Fish Sound Production: The Swim Bladder

Michael L. Fine and Eric Parmentier

Sound Production in Fishes

Sound production is nearly ubiquitous among various vertebrate taxa from fishes to mammals. However, although terrestrial vertebrates and marine mammals produce sounds that require air movement, fishes are unique in that they use a variety of mechanical systems that typically do not involve air movement. Indeed, the first vertebrates to produce sounds were likely primitive fishes, and the mechanisms of sound production had to be "reinvented" when vertebrates colonized land because fish sound-producing mechanisms likely did not produce enough acoustic energy to carry substantial distances in the low-density air environment (Gharhamani et al., 2014).

In fact, there is not "one" but many sound-producing mechanisms among the over 30,000 extant fish species (Rice et al., 2022). These range from high-speed contraction of muscles that vibrate a gas-filled chamber to stridulation or the rubbing of bones against one another (Fine and Parmentier, 2015).

Perhaps the best understood mechanisms for sound production in fishes involve the subject of this article, the swim bladder, a gas-filled chamber in the abdominal cavity of most bony fishes (sharks and rays do not have a swim bladder!) **(Figure 1)**. The primary role of the swim bladder is to control buoyancy so that fishes do not expend energy to maintain their vertical position in the water column (Pelster, 2021). However, in many species, the swim bladder has evolved for other functions including respiration (Pelster, 2021), hearing (Popper et al., 2021), and sound production (Parmentier and Fine, 2016).

Fish Sounds

Since the days of Aristotle, it has been recognized that fishes make sounds. Indeed, studies over decades
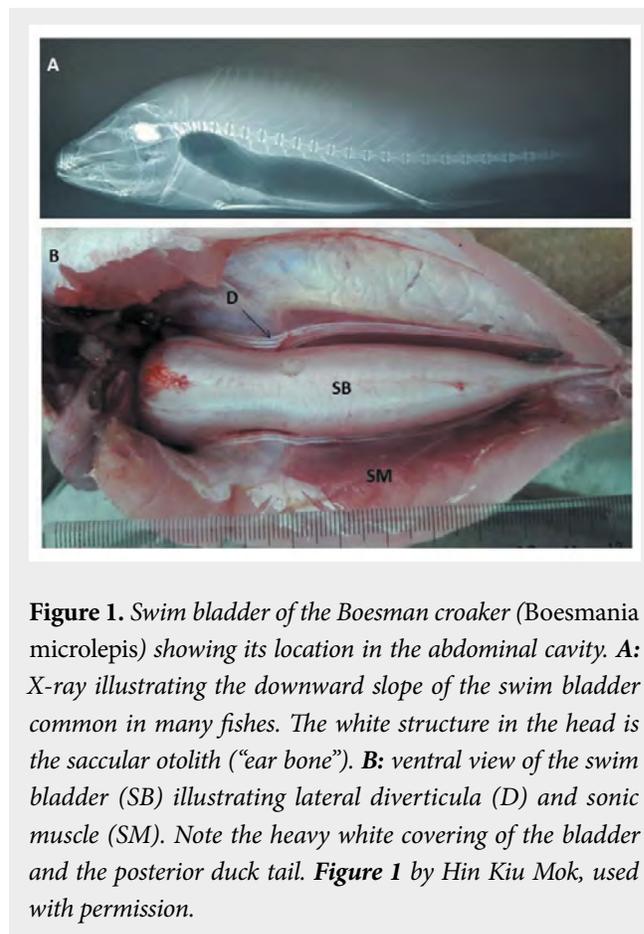

Figure 1. *Swim bladder of the Boesman croaker (*Boesmania microlepis*) showing its location in the abdominal cavity.* **A:** *X-ray illustrating the downward slope of the swim bladder common in many fishes. The white structure in the head is the saccular otolith ("ear bone").* **B:** *ventral view of the swim bladder (SB) illustrating lateral diverticula (D) and sonic muscle (SM). Note the heavy white covering of the bladder and the posterior duck tail.* **Figure 1** *by Hin Kiu Mok, used with permission.*

demonstrate that a substantial number of fish species produce sounds during courtship, disturbance, aggressive, and other contexts. Examples of fish sounds can be found at DOSITS.org (Discovery of the Sound in the Sea; see tinyurl.com/2s3ahwdp; fishsounds.net). Most fish sounds are a series of pulses that vary in frequency spectra and duration and are emitted with different temporal patterns (e.g., Winn, 1964). Some longer duration sounds can also have a well-developed harmonic structure. Moreover, many fish sounds are species specific, allowing potential call identification as with bird songs **(Figure 2)**.
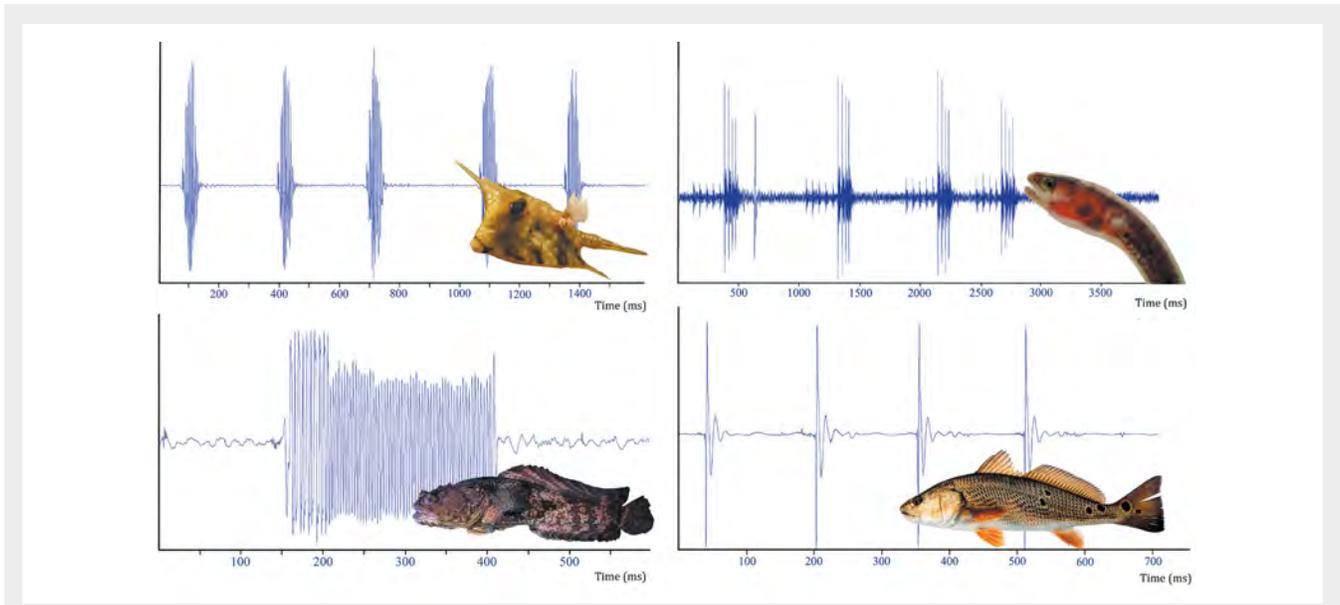
Figure 2. Oscillograms of sounds from four fish species. **Top left:** *longhorn cowfish* Lactoria cornuta. **Top right:** *red pearlfish* Encheliophis chardewalli. **Bottom right:** *red drum* Scieanops ocellatus *(see tinyurl.com/4yhcrec4).* **Bottom left:** *oyster toadfish* Opsanus tau *(see tinyurl.com/4j4rz4nk).*

