Multiple exaptations leading to fish sound production

Eric Parmentier | Rui Diogo | Michael L Fine

1 Laboratoire de Morphologie Fonctionnelle et Evolutive, Institut de Chimie—B6C, Université de Liège, Liège, Belgium
2 Department of Anatomy, College of Medicine, Howard University, Washington, DC, USA
3 Department of Biology, Virginia Commonwealth University, Richmond, VA, USA

Correspondence
Eric Parmentier, Laboratoire de Morphologie Fonctionnelle et Evolutive, Institut de Chimie—B6C, Université de Liège, Liège, Belgium. Email: E.Parmentier@ulg.ac.be

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Abstract
The term exaptation introduced by Stephen J. Gould and Elizabeth Vrba has been used infrequently. The high diversity of sound-producing mechanisms in fishes highlights a recurrent use of this process in unrelated taxa. We propose that sonic evolution typically involves exaptations: in many fish taxa, sound production was acquired by the independent modification of existing structures with other functions. These structures were modified into complex effectors for courtship and agonistic sound production without major changes to their gnathostome Bauplan. Existing anatomical structures (teeth, bones, etc.) were likely first used in non-voluntary sound production, which incidentally provided advantages and could then be selected specifically for signal production leading to the refinement of more sophisticated sonic organs. We postulate that in many if not most cases, sound-production specializations originated in fish taxa that took advantage of incidental non-voluntary sounds. We use different case-studies to show that exaptation may be a key, albeit largely unrecognized, agent of major morphological and behavioural changes.

Keywords
acoustic, adaptation, aptation, communication, evolution, teleost

1 INTRODUCTION

The ability to produce sounds for social communication has evolved inconsistently within multiple fish families. In some taxa (Bagridae, Batrachoididae, Carapidae, Doradidae Gadidae, Holocentridae, Pimelodidae, Pomacentridae, Sciaenidae and Triglidae for example), essentially all species have the ability to produce acoustic signals or are likely to call based on their anatomical structures (Fine & Parmentier, 2015; Parmentier & Fine, 2016). Conversely, large groups such as minnows (Cyprinidae) are mostly mute, but a couple of species produce socially relevant sounds (Holt & Johnston, 2014; Johnston & Johnson, 2000). Sound-producing mechanisms evolved independently and sporadically in various lineages (Fine & Parmentier, 2015). Due to the required constraints for sound production (mainly hard and osseous structures, or gas-containing structures such as the swim bladder), there are considerable sound-producing mechanisms that result from evolutionary convergences. The lack of homology however prevents a clear classification of sonic mechanisms, and categories are based mainly on appearances (Ladich & Fine, 2006).

The high diversity of mechanisms that has arisen independently in distantly related fishes indicates sound production plays an integral part of social communication and is important for reproductive success, fitness and speciation. However, although all fishes possess a hearing sense (Popper & Fay, 2011), the ability to produce sounds has not evolved in most species. Therefore, acoustic communication, even if advantageous, is not a vital function comparable to swimming, feeding, breathing or eating. Interestingly, as we will show below, many of the structures used in these vital functions can be modified for sound production. The hypothesis we develop here has been addressed in a book chapter that reviews sound production and sonic mechanisms in fishes (Parmentier & Fine, 2016). In this article, we further develop the concept of exaptation as a basis for evolution of sonic mechanisms in fishes believing it is a profitable model for other systems and taxa. We further elaborate our ideas and hope we can provoke debate on this frequently ignored concept that is central to the evolution of multiple functions in living systems.

