

Section I
*Acoustic and Chemical
Communication*

Section Editor
FRIEDRICH LADICH

*Dedicated to the memory of Professor Arthur
A. Myrberg Jr. (1933–2005), a wonderful human being
and pioneer in fish acoustic communication research
during the twentieth century. Unfortunately, he did not
live to see his chapters published.*

Sound-Generating Mechanisms in Fishes: A Unique Diversity in Vertebrates

Friedrich Ladich^{1*} and Michael L. Fine²

¹Department of Neurobiology and Behavior, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria. E-mail: friedrich.ladich@univie.ac.at

²Department of Biology, Virginia Commonwealth University, Richmond, VA, 23284-2012, USA. E-mail: mlfine@vcu.edu

ABSTRACT

Fishes have evolved the largest diversity of sonic organs among vertebrates. The main group of sound producing mechanisms is based on the swimbladder. These can be vibrated by intrinsic drumming muscles located in the wall of the swimbladder (toadfishes, searobins), or by extrinsic drumming muscles, which originate on structures such as the skull, vertebral processes or body wall musculature. Extrinsic drumming muscles insert either directly on the swimbladder (e.g. pimelodid catfish, tiger perches) or vibrate the swimbladder indirectly either via broad tendons (piranhas, drums) or via bony plates (elastic springs in doradid, mochokids and ariid catfishes).

Pectoral sound-producing mechanisms include vibration of the pectoral girdle (sculpins), rubbing of the enhanced pectoral spine in a groove of the shoulder girdle (catfishes), and plucking of enhanced fin tendons (croaking gouramis). In addition, sounds can be produced by other morphological structures such as dorsal fin spines, neck vertebrae and pharyngeal teeth grating. In a few taxa, such as catfishes, two different sound-producing mechanisms (swimbladder and pectoral) are present simultaneously. In several other well-known vocalizing taxa (damsel-fishes, gobies, loaches) the mechanisms remain unidentified.

Sound-generating mechanisms may be similarly developed in males and females (croaking gourami) or sexually dimorphic, in which case they are always better developed in males. In toadfishes males possess a relatively higher sonic muscle mass than females, whereas in some drum species muscles are totally absent in females. In the midshipman *Porichthys*

*Corresponding Author

notatus, territorial males possess larger sonic muscles than parasitic sneaker males, which steal fertilizations. In drums sonic musculature hypertrophies seasonally, a process apparently controlled by the hormone testosterone.

Drumming muscles vibrate the swimbladder at high rates (50–250 Hz), which results in emission of low-frequency harmonic sounds in which the contraction rates constitutes the fundamental frequency. In contrast, rubbing of bony structures against each other (stridulation) or tendon plucking results in production of broad-band pulsatile sounds with dominant frequencies at or above 1 kHz. The inability of fishes to vary their sound emissions by air flow modulations, as do birds and mammals, reduces the variation of sounds to differences in intensity, rate, and number and duration of pulses. Nevertheless, some species can emit up to five different sound types in different behavioral contexts.

Key Words: Swimbladder vibration; Pectoral mechanism; Physiology; Energetics; Fine structure; Sexual dimorphism; Sound characteristics; Sonic muscle; Stridulation.

1. HISTORICAL BACKGROUND

Fishes have evolved the largest diversity of sound-generating mechanisms among vertebrates. Investigation of this diversity proved difficult and controversial and took hundreds of years. First mentioned by Aristotle (Gohlke, 1957) in the fourth century B.C., sound-producing mechanisms were first extensively described in the nineteenth century by Müller (1857) and Dufossé (1874). Aristotle wrote that drums (sciaenids) and searobins (gurnards) produce sounds by rubbing and moving air within the body. Müller (1857) wrote a systematic overview of ‘*pisces vocales*’ (vocal fishes) in the mid-nineteenth century. His listing included representatives of seven mainly marine families—dactylopterids, triglids, sciaenids, cottids, zeids, batrachoidids, balistids, tetra- and diodontids—and three freshwater families—mochokids, cyprinids, and cobitids. He (Müller, 1857) successfully described the pectoral stridulatory mechanism in mochokid catfishes but failed with other groups, stating that nothing in the swimbladders of searobins and drums could explain sound generation. Seventeen years later Dufossé (1874) demonstrated anatomically (see Fig. 1.1) and with muting experiments that representatives of these taxa produce sounds by contracting specialized swimbladder muscles.

Müller (1842) and Bridge and Haddon (1889, 1892) described numerous muscles associated with the swimbladders in catfishes but incorrectly stated that these muscles adjust the swimbladder volume to compensate for changes in hydrostatic pressure. Sørensen (1895) opposed this view and demonstrated that they function in sound generation (see review by Fine and Ladich, 2003).

Thus at the beginning of the twentieth century major types of sound-producing mechanisms were known while others have been described more recently. However, many mechanisms still remain to be discovered, especially in well-known vocalizing taxa such as cobitids, cyprinids, pomacentrids, cichlids, and gobiids.

2. CLASSIFICATION (DIVERSITY) OF SONIC MECHANISMS

There exists no commonly accepted classification of sounds or sound-generating (sonic) mechanisms in fishes because it is not clear what should be regarded as a communication signal. Several studies have described unintentional noise, likely not used for intraspecific communication (Dijkgraaf, 1941). Another reason for the classification difficulty is that both morphological overlap and sometimes a large variation between the sonic apparatus of closely related taxa occur, as seen in the scorpaeniforms. Schneider (1961) differentiated between mechanisms based on a physical principle (stridulation) and those based on the swimbladder. Stridulatory mechanisms are based on friction of skeletal elements such as teeth, fin rays, and vertebrae. Tavalga (1971) differentiated between three major types—stridulatory, swimbladder (gas expulsion, extrinsic and intrinsic), and hydrodynamic sounds. Hydrodynamic sounds originally mentioned by Moulton (1960) are generated when objects such as the fins or body of fishes move through the water. Schaller and Kratochvil (1981) proposed a classification based primarily on physical principles: drumming muscle apparatus (direct and indirect types—not to be confused with intrinsic and extrinsic types), stridulatory, pneumatic, and plucking mechanisms. Pneumatic mechanisms produce sound by expulsion of air through small ducts or openings such as air from the swimbladder through the pneumatic duct in physostomous fishes or air from the intestine in cobitid fishes and clupeids (Müller, 1857; Dufossé, 1874; Dijkgraaf, 1941; Wilson et al., 2003). The fourth mechanism is based on plucking of stretched tendons (Kratochvil, 1978).

In the present overview we focus on acoustical communication and thus do not deal with unintentionally produced sounds such as those produced during swimming, feeding, breathing, or gas exchange. We suggest a classification based on morphological structures which have evolved exclusively for acoustical signaling. The main group of sonic organs utilizes swimbladder mechanisms with their innumerable variations. These are subdivided into intrinsic, extrinsic directly and extrinsic indirectly vibrating mechanisms. The second group comprises the pectoral mechanisms including pectoral spine rubbing, pectoral tendon plucking and pectoral girdle vibrations. The importance of additional sound-generating structures becomes less clear when nonspecialized morphological structures are involved, e.g. frequently pharyngeal mechanisms are postulated based on pharyngeal or jaw teeth grating (Lanzing, 1970; Ballantyne and Colgan, 1978). Recent studies on bubble release from the anus in herring during gas exchange indicate the possibility that these sounds may have a communicative function (Wahlberg and Westerberg, 2003; Wilson et al., 2003).

2.1 Swimbladder Mechanisms

Swimbladders are utilized in various ways in sound production. The best known example is vibration of the swimbladder by contraction of specialized muscles, called drumming or sonic muscles. Based on the origin and insertion of these muscles, various types are distinguished. Intrinsic drumming muscles attach solely to the swimbladder walls (i.e. there is no classical origin and insertion) whereas extrinsic types originate on other structures such as the skull, ribs, vertebrae, and reportedly muscles. Some fishes such as *Pterois* and searobins even possess both intrinsic and extrinsic muscles (Evans, 1973; Yabe, 1985). In some cases sonic muscles make no direct contact with the swimbladder but vibrate it indirectly via structures such as bony plates (elastic spring) or broad tendons. Therefore, we distinguish direct and indirect swimbladder vibrating mechanisms. There is not enough known about the evolution and function of intrinsic and extrinsic muscles at this point to allow comparisons. Fine and Ladich (2003) speculated that extrinsic muscles represent a step in the evolution of intrinsic ones, i.e. it would be easier to move the attachment of an existing muscle to the swimbladder than to create a new (de novo) muscle there. Intrinsic muscles are likely to be shorter and therefore have less inertia (i.e. series elastic element), which would facilitate rapid contraction and relaxation.

Besides the action of drumming muscles the swimbladder can be excited by beating or rubbing pectoral fins against areas of the body wall that cover it (Moulton, 1960; Salmon et al., 1968) although the beating explanation was questioned by Schneider (1961). In many cases swimbladders have been assumed to act as resonators that amplify sounds produced by other mechanisms such as stridulation (see below) (Tavolga, 1971; Demski et al., 1973), but this possibility requires experimental verification.

2.1.1. Intrinsic Drumming Muscles

Intrinsic drumming muscles are rather seldom found in fishes, but they are exceptionally well described, particularly in toadfishes (batrachoidids) (see below). Additionally, intrinsic muscles are found in dactylopterids (Dufossé, 1874), some gadids (Hawkins, 1986), and some scorpaeniforms, in particular triglids (Yabe, 1985) (Figs. 1.1 and 1.5C). Typically, two bands of muscles are firmly attached along the lateral surfaces of the swimbladder with fine striated fibers running dorsoventrally (Hawkins and Myrberg, 1983). The two muscles can be short and concentrated on the cranial poles of the swimbladder as in the burbot *Lota lota* (Hawkins, 1993) and the dory *Zeus faber* (Dufossé, 1874) or in the middle zone as in *Apistes* (Hallacher, 1974) or can even join each other at the caudal end as in the toadfish *Opsanus tau* (Schneider, 1967; Barimo and Fine, 1998). Recently, Dos Santos et al. (2000) found that the bladder is split into two rostrocaudal chambers connected by a canal in a Portuguese toadfish *Halobatrachus didactylus*, and the sonic muscles line the two lateral

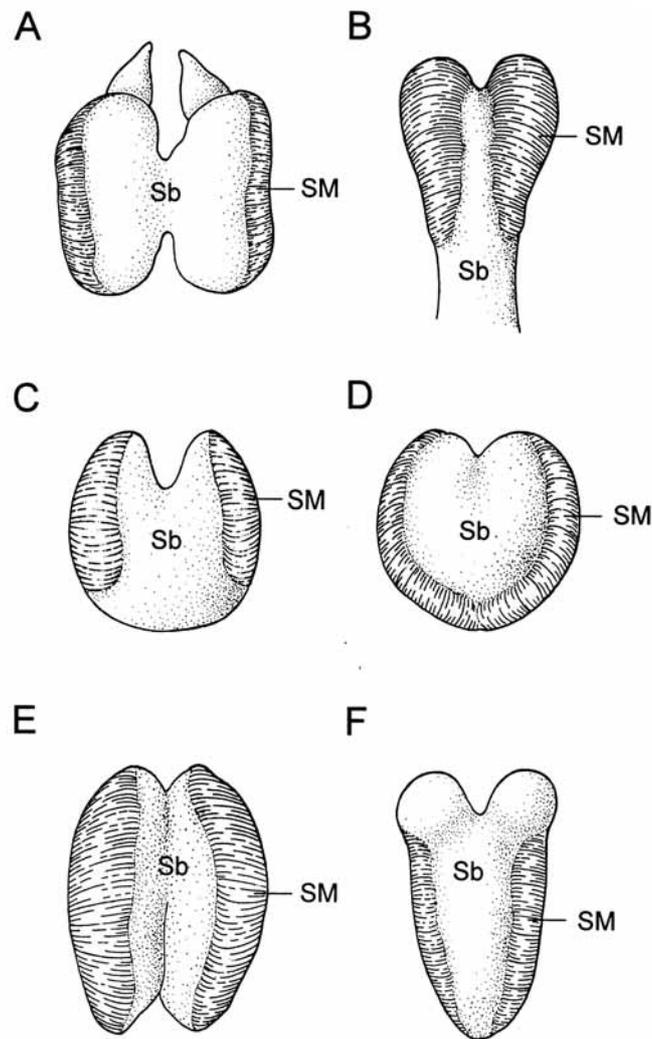


Fig. 1.1: Various types of intrinsic sonic swimbladder muscles in teleost fishes. Cranium always upward. A: *Dactylopterus* sp. (family Dactylopteridae); B: burbot, *Lota lota* (family Gadidae); C: midshipman, *Porichthys notatus* and D: toadfish, *Opsanus tau* (both family Batrachoididae); E: northern searobin, *Prionotus carolinus* and F: European gurnard (both family Triglidae). Sb—swimbladder, SM—sonic muscle. A, F—Redrawn from Dufossé (1874), B—after Hawkins (1986); C, D and E—after Bass and Baker (1991).

surfaces of the bladder. This situation looks much like the case in dactylopterids and triglids (Fig. 1.1A, E) except the two halves are almost completely separated by a small canal. It is not known whether these different shapes are due to morphological constraints, e.g. swimbladder size and shape (heart shape in toadfishes, two medially separated chambers in dactylopterids), or acoustical constraints, e.g. signaling duration, amplitude, etc. (Fig. 1.1). Position of the muscles and shape of the swimbladder have been related to directionality of the emitted sound field in the oyster toadfish (Barimo and Fine, 1998), and sound directionality is likely the selection force behind these different shapes.

The sonic nerve, a likely hypoglossal homolog, surrounded by its muscle forms in the occipital (neck) region, migrates down, and attaches to the swimbladder (Tracy, 1961; Galeo et al., 1987). Axons of sonic motoneurons exit via occipital nerve roots to innervate the sonic muscle, which is derived from occipital somites (Tracy, 1959; Lindholm and Bass, 1993; Bass and Baker, 1997).

2.1.2. *Extrinsic Drumming Muscles*

A greater variety is found within extrinsic mechanisms because muscles originate in a variety of places within the body. Large variations occur even within closely related groups, making it difficult to establish clear categories. This variation will be illustrated in two groups of otophysines—siluriforms and characiforms. Otophysines are characterized by Weberian ossicles, enhancing their auditory sensitivity and frequency range considerably (Nelson, 1994; Ladich, 1999; Ladich and Popper, 2004).

SILURIFORMES

Catfishes have at least four different types of swimbladder mechanisms (for a review, see Fine and Ladich, 2003) (Fig. 1.2). In pimelodid catfishes sonic muscles act directly. They originate on a flat tendon of the transverse process of the fourth vertebra and insert on the rostral and ventral surface of the swimbladder. The anterior half of the ventral surface is completely covered by a pair of flat sonic muscles (Schaller and Schachner, 1981; Heyd and Pfeiffer, 2000; Ladich, 2001) (for a sonogram, see Chapter 5). Drumming muscles are not, however, universally present in pimelodids and thus not a family characteristic. Bridge and Haddon (1889) observed atrophy and degeneration of the swimbladder in many species that lack sonic muscles.