Most fish sounds are generated by stridulation of bony structures or with the swim bladder (Parmentier and Fine, 2016). Stridulation sounds are typically higher pitched than swim bladder sounds and can be produced, for example, by rubbing a process on the base of the pectoral spine in catfish against the pectoral girdle (**Figure 3**) (Fine et al., 1997) or rubbing upper against lower pharyngeal teeth (toothlike structures located in the back of the mouth in fishes) (Bertucci et al., 2014).

Swim bladder sounds are typically generated by extremely fast sonic muscles that excite bladder vibrations (Fine and Parmentier, 2015). For example, a courtship boat whistle call of the oyster toadfish (*Opsanus tau*) with a fundamental frequency of 200 Hz would be stimulated by sonic muscle contractions at 200 Hz (see dosits.org/Oyster-Toadfish). Compared with a bird syrinx or mammalian larynx, the swim bladder, typically a closed structure, has little ability to vary sound frequency. A drop-off of several hertz during a tonal sound is due to muscle fatigue (Mitchell et al., 2008) rather than the ability to regulate tension as on a laryngeal membrane.

Sound production has evolved independently in various fish groups (Fine and Parmentier, 2015). Nearly two-thirds of fish species from over 100 families are known to produce

sounds, although future studies will likely identify many more sound-producing species (Looby et al., 2022). There is still much to be learned about fish sound production and acoustic behavior! Interestingly, the ability to produce sounds has evolved independently at least over 30 times (Parmentier et al., 2021a; Rice et al., 2022). Fish sonic structures

*Figure 3. **A:** pectoral spine of the channel catfish* Ictalurus punctatus, *illustrating stridulatory surfaces. Spine base is to the right and the dorsal process points upward. **B:** ridged undersurface of the process rubs against a rough surface on the cleithrum (a bone in the pectoral girdle) (**C**). **Inset:** magnified rough-rubbing surface that catches the ridges using a stick-slip mechanism similar to a moving bow on a violin (Mohajer et al., 2015). Scale bar, 1 mm in **A**; 0.5 mm in **B** and **C**. Modified from Fine et al. (1998), used with permission.*
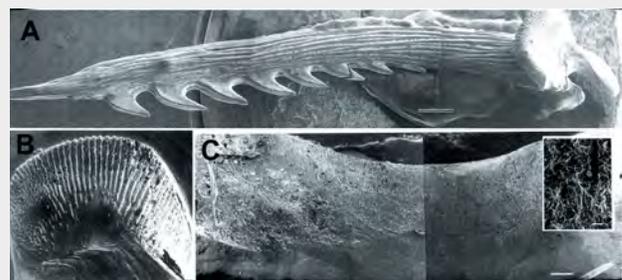
are thus highly variable and provide numerous examples of convergent evolution (independent evolution of similar traits in unrelated species), many of which center around the swim bladder.

Studies of fish sound production are going through a revolutionary period as they expand from a niche area with a small number of investigators. Reasons for this shift include the development of long-term recorders enabling the passive acoustic monitoring (PAM) (Mann, 2012) of species that cannot be easily observed, such as the monitoring of populations of Atlantic cod (*Gadus morhua*) and haddock (see dosits.org/Haddock) to locate breeding sites (e.g., Hawkins and Picculin, 2019). Using PAM thus provides ecological information on underwater habitats that would otherwise be difficult to obtain, e.g., nocturnal-burying or deep-living species that are hard to sample and cryptic species not resolved taxonomically (Parmentier et al., 2021b). Indeed, as early as the mid-twentieth century, the famous oceanographer N. B. Marshall (1967) identified muscles that are likely used for sound production in fishes living at great depth (macrourids and ophidiids), although we have yet to record identified sounds from these species in deep water.

The Swim Bladder

The swim bladder is situated below the vertebral column and forms as a dorsal outgrowth of the digestive tract. A major function is buoyancy; the internal gas counteracts the density of the heavier bone and muscle (Pelster, 2021). Like the digestive tract, the swim bladder wall is made up of cell types grouped in external and internal layers. Wall structure has not been correlated with acoustic function across teleost fishes, let alone been the subject of much experimentation. Swim bladders are practically transparent in shads (relatives of herring) that can hear 180-kHz ultrasounds (Popper et al., 2004) and have a heavy white external covering implicated in sound production and hearing in many fishes (Fine et al., 2016).

