts (one short, single-pulsed and two long, double-pulsed bursts). Modified after Ladich (2007). With permission from Elsevier

sound types—the loud advertisement chirp sound and the low-level grunt prior to spawning—were produced by males. This, however, raises the question why only female *T. vittata* are vocal during mating. This behaviour has either been overseen in other fish species due to a male-biased research approach or it is based on the unique biology of this species. One explanation for the difference between croaking gouramis and most other fish species might be that *T. vittata* is apparently monogamous. Although females are expelled from the nest vicinity after spawning, they regularly defend the nest site against conspecifics and occasionally pick up fry to bring them back to the nest (Ladich 2007). This represents a type of female nest and brood care in *T. vittata* which differs from cichlids and most other fish taxa.

In *T. schalleri*, aggressive sounds differed between sexes primarily in their temporal characteristics. Female sounds consisted of half as many bursts as male sounds (average 4 bursts versus 8) and burst periods were much shorter in females.

Fig. 5.10 Mean (+SE) number of bursts of male and female agonistic sounds and of female mating sounds. Different letters indicate significant differences between sexes and sound types. Modified after Ladich (2007). With permission from Elsevier

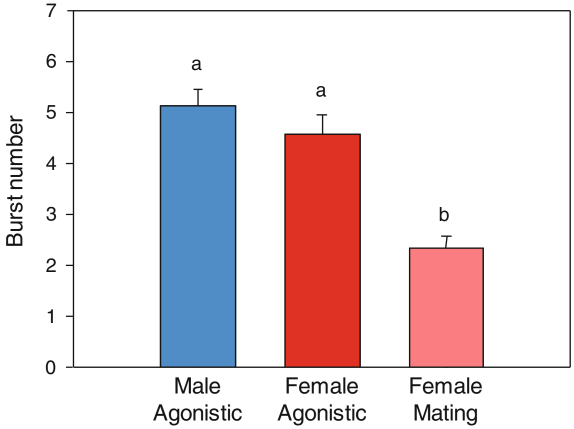
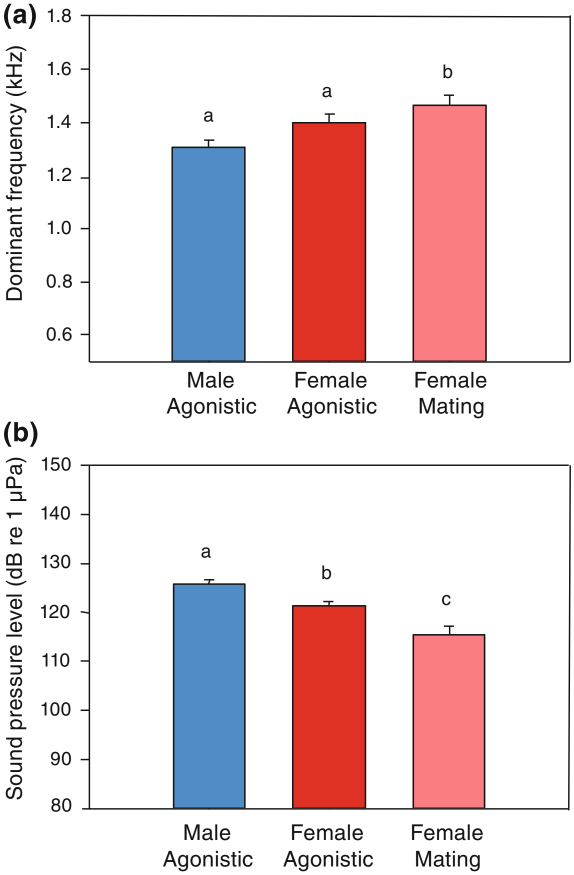


Fig. 5.11 Mean (+SE) **a** dominant frequency and **b** sound pressure level of male and female agonistic sounds and female mating sounds. Different letters indicate significant differences between sexes and sound types. Modified after Ladich (2007). With permission from Elsevier



Thus, female sounds were shorter and had a lower sound pressure level than male sounds (112.7 dB versus 118.2 dB) but they did not differ in dominant frequency (Schleinzer 1992). Mating behaviour has not been studied in this species.

5.3.7 Miscellaneous

It is assumed that females of many more perciform families emit sounds during agonistic behaviour, but data are sparse and insufficient to prove this assumption. Gerald (1971) mentioned that it is unknown if female centrarchids (sunfishes) produce sounds. Schneider (1964b) described threatening and drumming sounds in juvenile terapontids (tiger perches) without mentioning any sex-specific behaviour.

5.3.8 Gasterosteiformes

5.3.8.1 Syngnathidae—Seahorses

Seahorses produce clicking sounds in various behavioural contexts such as introduction into a new environment, during feeding and courtship. Anderson (2009) showed that both sexes of the lined seahorse *Hippocampus erectus* (family Syngnathidae) emitted clicks during courtship; these clicks may help to maintain reproductive pairs and identify sexually mature partners. Chakraborty et al. (2014) mentioned that males and females of the yellow seahorse *Hippocampus kuda* differed in the main energies of their feeding clicks. Peak frequencies of males covered a broader frequency range (1–4 kHz) than that of smaller females (1–2 kHz). This effect seems to be caused by size differences between sexes. Oliveira et al. (2014) showed that both sexes of the longsnout seahorse *Hippocampus reidi* produced clicks during feeding and courtship and previously undescribed growls in distress situations when animals were hand-held. Males and females were of similar size in their study and did not differ in most sound characteristics measured (pulse durations, pulse periods, dominant frequencies, sound pressure levels) except one: males produced louder courtship clicks than females.

5.4 Conclusion

A large gap exists in our knowledge of female sound production in fish. In order to close this gap, investigators need to put more emphasis on studying sound production in both sexes. It is quite unlikely that females of solely one out of 30,000 extant species vocalise during reproductive behaviour.

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Chapter 6
Habitat Acoustics and the Low-Frequency Communication of Shallow Water Fishes

Marco Lugli

Abstract Many teleosts known to produce sounds during territorial and breeding activities live in coastal, transitional, or freshwater habitats characterised by shallow, or very shallow, water. The variability of ambient noise levels and the complexity of sound propagation conditions make acoustic communication in such environments problematic, especially at lower frequencies. Yet, use of low frequencies for communication (sound signals and hearing) is common among these species (e.g. toadfishes, gobies, blennies, darters, sculpins). This chapter examines the relationships between environmental factors and the sound emitted by shallow water teleosts, focusing in particular on the role of the calling site and ambient noise for the sound frequencies employed for communication. Two ecological factors, nest site acoustics and noise windows, appear to favour the use of low-frequency sounds by teleosts living in shallow noisy habitats by providing higher signal-to-noise (S/N) ratios for communication. The final part of the chapter examines the variety of fish audiograms and emphasises the importance of ambient noise as a possible main environmental factor shaping the auditory sensitivity, especially among shallow water fishes. A theoretical argumentation is provided to explain how this would be accomplished.

6.1 Overview

Habitat acoustics concerns the study of the acoustic characteristics of the environment that affect the production, transmission, and reception (detection and recognition) of the sound emitted by a species in a given habitat. The way the acoustical environment affects the three stages of the acoustic communication process is examined to determine the type of environmental constraints and infer long-term (evolutionary) effects on sound and receptor systems. For instance, sound

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attenuation (spreading loss and absorption), degradation, and ambient noise may act as environmental constraints on acoustic communication (Wiley and Richards 1982). These factors are thought to be important for the evolution of long-distance vocalisations (the 'Acoustic Adaptation Hypothesis' of bird songs, Morton 1975, reviewed in Boncoraglio and Saino 2007), and may affect the detection and recognition of sounds. Evidence for the effects of environmental factors on acoustic signals and receptor systems has been provided for many terrestrial species, especially among birds and mammals (Bradbury and Vehrencamp 1998). For example, ambient noise (including mad-made noise) has been suggested to be a major constraint on the evolution of frequencies used in acoustic communication among birds and primates (e.g. Wiley and Richards 1982; Waser and Brown 1986; Slabbekoorn and Peet 2003; reviewed in Brumm and Slabbekoorn 2005; Brumm and Zollinger 2013).

Teleosts have the most diverse sound-producing mechanisms and hearing abilities, and live in a wider array of environments than other vertebrate groups. Yet, the relationships between the environmental constraints and sound communication are less understood than in land vertebrates. Three major reasons are the low accessibility for experimental investigation (for both technical and practical reasons; Myrberg 1996), the secretive, context-specific nature of fish sound production often characterised by low emission amplitudes (with some relevant exceptions, e.g., the midshipman humming sound; Bass 1990), and the acoustical complexity of the aquatic environment (Rogers and Cox 1988). Furthermore, although the sound-producing capability of certain fish species has long been recognised since the time of Aristotle, up until a few decades ago it was still questioned whether sound emission had any real functional significance for fish life. Consequently, the study of fish acoustic communication and the environmental pressures acting on it has lagged well behind that of land vertebrates.

In an influential paper on the physics of underwater sound propagation and detection by aquatic animals, Roger and Cox (1988) showed that general features of the fish sound production and hearing cannot be predicted by considerations simply based on the physical characteristics of the environment. For instance, sound pressure is much higher in water compared to air (about 60 times; Albers 1965) for a given value of the sound intensity. Therefore, the sensitivity to acoustic sound pressure typical of land vertebrates should also be a property of the fish ear. In fact, most fishes can detect only the particle displacement components associated with the sound wave (Kalmijn 1988; Roger and Cox 1988). Also, underwater ambient noise is highest at lower frequencies (Albers 1965). Thus, fishes should communicate acoustically using preferentially high frequencies. Another environmental constraint on the use of low frequencies for fish communication is represented by water depth because low frequencies cannot propagate in shallow waters (see below). Yet, available evidence indicates that many teleosts from the most diverse habitats, and especially those living in shallow environments (e.g. coastal areas, rivers, ponds), employ very-low–frequency sounds for territorial and mating purposes (e.g. Ladich 1989; Myrberg and Lugli 2006). Most knowledge of fish acoustic communication comes indeed from studies on the vocal behaviour of these shallow-water species (Fine et al. 1977; Ladich and Myrberg 2006; Myrberg and Lugli 2006). Because of its relevance for fish bioacoustics, the issue of low-frequency acoustic communication and possible relationships with habitat acoustics is thoroughly examined in the chapter. Before focussing on these topics, however, a few notes on acoustical features of the water medium and underwater sound transmission are necessary.

6.2 A Glimpse of Underwater Environment Acoustical Features Constraining Sound Propagation

The physics of sound propagation and the basic principles governing the interaction of sound with the physical environment are the same in air and in water (Albers 1965). However, the high density and low compressibility of water compared to air have important consequences regarding transmission of sound and acoustic information in aquatic environments. For instance, compared to air, a propagating sound wave travels faster (about five times) and with little absorption underwater. This bears two contrasting consequences for acoustic communication by aquatic animals. The sender of the sound may potentially extend the range of signal active space to distances not covered by sounds travelling in terrestrial environments (baleen whales are able to communicate acoustically over hundreds or even thousands of miles using low-frequency vocalisations). On the other side, the listener is easily, and often, exposed to a variety of noises generated by close and distant abiotic and biotic sources. Thus, an individual attending a sound relevant for fitness or survival is often faced with the problem of extracting the relevant information of the signal embedded in noise of changing and unpredictable form. When the sound is transmitted close to reflecting boundaries (i.e. air–water, water–bottom interfaces) further problems arise because direct and reflected paths of the sound may add or subtract, yielding fluctuations in the received sound level and introducing reverberations (Hawkins and Myrberg 1983; Spiesberger and Fristrup 1990). Thus, the effects of multipath propagation of the sound are prominent close to reflective surfaces (e.g. a sandy or rocky bottom) or in shallow habitats (coastal areas, small rivers, backwaters, ponds etc.), where most soniferous teleosts breed and interact acoustically (Hawkins and Myrberg 1983). For instance, the measurement of propagation of damselfish courtship sounds (*Dascyllus albisella*, Pomacentridae) conducted in a shallow reef environment revealed major alterations of spectral and temporal sound parameters at only a few metres from the source (Mann and Lobel 1997). Multipath propagation and signal degradation are not the only constraints on sound communication in shallow water. When the water depth is approximately one fourth the wavelength of the sound, the environment acts as a high-pass filter by allowing propagation only of frequencies above the critical frequency, that is, the frequency cutoff phenomenon (Officier 1958; Rogers and Cox 1988; Chap. 3, this volume). The value of the cutoff is also affected by bottom composition, being lower for hard substrates such as rocky or stony bottoms (Rogers and Cox 1988). Therefore, in shallow environments sound propagation becomes increasingly complex and strongly frequency and site dependent.

6.3 The Puzzling Paradox of Low-Frequency Communication of Shallow-Water Fishes

Soniferous fishes inhabit a variety of environments, from deep and open waters of oceans and lakes to very shallow streams and creeks, and emit sounds under different behavioural contexts (territory defense, mate attraction, distress, or antipredator reactions, etc.) and circumstances (alone in the nest or in aggregation, during schooling or chorusing, at dusk, etc.). However, a large number of species, including many of those spending most of their lifetime in deeper waters (e.g. the midshipman, *Porichthys notatus*), emit sounds mainly during reproductive activities taking place at breeding sites located near, or on, the bottom at shallow depths. Some of these species (e.g. majority of cyprinids) are substratum egg-scatterers and do not defend nest sites or care for eggs. Others, like many cichlids, lay demersal eggs on prepared surfaces that one or both parents defend. Still others spawn inside nest cavities (a hollow under a hard submerged object, a hole between rocks, etc.) and care for eggs. Examples of the latter group are numerous and include members of several teleost families, such as gobies, toadfishes, blennids, cottids, and darters, comprising mainly bottom-dwelling species. Nest sites of these species are often found in very shallow waters (depths of 1–2 m or less), for example, small rivers, streams, ponds, or coastal waters of lakes and sea, with complex bottom topography (presence of stones, boulders, changing slope conditions, etc.), and variable substrate composition. These environments are often characterised by high levels of low-frequency background noise (below) and/or short-range transmission of low-frequency sounds due to the frequency cutoff. Therefore, the finding that teleosts from shallow habitats produce sounds and have best hearing at frequencies well below 0.5 kHz is somewhat paradoxical (e.g. Fine et al. 1977; Myrberg 1981; Hawkins and Myrberg 1983; Fay and Popper 1999; Fig. 6.3; see review Ladich and Fay 2013). The presence of physiological constraints or short-range communication constitutes suggested explanations for the paradox (Fine and Lenhardt 1983; Bradbury and Vehrencamp 1998; Lugli and Fine 2003, 2007). The acoustic communication of the stream goby represents a case in point. Two small gobies, *Padogobius bonelli* (formerly, *P. martensii)* and *Gobius nigricans*, living in very shallow streams, respectively, in northern and central Italy, emit sounds with main frequencies in the 80–200 Hz band (Lugli et al. 1995, 1996b, 2003). These frequencies are well below the cutoff frequencies of the stream (0.8 kHz for water depth of 50 cm, over a rigid bottom; Officer 1958). Indeed, sound transmission measurements in the stream showed the level of the courtship sound of *P. bonelli* (Lugli and Fine 2007) attenuated by 15–20 dB over 20 cm (at a depth of 50 cm).

The effects of the high transmission loss in the field, the low sound amplitude (90–120 dB at 5–10 cm; Lugli et al. 1995, 2003), and low auditory sensitivity of *P. bonelli* and *G. nigricans* (see below) combine to restrict acoustic communication in these species to only a few decimetres from the emitter. Nonetheless, playback sounds of *P. bonelli,* when broadcast in small laboratory tanks, are capable of attracting conspecific receivers (aroused males and ripe females) as far as 40 cm away from the speaker (Lugli et al. 1996a, 2004). Results of a field study showed distance between nests of *P. bonelli* in the stream averaged about 60 cm (Lugli et al. 1992), and females were often found interspersed among male territories. Furthermore, laboratory observations showed most sounds are emitted by the territorial male goby close to the intended receiver (a ripe female or a rival male) after the latter has been visually or chemically detected (Torricelli et al. 1986; Lugli et al. 1996a, 2004). Thus, there is probably no need for long-distance acoustic communication in these species. Acoustic communication over short distances is not unique to gobies. Many other teleosts (cichlids, damselfishes, sculpins, gouramies, blennies, other gobies) emit vocalisations only after a nearby conspecific has been detected. Propagation distances of these sounds may vary from decimetres to few metres, but are unlikely to exceed 9–10 m (reviewed in Ladich and Bass 2003; Mann 2006) even under the most favourable environmental conditions (presence of low ambient noise levels, main sound frequencies above the cutoff; Crawford et al. 1997; Mann and Lobel 1997). Curiously, low-frequency vocalisations are also used by a few teleost species whose males call from the nest site to attract distant prospective mates. Two well-known examples of such sounds are the ‘hum’ call (main energy at around 100 Hz), produced by the male midshipman (*P. notatus*), and the boatwhistle call (main energy from 100 to 200 Hz), produced by the male toadfish (*Opsanus tau*, *O. beta*). These vocalisations are emitted from nests located in 1–5 m deep water (e.g. Bass 1990) or less (Fine and Lenhardt 1983). At such shallow depths, low frequencies may be near or below the cutoff, and the sound may decay quickly with distance (Fine and Lenhardt 1983). On the other hand, high-frequency sounds may be used by species that communicate in shallow water over distances of only 5–10 cm, for example, the sounds of croaking gouramies showing main energy between 1 and 2 kHz (Ladich 2007). From these few examples it would seem that environmental constraints on sound propagation operating in shallow habitats (e.g. water depth) cannot account for the widespread use of low frequencies among teleosts living in such environments.

Short-range propagation of teleost sounds does not necessarily imply that pressures from the environment are not important for other functions of the species’ acoustic communication system. In animal communication, signal efficacy is a useful measure of the success of a signal, that is, how strongly the signal affects the receiver’s behavior (Endler 2000). Signal amplitude is an important feature affecting all components of efficacy (i.e. efficiency and effectiveness). For instance, louder sounds not only propagate farther but may provide fitness benefits to the emitter also during close-range interactions. Studies on terrestrial species have shown that louder male vocalisations may be preferred by females (Castellano et al. 2008; Ritschard et al. 2010), and promote more effective territory defence. Among fishes, sound amplitude has been found to be tightly related to body size (e.g. Takemura 1984; Myrberg et al. 1993; Ladich 1998). Larger individuals are better able to acquire and defend resources important to females (e.g. Torricelli et al. 1988), including protection of eggs and embryos (Parmigiani et al. 1988). Indeed, it has been demonstrated that louder male vocalisations are preferred by gravid females (McKibben and Bass 1998) and are predictors of dominance during fights (Ladich 1998). However, a loud sound might be heard low by a receiver exposed to high levels of masking noise or with a frequency sensitivity mismatched to the spectrum of the sound. Thus, frequency composition of the sound may crucially influence the value of the signal-to-noise (S/N) ratio of communication. Consequently, sound spectrum is an important acoustic trait which may evolve in response to pressures from the environment other than, and independently of, those constraining propagation.