The majority of catfish families possess indirect vibrating mechanisms consisting of a thin bony plate that attaches to the swimbladder, termed a 'Springfederapparat' (elastic spring mechanism) by Müller (1842). Sonic muscles that originate on various structures insert on the elastic spring (also termed *ramus Mülleri*). The sonic muscles pull the elastic spring forward (therefore called protractor muscles), extending the swimbladder. When the muscles relax, a process slower than contraction, tension in the spring rapidly restores the swimbladder to its normal position. The elastic spring may

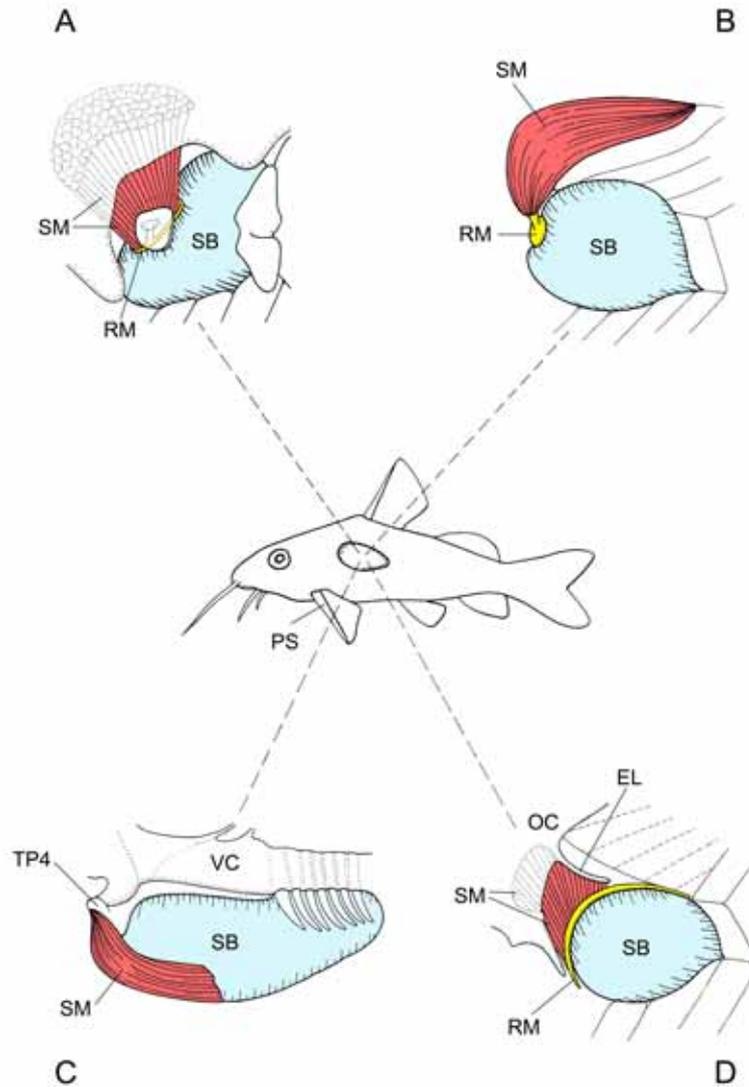


Fig. 1.2: Extrinsic swimbladder muscle types in catfishes (Siluriformes). A: Thorny catfish, *Platydoras costatus* (family Doradidae); B: upside-down catfish, *Synodontis* sp. (family Mochokidae); C: *Pimelodus* sp. (family Pimelodidae); D: sea catfishes, *Arius* sp. (family Ariidae). In the doradid *Platydoras* the first small dermal plate (P) and its short connection to the ramus Mülleri (RM) shown. For further details see text. EL—epiotic lamina; OC—occipital bone; P—dermal plates (scutes); PS—pectoral spine; RM—ramus Mülleri (=elastic spring); Sb—swimbladder; SM—sonic (= protractor) muscle; TP4—transverse process of the 4th vertebra; VC—vertebral column. Modified from Ladich and Bass, 1996, 1998 and Fine and Ladich, 2003; drawing by H.C. Grillitsch.

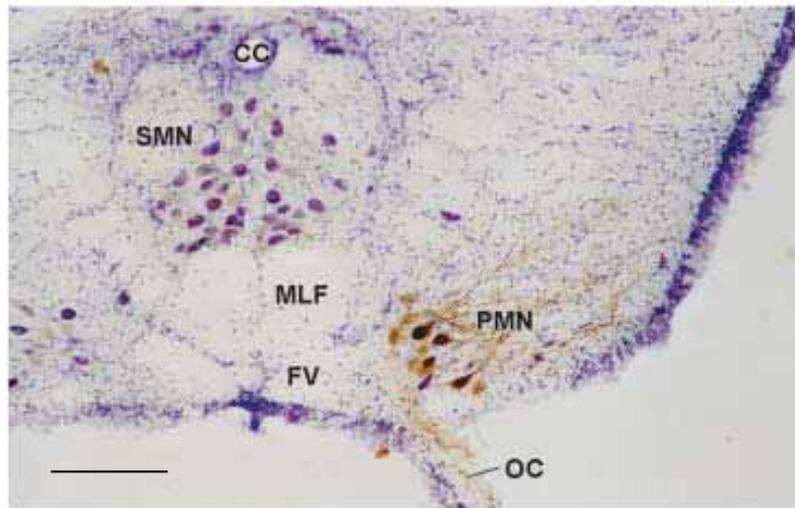


Fig. 1.3: Photomicrograph of biocytin-filled neurons (brown coloration) and fibers in brainstem of the mochokid catfish, *Synodontis nigromaculatus* after labeling of single pectoral spine-associated brachial nerve. Labeled pectoral spine motoneurons lie in the ventrolateral motor column (PMN), and nonlabeled swimbladder motoneurons (SMN) are located on midline below the central canal (CC). FV—ventral fasciculus; MLF—medial longitudinal fasciculus; OC—occipital nerve. Scale bar = 150 μ m. Reprinted from Fine and Ladich (2003).

therefore be seen as an adaptation for speed and may explain why intrinsic muscles have not evolved in catfishes. Families possessing an elastic spring mechanism were classified as 'arioids' by Lundberg (1993). Among 'arioids,' the shape of the tip of the elastic spring separates ariids from 'doradoids', a presumptive suborder which includes the African mochokids and the neotropical doradids and auchenopterids, two groups connected by several synapomorphic characters. Unlike the pointed elastic spring in ariids, the disk-shaped tip of the elastic spring in doradids and mochokids represents the more highly derived trait (see Fig. 1 in Lundberg, 1993).

In the ariids *Galeichthys* (=Arius) *felis* and *Bagre marinus* the sonic muscle originates on the occipital bone and the epiotic lamina (Fig. 1.2C) and inserts on the entire surface of the elastic spring, formed by a process of the fourth vertebra (Tavolga, 1962; Ladich and Bass, 1998). The spring is decurved and pointed, and its distal tip is movable. In representatives of the presumptive suborder doradoids, powerful muscles insert on the anterior side of the elastic spring. The shape and origin of the drumming muscle differ among families. In the mochokids, i.e. *Synodontis* spp., it originates on epaxial musculature ventral to the dorsal spine (Abu-Gideiri and Nasr, 1973; Ladich and Bass, 1996). The hook-shaped muscle extends rostrally and ventrally before inserting on

the elastic spring (Fig. 1.2B). In the doradid *Platydoras costatus* the disk-shaped spring is firmly connected to the rostradorsal swimbladder. The protractor muscles originate on the supraoccipital bone and insert dorsally on the elastic spring (Fig. 1.2A) (Kastberger, 1977; Ladich and Bass, 1998). The elastic spring is connected laterally via a short ligament to the first lateral plate, which is embedded in the lateral cutaneous area (exomembrane) between the occipital bone, cleithrum, and the large lateral plates (Ladich, 2001). Contraction of the protractor muscles causes the first lateral dermal plate and the swimbladder to vibrate, producing sound (Kastberger, 1977).

Sonic muscles are innervated by sonic motoneurons located in the hindbrain along the midline, ventral to the fourth ventricle and central canal in doradids and mochokids (Fig. 1.3) but lateral to the medial longitudinal fasciculus in ariids. Pimelodids have motoneurons in both locations (Ladich and Fine, 1994; Ladich and Bass, 1996, 1998).

CHARACIFORMES

Within characiforms, the sister group of siluriforms, several extrinsic drumming mechanisms evolved, which move the swimbladder indirectly. The most detailed anatomical description is given by Markl (1971) for the red piranha *Pygocentrus nattereri* and by Ladich and Bass (2005) for the black piranha *Serrasalmus rhombeus*. Sonic muscles originate on vertebral processes and insert on a broad tendon that surrounds the bladder ventrally, similar to a saddle girth (Fig. 1.4A). Thus contractions of these muscles vibrate the swimbladder via the tendon, as opposed to the bony plates in siluriforms (for a sonogram, see Chapter 5, this volume).

Contrary to the majority of sonic fishes, the sonic muscles in piranhas are innervated by the 3rd and 4th true spinal nerves (Markl 1971). Motoneurons are located in the spinal cord lateral to the central canal (Ladich and Bass, 2005).

In the jaraqui *Semaprochilodus* (= *Prochilodus*) *insignis* rapid contractions of well-developed intercostal muscles vibrate the swimbladder (Schaller, 1971), allowing these fish in the Amazonian river system to produce loud evening choruses. The intercostal muscles between the first four ribs are easily recognized by their deep red coloration in fresh specimens (Fig. 1.4B). In the closely related branquinha *Potamorhina* (= *Anodus*) *laticeps* a massive unpaired muscle surrounds the swimbladder cranially, running between the left and right thickened first ribs (Schaller and Kratochvil, 1981).

SCORPAENIFORMES

The largest diversity in sonic mechanisms is found in the marine order scorpaeniforms, ranging from intrinsic swimbladder muscles to pectoral muscles in species lacking swimbladders. There are extrinsic muscle types (Fig. 1.5A, B) that represent an intermediate stage between the intrinsic and extrinsic condition (Fig. 1.5C, D). Hallacher (1974) identified two categories of extrinsic "gasbladder muscles," types I and II, in scorpaenid rockfishes

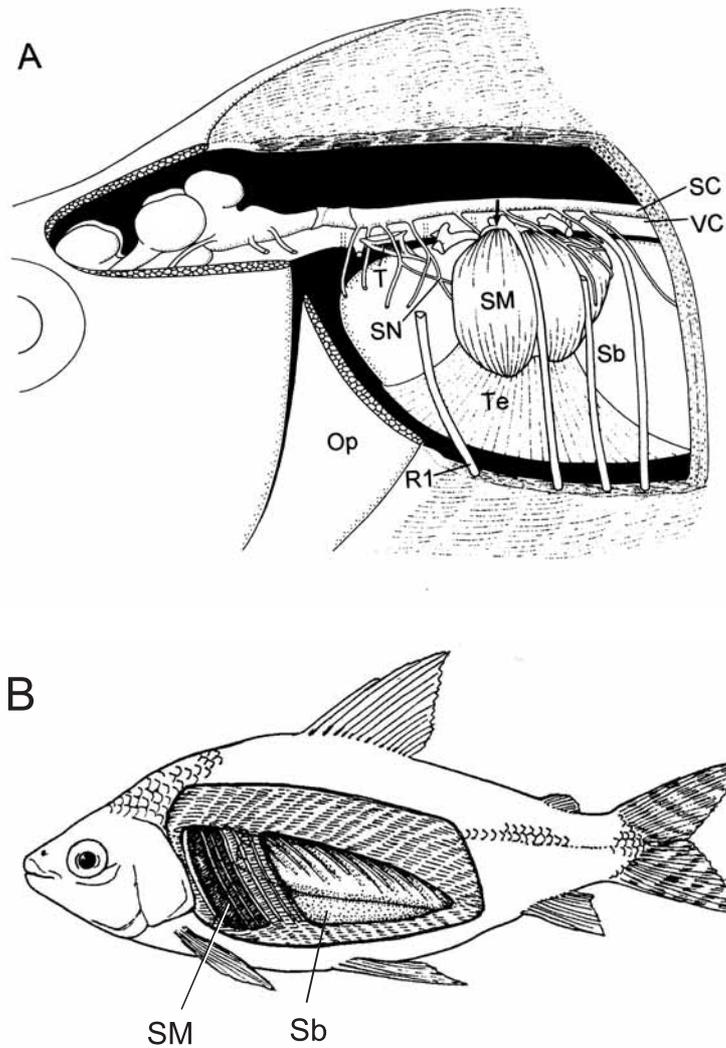


Fig. 1.4: Two extrinsic drumming muscle types in Characiformes. A: Lateral view of postcranial region of a black piranha, *Serrasalmus rhombeus* showing sonic muscle (SM) and its innervation. First and third pleural ribs partly removed to show innervation. Arrow indicates basal widening of 2nd rib where the sonic muscles originate; Op—operculum; R1—1st ventral rib; Sb—swim bladder; SC—spinal cord; SM—Sonic muscle; SN—sonic nerve; T—tripus; Te—tendon; VC—vertebral column. B: Jaraqui, *Semaprochilodus insignis* (Curimatidae). Well-vascularized intercostal drumming muscles (SM) shown. A—after Ladich and Bass (2005); B—from Schaller (1971).

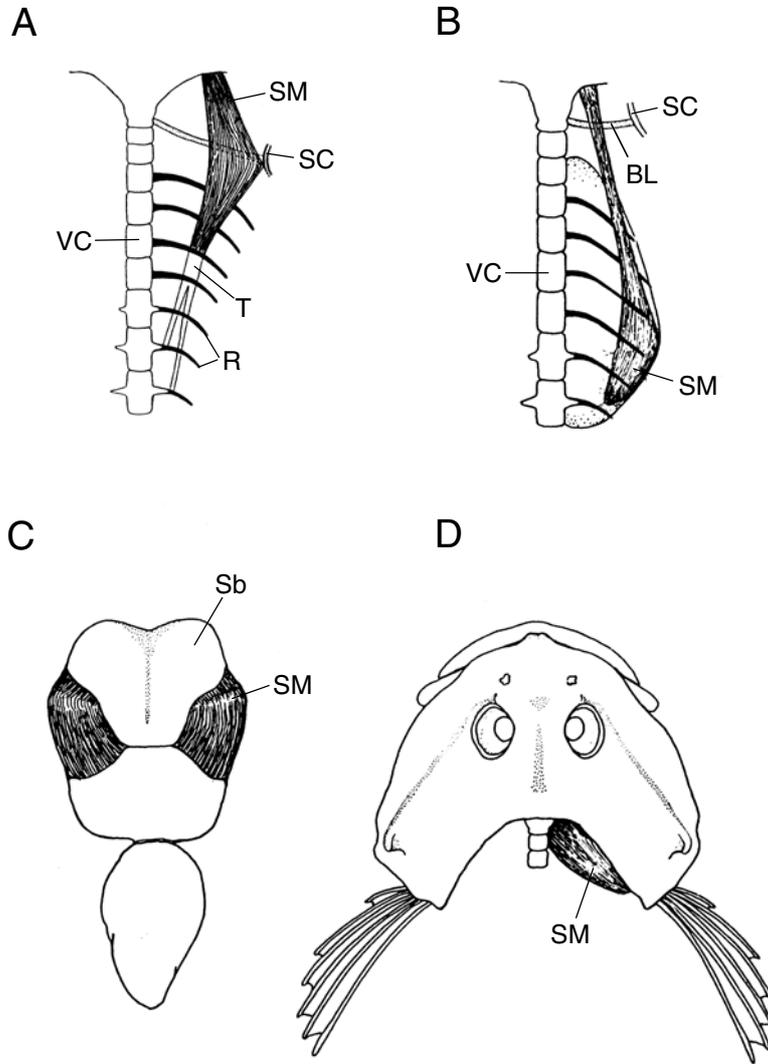


Fig. 1.5: Diversity of sonic (gasbladder) muscles in Scorpaeniformes (after Hallacher, 1974). A: Type I sonic muscles (SM) (e.g. *Sebastes*) showing characteristic attachment to pectoral girdle (SC) as the muscles pass posteriorly from their origin on the occipital to the insertion on ribs (R) and vertebrae (VC). B: Type II muscles (*Sebastes marmoratus*) bypass pectoral girdle (SC) and insert directly on the swimbladder (or vertebrae) (Both family Sebastidae). C: Gasbladder from *Apistus* showing the fully intrinsic muscle on the anterior lobe of the gasbladder (family Tetrarogidae). D: Dorsal view of right cranioclavical muscle (SM) in *Cottus asper* (family Cottidae), representative of a family lacking swimbladders. BL—Baudelot's ligament; Sb—swimbladder; SC—supracleithrum; T—tendon; VC—vertebral column.