The gas in the swim bladder provides an acoustic discontinuity (impedance mismatch) to water (Urick, 1975). The swim bladder has been treated as an underwater resonant bubble (Sand and Hawkins, 1973), a monopole that radiates sound equally in all directions (Harris, 1964). Moreover, the resonant frequency of a bubble decreases with size and increases with depth (Minnaert, 1933).

Historically, swim bladders were believed to aid hearing by translating vibrations resulting from incident sound to the ears in all species. Although on a continuum, fishes vary from auditory specialists to generalists (Popper et al., 2021). In specialists, swim bladders are close to or connected to the ears and support sensitive thresholds and hearing to several kilohertz. Specialist connections vary from bony Weberian ossicles that function something like the mammalian middle ear bones in otophysans (e.g., minnows, goldfish, and catfish) (Braun and Grande, 2008) to diverticula, or tubular connections, in other families (Parmentier et al., 2011). By contrast, generalists have no connections between the swim bladder and the ear, have less sensitive hearing and typically hear sounds below 1 kHz. Indeed, experiments in which the swim bladder was deflated in generalists (e.g., oyster toadfish, blue gourami, a goby) do not change the shape or sensitivity of audiogram threshold curves (Yan et al., 2000), indicating that generalist swim bladders are unlikely to enhance hearing.

Significantly, connections between the swim bladder and ear can vary even between closely related species. For example, some members of the taxonomic family Sciaenidae, a group of fishes often called drums or croakers because of the loud sounds they produce (e.g., see dosits.org/Silver-Perch), have long diverticula that terminate close to the ears (e.g., silver perch, weakfish). These species have lower thresholds and higher-frequency reception than the related spot and Atlantic croaker that have shorter diverticula (Horodysky et al., 2008).

Sonic Swim Bladder Exaptations

Except for hydrodynamic (swimming) sounds, sonic mechanisms appear to be exaptations, a term referring to a functional character that is co-opted for a new use (Gould and Verba, 1982). Structures with other functions have been repurposed into sonic organs while still maintaining their original functions (Parmentier and Fine, 2016). The first description of a sonic exaptation came from the clownfish (think Nemo from the movies; see dosits.org/Clownfish) with ligaments that cause jaw slams for prey capture (Parmentier et al., 2007). The slams originally produced sounds incidentally (Olivier et al., 2014), but they are now used during courtship and territorial defense (Parmentier et al., 2021b). Another example is the pharyngeal teeth at the back of the mouth

in many fishes, which are used to crush food and guide it into the esophagus. In haemulids, commonly known as grunts, these teeth have assumed an additional function and can generate a series of disturbance pulses apart from feeding (see dosits.org/Bluestriped-Grunt) (Bertucci et al., 2014).

Most sonic muscles are extrinsic; their morphological origin is on various bones (e.g., skull, vertebrae, ribs) and their insertion is on the swim bladder or structures that move the swim bladder. Based on forming from neck muscles in the oyster toadfish, extrinsic muscles likely gave rise to intrinsic ones found only on the walls of the swim bladder (Mok et al., 2011). The evolutionary process of attaching muscles to a swim bladder is unclear, with the possible exception of piranhas and related species (Melotte et al., 2016) in which intercostal horizontal muscles between ribs first modified their orientation and later hypertrophied. In the most derived species (e.g., those with the greatest divergence from ancestral species), the sound-producing system has two symmetric vertically oriented muscles coming from the vertebrae and connected by a tendon surrounding the ventral swim bladder. The muscles produce sounds by rapidly compressing the base of the anterior swim bladder (Melotte et al., 2016). Interestingly, sonic muscles in a related characiform group (tetras) maintained their primitive horizontal orientation and compressed the front of the swim bladder, illustrating that evolution likely occurred in stages (Borie et al., 2019).

In other species, the evolutionary stages are unknown, but developmental data support swim bladder muscles forming from head or body muscles. In toadfish, for example, the occipital-spinal nerves and sonic muscles migrate from the neck region and attach to the swim bladder embryologically, whereas in sciaenids with true spinal innervation, the sonic muscles grow down from the dorsal aponeurosis (a flat tendon overlying the swim bladder) during puberty. The two basic innervation patterns (occipital-spinal and true spinal) have evolved independently multiple times (Rice et al., 2022).

Swim Bladder Shape and Sound Production

One of the most remarkable things about sound production in fishes is the extraordinary diversity in swim bladder shape and associated structures that are found in various species. Indeed, this reflects the extraordinary number of different approaches evolution has taken. Different groups of fishes have independently found multiple ways to produce sounds.

Swim bladders are typically somewhat circular in cross section, taper toward the tail, and slope downward (**Figure 1**), effectively lowering a fish's center of buoyancy. Because the swim bladder is restricted to the body cavity, the downward slope may provide lift to the tail region and the taper greater postural stability than a sharp termination. Both nonsonic and some sonic species have swim bladders with this general shape.

Sciaenid bladders and some others often terminate in a pointed "duck tail" that should allow minimal sound radiation and reflect gas pressure forward during muscle contraction (**Figure 1**). Sound amplitude is determined by volume velocity, a product of surface area of the swim bladder and velocity (Bradbury and Vehrencamp, 1998). Thus, the small surface area and a thick tail will produce lower amplitudes than the larger swim bladder sides moved by sonic muscles. Because sonic muscles surround the mid-to-posterior swim bladder in many sciaenids, contraction will compress the bladder, increasing the internal pressure and causing expansion of the anterior region not covered by muscles.

Several sciaenids have caudally directed diverticula (Chao, 1986). For example, the small scale croaker with six long slender diverticula bilaterally (**Figure 1**) produces sounds with missing or attenuated lower frequencies, suggesting that the diverticula are acting as Helmholtz absorbers (e.g., high-pass filters; Mok et al., 2020). Black drum (Locascio and Mann, 2011) and some doradid catfish swim bladders have many short blind diverticula that increase the surface area and maybe sound amplitude (Birindelli et al., 2009).