Producing sound involves a vibration coupled to the medium (Bradbury & Vehrencamp, 1998). Five basic mechanisms have
been documented in teleost communication: (i) muscular vibrations of a membrane or sac (Fine, King, & Cameron, 2009; Millot, Vandewalle, & Parmentier, 2011), (ii) stridulation (Bertucci, Ruppé, Wassenbergh, Compère, & Parmentier, 2014; Fine, King, Friel, Loesser, & Newton, 1999; Parmentier et al., 2010), (iii) forced flow through a small orifice (Fish & Mowbray, 1970; Lagardère & Ernande, 2004; Wahlberg & Westerberg, 2003; Wilson, Batty, & Dill, 2003), (iv) muscular vibration of appendages (Colleye, Ovidio, Salmon, & Parmentier, 2013; Ladich, 1989; Parmentier et al., 2013) and (v) percussion on a substrate (Colleye et al., 2013). Moreover, although multiple submechanisms have been described, most fall into two categories: (i) muscles that directly or indirectly insert on the swim bladder and (ii) stridulatory mechanisms involving the rubbing of bones.

2 | BRIEF THOUGHTS ON THE EVOLUTION OF SOUND PRODUCTION IN FISHES

Because callers are present in distantly related taxa, and sound-producing mechanisms differ among fishes (Fine & Parmentier, 2015), we postulate the evolution of acoustic communication has been possible because fishes have taken advantage of particular anatomical features present in their ancestors. Essentially all teleost fishes have in common the following anatomical characteristics: bones, teeth, air sac (the gas or swim bladder), ligaments and more or less developed fins. These structures constitute the raw material for the development of sound production. All fishes have some ability to produce sounds. Swimming causes water movements that generate hydrodynamic sounds (Moulton, 1960), and eating requires movement of the buccal and pharyngeal jaws whose contacts create chewing sounds. The challenge is to demonstrate which sounds are incidental by-products and which are voluntarily used to communicate (mainly agonistic and courtship behaviour). The border between incidental sounds and ones used for social communication is thin. In another category, a classic example concerns women with high heels. Are the well-known sounds associated with these shoes used to send a message (communication) or are they just a by-product associated with locomotion? Some physostomes with a pneumatic duct between the swim bladder and the gut can produce sound by expressing air from the swim bladder (Lagardère & Ernande, 2004; Wahlberg & Westerberg, 2003), but it is unclear whether any of these sounds has evolved for communication or whether they are merely incidental.

Many of the swim bladder-based mechanisms result from evolutionary convergence or parallelism (Diogo, 2005) and utilize the same basic principle: muscles provoke the vibration of a gas-filled structure. Although diversity is high, the systems are analogous (some are homologous) and have been ascribed to two different mechanisms. The forced-response model (Fine, 2012; Fine, King, Ali, Sidker, & Cameron, 2016) poits that the contraction rate of superfast sonic muscles (called drumming muscles) force bladder wall vibration (Connaughton, 2004; Fine, Malloy, King, Mitchell, & Cameron, 2001; Millot et al., 2011) and determines sound fundamental frequency. On the other hand, the swim bladder rebound model applies to cases in which swim bladder sounds are driven by vibration of surrounding structures such as tendons, epineurals or ribs (Oliver & Lobel, 2013; Parmentier, Bouillac, Dragicevic, Dulcic, & Fine, 2010; Parmentier, Lagardère, Braquegnier, Vandewalle, & Fine, 2006). In this case, each muscle contraction causes a sound pulse, but frequencies are dictated by vibratory properties of the tendon or bone rather than the speed of the sonic muscle.

The second major category corresponds to the production of sounds by hard tissues. Stridulation mechanisms utilize friction of teeth or bones and produce irregular pulses containing a wider range of frequencies than from swim bladder sounds (Hawkins, 1993; Tavolga, 1971). The literature has focused mainly, but not exclusively (Kratochvil, 1985; Ladich, Bischof, Schleiner, & Fuchs, 1992), on two subtypes: rubbing of the pharyngeal teeth and friction of the pectoral fin against the shoulder girdle.