Two environmental factors may help to explain why low-frequency sound communication is so common among shallow-water fishes, namely sound amplification by the nest site and the environmental pressures from the ambient noise. Both factors appear to favour the use of particular frequency bands for sound production and reception, so as to increase the S/N ratio of communication. These are examined in detail below.

6.4 Nest and Spawning Sites Acoustics and Relationships with Low-Frequency Sound Communication

Among soniferous teleosts that spawn inside cavities below a hard submerged object, sounds are mostly produced by the male in the nest. Usually these species (toadfishes, gobies, blennies, etc.) are not very selective about the type of shelter used as a nest in the field. For instance, the male oyster toadfish *O. tau* may use stones, oyster shells, or artificial covers (including tin cans or pieces of cement; Michael L Fine, personal communication) as suitable nests. Therefore, among investigators studying the acoustical behaviour of these species in the laboratory or in the field, it is a common practice to provide males with artificial nest sites, such as terracotta tiles, halves of flowerpots, or plastic pipes. These enclosures have one or two openings and, therefore, may be considered semi-open systems analogous to organ pipes with one or two open ends. As such they could affect the amplitude and frequency spectrum of the sound produced inside them. However, until recently no study was conducted to explore the acoustic properties of natural and artificial nest cavities and their effect on the sound spectrum.

One of the first attempts to investigate the phenomenon was the study of Barimo and Fine (1998) on the propagation pattern of the oyster toadfish sound. They examined the radiation pattern in the field of the sound emitted by the male calling inside a terracotta tile open at both ends. They found an elongated and bilaterally symmetrical sound field around the fish and related the directional response of the system to the hearth-shaped swim bladder. A possible interference of the nest on the radiation pattern of the sound was excluded both on the basis of theoretical predictions, by equating the tile to a waveguide possibly amplifying the sound ahead of the two openings, and by noting the sound amplitude and spectrum of two sounds (a toadfish grunt and a croaker sound), emitted at 1 m by a free-swimming fish in a pen, was unaffected by the presence of tile above the receiver. Theoretically (Albers 1965; Bradbury and Vehrencamp 1998), this is an expected result because the small size of the shelter cannot produce significant scattering of the long wavelengths of these sounds (the shelter is virtually transparent to the sound).

In another study Parmentier et al. (2006) investigated the acoustic behaviour of two carapids that emit sounds (main frequencies comprised between 0.25 and 1.6 kHz) inside invertebrate hosts (sea cucumbers and sea stars) and were able to show that attenuation by the soft tissues of the sea cucumber was negligible at frequencies of the carapids' sound. The experiment consisted of feeding pure tones (200–1,000 Hz) into a transmitting hydrophone placed inside the cloacal cavity of the sea cucumber (*Holothuria stellati*) and examining whether the probe stimuli, collected by a receiving hydrophone placed at 25 cm from it, differed from the same stimulus transmitted after the cucumber was removed. What the authors essentially did was the computation of the frequency response of the system (Bradbury and Vehrencamp 1998) represented by the sea cucumber cavity and surrounding tegument. Results showed the amplitude of sounds recorded inside and outside the sea cucumber essentially overlapped (amplitude differences in the two conditions <0.5 dB).

Recently Lugli (2012) employed a similar method to investigate whether shelters commonly used by male gobies as calling and nest sites in the field (i.e. flat stones, bivalve shells) and in the laboratory (small terracotta flower pots, tunnel-shaped concrete blocks, plastic shelters, etc.) would affect the sound (main frequencies below 250 Hz, Fig. 6.3). Contrary to the lack of an effect reported in the two previous studies for the terracotta tile and the sea cucumber, Lugli (2012, 2013) found that the 'goby shelters' may exhibit remarkable 'amplification properties' towards these sounds. Because the phenomenon also may be potentially relevant to other fish species using cavities or enclosures for their low-frequency communication and for spawning findings of these studies are examined in some detail.

Anecdotal laboratory observations showed sounds emitted by a male freshwater goby (*P. bonelli*) inside the hollow under a stone sometimes appeared louder than those emitted by the male just outside it, suggesting that the stone cavity might have been responsible for the observed sound amplification. The phenomenon was explored by measuring the transfer function (frequency response) of the shelter within a laboratory tank under a variety of experimental conditions (described below), and using different types of probe stimuli (white noise, pure tones, artificial pulse trains) and shelters, from natural (stones, bivalve shells) to artificial (plastic covers, concrete blocks, halves of terracotta flower pots). Initially, shelters were stimulated by placing the sound source inside the cavity and the hydrophone just outside, an arrangement of the source and the receiver mimicking the situation of male fish emitting the sound from the cavity towards a nearby female (or rival male) in front of the nest. Results of the acoustical stimulation of the shelter hollow with white noise (the main driving stimulus used) showed that stones and shells, when placed on sand (all shelters) or gravel (stones) substrate, amplify sound frequencies below 200 Hz, the amplitude gain (from few dB up to 20 dB, or more) always peaking below 150 Hz (Fig. 6.1). Acoustical tests were also conducted on flat stones in the stream (Lugli 2012) and bivalve shells in the lagoon (Lugli unpublished data, Fig. 6.2) using pure tones as driving stimuli, with results similar to those obtained in the laboratory.

Compared to the natural shelters, the frequency response of artificial shelters was more variable, spanning from the marked low-frequency amplitude gain by, for example, terracotta flowerpots or concrete blocks, similar to that of stones (example in Fig. 6.1), to lack of gain by light plastic tiles, the latter leaving the frequency spectrum of the sound source unchanged (a useful property if characterisation of sound spectral quality is the focus of the investigation). The use of tiles and flowerpots as nest covers is common in studies on fish sound production conducted in the laboratory (e.g. Ladich 1989; Brantley and Bass 1994; Lindström and Lugli 2000; Amorim and Neves 2007) and field (Barimo and Fine 1998). Because low frequencies may be amplified substantially by the shelter, published spectra and frequency characteristics of sounds recorded from males from the nest cavity are likely to be biased towards lower frequencies.

A remarkable finding of the acoustical tests of shelters was that peak frequency (i.e. the frequency of maximum gain) did not differ significantly among shelters differing, often considerably, in shape or size. So, for example, the mean amplitude gain of stone and the small oyster shell (*Crassostrea gigas*) peaked in both cases at around 100 Hz (examples in Fig. 6.1). However, stones and heavier artificial shelters had higher gain values than shells or light plastic shelters. Interestingly, amplitude gain could be increased by putting a load above the shelter, or eliminated completely by experimentally decoupling the shelter from the substrate (e.g. by manually lifting the shelter a few millimetres above the substrate, Lugli 2012). Similarly, if sand is manually piled on top of the shelter, gain is enhanced further at lower frequencies (Lugli 2013; Fig. 6.2). This may be one reason why the sand goby males so eagerly dig and pile sand on the nest cover (typically, a small bivalve shell or a small stone). Male sand gobies (gen. *Pomatoschistus*, *Knipowitschia*) generally emit sounds only during the mating activities inside the nest cavity (Lugli and Torricelli 1999; Lindström and Lugli 2000). These vocalisations are low-frequency pulse trains with dominant frequencies in the range 80–200 Hz (e.g. Lugli et al. 1997; Malavasi et al. 2008), that is, the frequencies amplified by the nest (Fig. 6.3). Lugli (2013) showed an artificial sand pile on top of the shell may further amplify the sound up to 8–10 dB within the same frequency range. Notably, the sand pile enhanced these frequencies also in shelters without amplification properties (plastic tiles, *Mytilus* shells, Lugli 2013). Results of a correlative study of natural nest builds in the sand goby *Pomatoschistus minutus* showed amplification was higher in shelters constructed using larger amounts of sand. Producing louder sounds may confer advantages to the emitter in terms of enhanced male

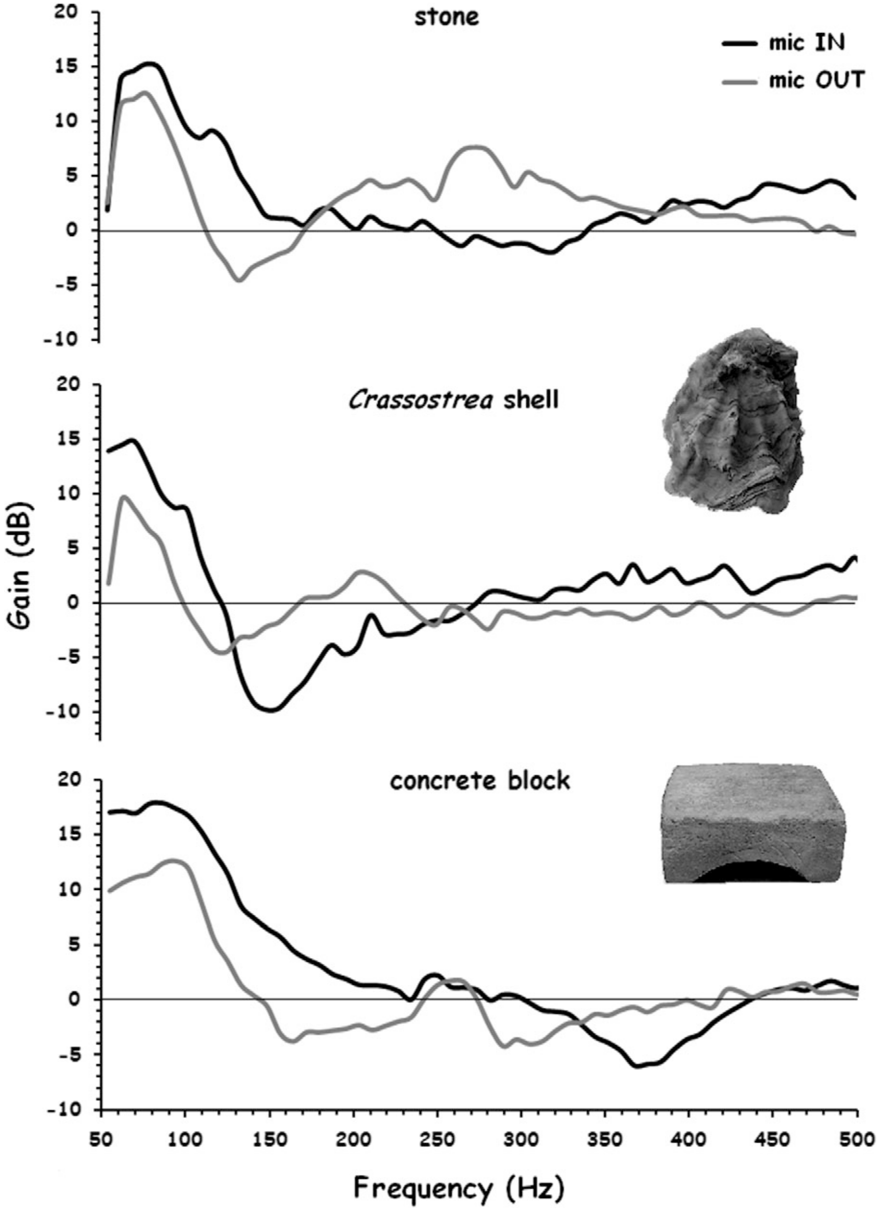

Fig. 6.1 Frequency response of a stream stone (weight: 1,400 g, basal surface: 180 cm^2), lagoon oyster shell, *Crassostrea gigas (*weight: 47.1 g, basal surface: 63 cm^2) and a small *concrete block* (weight: 290 g, see Lugli 2012 for dimensions) having a tunnel-shaped cavity, tested in laboratory twice: by positioning the hydrophone horizontally inside the cavity (mic IN) and, then, in the upright position at about 3 cm in front of the opening (mic OUT; see Lugli 2012 for experimental conditions and methods). Shelters not drawn to scale

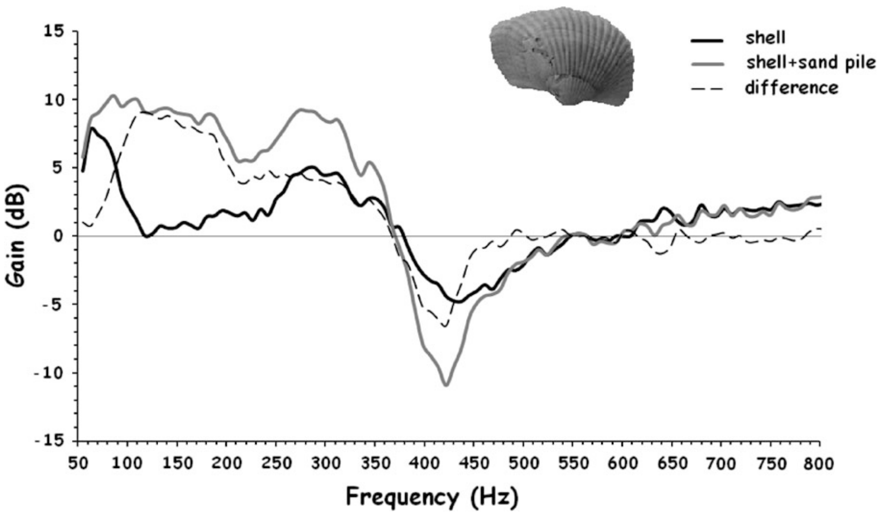

Fig. 6.2 Frequency response of a clam shell (*Scapharca inaequivalvis*, weight: 26.3 g, basal surface: 20.4 cm^2) tested in laboratory before (*black line*) and after (*grey line*) the shell was covered with an artificial sand pile. The difference between the two functions is the effect of the sand pile alone (*dashed line*; see Lugli 2013 for details)

attractiveness (McKibben and Bass 1998) and/or higher chances of attracting potential mates to the nest site due to larger active space of the sound signal. This suggests that sand piling by sand gobies might be an adaptation to increase sound amplitude and, hence, male attractiveness/reproductive success. It should be noted that gain properties of fish shelters were determined using sound frequencies below the cutoff recorded near the source (Lugli 2012). Thus, it is presently unknown whether the observed low-frequency sound enhancement by the nest is effective at greater distances and/or under conditions of sound propagation.

The use of stones or other hard underwater objects as a nest site is common to many cavity-nesting species from diverse fish families (Fig. 6.3). Therefore, the acoustical properties of the nest might have promoted low-frequency communication among these species. The presence of a close relationship between sound frequencies and gain properties of the nest may be observed by comparing the range of main frequencies of breeding sounds produced by these species (Table 6.1 in Myrberg and Lugli 2006) with the frequencies enhanced by the nest cavity (Lugli 2012; Fig. 6.3). Among the different fish taxa that use stones as a calling site the range of dominant frequencies of the sound matches, or fits, within the range of those enhanced by the stone. A similar relationship occurs between sounds of brackish sand gobies and the frequencies amplified by their nests (small bivalve shells with the sand pile, Lugli 2012, 2013). Notice among gobiids, the only two species known to spawn inside nests made of soft material (reeds, *Knipowitschia puctatissima*; burrows in the mud, *Zosterisessor ophiocephalus*), courtship sounds are produced at frequencies above those enhanced by a stone or shell

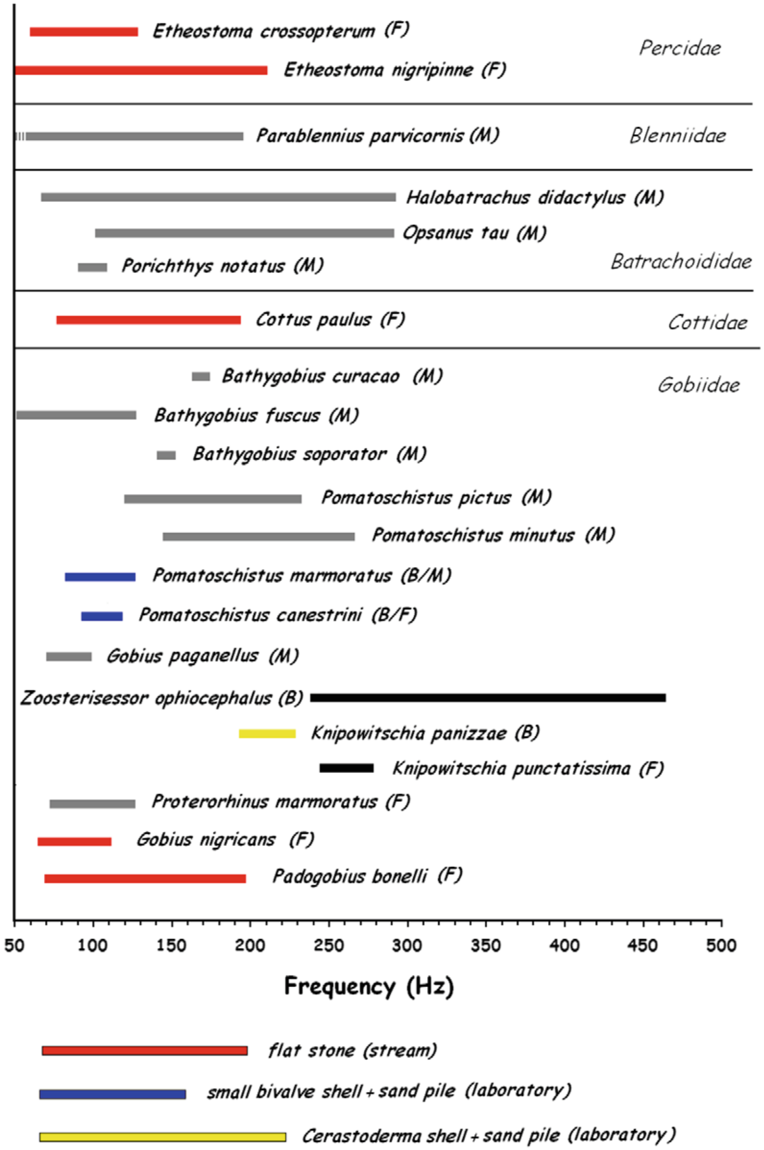

Fig. 6.3 The range of dominant frequencies (*horizontal bars*) of the courtship sounds emitted by cavity-nesting, egg-caring species from different habitats (*F* freshwater, *B* brackish lagoon, *M* coastal, marine; data from Myrberg and Lugli 2006; Lugli 2010; Amorim and Neves 2007; de Jong et al. 2007; Kierl and Johnston 2010). In all species but two (*Z. ophiocephalus*, *K. punctatissima*; *black bars*) the nest is a cavity below a hard object on the *bottom* (usually a stone or shell). For all species reported in the scheme, sound production occurs both inside and outside the nest cavity. The range of frequencies enhanced by the stream stone and lagoon bivalve shells is reported below the frequency axis for a comparison (the frequency ranges of species using these type of shelters are marked with coloured bars, whereas those of species potentially exploiting stone amplification are marked grey; data from Lugli 2012, 2013). Among gobiids, the high-frequency sounds of *Gobiosoma bosci* have been omitted from the scheme (see text)

[Note: in some cases—for instance, species producing broadband sound pulses in the nest, e.g. the sand gobies—the presence of the shelter might have biased the sound spectrum towards lower frequencies. This possibility is to be excluded for most of the goby species listed in the table (including all the sand gobies) because their sounds have always been recorded in the laboratory from males under light plastic shelters without amplification properties (Malavasi et al. 2008; Lugli 2012)].