(genus *Sebastes*). In all cases, the extrinsic swimbladder muscle originates on the occipital cranium and inserts on several vertebrae. Type I muscles attach to the pectoral girdle (supracleithrum) as they pass posteriorly to their insertion on ribs and vertebrae (Fig. 1.5A). Type II muscles do not connect to the pectoral girdle but attach instead directly to the swimbladder or vertebrae (Fig. 1.5B). Yabe (1985) found both extrinsic and intrinsic muscles in the scorpaeniforms *Pterois* and *Apistus*. Although the extrinsic and intrinsic muscles fuse in *Pterois*, they stay fully separated in *Apistus*.

Ontogenetic and neuroanatomical data suggest that extrinsic and intrinsic muscles in Scorpaeniformes are homologous. Rauther (1945) demonstrated that sonic muscles form from anterior hypaxial musculature embryonically and migrate to cover the swimbladder dorsally and to their origin on vertebrae and their cranial insertion on the pectoral girdle (cleithrum). (It is possible that these muscles form from occipital muscles as in toadfish (Tracy, 1961), and Rauther's work on early formation should be re-reviewed.) In later stages in *Trigla*, the attachment to skeletal elements degenerates and fully intrinsic muscles develop. Sonic motoneurons in all families are located within the ventral motor column (Ladich and Bass, 1998). Thus the diversity of sonic mechanisms in scorpaeniforms is not associated with different positions of sonic motoneurons (Ladich and Bass, 1998), indicating the central nervous system is more conservative, at least in this one point, than the peripheral (see also Ladich and Fine, 1992). Together, the foregoing data suggest that in the ancestral condition in scorpaeniforms, sonic muscles originate on the cranium, pass posteriorly with an attachment to the pectoral girdle, and finally insert by tendons to ribs, vertebrae, or the swimbladder. Degeneration of some attachment sites probably represents a derived state.

MISCELLANEOUS GROUPS

Swimbladder muscles similar to the extrinsic muscles in scorpaenids are present in nonrelated families of teleost fishes. In the squirrelfish *Holocentrus rufus* (family Holocentridae, order Beryciformes) a bilateral pair of extrinsic muscles originates on the skull near the auditory bulla and extends across the upper flattened part of the first two ventral ribs, which are firmly attached to the swimbladder, and ends on ribbon-like tendons just in front of the third rib (Winn and Marshall, 1963). Muscle contractions pull the air bladder forward. The sonic motoneurons are located in a ventrolateral position in the caudal medulla and rostral spinal cord, and axons exit via ventral occipital nerve roots (Carlson and Bass, 2000). In the tigerfish *Terapon jarbua* (family Terapontidae, order Perciformes) sonic muscles originate on the medial surfaces of the supracleithra, which are connected to the skull, and insert dorsally on the anterior half of the swimbladder beneath the fourth pair of ribs (Schneider, 1964) (Fig. 1.6). It is not clear whether these various muscle arrangements are homologous or have formed independently from different muscle precursors although they appear to have homologous innervation.

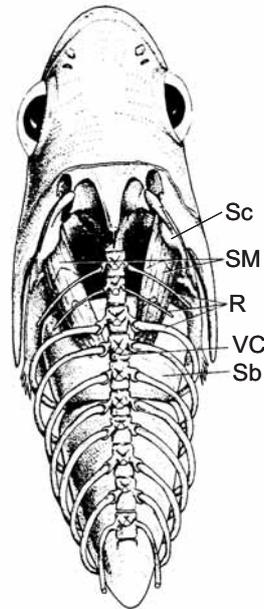


Fig. 1.6: Examples of extrinsic drumming muscles in Perciformes. Dorsal view of the tigerfish *Terapon jarbua* (family Terapontidae) showing origin of the drumming muscles (SM) on the supracleithra (Sc) and insertion on the swimbladder (Sb). R—rib, VC—vertebral column. Modified from Schneider (1964).

Extrinsic muscles lacking any contact with skeletal structures evolved in croakers (drum family Sciaenidae). Drumming muscles reportedly originate on the body wall lateral to the swimbladder and insert on a broad tendon, an aponeurosis, which attaches to the swimbladder dorsally (Schneider and Hasler, 1960; Ono and Poss, 1982; Hill et al., 1987) (Fig. 1.7). Actually in spot and croaker the origin is a small tendon on the ventral midline, which can be easily destroyed by dissection, and not hypaxial muscle (Fine, unpubl. obs.). A rapid contraction of the sonic muscles pulls the aponeurosis ventrally, thus forcing swimbladder movement indirectly. There is a large diversity within the family (Schneider and Hasler, 1960; Chao, 1978). Sonic muscles are present only in males of most species (Chao, 1978). In the Atlantic croaker *Micropogonius undulatus* however, they are present in both sexes although they grow larger in males (Hill et al., 1987). Adult kingfish (*Menthicirrus*) have no muscles and the swimbladder degenerates (Chao, 1978). In the freshwater drum, weakfish, spot, and croaker, the muscles form de novo and develop during puberty as juvenile indifferent gonads enlarge and develop into recognizable testes and ovaries (Schneider and Hasler, 1960; Hill et al., 1987). The muscles are

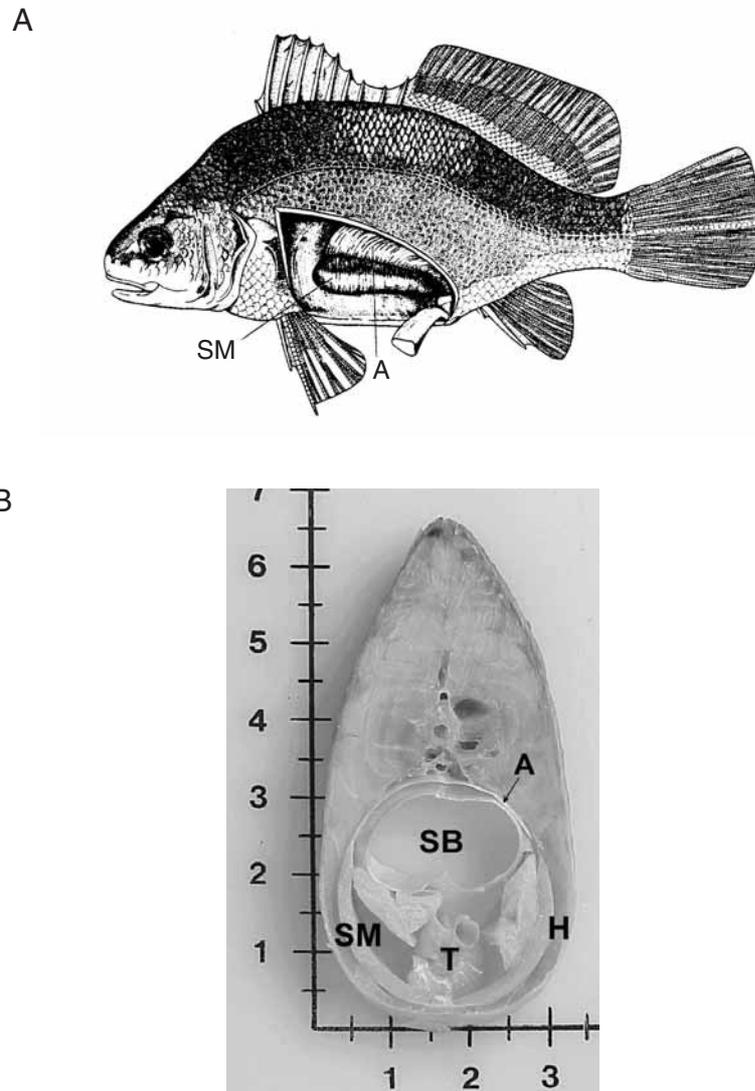


Fig. 1.7: Examples of extrinsic drumming muscles in Perciformes. A. Left sonic muscle (SM) attached to lateral trunk musculature and its insertion on the aponeurosis (A) in the freshwater drum *Aplodinotus grunniens* (family Sciaenidae) after removal of viscera. B. Cross section of a croaker illustrating the sonic mechanism. Note the sonic muscles (SM) originate on a tendon (T) on the ventral midline, follow the inner contour of the hypaxial muscles (H), and insert on the aponeurosis (A), a sheetlike tendon which fuses to the swimbladder (Sb). This section illustrates that the bladder and aponeurosis are separate structures. A—Modified from Schneider and Hasler (1960); and B—from Williams and Fine, unpublished.

innervated segmentally by true spinal nerves (Ono and Poss, 1982; Vance et al., 2002) and are innervated by a long column of motoneurons near the central canal that overlaps with epaxial and hypaxial trunk motoneurons (Hyman, Williams and Fine, unpubl.). The sonic muscle is likely a hypaxial derivative and is clearly not homologous to sonic muscles in other fishes, which are innervated by occipital spinal nerves. Finally, the sonic muscles undergo a yearly hypertrophy-atrophy cycle in which muscle fiber diameter, muscle thickness, various biochemical parameters, and sound amplitude are maximal during the peak of the mating season (Connaughton et al., 1997).

Extrinsic sonic systems connecting the skull to ribs and/or swimbladders have been described in several other families from different orders. In cod *Gadus morhua* three pairs of muscles insert on pleural ribs and separate lobes on the swimbladder (Brawn, 1961).

In the striped cusk-eel *Ophidion marginatum* (= *Rissola marginata*) (family Ophidiidae) two pairs of muscles originate at the otic region and insert on a vertebral process and cartilaginous caps of the swimbladder (Courtenay, 1971). In carapids primary sound-producing muscles originate within the orbits and insert on the swimbladder while the secondary muscle pair extends from the occipital bone to the underside of the first pair of ribs (Courtenay and McKittrick, 1970; Parmentier et al., 2003). In macrourids, as in other deep-sea fishes whose sounds have not been described, muscles attached to the swimbladder are a good indication of sound production and acoustical communication (Marshall, 1967). We know of no muscles attached to the swimbladder that do not have a sonic function.

2.2 Physiology and Fine Structure of Drumming Muscles

This section relates movement of sonic muscles to sound production. A surprisingly small amount of experimental work has been devoted to this subject. Involvement of the brain in sound production, concentrating on the midshipman *Porichthys notatus*, was recently reviewed (Bass and McKibben, 2003) and will not be treated extensively here.

2.2.1 Swimbladder Acoustics

The acoustics of swimbladders is central to diverse fields including acoustic communication in fishes, which involves both hearing and sound production (Tavolga, 1964, 1971; Demski et al., 1973; Fay and Popper, 1999; Zelik et al., 1999), passive acoustics to locate the calls of spawning fish (Connaughton and Taylor, 1995; Luczkovich and Sprague, 1999), and as targets to return scattered signals from sonar and echo sounders (Foote, 1997; Francis and Foote, 2003). Classically the swimbladder has been modeled as a pulsating underwater bubble (Harris, 1964; van Bergeijk, 1964), an omnidirectional, resonant monopole vibrated by incident sound that then radiates near-field vibrations to the ears or scatters sound back to sonar receivers. Underwater

bubbles are resonant structures with a high Q , a descriptor of sharpness of tuning. (Note a resonant structure like a bell or a crystal goblet efficiently produces sound at its natural or resonant frequency, and sound decays slowly (low damping) after excitation has stopped.) A low Q resonator, however, requires more energy for excitation but can produce a wider range of frequencies. It will follow the timing of a forcing stimulus (i.e. sonic muscle contraction) with greater fidelity. See Bradbury and Vehrencamp (1998) for more details. Swimbladder-bearing fishes have a lower Q , and vibrations decay more rapidly than in a free bubble (Weston, 1967); this discrepancy has traditionally been ascribed to damping by fish tissue surrounding the bladder. Numerous lines of evidence indicate that the resonant bubble model may be inappropriate in many, though not necessarily all cases. First, sonic muscles attached to swimbladders are the fastest muscles in vertebrates (see below), yet a resonant structure does not require extreme speed to excite it to resonance. Resonant frequency of an underwater bubble changes with size (bladders and sonic muscle size increase with fish growth) and depth and could create mismatches between communicating individuals. Note that choruses of toadfish, which include individuals of various sizes, produce calls with similar fundamental frequencies (Fine, 1978). Most fish sounds have a wide frequency spectrum and do not appear tuned (Winn, 1964; Fish and Mowbray, 1970); acoustical studies of fishes in an underwater sound field demonstrated a lower Q , i.e. broader tuning than an underwater bubble. A resonant bubble will continue to oscillate after sound termination and could interfere with temporal coding of fish sounds, most of which are of short duration and pulsed (Winn, 1964; Fine et al., 1977b; Wysocki and Ladich, 2003; Ladich, 2004). Finally, sonic swimbladders have a number of interesting shapes (i.e. heart shape in toadfish), which would not be logical for an omnidirectional source. Note that sounds from a catfish and a toadfish radiate directionally, not the omnidirectional pattern typically ascribed to the resonant bubble model (Tavolga, 1977; Barimo and Fine, 1998). A related phenomenon is that swimbladders have generally been assumed to function as accessory auditory organs, reradiating acoustic pressure to the ears (Bergeijk, 1964; Harris, 1964). This function has clearly been demonstrated in auditory specialists with connections between the swimbladder or a similar structure and the ears (Fay and Megela Simmons, 1999; Yan and Curtsinger, 2000; Fletcher and Crawford, 2001; Ladich and Wysocki, 2003). Studies in auditory generalists, fishes with no specialized connections such as cichlids, gobies, gouramis, and toadfish, indicate bladder deflation does not increase auditory thresholds (Fay and Popper, 1975; Yan et al., 2000; Lugli et al., 2003).

It therefore appears that the wall of the swimbladder has mechanical properties that can affect the presumably resonant bubble within. This notion was supported by Feuillade and Nero (1998) who modeled the bladder as an elastic tissue in a study of fish scattering in a sound field. We shall return to this subject later, integrating bladder and sonic muscle movement.

