Chapter 3
Mechanisms of Fish Sound Production

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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.

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3.2 Water as an Acoustic Medium

Because of its compressibility, water is often considered a 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 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

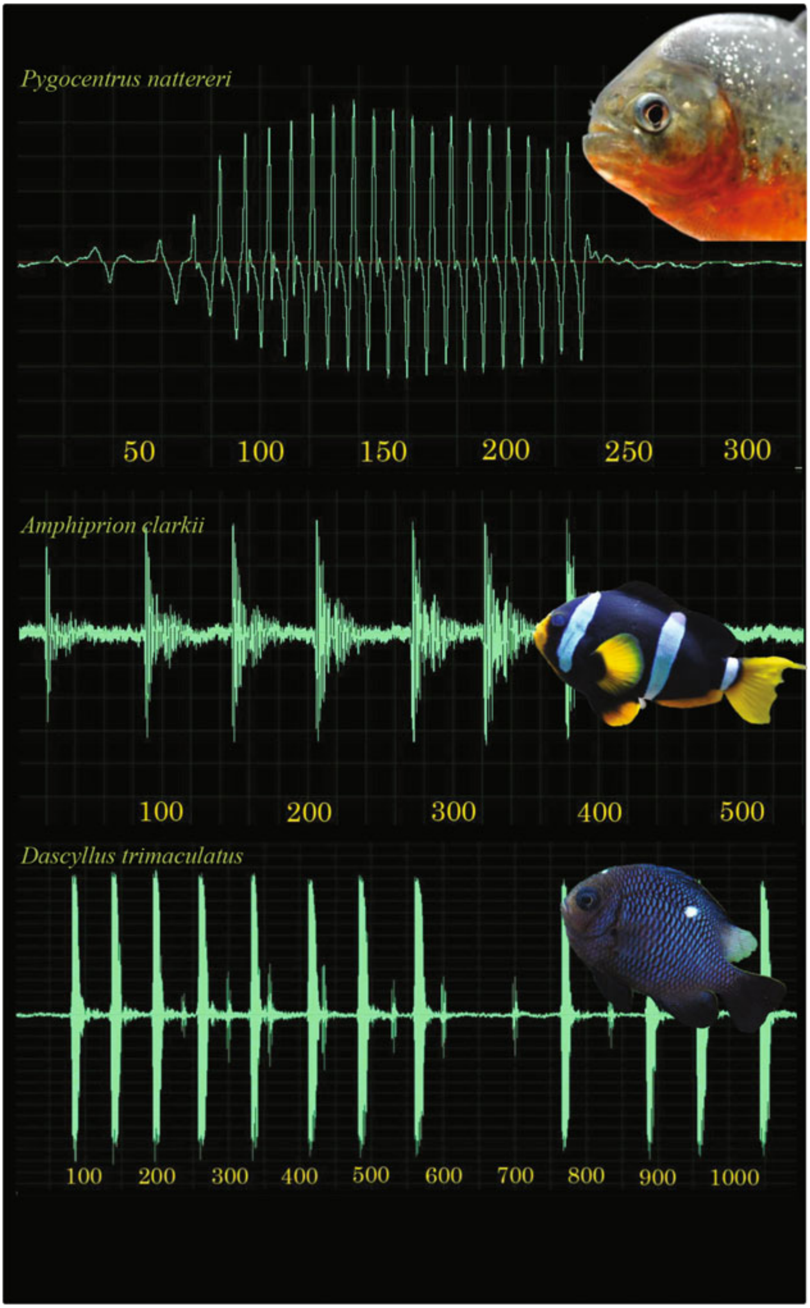

Fig. 3.1 Oscillograms (Voltage against time) of representative sounds for a piranah (*Pygocentrus*), two pomacentrid damselfish (*Amphiprion* and *Dascyllus*), a toadfish (*Opsanus*), a cusk-eel (*Ophidion*), and a butterfly fish (*Heniochus*). The piranah and toadfish sounds are tonal and the others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

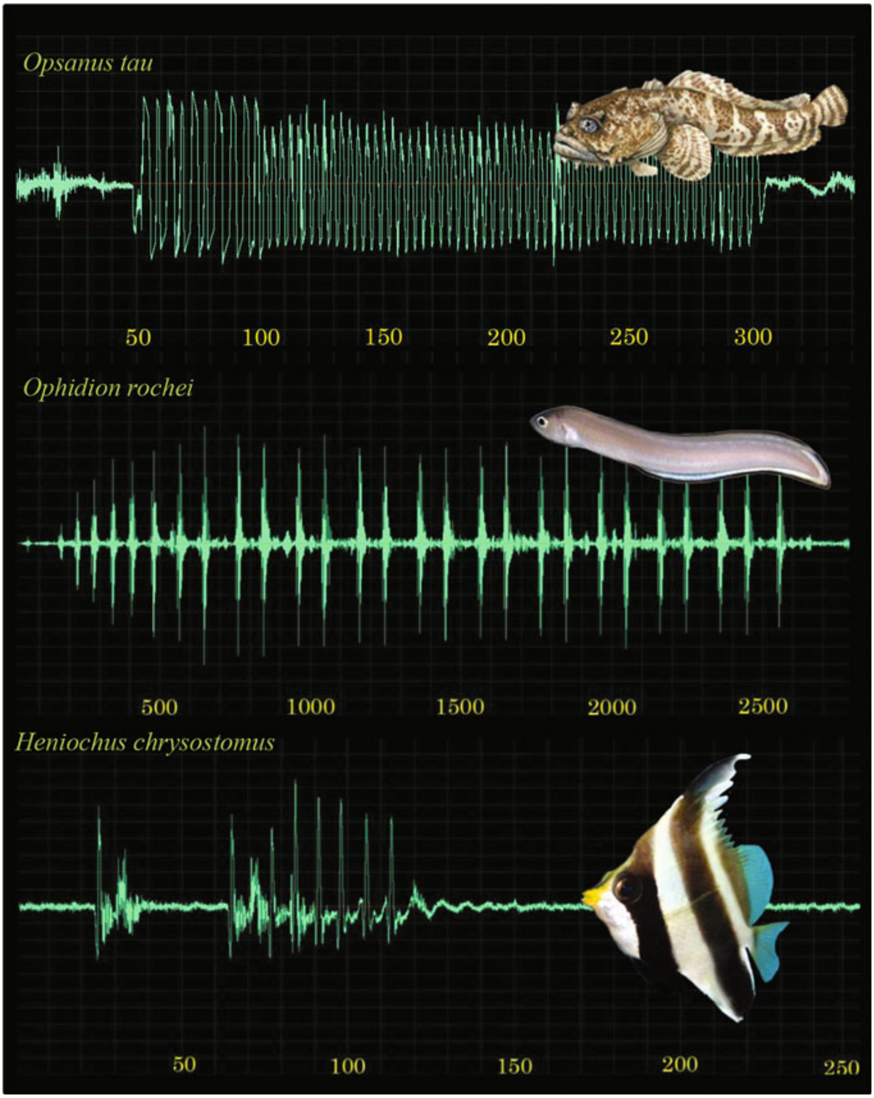

Fig. 3.1 (continued)

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).

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

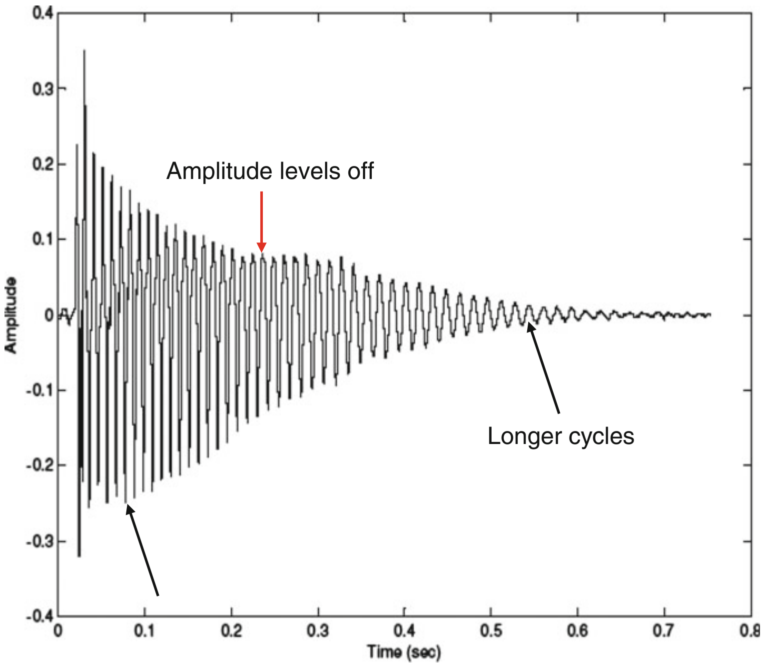

Fig. 3.2 Oscillogram of the advertisement call of the *black* drum *Pogonias cromis* modified from Locascio and Mann (2011). The *red arrow* above the waveform indicates that the amplitude levels off, which should not occur during exponential decay. The two *black arrows* below demonstrate that cycle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

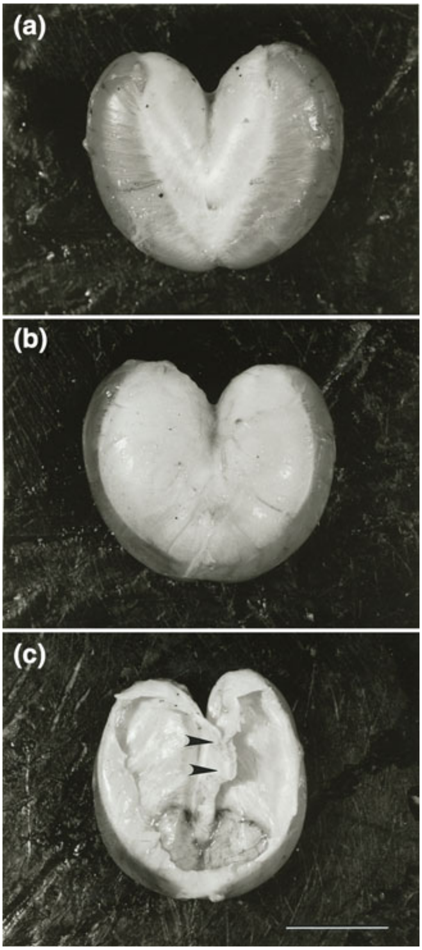

Fig. 3.3 Photographs of the swimbladder of the oyster toadfish *Opsanus tau* from Barimo and Fine (1998). **a** Dorsal view. **b** Ventral view. **c** Ventral view exposing the internal structure of the bladder. Note that the muscles are closer to the midline on the dorsal than the ventral surface and 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 dorso-lateral 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 small anterior and a larger 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.