To be considered communication, a signal must propagate to an individual able to perceive and interpret it. It then elicits a response by the receiver that is advantageous (at least) for the sender (Bradbury & Vehrencamp, 1998; Myrberg, 1981). Individuals able to generate signals should be favoured through evolutionary time because communication signals play important roles in species identification, sexual advertisement, mate attraction, territory defence, conflict resolution, location identification, information on potential fitness, etc. In teleosts however, data are currently insufficient to support acoustic communication as a major feature related to the evolutionary success of a taxon. There is no empirical evidence showing that a certain sound-producing structure A of taxon B was/is the subject of natural selection. Therefore, following Gould (Gould, 2002), one should be aware of not using terms such as “selected” in a gratuituous way, without clear, sound, backing evidence.

To be clear, swim bladder and stridulation mechanisms have evolved convergently to improve calling abilities because they face similar environmental constraints. This scheme can explain why distantly related families with different ancestral phenotypes have developed analogous systems allowing the production of sounds with high similarities in their frequency and temporal domains (Fine & Parmentier, 2015; Parmentier & Fine, 2016).

3 | THE CONCEPT OF EXAPTATION

According to Stephen Jay Gould and Elizabeth Vrba (Gould & Vrba, 1982), exaptation refers to a functional character previously acquired for a particular function that is later co-opted for a new use that will likely enhance fitness. More precisely, it involves two mechanisms (Pievani & Serrelli, 2011): the functional shift, by natural selection, of a structure with previously different purposes or the functional co-optation which expands functional diversity (McLennan, 2008). In this case, an emerging trait can be a non-adaptive side effect, a developmental constraint, a structural effect or a random insertion (Pievani & Serrelli, 2011). This is possible because the relationship between form
and function is not strictly one-to-one, but potentially redundant and flexible.

Exaptation was introduced to make a distinction between the current utility of a trait and its historical origin (Larson, Stephens, Tehrani, & Layton, 2013). Few examples are found in the literature (Cullen, Maie, Schoenfuss, & Blob, 2013; Ostrom, 1979; Patek, Baio, Fisher, & Suarez, 2013), probably because of the prevalence of an adaptationist view of evolution within evolutionary biologists (Gould, 2002). The main argument depends on the fact that every structure is a modification of some previous form, suggesting that all modifications are adaptations. In the case of exaptation, the new function did not emerge by natural selection to support or regulate the new function. Using legs for walking, swimming or flying is for example adaptations that require (deep) modifications of locomotor function. Classic examples of exaptation include bird feathers, which probably evolved for temperature regulation and display and were then co-opted for flight, and the jaws in trap ants (Odontomachus bauri, Formicidae) typically used in rapid closing strikes for prey-capture, which propel them into the air (Patek et al., 2013).

According to Gould (Gould, 2002), adaptation refers to the origin of a feature directly for a certain function, and importantly, its advantage within the context of natural selection related to that specific function. He defined also the term “adaption” which is quite different because it is neutral about whether or not there is a selective advantage for the feature within the context of that specific function. As Gould pointed out, it is almost impossible to prove that the origin of the feature several millions of years ago really increased the evolutionary fitness of a population/taxon A specifically because it allowed its members to perform a certain function B. So, for Gould, both adaptations and adaptations were subsets of “adaptation,” with exaptation concerning the later co-optation of the feature for another function. Basically, the difference between adaptation and exaptation is therefore essentially dependent on the timing and function to which we refer. For instance, in the case of dinosaurs/birds, when feathers first appeared, they were probably an adaptation for protection against the cold, and they would be considered an adaptation only if we can show that they directly increased the evolutionary fitness of the group by performing this specific function. Then, later, feathers became an exaptation for flight (new function). Although Gould’s definition of exaptation was not so strict, for authors such as Lauder (Lauder, 1996), feathers would only be considered an exaptation if we can show that they directly increased the evolutionary fitness of dinosaurs/birds by specifically allowing them to fly. That is, Lauder proposed four specific criteria to identify an exaptation to a current function such as flight: (i) current utility (function: flight) of the feature (feathers on wings), (ii) selection for that feature in its current environment, (iii) previous utility of the feature in ancestors with a different performance advantage (function: protection against cold) than the current one, and (iv) natural selection for that trait in the ancestral environment (selective advantage of that ancestral function).

