

Chapter 2

Fish Sound Production: Insights

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Abstract In addition to briefly reviewing sound-producing mechanisms, this chapter focuses on an under-appreciated evolutionary process, exaptation, which could aid in understanding the independent origins and high diversity of sound-producing mechanisms in fishes. Existing anatomical structures first used in non-voluntary sound production provide advantages that result in further selection and refinement of sophisticated sonic organs. Moreover, comparisons of the relationships between fish size and spectral features in multiple not phylogenetically related species highlight two acoustic patterns. In species using superfast muscles, the slope of the relationship between fish size and sound frequency is weak (1° – 5°) so that emitter size is unlikely inferred from call frequency. In other species that stridulate or use bones or tendons to stimulate the swimbladder, the high slopes (25° – 80°) indicate major differences in the call frequencies within a species. These signals likely convey important information (size and potential fitness of the emitter) to conspecific receivers.

Keywords Acoustic • Call • Communication • Evolution • Gas bladder • Mechanism • Message • Size effect • Sonic • Sonic muscle • Stridulation • Swim bladder • Teleost

2.1 Introduction

Although numerous sonic fishes produce many different sounds (Fig. 2.1), sound production for social communication occurs in a restricted number of families. In some taxa (Doradidae, Bagridae, Pimelodidae, Batrachoididae, Gadidae, Sciaenidae, Holocentridae, Pomacentridae, and Carapidae, for example) all, or almost all, species

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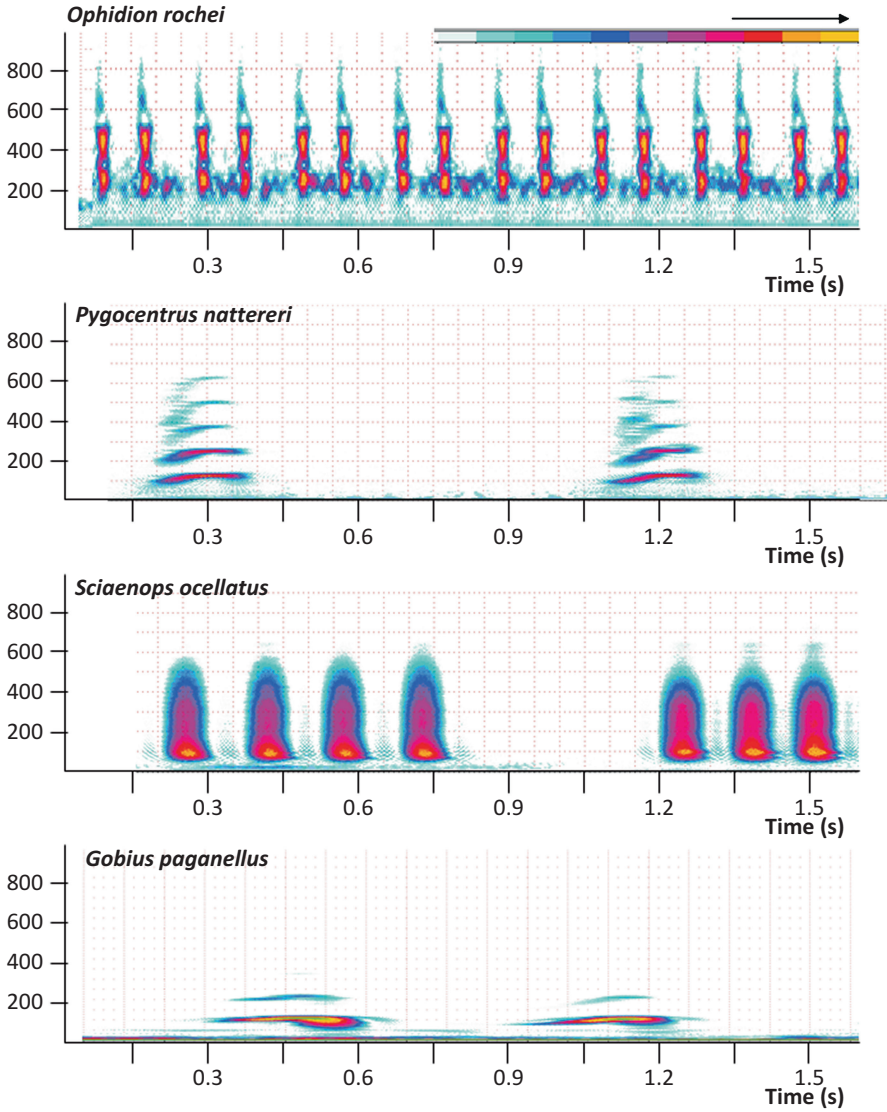


Fig. 2.1 Spectrogram of different fish sounds. Color scale: relative intensity

have the ability to call although mute species exist (Fine and Parmentier 2015). At the opposite extreme, large groups such as minnows (cyprinids) are mostly mute, but a few species produce socially relevant sounds (Johnston and Johnson 2000; Holt and Johnston 2014; Fine and Parmentier 2015). From a number of reviews devoted to the sound-producing mechanisms in fishes (Ladich and Fine 2006; Fine and Parmentier 2015) it is apparent that (1) sound-producing mechanisms have evolved

independently and sporadically in various lineages (Fine and Parmentier 2015) and (2) the variety of sound-producing mechanisms is so great that it has not been possible to classify these mechanisms satisfactorily in useful subcategories (Ladich and Fine 2006).

Many studies indicate advantages and even a necessity to produce sounds. However, the question remains: why are sounds produced in some taxa but not in others? Acoustic communication likely evolved in distantly related species because this function is important to reproductive success. This assumption is reinforced by the high diversity of mechanisms that fishes have developed independently, which leads to the suggestion that morphological characters promoting acoustic communication have evolved multiple times. These recurrent selections support the importance of the acoustic function to species fitness. Although all fishes possess the hearing sense and detect the acoustic scene (Popper and Fay 2011), most fish species lack the ability to produce sounds, indicating that acoustic communication may be advantageous but is not a vital function as is swimming, feeding, breathing or eating. Interestingly, many of the structures used in these vital functions can be modified for sound production.

Exaptation refers to a functional character previously shaped by natural selection for a particular function that is co-opted for a new use that enhances fitness (Gould and Vrba 1982). The term exaptation has been used once in the fish sound-production literature (Parmentier et al. 2007) in regard to the jaw-snapping mechanism in damselfishes. Recent descriptions of different mechanisms allow the suggestion that sound production mechanisms result from numerous and varied exaptations of existing structures. The parsimony principle states that a history involving a minimum number of changes in a set of sequences likely approximates the actual evolutionary history of the sequences (Fitch 1971; Hein 1990). We postulate that sound production appeared in fish taxa that were able to take advantage of their non-voluntary sounds. This hypothesis supports both observations of numerous unrelated mechanisms of sound production in fishes and that many species do not produce sounds.

Producing sound involves a vibration that is coupled to the medium (Bradbury and Vehrencamp 1998). There are five basic mechanisms for producing sounds, all of which are present in fishes: (1) muscular vibrations of a membrane or sac (Fine et al. 2009; Millot et al. 2011), (2) stridulation (Fine et al. 1999; Parmentier et al. 2010b; Bertucci et al. 2014), (3) forced flow through a small orifice (Wahlberg and Westerberg 2003; Lagardère and Ernande 2004), (4) muscular vibration of appendages (Kratochvil 1978, 1985; Ladich et al. 1992) and (5) percussion on a substrate (Colley et al. 2013).

Although multiple mechanisms have been described, most can be grouped into two categories: muscles that directly or indirectly connect to the swim bladder and stridulatory mechanisms involving the rubbing of bones. Additional mechanisms such as fin plucking in gouramis or jaw snapping in damselfish can be found in the literature (see Ladich and Fine 2006; Fine and Parmentier 2015). The two main groups can be split into multiple smaller categories that are quite different.

2.2 Swim Bladder Mechanisms

Many of the swim bladder-based mechanisms result from evolutionary convergence and are constructed around the same basic principle: fish have to provoke the vibration of a gas-filled structure whose base functions include buoyancy and respiration (Alexander 1966). Classically the swim bladder has been modeled as a pulsating underwater bubble (Harris 1964; van Bergeijk 1964), an omnidirectional and resonant monopole. Because of the compressibility of gas in the bladder compared with the surrounding water, an acoustic pressure wave is believed to excite the bladder into vibration that radiates particle motion to the ears (Sand and Hawkins 1973). Similarly, single muscle contractions would excite the swim bladder wall for sound production. Based on this logic, many investigators have assumed that the resonant properties of swim bladders can magnify sounds produced elsewhere in the body (Fish 1953; Demski et al. 1973; Smith and Croll 2011). Removing gas from toadfish (Tavolga 1964b), cichlid (Longrie et al. 2009), and damselfish swim bladders (Colleye et al. 2012) decreases sound amplitude but not fundamental frequency. In contrast, filling the swim bladder with fluid induces a significant decrease in pulse duration and a significant increase in dominant frequency (Colleye et al. 2012). These experiments indicate the importance of gas in the bladder to amplify and radiate movement of sonic muscles but do not support the logic of a resonant structure.