Modified swim bladder shapes may be related to sound production, audition, and/or gas secretion. Notably, the swim bladder of the oyster toadfish has a heart "cardiform" shape (**Figure 4**) with anterior protrusions on either side of the midline. Two hypotheses could explain this shape. The protrusions could direct sound detected by the swim bladder toward the ears, enhancing hearing. Alternatively, due to the absence of sonic muscles on the
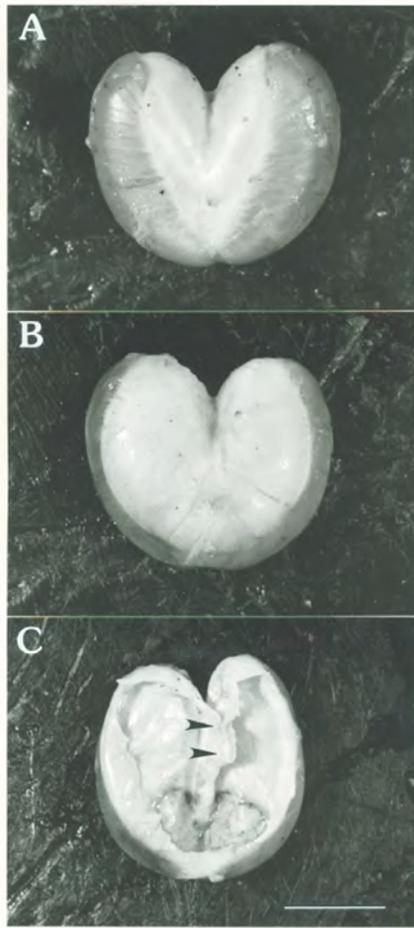
Figure 4. *Dissected swim bladder of the oyster toadfish* Opsanus tau. *Anterior (front) part is on* **top.** *A: dorsal view.* **B:** *ventral view.* **C:** *ventral view with swim bladder floor removed, illustrating the heavy column between the two anterior projections (**arrowheads**). Scale bar, 1 cm. From Barimo and Fine (1998), used with permission.*

1998). Additional sonic fishes with somewhat similarly shaped bladders likely impart a directional sound field (Ladich and Fine, 2006).

There are also swim bladders with variable heart or cardiform shapes in catfishes (Birindelli et al., 2009), species not related to the aforementioned oyster toadfish. These may support auditory function in concert with the Weberian ossicles that transfer swim bladder vibration to the ears (Chardon et al. 2003). Catfish swim bladders have two internal septa; a longitudinal septum runs from the back of the bladder forward and splits into a horizontal septum, forming a "T." The top of the T extends laterally from the midline without reaching the side walls, leaving lateral channels. Because the middle part of the anterior bladder (forward of the horizontal septum) is stiffer than lateral areas near the attachment of the first ossicle (Ali and Fine, unpublished data), the lateral channels are interpreted as an adaptation to aid hearing by amplifying vibrations near the ossicle attachment point.

The oyster toadfish and some other species including some cichlids have a horizontal septum with a small hole surrounded by a sphincter that separates the anterior gas-secreting and posterior gas-absorbing regions (Tracy, 1911). Likely, this septum functions exclusively in gas regulation with no acoustic role. It therefore appears that internal swim bladder structures can have various acoustic and nonacoustic functions.

Many otophysans and members of unrelated families have bladders with one or more chambers (Melotte et al., 2016). The anterior chamber is likely an acoustic specialization. Related channel and blue (*Ictalurus punctatus* and *Ictalurus furcatus*, respectively) catfish have one- and two-chambered bladders, respectively (Ghahramani et al., 2014), illustrating swim bladder plasticity. Again, there is an overlap in the occurrence of hearing and sound production. In species without sonic muscles, the anterior chamber would be strictly auditory in function while still aiding buoyancy.

Various ophidiiform fishes (cusk-eels and carapids) have little external variation but have numerous sexually dimorphic swim bladder adaptations that may help them find mates in the dark using sound (**Figure 5**). These include a fenestra (a thin pliable strip with no outer layer) that allows sonic muscles to pull the anterior part of the swim

anterior bladder and the thick column connecting the two protrusions (**Figure 4**), sound could be directed away from the ears so that they are not overstimulated when the fish calls.