As noted by Gould, under such a definition it is almost impossible to prove that any feature was an exaptation. In addition having to prove its selective advantage related to the origin of a specific function in the past, one would have to prove its selective advantage when it gained a—and specifically because of that—new function. Therefore, in this study we follow the less strict definition of exaptation of Gould, which basically refers to the change of function of a structure. That is, an exaptation is the sequence of at least two adaptions, one for the original function and subsequent ones for new functions, without any need to prove that the first adaption was really an adaptation. Moreover, one could argue that all complex structures are made of elements that were previously unrelated to the novel function (Larson et al., 2013). Therefore, we underline that, within the context of this work, co-option refers to the co-existence of functions. In the process of evolution, biological constraints can act in a different way on different species. Therefore, a function can develop further to the detriment of the co-existing function. Our purpose is not to predict but to explain evolutionary patterns.

Accordingly, in the examples we provide, sounds are made by structures that were initially related to functions other than producing sounds. The primary functions of a mouth, pectoral fins or swim bladder are eating, swimming (or manoeuvring) and buoyancy respectively. However, these organs can be used for sound production in fishes. As these original functions are absolutely necessary, the exaptation process is often related to functional decoupling, more than to a direct change of function A to function B: a new function B is added while the original function A remains in place. In this sense, these examples are somewhat similar to those of feathers: in most birds, feathers allow flight (or to show visual signals) but still maintain their original thermo-regulation function.

To our knowledge, the term exaptation has been used once in the fish sound-production literature (Parmentier et al., 2007) for a jaw-snapping mechanism in the Clark’s anemonefish (Amphiprion clarkii, Pomacentridae). However, many sonic mechanisms described in the literature appear to result from different exaptations. We postulate that acoustic communication appeared in fish taxa that gained an advantage from their incidental sounds. This hypothesis agrees with observations of numerous unrelated mechanisms of sound production in fishes and with the fact that many species do not produce sounds. Importantly, the concept of exaptation is highly interesting in this case because the mechanical units that change or incorporate new functions have the potential for rapid evolutionary change and may not require slow, stepwise macroevolutionary morphological transitions (McLennan, 2008). Sounds indicate the physiological state of the emitter and/or its readiness to engage in a behaviour. If the acoustic message is not self-sufficient, it can at least reinforce a colour pattern or a display (Parmentier, Kéver, Casadevall, & Lecchini, 2010; Ruppé et al., 2015). Teeth snapping or tail movement during a behaviour should have a greater effect on responding organisms if associated with the display of an associated sound (Bertucci, Attia, Beauchaud, & Mattheyon, 2012; Estramil et al., 2014).

We propose that in most, if not all, soniferous fish species, sound was likely an initial by-product of mechanical functions involved in feeding, locomotion or buoyancy. To be part of an operational system, sounds produced early in the evolution of the trait likely modified the behaviour of recipient individuals (conspecific or not). In this scheme,
behavioural responses would improve the fitness of the emitter although advantages likely accrued to the recipient as well. Upon the emergence of acoustic communication, natural selection can maximize the function to increase the efficiency of message transfer. Although this study concentrates on the evolution of sonic mechanisms, we realize that communication also involves sensory systems for the specificbehaviours that have also coevolved for communication. The specificbehaviour for example can be important to determine the best times and seasons for communication or to select the habitat that causes the least signal degradation with distance (Endler, 1992, 1993). Natural selection would favour increasing signal processing and decreasing signal degradation.