In Clark's anemonefish (*Amphiprion clarkii*), striking the ventral surface of the swim bladder with an impact hammer forces it inward, increasing pressure within the bladder. However, the compressed bladder does not rebound sufficiently to cause sound vibration, indicating that the swim bladder is an inefficient resonator (Colleye et al. 2012). Similar findings in oyster toadfish (*Opsanus tau*) and red-bellied piranha (*Pygocentrus nattereri*) (Fine et al. 2009; Millot et al. 2011) indicate that swim bladders are highly damped and thus prevented from prolonged resonant vibrations.

However, striking the rib cage of anemonefish (intimately surrounding the swim bladder) with an impact hammer generates sound waveforms similar to those of natural sounds (Colleye et al. 2012). Therefore, the vibrating ribs drive the swim bladder wall, which appears to function like a loudspeaker membrane driven by rib displacements (a forced response) rather than as an independent resonator. Furthermore, filling the swim bladder with physiological saline increased radiation mass and thus changes the properties of the swim bladder wall. Therefore, modifying the physical properties of the swim bladder should affect the vibrational properties of the rib cage. These considerations further support the notion that the swim bladder is not a resonant structure. Fine and Parmentier (2015) provide additional arguments showing conflicts between the resonant bubble model and different aspects of fish biology. Sonic muscles attached to swim bladders are among the fastest muscles in vertebrates (Skoglund 1961; Rome and Lindstedt 1998; Fine et al. 2001), yet a resonant structure such as a bell does not require extreme speed to excite it into resonance. The resonant frequency of an underwater bubble increases with depth (hydrostatic pressure) and decreases with bubble radius. Therefore swim bladder and sonic muscle size increases with fish growth could create mismatches

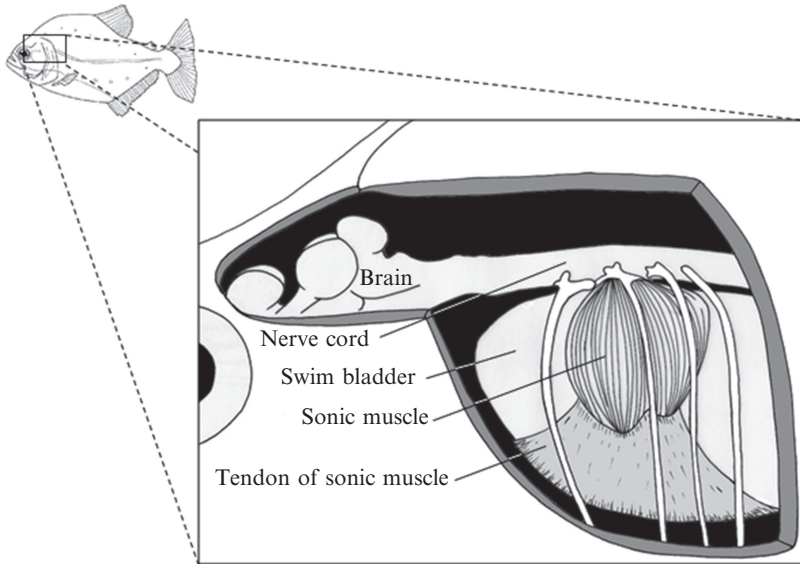


Fig. 2.2 Schematic *left lateral* view of the sound-producing mechanism (*black*) piranha (*Serrasalmus rhombeus*). Skull and vertebrae are not shown (Redrawn from Ladich and Bass 2005)

between communicating individuals. A resonant bubble will continue to oscillate after sound termination and would interfere with temporal coding of fish sounds, most of which are of short duration and pulsed. Finally, sonic swim bladders have a number of shapes (i.e., heart shaped in toadfish) or diverticula (Hawkins 1993; Barimo and Fine 1998; Ramcharitar et al. 2006; Schulz-Mirbach et al. 2013), which is not logical for an omnidirectional source (Fine 2012).

Sound production requires development of intrinsic or extrinsic muscles that deform the swim bladder to radiate sound. Mechanisms of swim bladder excitement are particularly diverse at various levels including muscle origins, insertions, ultra-structure, and contraction speed as well as in the sizes, shapes, and structures. Intrinsic muscles attach completely to large areas of the swim bladder. They are capable of producing short-duration pulsed-type sounds with single or a small number of contractions, but they are generally associated with production of long duration tonal notes. During a sustained contraction, the sonic muscle contraction rate can decrease slightly, causing a slight decrease (frequency modulation) of the fundamental frequency.

Extrinsic sonic muscles generally have their origins on various bones on the skull but also on the pectoral girdle, the ribs, or epineurals (Tavolga 1964a; Schneider 1967; Ladich and Fine 2006) and insert on the swim bladder or on a structure that attaches to the swim bladder. Sonic muscles in piranhas (Fig. 2.2) originate on the vertebral column and insert on a broad tendon that surrounds the ventral surface of the anterior chamber of the swim bladder (Markl 1971; Ladich and Bass 2005). In the red drum (*Sciaenops ocellatus*), sonic muscles are bilaterally symmetrical muscles

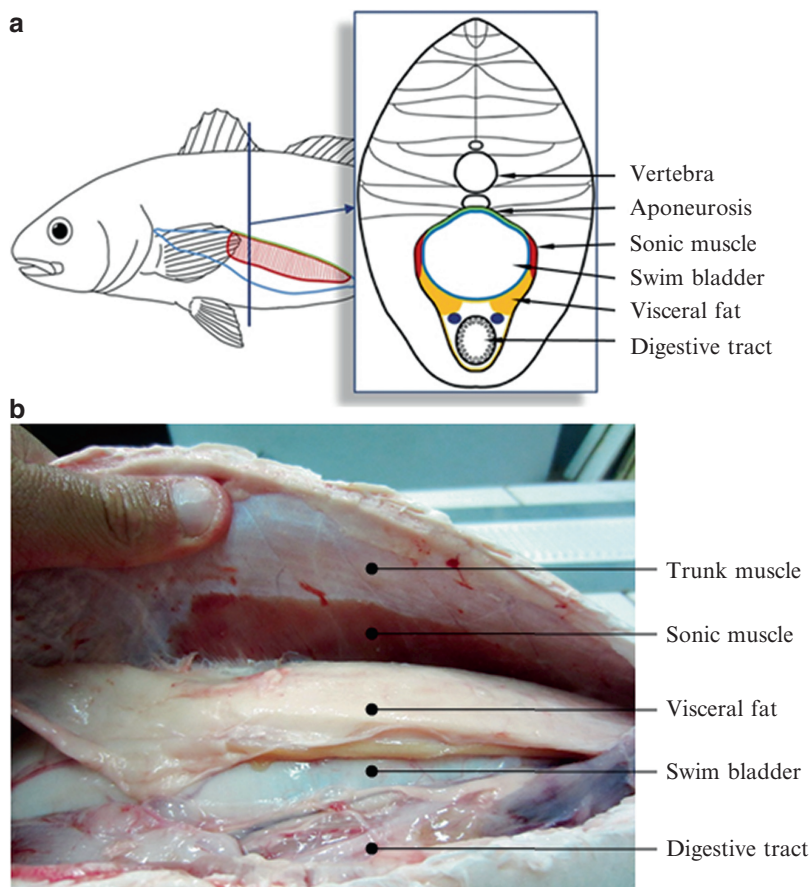


Fig. 2.3 (a) Schematic *left lateral view* of the sound-producing mechanism in the *red drum* (*Sciaenops ocellatus*). The *blue line* corresponds to the shape of the swim bladder and the *red lines* to the position of the sonic muscle. In the schematic cross section, *left and right* sonic muscles are dorsally united by the aponeurosis (in *green*). (b) Ventral view of the body cavity showing the relative position of the sonic muscle

that run perpendicular to the long axis of the fish. These muscles originate on the abdominal hypaxial musculature and insert on a central tendon that attaches to the dorsal swim bladder (Fig. 2.3). Alternately, extrinsic muscles can also insert between two bones, one of which is connected to the swim bladder via ligaments or connective tissue. This situation is found in some Scorpaenidae (Hallacher 1974) and Holocentridae (Parmentier et al. 2011b). In catfishes (Ladich and Fine 2006; Kaatz and Stewart 2012; Boyle et al. 2014), the sonic muscle inserts on variously derived elastic-spring mechanisms, the ramus Mülleri, a modified rib, that attaches to the bladder (Sørensen 1895; Chardon 1968). The muscle pulls the bladder forward directly or via the spring mechanism. Sound production is due to the pull and rebound from the spring mechanism and stretched bladder. In some ophidiiform

fishes the swim bladder insertion can be highly modified (Parmentier et al. 2002). In *Onuxodon* (Carapidae) and some *Ophidion* (Ophidiidae), for example (Fig. 2.4), the sonic muscles insert on a lima bean-shaped hard structure protruding from the anterior wall of the swim bladder (Parmentier et al. 2006a, 2008, 2010a).