2.2.2 Fine Structure of Swimbladder Muscles

In addition to their role in sound production, sonic muscles have been of interest because of their extreme speed; they are generally considered the fastest muscles in vertebrates (Tavolga, 1964; Rome and Linstedt, 1998). The ultrastructure of sonic muscles was first described in the oyster toadfish *Opsanus tau* (Fawcett and Revel, 1961), and this species is the model most examined. Its fibers have a number of morphological and biochemical adaptations for speed including an unusual radial morphology (Fawcett and Revel, 1961; Bass and Marchaterre, 1989a; Fine et al., 1993; Loesser et al., 1997), a sarcoplasmic reticulum (SR) constituting about a third of the fiber volume (Appelt et al., 1991), the fastest calcium spike in a vertebrate muscle (Rome et al., 1996), rapid cross-bridge detachment (Rome et al., 1999), huge activator stores of calcium (Somlyo et al., 1977; Feher et al., 1998), and multiple innervation of its muscle fibers (Gainer, 1969; Hirsch et al., 1998). Sonic fibers of toadfish and many other species have a classic morphology with a core of sarcoplasm surrounded by a radially arranged contractile cylinder comprised alternating ribbons of SR and myofibrils (Fig. 1.8). Fine et al. (1993) interpreted this arrangement as an adaptation for speed because it minimizes travel distance for calcium between the SR and myofibrils. There is clearly a tradeoff however because mitochondria (energy generating organelles) are excluded from the contractile cylinder (energy utilizing region), occurring instead in the central core and the periphery of the fiber. A surprisingly small number of mitochondria in this muscle (Appelt et al., 1991) appears to restrict endurance (see below) in this and many species although Bass and Marchaterre (1989a) discovered huge numbers of mitochondria in the midshipman *Porichthys notatus*, which produces unusual long duration hums that can last for tens of minutes. The transverse tubule in toadfish (Fawcett and Revel, 1961; Bass and Marchaterre, 1997a; Loesser et al., 1997), midshipman (Bass and Marchaterre, 1989a), searobin (Bass and Marchaterre, 1989b) and *Carapus acus* (Parmentier et al., 2003) is located at the A-I junction (two triads per sarcomere, generally considered an adaptation for speed) although it has been found at the Z line (the typical position in fish trunk muscle) in sonic muscles in tigerfish *Terapon jarbua* (Eichelberg, 1976), weakfish *Cynoscion regalis* (Ono and Poss, 1982), and catfishes *Pimelodus* and *Platydoras* (Ladich, 2001). Interestingly, Suzuki et al. (2003) found a single fiber has t tubules in both positions in the scorpion fish *Sebastiscus marmoratus*. The midshipman is also of note for having a dramatically expanded Z line, the largest ever found, in type I males, which produce long-duration hums (Bass and Marchaterre, 1989a; Lewis et al., 2003). Finally, within catfishes *Platydoras costatus* has a typical fiber with a radial arrangement around a central core, but *Pimelodus pictus* lacks the core and radial orientation (Ladich, 2001) (Fig. 1.8B). There are a number of similarities in morphology likely related to convergent adaptations for speed. Note that the toadfish and weakfish sonic muscles are clearly not homologous (e.g. their

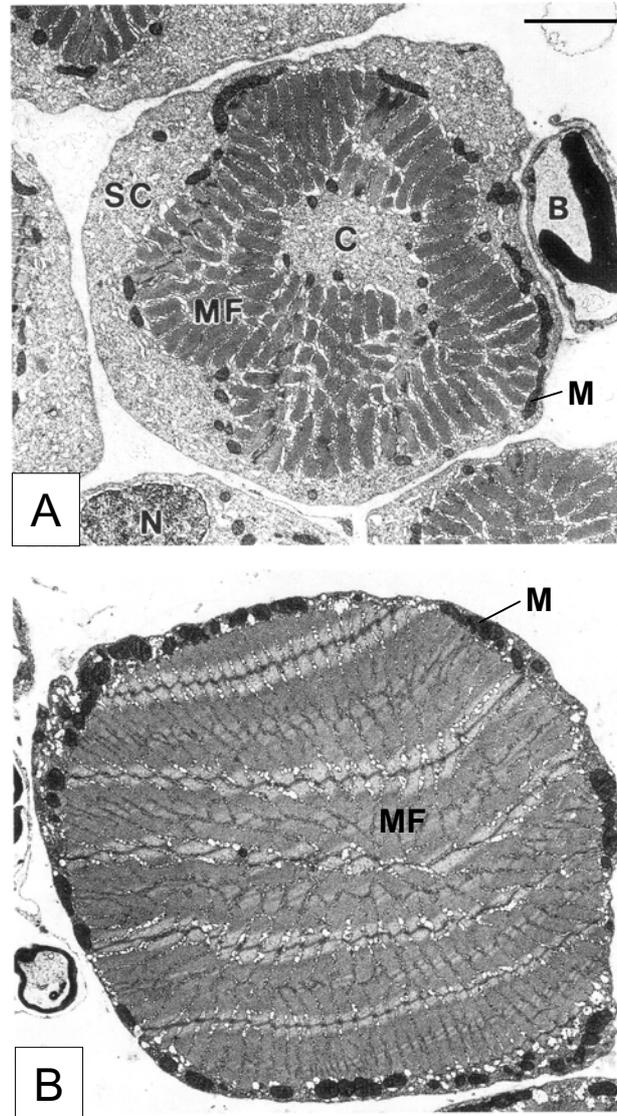


Fig. 1.8: Electron micrographs of drumming muscle fibers from catfishes. A: Doradid catfish *Platydoras costatus* illustrating a typical fish sonic muscle with a sarcoplasmic core surrounded by alternating ribbons of sarcoplasmic reticulum and myofibrils, B: Pimelodid catfish *Pimelodus pictus* illustrating a sonic fiber without a central core. Scale bar = 3 μm ; B—blood vessel; C—central core; M—mitochondria; MF—myofibrils; N—nucleus; SC—subsarcolemmal cytoplasm (from Ladich, 2001).

sonic muscles are innervated by occipital spinal and true segmental spinal nerves respectively), yet both have relatively similar ultrastructure. There is also a diversity of form in these fast muscles which has not been related to function. For instance, carapid sonic fibers have myofibrils with a twisted pattern at their periphery (Parmentier et al., 2003b). Some of the differences may relate to independent evolution.

2.2.3 Physiology

Tower (1908) performed an excellent experimental study in which he stimulated primarily weakfish but also toadfish and searobin sonic muscles and demonstrated that muscle movement and gas in the swimbladder were necessary for sound production. Little further work was done until the 1960s when there was a burst of activity. Fawcett and Revel (1961) examined the ultrastructure of sonic muscle, and Gainer and Klancher (1965) demonstrated multiple innervation of toadfish sonic muscle fibers. Investigators also found that stimulating a sonic muscle or its nerve with a single shock caused a sound pulse and that stimulating with a train of pulses determined the fundamental frequency of evoked sound, i.e. 100 pps stimulation produced a sound with a fundamental frequency of 100 Hz (Skoglund, 1961; Tavalga, 1964; Schneider, 1967). Reciprocal recording studies (electromyography) in a sonic muscle found a single action potential and therefore a single twitch occurred for each sound pulse (Packard, 1960; Skoglund, 1961; Winn and Marshall, 1963; Cohen and Winn, 1967; Crawford and Huang, 1999; Connaughton et al., 2000). They also demonstrated that sonic muscle pairs in these species contracted simultaneously because electrical synapses in the sonic motor nucleus synchronize the output to the muscles (Pappas and Bennett, 1966; Bass and Baker, 1990). An exception to this last generalization is provided by the searobin *Prionotus carolinus*, which has been shown to contract its muscles alternately (Bass and Baker, 1991; Connaughton, 2004). Alternate contraction doubles the call frequency with only a small decrease in amplitude (about 3 dB), yet permits the muscles to contract at half the frequency (Connaughton, 2004). Surprisingly, gray gurnards in the same family exhibit synchronous contraction (Bass and Baker, 1991; Amorim, 1996).

2.2.4 Toadfish and Weakfish Sound Generation

Countering the resonant bubble hypothesis (i.e. bigger fish produce lower frequency sound because of a larger swimbladder), recent work on the oyster toadfish indicates that its sound frequency is determined by a forced response to sonic muscle contraction rather than the natural frequency of the bladder (Fine et al., 2001). Fine and coworkers stimulated the sonic nerve with single shocks and trains of shocks, and recorded muscle action potentials, bladder movement with a laser vibrometer and evoked sound with a microphone above the fish, thus allowing bladder movement to be correlated with the waveform

of the evoked sound. Muscle twitches were extremely rapid, averaging 9.6 ms, but the time to peak pressure averaged 2.9 ms, which is less than the contraction time (4.5 ms) (Fig. 1.9). Differentiating the waveform of swimbladder displacement demonstrated that peak pressure occurs in the middle of contraction when velocity is maximal and acceleration zero (Fig. 1.10). Further, a twitch sound lasts for only 9.3 ms of the 38 ms movement, indicating that slow bladder movements do not generate recordable sound. Sound is generated inefficiently with a quadrupole-type motion (not the motion of a pulsating bubble): the curved sonic muscles lining the bladder push the sides in, building up internal pressure that pushes the bottom out, an inefficient pattern because there is no net volume change. Swimbladder vibrations decay rapidly with a damping coefficient equivalent to that of an automobile shock absorber, a device designed to prevent resonance. The rapid damping prevents expression of the natural frequency of the bladder and the sound frequency spectrum is broad. As previously stated, low Q resonators gain little advantage from resonance but follow timing extremely well (Bradbury and Vehrencamp, 1998), which supports the importance of temporal coding of sounds in fish communication (Winn, 1964).

Stimulation with 100 ms trains indicated that the muscle can contract at frequencies of 500 Hz and above, i.e. the muscle does not exhibit complete tetany (Fig. 1.11). A tetanized muscle would not move the bladder wall or produce sound. The muscle followed stimuli one-for-one at 400 Hz and

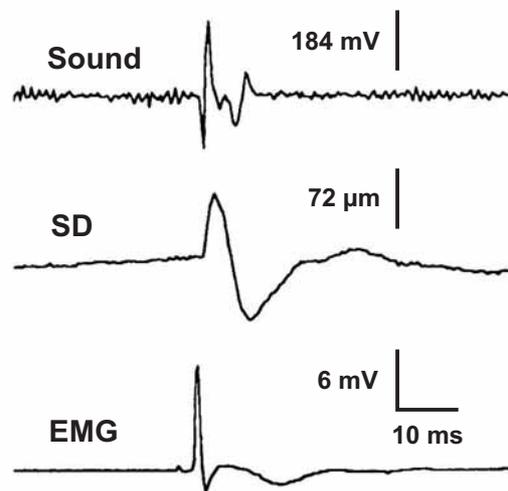


Fig. 1.9: Sound waveform, swimbladder displacement (SD), and muscle action potential of a twitch evoked by a single shock to the sonic nerve of a toadfish, *Opsanus tau*. Note that the sound terminates while the swimbladder is still in motion (from Fine et al., 2001).

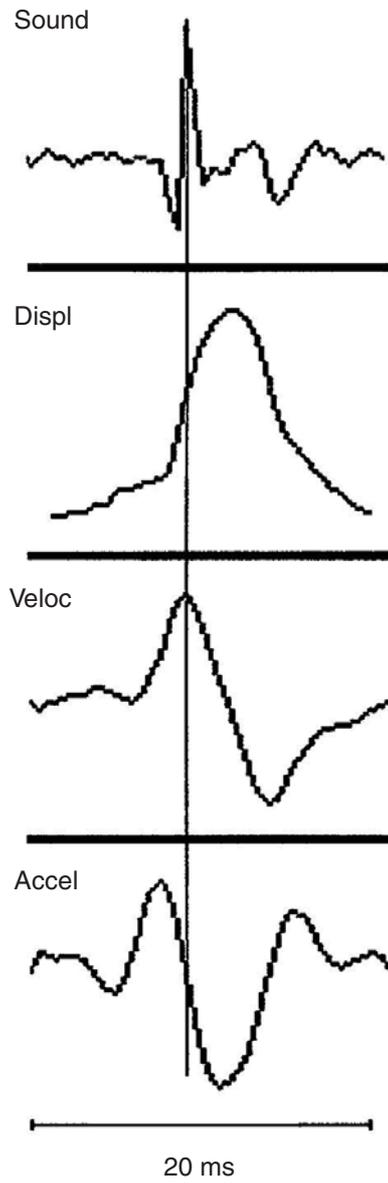


Fig. 1.10: Peak sound energy occurs in the middle of displacement (muscle contraction) when swimbladder velocity is maximal and acceleration is zero. Velocity and acceleration were obtained by differentiating the displacement waveform (from Fine et al., 2001).

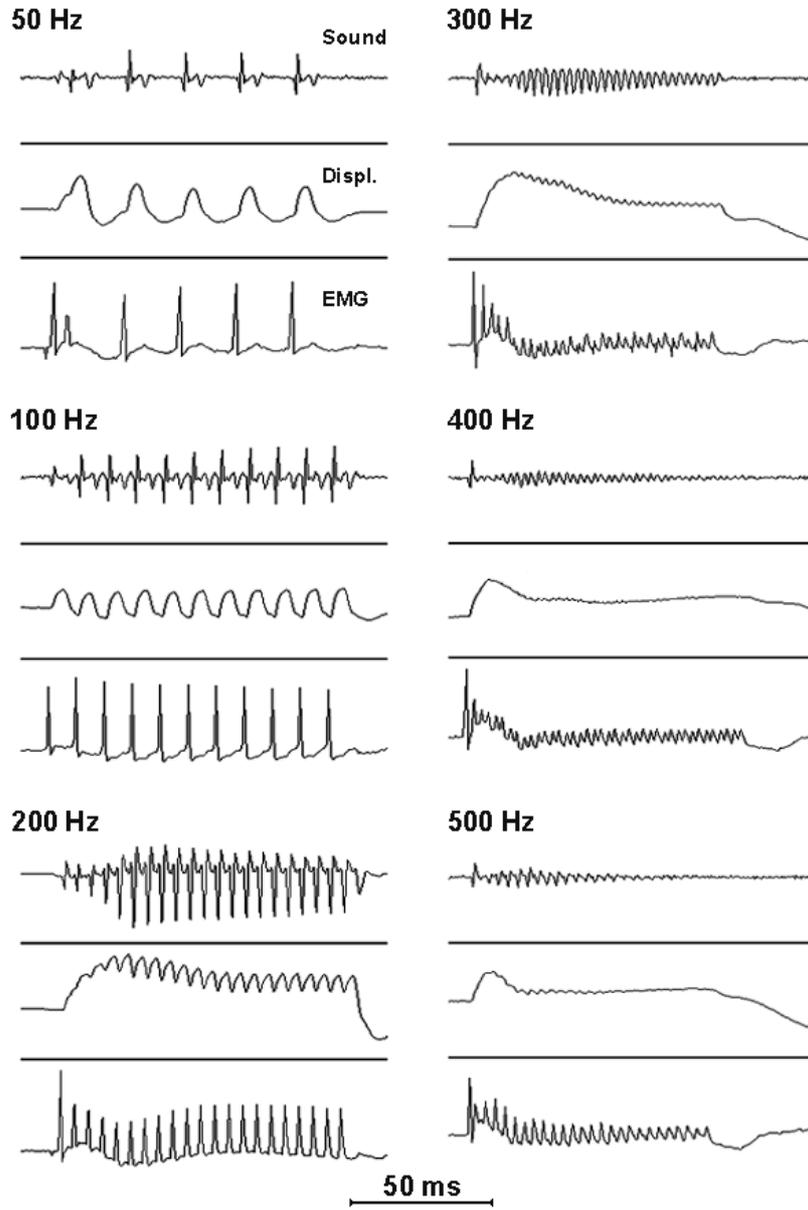


Fig. 1.11: Sound waveform, swimbladder displacement, and muscle action potentials evoked by 100 ms trains of stimuli (50–500 Hz) applied to the sonic nerve in the toadfish. The muscle is sufficiently fast that stimuli at 50 Hz and 100 Hz are equivalent to a series of individual twitches.

produced maximal sound amplitude at 150–175 Hz, frequencies that overlap the fundamental frequency of the boat whistle. Since the ratio of sound amplitude to movement amplitude increased at frequencies above the fundamental frequency of the boat whistle, Fine and coauthors (2001) concluded that sound amplitude is determined by muscle mechanics, i.e. a forced response, and not the natural frequency of the bladder. They suggested that the extreme speed of fish sonic muscles is an adaptation to generate sound from an inefficient, highly damped system. This argument is supported by data collected from sonic systems driven at a range of contraction rates (Tavolga, 1962; Fine et al., 2001; Connaughton, 2004).

In toadfish continuous contraction of the sonic muscle generates the fundamental frequency of sound (Skoglund, 1961; Fine et al., 2001), but many fish, such as the weakfish (*Cynoscion regalis*) produce sound pulses with single muscle twitches (Connaughton et al., 1997). This mechanism maximizes the opportunity to exhibit resonance. However, weakfish sounds, which change with fish size, temperature, and a yearly sonic muscle hypertrophy-atrophy cycle (Connaughton et al., 1997, 2000, 2002), likewise support the notion of sound generation by a forced contraction. The obvious interpretation, a decrease in dominant frequency with fish size because of the lower natural frequency of a larger bladder, was discounted for several reasons. The correlation of size and frequency ($r^2 = 0.38$), although significant, does not indicate a high degree of predictability, probably because of individual variation. However, the relationship of dominant frequency to pulse duration in these same fishes is much stronger ($r^2 = 0.94$), and the period of the dominant energy cycle predicts the dominant frequency almost perfectly. This finding supports an alternate hypothesis, namely that larger fish with larger muscles take longer to complete a single twitch (contraction and relaxation) and therefore generate a lower frequency sound. Further support is provided by an increase in dominant frequency with temperature, which does not affect the resonant frequency of an underwater bubble. Higher temperatures however, would support faster twitches, explaining the increase in frequency. Therefore, the mechanism of sound frequency generation in the weakfish is equivalent to that in toadfish, namely the timing of contraction and relaxation movements of the sonic muscle force bladder vibrations of that frequency, and that rapid damping of the swimbladder wall inhibits expression of the natural frequency of the bubble contained within the bladder.