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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 spectral 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

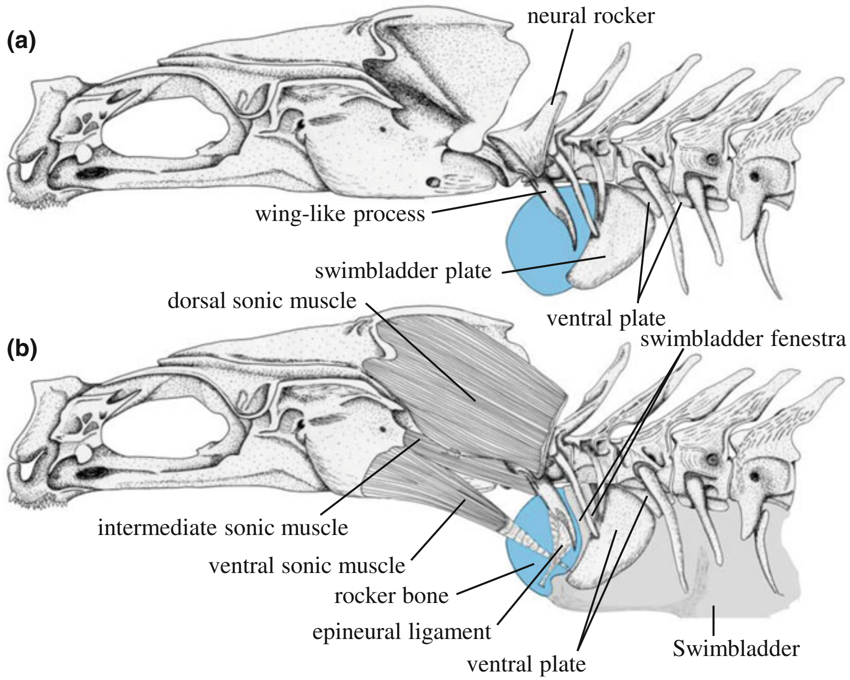

Fig. 3.4 Drawing of the skeleton, swimbladder, and sonic muscles of a representative ophidiid fish

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 dorsarostral 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 system

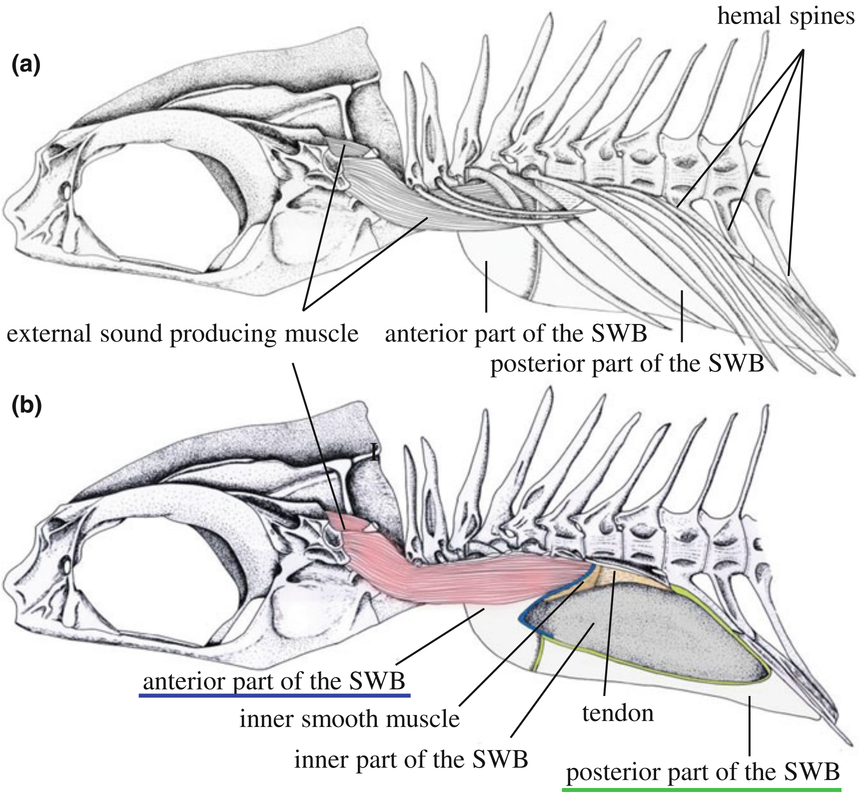

Fig. 3.5 Drawing of the skeleton, swimbladder, and sonic muscles of a glaucosomatid fish. Parallels between the glaucosomatid and the ophidiid in Fig. 3.4 include muscles attached to the dorsal anterior swimbladder, a swimbladder fenestra, and a rigid coupling of the posterior swimbladder to the vertebral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

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.

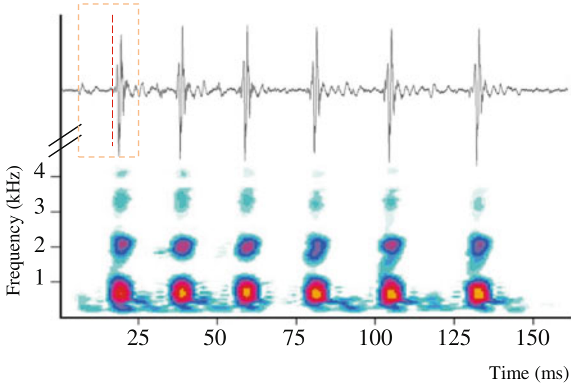

Fig. 3.6 Oscillogram and sonogram of a series of sound pulses evoked by touching the abdomen of the pearl perch *Glaucosoma buergeri*. The box in the oscillogram designates the first pulse, and the vertical *dashed line* separates pulse parts 1 and 2. From Mok et al. (2011)

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 cranio-clavicula 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. 2006); 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 1998) 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). Parvalbumin content is 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. in press).

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). 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. 2010a, b, c, d), 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 (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

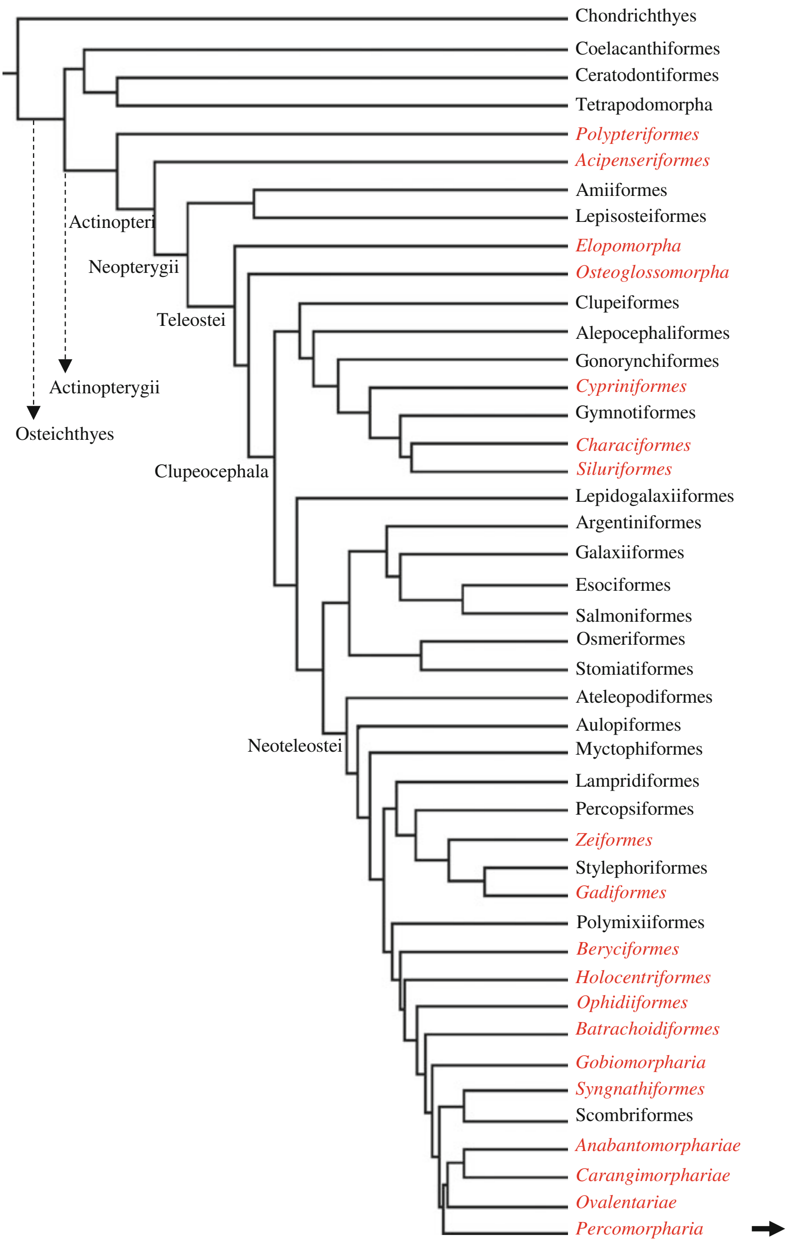

Fig. 3.7 Cladogram indicating groups of fishes that include sound producers (in *red* and italicized). The cladogram indicates that sound production has developed independently in multiple clades suggesting convergent evolution. Due to space considerations, the cladogram lumps diverse mechanisms including 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