Although there is generally one symmetrical pair of sonic muscles, some species have developed additional muscles (Fig. 2.4). In some Ophidiiformes such as the pearlfish *Carapus* and *Encheliophis*, for example, a pair of ventral muscles originates on the neurocranium (in the orbit ceiling) and inserts on the dorsal part of the swim bladder. Additionally a pair of dorsal muscles originates on the neurocranium and inserts on the first epineurals (Fig. 2.4), which connect to the swim bladder by ligaments (Parmentier et al. 2003a, b). In these fishes, contraction of the sonic muscles inserted directly on the swim bladder is the driving force for sonic emission, while the muscles inserted on the epineurals probably should modify the sounds.

In other Ophidiiformes, both dorsal and ventral muscles are required to produce sounds. Sustained contractions of dorsal muscles during the entire call place the swim bladder under tension, and a series of rapid contraction/relaxation cycles from the second pair of muscles creates multiple sound pulses (Fig. 2.5) (Parmentier et al. 2010a). This system is analogous to a bow. At rest, the string and the rod are separated; the contraction of the first pair of muscles would tense the rod with the string to stretch the bow, and the contraction and relaxation of the second set of muscles pulls and releases the bow string. This mechanism is experimentally supported by electromyographic recording from both muscles (Kéver et al. 2014b). The same kind of mechanism can apply in the glaucosomatid *Glaucosoma buergeri*. This fish also possesses two pairs of sonic muscles. The anterior sonic muscles originate on the skull and insert on the outside of the anterior-dorsal region of the swim bladder. The posterior muscle inserts on the inner side of the swim bladder and has the morphology of a typical smooth muscle (which is quite exceptional). Its contraction works as an antagonist to anterior skeletal muscles that extend the anterior swim bladder. The smooth muscle presumably functions to damp vibrations from the tendon, which would drive the swim bladder to produce sound (Mok et al. 2011).

Although diversity is high due to independent evolution, the systems correspond finally just to variations on a theme, and two main kinds of mechanisms will be highlighted.

The forced-response model (Fine 2012) posits that the frequency spectrum is dictated by contraction dynamics of superfast extrinsic or intrinsic sonic muscles (Fine et al. 2001; Connaughton 2004; Millot et al. 2011). This system, the drumming muscle system, can also involve bony or ligamentous attachments to the swim bladder if each contraction cycle generates a cycle of sound waveform. Drumming requires superfast muscles (Skoglund 1961; Rome et al. 1996; Fine et al. 2001) and can be found in various species of the Batrachoididae (Tower 1908; Rice and Bass 2009), Triglidae (Connaughton 2004), Serrasalminae (Markl 1971; Kastberger 1981a; Millot et al. 2011) and Zeidae (Onuki and Somiya 2004).

The swim bladder rebound model posits that swim bladder sounds are driven by vibration of surrounding structures such as epineurals or ribs (Parmentier et al. 2006b, 2010a; Oliver and Lobel 2013). In this case, the dominant frequency is determined by

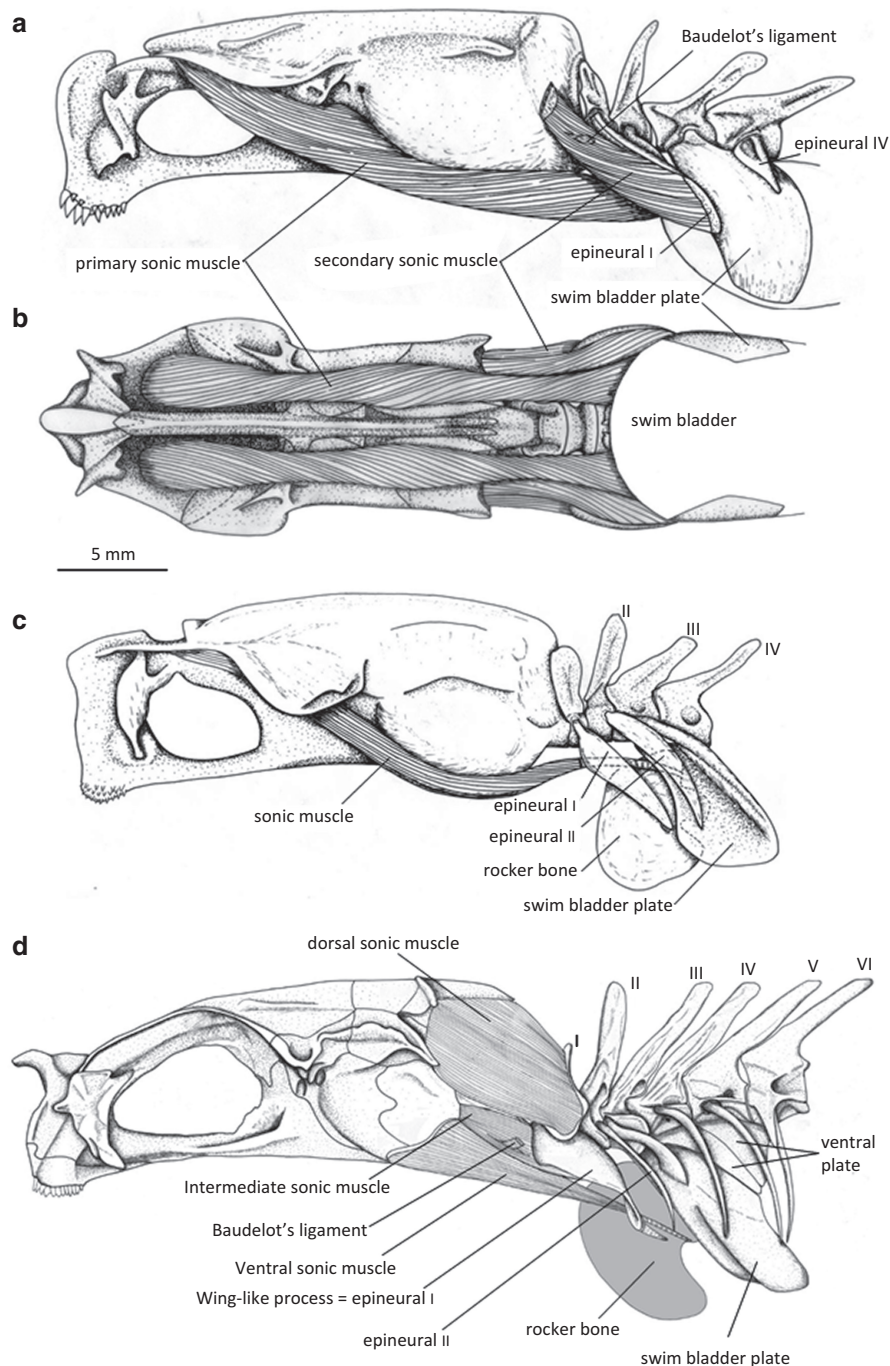


Fig. 2.4 Sound-producing mechanism in different ophidiiform fishes. *Left lateral (a) and ventral (b) view in *Carapus boraborensis*; (c) left lateral view in *Onuxodon fowleri* and (d) left lateral view in *Ophidion barbatum*. Swim bladders are not shown in c and d (Modified from Parmentier et al. 2002, 2006a)*