In testing these hypotheses, experiments in which the swim bladder was deflated did not show a change in auditory thresholds, failing to support the first hypothesis (Yan et al., 2000). By contrast, field recordings indicate that the sound amplitude is several decibels higher behind that of a toadfish as predicted by swim bladder shape and sonic muscle investment (Barimo and Fine,
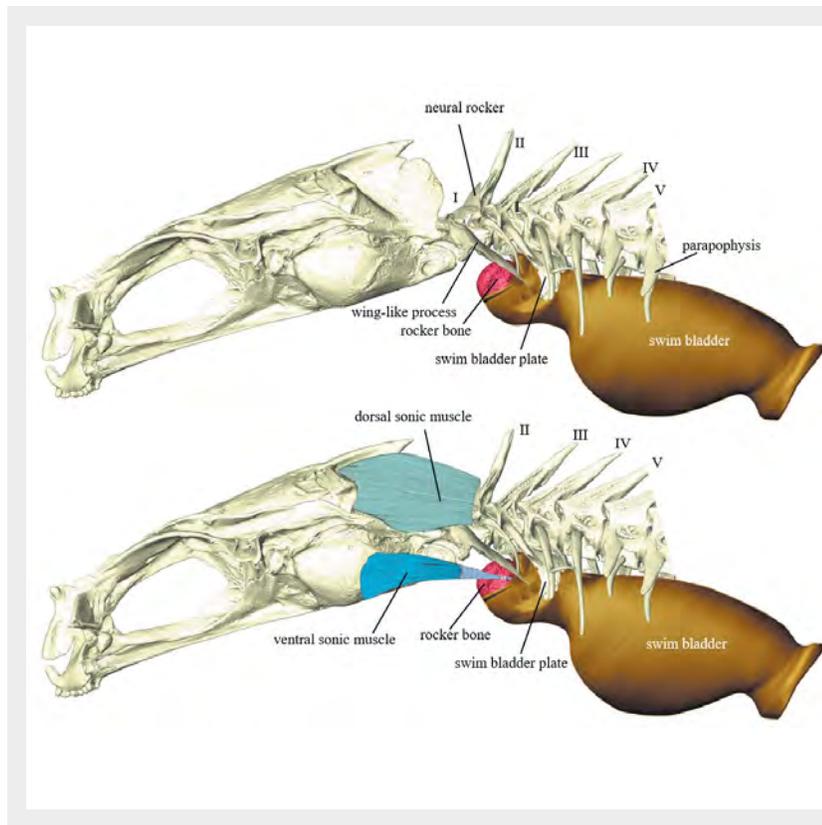
Figure 5. *Top:* *left lateral view of the sound-producing apparatus of a male cusk-eel* Ophidion rochei *(Roche's snake blenny), showing the skeleton and swim bladder.* **Bottom:** *same structures with sonic muscles attached.* **Numbers I to V:** *first five vertebrae. The neural rocker is the neural arch over the first vertebra that rotates forward when the dorsal sonic muscle contracts. This movement causes backward movement of the winglike process (a modified rib on the first vertebra) and counterclockwise movement of the rocker bone at the front of the swim bladder. In this way, the dorsal sonic muscle contraction allows arming the sound-producing apparatus. During sustained contraction of the dorsal sonic muscle, rhythmic contraction cycles of the ventral sonic muscle causes back and forth movements of the rocker bone and the corresponding production of pulses. Figure by Eric Parmentier, © 2022, all rights reserved.*

bladder forward without moving the posterior part (Fine et al., 2007; Parmentier et al., 2010). Other families also have a fenestra (Parmentier et al., 2016), indicating that this adaptation evolved multiple times. Additional male ophidiform adaptations that occur in some species include a bean-shaped "rocker bone" formed by modification and sclerification of the anterior swim bladder wall (Parmentier et al., 2008), swim bladder tubercles (Parmentier et al., 2018), and a posterior round membrane within a raised "donut" that appears to be a pressure-release system (Kever et al., 2014; Ali et al., 2016). Some also have a pivoting neural arch and winglike process on the first vertebra, which along with antagonistic muscle pairs move the swim bladder in opposite directions (Fine et al., 2007; Kever et al., 2014). Muscle antagonists are unusual in sonic fishes that rely primarily on internal gas pressure to restore bladder shape during muscle relaxation.

Swim Bladders and the Underwater Resonant Bubble

By the 1960s, the notion that fish swim bladders acted as a pulsating resonant bubble was so entrenched in fish bioacoustics (e.g., Harris, 1964; Weston, 1967; Sand and Hawkins, 1973) that questioning the resonance model

caused papers to be rejected for publication. Indeed, Tavolga (1971) supported resonance despite providing contrary evidence and suggested that the resonant frequency is close to the frequency produced by sonic muscles.

In the 1990s, we started to question the resonant bubble model as applied to sound production and hearing in the oyster toadfish. The bubble model predicts the swim bladder is an underdamped omnidirectional sound source that would emphasize a narrow frequency response based on size and depth. Findings of rapid damping had been attributed to swim bladder contact with surrounding fish tissue. Early work ignored the swim bladder wall, which is composed of collagen and elastin fibers (Morris and Albright, 1975). These fibers are woven in various directions and the wall contains about 80% water (Fine et al., 2016), therefore supporting the idea that viscous damping of the internal gas bubble inhibits the expression of resonance (Fine et al., 2016).

Our arguments and findings counter the traditional model and suggest a forced rather than a resonant response in toadfish and other species. These include the following observations.

(1) Most fish sounds are pulses with wide frequency spectra (Parmentier and Fine, 2016) rather than being concentrated at the swim bladder's resonant frequency. Tonal harmonic sounds such as the oyster toadfish boat whistle are caused by continuous contractions with a fundamental frequency that matches the muscle contraction rate (Fine et al., 2001). In fact, individual field recordings of male boat whistle choruses often have fundamental frequencies that vary by as little as 10 Hz, even though males are of different sizes (Fine, 1978). Therefore, muscle contraction rate rather than bladder size dictates fundamental frequency (Parmentier and Fine, 2016).

(2) The boat whistle fundamental frequency increases with temperature when muscles contract faster in toadfish (Fine, 1978) and other species (Ladich, 2018), although the resonant frequency of the internal bubble would be unaffected (Sprague et al., 2022).

(3) Toadfish sonic muscles are among the fastest vertebrate muscles and can be stimulated at 500 Hz without tetanizing (Fine et al., 2001). A resonant structure, however, does not require rapid excitation to set it into vibration (ding a crystal bowl).

(4) Toadfish calls terminate rapidly after muscle contractions stop (Fine et al., 2001), whereas a resonant structure would continue to ring, compromising the temporal nature of fish communication (Winn, 1964; Millot et al., 2011). Notably, toadfish can produce a grunt (acoustic tagging) within 41 ms in response to sounds from nearby toadfish or snapping shrimp (Thorson and Fine, 2002), suggesting precise temporal resolution that would be compromised by resonance.

(5) Oscillating bubbles are monopoles that produce an omnidirectional sound field (Harris, 1964). Yet the curved sonic muscles push the sides of the bladder inward, increasing the internal pressure that pushes the bottom outward (a quadrupole motion) (Fine et al., 2001). The sound radiation pattern in the wild is not uniform and follows the morphology of the heart-shaped swim bladder (Barimo and Fine, 1998).