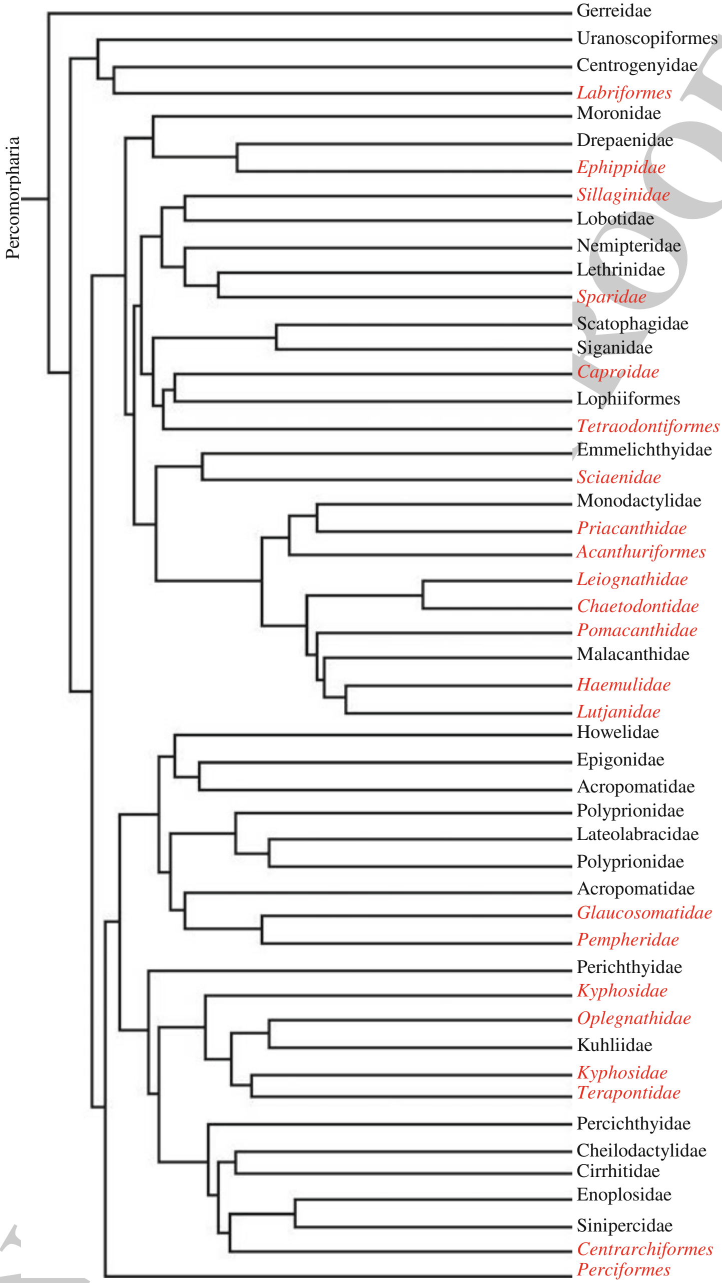

Fig. 3.7 (continued)

(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 AQ3

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. **AQ4**

References

Akamatsu T, Okumura T, Novarini N, Yan HY (2002) Empirical refinements applicable to the recording of fish sounds in small tanks. J Acoust Soc Am 112:3073–3082

Akster AH (1981) Ultrastructure of muscles fibres in head and axial muscles of the perch (*Perca fluviatilis* L.). Cell Tissue Res 219:111–131

Akster AH, Osse JWM (1978) Muscle fibre types in head muscles of the perch *Perca fluviatilis* (L), Teleostei. A histochemical and electromyographical study. Neth J Zool 28:94–110

Alexander RM (1966) Physical aspects of swimbladder function. Biol Rev 41:141–176

Alexander RM (1981) The chordates. Cambridge University Press, Cambridge

Amorim MCP (2006) Diversity of sound production in fish. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes, vol 1. Science Publishers, Endfield, pp 71–104 **AQ5**

Amorim MCP, Vasconcelos RO (2008) Variability in the mating calls of the Lusitanian toadfish *Halobatrachus didactylus*: cues for potential individual recognition. J Fish Biol 73:1267–1283. doi:10.1111/j.1095-8649.2008.01974

Amorim MCP, McCracken ML, Fine ML (2002) Metabolic costs of sound production in the oyster toadfish, *Opsanus tau*. Can J Zool 80:830–838

Amorim MCP, Vasconcelos RO, Parreira B (2009) Variability in the sonic muscles of the Lusitanian toadfish (*Halobatrachus didactylus*): acoustic signals may reflect individual quality. Can J Zool 87:718–725

Amorim MCP, Simoes JM, Mendonca N, Bandarra NM, Almada VC, Fonseca PJ (2010) Lusitanian toadfish song reflects male quality. J Exp Biol 213:2997–3004. doi:10.1242/jeb.044586

Appelt D, Shen V, Franzini-Armstrong C (1991) Quantitation of Ca ATPase, feet and mitochondria in superfast muscle fibres from the toadfish, Opsanus tau. J Muscle Res Cell Motil 12:543–552. doi:10.1007/bf01738442

Au WWL, Hastings MC (2008) Principles of marine bioacoustics. Springer, New York

Barber SB, Mowbray HM (1956) Mechanism of sound production in the sculpin. Science 124:219–220

Barimo JF, Fine ML (1998) Relationship of swim-bladder shape to the directionality pattern of underwater sound in the oyster toadfish. Can J Zool 76:134–143

Bass AH (1985) Sonic pathways in teleost fisher: a comparative HRP study. Brain Behav Evol 27:115–131

Bass AH, Chagnaud BP (2012) Shared developmental and evolutionary origins for neural basis of vocal–acoustic and pectoral–gestural signaling. Proc Natl Acad Sci 109:10677–10684. doi:10.1073/pnas.1201886109

Bass AH, Marchaterre MA (1989) Sound-generating (sonic) motor system in a teleost fish (*Porichthys notatus*): sexual in the ultrastructure of myofibrils. J Comp Neurol 286:141–153

Bass AH, Gilland EH, Baker R (2008) Evolutionary origins for social vocalization in a vertebrate hindbrain–spinal compartment. Science 321:417–421. doi:10.1126/science.1157632

Batzler WE, Pickwell GV (1970) Resonant acoustic scattering from gasbladder fishes. In: Farquhar GB (ed) Proceedings of an international symposium on biological sound scattering in the ocean. U.S. Government Printing Office, Washington, DC, pp 168–179

Bertucci F, Ruppé L, van Wassenbvergh S, Compère P, Parmentier E (2014) Sound production and role of the pharyngeal jaw apparatus in the French grunt, *Haemulon flavolineatum* (Haemulidae). J Exp Biol (in press)

Betancur-R R et al. (2013) The tree of life and a new classification of bony fishes, edn 1. PLOS currents tree of life

Lewis MK et al (2003) Concentric intermediate filament lattice links to specialized Z-band junctional complexes in sonic muscle fibers of the type I male midshipman fish. J Struct Biol 143:56–71. doi:10.1016/S1047-8477(03)00121-7

Birindelli JLO, Sousa LM, Sabaj Perez MH (2009) Morphology of the gas bladder in thorny catfishes (Siluriformes: Doradidae). Proc Acad Nat Sci Phila 158:261–296

Bosher B, Newton S, Fine M (2006) The spine of the channel catfish, *Ictalurus punctatus*, as an anti-predator adaptation: an experimental study. Ethology 112:188–195

Boyle KS, Tricas TC (2010) Pulse sound generation, anterior swim bladder buckling and associated muscle activity in the pyramid butterflyfish, *Hemitaurichthys polylepis*. J Exp Biol 213:3881–3893. doi:10.1242/jeb.048710

Boyle KS, Tricas TC (2011) Sound production in the longnose butterflyfishes (genus *Forcipiger*): cranial kinematics, muscle activity and honest signals. J Exp Biol 214:3829–3842. doi:10.1242/jeb.062554

Boyle KS, Dewan AK, Tricas TC (2013) Fast drum strokes: novel and convergent features of sonic muscle ultrastructure, innervation, and motor neuron organization in the pyramid butterflyfish (hemitaurichthys polylepis). J Morphol, 1097–4687. doi:10.1002/jmor.20096