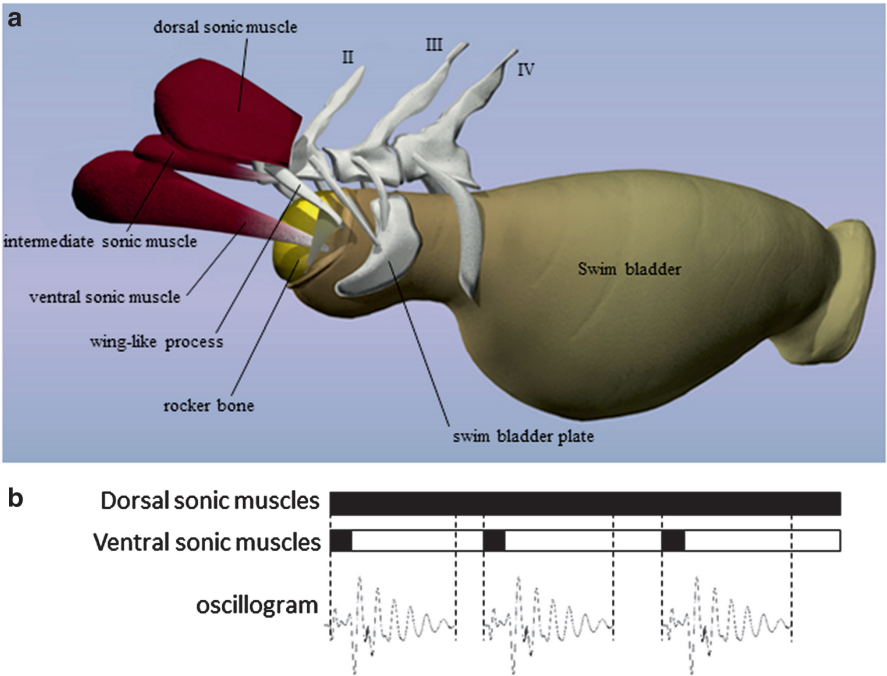


Fig. 2.5 Schematic view of the sound-producing mechanism in *Ophidion rochei* (a) and (b) schematic graph showing the muscle activity during sound production and the related oscillograms of calls. Dark areas correspond to the muscle activity

vibratory properties of the surrounding structure. Each muscle contraction causes a sound pulse but does not determine the sound’s frequency spectrum.

These two systems highlight dramatic differences in sonic muscle anatomy and physiology. Skeletal sonic muscles have varying contraction speeds, and maximal rates of contraction when stimulated electrically extend from 10 to 300 Hz (Gainer et al. 1965; Fine et al. 2001; Millot et al. 2011). In drumming fishes, the muscle contraction rate sets the fundamental frequency. For example, contraction of sonic muscles at 150 Hz will drive a sound with a fundamental frequency of 150 Hz and typically harmonics at multiples of 150 Hz. In this case a muscle twitch, the time for a contraction/relaxation cycle, is short: toadfish sonic muscles require about 10 ms for a twitch (Skoglund 1961; Fine et al. 2001). Additional studies on sonic muscles in the weakfish *Cynoscion regalis* (Sciaenidae), the leopard searobin *Prionotus scitulus* (Triglidae), the hardhead catfish *Arius felis* (Ariidae), the gafftopsail catfish *Bagre marinus* (Ariidae), and the tiger perch *Terapon jarbua* (Terapontidae) place them among the “champions” of contraction speed (Schneider 1967; Sprague 2000). The yellow pyramid butterflyfish (*Hemitaurichthys polylepis*) also produces rapid pulse train sounds with extrinsic high-speed swim bladder muscles (Boyle and Tricas 2010; Boyle et al. 2013).

The high-speed ability is related to morphological, physiological, and biochemical features of the muscles (Parmentier and Diogo 2006), which have an extremely fast relaxation rate (Rome and Lindstedt 1998). Skeletal muscle is composed of three major components (myofibrils, sarcoplasmic reticulum, and mitochondria) that comprise approximately 100 % of muscle fiber volume (less a small volume devoted to lipid and glycogen fuel) (Rome and Lindstedt 1998). Briefly stated, the volume occupied by myofibrils determines the force of contraction, sarcoplasmic reticulum allows high frequency contraction, and mitochondria fuel sustained performance (fatigue resistance). Functional specializations in muscle relate to the proportions of these three structures (Rome et al. 1996; Lindstedt et al. 1998; Rome and Lindstedt 1998). In comparison to white muscles (Ladich and Fine 2006), these muscles have the fastest 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), a different distribution of parvalbumins (Hamoir et al. 1980), specialized myosin isoforms (Hamoir and Focant 1981), an increased volume of sarcoplasmic reticulum (Bass and Marchaterre 1989; Appelt et al. 1991; Schaeffer et al. 1996), a reduced fiber and myofibril diameter (Evans 1973; Ono and Poss 1982; K  ver et al. 2014b), a higher content of mitochondria (Eichelberg 1977; Bass and Marchaterre 1989; Parmentier et al. 2013), multiple capillaries surrounding muscle fibers that maximize the supply of oxygen and exchange of other metabolites (Lewis et al. 2003).

The rebound system has been described mainly in ophidiiform and glaucosomatid fishes. In the rebound system, the mechanism of some carapid species utilizes slow muscles that tetanize at about 10 Hz (Parmentier et al. 2006b). Thus there is one slow muscle contraction for each sound pulse, and a resonant response (multiple cycles in the sound waveform) seems to be driven by a bone, the swim bladder plate, rather than the swim bladder. With slow muscles each muscle contraction generates a pulse but not the frequency within a pulse. 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. 2010a; K  ver et al. 2012, 2014a). Calls from the striped cusk-eel *Ophidion marginatum* have peak frequencies above 1 kHz (Mann et al. 1997; Sprague and Luczkovich 2001), which should be impossible even with superfast swim bladder muscles because twitches would have to occur in less than 1 ms, faster than any known direct muscle. As in *Carapus* species, calls would result from a release mechanism that utilizes three steps. The contraction of the dorsal muscle first pulls the epineurals, which are in close relationships with the anterior part of the swim bladder, backward. Second, contraction of sound-producing muscle stretches the anterior part of the swim bladder rostrally, creating a tension opposed to the action of the dorsal muscle. Third, sound-producing muscle relaxation combined with the caudally-acting force cause rapid rebound of the swim bladder (Parmentier et al. 2010a).

Other indirect swim bladder systems were recently summarized in Fine and Parmentier (2015). Sound production in the Nile tilapia (*Oreochromis niloticus*) occurs by contraction of a horizontal band of muscle that initiates movements of the

rib cage and the swim bladder (Longrie et al. 2009). Although sounds have been described in more than 30 cichlid species, the sound-producing mechanism is currently described only in one species. Additional studies are required to increase understanding of the mechanism(s) in this family.

2.3 Sounds and Information

Temporal patterns may be an important sound characteristic for acoustic communication in fishes, especially in noisy and/or shallow water where low frequencies do not propagate well and the spectral content of signals is easily altered (Mann 2006; Ghahramani et al. 2014). In many cases, temporal and spectral features are related to fish size, and therefore the calls can convey phenotypic differences between males: smaller individuals typically produce sounds of higher frequency and shorter duration than larger individuals (Myrberg et al. 1993; Connaughton et al. 2000).

However, the relationship between these variables and size is not invariant. In some species, the fundamental frequency may not change with fish size because muscle contraction rate determines the fundamental frequency (Skoglund 1961; Fine et al. 2001). Grunt fundamental frequency did not change with size in toadfish varying from 29 to 760 g (Fine and Waybright 2015), and choruses of toadfish in nature, composed of different sized fish, can have fundamental frequencies varying over as little as 10 Hz (Fine 1978). At the opposite extreme, fundamental frequency in *Amphiprion clarkii* decreases by 500 Hz in individuals between 30- and 90-mm total length.

In Fig. 2.6, data from published studies were collected to compare the slopes of the relationships between fish size and fundamental frequency. When the equation was given, slopes were drawn on the basis of the specimen sizes in the study. For other studies, the slopes were calculated based on data in the graphs, in which case data from the smallest and largest individuals were used. These slopes should be considered approximations. Figure 2.6a includes fishes in which the sound-producing mechanism is based on superfast muscles. In these examples sound frequencies are dependent on the sonic muscle contraction rate. The species in this group have negative slopes between 1 and 10°. Moreover, highest slopes are found in studies comparing adults and larvae in which the sound-producing system is not completely developed (Vasconcelos and Ladich 2008; Parmentier et al. 2011b). The sound production mechanism of the rock-pool blenny (*Parablennius parvicornis*) is unknown (De Jong et al. 2007). Interestingly, the slope of the relationship in this species is greater than 10°, and these blennies produce harmonic calls, suggesting mechanism involving high-speed muscles.