What about the many vocal species not spawning inside cavities? A quick survey of their breeding sounds reveals these teleosts (e.g. cichlids, damselfishes, gurnards and searobins, croakers and drums, catfishes, croaking gouramis; see Table 6.1 in Myrberg and Lugli 2006; Ramcharitar et al. 2006) emit sounds with dominant frequencies usually extending well above 200 Hz. For instance, sound production among cichlids has been documented in more than 12 species belonging to different genera and differing for reproductive style (from substrate-spawning to mouth brooding) and habitat. Yet, main sound frequencies are above 300 Hz (up to few kHz), with the presence of significant acoustic energy below 200 Hz being observed in a few sounds (mainly agonistic) from a limited number of species (e.g. *Herotilapia multispinosa*, Brown and Marshall 1978).

In sum, this cursory analysis shows that species calling from cavities under cover (stones, shells) on the substrate emit low-frequency sounds with dominant frequencies below 200 Hz (the frequency range amplified by these shelters), whereas noncavity-spawning species tend to emit sounds at higher frequencies. There are, of course, exceptions to this 'rule', within each 'category'. The male naked goby (*Gobiosoma bosci*) uses oyster shells as a nest site and courts ripe females by producing 'clicking' sounds with main energy around 2 and 4 kHz, a case of high-frequency communication unique among gobiids (Mok 1981). However, many *G. bosci* sounds in the original recordings contained a great deal of low-frequency energy heavily corrupted by background noise. Considering that all goby species whose hearing has been investigated up to now are maximally sensitive to sound frequencies below 0.5 kHz (see Ladich and Fay 2013), a study of the hearing abilities and a redescription of sounds by the naked goby would be desirable. An intriguing example of noncavity-spawning species producing low-frequency sounds is represented by the group of cyprinids living in small streams and creeks (genera *Cyprinella*, *Codoma*). These fishes are, with a few exceptions (e.g. the cavity-nesting minnow, *Codoma ornata*, Johnstone and Vives 2003), crevice-spawners, non-guarding species; yet, the territorial male emits very-low–frequency sounds (main energy below 100 Hz, typically from 40 to 80 Hz) associated with mating and territory defence (Phillips and Johnston 2009). In this case one explanation may be these species would fit the sound energy within the quiet window at around 100 Hz in the stream ambient noise (see below). However, sound emission among these species often occurs in proximity to the spawning site (a crevice in a rock, a space between stones, which rarely form a flat surface in the field). Acoustical tests conducted in the laboratory (Lugli unpublished data) showed a depression between two rocks or semi-open cavities may indeed exhibit amplitude enhancement of low frequencies when acoustic stimuli are broadcast from a speaker placed close to, or inside, these 'crevices'. Further studies on the acoustics of the spawning environment of these species are clearly needed and results might reveal interesting and unexpected relationships with the sound.

In conclusion, cavity-spawning teleosts seem to have exploited the acoustic properties of the nest for increasing the amplitude of their sounds and, hence, the S/N ratio of acoustic communication, at least over short distances from the source. Thus, the acoustic environment of the nest site might play an important role in the evolution of low-frequency communication among these species. Because these fishes usually inhabit noisy environments, another potential environmental pressure for the low-frequency acoustic communication is represented by the habitat ambient noise. The constraining role of ambient noise on low-frequency communication is examined below.

6.5 Characteristics and Variability of Ambient Noise in Shallow Environments: Importance of Noise Windows for Sound Communication

There is an abundant literature on main sources and characteristics of ambient noise (including man-made noise) in the ocean and shallow marine environments. The topic has been reviewed by many authors (e.g. Wenz 1962; Urick 1983; Dahl et al. 2007). However, the vast majority of soniferous teleosts live and/or reproduce in very shallow marine and freshwater habitats (water depth of a few metres or below; see above), for which noise literature has only recently begun to accumulate. Furthermore, unlike land species, bioacoustical studies on vocalising fishes have seldom included a detailed characterisation of the habitat ambient noise, a necessary step towards the understanding of the role of ambient noise as a constraint for fish acoustic communication. Characterisation of the ambient noise at specific locations inhabited by fish species communicating acoustically has been recently done for very shallow, noisy environments (e.g. stony streams, near-shore marine areas, brackish lagoons, water depth <1 m; Lugli and Fine 2003; Wysocki et al. 2007; Lugli 2010; Speares et al. 2011). These habitats are probably the most unfavourable ones for acoustical communication to take place, being characterised by high noise levels (mainly from sources of bubble noise) and no sound propagation at frequencies below the cutoff (see above). Yet, a number of species from different teleost families have adapted and communicate acoustically in such environments.

Lugli and Fine (2003) measured several noise spectra at both quiet and noisy places of two Italian streams (the Stream Stirone and River Serchio), each inhabited by a different stream goby species (*P. bonelli* and *G. nigricans*, respectively). The streams were remarkably quiet in places where the water surface was unbroken (spectrum levels from 40 to 60 dB re: 1 μPa in the frequency range 0.1–1 kHz). However, at places where the water surface breaks, trapping air underwater, background noise increases significantly at all frequencies, with the highest increments in the 200–500 Hz band (Figs. 6.4 and 6.5). The spectrum levels at the

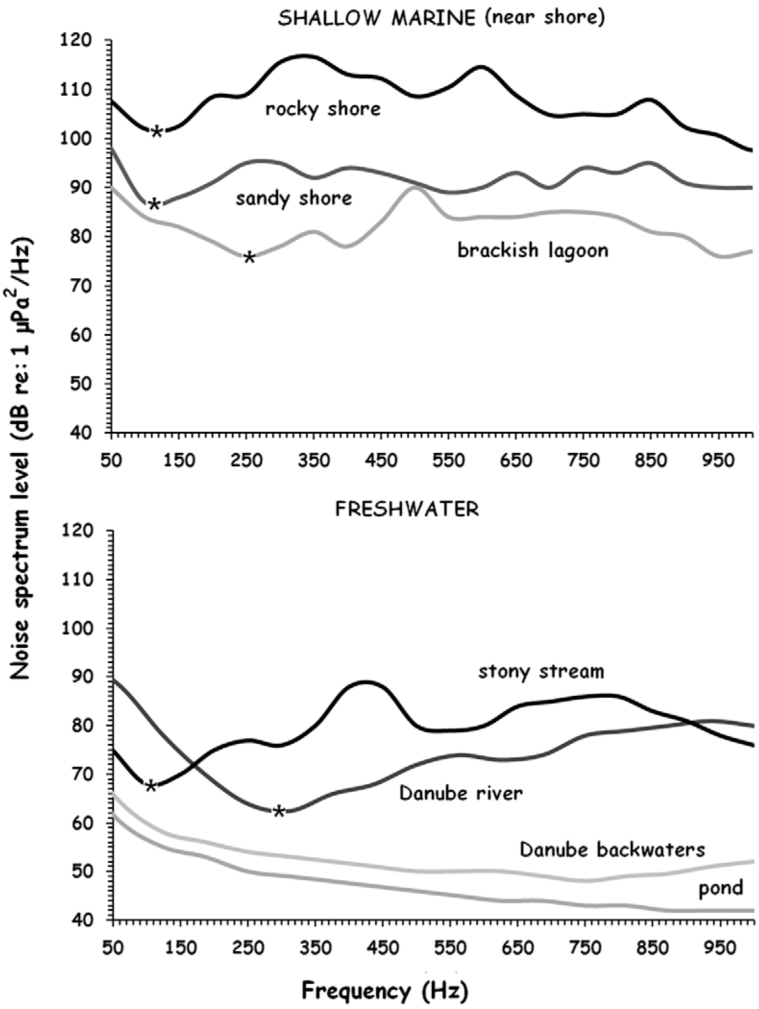

Fig. 6.4 Individual low-frequency ambient noise pressure spectra representative of the noise conditions found in very shallow marine (*upper plot*) and freshwater (*lower plot*) habitats inhabited by soniferous fishes (from Lugli and Fine 2003; Lugli 2007; Wysocki et al. 2007). Notice the presence of a frequency region with lower noise levels (termed ‘*noise window*’ by Lugli and Fine 2003) in the noise spectrum of noisy marine and freshwater habitats (an *asterisk marks the center of the* ‘*window*’), and the lack of it in the two quiet freshwater habitats

noisiest places (i.e. near cascades, small rapids, pools below a small waterfall) differed up to 35 dB between different frequencies in the 0.03–1 kHz band of a spectrum, the maximum noise levels often being comparable to, or even exceeding, levels measured in the shallow ocean at higher sea states or during heavy shipping (i.e. 80–90 dB). Furthermore, the noise spectrum could vary remarkably in both shape and level among nearby locations (Fig. 6.5). Large short-range variations in

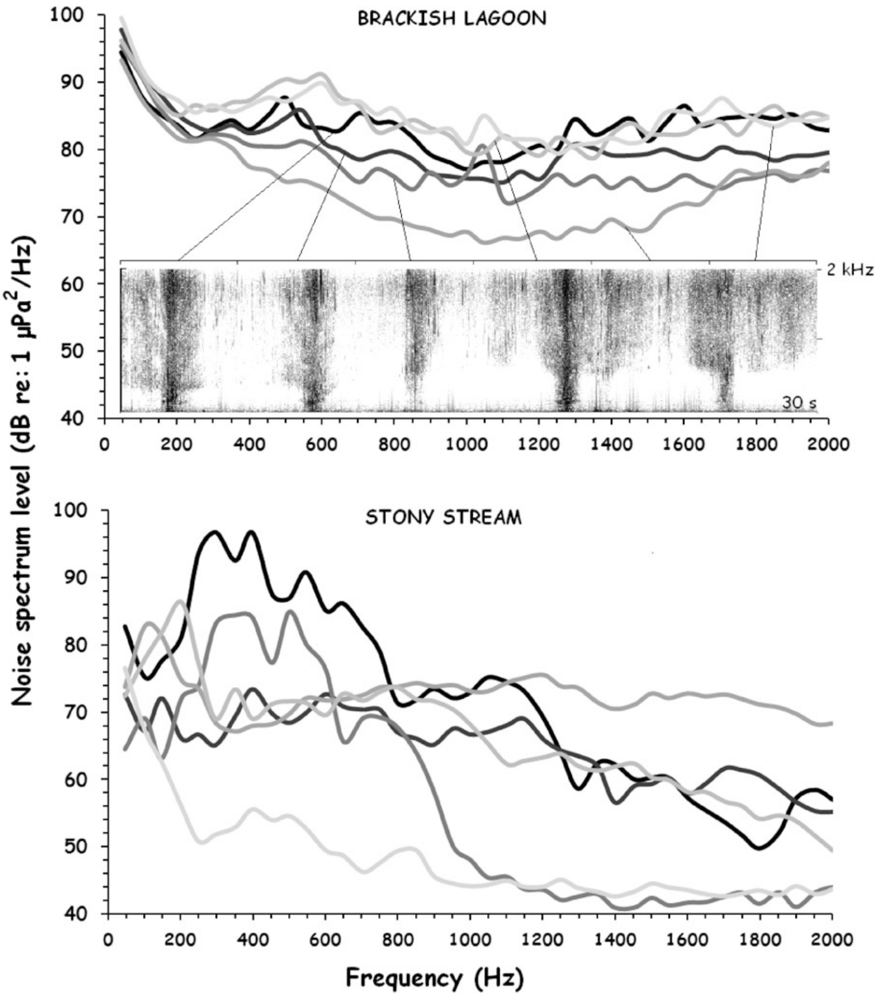

Fig. 6.5 Examples of variability of ambient noise spectrum in a lagoon (*upper plot*) and stream (*lower plot*) inhabited by soniferous gobies. *Upper plot* Temporal variability of noise spectrum determined for each subsequent 5-s segment of a 30-s continuous underwater noise recording at a fixed location of the lagoon (Sacca del Canarin, river Po delta, Northern Italy, water depth ~50 cm). Ambient noise consisted mainly of bursts of bubble noise produced by travelling breaking waves (*spectrogram below*) passing nearby the measurement location (see Lugli 2010 for further information). *Lower plot* Variability of stream ambient noise spectrum between nearby recording locations (*Stream Stirone*). Most locations were close to sources of underwater bubble noise (see Lugli and Fine 2003, 2007 for further information)

ambient noise levels and spectrum are expected in such very shallow and complex habitats with many noise sources and exponential decay of low-frequency noise energy due to frequency cutoff (Akamatsu et al. 2002; Lugli and Fine 2003). A notable feature of stream ambient noise was the presence of a relatively quiet

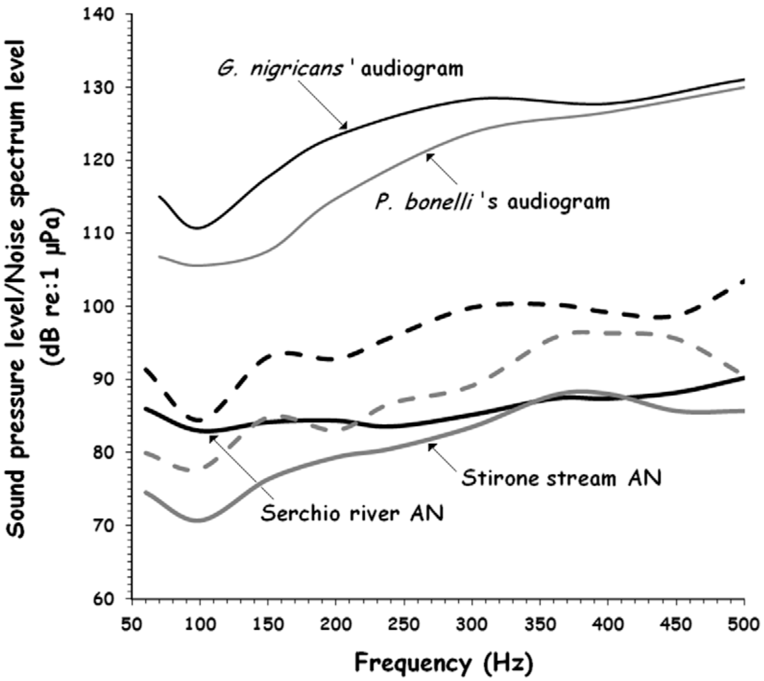

Fig. 6.6 The pressure audiogram of two allopatric stream goby species (*thin lines*) and average (*continuous thick line*) +1 SD (*dotted line*) ambient noise pressure spectrum from noisy locations of the corresponding stream (*P. bonelli* and Stream Stirone: *grey lines*; *G. nigricans* and River Serchio: *black lines*). Note the low-frequency noise window around 100 Hz in Stream Stirone and the standard deviation curves of the ambient noise of both streams matching the audiogram's profile. The matching improves using data from the noisiest locations of the stream (see text for further explanations). The data suggest that hearing is influenced by common selective pressures from the environment

window around 100 Hz in many noisy locations (particularly in Stream Stirone). The window, about 130 Hz wide in Stream Stirone, was more sharply tuned at 100 Hz, that is, resembling a notch, in River Serchio (Fig. 6.6). This quieter noise spectral region is exploited by the two gobies for communication: the main sound frequencies matched the window/notch frequencies (Lugli 2010; compare also Fig. 6.6 with Fig. 6.3); furthermore, the goby hearing sensitivity also peaked at 100 Hz (Fig. 6.6). It should be noted that the window band overlaps the range of frequencies enhanced by the stone. Thus, in the stream goby both ambient noise and nest/calling site appear to act synergistically to increase the S/N ratio of acoustic communication (see discussion below).

A subsequent study (Lugli 2010) examined the spectral features of ambient noise in freshwater, brackish, and shallow marine habitats inhabited by other vocal gobies and often characterised by elevated noise levels. The habitats investigated, among others, were two brackish lagoons, a near-shore sandy bottom, and a rocky shore.

In these habitats the main noise source was the bubble noise generated by breaking ripples and wave splashes. Overall, noise levels were higher (80–110 dB, re: 1 μPa) than those measured in the stream. However, because of the repetitive and unpredictable nature of waves, noise levels showed high short-time variability associated with the presence of a wave-breaking event at or near the recording position (Fig. 6.5). Bubble noise energy concentrated mostly in the 0.03–4 kHz band and peaked usually below 500 Hz. Like the stream bubble noise, the noise spectrum of breaking ripples and wave splashes featured a low-frequency 'quiet window' in all habitats surveyed. The window, about 100–150 Hz wide, was tuned at 100 Hz in the coastal habitats surveyed, and at 200 Hz in the lagoon. The spectral features of the window were then correlated with the range of dominant frequencies of sounds used by gobies reproducing in these environments. Results showed the dominant frequencies of sounds of the two marine gobies (*Gobius paganellus*, *G. cobitis*) showed the best fit within the quiet window at around 100 Hz in the noise spectrum of marine areas, whereas those of four brackish gobies (*K. panizzae*, *P. marmoratus*, *P. canestrinii* and *Z. ophiocephalus*), better fitted the quiet window at around 200 Hz in the noise spectrum of the lagoon (Fig. 6.7).

It should be noted that these studies (Lugli and Fine 2003; Lugli 2010) were conducted using acoustic pressure as the measurement unit. However, gobies, as are many other teleosts with 'poor' hearing that communicate at close distance (i.e. in the near field), are primarily or exclusively particle-motion–sensitive species. In the near field, acoustic pressure and particle velocity do not have a constant relationship but vary with the characteristics of sound source and propagation distance in complex, site-dependent ways (Kalmijn 1988). Thus, the measurement of the sound and ambient noise in terms of particle velocity is therefore required. This has been done for the stream ambient noise and *P. bonelli* sounds (Lugli and Fine 2007) using a pressure (p)-velocity (u) sensor in the stream. Results showed the noise spectrum was similar for p and u (including the quiet window at noisy locations). The energy distribution of the sound was quite similar for p and u spectra. Most important, the sound/ambient noise window match occurred for both p and u, the matching being shifted 50 Hz higher for u. Overall, results of this study validated conclusions about sound communication derived by measuring only acoustic pressure.