Bradbury J, Vehrencamp S (1998) Principles of animal communication. Sinauer Associates Inc, Sunderland

Brantley R, Tseng J, Bass A (1993) The ontogeny of inter- and intrasexual vocal muscle dimorphisms in a sound producing fish. Brain Behav Evol 42:336–349

Breedlove SM, Arnold AP (1980) Hormone accumulation in a sexually dimorphic nucleus of the rat spinal cord. Science 210:564–566

Burkenroad MD (1930) Sound production in the Haemulidae. Copeia 1930:17–18

Burkenroad MD (1931) Notes on the marine sound-producing fish of Louisiana. Copeia 1931:20–28

Butler A, Saidel W (2000) Defining sameness: historical, biological, and generative homology. BioEssays 22:846–853

Carlson B, Bass A (2000) Sonic/vocal motor pathways in squirrelfish (Teleostei, Holocentridae). Brain Behav Evol 56:14–28

Casadevall M, Matallanas J, Carrasson M, Munoz M (1996) Morphometric, meristic and anatomical differences between Ophidion barbatum L., 1758 and O. rochei Muller, 1845 (Pisces, Ophidiidae). Publ Especiales Inst Esp Oceanogr 21:45–61

Chagnaud BP, Baker R, Bass AH (2011) Vocalization frequency and duration are coded in separate hindbrain nuclei. Nat Commun 2:346

Chagnaud BP, Zee MC, Baker R, Bass AH (2012) Innovations in motoneuron synchrony drive rapid temporal modulations in vertebrate acoustic signaling. J Neurophysiol 107:3528–3542. doi:10.1152/jn.00030.2012

Chardon M (1968) Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. Ann Mus R Afr Centr 169:1–273

Chen SF, Huang BQ, Chien YY (1998) Histochemical characteristics of sonic muscle fibers in Tigerperch, *Terapon jarbua*. Zool Stud 37:56–62

Chiu K-H, Hsieh F-M, Chen Y-Y, Huang H-W, Shiea J, Mok H-K (2013) Parvalbumin characteristics in the sonic muscle of a freshwater ornamental grunting toadfish (Allenbatrachus grunniens). Fish Physiol Biochem 39:107–119. doi:10.1007/s10695-012-9683-4

Cohen M, Winn H (1967) Electrophysiological observations on hearing and sound production in the fish, *Porichthys notatus*. J Exp Biol 165:355–370

Colleye O, Frederich B, Vandewalle P, Casadevall M, Parmentier E (2009) Agonistic sounds in the skunk clownfish *Amphiprion akallopisos*: size-related variation in acoustic features. J Fish Biol 75:908–916. doi:10.1111/j.1095-8649.2009.02316.x

Colleye O, Vandewalle P, Lanterbecq D, Lecchini D, Parmentier E (2011) Interspecific variation of calls in clownfishes: degree of similarity in closely related species. BMC Evol Biol 11:365

Colleye O, Nakamura M, Frédérich B, Parmentier E (2012) Further insight into the sound-producing mechanism of clownfishes: what structure is involved in sound radiation? J Exp Biol 215:2192–2202. doi:10.1242/jeb.067124

Colson D, Patek S, Brainerd E, Lewis S (1998) Sound production during feeding in *Hippocampus* seahorses (Syngnathidae). Environ Biol Fishes 51:221–229. doi:10.1023/a:1007434714122

Connaughton MA (2004) Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. J Exp Biol 207:1643–1654. doi:10.1242/jeb.00928

Connaughton MA, Taylor MH (1995) Seasonal and daily cycles in sound production associated with spawning in weakfish, *Cynoscion regalis*. Environ Biol Fishes 42:233–240

Connaughton MA, Fine ML, Taylor MH (1997) The effect of seasonal hypertrophy and atrophy of fiber morphology, metabolic substrate concentration and sound characteristics of the weakfish sonic muscle. J Exp Biol 200:2449–2457

Connaughton MA, Fine ML, Taylor MH (2002) Weakfish sonic muscle: influence of size, temperature and season. J Exp Biol 205:2183–2188

Coombs S, Popper AN (1979) Hearing differences among Hawaiian squirrelfish (family Holocentridae) related to differences in the peripheral auditory system. J Comp Physiol A 132:203–207. doi:10.1007/bf00614491

Courtenay W (1971) Sexual dimorphism of the sound producing mechanism of the striped cusk eel, Rissola marginata (Pisces: Ophidiidae). Copeia 2:259–268

Crockford T, Johnston IA (1993) Developmental changes in the composition of myofibrillar proteins in the swimming muscles of Atlantic herring, *Clupea harengus*. Mar Biol 115:15–22. doi:10.1007/bf00349381

De Jong K, Bouton N, Slabbekoorn H (2007) Azorean rock-pool blennies produce size-dependent calls in a courtship context. Anim Behav 74:1285–1292

Demski LS, Gerald JW (1972) Sound production evoked by electrical stimulation of the brain in toadfish (*Opsanus beta*). Anim Behav 20:504–513

Demski LS, Gerald JW (1974) Sound production and other behavioral effects of midbrain stimulation in the free-swimming toadfish, *Opsanus beta*. Brain Behav Evol 9:41–59

Demski LS, Gerald JW, Popper AN (1973) Central and peripheral mechanisms of teleost sound production. Am Zool 13:1141–1167

Devincenti CV, Diaz AO, Goldenberg AL (2000) Characterization of the swimming muscle of the anchovy *Engraulis anchoita* (Hubbs and Martini 1935). Anat Histol Embryol 29:197–202

Eichelberg H (1976) The fine structure of the drum muscles of the tigerfish *Therapon jarbua*, as compared with the trunk musculature. Cell Tissue Res 174:453–463

Eichelberg H (1977) Fine structure of the drum muscles of the piranha (Serrasalminae, Characidae). Cell Tissue Res 185:547–555. doi:10.1007/bf00220658

Evans RR (1973) The swimbladder and associated structures in Western Atlantic sea robins (Triglidae). Copeia 1973:315–321

Fänge R, Wittenberg JB (1958) The swimbladder of the toadfish (*Opsanus tau* L.). Biol Bull 115:172–179

Fawcett DW, Revel JP (1961) The sarcoplasmic reticulum of a fast-acting fish muscle. J Biophys Biochem Cytol 10:89–109

Feher J, Waybright T, Fine M (1998) Comparison of sarcoplasmic reticulum capabilities in toadfish (*Opsanus tau*) sonic muscle and rat fast twitch muscle. J Muscle Res Cell Motil 19:661–674. doi:10.1023/a:1005333215172

Feuillade C, Nero RW (1998) A visco-elastic swimbladder model for describing enhanced-frequency resonance scattering from fish. J Acoust Soc Am 103:3245–3255. doi:10.1121/1.423076

Fine ML (1978a) Geographical variation in sound production evoked by brain stimulation in the oyster toadfish. Naturwissenschaften 65:493. doi:10.1007/bf00702846

Fine ML (1978b) Seasonal and geographical variation of the mating call of the oyster toadfish *Opsanus tau* L. Oecologia 36:45–57

Fine ML (1997) Endocrinology of sound production in fishes. Mar Freshw Behav Physiol 29:23–45

Fine ML (2012) Swimbladder sound production: the forced response versus the resonant bubble. Bioacoustics 21:5–7

Fine ML, Ladich F (2003) Sound production, spine locking and related adaptations. In: Kapoor BG, Arratia G, Chardon M, Diogo R (eds) Catfishes. Science Publishers, Enfield, pp 248–290

Fine ML, Lenhardt ML (1983) Shallow-water propagation of the toadfish mating call. Comp Biochem Physiol A Physiol 76:225–231 doi:10.1016/0300-9629(83)90319-5

Fine ML, Pennypacker KR (1988) Histochemical typing of sonic muscle from the oyster toadfish. Copeia 1988:130–134

Fine ML, Winn HE, Joest L, Perkins PJ (1977a) Temporal aspects of calling behavior in the oyster toadfish, *Opsanus tau*. Fish Bull 75:871–874

Fine ML, Winn HE, Olla BL (1977b) Communication in fishes. In: Sebeok T (ed) How animals communicate. Indiana University Press, Bloomington, pp 472–518

Fine ML, Keefer D, Leichnetz GR (1982) Testosterone uptake in the brainstem of a sound-producing fish. Science 215:1265–1267

Fine ML, Economos D, Radtke R, McClung JR (1984) Ontogeny and sexual dimorphism of the sonic motor nucleus in the oyster toadfish. J Comp Neurol 225:105–110. doi:10.1002/cne.902250111

Fine M, Burns N, Harris T (1990) Ontogeny and sexual dimorphism of sonic muscle in the oyster toadfish. Can J Zool 68:1374–1381

Fine ML, Bernard B, Harris TM (1993) Functional morphology of toadfish sonic muscle fibers: relationship to possible fiber division. Can J Zool 71:2262–2274. doi:10.1139/z93-318

Fine ML, McKnight JW Jr, Blem CR (1995) Effect of size and sex on buoyancy in the oyster toadfish. Mar Biol 123:401–409. doi:10.1007/bf00349218

Fine ML, McElroy D, Rafi J, King CB, Loesser KE, Newton S (1996) Lateralization of pectoral stridulation sound production in the channel catfish. Physiol Behav 60:753–757. doi:10.1016/0031-9384(96)00092-3

Fine ML, Friel J, McElroy D, King C, Loesser K, Newton S (1997) Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus*. Copeia 1997:777–790