In the second group (Fig. 2.6b), the relationships between dominant frequency and fish size have steeper slopes, between 25 and 80°. Species in this group belong to distantly related taxa: cichlids (Amorim et al. 2003, 2004; Bertucci et al. 2012), pomacentrids (Myrberg et al. 1993; Colley et al. 2011), and gobiids (Malavasi et al. 2003). Although it was not possible to place them on the graph because the authors used the swim bladder size or the body weight rather than body length, similar

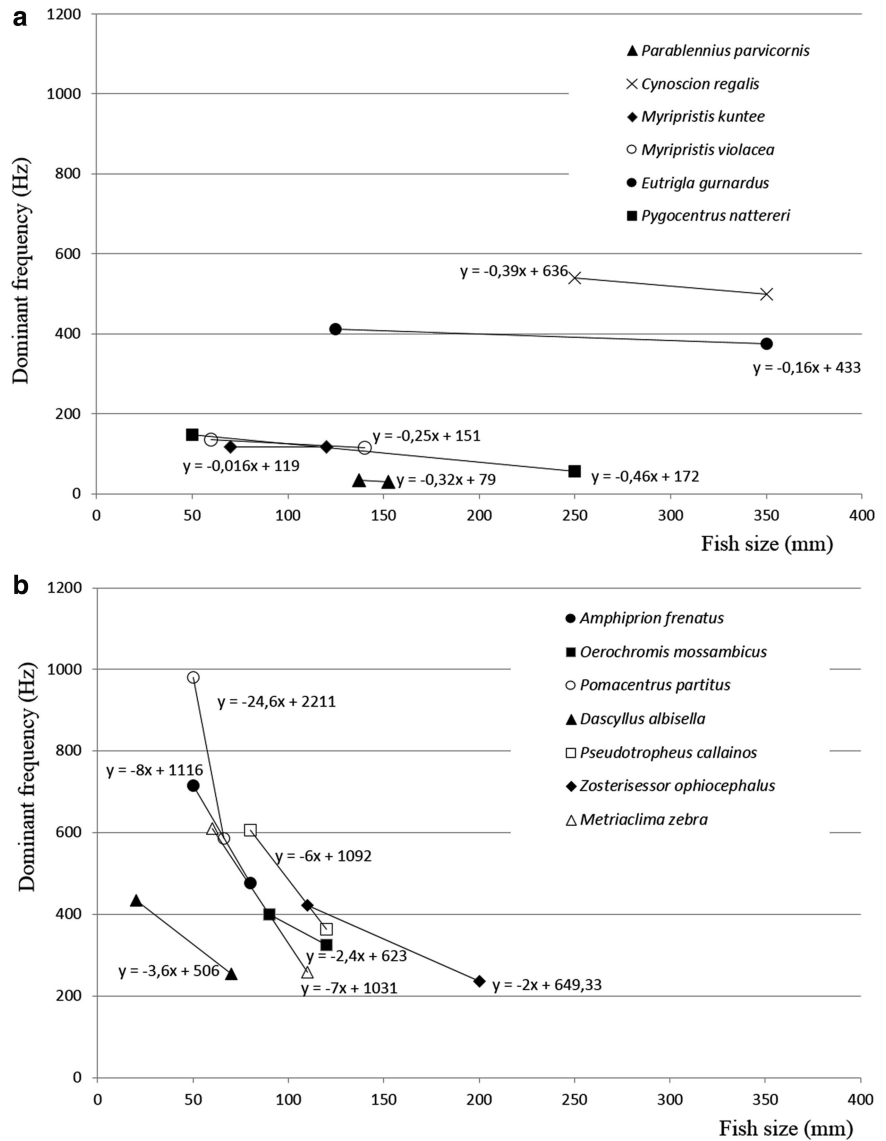


Fig. 2.6 Relationships between dominant frequency and fish size in different species. **(a)** Fishes in which the sound-producing mechanism is based on superfast muscles. The mechanism is, however, not yet known in *P. parvicornis*. All the fish species in this group have a negative slope between 1 and 5°. **(b)** Fishes in which the sound-producing mechanism is not based on fast-contracting muscles. The relationships between dominant frequency and fish size have slopes between 60 and 87°

relationships are found in the Carapidae (Parmentier et al. 2006b), Mormyridae (Crawford 1997), and Ophiidiidae (Kéver et al. 2014a). Moreover, similar steep slopes are also found in fishes producing stridulatory sounds as in Osphronemidae (Henglmüller and Ladich 1999).

Comparison of Fig. 2.6a, b suggests another way that the sound-producing mechanism can be used to group fishes, namely size information in their calls. In fishes of the first group (Holocentridae, Sciaenidae, Batrachoididae), fish size would not be inferred from the main frequency by conspecifics whereas it would be possible in fishes from the second group. In the lattice soldierfish (*Myripristis violacea*), for example, 60- and 130-mm individuals produce the same main frequency (Parmentier et al. 2011b). As a comparison, the calling frequency of 60-mm skunk clownfish (*Amphiprion akallopisos*) is 700 Hz but less than 400 Hz in 130-mm specimens (Colleye et al. 2009). The high slopes in the second group, indicate that frequency can provide information on emitter size. Teleost fishes such as the black goby (*Gobius niger*, Gobiidae) and the annular seabream (*Diplodus annularis*, Sparidae) are able to discriminate tonal sounds differing in frequency by approximately 10 %, equivalent to 40 Hz for a 400-Hz sound (Fay 1988). Similar frequency discrimination occurs in bicolor damselfish (*Stegastes partitus*); females preferentially respond to lower frequency chirps of larger males (Myrberg et al. 1986). In the sergeant major (*Abudefduf saxatilis*), fish size affects auditory sensitivity (Egner and Mann 2005); all fish are most sensitive to low frequencies (100–400 Hz), but larger fish are more likely to respond to higher frequencies (800–1600 Hz). On the other hand, females of Hawaiian dascyllus (*Dascyllus albisella*) choose their mate on the basis of their courtship rate and not on phenotypic characters such as weight size, or dominant frequency (Oliver and Lobel 2013).

Despite these comments, slopes from group 1 species (Fig. 2.2) were all negative. This shared phenomenon is likely a scaling effect because longer muscles, presumably with longer fibers, from larger fish would take longer to complete a twitch (Connaughton et al. 2000).

An important set of studies in the Lusitanian toadfish (*Halobatrachus didactylus*) provides more information on this kind of vocal behavior (Amorim and Vasconcelos 2008). The acoustic features that consistently best discriminate individual toadfish are the dominant frequency of the middle tonal segment of the boat whistle and dominant frequency modulation. If scientists can recognize individuals based on their calls, it is likely that the fish can too, and evidence of individual recognition has been demonstrated in the Gulf toadfish *Opsanus beta* (Thorson and Fine 2002). However, these frequencies are related to the pulse period (i.e., the rate of muscle contraction) and not fish size. Moreover, the pulse period has low variability in this taxa, which is consistent with their vocal central pattern generator (Bass and Baker 1990; Barimo and Fine 1998; Amorim et al. 2010). In *Halobatrachus didactylus*, reproductive success appears to be determined by calling rate and calling effort (i.e., the highest percentage of time spent calling). These parameters indicate male condition (Vasconcelos et al. 2012), as reflected in sonic muscle hypertrophy and larger gonads (Amorim et al. 2010). In this case, the sonic muscle mass would allow long periods of calling but not affect main frequency. In other words, sounds would be related to male quality, that is to males that are likely to confer greater fitness on their offspring (Amorim and Vasconcelos 2008; Amorim et al. 2010) but not to its size.

2.4 Stridulation Mechanisms

These mechanisms work by friction caused by rubbing skeletal elements (teeth or bones), which produce a series of irregular pulses containing a wide range of frequencies (Tavolga 1971; Hawkins 1993). Two examples have dominated the literature: rubbing of the pharyngeal teeth and friction of the pectoral fin against the shoulder girdle (Fig. 2.7).