Because some of the previous physiology was done with the swimbladder exposed to air, Fine and colleagues (2004) examined individual croakers *Micropogonius undulatus* (a sciaenid relative of the weakfish) both in air and underwater in a large shallow boat harbor. Pulse repetition rate and dominant frequency did not change in individual fish under the two conditions although Qs were higher and damping lower in air than in water (sound pulses exhibited an extra cycle).

2.2.5 Energetics

Advertisement calling is a costly activity in some insects and frogs (Prestwich, 1994), but may not be as expensive in some birds (Horn et al., 1995). Researchers have assumed that the rapid contraction of fish sonic muscle would be extremely expensive (Zelick et al., 1999). However, Amorim et al. (2002) found electrically stimulated calls at the most rapid rate induced by playbacks to calling male toadfish (e.g. 15 min⁻¹) did not result in increased oxygen consumption in a respirometer. This surprising result is explained by the small amount of sonic muscle mass (about 1% fish weight) (Johnson et al., 2000) and its intermittent use in sound production. Presuming 15 calls min⁻¹ (Fish, 1972) and 300 ms call⁻¹, a typical duration for York River, VA, toadfish (Fine, 1978), sonic muscles would be active for only 4.5 s per minute. Further, individuals spend most of their time in silence or producing 1–2 calls min⁻¹ (Fine et al., 1977a; Thorson and Fine, 2002). Smaller caloric expense than expected is supported by measurements of modest ATP utilization for rapid twitches (Rome and Klimov, 2000) and the small volume (about 4%) of mitochondria in sonic fibers (Appelt et al., 1991).

The toadfish is relatively unusual in producing a long duration call involving multiple muscle contractions (Winn, 1964). More commonly, fishes produce short duration pulsatile calls as in the weakfish, which produces trains of 2–15 pulses, each caused by a single muscle contraction, at a rate of 20 Hz (Connaughton et al., 2000). Therefore, a full second of these pulses would require 20 muscle contractions, as opposed to 60 contractions for a single toadfish boat whistle with a fundamental frequency (i.e. muscle contraction rate) of 200 Hz (300 ms × 200 Hz). Considering many frogs and insects can maintain the most rapid rate a toadfish can produce for about a minute (Fish, 1972; Thorson and Fine, 2002) for multiple hours in an evening chorus (Pough et al., 1992; Prestwich, 1994), there appear to be major energetic differences between producing sound by blowing air over a membrane—as in frogs, birds, and humans—and contracting sonic muscles on a swimbladder. Although the fish condition is paradoxically inexpensive, extreme adaptations for speed allow for few mitochondria and therefore diminished fatigue resistance (Rome and Linstedt, 1998).

An exception to the above analysis is provided by *Porichthys notatus*, a toadfish in another subfamily that produces relatively low frequency hums (90–100 Hz sonic muscle contractions) that can last for minutes or even tens of minutes (Ibara et al., 1983; Bass et al., 1999). All fast muscles are not equivalent. *Porichthys* fibers, similar to rattlesnake shaker fibers, are surrounded by banks of mitochondria (Bass and Marchaterre, 1989) and contract at considerably lower speeds than in the oyster toadfish (*Opsanus tau*). It also appears to increase its acoustic power by pumping gas into the swimbladder during bouts of continuous calling (Bass, pers. comm.; Ibara, pers. comm.), which would increase its stiffness and effectiveness at sound radiation.

2.3 Pectoral Sound Generating Mechanisms

Teleost fishes have evolved a number of pectoral adaptations for sound production. These modifications can affect the pectoral girdle, pectoral fin rays, and fin tendons.

2.3.1 *Sculpins*

The mostly marine scorpaenid family Cottidae (sculpins) lack a swimbladder but vibrate the pectoral girdle by rapidly contracting a muscle extending between the skull and the cleithrum (Barber and Mowbray, 1956; Ladich, 1989; Bass and Baker, 1991) (Fig. 1.5D). Barber and Mowbray (1956) described this mechanism in the longhorn sculpin *Myoxocephalus octodecimspinosus*. The cranioclavicular muscles originate on the ventral surface of the skull and insert on the anterior edge of the cleithrum near its articulation with the supraclavicle. Contraction produces an adduction of the pectoral girdle relative to the skull. The resultant periodic movements of the pectoral girdle are believed to produce the actual sound although this system deserves further study. In the European river bullhead *Cottus gobio* individual contractions generate a single knock sound. Fish in a state of heightened arousal rapidly contract the girdle resulting in growling sounds of approximately 250 ms duration (Ladich, 1989).

2.3.2 *Croaking gouramis*

Croaking gouramis, representatives of labyrinth fishes (family Osphronemidae, suborder Anabantoidae), generate pulsed sounds by two enhanced pad-like tendons of the fourth and fifth pectoral fin ray (Fig. 1.12) (Kratochvil, 1978). Two sound pulses (= double pulse) are emitted during abduction when the enhanced superficial adductor muscle stretches both tendons of one fin and snaps them over bony elevations of the base of the second and third fin ray. Alternate beating of both fins would result in the emission of a series of double pulses comprising a croaking sound (Fig. 1.12). This mechanism is similar to the plucking of guitar strings and has evolved exclusively in the genus *Trichopsis*, comprising three species (Kratochvil, 1985). Cutting of the two hypertrophied tendons mutes the fish, and regeneration of these tendons restores the sound (Ladich et al., 1992b).

2.3.3 *Catfishes*

A more profound modification of the pectoral fins has evolved in numerous catfish species; in addition to producing sounds the pectoral spine can be locked and serve as a defensive weapon (Fine and Ladich, 2003). Representatives of the majority of catfish families possess an enhanced first pectoral fin ray, the spine, which is moved by large adductor and abductor muscles (Schachner and Schaller, 1981). The base of the spine has a dorsal process that bears a

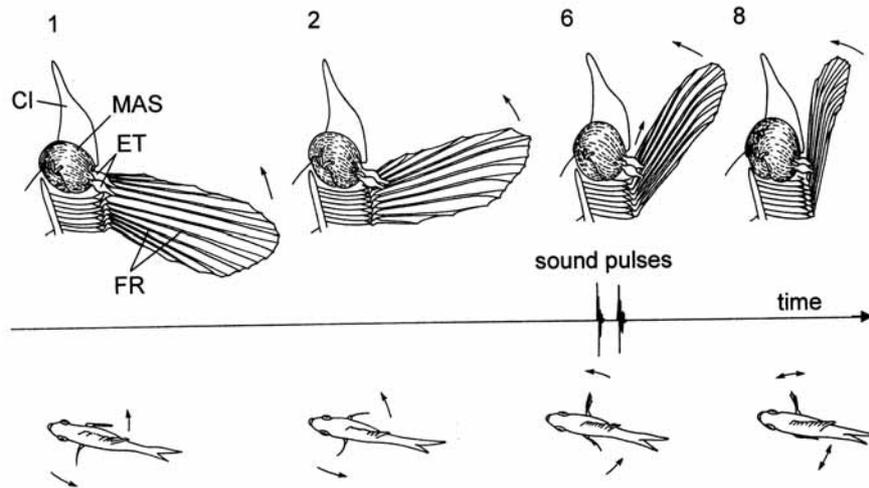


Fig. 1.12: Pectoral tendon plucking mechanism and sound generation in the croaking gourami *Trichopsis vittata* (family Osphronemidae). Lower picture row represents four frames from a film (180 frames/s) showing movement of the pectoral fins, while upper row shows contraction of the superficial adductor muscle (MAS), stretching of both enhanced tendons (ET) and abduction of the fin rays (FR) in more detail. Oscillogram between picture rows illustrates the moment of sound emission during forward movement of the right fin. Due to muting of left side both sound pulses could only be generated by the right fin. Frames were numbered accordingly. Cl—cleithrum. Redrawn from Kratochvil (1985).

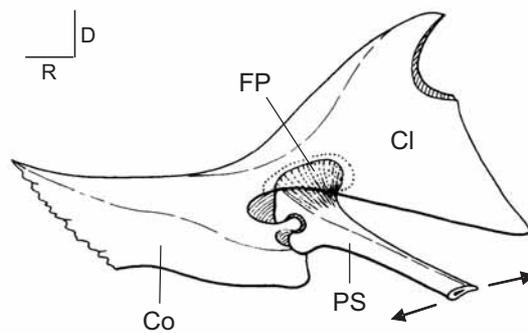


Fig. 1.13: Pectoral stridulatory mechanism in catfishes. Lateral view of left pectoral girdle in the catfish *Rhamdia quelen* (family Pimelodidae) showing enhanced first fine ray (PS—pectoral spine) and dorsal friction process (FP) with a series of ridges. Cl—cleithrum, Co—Coracoid. Redrawn from Schachner and Schaller (1981).

series of ridges on the lateroventral surface (Figs. 1.13, 1.14). The dorsal process slides within a groove in the cleithrum without contact during normal movement. Pressing the ridges against the groove, which has an unspecialized but rough surface in channel catfish (Fine et al., 1997) during a fin sweep results in the production of a series of short pulses (Pfeiffer and Eisenberg, 1965; Ladich 1997a; Heyd and Pfeiffer, 2000). Fine and coworkers (1997) believed each sound pulse is generated by a collision of a single ridge against the rough surface (Fig. 1.14B, C). This suggestion has not been verified experimentally. Partial support comes from the observation that the ridges grow further apart in larger fish, which produce sounds with longer intervals between pulses during a pectoral fin sweep (Fine et al., 1999). Additionally, the fused pectoral girdle is the sound radiator, i.e. striking the girdle with a piezoelectric hammer generated a frequency spectrum similar to that of pulses from the same fish when alive (Fine et al., 1997).

Different species utilize different combinations of muscle movements to produce sound. Ladich (1997a) and Heyd and Pfeiffer (2000) found that spines are moved in both directions (adduction and abduction) to generate sounds in bagrids, mochokids, doradids, and aspredinids, in contrast to ariids, pimelodids, callichthyids, and loricariids, which only stridulate when pectoral spines are spread (abducted). Although channel catfish utilize both fins in sound production, some individuals are right or left handed (Fine et al., 1996). Interfamilial comparisons revealed that sound duration correlated

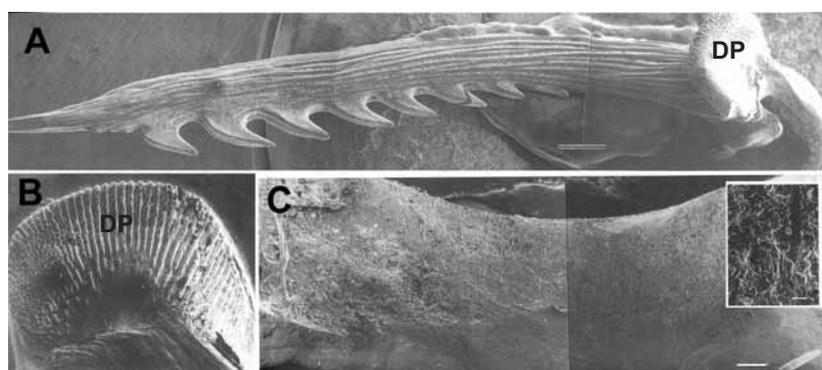


Fig. 1.14: Scanning electron micrographs of modified pectoral spine of the channel catfish *Ictalurus punctatus* used for sound production and locking. A: Dorsal view of pectoral spine; medial toward the right and anterior toward the top. Dorsal process (DP) at spine base (pointing up in the Figure) is used for sound production. B: Ventrolateral surface of dorsal process (hidden in A) containing a series of ridges. C: Rubbing surface on a channel in the cleithrum. Inset a close-up view illustrating its rough surface. Pressing the ridges of the dorsal process against this surface during a fin abduction results in a series of pulses. Scale bar = 1 mm in A, 0.5 mm in B, 0.68 mm in C and 50 μ m for the inset in C. Modified from Fine et al. (1997).

positively with the size of pectoral spines (Ladich, 1997), and the number of pulses correlated with the number of ridges. Kaatz (1999) found that aspredinids with few large ridges produce the smallest number of sound pulses, and callichthyids with a large number of small ridges produce the greatest number.

Dominant frequency of stridulatory sounds decreased with fish size in *Platydoras* and *Ictalurus*, but such a correlation was not demonstrated in several other species (Ladich, 1997; Fine et al., 1999; Fine and Ladich, 2003). Deflation of the swimbladder does not change frequency spectrum or amplitude.

Pectoral spine-associated motoneurons are located in the ventral motor column similar to scorpaeniforms (Ladich and Bass, 1998) (see Fig. 1.3).

2.4 Other Sonic Mechanisms

Sounds most likely used for communicative purposes are generated in numerous other ways. Several of these mechanisms have been described, sometimes without clear details or experimental evidence, and a behavioral context is not always evident.

In the catfish *Sisor rhabdophorus* (family Sisoridae) a dorsal fin stridulating mechanism is based on rubbing of a radial or pterygophore on an interspinous bone having file-like ridges (Mahajan, 1963). In the triggerfish *Balistes* erection of the dorsal spine results in sound production (Schneider, 1961). Fish (1953) mentioned sound production in the northern seahorse *Hippocampus hudsonius* (family Syngnathidae) by friction of neck vertebrae against the posterior margin of the skull.

Several investigations proposed a sound-producing mechanism based on pharyngeal teeth, which occur in the majority of fishes, in particular in perciforms. No special adaptation for sound generation has been described nor has anyone carefully examined tooth movement during sound generation. Burkenroad (1931) suggested pharyngeal teeth stridulation for carangids and haemulids, Fish and Mowbray (1970) for labrids, pomacentrids, scarids, Lanzing (1970) for cichlids, and Ballantyne and Colgan (1978) for centrarchids. Burkenroad (1931) mentioned incisor teeth stridulation in tetraodontids and diodontids. Analysis of sound characteristics revealed broadband pulsed sounds in cichlids and sunfishes, but less so in carangids and haemulids. Sound characteristics support to some degree the assumed pharyngeal explanation for sound production. Rice and Lobel (2002) found a sexually dimorphic muscle and enzymatic activity in the pharyngeal jaw, providing indirect support for a pharyngeal mechanism.

Several other mechanisms have been proposed, but they require additional experimental support. Loaches produce loud clicking or knocking sounds during agonistic interactions, which appear to be produced by an opercular mechanism (Valinsky and Rigley, 1981) since sound production ceased when opercles are fixed with a steel wire. No further anatomical details were given.

Another apparatus based on air-gulping and involvement of gills was suggested for the characid *Mimagoniates* (= *Glandulo cauda*) *inequalis* (Nelson, 1964). Lastly a recent study states that low-frequency sounds are produced by water expulsion through the gill cover in a goby (Stadler, 2002). Bubbles emitted from the anus in herring, which produce a stereotyped series of high-frequency pulses, might have some communicative value in addition to hydrostatic, but that needs to be demonstrated (Wahlberg and Westerberg, 2003; Wilson et al., 2003). The mechanism used by cod to produce high-frequency clicks (7 kHz) is not known (Vester et al., 2004).

2.5 Sexual Dimorphism

Sound-generating mechanisms are often sexually dimorphic and may be present exclusively in males, as in many sciaenids (Chao, 1978), or more commonly better developed in males. Although sound production is commonly associated with male courtship, females with smaller sonic muscles vocalize in the majority of fishes, particularly during agonistic interactions (Ladich, 1997b; see Chapter 5).