Spectral features of ambient noise and their relationships with fish sounds have also been examined in other species. Speares et al. (2011) examined ambient noise characteristics of two separate North American creeks inhabited by sound-producing fishes belonging to the genus *Etheostoma* (darters, family Percidae). In these streams noise levels were high (up to 100 dB), below 100 Hz, and decreased with frequency more quickly in quieter places (pools and runs) than in fast-flowing riffles, where underwater bubbles formed from the breaking of the water surface. As with the Italian streams, the noise spectrum at the noisiest places of one stream (the riffles of Cypress Creek) featured a low-frequency band, between 150 Hz and 330 Hz, with quieter noise levels. The dominant frequency of the aggressive vocalisations of the species inhabiting these riffles (*E. flabellare*) fell within the quiet window. The second species investigated (*E. crossopterum*) produced vocalisations

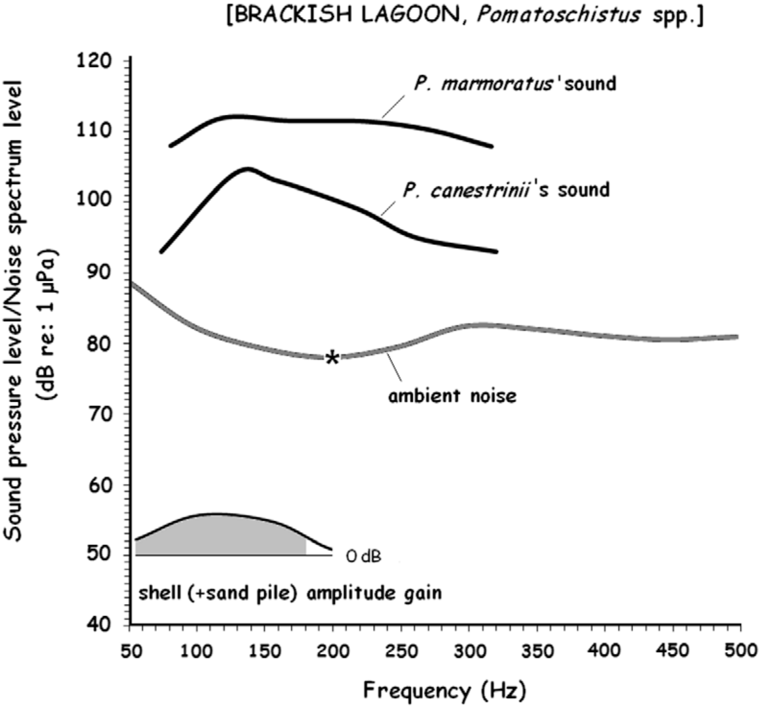

Fig. 6.7 The mean sound spectrum of two brackish sand gobies (the Marmoreal goby, *Pomatoschistus marmoratus*, and Canestrini goby, *P. canestrinii*, *dark lines*) and the 50–500 Hz mean (*pale line*) spectrum of the breaking wave noise in the lagoon (data from Lugli 2013). The asterisk marks the center frequency of the quiet window in the low-frequency ambient noise spectrum (approx. 100–270 Hz). Superimposed on the plot is the mean amplitude gain (dB) from the bivalve shell with a sand pile above, the typical nest site of these species (Lugli 2013). Axes have the same units of the main plot except that dB units on the *Y*-axis are relative to the 0 dB gain line

with lower average frequency and wider frequency range, more suitable for communication in the much quieter environment of the pool (spectrum levels at frequencies above 100 Hz well below 70 dB) with a not clear quiet noise window. The authors concluded that both species produce vocalisation with dominant frequencies working within the acoustic constraints of their respective microhabitats. Because both species call and spawn below stones (Speares et al. 2011) it remains to be seen whether and to what extent their sounds are also amplified by the nest cavity.

A much wider quiet noise window was described in the background noise of African floodplains inhabited by the weakly electric fish *Pollimyrus isidori* (family: Mormyridae; Crawford et al. 1997). The window (from 0.2 to 3 kHz) was supposed to result from low-frequency noise due to water motion and other unidentified sources, and from a high-frequency noise produced by aquatic insects stridulating underwater. A significant amount of energy of the courtship sounds (moans, grunts) of *P. isidori* falls within this noise window (Crawford et al. 1997).

The presence of quiet noise windows has been reported for other freshwater habitats. Wysocki et al. (2007) determined the underwater noise spectrum of 12 aquatic environments in Austria, from noisy fast-running streams to quiet ponds and river backwaters. Although the study did not capture the ambient noise variability of each habitat, nonetheless results showed large variations of noise level and spectrum between different environments consistent with the different water flow regimes. The spectrum levels of stagnant habitats (lakes, backwaters, ponds) were higher at frequencies below 100 Hz and decreased with increasing frequency, resting generally below 60 dB in the frequency band 0.1–5 kHz (Fig. 6.4). The noise spectra of running water habitats, on the other hand, showed higher noise levels at lower frequencies, a rapid decline of the spectrum levels to a minimum, followed by an increase again towards a peak (around 80 dB) or a plateau (at around 100 dB, Danube river at Orth), thus defining an area of lower spectral levels (i.e. a 'noise window') at frequencies from 170 to 450 Hz (Fig. 6.4). The spectral energy above the window was believed to originate from noise produced by transport of sediment and cavitation. The authors also noted noisy habitats exhibited large differences in the noise spectrum, whereas stagnant habitats had a similar noise profile, an observation supported by the results of investigations of stream ambient noise discussed above. However, they did not specifically relate the presence of these windows to sounds produced by teleosts inhabiting these environments.

In sum, the occurrence of low-frequency regions with lower noise levels (termed 'noise windows'; Lugli and Fine 2003) is a recurrent feature of noise spectra in shallow-water habitats with intermittent or continuous sources of elevated noise levels. The number of teleosts living in such noisy shallow environments is numerous, and studies exploring the relationships between their sounds and ambient noise characteristics could reveal further cases of sound/ambient noise matching. A cursory examination of these relationships was attempted by Lugli (2010) using published data on sounds produced by other teleosts breeding in small streams, creeks, and very shallow marine habitats similar to those examined above. The species surveyed belonged to families as diverse as cottids, batrachoidids (*Porichthys*, *Opsanus*), and cyprinids (genus: *Cyprinella*). The range of the main frequencies of sound produced by these species was superimposed on a generic noise spectrum of a breaking wave and a stream waterfall, two main sources of elevated background noise of these environments both featuring the quiet window around 100 Hz. In all species the main frequencies of the sound fitted within the quiet window, including two stream cyprinids, a teleost family well known for including many species living in quiet environments (e.g. backwaters, ponds) and characterised by well-developed hearing and typical sound frequencies well above 100–200 Hz (reviewed in Amorim 2006). Thus, these data indicate that the sound/ambient noise match may be widespread among marine and freshwater species breeding in shallow noisy environments.

A match between call energy and ambient noise has also been described in marine mammals (baleen whales) communicating in shallow coastal habitats (Bass and Clark 2003), and in many land vertebrates (birds, primates, frogs; Brenowitz 1982; Ryan and Brenowitz 1985; Waser and Brown 1986; Brumm and Zollinger 2013). Ambient noise therefore may act as a main constraint upon frequencies used for acoustic communication in both marine and terrestrial species.

6.6 Fish Low-Frequency Communication Explained by Habitat Acoustics?

Attempts to explain the widespread use of low-frequency sounds by teleosts in terms of adaptation to environmental factors have already been made in the past. Bass and Clark (2003) interpreted low-frequency signalling by developing a set of complementary explanations linking environmental to behavioural and structural factors. Thus, for instance, the constraining effect of water depth on sound transmission was taken as an example of an ecological factor favouring the use of low frequencies for short-range communication in shallow waters. The short propagation distance of frequencies below the cutoff might avoid degradation of sound signals caused by multipath propagation and limit interception by competitors or predators. There is no compelling evidence in support of this behavioural–ecological explanation, however. For example, stream gobies (*P. bonelli*, *G. nigricans*) do not have aquatic predators (with the possible exception of the collared snake, *Natrix natrix,* whose hearing capabilities are unknown) and sound interception by competitors occurs despite the very short propagation distance (few decimetres) of their low-frequency sounds (Lugli 1997). Bass and Clark (2003) indicated as an example of an ecological–structural mechanism favouring low-frequency acoustic signalling, the maintenance of the inner ear's most fundamental function of low-frequency particle motion detector in the near field in many extant species, as hypothesised by Kalmijn (1988). Inasmuch as the lateral line detects the local hydrodynamic flow in the very near field, the inner ear might have evolved originally to extend the detection range and frequency sensitivity of the lateral line to the remaining part of the near field. The strength of the local flow and extension of the near field are greater for sounds with longer wavelengths (Kalmijn 1988). Thus, fishes are expected to use preferentially low-frequency vocalisations for near-field acoustic communication. Another explanation for low-frequency acoustic communication relates to the physiology of sound production. Many fishes produce sounds by contraction of sonic muscles (often attached to the swim bladder) whose contraction rate translates into the sound's fundamental frequency. The maximum sustainable repetition rate of these muscles (up to 300 Hz among batrachoidids; Skoglund 1961) would set an upper limit to the main frequency of the sound, a behavioural–structural explanation for the occurrence of low-frequency communication among these species (Bass 1998). However, there are many ways by which a fish can extend the frequency range of the sound originated by muscular contraction (e.g. Ladich and Bass 2011).

In the two previous sections we have shown that two ecological factors, nest site acoustics and occurrence of noise windows, may favour the use of low-frequency sounds by teleosts living in shallow noisy habitats by providing higher S/N ratios for communication. For example, the main frequencies of sound of the male stream goby, *P. bonelli*, fit within the 10-dB–deep noise window at around 100 Hz of the stream noise and, curiously, are also those maximally amplified by the stone hollow (around 12 dB, on average, for a 100 Hz tone, Lugli 2012). The joint contribution of these two environmental factors might increase the S/N ratio of the 100 Hz pitched sound signal emitted by the male *P. bonelli* inside the nest site substantially (from 10 to 20 dB, when compared to a higher pitched sound). A similar fortunate circumstance occurs among sand gobies of the genus *Pomatoschistus*, where the frequencies enhanced by the nest (a shell with sand pile) happen to be within the noise window of the lagoon ambient noise. As expected, the sound spectrum of these species fits within the broad noise window of the lagoon ambient noise, but the peak frequency of the sound matches the frequency of maximum gain of the nest (Fig. 6.7). Thus, it would seem that both ambient noise and nest acoustics jointly operate to increase the S/N ratio of goby acoustic communication in the presence of elevated noise levels. Like gobies, many other teleosts (e.g. toadfishes, sculpins, darters, blennies) live in shallow noisy habitats and communicate acoustically over short, or very short distances. In addition, in many of these species the male calls from cavities under stones or other submerged objects used as a nest site. Thus, the widespread use of low frequencies for communication among these fishes may be promoted by one or both of the above acoustical features of the habitat.

However, in order to be effective, acoustic communication requires that the sound must be detected and clearly recognised by intended listeners (e.g. a potential mate). Both detection and recognition depend on the S/N ratio. Thus, the next section explores the importance of ambient noise on hearing sensitivity.

6.7 Environmental Pressures Operating on Receiver Auditory Sensitivity

An unresolved mystery of fish acoustic communication is the great variability of hearing sensitivities found among different, in some cases also closely related, species (e.g. Fay and Megela-Simmons 1999; Ladich 2014). The variety of fish auditory sensitivities (Fig. 6.8) is much higher than that found among other vertebrate groups, where the audiogram form usually shows only minor changes among related species. To a large extent, these differences are related to the way the sound is processed by the inner ear of the fish. The fish ear responds to acoustic particle motion associated with the incoming sound wave passing through the acoustically transparent fish tissues. Hair cells of the inner ear function as low-frequency, particle motion detectors (Kalmijn 1988). In terms of hearing sensitivity fishes can be classified into two main categories: the hearing specialists, like the goldfish, show high sensitivity, extended hearing range towards higher frequencies (up to several kHz), and higher frequency discrimination; on the contrary, the hearing nonspecialists (also referred to as 'generalists'; e.g. the perch), have poor hearing sensitivity, a narrow hearing range restricted to lower frequencies (100–300 Hz), and poor frequency discrimination (e.g. Ladich and Popper 2004; Fig. 6.8). Species belonging to the first group (e.g. cyprinids, mormyrids, anabantoids), have developed accessory hearing structures (like the Weberian ossicle chain of otophysans) connecting the inner ear with the swim bladder, or other pressure-to-displacement conversion mechanisms (e.g. auditory bullae of mormyrids), enabling them to detect the acoustic pressure from distant sound sources and the associated far-field acoustical information. Auditory specialists are mainly found in quiet freshwater habitats (lakes, ponds, large slow-flowing rivers). Those of the second group (e.g. toadfishes, blennids, gobies, darters) can only detect the particle motion components of the near field generated by a close sound source (a task also accomplished by auditory specialists). Auditory nonspecialists are typically found in noisy freshwater habitats (streams, creeks, small rivers) and in shallow marine environments (coastal areas, lagoons). Between these two broad categories there is a third group of species showing intermediate hearing sensitivity. These fishes appear to be sensitive to sound pressure but lack morphological adaptations for hearing enhancement (e.g. damselfishes). The above distinctions do not have to be considered too rigidly as one category may grade into the other (Smith et al. 2004; Ladich 2014). Interestingly, remarkable differences in sensitivity also exist between closely related members of the same family, both with and without hearing specialisations (e.g. Ladich and Yan 1998; Schulz-Mirbach et al. 2013).

Until recently, the causes of variability of fish audiograms has remained a matter of speculation and largely unexplained (reviewed in Ladich and Bass 2003). Factors unrelated to the natural environment, such as differences in the testing procedures, methods, or the acoustic units used to assess auditory sensitivity of a particular species (Hawkins and Myrberg 1983; Fay and Megela-Simmons 1999; Ladich 2014) may partly account for such variability. However, there are indications that the acoustical characteristics of the species' habitat may also play an important role. I have shown before that fishes live in environments differing greatly for sound propagation and ambient noise characteristics. The importance of the acoustic environment in the evolution of fish auditory sensitivity has been emphasised by few investigators (Hawkins and Myrberg 1983; Rogers and Cox 1988; Schellart and Popper 1992; Ladich 2014). Myrberg (1980) noted among fishes with good hearing abilities the auditory thresholds below the point of greatest sensitivity parallels those of the spectrum-level noise, the levels of the audiogram resting from 15 to 20 dB above the ambient noise curve (sea state 1). He also noted that adding only a few dB to the noise levels would affect sensitivity and impair hearing within the region of greatest sensitivity (400–600 Hz), and concluded that low-frequency auditory sensitivity among fish with good hearing appears to be governed by the

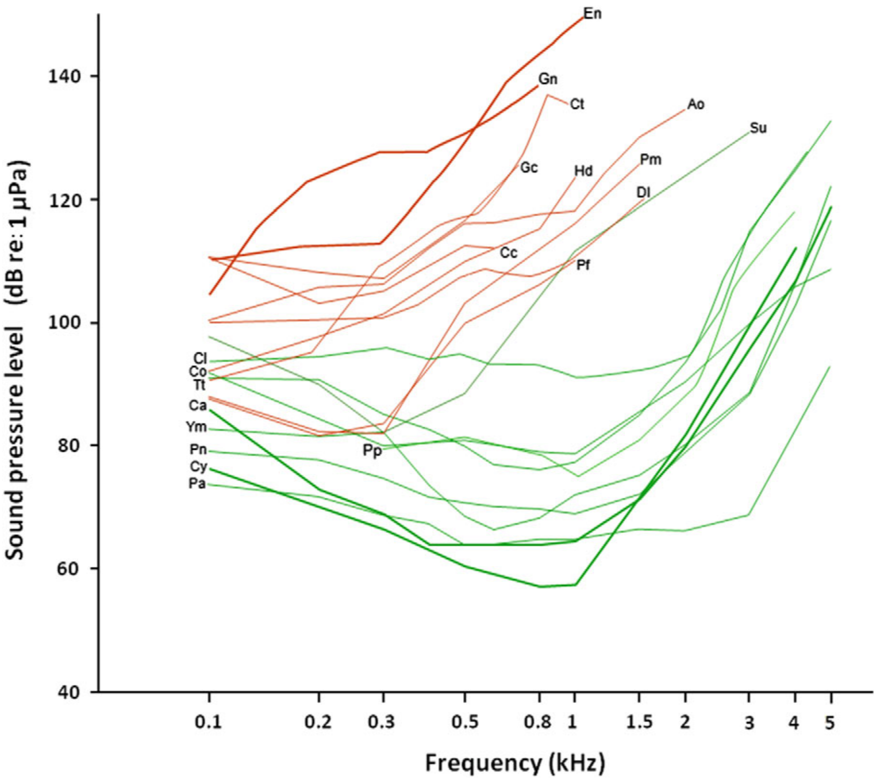

Fig. 6.8 Pressure audiograms for 20 representative auditory specialists (*green lines*) and nonspecialists (*dark red lines*) teleosts (*species initials in brackets, see below*) living in shallow or very shallow habitats. Audiograms of species living in very noisy (streams, creeks: *thick red lines*) or very quiet (ponds, stagnant waters; *thick green lines*) habitats are highlighted. All thresholds curves were obtained using AEP technique (Kenyon et al. 1998). Ao, *Astronotus ocellatus*; Ca, *Carassius auratus*; Cc, *Chromis chromis*; Cl, *Colisa lalia*; Co, *Corydoras aeneus*; Ct, *Cottus carolinae*; Cy, *Cyprinus carpio*; Dl, *Dicentrarchus labrax*; En, *Etheostoma neopterum;* Gn, *Gobius nigricans;* Gc, *Gobius cruentatus;* Hd, *Halobatrachus didactylus*; Pa, *Platydoras armatulus*; Pf, *Perca fluviatilis*; Pm, *Poecilia mexicana*; Pn, *Pygocentrus nattereri*; *Pp, Pimephales promelas*; Su, *Sciaena umbra*; Tt, *Trichogaster trichopterus*; Ym, *Yasuhikotakia modesta* (Modified from Ladich 2014; further references: Zeyl et al. in press, Ct, En; Ladich and Yan 1998, Cl; Lugli et al. 2003, Gn; Scholik and Yan 2001, Pp; Lovell 2003, Dl)

slope of the ambient noise. Hawkins and Myrberg (1983) argued that there is no advantage in having sensitive hearing when noise masks the auditory system, implicitly advocating the importance of ambient noise in the evolution of hearing sensitivity.

Investigators have considered the possible relationships of hearing abilities with vocal activity and spectral characteristics of species' sound, with contrasting results. For instance, in anabantoid fishes (*Trichopsis vittata*, *Colisa lalia*) there is a general agreement between the main energies of the high-pitched sounds and the best hearing sensitivity of the fish (Ladich and Yan 1998). However, best hearing and main sound energy are mismatched in several other teleost groups, regardless of the presence of hearing aids (Ladich 2000). Furthermore, within-family comparisons (e.g. among Cyprinids) showed nonvocal species (e.g. the goldfish) do not have poorer hearing than vocal ones (Ladich 2000). These results are consistent with the hypothesis that the hearing function is more primitive than sound production (Kalmijn 1988), implying that other factors are responsible for the evolution of hearing sensitivity.