Likely all fishes can produce sounds using their pharyngeal teeth during feeding movements or substrate manipulations, and therefore it is not always easy to relate sound production to communication. These sounds, however, can be used by other species (interception or eaves dropping), which may be inimical to communication because the beneficiary is not the sender (Myrberg 1981). Unfortunately in many fishes without obviously distinct sound-producing elements, the sonic mechanism

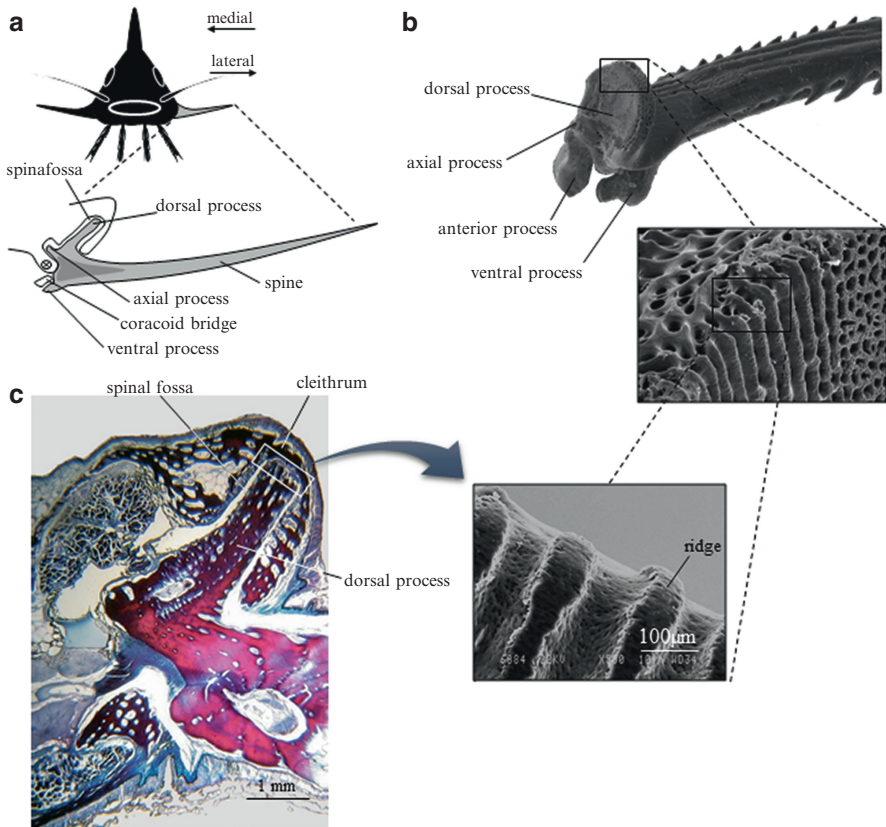


Fig. 2.7 (a) Frontal schematic view of the *left* pectoral spine and the position of its dorsal process in the spinal fossa in mochokid catfish. (b) Scanning electron micrographs of a mochokid catfish with enlarged views of the ridges situated on the dorsal process. (c) Cross section at the level of the dorsal process of the pectoral spine (Modified from Parmentier et al. 2010b)

has been attributed, without explicit evidence, to sounds from the pharyngeal jaws and a resonating effect of the swim bladder (Fine and Parmentier 2015). In this regard the swimbladder does not appear to radiate stridulatory sounds in the tiger-tail seahorse (Lim et al. 2015) or in channel catfish (Fine et al. 1997). To the best of our knowledge, the use of rubbing teeth in communication process can be found in haemulid grunts (Burkenroad 1930; Bertucci et al. 2014), but additional experiments are required to understand the related behaviors.

A second stridulatory mechanism utilizes pectoral spines in catfishes (Sørensen 1895; Schachner and Schaller 1981; Fine and Ladich 2003). During abduction and in some species adduction of the fins, sweep movements of the pectoral spine produce a number of discrete pulses with varying waveforms (Fine et al. 1996, 1999; Vance 2000). Sounds are produced by microscopic bony ridges on the dorsal process (Schachner and Schaller 1981; Fine et al. 1997; Parmentier et al. 2010b) coming into contact with the cleithrum (Parmentier et al. 2010b).

Seahorses produce sounds by rubbing the exoccipital bone on the back of the skull against a coronet (Colson et al. 1998; Oliveira et al. 2014; Lim et al. 2015).

Some species of croaking gouramis (*Trichopsis vittata*) provide another kind of pectoral mechanism. Rather than bone against bone, the pectoral fin has two hypertrophied tendons that rub against other fin rays, producing a double-pulsed sound (Kratochvil 1985; Ladich et al. 1992).

2.5 A Thought About Evolution of Sound Production

Although callers are present in distantly related taxa and in some basal groups of bony fishes (Fine and Parmentier 2015), there is no phylogenetic continuity, as with the syrinx of birds and the larynx of mammals. The development of acoustic communication in fishes is possible because required morphological characters were present as precursors. Quite all teleosts have bones, teeth, an air sac, inner ears with otoliths (and three semicircular canals) and more or less developed fins that constitute the raw material for the development of sound-producing structures. We note that the swim bladder may be lost in certain benthic or deep-water forms. In fact, all fishes can produce sounds if we consider ones produced by hydrodynamic movements (Moulton 1960) and chewing sounds, but the challenge is to demonstrate which sounds are incidental byproducts and which are voluntarily used to communicate (mainly agonistic and courtship behavior). Some physostome fishes, with connections between the swim bladder and the gut, can produce sound by shuttling gas from the swim bladder (Wahlberg and Westerberg 2003; Lagardère and Ernande 2004), but it is unclear if any such sounds have evolved for communication or are merely incidental, as in gut rumbling in humans.

A signal can be selected for communication if it fulfills the following conditions: (1) it can be generated at relatively low cost, (2) it can propagate to an individual able to perceive and interpret it, and (3) it elicits a response of the receiver that is advantageous for the sender (Myrberg 1981; Bradbury and Vehrencamp 1998).

Individuals able to elicit, modify, or generate informative signals should be favored through evolutionary history because they can inform conspecifics about their location, intentions, and potential fitness. Data are, however, currently insufficient to show which groups have taken advantage of this ability to evolve more rapidly or to produce a higher specific diversity. Catfishes, for instance, have many species capable of sound production, but they also have other adaptations (electro- and chemoreception), and therefore it is not possible to claim that sound production is responsible for their diversity. In terms of adaptive radiation, evolving sound production does not generally open up new avenues leading to diversification, but this question has never been studied systematically.

Production of underwater acoustic signals is subject to constraints that differ between swim bladder and stridulation mechanisms. Further, these systems likely evolved convergently to improve calling abilities. This scheme can also explain why distantly related families such as sciaenids (Connaughton et al. 2000; Ramcharitar et al. 2006; Parmentier et al. 2014), characids (Markl 1971; Kastberger 1981a; Ladich and Bass 2005; Millot et al. 2011), or batrachoidids (Fine et al. 2001; Rice and Bass 2009) share similar characteristics. In drums (Sciaenidae), the swim bladder is surrounded laterally by bilaterally symmetrical sonic muscles originating from a ventral tendon or the hypaxial musculature and inserting on a large, flattened central tendon that attaches to a large extent of the dorsal swim bladder (Fig. 2.3) (Hill et al. 1987; Parmentier et al. 2014). In piranhas, a broad tendon is not dorsal but ventral to the swim bladder (Fig. 2.2), and lateral sonic muscles insert on transverse expansions at the base of the second pair of ribs (Ladich and Bass 2005; Millot et al. 2011). In black drum (unlike in typical sciaenids), toadfishes, and searobins sonic muscles are intrinsic and attach exclusively to the swim bladder (Fine et al. 2001; Rice and Bass 2009). Despite these differences, the frequency spectrum is dictated by contraction dynamics of superfast sonic muscles acting on the damped swim bladder. Similarities in ultrastructure of nonhomologous sonic muscle fibers are particularly striking in weakfish, a sciaenid (Ono and Poss 1982), and the oyster toadfish (Fawcett and Revel 1961; Appelt et al. 1991; Fine et al. 1993) although the sciaenid is innervated segmentally by true spinal nerves and the toadfish by occipital spinal nerves. Again, evolution has produced muscles with convergent abilities to contract rapidly (Rome et al. 1996; Young and Rome 2001; Parmentier and Diogo 2006).

Similar variability occurs in stridulatory mechanisms of sound production that involve movements of pectoral and dorsal fins, pharyngeal teeth, buccal teeth, neurocranium, and so forth (see Fine and Parmentier 2015 for a review). Therefore caution is required in assuming homologous characters involved with sound-producing mechanisms in phylogenetic studies; similar functions can be produced by convergent structures whose similarity is superficial, as is often the case with morphology (Kocher et al. 1993; Rüber and Adams 2001; Frédérick et al. 2013). In other words, fishes using swim bladder mechanisms are not phylogenetically closer than ones using stridulatory mechanisms. Some taxa even employ both mechanisms. For instance some catfishes (Siluriformes) produce sounds using swim bladder muscles (Sørensen 1895; Tavalga 1977; Parmentier and Diogo 2006) or

pectoral (Kaatz et al. 2010; Parmentier et al. 2010b) or dorsal spines (Mahajan 1963; de Pinna 1996). However, no catfish possesses all of these mechanisms, and some employ one, two or none of them (Fine and Ladich 2003; Parmentier and Diogo 2006). Even within swim bladder mechanisms, some catfishes have muscles connected directly to the swim bladder whereas in others they insert on a modified rib (the Springfederapparat or elastic spring mechanism), which then attaches to the bladder.