In toadfishes numerous studies have found differences in size of swimbladders, intrinsic swimbladder muscles, in fine structure of muscle fibers, in the morphology and physiology of sonic motoneurons, and sonic motor axons (Fine et al., 1984; Bass and Marchaterre, 1989; Bass and Baker, 1990; Fine et al., 1990; Bass and Andersen, 1991). This dimorphism arises developmentally: sonic structures in juveniles are similar in males and females and subsequent to puberty start to grow at different rates (Brantley et al., 1993; Fine, 1997). Unlike mammals, toadfish add neurons and muscle fibers postembryonically for years (Brantley et al., 1993; Fine, 1997; Loesser et al., 1997). Sonic muscles exhibit a seasonal cycle in the Lusitanian toadfish *Halobatrachus didactylus*, with maximal weight during the spawning season when androgens are elevated (Modesto and Canario, 2003), but sonic muscles do not change seasonally in the oyster toadfish (Johnson et al., 2000). Differences also exist between two alternatively reproducing male morphs in the midshipman *Porichthys notatus* (Bass and McKibben, 2003). Territorial type I males are larger, advertise their territory acoustically and possess larger sonic muscles (both in absolute and relative terms, that is after being corrected for body weight differences) than parasitic sneaker males, which steal fertilizations and avoid costs for brood care (Bass and Marchaterre, 1989; Bass and Baker, 1990). Type I males have larger sonic motor neurons, differences in sonic muscle ultrastructure and are more vocal than type II males and females (Bass and Marchaterre, 1989a,b; Brantley and Bass, 1994). Similar differences in sonic motoneuron size have been found in the oyster toadfish and the Lusitanian toadfish (Fine et al., 1984; Modesto and Canario, 2003) but have not been related to spawning behavior or sound production.

Differences between sexes in intrinsic swimbladder muscles are also known in the cod family. In the haddock *Melanogrammus aeglefinus*, Templeman and Hodder (1958) described a 6–9 times larger drumming muscle volume in males than in females. The drumming muscle mass in males varies seasonally. The muscles are nearly twice as large during the prespawning and spawning period May and June as they are in October and November.

Sexual dimorphism is also found in several families possessing extrinsic swimbladder mechanisms. It is not clear to what degree sexually dimorphic organs are characteristic of whole families. Schneider and Hasler (1960) observed a large variety among the sciaenid or drum family: muscles are either only present in males (*Cynoscion*) or in both sexes such as in *Micropogonius*. The sonic musculature in the weakfish *Cynoscion regalis* is fully developed during their seasonal period of sexual maturity and subsequently degenerates (Ono and Poss, 1982; Connaughton et al., 1997). This seasonal hypertrophy is hormonally controlled by androgens, and Connaughton and Taylor (1995) observed a two-and-a-half-fold increase in sonic muscle mass over a period of three weeks after testosterone implantation. Differences in number and size of sonic muscles between sexes are found in cusk-eels, which according to Courtenay (1971) is characteristic of the ophidiine subfamily.

Sexual dimorphism is also found in fishes with pectoral mechanisms. In callichthyid catfishes pectoral fins are longer in males than those of females standardized to body length and differences in sound characteristics were observed (Pruzsinszky and Ladich, 1998). In croaking gouramis (genus *Trichopsis*) sexual dimorphism is not genus but species-specific. A small difference exists between sexes in *T. vittata*, but the sound-generating mechanism is rudimentary in the female pygmy gourami *T. pumila* (Kratochvil, 1980).

3. SOUND CHARACTERISTICS

Because of the long wavelength of underwater sound, propagation of low-frequency sounds is severely restricted in shallow water where the majority of vocalizing fishes live (Bass and Clark, 2003; Ladich and Bass, 2003; see Chapter 4). Additionally background noise is highest at low frequencies. Rogers and Cox (1988) therefore predicted that fish should evolve the ability to produce and hear higher frequency sound if they communicate over longer distances. However, this is generally not the case. The majority of communicative sounds are produced by sonic swimbladder muscles, and are low in frequency (most energy below 1000 Hz), pulsed, and repetitious. These characteristics contrast with the majority of terrestrial vertebrate and insect signals, which contain higher frequencies (> 1 kHz), are tonal, and often distinctly frequency modulated. This pulsatile low frequency character of fish sounds appears to be caused by morphological constraints determined by sonic muscle

physiology and swimbladder acoustics. Sound frequencies cannot be too low because of inefficiencies in the swimbladder as an acoustic source (it will not produce sounds when moved at a low speed) or too high because of limitations in contraction rate of the sonic muscle (Fine et al., 2001; Lugli et al., 2003).

Acoustic signals generated by swimbladder drumming mechanisms typically possess 3–5 harmonics at multiples of the fundamental frequency and the spacing between harmonics equals the drumming muscle contraction rate (see physiology). The fundamental frequency of drumming sounds varies from 50 to greater than 250 Hz with most sound energy in the first harmonic, and sometimes in the second or third (Ladich, 1997a, 1999). In the midshipman *Porichthys notatus* (family Batrachoididae) the fundamental frequency of courtship hums is 80–100 Hz depending on temperature (Brantley and Bass, 1994; McKibben and Bass, 1998). In the closely related oyster toadfish it varies from less than 150 Hz to over 250 Hz, depending on temperature and undescribed seasonal factors (Fine, 1978). Differences in fundamental frequency and thus pulse repetition rate are also found in closely related catfish families. In the pimelodid catfish frequency is higher (165–177 Hz) than in doradid catfish (96–114 Hz) (Ladich, 1997). Drumming sounds in both families also exhibit a small degree of frequency modulation, a feature relatively unusual in fishes compared to birds and mammals (Fine et al., 1977). Spawning calls of the male haddock *Melanogrammus aeglefinus* (family Gadidae) and the male mormyrid *Pollimyrus isidori* exhibit distinct frequency modulations (Hawkins and Rasmussen, 1978; Crawford et al., 1986). Changes in fundamental frequency (muscle contraction rate) have been ascribed to lower levels of excitement and muscle fatigue (Hawkins, 1993; Brantley and Bass, 1994). Muscle fatigue however, is more likely to be represented as a decrease in amplitude rather than in frequency.

Fishes are not able to modify or modulate their sound output by changes in air flow mediated by vocal membranes and vocal tract resonating structures as in birds and mammals (Fitch and Hauser, 2003). Sound generation by sonic muscle contraction rate depends on pattern generators in the central nervous system (Bass and Baker, 1990), and therefore sound frequency of swimbladder sounds is unlikely to be related to fish size although a larger fish should be able to produce higher amplitude sounds (Fine, 1978; Waybright et al., 1990). The rather simple sound-generating process of the swimbladder mechanism reduces variation of sounds to differences in intensities, rate, and number of muscle contractions. Nevertheless, the majority of species produce several sound types. Territorial male midshipman *P. notatus* produces hums, growls and grunts, whereas males of the electric fish *Pollimyrus adspersus* produce three different sound types even within one courtship vocalization—moans, hoots, and growls—and two additional sound types during aggression (Crawford et al., 1986; Bass and Ladich, 2003; Bass and McKibben, 2003). Although frequency can be a factor, most of these differences are caused by temporal changes in muscle contraction patterns (Winn, 1964).

Pectoral sound characteristics differ depending on how sounds are generated. Pectoral girdle vibration results in the emission of low-frequency knocking or growling sounds in the European river bullhead *Cottus gobio*, with main energies found below 500 Hz (Ladich, 1989). More typically, sounds produced by pectoral fins consist of a series of short broadband pulses, with main energies concentrated at frequencies above 1 kHz. Croaking gouramis produce series of double pulses with dominant frequencies inversely correlated to species- and body size (Ladich et al., 1992a). Mean frequencies were found at 1.3 kHz in the largest species *T. vittata*, and 2.5 kHz in *T. pumila*, the smallest one. Species also differ in their pulse periods and number of pulses. Intraspecific differences were furthermore found between aggressive and courtship sounds and during growth. Henglmüller and Ladich (1999) and Wysocki and Ladich (2001) demonstrated that the dominant frequency, pulse periods, and pulse numbers change during ontogenetic development in *T. vittata* (for sonograms of various sound types see Chapter 5).

In catfishes sounds produced by rubbing of pectoral spines in grooves of the shoulder girdle result in high-frequency stridulations. Stridulation in doradids, pimelodids and mochokids are pulsatile, with durations ranging from 25 to 100 ms and main energy concentrated between 2 and 3.6 kHz (Ladich, 1997). A negative correlation between body size and dominant frequency was found in only one of the six species, the doradid *Platydoras costatus*. Larger channel catfish, ictalurids, do produce somewhat lower frequency sound although the picture is complicated because sound energy occurs in several frequency bands, and the individual bands decrease in frequency in larger fish (Fine et al., 1999).

Several groups of mostly freshwater fishes (otophysines, mormyrids, and gouramis) have evolved accessory hearing structures and possess the ability to detect sound frequency up to several kilohertz. These hearing specializations might have been selected by environmental constraints such as low ambient noise levels at these higher frequencies (Schellart and Popper 1992; Ladich and Popper, 2004). However, we do not know whether and to what degree sound-generating mechanisms and thus particular sound types evolved because of hearing abilities or environmental constraints (Ladich, 2000).

4. EVOLUTIONARY CONSIDERATIONS

The evolutionary constraints and phylogeny resulting in the enormous diversity of sonic organs in fishes are not known. Such a diversity is atypical for vertebrates: amphibians and mammals generate sounds primarily with one sonic organ, the larynx, and birds by the syrinx. Bass and Baker (1997) suggested that the vocal muscles associated with sound production in vertebrates have a common embryonic origin because they originate from

occipital somites. A purely cladistic analysis however, would indicate that sonic abilities occur sporadically among fish families, suggesting independent evolution. This discrepancy could be settled if all fishes possessed a hypoglossal nerve embryonically, and the nerve was lost in most adult fish species that lack the ability to produce sound. If this scenario were true then all nonsonic fish species would be preadapted to develop swimbladder muscles and produce sound. Bass and Baker's generalization may hold for fishes with sonic swimbladder muscles innervated by occipital nerves which are likely homologous to the hypoglossal nerve of tetrapods, but it excludes the pectoral and true spinal mechanisms in fishes.

A more detailed analysis of the vocal pathways of sonic mechanisms in fishes revealed multiple innervation patterns, which are not necessarily restricted to particular families. In *Batrachoidiformes* and *Siluriformes* the sonic motor nuclei occupy a medial position, being located either on the midline ventral to the central canal (*Batrachoididae*, *Mochokidae*), slightly lateral of the midline (*Ariidae*), or in both positions (*Pimelodidae*). Midline vagal motor neurons dorsal to the central canal were described for a mormyrid (Bass, 1985; Bass and Baker, 1991; Ladich and Bass, 1998).

Sound-generating organs in holocentrids, scorpaeniforms (cottids, triglids, scorpaenids), croaking gouramis (osphronemids), and catfishes (pectoral spines) are innervated by motoneurons located in the ventral motor column of the hindbrain and rostral spinal cord whose axons exit via ventral occipital nerve roots (Bass and Baker, 1991; Ladich and Fine, 1992, 1994; Ladich and Bass, 1996, 1998; Carlson and Bass, 2000). Catfish and croaking gourami pectoral organs are innervated by neurons in the pectoral motor column. However, there are two possible interpretations for ventrolateral neurons innervating swimbladder muscles, one being a pectoral affinity. The second possibility is that the neurons have a hypoglossal affinity as in catfish and toadfish, but the neurons have migrated from the ancestral midline position. The hypoglossal hypothesis is more parsimonious, but the issue must be resolved by embryonic observations and experimental techniques to indicate neuron birthdays and origins (i.e. Galeo et al., 1987).

Another major pattern occurs in piranhas (*Characidae*) and the nonrelated drums (*Sciaenidae*), whose sonic muscles are innervated by pure spinal nerves (Markl, 1971; Ono and Poss, 1982; Vance et al., 2002; Ladich and Bass, 2005).

These various innervation patterns imply that similar end organs, such as intrinsic swimbladder muscles in triglids and toadfishes may or may not be homologous since there are differences in their sonic motor nuclei, and muscles appear to undergo different developmental processes (Rauther, 1945; Tracy, 1961). Therefore a systematic separation of vocalizing fish taxa, which involve independent evolution and possible sporadic occurrences of homologous organs, may not be possible.

Acknowledgments

We thank Heidemarie Grillitsch for the drawings in Figures 1.1, 1.2, 1.12 and 1.13 and Livia Rudoll for her help with Figure 1.2. FL's research was supported by the Austrian Science Fund (FWF no. 15873) and MLF by NIH and the Virginia Marine Resources Commission.

REFERENCES

- Abu-Gideiri, J.B. and D.H. Nasr. 1973. Sound production by *Synodontis schall* (Bloch-Schneider). *Hydrobiologia* 43: 415–428.
- Amorim, M.C.P. 1996. Acoustic communication in triglids and other fishes. Ph.D. Thesis. University of Aberdeen, UK.
- Amorim, M.C.P., M.L. McCracken and M.L. Fine. 2002. Metabolic costs of sound production in the oyster toadfish, *Opsanus tau*. *Can. J. Zool.* 80: 830–838.
- Appelt, D., V. Shen and C. Franzini-Armstrong. 1991. Quantitation of Ca ATPase, feet and mitochondria in super fast muscle fibers from the toadfish, *Opsanus tau*. *J. Muscle Res. Cell Motil.* 12: 543–552.
- Ballantyne, P.K. and P.W. Colgan. 1978. Sound production during agonistic and reproductive behaviour in the pumpkinseed (*Lepomis gibbosus*), the bluegill (*Lepomis macrochirus*) and their hybrid sunfish. I. Context. *Biol. Behav.* 3: 113–135.
- Barber, S. B. and W.H. Mowbray. 1956. Mechanism of sound production in the sculpin. *Science* 124: 219–220.
- Barimo, J.F. and M.L. Fine. 1998. Relationship of swimbladder shape to the directionality pattern of underwater sound in the oyster toadfish. *Can. J. Zool.* 76: 134–143.
- Bass, A.H. 1985. Sonic motor pathways in teleost fishes: A comparative HRP study. *Brain Behav. Evol.* 27: 115–131.
- Bass A.H. and K. Andersen 1991. Inter- and Intra-sexual dimorphisms in the sound generating motor system in a vocalizing fish: Motor axon number and size. *Brain Behav. Evol.* 37: 204–214.
- Bass, A.H. and R. Baker. 1990. Sexual dimorphisms in the vocal control system of a teleost fish: morphology of physiologically identified neurons. *J. Neurobiol.* 21: 1155–1168.
- Bass, A.H. and R. Baker. 1991. Evolution of homologous vocal control traits. *Brain Behav. Evol.* 38: 240–254.
- Bass, A.H. and R. Baker. 1997. Phenotypic specification of hindbrain rhombomeres and the origin of rhythmic circuits in vertebrates. *Brain Behav. Evol.* 50 (Suppl. 1): 3–16.
- Bass, A.H. and C.W. Clark. 2003. The physical acoustics of underwater sound communication. In: *Acoustic Communication*. A. Megela Simmons, A.N. Popper and R.R. Fay (eds.). Springer-Verlag, New York, pp. 15–64.
- Bass, A.H. and M.A. Marchaterre. 1989a. Sound-generating (sonic) motor system in a teleost fish (*Porichthys notatus*): sexual polymorphism and general synaptology of a sonic motor nucleus. *J. Comp. Neurol.* 286: 154–169.
- Bass, A.H. and M.A. Marchaterre. 1989b. Sound-generating (sonic) motor system in a teleost fish (*Porichthys notatus*): sexual polymorphism in the ultrastructure of myofibrils. *J. Comp. Neurol.* 286: 241–253.
- Bass, A.H. and J.R. McKibben. 2003. Neural mechanisms and behaviors for acoustic communication in teleost fish. *Prog. Neurobiol.* 69: 1–26.
- Bass, A.H., D. Bodnar and M.A. Marchaterre. 1999. Complementary explanations for existing phenotypes in an acoustic communication system. In: *The Design of Animal Communication*. M.D. Hauser and M. Konishi (eds.). MIT Press, Cambridge, MA, pp. 493–514.