A study of Lugli et al. (2003) supported the Hawkins and Myrberg (1983) insight on the importance of ambient noise for shaping the species' hearing sensitivity. They found in the two stream gobies, *G. nigricans* and *P. bonelli*, the main sound frequencies and the region of greatest sensitivity of the fish audiogram fitted within the low-frequency quiet region of the stream noise (i.e. the 100 Hz 'notch' of the *G. nigricans*' stream noise and the quiet window of *P. bonelli*'s stream noise, Fig. 6.6), a set of related adaptations enhancing the signal-to-noise of acoustic communication in line with principles of optimal communication in a noisy environment (e.g. Wiley and Richards 1982; Endler 1992). They also found that higher noise levels in the 100 Hz notch correctly predicted the lower sensitivity and the narrow range of best hearing of *G. nigricans* in comparison to those of *P. bonelli* (Fig. 6.6). Furthermore, in each species the absolute auditory sensitivity tracked the mean ambient noise spectrum level determined at noisy locations of the species' stream (Fig. 6.6). The presence of fine audiogram/noise matching in the two gobies addresses the importance of ambient noise in shaping the form of the stream goby's hearing sensitivity. Lugli (2002) noted the presence of similar audiograms in other hearing nonspecialist species living in noisy shallow water habitats (e.g. the European perch, *Perca fluviatilis,* reviewed in Popper and Fay 1973), and argued the habitat ambient noise may represent an important environmental constraint upon the evolution of fish hearing sensitivity in general. Subsequent investigations supported this view. Amoser and Ladich (2005) found that hearing thresholds of a hearing nonspecialist (the European perch, Percidae, audiogram in Fig. 6.8), were only slightly affected by the highest noise levels of noisy freshwater habitats (stream, small river), whereas those of a hearing specialist (the common carp, Cyprinidae, audiogram in Fig. 6.8) were masked also by the low noise levels of quiet standing waters (backwaters, lake, pond). They concluded that only the low noise levels of quiet habitats would facilitate the evolution of auditory specialisations that broadened the hearing sensitivity to higher frequencies (the only ones propagating above the cutoff frequency in shallow habitats), in order to detect the acoustic pressure from distant sound sources produced by relevant biotic (e.g. predators) and abiotic (waves, splashes) sources (Amoser and Ladich 2005). Recently, Ladich and Schulz-Mirbach (2013) reviewed the results of comparative studies on the effect of noise masking on hearing, and noted that major threshold shifts occurred only under noisy conditions among fishes with hearing specialisations. However, situations characterised by the presence of elevated noise levels are rare in quiet habitats (excluding the presence of anthropogenic noise), but common in noisy ones (examples in Fig. 6.4). As already pointed out by Lugli et al. (2003)

for the stream goby, there might not be a strong selective advantage for a species with limited hearing ability and low-frequency sensitivity to change the status quo if the fish is likely to encounter high levels of background noise, and other unfavourable acoustic conditions (e.g. multipath propagation) constraining long-distance communication in these environments. In this regard, the results of a recent study on amblyopsid cavefishes living in noisy subterranean streams are notable in that they showed that moving from quiet habitats to a noisy one may lead to decreased auditory sensitivity at frequencies where ambient noise is highest (Niemiller et al. 2013). This is a remarkable and unexpected finding considering these fishes are blind, because of the total darkness of the cave environment, and must rely on auditory function for orientation and communication. The picture that emerges from these observations indicates that the auditory sensitivity of fishes might indeed be well suited to cope with the prevailing ambient noise conditions of their habitats. This conclusion is further strengthened by examination of audiogram/ambient noise relationships in two unrelated vocal species (the red-mouthed goby *Gobius cruentatus,* and the damselfish *Chromis chromis*) breeding within the same marine shallow area (Picciulin et al. 2010). These species have a similar audiogram (Wysocki et al. 2009) and absolute hearing thresholds that appear to track the profile of the ambient noise of the breeding area (a coastal rocky reef, Fig. 6.9). The importance of ambient noise conditions in the evolution of hearing sensitivities in fishes (and less so acoustic communication) has also been emphasised by Ladich (2014), who labeled the issue as 'ecoacoustical constraints hypothesis'.

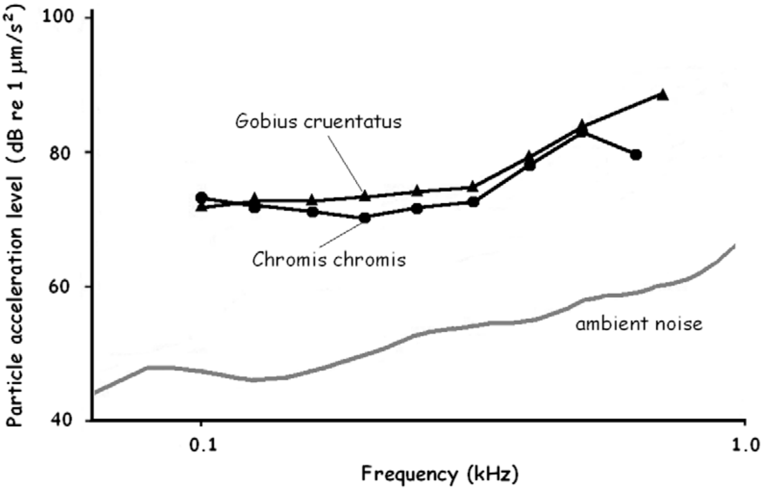

Fig. 6.9 The particle acceleration audiogram (AEP method) of *C. chromis* (Pomacentridae, *filled circles*) and *G. cruentatus* (Gobiidae) (*filled triangles*) shown together with particle acceleration level underwater ambient noise spectrum measured close to a coastal rocky reef (150 m long), within an area where both species live and reproduce (water depth: 3–7 m). All analyses are done in 1/3 octave bands (modified from Picciulin et al. 2010)

This hypothesis attempts to explain why numerous vocalising taxa such as toadfish, gobies, and sculpins possess poor hearing abilities and why nonvocalising species such as many cyprinids (goldfish, carps, etc.) evolved specialisations for the improvement of hearing such as auditory ossicles.

But why and how should the auditory sensitivity of a species be well matched to the habitat ambient noise? In particular, what are (if any) the costs for an individual fish by listening with a too-sensitive ear for the noise conditions encountered in the species' habitat? A potential advantage for a fish having thresholds above the prevailing ambient noise levels is the avoidance of sensory overstimulation and deleterious effects of elevated noise levels on the auditory system such as hair cell damage (Popper and Clarke 1976; Enger 1981; Hastings et al. 1996). Studies conducted on teleosts with good hearing have shown that longer exposure to moderately loud noises may produce sensory cell damage and lead to permanent loss of hearing (e.g. Hastings et al. 1996). Thus, a fish with a sensitive ear living in noisy environments would be frequently exposed to elevated noise levels which might have deleterious consequences for reproduction and survival, from alteration of normal behavioural activities and chronic stress, to permanent loss of hearing in the long run. This possibility has yet to be tested experimentally, however. Interestingly, Hopkins (1988) interpreted low sensitivity of electroreceptors in African freshwater electric fishes as an adaptation to avoid sensory overstimulation from the more or less continuous electrical noise of lightning storms.

However, the adverse effects of noise on auditory performances may be more subtle and occur at much lower levels than those required to damage the functionality of the inner ear. It is well known that noise can impair the perception of sound by masking auditory thresholds and cause temporary hearing loss (Yost 1994; Ladich 2013). Studies conducted among vertebrates over the last 20–30 years have clearly demonstrated the detrimental effects of noise masking on auditory performances of great adaptive value, such as the ability to assess correctly the overall intensity and spectral shape of the sound. The correct assessment of the intensity of multiple frequency components of the sound is fundamental for the reliable identification of the sound source, classification of acoustic events, or assessment of mate quality through comparison of sounds from different individuals (e.g. Bregman 1990; Wolleman and Wiley 2002). Because classification processes of acoustical stimuli by the receiver's auditory system must rely upon the perceived quality of the sound embedded in noise, one might expect a lowered ability to discriminate acoustic variants by a hearing-sensitive receiver when the masking background noise spectrum varies at, or between, locations at which sound detection occurs. We have seen (Fig. 6.5) that noise levels in shallow water environments, such as a stream waterfall, may vary unpredictably even at short temporal and/or spatial scales. Such fluctuations in level and spectrum of the noise give rise to complex masking patterns in a sensitive ear that may greatly alter the spectral appearance of the sound and, hence, affect the subjective perception of the sound quality, even at a close distance from the source. Animals have developed many peripheral and central adaptations to cope with the negative effects of noise masking on signal perception (e.g. peripheral auditory filtering, auditory templates and feature detectors, cross channel analysis, and comodulation masking release; reviewed in Brumm and Slabbekoorn 2005). However, there is no way a sound embedded in noise can be reconstructed by the hearing system into its original spectrum, a process known as noise spectral subtraction (Boll 1979). These observations suggest a potential advantage of having absolute sensitivity above the prevailing ambient noise conditions of the environment is to avoid, or minimise, the negative effects of noise masking on complex auditory performances (such as signal recognition). The cost to be paid, of course, would be a lowered capability of the hearing system to detect potentially relevant sound stimuli. Thus, a tradeoff between the detection and recognition or discrimination of sound signals might take place when communication occurs under variable masking conditions. Furthermore, the tradeoff between these two functions might operate to set the optimal hearing sensitivity within the constraints of the species' environment (ambient noise characteristics, sound transmission properties, etc.).

6.8 Concluding Remarks

This chapter focused on acoustic communication by shallow-water fishes and the environmental factors promoting the use of low frequencies by these species. The constraining role of ambient noise, and the amplitude gain of the nest favouring the use of low frequencies by many cavity-nesting species, have been emphasised. Ambient noise appears to function as a constraining factor not only for the use of appropriate low-frequency bands for acoustic communication but also for the development of an optimal hearing sensitivity within a particular underwater environment.

Not all soniferous fishes live in very shallow waters, however. For instance, gadoid fish (e.g. cod, haddock) emit low-frequency sounds close to the bottom at great depths (Hawkins and Rasmussen 1978). Similarly, not all shallow-water fishes communicate using low frequencies. Environmental factors promoting the use of high frequencies by these species (i.e. predator detection, propagation conditions) have also been discussed by other authors (e.g. Ladich and Bass 2003). In the present chapter, sound transmission properties of the underwater environment and their effects on acoustic communication in different habitats have been only briefly mentioned. Again, this topic is examined in more detail in other reviews (Fine and Parmentier, this volume, Bass and Clark 2003).

Frequency composition aside, there are many other sound features (e.g. duration, temporal structure, amplitude and frequency modulation, emission rate) that may potentially evolve in response to acoustical properties of the environment in order to convey acoustic information reliably to intended receivers. For example, many teleosts (e.g. some gobies, toadfishes) produce mating sounds characterised by slow frequency modulation, concentration of acoustic energy at a main (low) frequency, and high repetition rates. These characteristics are typical of bird and mammal vocalisations that must propagate with little distortion through an environment characterised by reverberations and irregular amplitude fluctuations (Wiley and Richards 1982). Unfortunately, there is a paucity of experimental and comparative studies addressing the effect of acoustical environment on these sound traits amongst teleosts.

A number of studies have addressed the issue of short-term effects of both ambient and man-made noise on fish behaviour and hearing. Current evidence indicates that both types of noise may potentially impair fish sound detection and hearing, thereby hampering information-gathering processes important for acoustic communication (and orientation; reviewed in Ladich 2013). However, the long-term effects of increased noise levels on acoustic behaviour, perceptual abilities (including auditory scene analysis), and survival of fishes in their natural environments are largely unknown. For instance, although fishes show avoidance reactions in response to loud underwater noises (e.g. Picciulin et al. 2010), there are with one exception (Holt and Johnston 2014) no fish studies showing the presence of adaptive responses to increased noise levels, such as increased signal output, frequency shift, and the like, as observed in birds or mammals.

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Chapter 7
Sex Steroid-Dependent Modulation of Acoustic Communication Systems in Fishes

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Abstract Acoustic communication is widespread among fishes, the largest extant group of vertebrates, and in many vocal teleost species it is essential for their reproductive and social behaviors. Recent evidence suggests that a fish's internal hormonal state can profoundly influence its ability to produce and perceive social acoustic signals. Here, we review the current knowledge of how sex steroids can influence the auditory capabilities and vocal motor production of acoustic social signals in two incipient model teleosts, the plainfin midshipman fish *Porichthys notatus* and the African cichlid *Astatotilapia burtoni.* Studies of these model systems show that steroid-mediated improvements in vocal-acoustic processing are typically associated with reproductive readiness. This especially holds true for species that rely heavily on acoustic signaling during seasonal breeding such as the midshipman fish, as well as non-seasonally breeding species like cichlids that appear to use sound production as one component of a more complex multimodal courtship repertoire. Evidence for reproductive-state dependent plasticity in midshipman and cichlids is supported by changes in gonadal state, circulating sex-steroids (testosterone, 11-ketotestosterone, and estradiol), and steroid receptor expression in peripheral and central auditory structures that are concurrent with changes in auditory sensitivity and vocal motor production. This form of steroid-dependent vocal-acoustic plasticity is proposed to be an evolutionary labile solution for enhancing the detection and production of social acoustic signals. The abundance and diversity of vocal fish present unique future opportunities to explore how this solution may have shaped sexual selection and the evolution of acoustic communication systems in fishes.

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7.1 Introduction—Sex Steroids and Acoustic Communication Systems in Fishes

Sex steroids are a class of hormones that have profound organizational and activational effects on the vertebrate central nervous system (CNS) and are known to shape the expression of many social behaviors including those involved in courtship, reproduction, parental care, aggression, and communication. Sex steroids are derived from cholesterol and are synthesized in the brain, adrenal gland, and gonads (Schlinger and Remage-Healey 2012). Recent work suggests that the CNS may be modulated by both brain-derived steroids or "neurosteroids" and peripherally synthesized steroids or "neuroactive steroids". These activating hormones can regulate behavior by inducing an array of physiological and morphological changes in the CNS to shape the expression of behaviors such as those used in social communication.

Sex steroids such as androgens and estrogens are well-known modulators of vocal motor behaviors used during social and reproductive communication. These same steroid hormones are also known to greatly influence the production and reception of social acoustic signals leading to a more efficient exchange of information during communication. This steroid-dependent form of auditory plasticity is proposed to be an evolutionary labile solution for enhancing the detection of social acoustic signals during reproductive cycles in fishes (Sisneros et al. 2004a; Maruska et al. 2012). However, sensory plasticity related to reproductive-state and sex steroid levels is known to be widespread among vertebrates, including humans (Sisneros et al. 2004a; Walpurger et al. 2004; Hau et al. 2008; Arch and Narins 2009; Caras 2013).

Our review focuses on sex-steroid induced plasticity of the vocal-motor production and auditory reception of social acoustic signals during the reproductive cycle of fishes to enhance acoustic communication. We primarily report on recent evidence in two vocal teleost species, the plainfin midshipman fish (*Porichthys notatus*) and the African cichlid (*Astatotilapia burtoni*).

7.2 Reproduction, Sex Steroids, and the Midshipman Auditory System

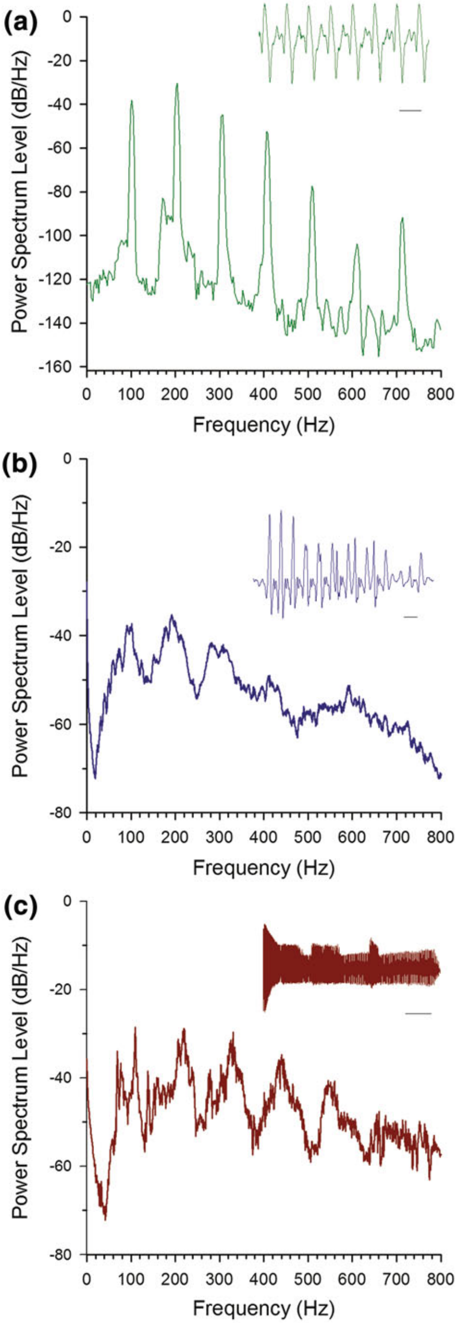
7.2.1 *Reproduction and Acoustic Communication in the Plainfin Midshipman Fish*

The plainfin midshipman is a marine teleost species that has become a productive neuroethological model for investigating the neural and endocrine mechanisms of acoustic communication among vertebrates, in part because the reception and production of social vocalizations is essential to their reproduction. Plainfin midshipman are vocal fish from the Family Batrachoididae (order Batrachoidiformes) that migrate seasonally during the spring and summer from the deep ocean off the west coast of British Columbia and the United States into the sub-tidal and shallow rocky intertidal zones where they breed (Miller and Lea 1972; Bass 1990, 1996). This species is known to have three adult morphs that include two types of males (types I and II) and females; each male morph employs a different reproductive tactic (Brantley and Bass 1994; Bass et al. 1999). Type I or "singing" males build and defend nests that are constructed under rocky shelters in the sub-tidal and rocky intertidal zones during the spring and summer breeding season (May–July). At night from their nests, type I males produce long-duration advertisement calls also known as "hums" to attract potential mates for spawning (Bass et al. 1999). This seasonal advertisement call is a multiharmonic social acoustic signal with a fundamental frequency (F_0) that is established by the contraction rate of the sonic muscles attached to the swim bladder, which acts as a resonant structure in the midshipman fish to help propagate the vocal-acoustic signals. The advertisement calls are relatively long in duration on the order of several minutes to 1 h with a F_0 of 90–100 Hz at temperatures of 15–16 °C (Ibara et al. 1983; Bass et al. 1999), however the F_0 is temperature dependent and is known to vary linearly with ambient temperature (Bass and Baker 1991; Brantley and Bass 1994). The harmonics of the advertisement call extend up to 800 Hz (Fig. 7.1a) and are very stable (Bass et al. 1999). Typically the hum's dominant harmonics range up to approximately 400 Hz, can contain more or equal spectral energy as the F_0, and have been hypothesized to be used by females in the localization of male advertisement calls during the reproductive season (Sisneros and Bass 2003; Sisneros 2009a). McKibben and Bass (1998) showed that females can respond selectively in two-choice tests and are capable of differentiating and choosing between acoustic signals that differ in duration, frequency, amplitude, and spectral/temporal content. Taken together, the results from McKibben and Bass (1998, 1999, 2001a, b) suggest that females could potentially utilize acoustic information in male advertisement calls to access mate quality and facilitate mate-choice decisions.