Fine ML, King C, Friel J, Loesser K, Newton S (1999) Sound production and locking of the pectoral spine of the channel catfish. Am Fish Soc Symp 24:105–114

Fine ML, Malloy KL, King CB, Mitchell SL, Cameron TM (2001) Movement and sound generation by toadfish swimbladder. J Comp Physiol A 187:371–379

Fine ML, Schrinel J, Cameron TM (2004) The effect of loading on disturbance sounds of the Atlantic croaker *Micropogonius undulatus*: air versus water. J Acoust Soc Am 116:1271–1275

Fine ML, Lin H, Nguyen BB, Rountree RA, Cameron TM, Parmentier E (2007) Functional morphology of the sonic apparatus in the fawn cusk-eel *Lepophidium profundorum* (Gill 1863). J Morphol 268:953–966. doi:10.1002/jmor.10551

Fine ML, King CB, Cameron TM (2009) Acoustical properties of the swimbladder in the oyster toadfish *Opsanus tau*. J Exp Biol 212:3542–3552. doi:10.1242/jeb.033423

Fine ML et al (2011) A primer on functional morphology and behavioural ecology of the pectoral spine of the channel catfish. Am Fish Soc Symp 77:745–753

Fine ML, Lahiri S, Sullivan ADH, Mayo M, Newton SH, Sismour EN (2014) Reduction of the pectoral spine and girdle in domesticated channel catfish is likely caused by changes in selection pressure. Evolution 68:2102–2107. doi:10.1111/evo.12379

Finger TE, Kalil K (1985) Organization of motoneuronal pools in the rostral spinal cord of the sea robin, *Prionotus carolinus*. J Comp Neurol 239:384–390

Fish MP (1953) The production of underwater sounds by the northern seahorse, *Hippocampus hudsonius*. Copeia 1953:98–99

Fish MP (1954) The character and significance of sound production among fishes of the Western North Atlantic Ocean. Bull Bingham Oceanogr Col 14:1–109

Fish JF (1972) The effect of sound playback on the toadfish. In: Winn HE, Olla BL (eds) Behavior of marine animals, vol 2. Plenum Press, New York, pp 386–434

Fish MP, Mowbray HM (1970) Sounds of Western North Atlantic fishes. The Johns Hopkins Press, Baltimore

Focant B, Huriaux F, Vandewalle P, Castelli M, Goessens G (1992) Myosin, parvalbumin and myofibril expression in barbel (*Barbus barbus* L.) lateral white muscle during development. Fish Physiol Biochem 10:133–143. doi:10.1007/bf00004524

Focant B, Vandewalle P, Huriaux F (2003) Expression of myofibrillar proteins and parvalbumin isoforms during the development of a flatfish, the common sole *Solea solea*: comparison with the turbot *Scophthalmus maximus*. Comp Biochem Physiol Part B Biochem Mol Biol 135:493–502. doi:10.1016/S1096-4959(03)00116-7

Francis DTI, Foote KG (2003) Depth-dependent target strengths of gadoids by the boundary-element method. J Acoust Soc Am 114:3136–3146. doi:10.1121/1.1619982

Gainer H (1969) Multiple innervation of fish skeletal muscle. In: Kerkut GA (ed) Experiments in physiology and biochemistry, vol 2. Academic Press, New York, pp 191–208

Gerday C (1982) Soluble calcium-binding proteins from fish and invertebrate muscle. Mol Physiol 2:63–87

Gill T (1905) The life history of the sea-horses (hippocampids). Proc US Natl Mus 28:805–814

Gilland E, Baker R (1993) Conservation of neuroepithelial and mesodermal segments in the embryonic vertebrate head. Acta Anat 148:110–123

Gkenas C, Malavasi S, Georgalas V, Leonardos ID, Torricelli P (2010) The reproductive behavior of *Economidichthys pygmaeus*: secondary loss of sound production within the sand goby group? Environ Biol Fishes 87:299–307

Gray GA, Winn HE (1961) Reproductive ecology and sound production of the toadfish, *Opsanus tau*. Ecology 42:274–282

Guest WC, Lasswell JL (1978) A note on courtship behavior and sound production of red drum. Copeia 1978:337–338

Hamoir G, Focant B (1981) Proteinic differences between the sarcoplasmic reticulum of the superfast swimbladder and the fast skeletal muscles of the toadfish *Opsanus tau*. Mol Physiol 1:353–359

Hamoir G, Gerardin-Otthiers N, Focant B (1980) Protein differentiation of the superfast swimbladder muscle of the toadfish *Opsanus tau*. J Mol Biol 143:155–160. doi:10.1016/0022-2836(80)90129-1

Harris GG (1964) Considerations on the physics of sound production by fishes. In: Tavolga WN (ed) Marine bio-acoustics, vol 1. Pergamon Press, New-York, pp 233–247

Hawkins AD (1993) Underwater sound and fish behaviour. In: Pitcher TJ (ed) Behaviour of teleost fishes, 2nd edn. Chapman & Hall, London, pp 129–169

Heyd A, Pfeiffer W (2000) Über die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihren Zusammenhang mit der Phylogenese und der Schreckreaktion. Rev Suisse Zool 107:165–211

Hirsch JE, Bigbee JW, Fine ML (1998) Continuous adult development of multiple innervation in toadfish sonic muscle. J Neurobiol 36:348–356

Horch K, Salmon M (1973) Adaptations to the acoustic environment by the squirrelfish *Myripristis violaceus* and *M. pralinius*. Mar Behav Physiol 2:121–139

Howes G (1992) Notes on the anatomy and classification of Ophidiiform fishes with particular reference to the abyssal genus *Acanthonus* Günther, 1878. Bull Br Mus Nat Hist 58:95–131

Huriaux F, Baras E, Vandewalle P, Focant B (2003) Expression of myofibrillar proteins and parvalbumin isoforms in white muscle of dorada during development. J Fish Biol 62:774–792. doi:10.1046/j.1095-8649.2003.00064.x

Johnston IA (1981) Structure and function of fish muscles. Symp Zool Soc Lond 48:71–113

Johnston CE, Johnson DL (2000a) Sound production during the spawning season in cavity-nesting darters of the subgenus *Catonotus* (Percidae: *Etheostoma*). Copeia 2000:475–481

Johnston CE, Johnson DL (2000b) Sound production in *Pimephales notatus* (Rafinesque) (Cyprinidae). Copeia 2000:567–571

Johnston C, Vives S (2003) Sound production in *Codoma ornata* (Girard) (Cyprinidae). Environ Biol Fishes 68:81–85. doi:10.1023/a:1026067913329

Johnston IA, Patterson S, Ward PS, Goldspink G (1974) The histochemical demonstration of myofibrillar adenosine triphosphatase activity in fish muscle. Can J Zool 52:871–877

Jordão JM, Fonseca PJ, Amorim MCP (2012) Chorusing behaviour in the Lusitanian toadfish: should I match my neighbours' calling rate? Ethology 118:885–895. doi:10.1111/j.1439-0310.2012.02078.x

Josephson R (2006) Comparative physiology of insect flight muscle. In: Nature's versatile engine: insect flight muscle inside and out. Molecular biology intelligence unit. Springer, Berlin, pp 34–43. doi:10.1007/0-387-31213-7_3

Kaatz IM, Stewart DJ (1997) The evolutionary origin and functional divergence of sound production in catfishes: stridulation mechanisms. J Morphol 232:272

Kaatz IM, Stewart DJ (2012) Bioacoustic variation of swimbladder disturbance sounds in neotropical doradoid catfishes (Siluriformes: Doradidae, Auchenipteridae): potential morphological correlates. Curr Zool 58:171–188

Kaatz IM, Stewart DJ, Rice AN, Lobel PS (2010) Differences in pectoral fin spine morphology between vocal and silent clades of catfish (order Siluriformes): ecomorphological implications. Curr Zool 56:73–89

Kastberger G (1981a) Economy of sound production in piranhas (Serrasalminae, Characidae): I. Functional properties of sonic muscles. Zool Jahrb Physiol 85:113–125

Kastberger G (1981b) Economy of sound production in piranhas (Serrasalminae, Characidae): II Functional properties of sound emitter. Zool Jb Physiol 85:393–411

Kasumyan AO (2008) Sounds and sound production in fishes. J Ichthyol 48:981–1030

Kéver L, Boyle K, Dragicevic B, Dulcic J, Casadevall M, Parmentier E (2012a) Sexual dimorphism of sonic apparatus and extreme intersexual variation of sounds in *Ophidion rochei* (Ophidiidae): first evidence of a tight relationship between morphology and sound characteristics in Ophidiidae. Front Zool 9:34

Kéver L, Boyle KS, Dragičević B, Dulčić J, Casadevall M, Parmentier E (2012b) Sexual dimorphism of sonic apparatus and extreme intersexual variation of sounds in *Ophidion rochei* (Ophidiidae): first evidence of a tight relationship between morphology and sound characteristics in Ophidiidae. Front Zool 9:1–16

Kéver L, Boyle KS, Bolen G, Dragičević B, Dulčić J, Parmentier E (2014) Modifications in call characteristics and sonic apparatus morphology during puberty in *Ophidion rochei* (actinopterygii: Ophidiidae). J Morphol 275:650–660. doi:10.1002/jmor.20245

Klug GA, Leberer E, Leisner E, Simoneau J, Pette D (1988) Relationship between parvalbumin content and the speed of relaxation in chronically stimulated rabbit fast-twitch muscle. Pflugers Arch 411:126–131