Modifications in behaviour can act as a driver of evolutionary diversification by changing the way individuals interact with their environment, exposing individuals to divergent selection pressures on populations that promote adaptive divergence (Lapièdra, Sol, Carranza, & Beaulieu, 2013; Wcislo, 1989). Corresponding to a modification in the behaviour, the development of the ability to produce sound allows the fish to enter a new adaptive zone, an environmental space that is exploitable after the acquisition of morphological and/or physiological characters. For instance, wing development permitted birds to enter a new adaptive zone (the aerial way of life), and then minor morphological modifications allowed them to colonize various milieus (Mayr, 1989). In parallel, calling species adopt new ways to allow enhancement of their fitness by the development of a system that improves (or creates), for example, identification, attraction of sexual partners or territorial defence, thus providing evolutionary advantages enabling the taxa to diversify into different forms. Historically, the ability to switch into a new adaptive zone resulted from one or several modifications to an ancestral plan (Zeldicht & Fink, 1996) or from the emergence of novelties (Futuyma, 1986; Heard & Hauser, 1995). Then, the evolutionary success of a taxa with a new ecological opportunity would relate to key innovations (Dumont et al., 2012). Using an exaptation to gain a new adaptive zone can be a parsimonious process as the morphological features do not require extensive modifications or novelties. Behavioural changes related to the new adaptive zone would be followed by morphological and physiological evolution that may drive evolution in novel directions (Price, Qvarnström, & Irwin, 2003). We hypothesize that sound production could be involved in the radiation of some taxa such as cichlids or pomacentrids for instance, but further studies are required.

Striking sound-producing mechanisms arose in many taxa, notably in Ophidiform (Courtenay, 1971; Parmentier, Fontenelle, Fine, Vandewalle, & Henrist, 2006; Parmentier, Bouillac et al., 2010) and Batrachoidiform (Fine et al., 2001; Rice & Bass, 2009; Skoglund, 1961) fishes. Their peculiar morphology allows classification as a calling species, even without sound recordings (Fine et al., 2007; Nguyen, Lin, Parmentier, & Fine, 2008). Conversely, the identification of a sonic mechanism can be puzzling in many taxa without obvious sonic mechanical structures. Cichlids (Longrie, Van Wassenbergh, Vandewalle, Mauguit, & Parmentier, 2009; Rice & Lobel, 2003), gobids (Parmentier et al., 2013; Stadler, 2002), cottois (Colley et al., 2013) and cyprinids (Holt & Johnston, 2014; Johnston & Johnson, 2000; Ladich, 1988) include calling species. Yet their anatomy is similar to that of mute relatives. Therefore, sounds can be produced with only minor, or undetected morphological modifications of the teleost Bauplan. These examples can be related to exaptation as minor morphological or physiological modifications of (pre)existing structures provide new functions.

3.1 | Sound production from a swim bladder

The following sections will discuss several specific examples of taxa that have taken advantage of their incipient abilities to produce voluntary communication signals. The use of the swim bladder in sound production can be an exaptation because the primary role of this organ is buoyancy (Alexander, 1966); that is, its use for sound production is a secondary, derived feature. In the oyster toadfish (Opsanus tau, Batrachoididae), the swim bladder continues to provide buoyancy with no conflict between this traditional role and the added one of sound production (Fine, McKnight, & Blem, 1995). It is worth mentioning that service as an accessory auditory organ in otophysine fishes is another derived feature of this organ (Ladich, 2014; Popper & Fay, 2011). In many cases, the swim bladder needs fast contracting muscle to produce sounds as slow bladder movements are silent. Skeletal muscles with a number of convergent morphological and biochemical adaptations for speed are found in many unrelated taxa (Fine & Parmentier, 2015), but the development leading to this kind of muscle is not yet clearly explained. Sonic muscles appear to have evolved from occipital, epaxial, hypaxial or pectoral girdle muscles. Therefore, emerging sonic muscles were derived from a primary function related to locomotion. The family Triglidae, for example, has species with variations in the organization of sonic muscles and in their relation to the swim bladder. Ontogenetic data indicate that extrinsic and intrinsic muscles in triglids are homologous and are derived from hypaxial musculature (Ladich & Bass, 1998; Rauther, 1945). This is a further example of functional uncoupling, because fish retain the ability to move, but these muscles are no longer related to that original function but are now devoted to the new (sonic) function. Similarly in toadfish, the sonic muscle forms in the occipital regions and secondarily migrates and attaches to the sides of the swim bladder (Tracy, 1961).