Type I males are also known to produce "grunt" trains and "growls". While all adult morphs (females and both male types) are capable of producing "grunts" (Fig. 7.1b) or short duration ($\sim$50–200 ms) broad band acoustic signals during agonistic interactions (Ibara et al. 1983; Brantley and Bass 1994), only type I males produce grunt trains or rapid succession of single grunts at a rate that ranges from 97 to 110 Hz (Brantley and Bass 1994; Bass et al. 1999). Type I males often use grunt trains to ward off nest intruders during the reproductive season. "Growls" are also agonistic calls and are often used in the defensive of a nest. Like the advertisement call, "growls" are only produced by type I males and are long-duration multiharmonic calls. Growls (Fig. 7.1c) begin with a grunt-like signal component followed by a multiharmonic component with a F_0 of 59–116 Hz that changes over that duration of the call (Bass et al. 1999). Type I males often produce growls during the early breeding season when these males are highly aggressive and territorial as they establish their nest sites.

Type II males also known as "sneaker" males employ an alternative reproductive and behavioral tactic during the breeding season. Type II males do not produce

Fig. 7.1 Power spectra and waveforms (insets) of representative vocalizations of the plainfin midshipman fish (*Porichthys notatus*) that include the hum, grunt, and growl recorded at 16°C from a nesting type I male. **a** The advertisement call or "hum" (inset, bar = 10 ms). **b** Grunt (inset, bar = 10 ms). **c** Growl (inset, bar = 500 ms)



advertisement calls or court females but instead satellite and/or "sneak" spawn in competition with type I males (Brantley and Bass 1994). Sneaker males invest less energy in body growth and instead invest more energy in the development of their gonads. Type II males can have testes as large as 15–20 % of their body mass which can presumably result in greater sperm production (Bass 1996; Brantley and Bass 1994; and JAS personal observation).

Reproductive females do not produce grunt trains, growls, or advertisement calls but instead are passive listeners that use audition to locate "singing" type I males to mate with during the breeding season. After a gravid female (full of eggs) has spawned with a type I male and has deposited all her eggs, she will then leave the intertidal nesting environment and return to deep offshore sites. Type I males remain with the fertilized eggs in the nest and will then continue to court and spawn with additional females over the course of the breeding season until their nests are filled with multiple clutches of eggs and developing larvae (DeMartini 1988; Brantley and Bass 1994; Bass and McKibben 2003; Sisneros et al. 2009a). The nesting type I males provide all the parental care of the nest eggs and larvae which include fanning and brushing the fertilized eggs to keep them free of detritus and bacteria. Nesting type I males vigorously defend and guard their nests from predators until the developing larvae have absorbed their yolk, detached from the nest, and become free swimming after approximately 50–60 days post fertilization at a relatively constant temperature of 15 °C (Alderks and Sisneros 2013).

The primary end organ used for hearing in the midshipman is the saccule. The midshipman inner ear, like other teleost fishes, includes three semicircular canals and three otolithic acoustic end organs: the utricle, lagena, and saccule. All three otolithic end organs are innervated by cranial nerve VIII, but the saccule serves as the main hearing organ in most teleost fishes (Popper 2011). The sensitivity and frequency response of the midshipman auditory peripheral nervous system (PNS) including the hair cells and afferents of the saccule have been extensively quantified (McKibben and Bass 1999, 2001a; Sisneros and Bass 2003, 2005; Sisneros 2009b). In general, the hair cells and afferents of the saccule are broadly tuned with peak frequency sensitivity at low frequencies (<150 Hz) associated with midshipman vocalizations (McKibben and Bass 1999; Sisneros and Bass 2005; Sisneros 2007). Ontogenetic comparisons of saccular afferent data from adult and juvenile midshipman indicate that the saccular primary afferents of juveniles, like those of nonreproductive adults, are best adapted to temporally encode the low frequencies within midshipman vocalizations (Sisneros and Bass 2005).

7.2.2 Seasonal Plasticity of the Midshipman Auditory System

Behavioral studies of the midshipman's spawning behavior and acoustic playback responses showed that reproductive females (full of eggs) exhibit strong phonotaxis to natural and synthetic advertisement calls, whereas recently spawned females (void of eggs) do not respond to the advertisement call (McKibben and Bass 1998, 2001b;

Zeddies et al. 2010, 2012). Based on these experiments and the fact that nocturnally-active females rely on audition to locate mates, Sisneros and Bass (2003) tested the hypothesis that seasonal reproductive state (gravid vs. non-gravid) influenced the frequency response and sensitivity of the auditory system (Sisneros and Bass 2003). Results from Sisneros and Bass (2003) showed that saccular afferents from summer reproductive females exhibited greater phase-locking accuracy to frequencies of 120–400 Hz and had higher peak frequency sensitivity than that recorded for winter nonreproductive females. In addition, Sisneros (2009b) showed that in reproductive females saccular hair cells were more sensitive (i.e., lower thresholds, ~8–13 dB or 2.5–4.5 times lower) than nonreproductive females to frequencies 75–385 Hz. Together these studies showed that the sensitivity of the midshipman's peripheral auditory system was related to the female reproductive cycle such that breeding females were better adapted than non-breeding females to perceive the dominant harmonic frequencies in the male's mate call (Sisneros and Bass 2003; Sisneros 2009b).

The detection of male advertisement call harmonics by reproductive females likely increases the probability of mate localization due to the sound transmission properties of shallow water acoustic environments like those where plainfin midshipman court and breed. The harmonics of the advertisement call have been proposed to provide enhanced signal detection of the advertisement call for females because the call's dominant harmonics (200–400 Hz) will propagate farther than the lower F_0 (~80–100 Hz) in shallow water environments due to an inverse relationship between water depth and the cutoff frequency of sound transmission (Fine and Lenhardt 1983; Roger and Cox 1988; Sisneros and Bass 2003; Sisneros 2009c) (see also Chap. 6 by Lugli this volume). In very shallow water (<3 m), substrate composition (e.g., rocky substrate like that found in the midshipman's nesting environment) also becomes an important factor that is likely to affect the cutoff frequency of signal propagation and attenuate the transmission of acoustic signals less than 150 Hz (Roger and Cox 1988; Bass and Clark 2003). In addition, the harmonics of the mate call produce by males may also affect the receiver's detection of the signal when near the source of the advertisement call. McKibben and Bass (2001a) showed that saccular afferent detection of a tone at or near the F_0 of the mate call was improved when tones similar to harmonics were added to the presentation stimuli. In sum, this seasonal enhancement of auditory sensitivity likely represents an adaptation of the teleost auditory system to facilitate the detection of advertisement calls and enable females to acquire acoustic information needed for the recognition, identification, and localization of potential mates.

Recently, Coffin et al. (2012) showed that females undergo seasonal changes in hair cell sensitivity that were concurrent with changes in hair cell density in the midshipman saccule. Summer reproductive females were found to have greater hair cell receptor density in the saccule than winter nonreproductive females (Fig. 7.2a), but this change in receptor density did not occur in the other two inner end organs, the utricle, and lagena. The seasonal change in hair cell addition was not dependent on fish body size and the increase in saccular hair cell density was consistent across the size range of fish sampled. Coffin et al. (2012) also observed a seasonal increase

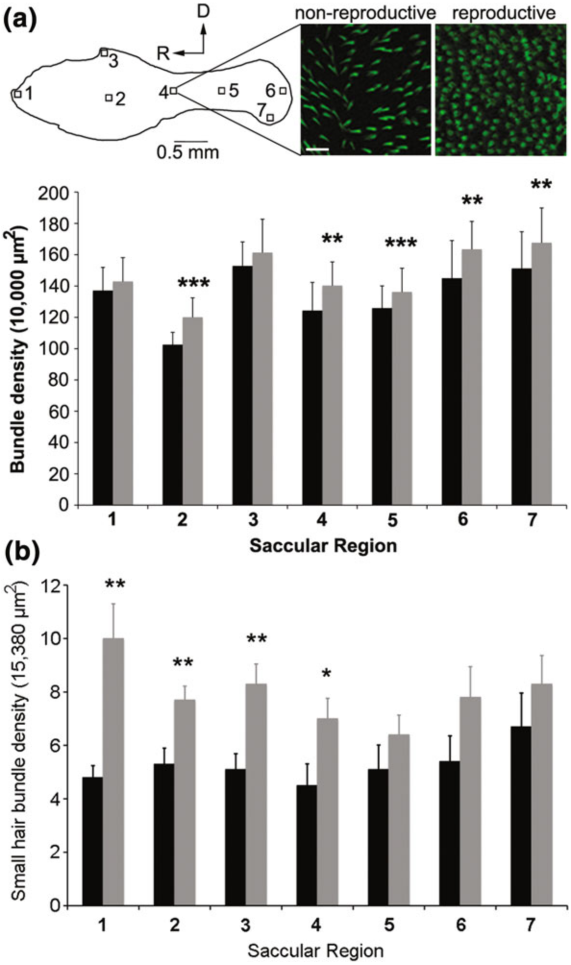


Fig. 7.2 Seasonal differences in hair bundle density and in the number of small hair bundles in the saccule of female midshipman (*P. notatus*). All data are plotted as means + 1 SE. **a** Phalloidin-labeled hair bundles were counted in 10,000 μm^2 areas from seven regions across the saccule, as indicated by the numbered boxes on the line drawing (*top portion of figure*). The micrographs (*top right*) show representative images from the *middle* of the saccule from a nonreproductive and reproductive female. Hair bundle quantification from these seven saccular regions (*bottom portion of figure*) shows significantly more hair cells in noted regions (** $p < 0.01$; *** $p < 0.001$). Note: *black bars*, nonreproductive females; *gray bars*, reproductive females. (Modified from Coffin et al. 2012). **b** Small hair bundles were counted in seven 15,380 μm^2 regions of ten saccules from both reproductive (*gray bars*) and nonreproductive (*black bars*) females. There were significantly higher densities of small hair bundles between reproductive and nonreproductive females in the noted saccular regions (* $p < 0.05$; ** $p < 0.01$). (Modified from Coffin et al. 2012)

in the number of small saccular hair bundles in reproductive females (Fig. 7.2b) that were hypothesized to be either mature hair cells with a distinct subtype of morphology or potentially immature hair cells. One possible explanation suggested by the authors was that the smaller hair bundles in breeding females represented immature saccular hair cells that were the product of increased hair cell proliferation that occurred earlier in the spring during the pre-nesting period (Sisneros et al. 2004b). The seasonal increase in saccular hair cell density observed in reproductive females occurred concurrently with increases in the magnitude of the evoked potentials of the saccule and had a corresponding decrease in the auditory thresholds of saccular hair cells (Fig. 7.3). This recent demonstration of concurrent seasonal change in hair cell receptor density and auditory sensitivity may represent one of the mechanisms that contribute to the increased saccular sensitivity observed seasonally in reproductive female midshipman.

In addition to seasonal changes in female auditory sensitivity, seasonal auditory plasticity is also known to occur in type I nesting males. Rohmann and Bass (2011) showed that the saccular hair cell thresholds of reproductive type I males were significantly lower than that of nonreproductive type I males at frequencies greater than 145 Hz. This seasonal frequency-dependent change in auditory sensitivity was most apparent at frequencies that were associated with the dominant harmonics in the male advertisement call (approx. 180–400 Hz) (Rohmann and Bass 2011).

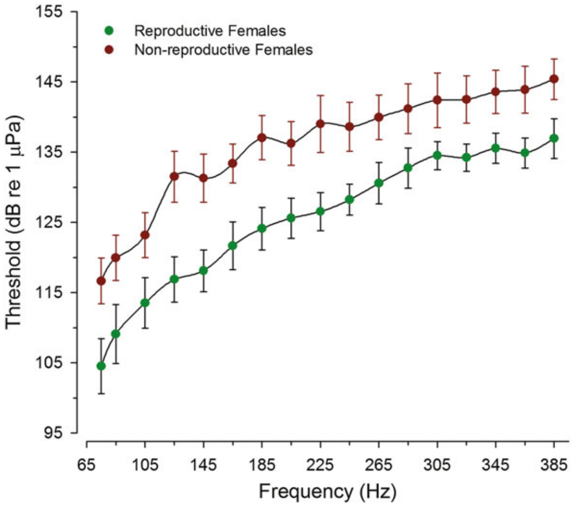


Fig. 7.3 Auditory threshold tuning curves for reproductive and nonreproductive female midshipman (*P. notatus*) based on the evoked potentials recorded from the saccule. All data are plotted as means ±95 % CL. The sample size for the reproductive females (*green circles*) was 12 animals (16 recordings) while the sample size for the nonreproductive females (*red circles*) was 12 animals (20 recordings). Auditory threshold at each stimulus frequency was determined as the lowest stimulus intensity in decibels (re 1 µPa) that evoked a saccular potential that was at least 2 SD above the background noise measurement. (Modified from Coffin et al. 2012)

One adaptive function for this seasonal enhancement of hearing in type I males may be to assess other males during intraspecific male competition and during nest establishment in the breeding season. The future work needs to determine whether or not seasonal changes in auditory sensitivity also occur in type II sneaker males. There is no reason to expect that such changes would be limited to females and type I males. One could hypothesize that the seasonal increase in auditory sensitivity would also benefit type II males in their ability to detect and assess calling type I males for the selection of cuckoldry sites during the breeding season.

7.2.3 Steroid-Dependent Plasticity of Midshipman Auditory System

In natural populations of plainfin midshipman, sex steroids levels are known to fluctuate seasonally with the reproductive cycle and correspond to seasonal changes in reproductive biology and behavior (Brantley et al. 1993; Knapp et al. 1999; Sisneros et al. 2004b). There are four time periods that correspond to the annual reproductive cycle in the plainfin midshipman: the nonreproductive, prenesting, nesting, and postnesting periods (Sisneros et al. 2004b). The nonreproductive period occurs in the winter from December to February when females have a low gonadal somatic index (GSI, ratio of gonad to body mass) with ovaries containing undeveloped oocytes and low estradiol (E_2) and testosterone (T) plasma levels, whereas type I males have a similar low GSI with no sperm present and low T and 11-ketotestosterone (11-KT) plasma levels. The prenesting period occurs in the spring (March–April) when both females and type I males exhibit seasonal development of the ovaries and testes, respectively, with females exhibiting a brief spike of E_2 and T plasma levels in April about 1 month prior to the summer breeding season while type I males continue to show a gradual increase in T and 11-KT plasma levels during gonadal recrudescence. The nesting period occurs in late-spring and summer (May–August) when breeding females have high GSI with well-developed eggs ($\sim$5 mm diameter) and low T and E_2 levels while type I males exhibit an intermediate GSI with T and 11-KT levels that peak at the start of the summer nesting season (May–June). During the nesting period, "humming" type I males have significantly higher plasma levels of 11-KT than non-humming males (Genova et al. 2012). The postnesting period occurs in the fall months (September–October) when females and type I males show a marked decrease in GSI and in E_2, T, and 11-KT plasma levels.

The spring prenesting peak of circulating blood levels of E_2 and T exhibited by females, which occurs approximately 30 days before the reproductive season begins, led Sisneros et al. (2004a) to hypothesize that E_2 and T could induce seasonal changes in peripheral auditory sensitivity via enhancements in phase-locking accuracy and changes in peak frequency sensitivity of saccular afferents in nonreproductive individuals. Sisneros et al. (2004a) showed that ovariectomized

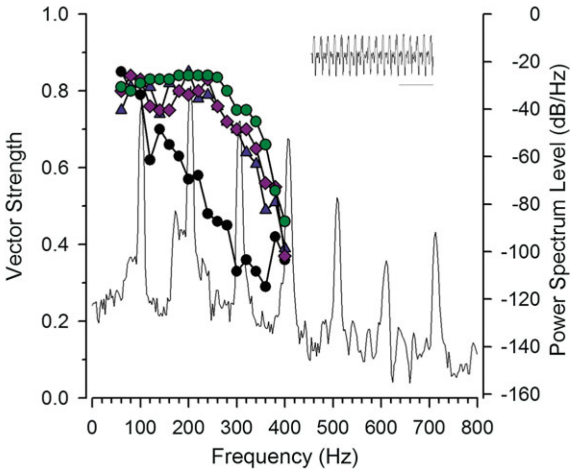


Fig. 7.4 The adaptive coupling between the frequency encoding of saccular afferents and the dominant harmonic components in the male advertisement call of the plainfin midshipman fish (*P. notatus*). The type I male midshipman advertisement call or "hum" recorded at 16 C is shown in the *inset* (bar = 10 ms) above the main combined plot of the phase-locking precision of saccular afferents as a function of the vector strength of synchronization (*VS, left y-axis*) and the power (*amplitude*) spectrum level of the hum (*right y-axis, in relative dB values*) from a nesting type I male. Plotted are the median Vector Strength values of the saccular afferents emphasizing the overlap in frequency sensitivity between testosterone-treated (*blue triangles*) and 17β-estradiol-treated (*pink diamonds*) nonreproductive females and wild-caught reproductive females (*green circles*). Steroid-treated and wild-caught reproductive females show robust encoding of the fundamental frequency (~100 Hz) and the second (~200 Hz) and third (~300 Hz) harmonics of the hum. In contrast, winter nonreproductive females (*black circles*) show comparable encoding only for frequency close to the fundamental frequency at approximately 100 Hz. Adapted from Sisneros et al. (2004b)

nonreproductive females implanted with either E_2 or T capsules to produce prenesting steroid levels resulted in an improvement of phase-locking accuracy of saccular afferents at higher frequencies within the midshipman hearing range. These steroid induced changes improved the encoding of saccular afferents at frequencies that corresponded to the major harmonic components of the advertisement call and was similar to the female reproductive auditory phenotype (Fig. 7.4). Furthermore, an estrogen receptor alpha (ERα) specific for midshipman was cloned and identified by real-time reverse transcription polymerase chain reaction in the sensory macula of the saccule and provides further evidence for direct effects of sex steroids on the peripheral auditory system of teleosts (Sisneros et al. 2004a).

One mechanism that could explain the seasonal change in hair-cell frequency sensitivity (Sisneros 2009b; Rohmann et al. 2011) is a reproductive-state dependent change in ion channel expression of midshipman saccular hair cells (Rohmann et al. 2013), which is almost certainly linked to seasonal fluctuations in steroid hormone levels. Rohmann et al. (2013) recently demonstrated that reproductive midshipman show increased abundance of Ca^+-activated potassium (BK) channels in saccular hair cells which are thought to enhance the midshipman's ability to "hear" social acoustic signals during the reproductive season. The large conductance BK channels are known to underlie the primary outward hair cell current and influence the electrical resonance and frequency tuning of hair cells in nonmammals (Fettiplace and Fuchs 1999). Rohmann et al. (2013) showed pharmacological manipulation that reduced BK currents replicated the natural range of hair cell sensitivity of the saccule in midshipman. These pharmacological manipulations targeting BK channels, together with the increased measures of BK transcript abundance, could explain the observed seasonal increase in auditory sensitivity to the higher harmonics of the midshipman vocalizations (Rohmann et al. 2013).