Korneliussen H, Dahl HA, Paulsen JE (1978) Histochemical definition of muscle fibre types in trunk musculature of a teleost fish (cod, Gadus morhua, L.). Histochem Cell Biol 55:1–16

Kratochvil H (1978) Der Bau des Lautapparates vom Knurrenden Gurami (*Trichopsis vittatus* Cuvier & Valenciennes) (Anabantidae, Belontiidae). Zoomorphologie 91:91–99

Kratochvil H (1985) Beiträge zur Lautbiologie der Anabantoidei—Bau, Funktion und Entwicklung von lauterzeugenden Systeme. Zool Jahrb Physiol 89:203–255

Ladich F (1988) Sound production by the gudgeon, Gobio gobio L., a common European freshwater fish (Cyprinidae, Teleostei). J Fish Biol 32:707–715. doi:10.1111/j.1095-8649.1988.tb05411.x

Ladich F (1997) Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. Bioacoustics 8:185–208

Ladich F (2001) Sound-generating and -detecting motor system in catfish: design of swimbladder muscles in doradids and pimelodids. Anat Rec 263:297–306

Ladich F (2013) Effects of noise on sound detection and acoustic communication in fishes. In: Brumm H (ed) Animal communication and noise. Springer, Berlin, pp 65–90

Ladich F (2014) Diversity in hearing in fishes: ecoacoustical, communicative, and developmental constraints. In: Köppl C, Manley GA, Popper AN, Fay RR (eds) Insights from comparative hearing research. Springer handbook of auditory research, vol 49. Springer, New York, pp 289–321

Ladich F, Bass AH (2005) Sonic motor pathways in piranhas with a reassessment of phylogenetic patterns of sonic mechanisms among teleosts. Brain Behav Evol 66:167–176

Ladich F, Fine ML (1992) Localization of pectoral fin motoneurons (sonic and hovering) in the Croaking Gourami (*Trichopsis vittatus*). Brain Behav Evol 39:1–7

Ladich F, Fine ML (1994) Localization of swim bladder and pectoral motoneurons involved in sound production in pimelodid catfish. Brain Behav Evol 44:86–100

Ladich F, Fine M (2006) Sound-generating mechanisms in fishes: a unique diversty in vertebrates. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes, vol 1. Science Publishers, Enfield, pp 3–34

Ladich F, Myrberg AAJ (2006) Agonistic behavior and acoustic communication. In: Ladich F, Collin S, Moller P, Kapoor B (eds) Communication in fishes. Science Publishers, Enfield, pp 122–148

Ladich F, Tadler A (1988) Sound production in *Polypterus* (Osteichthyes: Polypteridae). Copeia 1988:1076–1077

Ladich F, Wysocki LE (2003) How does tripus extirpation affect auditory sensitivity in goldfish? Hear Res 182:119–129

Ladich F, Bischof C, Schleinzer G, Fuchs A (1992) Intra- and interspecific differences in agonistic vocalization in croaking gouramis (Genus: *Trichopsis*, Anabantoidei, Teleostei). Bioacoustics 4:131–141

Lagardère JP, Mariani A (2006) Spawning sounds in meagre *Argyrosomus regius* recorded in the Gironde estuary. Fr J Fish Biol 69:1697–1708

Lagardère JP, Mallekh R, Mariani A (2004) Acoustic characteristics of two feeding modes used by brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*) and turbot (*Scophthalmus maximus*). Aquaculture 240:607–614

Lechner W, Ladich F (2008) Size matters: diversity in swimbladders and Weberian ossicles affects hearing in catfishes. J Exp Biol 211:1681–1689

Lindstedt SL, McGlothlin T, Percy E, Pifer J (1998) Task-specific design of skeletal muscle: balancing muscle structural composition. Comp Biochem Physiol Part B Biochem Mol Biol 120:35–40. doi:10.1016/S0305-0491(98)00021-2

Lobel PS (2001) Acoustic behaviour of cichlid fishes. J Aquaric Aquat Sci 9:167–186

Lobel PS, Mann DA (1995) Spawning sounds of the damselfish, *Dascyllus albisella* (Pomacentridae), and relationship to male size. Bioacoustics 6:187–198

Lobel PS, Kaatz I, Rice AN (2010) Acoustical behavior of reef fishes. In: Cole KS (ed) Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Berkeley, pp 307–387

Locascio JV, Mann DA (2005) Effects of Hurricane Charley on fish chorusing. Biol LetT 1:362–365. doi:10.1098/rsbl.2005.0309

Locascio JV, Mann DA (2011) Diel and seasonal timing of sound production by black drum (*Pogonias cromis*). Fish Bull 109:327–338

Loesser KE, Rafi J, Fine ML (1997) Embryonic, juvenile, and adult development of the toadfish sonic muscle. Anat Rec 249:469–477

Longrie N, Van Wassenbergh S, Vandewalle P, Mauguit Q, Parmentier E (2009) Potential mechanism of sound production in *Oreochromis niloticus* (Cichlidae). J Exp Biol 212:3395–3402. doi:10.1242/jeb.032946

Luczkovich JJ, Sprague MW, Johnson SE, Pullinger RC (1999) Delimiting spawning areas of weakfish, *Cynoscion regalis* (family Sciaenidae) in Pamlico Sound, North Carolina using passive hydroacoustic surveys. Bioacoustics 10:143–160

Lugli M (2008) Role of ambient noise as a selective factor for frequencies used in fish acoustic communication. Bioacoustics 17:40–42

Lugli M (2010) Sounds of shallow water fishes: pitch within the quiet window of the habitat ambient noise. J Comp Physiol A 196:439–451. doi:10.1007/s00359-010-0528-2

Lugli M, Fine ML (2003) Acoustic communication in two freshwater gobies: ambient noise and short-range propagation in shallow streams. J Acoust Soc Am 114:512–521

Lugli M, Pavan G, Torricelli P, Bobbio L (1995) Spawning vocalisations in male freshwater gobiids (Pisces, Gobiidae). Environ Biol Fishes 43:219–231

Lugli M, Yan HY, Fine ML (2003) Acoustic communication in two freshwater gobies: the relationship between ambient noise, hearing thresholds and sound spectrum. J Comp Physiol A 189:309–320

Luther PK, Munro PMG, Squire JM (1995) Muscle ultrastructure in the teleost fish. Micron 26:431–459

Mahajan CL (1963) Sound producing apparatus in an Indian catfish *Sisor rhabdophorus* Hamilton. J Linn Soc Lond Zool 43:721–724

Malavasi S, Collatuzzo S, Torricelli P (2008) Interspecific variation of acoustic signals in Mediterranean gobies (Perciformes, Gobiidae): comparative analysis and evolutionary outlook. Biol J Linn Soc 93:763–778. doi:10.1111/j.1095-8312.2008.00947.x

Mann DA (2006) Propagation of fish sounds. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes, vol 1. Science Publishers, Endfield, pp 107–120

Mann DA, Jarvis SM (2004) Potential sound production by a deep-sea fish. J Acoust Soc Am 115:2331–2333

Mann D, Lobel P (1997) Propagation of damselfish (Pomacentridae) courtship sounds. J Acoust Soc Am 101:3783–3791

Mann D, Bowers-Altman J, Rountree R (1997) Sounds produced by the striped cusk-eel *Ophidion marginatum* (Ophidiidae) during courtship and spawning. Copeia 1997:610–612

Mann DA, Locascio JV, Coleman FC, Koenig CC (2009) Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. Endangered Species Res 7:229–236. doi:10.3354/esr00109

Markl H (1971) Schallerzeugung bei Piranhas (Serrasalminae, Characidae). J Comp Physiol A 74:39–56. doi:10.1007/bf00297789

Marshall NB (1962) The biology of sound-producing fishes. Symp Zool Soc Lond 7:45–60

Marshall NB (1967) Sound-producing mechanisms and the biology of deep-sea fishes. In: Tavolga WN (ed) Marine bio-acoustics, vol 2. Pergamon, Oxford, pp 123–133

McCartney BS, Stubbs AR (1970) Measurement of the target strength of fish in dorsal aspect, including swimbladder resonance. In: Farquhar GB (ed) Proceedings of an international symposium on biological sound scattering in the ocean. US government printing office, Washington, DC, pp 180–211

McKibben JR, Bass AH (1998) Behavioral assessment of acoustic parameters relevant to signal recognition and preference in a vocal fish. J Acoust Soc Am 104:3520–3533

Meyer-Rochow VB, Ishihara Y, Ingram JR (1994) Cytochemical and histological details of muscle fibres in the southern smelt *Retropinna retropinna* (Pisces; Galaxioidei). Zool Sci 11:55–62

Miano JP, Loesser-Casey KE, Fine ML (2013) Description and scaling of pectoral muscles in ictalurid catfishes. J Morphol 274:467–477

Millot S, Vandewalle P, Parmentier E (2011) Sound production in red-bellied piranhas (*Pygocentrus nattereri*, Kner): an acoustical, behavioural and morphofunctional study. J Exp Biol 214:3613–3618. doi:10.1242/jeb.061218

Mitchell S, Poland J, Fine ML (2008) Does muscle fatigue limit advertisement calling in the oyster toadfish *Opsanus tau*? Anim Behav 76:1011–1016. doi:10.1016/j.anbehav.2008.03.024

Mok HK, Gilmore RG (1983) Analysis of sound production in estuarine fish aggregations of *Pogoniascromis*, *Bairdiella chrysoura*, and *Cynoscion neubulosus* (Sciaenidae). Bull Inst Zool Acad Sin 22:157–186