In muscles, myofibril volume determines the force of contraction, the volume of sarcoplasmic reticulum allows rapid contraction and the volume of mitochondria sets the level of sustained performance (Rome & Lindstedt, 1998). In the red piranha (Pygocentrus nattereri, Serrasalmidae), muscle development has been studied in 3 mm specimens (1 day post-hatching) to adults of 260 mm. High-speed sonic muscles are skeletal muscles with delayed development compared to hypaxial muscles. This delay restricts the quantity of myofibrils and maintains a high proportion of sarcoplasmic reticulum (Milhot & Parmentier, 2014). Delayed development could account for high-speed sonic muscles that have evolved repeatedly in different lineages. This finding should be confirmed in other species. In spot croaker (Leiostomus xanthurus, Sciaenidae), Atlantic croaker (Micropogonias undulatus, Sciaenidae) and weakfish (Cynoscion regalis, Sciaenidae), sonic muscles develop at puberty on a central tendon overlying the
dorsal surface of the swim bladder (Hill, Fine, & Musick, 1987). These trunk muscles migrate around the sides of the swim bladder before forming the origin on a small strip of connective tissue on the ventral midline. Muscle development in the toadfish _O. tau_ however is different indicating convergence. Axons surrounded by presumptive sonic muscle migrate from the occipital spinal cord (Galeo, Fine, & Stevenson, 1987) and attach to the swim bladder (Tracy, 1961). In this functional uncoupling, muscles become involved in the new function (sound production) instead of the original function (locomotion). Motion continues to be accomplished by other muscles and therefore requires partial reorganization of the Bauplan.

Mochokid catfishes provide an interesting example of multiple exaptations. The elastic spring apparatus of catfishes such as Ariidae, Doradidae and Mochokidae (Hagedorn, Womble, & Finger, 1990; Ladich & Bass, 1998) is composed of a pair of protractor muscles, which inserts on the transverse processes (Müllerian ramus) of the fourth vertebra. Because the transverse processes are connected to the swim bladder wall, rapid contractions of the protractor muscles result in sound production (Ladich & Bass, 1998). However, Boyle, Colleye, and Parmentier (2014) recently demonstrated that the highly specialized fibres of the protractor muscle are also responsible for electric organ discharges in some squeakers (Synodontis spp., Mochokidae).

During agonistic encounters, some species produce sounds, others produce electric discharges and some do both although not simultaneously (Boyle et al., 2014). Therefore, this example highlights a case of multiple exaptations leading to complex systems through stepwise evolutionary transitions between the original function and the new, modified functions. In particular, in this catfish family (Mochokidae) the teleost Bauplan was first exapted for a new function, (sound production), and later co-opted for a new use (electric discharge) suggesting the fish benefitted from the development of a second pathway of communication (Boyle et al., 2014).

### 3.2 Pomacentridae: sound production from buccal jaws

Damselﬁsh (Pomacentridae) produce sounds in different behavioural contexts (Colleye & Parmentier, 2012; Mann & Lobel, 1998; Myrberg, Spanier, & Ha, 1978). Their sonic mechanism is unique to this family and causes mouth closing movements inducing teeth collisions (Parmentier et al., 2007). Jaw snapping causes sound onset, but the resulting vibrational wave appears to be transferred to the rib cage. Vibrating ribs then drive oscillations of the swim bladder wall (Colleye, Nakamura, Frederich, and Parmentier, 2012). Rapid mouth closure is forced by a synapomorphic ceratombardibular ligament (Stiassny, 1981) joining the lateral side of the hyoid bar to the medial side of the mandible. Experiments on anesthetized specimens show the jaw slam is caused by the stretched ligament and does not require adductor muscle contraction (Olivier, Frédéric, Spanopoulos-Zarco, Balart, & Parmentier, 2014). Further, cutting the ceratombardibular ligaments prevents both feeding and sound production.