(6) Deflation of the toadfish swim bladder does not affect the auditory threshold curve, although the swim bladder is several centimeters behind the ears (Yan et al., 2000).

Although a larger bubble will have a lower resonant frequency, low-frequency calls can occur for other reasons (Parmentier and Fine, 2016). Sonic muscles and swim bladders grow with fish size (Fine et al., 1990), and longer muscles take longer to contract, driving lower frequency sounds in weakfish (Connaughton et al., 2000) and other sciaenids (Tellechea et al., 2010). In a carapid fish, slow sonic muscles pull the anterior swim bladder forward, stretching the swim bladder fenestra that snaps back when a catch is released (Parmentier et al., 2006). The snap excites an overlying bony plate that, in turn, vibrates the swim bladder. The peak frequency of their sounds is close to twice that predicted by the bubble equation and is likely caused by tuning of the swim bladder plate. Finally, a cusk-eel living down to 5,000 m has short sonic muscles that terminate in a long tendon occupying 70% of the distance between the head and the swim bladder (Fine et al., 2018). Tendons require fewer calories than muscles and likely drive swim bladder sounds after the muscle contraction ends.

Clearly, there is support for both the forced response in sound production and hearing and the resonance model in sound fields. With depth, a bubble's resonant frequency will increase due to a higher hydrostatic pressure (Minnaert, 1933) and the gas will dominate so that the bladder wall will contribute less to the overall stiffness (Sprague et al., 2022). It therefore appears that the gas bubble resonance inside the bladder becomes increasingly important with depth, and both models likely apply, albeit under different environmental conditions.

Conclusion

Analogous to the syrinx in birds and larynx in mammals, the swim bladder is a major sound-producing organ in fishes. It also functions in hearing and is responsible for most returns from sonar. Historically, the swim bladder has been modeled as an underwater resonant bubble, whereas we provide evidence for a forced-response model in which viscous damping of the bladder wall inhibits resonance of the internal bubble. Further experimental work on the shape, wall structure, and mechanical behavior of the swim bladder is required.

References
Ali, H., Mok, H. K., and Fine, M. L. (2016). Development and sexual dimorphism of the sonic system in deep sea neobythitine fishes: The upper continental slope. *Deep-Sea Research Part I: Oceanographic Research Papers* 115, 293-308.

Barimo, J. F., and Fine, M. L. (1998). Relationship of swim-bladder shape to the directionality pattern of underwater sound in the oyster toadfish. *Canadian Journal of Zoology* 76, 134-143.

Bertucci, F., Ruppé, L., Van Wassenbergh, S., Compère, P., and Parmentier, E. (2014). New insights into the role of the pharyngeal jaw apparatus in the sound-producing mechanism of *Haemulon flavolineatum* (Haemulidae). *Journal of Experimental Biology* 217, 3862-3869.

Birindelli, J. L., Sousa, L. M., and Sabaj Perez, M. H. (2009). Morphology of the gas bladder in thorny catfishes (Siluriformes: Doradidae). *Proceedings of the Academy of Natural Sciences of Philadelphia* 158, 261-296.

Borie, A., Hungria, D. B., Ali, H., Doria, C. R., Fine, M. L., and Travassos, P. E., (2019). Disturbance calls of five migratory Characiformes species and advertisement choruses in Amazon spawning sites. *Journal of Fish Biology* 95, 820-832.

Bradbury, J. W., and Vehrencamp, S. L. (1998). *Principles of Animal Communication.* Sinauer Associates, Sunderland, MA.

Braun, C. B., and Grande, T. (2008). Evolution of peripheral mechanisms for the enhancement of sound reception. In Webb. J. F., Popper, A. N., and Fay, R. R. (Eds.), *Fish Bioacoustics.* Springer, New York, NY, pp. 99-144.

Chao, N. L. (1986). A synopsis on zoogeography of Sciaenidae. In Uyeano, T., Arai, R., Taniuchi, T., and Matsuura, K. (Eds.), *Indo-Pacific Fish Biology. Proceedings of the Second International Conference on Indo-Pacific Fishes*, Ichthyological Society of Japan, Tokyo, July 28 to August 3, 1985, pp. 570-589.

Chardon, M., Parmentier, E., and Vanderwalle, P. (2003). Morphology, development and evolution of the Weberian apparatus in catfish. In Arratia, G., Kapoor, B. G., Chardon, M., and Diogo, R. (Eds.), *Catfishes*, vol. 1. Science Publishers, Inc., Enfield, NH, pp. 71-120.

Connaughton, M. A., Taylor, M. H., and Fine, M. L. (2000). Effects of fish size and temperature on weakfish disturbance calls: Implications for the mechanism of sound generation. *Journal of Experimental Biology* 203, 1503-1512.

Fine, M. L. (1978). Seasonal and geographic variation of the mating call of the oyster toadfish *Opsanus tau. Oecologia* 36, 45-57.

Fine, M. L., and Parmentier, E. (2015). Mechanisms of fish sound production. In Ladich, F. (Ed.), *Sound Communication in Fishes.* Springer, Vienna, Austria, pp. 77-126.

Fine. M. L., Ali, H. A., Nguyen, T. K., Mok, H. K., and Parmentier, E. (2018). Development and sexual dimorphism of the sonic system in three deep-sea neobythitine fishes and comparisons between upper mid and lower continental slope. *Deep-Sea Research Part I: Oceanographic Research Papers* 131, 41-53.

Fine, M. L., Burns N. M., and Harris, T. M. (1990). Ontogeny and sexual dimorphism of the sonic muscle in the oyster toadfish. *Canadian Journal of Zoology* 68, 1374-1381.

Fine, M. L., Friel, J. P., McElroy, D., King, C. B., Loesser, K. E., and Newton, S. (1997). Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus. Copeia* 1997, 777-790.

Fine, M. L., King, T. L., Ali, H., Sidker, N., and Cameron, T. M. (2016). Wall structure and material properties cause viscous damping of swimbladder sounds in the oyster toadfish *Opsanus tau. Proceedings of the Royal Society of London B: Biological Sciences* 283, 1-9.