Moyes CD, Buck LT, Hochachka PW, Suarez RK (1989) Oxidative properties of carp red and white muscle. J Exp Biol 143:321–331

Moyes CD, Schulte PM, Hochachka PW (1992) Recovery metabolism of trout white muscle: role of mitochondria. Am J Physiol 262:295–304

Munk WH (1974) Sound channel in an exponentially stratified ocean, with application to SOFAR. J Acoust Soc Am 55:220–226. doi:10.1121/1.1914492

Myrberg AA (1981) Sound communication and interception in fishes. In: Tavolga WN, Popper AN, Fay RR (eds) Hearing and sound communication in fishes. Springer, New York, pp 395–426

Myrberg AA, Lugli M (2006) Reproductive behavior and acoustic communication. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes, vol 1. Science Publishers, Endfield, pp 149–176

Myrberg AA, Spires JY (1980) Hearing in damselfishes: an analysis of signal detection among closely related species. J Comp Physiol 140:135–144

Myrberg A, Spanier E, Ha S (1978) Temporal patterning in acoustic communication. In: Reese ES, Lighter FJ (eds) Contrasts in behaviour. Wiley, New York, pp 137–177

Myrberg AA, Ha SJ, Shamblott MJ (1993) The sounds of bicolor damselfish (*Pomacentrus partitus*): predictors of body size and a spectral basis for individual recognition and assessment. J Acoust Soc Am 94:3067–3070

Nguyen TK, Lin H, Parmentier E, Fine ML (2008) Seasonal variation in sonic muscles in the fawn cusk-eel *Lepophidium profundorum*. Biol Lett 4:707–710. doi:10.1098/rsbl.2008.0383

Ono RD, Poss SG (1982) Structure and innervations of the swimbladder musculature in the weakfish, *Cynoscion regalis* (Teleostei: Sciaenidae). Can J Zool 60:1955–1967

Onuki A, Somiya H (2007) Innervation of sonic muscles in teleosts: occipital versus spinal nerves. Brain Behav Evol 69:132–141

Papes S, Ladich F (2011) Effects of temperature on sound production and auditory abilities in the striped raphael catfish *Platydoras armatulus* (Family Doradidae). PLoS ONE 6:1–10

Parmentier E, Diogo R (2006) Evolutionary trends of swimbladder sound mechanisms in some teleost fishes. In: Ladich F, Collin SP, Moller P, BG K (eds) Communication in fishes, vol 1. Science Publishers, Enfield, pp 45–70

Parmentier E, Genotte V, Focant B, Goffinet G, Vandewalle P (2003a) Characterization of the primary sonic muscles in *Carapus acus* (Caparidae): a multidisciplinary approach. Proc R Soc Biol Sci Ser B 270:2301–2308

Parmentier E, Vandewalle P, Lagardère JP (2003b) Sound-producing mechanisms and recordings in Carapini species (Teleostei, Pisces). J Comp Physiol A 189:283–292

Parmentier E, Fine ML, Vandewalle P, Ducamp J-J, Lagardere J-P (2006a) Sound production in two carapids (*Carapus acus* and *C. mourlani*) and through the sea cucumber tegument. Acta Zool 87:113–119

Parmentier E, Fontenelle N, Fine ML, Vandewalle P, Henrist C (2006b) Functional morphology of the sonic apparatus in *Ophidion barbatum* (Teleostei, Ophidiidae). J Morphol 267:1461–1468

Parmentier E, Lagardere J-P, Braquegnier J-B, Vandewalle P, Fine ML (2006c) Sound production mechanism in carapid fish: first example with a slow sonic muscle. J Exp Biol 209:2952–2960

Parmentier E, Colleye O, Fine M, Frederich B, Vandewalle P, Herrel A (2007) Sound production in the clownfish *Amphiprion clarkii*. Science 316:1006

Parmentier E, Compere P, Casadevall M, Fontenelle N, Cloots R, Henrist C (2008a) The rocker bone: a new kind of mineralised tissue? Cell Tissue Res 334:67–79

Parmentier E, Lagardère JP, Chancerelle Y, Dufrane D, Eeckhaut I (2008b) Variations in sound-producing mechanism in the pearlfish Carapini (Carapidae). J Zool 276:266–275. doi:10.1111/j.1469-7998.2008.00486.x

Parmentier E, Lecchini D, Frederich B, Brie C, Mann D (2009) Sound production in four damselfish (*Dascyllus*) species: phyletic relationships? Biol J Linn Soc 97:928–940. doi:10.1111/j.1095-8312.2009.01260.x

Parmentier E, Bouillac G, Dragičević B, Dulčić J, Fine M (2010a) Call properties and morphology of the sound-producing organ in Ophidion rochei (Ophidiidae). J Exp Biol 213:3230–3236. doi:10.1242/jeb.044701

Parmentier E, Bouillac G, Dragičević B, Dulčić J, Fine ML (2010b) Call properties and morphology of the sound-producing organ in *Ophidion rochei* (Ophidiidae). J Exp Biol 213:3230–3236

Parmentier E, Fabri G, Kaatz I, Decloux N, Planes S, Vandewalle P (2010c) Functional study of the pectoral spine stridulation mechanism in different mochokid catfishes. J Exp Biol 213:1107–1114. doi:10.1242/jeb.039461

Parmentier E, Kéver L, Casadevall M, Lecchini D (2010d) Diversity and complexity in the acoustic behaviour of *Dacyllus flavicaudus* (Pomacentridae). Mar Biol 157:2317–2327. doi:10.1007/s00227-010-1498-1

Parmentier E, Boyle KS, Berten L, Brié C, Lecchini D (2011a) Sound production and mechanism in *Heniochus chrysostomus* (Chaetodontidae). J Exp Biol 214:2702–2708. doi:10.1242/jeb.056903

Parmentier E, Mann K, Mann D (2011b) Hearing and morphological specializations of the mojarra (*Eucinostomus argenteus*). J Exp Biol 214:2697–2701

Parmentier E, Vandewalle P, Brie C, Dinraths L, Lecchini D (2011c) Comparative study on sound production in different Holocentridae species. Front Zool 8:12

Parmentier E, Kéver L, Boyle K, Corbisier Y-E, Sawelew L, Malavasi S (2013) Sound production mechanism in *Gobius paganellus* (Gobiidae). J Exp Biol 216:3189–3199. doi:10.1242/jeb.087205

Parmentier E, Tock J, Falguière JC, Beauchaud M (2014) Sound production in *Sciaenops ocellatus*: preliminary study for the development of acoustic cues in aquaculture. Aquaculture 432:204–211

Patterson S, Johnston IA, Goldspink G (1975) A histochemical study of the lateral muscles of five teleost species. J Fish Biol 7:159–166

Popper AN, Fay RR (2011) Rethinking sound detection by fishes. Hear Res 273:25–36. doi:10.1016/j.heares.2009.12.023

Ramcharitar J, Gannon D, Popper A (2006) Bioacoustics of fishes of the family Sciaenidae (croackers and drums). Trans Am Fish Soc 135:1409–1431

Remage-Healey L, Nowacek DP, Bass AH (2006) Dolphin foraging sounds suppress calling and elevate stress hormone levels in a prey species, the Gulf toadfish. J Exp Biol 209:4444–4451. doi:10.1242/jeb.02525

Rice AN, Bass AH (2009) Novel vocal repertoire and paired swimbladders of the three-spined toadfish, *Batrachomoeus trispinosus*: insights into the diversity of the Batrachoididae. J Exp Biol 212:1377–1391. doi:10.1242/jeb.028506

Rome LC (2006) Design and function of superfast muscles: new insights into the physiology of skeletal muscle. Annu Rev Physiol 68:193–221

Rome LC, Linstedt SL (1998) The quest for speed: muscles built for high-frequency contractions. News Physiol Sci 13:26–268

Rome LC, Syme DA, Hollingworth S, Lindstedt S, Maylor SM (1996) The whistle and the rattle: the design of sound producing muscles. Proc Natl Acad Sci 93:8095–8100

Rome LC et al (1999) Trading force for speed: why superfast crossbridge kinetics leads to superlow forces. Proc Natl Acad Sci 95:5826–5831

Rosenthal GG, Lobel PS (2006) Communication. In: Sloman KA, Wilson RW, Balshine S (eds) Behaviour and physiology of fish, vol 24. Fish physiology. Elsevier, New York, pp 39–78

Salmon M (1967) Acoustical behavior of the mempachi, *Myripristis berndti*, in Hawaii. Pac Sci 21:364–381

Sand O, Hawkins AD (1973) Acoustic properties of the cod swimbladder. J Exp Biol 58:797–820

Schachner G, Schaller F (1981) Schallerzeugung and Schallreaktionen beim Antennenwels (Mandim) *Rhambdia sebae sebae*. Zool Beitr 27:375–392

Schaeffer P, Conley K, Lindstedt S (1996) Structural correlates of speed and endurance in skeletal muscle: the rattlesnake tailshaker muscle. J Exp Biol 199:351–358

Scholz K, Ladich F (2006) Sound production, hearing and possible interception under ambient noise conditions in the topmouth minnow *Pseudorasbora parva*. J Fish Biol 69:892–906. doi:10.1111/j.1095-8649.2006.01168.x