2.5.1 Concept of Exaptation

A phenotype is composed of modular units that integrate functionally related characters into units of evolutionary transformation. These units may emerge spontaneously (large-effect mutations of homeobox genes, for example) and are then acted on by natural selection (Wagner 1996). Functional modularity refers to the interactions of traits in performing one or more functions (Klingenberg 2008). The teleost head, for example, is used for prey capture and breathing. Motor patterns allowing these movements are usually based on the same mechanical principle that allows gill ventilation. In teleosts and sharks, feeding movements may be exaggerations of ones used in breathing (Hughes 1960; Liem 1985; Ferry-Graham 1999). By introducing the term exaptation, Stephen Jay Gould and Elizabeth Vrba published a provocative challenge to orthodox evolutionary theory (Larson et al. 2013). Exaptation refers to a functional character previously shaped by natural selection for a particular function that is co-opted for a new use that enhances fitness (Gould and Vrba 1982). However, the character can retain its plesiomorphic (ancestral) form while taking on a new function, thus expanding functional diversity (McLennan 2008). Exaptation has not been used widely in the biological sciences (Larson et al. 2013), mainly because few concrete examples have been properly demonstrated (Ostrom 1979; Cullen et al. 2013; Patek et al. 2013). Bird feathers are usually used to support the concept because they probably evolved for temperature regulation and display functions and later co-opted for flight. The jaws in trap-ants are typically used in rapid closing strikes for prey capture but also allow ants to propel themselves into the air (Patek et al. 2013).

The concept of exaptation is highly interesting because the mechanical units that change or incorporate new functions have the potential for rapid evolutionary change and may not require transitional forms (McLennan 2008). In fish species, sound was likely an initial byproduct of mechanical functions involved in feeding or locomotion. To be part of an operational system, sounds produced early in the evolution of the trait likely evoked modifications in the behavior of the recipient individuals (conspecific or not). In this scheme, behavioral responses would have improved the fitness of the emitter although advantages likely accrued to the recipient as well. The ability to produce sound allows the fish to enter a new adaptive zone, an environmental (not necessarily new) space that is exploitable after the acquisition of morphological and/or physiological characters. For instance, wing development permitted birds

to enter a new adaptive zone (the aerial way of life), and then minor morphological modifications allowed them to colonize various milieus (Mayr 1989). This process allows the acceleration of diversification by ecological opportunity, such as dispersal into newly opened territory, extinction of competitors, or adoption of a new way of life (Simpson 1953), which for the purpose of this chapter involves sound production. Calling species do not necessarily develop new ecological opportunities but increase attraction of sexual partners, discourage predators, or improve territorial defense, thus providing evolutionary advantages. Historically, morphological modifications that permit entrance into a new adaptive zone were thought to result from one or several changes to an ancestral plan (Zelditch and Fink 1996) or from the emergence of novelties (Futuyama 1986; Heard and Hauser 1995). However, the establishment of a relationship between exaptation and an adaptive zone might allow an adaptation such as sound production to develop rapidly because extensive modification of morphology may be unnecessary, particularly if fish sound-producing mechanisms arose from pre-existing structures adapted for other functions. Once sounds have been incorporated into a species' behavior, natural selection can reinforce calling behavior through morphological and physiological modifications. Beautiful and surprising sound-producing mechanisms arose in many taxa, notably in ophidiiform (Courtenay 1971; Parmentier et al. 2006a) and batrachoidiform fishes (Skoglund 1961; Fine et al. 2001; Rice and Bass 2009). In these taxa, a well-developed mechanism allows rapid identification of its structural components, for example, muscles on a swim bladder. On the other hand, many taxa are deprived of obvious mechanical structures that would cause sound production. Cichlids (Rice and Lobel 2003; Longrie et al. 2009), pomacentrids (Parmentier et al. 2007), gobiids (Stadler 2002; Parmentier et al. 2013), cottids (Colleye et al. 2013), chaetodontids (Boyle and Tricas 2010, 2011; Parmentier et al. 2011a), and cyprinids, for example, all include species capable of sound production, but these species do not exhibit major modifications of their Bauplan. The anatomy of these fishes is similar to that of mute relatives. Surprisingly, in some groups the responsible anatomical structures are unknown, and it is difficult to determine which parts of the body to investigate. Therefore sounds can be produced with only minor modifications of fish morphology. Sections 2.5.1.1–2.5.1.5 discuss several interesting examples highlighting taxa that have taken advantage of their incipient abilities to produce voluntary communication signals.

2.5.1.1 Damsel fish (Pomacentridae)

Damsel fish are well-known vocal species that produce sounds in courtship and agonistic contexts (Myrberg et al. 1978; Mann and Lobel 1998; Colleye and Parmentier 2012). The sonic mechanism appears unique among teleosts and results from teeth collisions induced by a fast jaw slam (Parmentier et al. 2007). The vibration is radiated through the ribs and induces oscillations of the swim-bladder wall (Colleye et al. 2012). Rapid mouth closure is forced by an apomorphic ceratomandibular ligament (Stiassny 1981) that connects the medial face of the lower jaw and the lateral face of the ceratohyal (Fig. 2.8). The ligament, stretched when the oral jaws

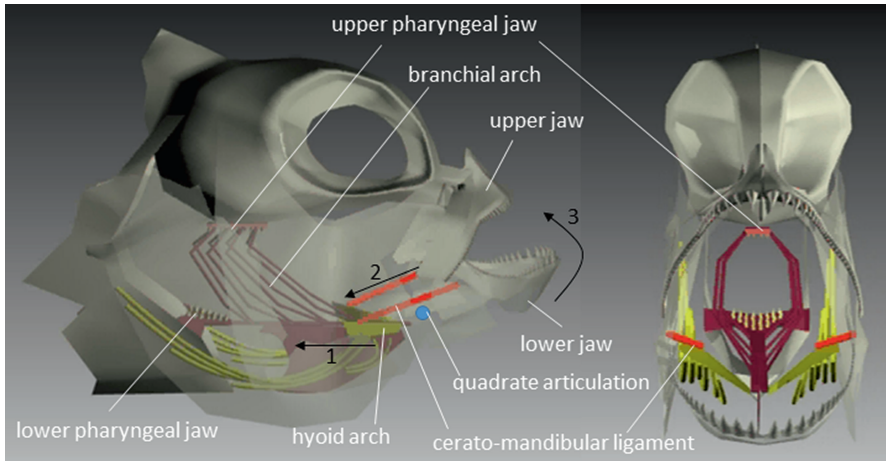


Fig. 2.8 Schematic *right lateral view* (a) and *rostral view* (b) of the sound-producing mechanism illustrating the relative movement of skeletal components in clownfish. Lowering the hyoid bar (1) stretches the sonic ligament (2), and the jaw closes the mouth (3) by rotating around the mandible articulation on the quadrate (Modified from Parmentier et al. 2007)

are opened, enables rapid closure causing teeth collisions and sound production (Parmentier et al. 2007; Colleye et al. 2012; Fr  d  rich et al. 2014). Manual manipulation of fresh specimens indicates mouth closure is caused by the stretched ligament and does not require adductor muscle contraction, as in other teleosts (Olivier et al. 2014). Further, cutting the ceratomandibular ligaments prevents both feeding and sound production.