Fine, M. L., Lin, H., Nguyen, B. B., Rountree, R. A., Cameron, T. M., and Parmentier, E. (2007). Functional morphology of the sonic apparatus in the fawn cusk-eel *Lepophidium profundorum* (Gill, 1863). *Journal of Morphology* 268, 953-966.

Fine, M. L., Malloy, K. L., King, C. B., Mitchell, S. L., and Cameron, T. M. (2001). Movement and sound generation by the toadfish swimbladder. *Journal of Comparative Physiology A* 187, 371-379.

Ghahramani, Z. N., Mohajer, Y. J., and Fine, M. L. (2014). Developmental variation in sound production in water and air in the blue catfish *Ictalurus furcatus. Journal of Experimental Biology* 217, 4244-4251.

Gould, S. J., and Vrba, E. S. (1982). Exaptation — A missing term in the science of form. *Paleobiology* 8, 4-15.

Harris, G. G. (1964). Considerations on the physics of sound production by fishes. In Tavolga, W. N. (Ed.), *Marine Bio-Acoustics.* Pergamon Press, New York, NY, pp. 233-247.

Hawkins, A. D., and Picciulin, M. (2019). The importance of underwater sounds to gadoid fishes. *The Journal of the Acoustical Society of America* 146(5), 3536-3551. https://doi.org/10.1121/1.5134683.

Horodysky, A. Z., Brill, R. W., Fine, M. L., Musick, J. A., and Latour, R. J. (2008). Acoustic pressure and particle motion thresholds in six sciaenid fishes. *Journal of Experimental Biology* 211, 1504-1511.

Kever, L., Boyle, K. S., Bolen, G., Dragicevic, B., Dulčić, J., and Parmentier, E. (2014). Modifications in call characteristics and sonic apparatus morphology during puberty in *Ophidion rochei* (Actinopterygii: Ophidiidae). *Journal of Morphology* 275, 650-660.

Ladich, F. (2018). Acoustic communication in fishes: Temperature plays a role. *Fish and Fisheries* 19(4), 598-612.

Ladich, F., and Fine, M. L. (2006). Sound-generating mechanisms in fishes: A unique diversity in vertebrates. In Ladich, F., Colin, S. P., Moller, P., and Kapoor, B. G. (Eds.), *Communication in Fishes.* Science Publishers, Inc., Enfield, NH, pp. 3-43.

Locascio, J. V., and Mann, D. A. (2011). Localization and source level estimates of black drum (*Pogonias cromis*) calls. *The Journal of the Acoustical Society of America* 130, 1868-1879.

Looby, A., Cox, K., Bravo, S., Rountree, R., Juanes, F., Reynolds, L. K. and Martin, C. W., (2022). A quantitative inventory of global soniferous fish diversity. *Reviews in Fish Biology and Fisheries* 32, 581–595. https://doi.org/10.1007/s11160-022-09702-1.

Mann, D. A. (2012). Remote sensing of fish sounds using passive acoustic monitoring. *Acoustics Today* 8(3), 8-15.

Marshall, N. B. (1967). Sound-producing mechanisms and the biology of deep-sea fishes. In Tavolga, W. N. (Ed.), *Marine Bio-Acoustics,* vol. 2. Pergamon Press, New York, NY, pp. 123-133.

Melotte, G., Virourous, R., Michel, C., and Parmentier, E. (2016). Interspecific variation of warning calls in piranhas: A comparative analysis. *Science Reports* 6, 36127.

Millot, S., Vandewalle, P., and Parmentier, E. (2011). Sound production in red-bellied piranhas (*Pygocentrus natteri*, Kner): An acoustical, behavioural and morphofunctional study. *Journal of Experimental Biology* 214, 3613-3618.

Minnaert, F. (1933). On musical air bubbles and the sounds of running water. *The Philosophical Magazine: A Journal of Theoretical Experimental and Applied Physics* 16, 235-248.

Mitchell, S., Poland, J., and Fine, M. L. (2008). Does muscle fatigue limit advertisement calling in the oyster toadfish *Opsanus tau*? *Animal Behaviour* 76, 1011-1016.

Mohajer, Y., Ghahramani, Z., and Fine, M. L. (2015). Pectoral sound generation in the blue catfish *Ictalurus furcatus. Journal of Comparative Physiology A* 201, 305-315.

Mok, H. K., Parmentier, E., Chiu, K. H., Tsai, K. E., Chiu, P. H., and Fine, M. L. (2011). An intermediate in the evolution of superfast sonic muscles. *Frontiers in Zoology* 8, 1-8.

Mok, H. K., Wu, S. C., Sirisuary, S., and Fine, M. L. (2020). A sciaenid swim bladder with long skinny fingers produces sound with an unusual frequency spectrum. *Science Reports* 10, 18619.

Morris, S. M., and Albright, J. T. (1975). The ultrastructure of the swimbladder of the toadfish, *Opsanus tau* L. *Cell and Tissue Research* 164, 85-104.

Olivier, D., Frédéric, B., Zarco, M. S., Balart, E. F., and Parmentier, E. (2014). The cerato-mandibular ligament: A key functional trait for grazing in damselfish (Pomacentridae). *Frontiers in Zoology* 11, Article 63.

Parmentier, E., and Fine, M. L. (2016). Fish sound production: Insights. In Suthers, R. A., Fitch, W. T., Fay. R, R., and Popper, A. N. (Eds.), *Vertebrate Sound Production and Acoustic Communication.* Springer, Cham, Switzerland, pp. 19-49.

Parmentier, E., Bahrib, M. A., Plenevaux A., Fine, M. L., and Estradad, J. M. (2018). Sound production and sonic apparatus in deep-living cusk-eels (*Genypterus chilensis* and *Genypterus maculatus*). *Deep-Sea Research Part I: Oceanographic Research Papers* 141, 83-92.