Schulz-Mirbach T, Heß M, Metscher B, Ladich F (2013) A unique swim bladder-inner ear connection in a teleost fish revealed by a combined high-resolution microtomographic and three-dimensional histological study. BMC Biol 11:75

Sismour EN, Nellis SC, Newton SH, Da Mays, Fine ML (2013) An experimental study of consumption of channel catfish *Ictalurus punctatus* by largemouth bass *Micropterus salmoides* when alternative prey are available. Copeia 2013:277–283. doi:10.1643/ce-12-052

Sisneros JA, Forlano PM, Deitcher DL, Bass AH (2004) Steroid-dependent auditory plasticity leads to adaptive coupling of sender and receiver. Science 305:404–407

Skoglund C (1961) Functional analysis of swimbladder muscles engaged in sound production of the toadfish. J Biophys Biochem Cytol 10:187–200

Somlyo AV, Shurman H, Somlyo AP (1977) Composition of sarcoplasmic reticulum in situ by electron probe X-ray microanalysis. Nature 268:556–558

Sörensen W (1895) Are the extrinsic muscles of the air-bladder in some Siluroidae and the “elastic spring” apparatus of others subordinate to the voluntary production of sounds? What is, according to our present knowledge, the function of the Weberian ossicles? J Anat Physiol 29:205–229, 399–423, 518–552

Speares P, Johnston C (2011) Sound production in *Etheostoma oophylax* (Percidae) and call characteristics correlated to body size. Environ Biol Fishes 92:461–468

Sprague MW (2000) The single sonic muscle twitch model for the sound-production mechanism in the weakfish. Cynoscion regalis J Acous Soc Am 108:2430–2437

Sprague MW, Luczkovich JJ (2001) Do striped cusk-eels *Ophidion marginatum* (Ophidiidae) produce the “chatter” sound attribuated to weakfish *Cynoscion regalis* (Scianidae)? Copeia 2001:854–859

Sprague MW, Luczkovich JJ, Pullinger RC, Johnson SE, Jenkins T, Daniel HJ (2000) Using spectral analysis to identify drumming sounds of some North Carolina fishes in the family Sciaenidae. J Elisha Mitchell Sci Soc 116:124–145

Stiassny MLJ (1981) The phyletic status of the family Cichlidae (Pisces, Perciformes): a comparative anatomical investigation. Neth J Zool 31:275–314

Stout JF (1963) The significance of sound production during the reproductive behaviour of Notropis analostanus (family cyprinidae). Anim Behav 11:83–92 doi:10.1016/0003-3472(63)90014-9

Taverne L, Aloulou-Triki A (1974) Étude anatomique, myologique et ostéologique du genre *Synodontis* Cuvier (Pisces: Siluriformes, Mochokidae). Annales du Museum Royal d’Afrique Centrale 210:1–69

Tavolga WN (1964) Sonic characteristics and mechanisms in marine fishes. In: Tavolga WN (ed) Marine Bio-acoustics. Pergamon Press, Oxford, pp 195–211

Tavolga WN (1971a) Acoustic orientation in the sea catfish, *Galeichthys felis*. Ann N Y Acad Sci 188:80–97. doi:10.1111/j.1749-6632.1971.tb13091.x

Tavolga WN (1971b) Sound production and detection. In: Hoar WS, Randall DJ (eds) Fish physiology, vol 5. New York, pp 135–205

Tavolga WN (1976) Acoustic obstacle detection in the sea catfish (*Arius felis*). In: Schuijf A, Hawkins AD (eds) Sound reception in fish. Elsevier, Amsterdam, pp 185–204

Tavolga WN (1977) Mechanisms for directional hearing in the sea catfish (*Arius felis*). J Exp Biol 67:97–115

te Kronnie G, Tatarczuch L, van Raamsdonk W, Kilarski W (1983) Muscle fibre types in the myotome of stickleback, *Gasterosteus aculeatus* L.: a histochemical, immunohistochemical and ultrastructural study. J Fish Biol 22:303–316

Thorson RF, Fine ML (2002a) Crepuscular changes in emission rate and parameters of the boatwhistle advertisement call of the gulf toadfish *Opsanus beta*. Environ Biol Fish 63:321–331

Thorson RF, Fine ML (2002b) Acoustic competition in the gulf toadfish *Opsanus beta*: acoustic tagging. J Acoust Soc Am 111:2302–2307

Tikunov B, Rome L (2009) Is high concentration of parvalbumin a requirement for superfast relaxation? J Muscle Res Cell Motil 30:57–65. doi:10.1007/s10974-009-9175-z

Tower RW (1908) The production of sound in the drumfishes, the searobin and the toadfish. Ann N Y Acad Sci 18:149–180

Tracy HC (1959) Stages in the development of the anatomy of motility of the toadfish (Opsanus tau). J Comp Neurol 111:27–81. doi:10.1002/cne.901110103

Tricas T, Kajiura S, Kosaki R (2006) Acoustic communication in territorial butterflyfish: test of the sound production hypothesis. J Exp Biol 209:4994–5004

Urick RJ (1975) Principles of underwater sound. McGraw-Hill, New York

van Bergeijk WA (1964) Directional and nondirectional hearing in fish. In: Tavolga WN (ed) Marine bioacoustics. Pergamon Press, New York, pp 281–299

Vance T (2000) Variability in stridulatory sound production in the channel catfish, *Ictalurus punctatus*. BIOS 71:79–84

Vance TL, Hewson JM, Modla S, Connaughton MA (2002) Variability in sonic muscle size and innervation among three sciaenids: spot, Atlantic croaker, and weakfish. Copeia 2002:1137–1143

Vasconcelos RO, Ladich F (2008) Development of vocalization, auditory sensitivity and acoustic communication in the Lusitanian toadfish *Halobatrachus didactylus*. J Exp Biol 211:502–509

Wall CC, Lembke C, Mann DA (2012) Shelf-scale mapping of sound production by fishes in the eastern Gulf of Mexico, using autonomous glider technology. Mar Ecol Prog Ser 449:55–64. doi:10.3354/meps09549

Wall CC, Simard P, Lembke C, Mann DA (2013) Large-scale passive acoustic monitoring of fish sound production on the West Florida Shelf. Mar Ecol Prog Ser 484:173–188. doi:10.3354/meps10268

Wall CC, Rountree RA, Pomerleau C, Juanes F (2014) An exploration for deep-sea fish sounds off Vancouver Island from the NEPTUNE Canada ocean observing system. Deep Sea Res Part I Oceanogr Res Pap 83:57–64. doi:10.1016/j.dsr.2013.09.004

Walsh PJ, Bedolla C, Mommsen TP (1987) Reexamination of metabolic potential in the toadfish sonic muscle. J Exp Zool 241:133–136. doi:10.1002/jez.1402410116

Walsh PJ, Mommsen TP, Bass AH (1995) Biochemical and molecular aspects of singing in Batrachoidid fishes. In: Hochachka PW, Mommsen TP (eds) Biochemistry and molecular biology of fishes, metabolic and adaptational biochemistry, vol IV. Elsevier, New York, pp 279–289

Watkins WA (1967) The harmonic interval: fact or artifact in spectral analysis of pulse trains. In: Tavolga WN (ed) Marine bio-acoustics, vol 2. Pergamon Press, New York, pp 15–43

Waybright TD, Kollenkirchen U, Fine ML (1990) Effect of size and sex on grunt production in the oyster toadfish. Abstr Soc Neurosci 16:578

Weber M (1913) Die Fische der Siboga-Expedition. Siboga-Expeditie 32:1–710

Weston D (1967) Sound propagation in the presence of bladder fish. In: Albers V (ed) Underwater acoustics, vol 2. Plenum, New York, pp 55–88

Winn HE (1964) The biological significance of fish sounds. In: Tavolga WN (ed) Marine bio-acoustics. Pergamon Press, New York, pp 213–231

Winn HE (1967) Vocal facilitation and the biological significance of toadfish sounds. In: Tavolga WN (ed) Marine bio-acoustics. Pergamon Press, New York, pp 283–304

Winn HE, Marshall JA (1963) Sound producing organ of the squirrelfish *Holocentrus rufus*. Physiol Zool 36:34–44

Winn HE, Stout JF (1960) Sound production by the satinfin shiner, *Notropis analostanus* and related fishes. Science 132:222–223

Winn HE, Marshall JA, Hazlett B (1964) Behavior, diel activities, and stimuli that elicit sound production and reactions to sounds in the longspine squirrelfish. Copeia 1964:413–425

Yan HY (1998) Auditory role of the suprabranchial chamber in gourami fish. J Comp Physiol A 183:325–333. doi:10.1007/s003590050259

Yan HY, Fine ML, Horn NS, Colón WE (2000) Variability in the role of the gasbladder in fish audition. J Comp Physiol A 186:435–445. doi:10.1007/s003590050443

Yoshimoto M, Kikuchi K, Yamamoto N, Somiya H, Ito H (1999) Sonic motor nucleus and its connections with octaval nuclei of the medulla in a rockfish, *Sebasticus marmoratus*. Brain Behav Evol 54:183–204

Young IS, Rome LC (2001) Mutually exclusive muscle designs: the power output of the locomotory and sonic muscles of the oyster toadfish (*Opsanus tau*). Proc Roy Soc Lond Series B: Biol Sci 268:1965–1970. doi:10.1098/rspb.2001.1731

Zelick R, Mann DA, Popper AN (1999) Acoustic communication in fishes and frogs. In: Fay RR, Popper AN (eds) Comparative hearing: fish and amphibians. Springer, New York

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