In addition to their effects on the midshipman auditory system, sex steroids are also known to have both rapid and long-term effects on the vocal motor behavior and activity of the central pattern generator of the vocal motor system in type I males. Androgens (T and 11-KT) and estrogen have been shown to regulate vocal motor output and call production in the midshipman and the closely related Gulf toadfish (*Opsanus beta*). For a more detailed review of the sonic motor behaviors and the effects of sex steroids on the associated neural mechanisms of the vocal motor system in midshipman and toadfish see Bass et al. (Chap. 2 in this volume), Bass and McKibben (2003), and Bass and Ladich (2008).

The distribution of estrogen and androgen receptors has been described extensively for the vocal and auditory networks in the midshipman (for more detailed descriptions see Forlano et al. 2005, 2010; Fergus and Bass 2013). In sum, Forlano et al. (2005) described the distribution of ERα mRNA in the saccule and brain of reproductive females and type I males and identified transcripts in liver and ovary, the CNS, and in the VIII nerve branches of the saccule proximal to the sensory epithelium. More recently, Fergus and Bass (2013) identified estrogen receptors ERβ1 and ERβ2 in midshipman vocal–acoustic networks of the CNS and in the saccule. In that study, Fergus and Bass (2013) developed antibodies to localize protein expression in the vocal-acoustic areas of the peripheral and central nervous systems and showed that ERβ1 and ERβ2 receptors were expressed in the telencephalon, hypothalamus, and in other vocal–acoustic brain regions shown previously to exhibit expression of ERα and aromatase. In addition, both ERβ1 and ERβ2 were expressed within the hair cells of the saccular epithelium with ERβ1 being expressed in a very small region at the apical end of hair cells immediately adjacent to the hair bundle while ERβ2 was expressed more broadly within hair cells and within the ganglion cells of the VIII nerve proximal to the sensory macula of the saccule (Fergus and Bass 2013). Forlano et al. (2010) described the distribution of androgen receptor mRNA throughout the CNS with transcripts found in the vocal pre pacemaker nucleus, dorsal periphery of the vocal motor nucleus, and in the saccule.

An additional candidate site for sex steroid effects on the auditory system may include the saccular efferents that project from hindbrain and diencephalic efferent nuclei to the base of saccular hair cells (Forlano et al. 2014). Saccular efferent neurons provide inhibitory input to the saccular afferents and their hair cells from the CNS and can modulate the sensitivity or gain of the saccule (Furukawa and

Matsura 1978; Lin and Faber 1988). Xiao and Suga (2002) showed that auditory neurons in the mammalian cortex are able to modulate the frequency response and sensitivity of hair cells in the cochlea. Future work that examines the steroid-dependent effects of efferent modulation of the midshipman PNS may prove fruitful. In sum, the distribution of estrogen and androgen receptors in the inner ear saccule and brain strongly supports the role of these sex steroids as neuromodulators of behaviorally defined auditory, vocal, and neuroendocrine circuits in the midshipman and teleost fishes in general.

7.3 Sex Steroids and the Cichlid Auditory System

7.3.1 Acoustic Communication in Cichlids

Cichlids represent a large and diverse group of freshwater fishes, well-known for their flashy coloration patterns and visually conspicuous behavioral displays. Recently, however, the importance of non-visual signaling (acoustic, chemosensory, mechanosensory, tactile) during social interactions such as aggression and mating has come to the forefront. Previous studies suggest that single traits, such as those involved in visual signaling, are often insufficient to explain phenotypic diversity in cichlids, and that species richness is a function of the number of traits involved in diversification (i.e., the “multifarious selection” hypothesis) (Blais et al. 2009; Nosil and Harmon 2009; Nosil et al. 2009). Thus, the use of multimodal communication systems for social interactions provides more traits on which sexual selection can act, possibly contributing to the high diversity of cichlid fishes (Blais et al. 2009; Sturmbauer et al. 2011). Consequently, there has been significant recent interest in understanding the function and diversity of acoustic signaling in cichlids, with sound production and/or hearing abilities now described for a number of African, American, and Asian cichlid species (Yan and Popper 1992; Ripley et al. 2002; Amorim et al. 2004; Amorim 2006; Simoes et al. 2008; Maruska et al. 2012; Schulz-Mirbach et al. 2012).

Many cichlid fishes use sounds for species or individual recognition (Amorim et al. 2008; Verzijden et al. 2010; Bertucci et al. 2012a; Longrie et al. 2013), during territorial or agonistic interactions (Amorim 2006; Simoes et al. 2008; Bertucci et al. 2012b), and during reproductive courtship contexts (Amorim et al. 2003, 2008; Maruska et al. 2012). Cichlids are one of the most visually conspicuous groups of fishes, with complex coloration patterns and elaborate courtship behavioral displays. Thus, visual communication is extremely important in this group, and sounds are likely used as a supplement to this rich visual information, which differs from the case in batrachoidid fishes (toadfish, midshipman) that use acoustic signaling as a primary sensory channel. Descriptions of sound production in cichlids thus far show that sounds are not typically used alone, but are produced concurrent with visual display behaviors (Ripley and Lobel 2004; Maruska et al. 2012; Longrie et al. 2013).

For example, in the Lake Malawi cichlid *Metriaclima zebra*, sounds produced during male-male interactions reduced opponent aggression as a complement to visual displays, thereby potentially lowering the risk of escalated fights (Bertucci et al. 2010). In the Lake Victoria cichlid *Pundamilia nyererei*, playback experiments showed that while both males and females can discriminate conspecific sounds compared to noise controls, females do not display phonotaxis toward courtship sounds without the presence of a live male (Estramil et al. 2013). In the African cichlids *P. nyererei* and *A. burtoni*, however, playback experiments that consisted of visual and acoustic signals that were temporally uncoupled from each other showed that courtship sounds alone influenced a female's preference before she could see the male (Verzijden et al. 2010; Maruska et al. 2012). These experiments suggest that while a live male may be required to elicit receptive behaviors in a female and ultimately determine her mate choice decision, simply overhearing courtship sounds alone may provide the female with some valuable information such as the presence and relative quality of a courting male in the area. Nevertheless, sound production in cichlids is likely one component of a complex multimodal signaling system that complements visual, chemosensory, mechanosensory, and tactile cues.

7.3.2 Steroids and Acoustic Communication in the Model African Cichlid Astatotilapia burtoni

The African cichlid fish *A. burtoni* is an excellent and emerging model for studying the role of acoustic communication as part of a multimodal signaling system used during reproduction, and for investigating the role of internal hormonal state on auditory processing. Importantly, this species already has a wealth of available information on its social behaviors, reproductive physiology, steroid cycling, and communication modalities, as well as an understanding of the remarkable plasticity in behavior and physiology associated with changes in social status and reproductive state [reviewed in (Maruska and Fernald 2011a, 2013; Fernald and Maruska 2012)]. Further, genomic resources for *A. burtoni* are now available, along with those of four other African cichlid species, providing important molecular tools for understanding the mechanisms of putative steroid-induced plasticity in behavior and sensory processing in comparative and evolutionary contexts.

7.3.2.1 Natural History and Social Behavior of *A. burtoni*

Astatotilapia burtoni is endemic to Lake Tanganyika, the oldest, deepest, and most diverse lake within the rift valley system of Eastern Africa. This species lives primarily in shallow shore pools and river estuaries, where visual conditions are often variable, and environmental parameters are dynamic (Fernald and Hirata 1977).

Adult males exist in two distinct but reversible phenotypes, which differ in appearance, behavior, morphology, activity of their brain-pituitary-gonadal axis, and ultimately reproductive capacity [reviewed in (Fernald 2009; Maruska and Fernald 2011a, 2013; Fernald and Maruska 2012). Dominant (also called territorial) males represent a small percentage of the adult male population (~ 10–30 %), are brightly colored (blue or yellow) with a black stripe through the eye (eye-bar), an opercular black spot at the caudal tip of the gill cover, prominent egg-spots on the anal fin, and a red humeral patch on the side of the body. These dominant males hold territories that they defend vigorously from rival males, and spend significant amounts of time engaged in courtship displays and eventually spawning with females (Fernald 1977; Fernald and Hirata 1977). In contrast, subordinate (also called non-territorial) males make up the majority of the adult male population (~ 70–90 %), are more dull in coloration and similar to females (lacking eye-bar and humeral patch), do not hold territories or typically reproduce, school with females and other subordinate males, and flee from the aggressive attacks of dominant males.

Astatotilapia burtoni lives in a lek-like social system where dominant males defend clustered territories to guard food, shelter, and spawning substrates from rival males (Fernald 1977). Dominant males establish a spawning area by digging a pit in their territory, engage in agonistic threat displays and border disputes with neighboring dominant males, chase subordinate males away from their territory, and perform courtship quivers toward passing females in an attempt to lead them into their territory to spawn. Since defendable territories for spawning and feeding are often limited, and females are less likely to mate outside the protection of a spawning shelter, there is fierce competition for this resource. As a result, only a minority of males at any one time will defend a territory and successfully mate with females. Typical territory tenure lasts about 4–6 weeks (Fernald and Hirata 1977; Hofmann et al. 1999), and if a dominant male is either challenged by a subordinate male, or disappears from the population, a subordinate male will rise in social rank, and within minutes, display dominance and reproductive behaviors (Burmeister et al. 2005; Maruska and Fernald 2010a). Once a receptive (gravid, "ripe with eggs") female follows a dominant male into his territory and is appropriately stimulated, she will deposit eggs on the substrate and then immediately turn around and collect them into her mouth. The male then displays the egg-spots on his anal fin in front of her, and while she attempts to collect these egg-spots, the male releases sperm near her mouth to fertilize the eggs inside. There are typically several bouts of egg-laying and fertilization that may be briefly interrupted as the dominant male chases away intruders or interacts with neighboring males. During these spawning bouts, subordinate males will also attempt to interrupt the pair and "sneak" fertilization attempts; although these subordinate males do not defend territories, they do maintain sperm in their testes during social suppression (Maruska and Fernald 2011b; Kustan et al. 2012). When spawning and fertilization are complete, the dominant male resumes his territorial defense and continues to court other receptive females, while the female leaves the territory to brood the young in her mouth (mouth-brooding) for ~ 2 weeks until releasing them as fully-developed fry. Following brood release, females will resume feeding and immediately begin ovarian recrudescence to prepare for subsequent spawning. In contrast to the seasonally breeding midshipman fish described above, *A. burtoni* is a non-seasonal breeder, and while individual females cycle between spawning and brooding every ~28 days (Kidd et al. 2013), dominant males maintain territories and are continuously available for receptive females year-round.

7.3.2.2 Acoustic Communication in *A. burtoni*

As in many cichlids, social communication in *A. burtoni* relies heavily on visual signals (Fernald 1977; Fernald and Hirata 1977; Fernald 1984; Clement et al. 2005), but several studies have now demonstrated the importance of multimodal signaling, including chemosensory and acoustic communication (Crapon de Caprona 1974, 1980; Nelissen 1977; Robison et al. 1998; Maruska and Fernald 2010b, c, 2012; Maruska et al. 2012). Dominant male *A. burtoni* produce pulsed (range, 2–19 pulses; mean, 8.5 pulses per sound) relatively broadband (peak frequency range, 129–904 Hz; mean, 500 Hz) sounds during body quivers associated with courtship behaviors (Maruska et al. 2012) (Fig. 7.5a, b). These sounds are similar to courtship sounds described in other cichlid species (Amorim et al. 2003, 2008; Verzijden et al. 2010), and are intentional (not merely a by-product of body movements), because while sounds are only produced during quivers, not all quiver behaviors are associated with sound production (Fig. 7.5c). Dominant males typically swim out rapidly from their territory shelter toward a receptive female, perform a visual-acoustic quiver display in close proximity to the female (Fig. 7.5a), and then turn around and swim back toward the territory with an exaggerated tail waggle in an attempt to lead the female into the shelter for spawning. The close-proximity of signaling individuals to receivers, as well as the low intensity and rapid attenuation of these courtship sounds, suggests they are used primarily for close-range communication. Larger males produce courtship sounds with lower peak frequencies compared to smaller males, potentially providing females, subordinate males, and neighboring dominant males with an honest indicator of signaler body size (Maruska et al. 2012). Larger dominant males also show a greater percentage of visual quiver displays that are associated with sound production compared to smaller males, suggesting that male experience or age may play a role in acoustic signaling during reproduction. Whether or not female *A. burtoni* also produce sounds, or whether sounds are produced during male–male agonistic interactions or other specific behaviors requires further testing.

Auditory evoked potential (AEP) recordings in *A. burtoni* show that both males and females are most sensitive to low frequency sounds (~200–600 Hz; best frequency, 200–300 Hz), which overlaps the spectral content of the courtship sounds produced by dominant males (Maruska et al. 2012) (Fig. 7.6a, b). Playback experiments also demonstrate that gravid females prefer males associated with courtship sound production over males without sounds or males associated with noise control sounds, suggesting that they gain some valuable information on male

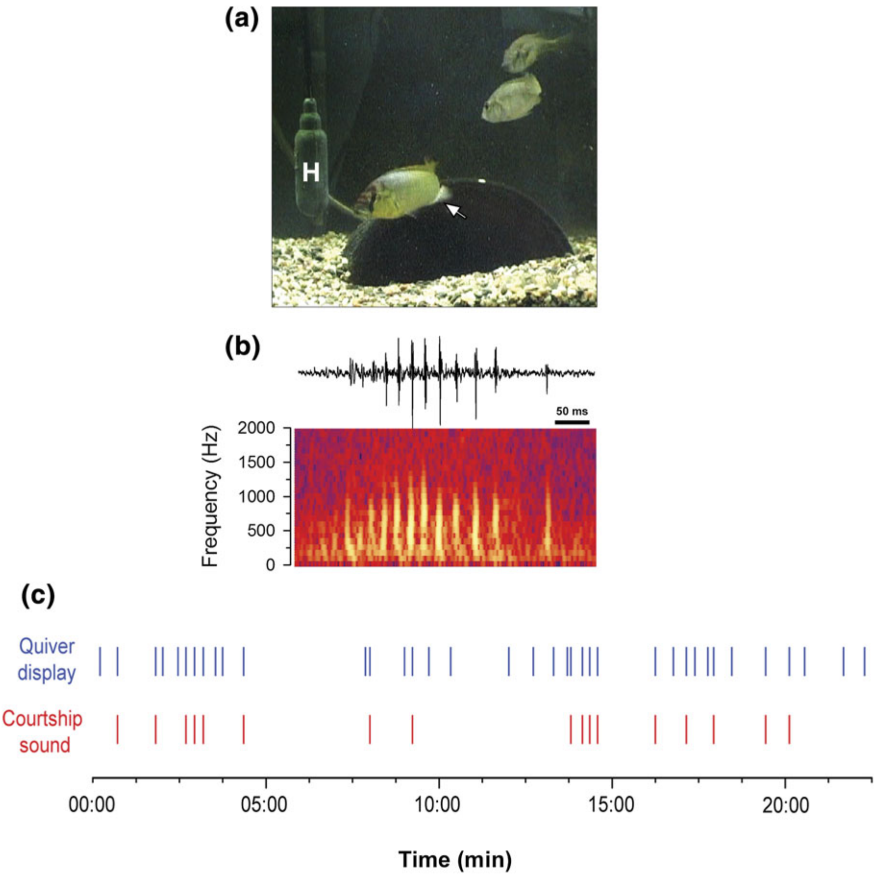


Fig. 7.5 *Brightly-colored* dominant male cichlids, *Astatotilapia burtoni*, produce pulsed sounds during body quiver behavior as part of visual-acoustic courtship displays. **a** Photograph of a *yellow* dominant male in front of his territory shelter performing a quiver and courtship sound while presenting his anal fin egg spots (*arrow*) toward attentive reproductively-receptive females. H, hydrophone. **b** Representative waveform and spectrogram of a pulsed broadband courtship sound produced by a dominant male. **c** Temporal sequence of courtship sounds (*red lines*) and visual quiver displays (*blue lines*) produced by an individual dominant male shows that not all quivers are associated with sound production. The percentage of visual quivers associated with sound production is also positively correlated with male body size in *A. burtoni*. (Modified from Maruska et al. 2012)

quality, status, or motivation from his sounds (Maruska et al. 2012) (Fig. 7.7). Thus, *A. burtoni* dominant males use sound production as part of their multimodal courtship repertoire, and females are attending to these sounds. What type of information these sounds provide to females and how it is integrated with other sensory channels in the brain to control mating decisions requires further study.