In the clownfish (*Amphiprion clarkii*) and the filamentous algae grazer (*Stegastes rectifraenum*), the slam occurs during feeding, likely the precursor behavior, and sound production (Olivier et al. 2014, 2015). In *Stegastes rectifraenum*, the buccal jaw slam probably plays a major role in farming activity enabling accurate strikes on small filamentous algae (Olivier et al. 2014). Kinematic analysis has demonstrated that similar jaw slams and sounds are produced during biting of filamentous algae and agonistic behavior. Similar movements are also found in sound production and biting in *Amphiprion*, and the characters and motor patterns used in feeding have been co-opted for sound production. Based on feeding movements and parsimony, the ancestral call was likely a single pulse. Different sequences of pulses are produced in different behaviors although they all utilize the c-md ligament. Sounds generally occur simultaneously with aggressive actions related to territorial defense. In all studied species, a single jaw slam occurs during fighting and produces a single pulse. The origin of sound production would come from a biting action for two reasons. (1) Fighting sounds usually occur before the display of aggressive behavior with biting (Parmentier et al. 2010c). (2) Alternatively, biting occurs during foraging activities in *Stegastes rectifraenum* (Olivier et al. 2014). Intact individuals were able to produce sounds and maintain their territorial boundaries

whereas muted individuals did not deter intruders from entering their shelter sites despite appropriate visual displays (Myrberg 1997).

Initial communicative sounds were probably single pulses, which were selected because they resulted in successful territory and nest defense. Currently, one or two pulse sounds are used to deter conspecifics and heterospecifics, and courtship dips or visiting calls utilize trains of pulses that result from repetition of the same motor pattern.

2.5.1.2 Piranhas (Serrasalminae)

Piranhas produce drumming calls by contracting high-speed swim bladder muscles in several species (Markl 1971; Kastberger 1981a, b). One species, *Pygocentrus nattereri*, has been shown to produce a different sound when an individual snapped its jaws to bite a conspecific (Millot et al. 2011). The sound has a single pulse with a dominant frequency of approximately 1740 Hz. In videos, 90 % of the sounds occurred when chasing a conspecific. Further studies are required to determine if these teeth sounds have a communication function.

2.5.1.3 Grunt (Haemulidae)

Stridulation is based on friction of skeletal elements such as teeth, fin rays, and vertebrae (Burkenroad 1930; Tavalga 1971). Haemulids produce stridulatory sounds when the upper and lower pharyngeal teeth grate against each other (Burkenroad 1930; Moulton 1958). These sounds are also made when the fish are handheld, and to the best of our knowledge, sound production under natural conditions has not been observed. Therefore the function of these sounds is unknown although the association with being grabbed suggests they are emitted in stressful situations. The detailed cyclic pharyngeal jaw movement pattern during food processing has been described in nine haemulid species (Wainwright 1989a, b). In the French grunt (*Haemulon flavolineatum*) Bertucci and colleagues found similar sounds produced during food processing and when fish are handheld (Bertucci et al. 2014). High-speed X-ray videos confirmed sounds result from the rubbing of teeth located on the upper and lower pharyngeal jaws, and the cyclic movements during sound production correspond to those made during food processing (Bertucci et al. 2014).

In the Haemulidae, as in many perciform fishes (Vandewalle et al. 1992, 1995), the motion of the upper jaw is generally greater than that of the lower jaw. During the rhythmic pharyngeal transport of food to the esophagus, the upper jaw sweeps dorsally from the posterior pharyngeal cavity forward, descends, and then returns to its initial position. The lower pharyngeal jaws move similarly. The upper and lower jaws meet during the posterior movement of the upper and anterior movement of the lower jaws, creating a sheering action. Without food, these movements provoke sound production. We hypothesize incidental sounds produced during food processing assumed a communication function that was favored over time.

2.5.1.4 Sea Horses (Syngnathidae)

Sea horses and pipefishes produce stridulation clicks during feeding strikes but also in courtship, male–male competition, and when held out of water (Fish 1953; Colson et al. 1998; Ripley and Foran 2007). Observations of head movements with high-speed video and synchronous sound recording indicate sound clicks and feeding strikes are due to a bony articulation: ridges of the supraoccipital bone slide under the groove in the coronet (bony plate at the back of the head) during rapid head elevation (Colson et al. 1998; Lim et al. 2015). In pipefishes, feeding strikes evoke click production (Ripley and Foran 2007), but the functional significance of the feeding click is unknown. The incidental byproduct hypothesis has been rejected because clicks may increase predation risk (Oliveira et al. 2014), although the balance between risk and benefit has not been studied. The benefit should be more important than the risk for the caller, and the feeding sounds may help maintain proximity between male–female pairs since these fish swim slowly. Once more, the parsimony principle implies sound production was first a byproduct of feeding strikes and has been selected for use in courtship and pair maintenance. It may have contributed to the complex courtship behavior found in many members of the family.

2.5.1.5 Catfish (Siluriformes)

Catfishes (Fig. 2.7) use large, complex, and armored pectoral spines that can be bound and locked as antipredator adaptations (Fine and Ladich 2003). A locked spine more than doubles the width of a juvenile channel catfish and complicates ingestion by gape-limited fish predators (Bosher et al. 2006; Sismour et al. 2013). In fact, dead fish, snakes, and birds have been found with spines stuck in their tissues (Sismour et al. 2013). Furthermore, spine and pectoral girdle mass have decreased in domesticated channel catfish that have experienced reduced predation for a number of generations. Selection for fast growing individuals may have also played a part in pectoral reduction (Fine et al. 2014). In addition, catfishes have evolved toxins multiple times that can be delivered by the pectoral spines (Burkhead 1972; Wright 2009).

The base of catfish spines has apomorphic dorsal, anterior, and ventral processes that are not present in related taxa such as characids and cyprinids (Hubbs and Hibbard 1951; Fine and Ladich 2003). The processes mate with complementary surfaces on the cleithrum and coracoid of a fused pectoral girdle (Brousseau 1978; Diogo et al. 2001; Miano et al. 2013) that provides support to anchor the spines (Schaefer 1984). Fossils of well-developed pectoral spines and girdles date back to the Cretaceous (Gayet and Van Neer 1990; Lundberg 1997; Gayet and Meunier 2003); therefore no direct information exists on the formation of these processes from a typical pectoral first spine. The dorsal and anterior processes likely evolved from the dorsal half of the first lepidotrich and the ventral process from the ventral half (John Lundberg and John Friel, pers. comm., 2014).

In a distress situation, pectoral spines are bound after partial and locked after complete abduction. The locked spine resists any linear motion, and unlocking requires posterodorsal rotation of the spine followed by adduction (Fine et al. 1997). The deployment of an enlarged spine provided some degree of protection. However, the spine function does not seem limited to this function in all Siluriformes. Numerous catfish species use also the dorsal process of the pectoral spine to stridulate, producing a series of pulses when grabbed by a predator (Bosher et al. 2006) or when handheld (Heyd and Pfeiffer 2000; Kaatz et al. 2010). The fused pectoral girdle, in addition to providing a rigid platform to anchor the spine (Schaefer 1984), has secondarily become specialized as a sound radiator. Species capable of sound production have developed ridges, visible with scanning electron microscopy, on the under surface of the dorsal process (Fine et al. 1997; Kaatz et al. 2010; Parmentier et al. 2010b). In these species, sounds are caused by a slip-stick mechanism: Small jerk-like motions of ridges against the cleithrum stimulate the pectoral girdle to vibrate (Parmentier et al. 2010b; Ghahramani et al. 2014; Mohajer et al. 2015). Initially the sound is of low amplitude, which then increases after termination of the jerk suggesting constructive interference, when the spine is immobile (Mohajer et al. 2015).

Most catfish species produce sound during spine abduction although a number of families have members that stridulate during abduction and adduction (Heyd and Pfeiffer 2000; Kaatz et al. 2010; Parmentier et al. 2010b). The channel catfish stridulates only during abduction although one adduction sound was videotaped out of 256 recorded (Fine et al. 1996). Therefore existing morphology will support adduction sounds, which would require amended neural programming. In this light it is interesting to note that the blue catfish, which produces only abduction sounds, first adducts its spine silently before stridulating (Ghahramani et al. 2014; Mohajer et al. 2015), suggesting the possibility of an existing step that may have occurred in those species that produce sound by stridulating in both directions.

The enlarged dorsal process, the rough surface of the channel in the cleithrum, and the fused pectoral girdle required to bind and lock the spines were co-opted to make sounds in most catfishes. Sound production was likely added secondarily to the defense function, and in many species sounds were further co-opted as agonistic and courtship signals.

2.6 Conclusion

In addition to reviewing the topic generally this chapter proposes a novel conceptual path to explore evolution of sound-producing mechanisms and propose the concept of exaptation as an entry to understand the myriad forms and solutions employed by fishes. Existing anatomical structures are first used in nonvoluntary sound production, which provides advantages and results in further selection and refinement of more sophisticated sonic organs. The examples have focused on fishes using stridulatory mechanisms to produce sounds but make it clear that a similar evolutionary history likely applies to mechanisms based on swim bladder and sound-producing muscles.

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