- Bradbury, J.W. and S.L. Vehrencamp. 1998. *Principles of Animal Communication*. Sinauer, Sunderland, MA.
- Brantley, R.K. and A.H. Bass. 1994. Alternative male spawning tactics and acoustic signalling in the plainfin midshipman fish, *Porichthys notatus*. *Ethology* 96: 213–232.
- Brantley, R.K., J. Tseng and A.H. Bass. 1993. The ontogeny of inter- and intrasexual vocal muscle dimorphisms in a sound-producing fish. *Brain Behav. Evol.* 42: 336–349.
- Brawn, V.M. 1961. Sound production by the cod (*Gadus callarias* L.). *Behaviour* 18: 177–198.
- Bridge, T.W. and A.C. Haddon. 1889. Contribution to the anatomy of fishes. I. The airbladder and Weberian ossicles in the Siluridae. *Proc. Roy. Soc. Lond.* 46: 209–227.
- Bridge, T.W. and A.C. Haddon. 1892. Contribution to the anatomy of fishes. I. The airbladder and Weberian ossicles in the Siluridae. *Proc. Roy. Soc. Lond.* 52: 139–157.
- Burkenroad, H.D. 1931. Notes on the sound-producing marine fishes of Louisiana. *Copeia* 1931: 20–28.
- Carlson, B.A. and A.H. Bass. 2000. Sonic/vocal motor pathways in squirrelfish (Teleostei, Holocentridae). *Brain Behav. Evol.* 56: 14–28.
- Chao, L. N. 1978. A basis for classifying Western Atlantic Sciaenidae (Teleostei: Perciformes). NOAA Technical Report, Circular 415. Washington DC: US Dept. Comm., Natl. Oceanic Atmospheric Administration, National Marine Fisheries Services, pp. 65.
- Cohen, M.J. and H.E. Winn. 1967. Electrophysiological observation on hearing and sound production in the fish *Porichthys notatus*. *J. Exp. Zool.* 165: 355–370.
- Connaughton, M.A. 2004. Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. *J. Exp. Biol.* 207: 1643–1654.
- Connaughton, M.A. and M.H. Taylor. 1995. Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. *Env. Biol. Fish.* 42: 233–240.
- Connaughton, M.A., M.L. Fine and M.H. Taylor. 1997. The effects of seasonal hypertrophy and atrophy on fiber morphology, metabolic substrate concentration and sound characteristics of the weakfish sonic muscle. *J. Exp. Biol.* 200: 2449–2457.
- Connaughton, M.A., M.H. Taylor and M.L. Fine. 2000. Effects of fish size and temperature on weakfish disturbance calls: implications for the mechanism of sound generation. *J. Exp. Biol.* 203: 1503–1512.
- Connaughton, M.A., M.L. Fine and M.H. Taylor. 2002. Use of sound for localisation of spawning weakfish in Delaware Bay (USA) and effects of fish size, temperature and season on sound parameters. *Bioacoustics* 12: 294–296.
- Courtenay, W.R. 1971. Sexual dimorphism of the sound producing mechanism of the striped cusk-eel, *Rissola marginata* (Pisces: Ophidiidae). *Copeia* 1971: 259–268.
- Courtenay, W.R. and F.A. McKittrick. 1970. Sound producing mechanisms in carapid fishes, with rates on phylogenetic implications. *Mar. Biol.* 7: 131–137.
- Crawford, J.D. and X. Huang. 1999. Communication signals and sound production mechanisms of mormyrid electric fish. *J. Exp. Biol.* 202: 1417–1426.
- Crawford, J.D., M. Hagedorn and C.D. Hopkins. 1986. Acoustic communication in an electric fish, *Pollimyrus isidori* (Mormyridae). *J. Comp. Physiol. A* 159: 297–310.
- Demski, L.S., J.W. Gerald and A.N. Popper. 1973. Central and peripheral mechanisms of teleost sound production. *Amer. Zool.* 13: 1141–1167.
- Dijkgraaf, S. 1941. Haben die Lautäußerungen der Elritze eine biologische Bedeutung? *Zool. Anz.* 136: 103–106.
- Dos Santos, M.E., T. Modesto, R.J. Matos, M.S. Grober, R.F. Oliviera and A. Canario. 2000. Sound production by the Lusitanian toadfish, *Halobatrachus didactylus*. *Bioacoustics* 10: 309–321.
- Dufossé, M. 1874. Recherches sur les bruits et les sons expressifs que font entendre les poissons d'Europe et sur les organes producteurs de ces phenomenes acoustiques ainsi que sur les appareils de l'audition de plusieurs de ces animaux. *Ann. Sci. Nat.* 19: 1–53.
- Eichelberg, H. 1976. The fine structure of the drum muscles of the tigerfish, *Therapon jarbua*, as compared with the trunk musculature. *Cell Tiss. Res.* 174: 453–463.

- Evans, R.R. 1973. The swimbladder and associated structures in Western Atlantic searobins (Triglidae). *Copeia* 1973: 315–321.
- Fawcett, D.W. and J. P. Revel. 1961. The sarcoplasmic reticulum of a fast-acting muscle. *Biophys. Biochem. Cytol.* 10: 89–109.
- Fay, R.R. and A.N. Popper. 1975. Modes of stimulation of the teleost ear. *J. Exp. Biol.* 62: 379–387.
- Fay, R.R. and A.N. Popper. 1999. *Comparative Hearing: Fish and Amphibians*. Springer-Verlag, New York.
- Fay, R.R. and A. Megela Simmons. 1999. The sense of hearing in fishes and amphibians. In: *Comparative Hearing: Fish and Amphibians*, R.R. Fay and A.N. Popper (eds.). Springer-Verlag, New York, pp. 269–318.
- Feher, J.J., T.D. Waybright and M.L. Fine. 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.
- Feuillade, C. and R.W. Nero. 1998. A viscous-elastic swimbladder model for describing enhanced-frequency resonance scattering from fish. *J. Acoust. Soc. Amer.* 103: 3245–3255.
- 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. 1997. Endocrinology of sound production in fishes. *Mar. Fresh. Behav. Physiol.* 29: 23–45.
- Fine, M.L. and F. Ladich. 2003. Sound production, spine locking and related adaptations. In: *Catfishes*, G. Arratia, B.G. Kapoor, M. Chardon and R. Diogo (eds.). Science Publishers, Inc., Enfield (NH) USA, vol. 1, pp. 249–290.
- Fine, M.L., H.E. Winn, L. Joest and P.J. Perkins. 1977a. Temporal aspects of calling behavior in the oyster toadfish, *Opsanus tau*. *Fish. Bull.* 75: 871–874.
- Fine, M.L., H.E. Winn and B.L. Olla. 1977b. Communication in fishes. In: *How Animals Communicate*. T.A. Sebeok (ed.). Indiana Univ. Press, Bloomington. pp. 472–518.
- Fine, M.L., D. Economos, R. Radtke and J.R. McClung. 1984. Ontogeny and sexual dimorphism of the sonic motor nucleus in the oyster toadfish. *J. Comp. Neurol.* 225: 105–110.
- Fine, M.L., N.M. Burns and T.M. Harris. 1990. Ontogeny and sexual dimorphism of the sonic muscle in the oyster toadfish. *Can. J. Zool.* 68: 1374–1381.
- Fine, M.L., B. Bernard and T.M. Harris. 1993. Functional morphology of toadfish sonic muscle fibers: relationship to possible fiber division. *Can. J. Zool.* 71: 2262–2274.
- Fine, M.L., D. McElroy, J. Rafi, C.B. King, K.E. Loesser and S. Newton. 1996. Lateralization of pectoral sound production in the channel catfish. *Behav. Physiol.* 60: 753–757.
- Fine, M.L., J.P. Friel, D. McElroy, C.B. King, K.E. Loesser and S. Newton. 1997. Pectoral spine locking and sound production in the channel catfish (*Ictalurus punctatus*). *Copeia* 1997: 777–790.
- Fine, M.L., C.B. King, J.P. Friel, K.E. Loesser and S. Newton. 1999. Sound production and locking of the pectoral spine of the channel catfish. *Amer. Fish. Soc. Symp.* 24: 105–114.
- Fine, M.L., K.L. Malloy, C.B. King, S.L. Mitchell and T.M. Cameron. 2001. Movement and sound generation by the toadfish swimbladder. *J. Comp. Physiol. A* 187: 371–379.
- Fine, M.L., J. Schrinel and T.M. Cameron. 2004. The effect of loading on disturbance sounds of the Atlantic croaker *Micropogonius undulatus*: Air vs. water. *J. Acoust. Soc. Amer.* 116: 1271–1275.
- Fish, J.F. 1972. The effect of sound playback on the toadfish. In: *Behavior of Marine Animals*, H.E. Winn and B. Olla (eds.). Plenum Press, New York, vol. 2, pp. 386–434.
- Fish, M.P. 1953. The production of underwater sounds by the northern seahorse, *Hippocampus hudsonius*. *Copeia* 1953: 98–99.
- Fish, M.P. and W.H. Mowbray. 1970. *Sounds of Western North Atlantic Fishes*. John Hopkins Press, Baltimore.
- Fitch, W.T. and M.D. Hauser. 2003. Unpacking “Honesty”: Vertebrate vocal production and the evolution of acoustic signals. In: *Acoustic Communication*, A.M. Simmons, A.A. Popper and R.R. Fay (eds.). Springer-Verlag, New York, pp. 65–137.

- Fletcher, L.B. and J.D. Crawford. 2001. Acoustic detection by sound-producing fishes (Mormyridae): the role of gas-filled tympanic bladders. *J. Exp. Biol.* 204: 175–183.
- Foote, K.G. 1997. Target strength of fish. In: *Encyclopedia of Acoustics*, M.J. Crocker (ed). John Wiley & Sons, New York, pp. 493–500.
- Francis, D.T. and K.G. Foote. 2003. Depth-dependent target strengths of gadoids by the boundary-element method. *J. Acoust. Soc. Amer.* 114: 3136–3146.
- Gainer, H. 1969. Multiple innervation of fish skeletal muscle. In: *Experiments in Physiology and Biochemistry*, G.A. Kerkut (ed.). Academic Press, New York, vol. 2, pp. 191–208.
- Gainer, H. and J.E. Klancher. 1965. Neuromuscular junctions in a fast-contracting fish muscle. *Comp. Biochem. Physiol.* 15: 159–165.
- Galeo, A.J., M.L. Fine and J.A. Stevenson. 1987. Embryonic and larval development of the sonic motor nucleus in the oyster toadfish. *J. Neurobiol.* 18: 359–373.
- Gohlke, P. (ed.). 1957. *Aristoteles. Tierkunde*. 2nd ed. Ferdinand Schöningh, Paderborn, Germany.
- Hallacher, L.E. 1974. The comparative morphology of extrinsic gasbladder musculature in the scorpionfish genus *Sebastes* (Pisces: Scorpaenidae). *Proc. Cal. Acad. Sci.* 40: 59–86.
- Harris, G.G. 1964. Considerations on the physics of sound production by fishes. In: *Marine Bioacoustics*, W. N. Tavolga (ed.). Pergamon Press, New York, pp. 233–247.
- Hawkins, A.D. 1993. Underwater sound and fish behaviour. In: *Behaviour of Teleost Fishes*, T. J. Pitcher (ed.). Chapman & Hall, London, pp. 129–169.
- Hawkins, A.D. and K.J. Rasmussen. 1978. The calls of gadoid fish. *J. Mar. Biol. Assoc. UK*, 58: 891–911.
- Hawkins, A.D. and A.A. Myrberg. 1983. Hearing and sound communication underwater. In: *Bioacoustics, a Comparative Approach*. Academic Press, London, pp. 347–405.
- Heyd, A. and W. Pfeiffer. 2000. Über die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihren Zusammenhang mit der Phylogenie und der Schreckreaktion. *Rev. Suisse Zool.* 107: 165–211.
- Hill, G.L., M.L. Fine and J.A. Musick. 1987. Ontogeny of the sexually dimorphic sonic muscle in three sciaenid species. *Copeia* 1987: 708–713.
- Hirsch, J.E., J.W. Bigbee and M.L. Fine. 1998. Continuous adult development of multiple innervation in toadfish sonic muscle. *J. Neurobiol.* 36: 348–356.
- Horn, A.G., M.L. Leonard and D.M. Weary. 2002. Oxygen consumption during crowing by roosters: talk is cheap. *Anim. Behav.* 50: 1171–1175.
- Ibara, R.M., L.T. Penny, A.W. Ebeling, G. Van Dykhuizen and G. Cailliet. 1983. The mating call of the plainfin midshipman fish, *Porichthys notatus*. In: *Predators and Prey in Fishes*, D.L. Noakes, D.G. Linquist, G.S. Helfman and J.A. Ward (eds.). Dr. W. Junk Publishers, The Hague, pp. 205–212.
- Johnson, M.S., T.D. Waybright, D.W. Matt, J.J. Feher and M.L. Fine. 2000. Absence of a seasonal cycle in the sonic neuromuscular system of the oyster toadfish. *J. Fish Biol.* 56: 211–215.
- Kaatz, I.M. 1999. The behavioral and morphological diversity of ACOUSTIC communication systems in a clade of tropical catfishes (Pisces: Siluriformes). Ph.D. thesis. University of Syracuse, NY.
- Kastberger, G. 1977. Der Trommelapparat der Doradiden (Siluriformes, Pisces). *Zool. Jahrb. Physiol.* 81: 281–309.
- Kratochvil, H. 1978. Der Bau des Lautapparates vom Knurrenden Gurami (*Trichopsis vittatus* Cuvier et Valenciennes) (Anabantidae, Belontiidae). *Zoomorphologie* 91: 91–99.
- Kratochvil, H. 1980. Geschlechtsdimorphismus beim Lautapparat des Knurrenden Zwerggurami *Trichopsis pumilus* Arnold (Anabantidae, Teleostei). *Zoomorphologie* 94: 204–208.
- Kratochvil, H. 1985. Beiträge zur Lautbiologie der Anabantoidei—Bau, Funktion und Entwicklung von lauterzeugenden Systeme. *Zool. Jahrb. Physiol.* 89: 203–255.
- Ladich, F. 1989. Sound production by the river bullhead *Cottus gobio* L. (Cottidae, Teleostei). *J. Fish Biol.* 35: 531–538.
- Ladich, F. 1997a. Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. *Bioacoustics* 8: 185–208.