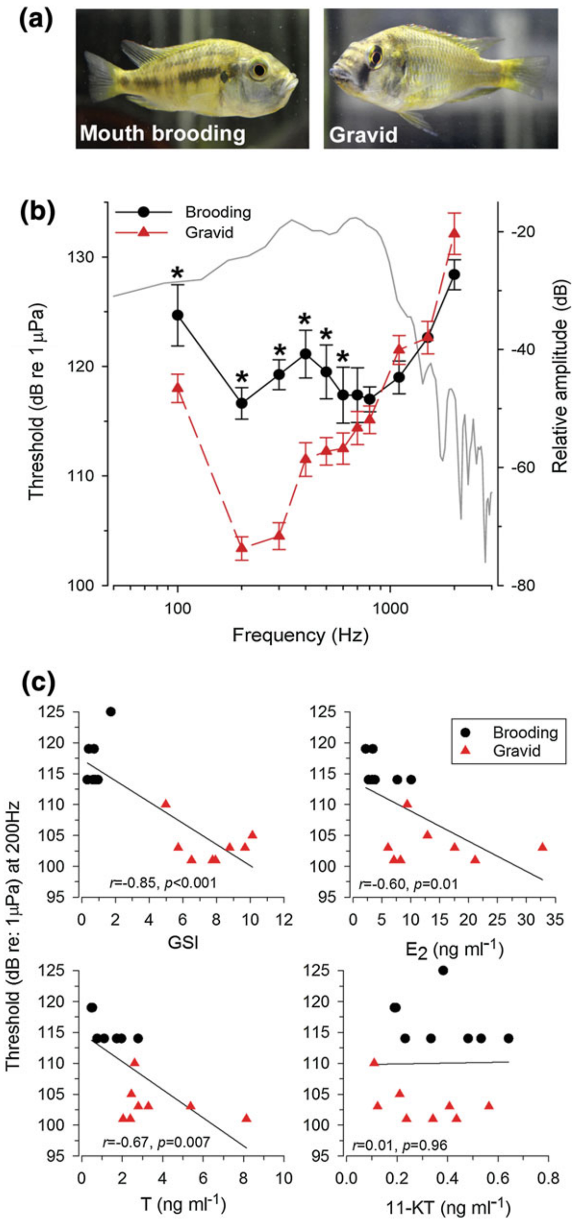


Fig. 7.6 Hearing thresholds in *A. burtoni* differ with female reproductive state and circulating sex-steroid levels. **a** Photographs of a reproductively-receptive gravid female and a parental care phase mouth-brooding female cichlid. **b** Hearing thresholds measured via auditory evoked potentials (AEP) show that gravid females have lower thresholds at low frequencies from 100 to 600 Hz compared to mouth-brooding females, which overlaps the spectral content found in male courtship sounds. Data are plotted as mean ± SE (*left axis*) and *asterisks* indicate statistical differences between female reproductive states within a frequency. *Gray line* represents the power spectra of a representative male courtship sound for comparison. **c** Auditory thresholds at best frequency (200 Hz) are also negatively correlated with gonadosomatic index (GSI), and plasma levels of T and E_2, but not 11KT, suggesting that receptive females with higher steroid titers have improved hearing sensitivity. (Modified from Maruska et al. 2012)

7.3.2.3 Steroid Cycling and Sex-Steroid Receptors in *A. burtoni*

In contrast to the seasonally-breeding midshipman fish, *A. burtoni* breeds year-round, but both males and females still undergo cyclical changes in circulating sex-steroid levels related to social status and gonadal state (Parikh et al. 2006; Maruska and

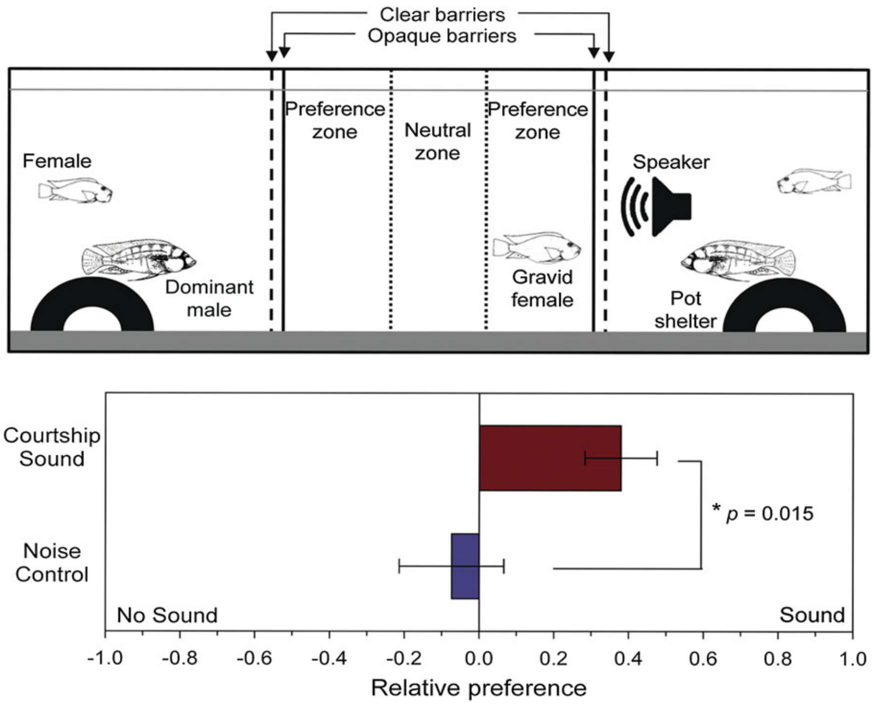


Fig. 7.7 Gravid receptive female cichlids prefer to affiliate with males associated with playbacks of courtship sounds compared to no sounds and noise controls. *Top* shows the experimental tank setup used for female preference trials. *Bottom* shows the relative preference (mean ± SE, $N = 10$ females per sound condition) of gravid females for males associated with playback of courtship sounds compared to playbacks of control noise sounds. (Modified from Maruska et al. 2012)

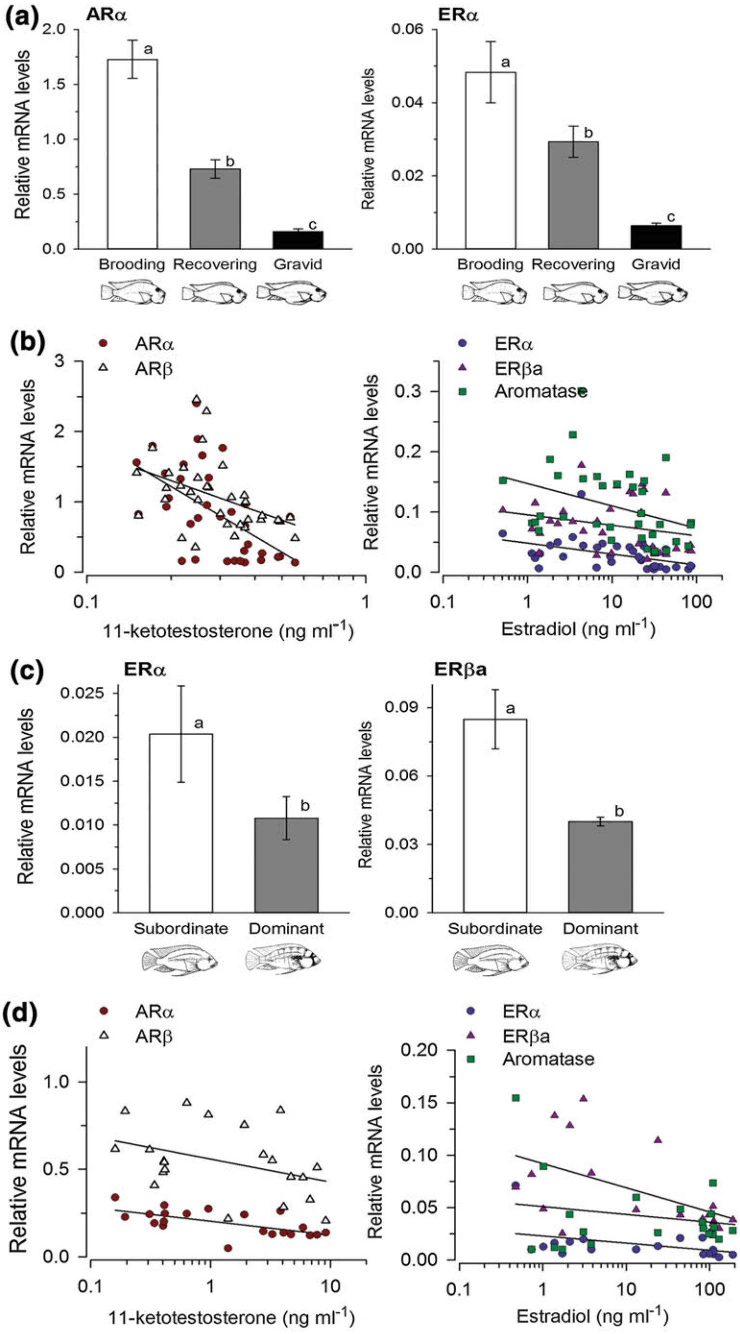
Fernald 2010c; Grone et al. 2012; O'Connell and Hofmann 2012; Renn et al. 2012; Maruska et al. 2013). For example, dominant reproductively-active males have higher plasma levels of testosterone (T), 11-ketotestosterone (11-KT; a potent fish-specific androgen), 17β-estradiol (E_2), and progesterone compared to subordinate males. Similarly, gravid females have higher circulating levels of androgens (T and 11-KT) and E_2 than recovering females (midway between brooding and gravid states), which in turn, have higher steroid levels than mouth-brooding females. Further, relative steroid sensitivity, measured by changes in sex-steroid receptor mRNA levels, also varies with reproductive state in both the saccule of the inner ear and within specific nuclei in the brain (although auditory processing regions have not yet specifically been examined) (Fig. 7.8a, b) (Maruska and Fernald 2010c; Maruska et al. 2013). In the saccule of males, for example, mRNA levels of the estrogen receptors (ER), ERα and ERßa, are higher in subordinate compared to dominant individuals (Fig. 7.8c), while there are no social status differences in androgen receptor (AR) subtypes, ERßb, or aromatase. Females also have higher relative mRNA levels of aromatase, ARα, ARß, and ERα, but not ERßa or ERßb, in the saccule compared to males (Maruska and

Fernald 2010c). These receptor expression levels in females are also negatively correlated with circulating androgen and estradiol levels, suggesting down-regulation of ARs and ERs by elevated sex-steroids produced by the developing ovaries as females approach spawning (Fig. 7.8b). Similarly, the same receptor expression levels are also negatively correlated with circulating androgen and estradiol levels in males (Fig. 7.8d). Saccular levels of some steroid receptors (ARα, ARß, ERα, ERßa, aromatase), but not others (ERßb), differ among reproductive states in female *A. burtoni*, with mouth-brooding individuals always having higher receptor expression compared to gravid individuals (Fig. 7.8a). These reproductive and social state changes in hormone cycling and relative steroid sensitivity provide the substrate for steroid-induced plasticity of acoustic communication in this species.

7.3.2.4 Sex Steroids and Hearing in *A. burtoni*

Gravid sexually-receptive female *A. burtoni* have lower hearing thresholds (~5–15 dB SPL re: 1 µPa lower) at low frequencies (100–600 Hz) compared to mouth-brooding females in the parental care phase of the reproductive cycle, while thresholds at higher frequencies (>600 Hz) do not differ between female states (Maruska et al. 2012) (Fig. 7.6a, b). This improved hearing in the spectral range of male courtship sounds may allow females to detect courting males at greater distances, or to better discriminate individual male qualities within the lek, both of which can lead to more informed mating decisions and increased reproductive fitness. Hearing thresholds are similar between dominant and subordinate males, but subordinate males have slightly lower thresholds (~3–6 dB) at high frequencies between 600 and 800 Hz. The biological significance of this difference is unclear, but one hypothesis is that improved hearing near the upper spectral range of male courtship sounds could allow subordinate males to better locate territories of smaller dominant males (e.g., individuals that produce higher frequency sounds) where they might have a better chance for sneak fertilization attempts, or of winning a challenge with a smaller resident male to then acquire his territory.

Hearing thresholds in *A. burtoni* are also correlated with circulating sex-steroid levels in both females and males, but in different directions (Maruska et al. 2012). In females, higher hearing thresholds at best frequency (200 Hz) are negatively correlated with gonadosomatic index and plasma levels of T and E_2, but not 11-KT (Fig. 7.6c). This suggests that high circulating T and E_2 produced by the developing ovaries as females approach spawning could contribute to the twofold to fivefold improved hearing sensitivity observed in gravid females compared to brooding females. As mentioned above, gravid females also have lower mRNA levels of several ER subtypes and ARs in the saccule compared to brooding females (Fig. 7.8a). Thus, as females approach spawning readiness, circulating sex-steroid levels increase, relative steroid sensitivity of the saccule decreases (e.g. lower mRNA levels of steroid receptors), but overall hearing sensitivity is improved (Fig. 7.9). Interestingly, relative sex-steroid sensitivity of the whole brain is higher


(a)
ARα
Relative mRNA levels
0.0
0.5
1.0
1.5
2.0
a
b
c
Brooding
Recovering
Gravid
ERα
Relative mRNA levels
0.00
0.02
0.04
0.06
a
b
c
Brooding
Recovering
Gravid
(b)
ARα
ARβ
Relative mRNA levels
0
1
2
3
0.1
1
11-ketotestosterone (ng ml^{-1})
ERα
ERβa
Aromatase
Relative mRNA levels
0.0
0.1
0.2
0.3
0.1
1
10
100
Estradiol (ng ml^{-1})
(c)
ERα
Relative mRNA levels
0.000
0.005
0.010
0.015
0.020
0.025
a
b
Subordinate
Dominant
ERβa
Relative mRNA levels
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0.06
0.09
a
b
Subordinate
Dominant
(d)
ARα
ARβ
Relative mRNA levels
0.0
0.5
1.0
0.1
1
10
11-ketotestosterone (ng ml^{-1})
ERα
ERβa
Aromatase
Relative mRNA levels
0.00
0.05
0.10
0.15
0.20
0.1
1
10
100
Estradiol (ng ml^{-1})

◀**Fig. 7.8** Sex-steroid receptor expression in the saccule of the *A. burtoni* inner ear differs with reproductive state in females and social status in males. **a** mRNA levels of several steroid receptor subtypes differ in the saccule of gravid, recovering, and mouth-brooding female cichlids. mRNA levels of ARα and ERα are shown, measured via quantitative PCR and referenced to the geometric mean of the reference genes 18s and g^3pdh. **b** Correlations between circulating steroid levels (11-ketotestosterone, estradiol) and steroid receptor mRNA levels in the saccule of female cichlids. **c** mRNA levels of estrogen receptor subtypes (ERα, ERβa) that differ between reproductively-active dominant and reproductively-suppressed subordinate male *A. burtoni*. **d** Correlations between circulating steroid levels (11-ketotestosterone, estradiol) and receptor mRNA levels in the saccule of male cichlids. ARα, androgen receptor α; ARβ, androgen receptor β; ERα, estrogen receptor α; ERβa, estrogen receptor βa. Different *letters* above *bars* in (**a**) and (**c**) indicate statistical differences at $p < 0.05$, and $N = 11–12$ fish per group. (Modified from Maruska and Fernald 2010a, b, c)

in gravid females compared to mouth-brooders, but the exact neuroanatomical locations of these changes in mRNA receptor levels are unknown (Maruska and Fernald 2010b). It is possible, therefore, that the improved hearing in gravid females is due to plasticity in central processing regions, or in peripheral auditory structures (inner ear), or both. In males, however, increased hearing thresholds at best frequency are positively correlated with plasma levels of androgens (11-KT and T), but not E_2, suggesting that individuals with lower circulating androgens have better hearing. In *A. burtoni*, subordinate males have smaller testes with lower plasma levels of all sex-steroids compared to dominant males, raising the possibility that low androgens (or removal of an androgen-dependent inhibition in the auditory system) contribute to improved hearing at the high frequencies observed in the AEP experiments. In contrast to estrogens (Al-Mana et al. 2008; Sisneros 2009a; Maney and Pinaud 2011; Caras 2013), however, relatively little is known about how androgens influence auditory processing and hearing thresholds in vertebrates (McFadden 2009; Forlano et al. 2010; Snihur and Hampson 2012). As mentioned above, *A. burtoni* does express androgen receptors in the saccule of the inner ear, and in several auditory processing nuclei of the brain (Maruska and Fernald 2010c; Munchrath and Hofmann 2010; Maruska et al. 2012), which may serve as neural substrates for changes in androgen-related hearing ability associated with social status. Nevertheless, these sex differences also suggest there may be different mechanisms controlling steroid-induced plasticity in the auditory system of males versus females that requires further study.

While direct manipulations are needed to determine causation between steroids and auditory processing in *A. burtoni*, the studies thus far suggest that circulating sex-steroids may regulate cyclical changes in auditory perception such that females show enhanced sensitivity to male courtship signals when they approach spawning readiness. This hypothesis is supported by the fact that there are similar examples of changes in hearing ability associated with variations in reproductive state and circulating steroids, particularly estrogens, in females of every major vertebrate group (Sisneros et al. 2004a; Al-Mana et al. 2008; Maney et al. 2008; Arch and Narins 2009; Sisneros 2009b; Caras 2013). Future work examining where improved

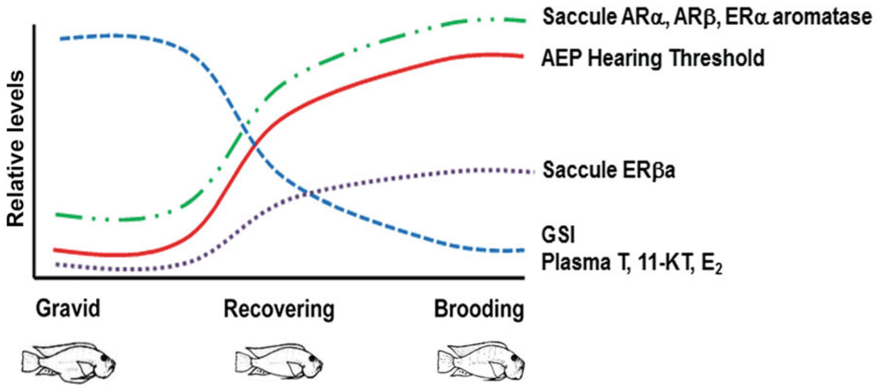

Fig. 7.9 Schematic summary of relationships between hearing thresholds, circulating steroids, and steroid receptor levels in the saccule across the female *A. burtoni* reproductive cycle. In gravid receptive females, plasma steroid levels are high, hearing sensitivity to low frequencies is improved (lower thresholds), and mRNA levels of some steroid receptors in the saccule are low. In parental mouth-brooding females, these relationships are primarily opposite in relative value. Data is compiled from Maruska and Fernald (2010a, b, c) and Maruska et al. (2012)

hearing sensitivity occurs along the auditory pathway, and what cellular and molecular mechanisms are involved, will shed light on the biological significance of steroid-induced auditory plasticity in this important model cichlid species.

7.4 Summary, Conclusions, and Future Directions

Acoustic communication is widespread in fishes, and recent interest in this topic has revealed that internal hormonal state can profoundly influence the ability of individuals to produce and perceive sounds in the aquatic environment. While steroid-mediated plasticity in vocal-acoustic processing exists in many taxa, we have only just begun to explore the importance, mechanisms, and diversity of this plasticity in fishes, the largest group of vertebrates. Here we reviewed the current knowledge on how sex-steroid hormones can influence auditory capabilities and vocal-motor patterning using examples from two incipient model teleosts, the plainfin midshipman fish *P. notatus* and the African cichlid *A. burtoni*.

One common emerging theme from this review is that steroid-mediated improvements in vocal-acoustic processing are typically associated with reproductive readiness. This holds true for species that rely heavily on acoustic signaling during seasonal breeding such as the midshipman fish, as well as non-seasonally breeding species like cichlids that appear to use sound production as one component of a more complex multimodal courtship repertoire. This reproductive-associated plasticity is supported by changes in gonadal state, circulating sex-steroids, and steroid receptor expression in peripheral and central auditory structures. In addition to cichlids and midshipman fish, studies in other species such as the round goby

Neogobius melanostomus also demonstrate sex-steroid associated changes in auditory processing (Zeyl et al. 2013). Thus, the continued examination of diverse fish species should reveal conserved and divergent cellular and molecular mechanisms mediating steroid-auditory plasticity. Further, while this review has concentrated on the influence of sex-steroids on vocal-acoustic processing, there is also evidence for biologically-relevant roles for stress hormones such as cortisol (Remage-Healey and Bass 2005; Arterbery et al. 2010; Maruska and Fernald 2010b; Genova et al. 2012) and neuropeptides such as gonadotropin-releasing hormone (Maruska and Tricas 2011) modulating acoustic communication in fishes that requires further attention. Importantly, this review has highlighted how little is known about steroid-mediated auditory plasticity in the >30,000 species of fishes and future work should focus on exploring both the phylogenetic extent of this phenomenon, as well as the molecular and cellular mechanisms mediating changes at different locations along the auditory pathway. The widespread presence of steroid-dependent auditory plasticity in all vertebrate groups suggests it is an evolutionary labile solution, but future work on diverse fish species are needed to fully appreciate how this solution may have contributed to sexual selection and evolution of the mechanisms to support hormone-mediated vocal-acoustic plasticity across taxa.

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Index

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