Parmentier, E., Bertucci, F., Bolgan, M., and Lecchini, D. (2021a). How many fish could be vocal? An estimation from a coral reef (Moorea Island). *Belgian Journal of Zoology* 151, 1-29.

Parmentier, E., Bouillac, G., Dragicevic, B., Dulcic J, and Fine, M. (2010). Call properties and morphology of the sound producing-organ in *Ophidion rochei* (Ophidiidae). *Journal of Experimental Biology* 213, 3230-3236.

Parmentier, E., Colleye, O., Fine, M. L., Frédérich, B., Vanderwalle, P., and Herrel, A. (2007). Sound production in the clownfish *Amphirprion clarkii. Science* 316, 1006.

Parmentier, E., Compère, P., Casadevall, M., Fontenelle, N., Cloots, R., and Henrist, C. (2008). The rocker bone: A new kind of mineralised tissue? *Cell and Tissue Research* 334, 67-79.

Parmentier, E., Fine, M. L, and Mok, H. K. (2016). Sound production by a recoiling system in the Pempheridae and Terapontidae. *Journal of Morphology* 277, 717-724.

Parmentier., E., Lagardère, J. P., Braquegnier, J. B., Vandewalle, P., and Fine, M. L. (2006). Sound production mechanism in carapid fish: First example with a slow sonic muscle. *Journal of Experimental Biology* 209, 2952-2960.

Parmentier, E., Mann, K. A., and Mann, D. A. (2011). Hearing and morphological specializations of the mojarra (*Eucinostomus argenteus*). *Journal of Experimental Biology* 214, 2697-2701.

Parmentier, E., Scalbert, R., Raick, X., Gache, C., Frédérich, B., Bertucci, F., and Lecchini, D. (2021b). First use of acoustic calls to distinguish cryptic members of a fish species complex. *Zoological Journal of the Linnean Society* 195(3), 964-975.

Pelster, B. (2021) Using the swimbladder as a respiratory organ and/or a buoyancy structure—Benefits and consequences. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 335, 831-842.

Popper, A. N., Hawkins, A. D., and Sisneros, J. A. (2021). Fish hearing "specialization" — A re-evaluation. *Hearing Research* 108393. https://doi.org/10.1016/j.heares.2021.108393.

Popper, A. N., Plachta, D. T., Mann, D. A., and Higgs, D. (2004). Response of clupeid fish to ultrasound: A review. *ICES Journal of Marine Science* 61, 1057-1061.

Rice, A. N., Farina S. C., Makowski, A. J., Kaatz, I. M., Lobel, P. S., Bemis, W. E., and Bass, A. H. (2022). Evolutionary patterns in sound production across fishes. *Ichthyology and Herpetology* 110, 1-12.

Sand, O., and Hawkins, A. D. (1973). Acoustic properties of the cod swim bladder. *Journal of Experimental Biology* 58, 797-820.

Sprague, M. W., Fine, M. L.,and Cameron, T. M. (2022). An investigation of bubble resonance and its implications for sound production by deepwater fishes. *PLoS ONE* 17(7), e0267338.

Tavolga. W. N. (1971). Sound production and detection. In Hoar, W. S., and Randall, D. J. (Eds.), *Fish Physiology*. Academic Press, New York, NY, pp. 135-205.

Tellechea, J. S., Martinez, C., Fine, M. L., and Norbis, W. (2010). Sound production in the whitemouth croaker and relationship between fish size and call characteristics. *Environmental Biology of Fishes* 89, 163-172.

Thorson, R. F., and Fine, M. L. (2002). Acoustic competition in the gulf toadfish *Opsanus beta*: Acoustic tagging. *The Journal of the Acoustical Society of America* 111, 2302-2307.

Tracy, H. C. (1911). The morphology of the swim bladder in teleosts. *Annals of the New York Academy of Sciences* 38, 600-606, 638-649.

Urick, R. J. (1975). *Principles of Underwater Sound.* McGraw-Hill, New York, NY.

Weston, D. E. (1967). Sound propagation in the presence of bladder fish. In Albers, V. M. (Ed.), *Underwater Acoustics,* vol. 2. Plenum Press, New York, NY, pp. 55-88.

Winn, H. E. (1964). The biological significance of fish sounds. In Tavolga, W. N. (Ed.), *Marine Bio-Acoustics*. Pergamon Press, New York, NY, pp. 213-231.

Yan, H. Y., Fine, M. L., Horn, N. S., and Colon, W. E. (2000). Variability in the role of the gasbladder in fish audition. *Journal of Comparative Physiology A* 186, 435–445.

About the Authors

Michael L. Fine mfine@vcu.edu

Department of Biology
Virginia Commonwealth University
Richmond, Virginia 23062, USA

Michael L. Fine is a professor emeritus in the Department of Biology, Virginia Commonwealth University (Richmond). Dr. Fine received his BS in zoology from the University of Maryland, College Park (College Park), his MA in marine science from the College of William and Mary (Williamsburg, Virginia), and his PhD in oceanography from the University of Rhode Island (Kingston). He did a postdoc in auditory neurophysiology at Cornell University (Ithaca, New York), recording from the toadfish VIIIth nerve. At Virginia Commonwealth University, he worked on anatomy, sonic muscle physiology, and sound production in the oyster and gulf toadfish and later in other fish species.

Eric Parmentier
E.Parmentier@uliege.be

Department of Biology, Environment and Ecology
University of Liège
B-4000 Liège, Belgium

Eric Parmentier is a full professor and the principal investigator in the Laboratory of Functional and Evolutionary Morphology, University of Liège (Liège, Belgium). Prof. Parmentier received his PhD in science from the University of Liège. He did a postdoc in acoustic communication at Virginia Commonwealth University (Richmond) and on hearing abilities in fishes at the University of South Florida (Tampa). He is working on acoustic communication, the anatomy of sound-producing muscles in different teleost species, and passive acoustic monitoring.