- Ladich, F. 1997b. Agonistic behaviour and significance of sounds in vocalizing fish. *Mar. Fresh. Behav. Physiol.* 29: 87–108.
- Ladich, F. 1999. Did auditory sensitivity and vocalization evolve independently in otophysan fishes? *Brain Behav. Evol.* 53: 288–304.
- Ladich, F. 2000. Acoustic communication and the evolution of hearing in fishes. *Phil. Trans. Roy Soc. Lond. B* 355: 1285–1288.
- 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. 2004. Sound production and acoustic communication. In: *The Senses of Fish. Adaptations for the Reception of Natural Stimuli*, G. von der Emde, J. Mogdans and B.G. Kapoor (eds.). Narosa, New Delhi/Kluwer, Dordrecht/Springer-Verlag, Heidelberg, pp. 210–230.
- Ladich, F. and A.H. Bass. 1996. Sonic/vocal-acousticolateralis pathways in teleost fishes: a transneuronal biocytin study in mochokid catfish. *J. Comp. Neurol.* 374: 493–505.
- Ladich, F. and A.H. Bass. 1998. Sonic/vocal motor pathways in catfishes: Comparison with other teleosts. *Brain Behav. Evol.* 51: 315–330.
- Ladich, F. and A.H. Bass. 2003. Underwater sound generation and acoustic reception in fishes with some notes on frogs. In: *Sensory Processing in Aquatic Environments*, S.P. Collin and N.J. Marshall (eds.). Springer-Verlag, New York, pp. 173–193.
- Ladich, F. and A.H. Bass. 2005. Sonic/vocal motor pathways in piranhas (family Characidae) with a comparison to other teleosts. *Brain Behav. Evol.* 66: 167–176.
- Ladich, F. and M.L. Fine. 1992. Localization of pectoral fin motoneurons (sonic and hovering) in the croaking gourami *Trichopsis vittatus*. *Brain Behav. Evol.* 39: 1–7.
- Ladich, F. and M.L. Fine. 1994. Localization of swimbladder and pectoral motoneurons involved in sound production in pimelodid catfish. *Brain Behav. Evol.* 44: 86–100.
- Ladich, F. and A.N. Popper. 2004. Parallel evolution in fish hearing organs. In: *Evolution of the Vertebrate Auditory System*, G. Manley, A.N. Popper and R.R. Fay (eds.). Springer-Verlag, New York, pp. 85–127.
- Ladich, F. and E.L. Wysocki. 2003. How does tripus extirpation affect auditory sensitivity in goldfish? *Hear. Res.* 182: 119–129.
- Ladich, F., C. Bischof, G. Schleinzler and A. Fuchs. 1992a. Intra- and interspecific differences in agonistic vocalization in croaking gouramis (Genus: *Trichopsis*, Anabantoidei, Teleostei). *Bioacoustics* 4: 131–141.
- Ladich, F., W. Brittinger and H. Kratochvil. 1992b. Significance of agonistic vocalization in the croaking gourami (*Trichopsis vittatus*, Teleostei). *Ethology* 90: 307–314.
- Lanzing, W.S.R. 1974. Sound production in the cichlid *Tilapia mossambica* Peters. *J. Fish. Biol.* 6: 341–347.
- Lewis, M.K., P.C. Nahimey, V. Chen, B.B. Adikari, J. Wright, A.H. Bass and K. Wang. 2003. Concentric intermediate filament lattice links to specialized Z band-junctional complexes in sonic muscle fiber of the type I male midshipman fish. *J. Struct. Biol.* 143: 56–71.
- Lindholm, M.M. and A.H. Bass. 1993. Early events in myofibrillogenesis and innervation of skeletal sound-generating muscle in a teleost fish. *J. Morph.* 216: 225–239.
- Loesser, K.E., J. Rafi and M.L. Fine. 1997. Embryonic, juvenile, and adult development of the toadfish sonic muscle. *Anat. Rec.* 249: 469–477.
- Luczkovich, J. and M.W. Sprague. 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., H.Y. Yan and M.L. Fine. 2003. Acoustic communication in two freshwater gobies: the relationship between ambient noise, hearing and sound spectrum. *J. Comp. Physiol. A* 189: 309–320.
- Lundberg, J.G. 1993. African-South American freshwater fish clades and continental drift: problem with a paradigm. In: *Biological Relationship between Africa and South America*, P. Goldblatt (ed.). Yale University Press, New Haven, pp. 156–199.

- Mahajan, C.L. 1963. Sound producing apparatus in an Indian catfish *Sisor rhabdophorus* Hamilton. *J. Linn. Soc. (Zool.)* 43: 721–724.
- Markl, H. 1971. Schallerzeugung bei Piranhas (Serrasalminae, Characidae). *Z. vergl. Physiol.* 74: 39–56.
- Marshall, N.B. 1967. Sound-producing mechanisms and the biology of deep-sea fishes. In: *Marine Bio-Acoustics*, W.N. Tavolga (ed.). Pergamon Press, Oxford, pp. 123–133.
- Modesto, T. and A. Canario. 2003. Morphometric changes and sex steroid levels during the annual reproductive cycle of the Lusitanian toadfish, *Halobatrachus didactylus*. *Gen. Comp. Endocrinol.* 131: 220–231.
- Moulton, J.M. 1960. Swimming sounds and the schooling of fishes. *Biol. Bull.* 119: 210–223.
- Müller, J. 1842. Beobachtungen über die Schwimmblase der Fische, mit Bezug auf einige neue Fischgattungen. *Arch. Anat. Physiol.* 307–329.
- Müller, J. 1857. Über die Fische, welche Töne von sich geben und die Entstehung dieser Töne. *Arch. Anat. Physiol. Wiss. Med.* 249–279.
- Myrberg, A.A., S.J. Ha and H.S. Shablott. 1993. The sounds of bicolor damselfish (*Pomacentrus partitus*): predictors of body size and a spectral basis for individual recognition and assessment. *J. Acoust. Soc. Amer.* 94: 3067–3070.
- Nelson, J.S. 1994. *Fishes of the World*. John Wiley & Sons, New York, (3rd Edn.).
- Nelson, K. 1964. The evolution of sound production associated with courtship in the characid fish, *Glandulocauda inequalis*. *Evolution* 18: 526–540.
- Ono, R.D. and S.G. Poss. 1982. Structure and innervation of the swimbladder musculature in the weakfish, *Cynoscion regalis* (Teleostei: Sciaenidae). *Can. J. Zool.* 60: 1955–1967.
- Packard, A. 1960. Electrophysiological observations on a sound-producing fish. *Nature* (London) 187: 63–64.
- Pappas, G.D. and M.V.L. Bennett. 1966. Specialized junctions involved in electrical transmission between neurons. *Ann. NY Acad. Sci.* 137: 203–236.
- Parmentier, E., P. Vandewalle and J.P. Lagardere. 2003a. Sound-producing mechanisms and recordings in Carapini species (Teleostei, Pisces). *J. Comp. Physiol. A* 189: 283–292.
- Parmentier, E., V. Gennotte, B. Focant, G. Goffinet, and P. Vandewalle. 2003b. Characterization of the primary sonic muscles in *Carapus acus* (Carapidae): a multidisciplinary approach. *Proc. Roy. Soc. Lond. B* 270: 2301–2308.
- Pfeiffer, W. and J.F. Eisenberg. 1965. Die Lauterzeugung der Dornwelse (Doradidae). *Z. Morph. Ökol. Tiere.* 54: 669–679.
- Pough, F.H., W.E. Magnusson, M.J. Ryan, W.D. Wells and T.L. Taigen. 1992. Behavioral energetics. In: *Environmental Physiology of Amphibians*, M.E. Feder and W.N. Burggren (eds.). University of Chicago Press, Chicago, pp. 395–436.
- Prestwich, K.N. 1994. The energetics of acoustic signalling in anurans and insects. *Amer. Zool.* 34: 625–643.
- Rauther, M. 1945. Über die Schwimmblase und die zu ihr in Beziehung tretenden somatischen Muskeln bei den Trigliden und anderen Scleroparei. *Zool. Jahrb. Anat.* 69: 159–250.
- Rice, A.N. and P.S. Lobel. 2002. Enzyme activities of pharyngeal jaw musculature in the cichlid *Tramitichromis intermedius*: implications for sound production in cichlid fishes. *J. Exp. Biol.* 205: 3519–3523.
- Rogers, P.H. and M. Cox. 1988. Underwater sounds as a biological stimulus. In: *Sensory Biology of Aquatic Animals*, J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga (eds.). Springer-Verlag, New York, pp. 131–149.
- Rome, L.C. and S.L. Linstedt. 1998. The quest for speed: muscles built for high-frequency contractions. *News Physiol. Sci.* 13: 261–268.
- Rome, L.C. and A.A. Klimov. 2000. Superfast contractions without superfast energetics: ATP usage by SR-CA²⁺ pumps and crossbridges in toadfish swimbladder muscle. *J. Physiol.* 526: 279–298.

- Rome, L.C., D.A. Syme, S. Hollingworth, S.L. Lindstedt and S.M. Baylor. 1996. The whistle and the rattle: The design of sound producing muscles. *Proc. Natl. Acad. Sci. USA*. 93: 8095–8100.
- Rome, L.C., C. Cook, D.A. Syme, M.A. Connaughton, M. Ashley-Ross, A. Klimov, B. Tikunov and Y.E. Goldman. 1999. Trading force for speed: Why superfast crossbridge kinetics leads to superlow forces. *Proc. Natl. Acad. Sci. USA*. 96: 5826–5831.
- Salmon, M., H.E. Winn and N. Sorgente. 1968. Sound production and acoustical behavior in triggerfish. *Pac. Sci.* 12: 11–20.
- Sand, O. and A. D. Hawkins. 1973. Acoustic properties of the cod swimbladder. *J. Exp. Biol.* 58: 797–820.
- Schachner, G. and F. Schaller. 1981. Schallerzeugung und Schallreaktionen beim Antennenwels (Mandim) *Rhamdia sebae sebae* Val. *Zool. Beitr.* 27: 375–392.
- Schaller, F. 1971. Über den Lautapparat von Amazonas-Fischen. *Naturwissenschaften* 58: 573–574.
- Schaller, F. and H. Kratochvil. 1981. Lautbildung bei Fischen. *Biologie in unserer Zeit* 11: 43–47.
- Schellart, N.A.M. and A.N. Popper. 1992. Functional aspects of the evolution of the auditory system of actinopterygian fish. In: *Evolutionary Biology of Hearing*, D.E. Webster, R.R. Fay and A.N. Popper (eds.). The Springer-Verlag, New York, pp. 295–322.
- Schneider, H. 1961. Neuere Ergebnisse der Lautforschung bei Fischen. *Die Naturwissenschaften* 15: 513–518.
- Schneider, H. 1964. Physiologische und morphologische Untersuchungen zur Bioakustik der Tigerfische (Pisces, Theraponidae). *Z. vergl. Physiol.* 47: 493–558.
- Schneider, H. 1967. Morphology and physiology of sound-producing mechanisms in teleost fishes. In: *Marine Bio-Acoustics*. W.N. Tavolga (ed.). Pergamon Press, New York, vol. 2, pp. 135–158.
- Schneider, H. and A.D. Hasler. 1960. Laute und Lauterzeugung beim Süßwassertrommler *Aplodinotus grunniens* Rafinesque (Sciaenidae, Pisces). *Z. vergl. Physiol.* 43: 499–517.
- Skoglund, C.R. 1961. Functional analysis of swimbladder muscles engaged in sound production of the toadfish. *J. Biophys. Biochem. Cytol.* 10: 187–200.
- Somlyo, A.V., H. Shurman and A.P. Somlyo. 1977. Composition of sarcoplasmic reticulum in situ by electron probe X-ray microanalysis. *Nature* (London) 268: 556–558.
- Sørensen, W. 1895. Are the extrinsic muscles of the air-bladder in some Siluroidea 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.
- Stadler, J.M. 2002. Evidence for a hydrodynamic mechanism of sound production by courting males of the notchtongue goby, *Bathygobius curacao* (Metzlaar). *Bioacoustics* 13: 145–152.
- Suzuki, S., H. Nagayoshi, K. Ishino, N. Hino and H. Sugi. 2003. Ultrastructural organization of the transverse tubules and the sarcoplasmic reticulum in a fish sound-producing muscle. *J. Electron Microsc.* 52: 337–347.
- Tavolga, W.N. 1962. Mechanisms of sound production in the ariid catfishes *Galeichthys* and *Bagre*. *Bull. Amer. Mus. Nat. Hist.* 24: 1–30.
- Tavolga, W.N. 1964. Sonic characteristics and mechanisms in marine fishes. In: *Marine Bio-Acoustics*, W.N. Tavolga (ed.). Pergamon Press, New York, pp. 195–211.
- Tavolga, W.N. 1971. Sound production and detection. In: *Fish Physiology. Sensory Systems and Electric Organs*, W.S. Hoar and D.J. Randall (eds.). Academic Press, London, vol. 5, pp. 135–205.
- Tavolga, W.N. 1977. Mechanisms for directional hearing in the sea catfish (*Arius felis*). *J. Exp. Biol.* 67: 97–115.
- Templeman, W. and V.M. Hodder. 1958. Variation with fish length, sex, stage of sexual maturity, and season in the appearance and volume of the drumming muscle of the swimbladder in the haddock, *Melanogrammus aeglefinus* (L.). *J. Fish. Res. Bd. Can.* 15: 355–390.

- Thorson, R.F. and M.L. Fine. 2002. Crepuscular changes in emission rate and parameters of the boat whistle advertisement call of the gulf toadfish, *Opsanus beta*. *Env. Biol. Fish.* 63: 321–331.
- Tower, R.W. 1908. The production of sound in the drumfishes, the sea-robin and the toadfish. *Ann. NY Acad. Sci.* 18: 149–180.
- Tracy, H.C. 1959. Stages in the development of the anatomy of motility of the toadfish (*Opsanus tau*). *J. Comp. Neurol.* 111: 27–81.
- Tracy, H.C. 1961. Development of the spinal crest, nerves and muscles in the toadfish (*Opsanus tau*). *J. Comp. Neurol.* 111: 27–82.
- Valinsky, W. and L. Rigley. 1981. Function of sound production by the skunk loach *Botia horae* (Pisces, Cobitidae). *Z. Tierpsychol.* 55: 161–172.
- Van Bergeijk, W.A. 1964. Directional and nondirectional hearing in fish. In: *Marine Bio-Acoustics*, W.N. Tavolga (ed.). Pergamon Press, New York, pp. 281–299.
- Vance, T.L., J.M. Hewson, S. Modla and M.A. Connaughton. 2002. Variability in sonic muscle size and innervation among three sciaenids: spot, Atlantic croaker, and weakfish. *Copeia* 2002: 1137–1143.
- Vester, H.J., L.P. Folkow and A.S. Blix. 2004. Click sounds produced by cod (*Gadus morhua*). *J. Acoust. Soc. Amer.* 115: 914–919.
- Wahlberg, M.H. and H. Westerberg. 2003. Sounds produced by herring (*Clupea harengus*) bubble release. *Aquat. Living Res.* 16: 271–275.
- Waybright, T.D., U. Kollenkirchen and M.L. Fine. 1990. Effect of size and sex on grunt production in the oyster toadfish. *Soc. Neurosci. Abstr.* 16: 578.
- Weston, D.E. 1967. Sound propagation in the presence of bladder fish. In: *Underwater Acoustics*. V.M. Albers (ed.). Plenum Press, New York, vol. 2, pp. 55–88.
- Wilson, B., R.S. Batty and L.M. Dill. 2004. Pacific and Atlantic herring produce bursts pulse sounds. *Proc. Roy. Soc. Lond. B (Suppl.)* 271: 95–97.
- Winn, H.E. 1964. The biological significance of fish sounds. In: *Marine Bio-Acoustics*, W.N. Tavolga (ed.). Pergamon Press, New York, pp. 213–231.
- Winn, H.E. and J.A. Marshall. 1963. Sound-producing organ of the squirrelfish, *Holocentrus rufus*. *Physiol. Zool.* 36: 36–44.
- Yabe, M. 1985. Comparative osteology and myology of the subfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. *Mem. Fac. Fish. Hokkaido Univ.* 32: 1–130.
- Yan, H.Y. and W.S. Curtsinger. 2000. The otic gas bladder as an ancillary auditory structure in a mormyrid fish. *J. Comp. Physiol. A* 186: 595–602.
- Yan, H.Y., M.L. Fine, N.S. Horn and W.E. Colon. 2000. Variability in the role of the gasbladder in fish audition. *J. Comp. Physiol. A* 187: 371–379.
- Zelick, R., D.A. Mann and A.N. Popper. 1999. Acoustic communication in fishes and frogs. In: *Comparative Hearing: Fish and Amphibians*, R.R. Fay and A.N. Popper (eds.). Springer-Verlag, New York, pp. 363–411.