Beside sound production, the function of the ceratombardibular ligament, a morphological novelty, provides a diversiﬁcation in the feeding mechanism (Frédéric, Olivier, Litsios, Alfaro, & Parmentier, 2014; Olivier, Frédéric, Herrel, & Parmentier, 2015). In the filamentous algae grazer Cortez damselfish (_Stegastes rectifaeria_um Pomacentridae), the slam occurs during feeding and simultaneously produces sounds (Olivier et al., 2014). The same morpho-functional process occurs in the anemonefish _A. clarkii_. However, the ceratombardibular ligament appears to be vital for feeding in the grazer, but not in the anemone-fish that uses different feeding mechanisms depending on the prey (Olivier et al., 2015). We postulate characters and motor patterns used in feeding have been secondarily co-opted for sound production. (i) Sounds can be made during feeding and are therefore a by-product. (ii) In all studied species, a single jaw slam is related to feeding and produces a single pulse; fighting sounds usually occur before elevated aggressive behaviour with biting (Mann & Lobel, 1998; Olivier et al., 2014; Parmentier, Kéver et al., 2010). (iii) Biting occurs during foraging activities in Cortez damselfish (Olivier et al., 2014). Further, intact (calling) individuals maintain their territorial boundaries whereas muted ones did not deter intruders from entering their shelter sites despite appropriate visual displays (Myrberg, 1997).

We hypothesize that initially sounds were single pulses produced during feeding activities. These by-product sounds were selected because they contributed to successful territory defence. The production of sounds informs the intruder of the emitter’s presence and elicits an (escape) response, favouring its selection for territorial defence. Secondly, the teeth snapping is produced in non-feeding behaviours, using the ancestral motor pattern. Currently, one or two pulse sounds are used by many damselfishes to deter conspeciﬁcs and heterospeciﬁcs (Parmentier, Lecchini, & Mann, 2016). Finally, courtship dips, chases or visiting calls utilize trains of pulses that result from repetition of the same motor pattern.

### 3.3 Haemulidae: sound production from pharyngeal jaws

In teleosts, pharyngeal jaw movements are used in chewing, processing and transportation of food from the pharyngeal cavity to the oesophagus (Vandewalle, Parmentier, & Chardon, 2000). This pharyngeal transport comprises repeated cycles of motor patterns supporting similar muscle activity and pharyngeal jaw movements. Electromyographic recordings indicate these movements are highly conserved among closely related Haemulidae species (Wainwright, 1989a,b). Grunt is the vernacular name for fishes in this family as a reflection of their well-known sounds. They produce these sounds in distress situation as recordings have been made in hand-held fish. Rubbing of upper and lower pharyngeal teeth produces stridulatory sounds (Burkenroad, 1930; Moulton, 1958). Bertucci et al. (2014) performed a study on the French grunt (_Haemulon flavolineatum_, Haemulidae) using hydrophones to record sounds, high-speed X-ray videos (to see bone movements inside the buccal cavity) and electron microscopy to study the teeth of the pharyngeal jaws was realized. Quantitative comparisons indicate the same sounds are produced during food processing as in distress situations. Videos showed cyclic movements during sound production were similar to movements employed in food processing,
and electron microscopy revealed traces of erosion on different teeth of the pharyngeal jaws (Bertucci et al., 2014).

As sound production in pomacentrids is related to feeding movements of the buccal cavity, we postulate that haemulids were able to take advantage of the incidental sounds produced during food processing to develop a communication function. Most fishes with pharyngeal teeth can produce acoustic signals during food processing, but acoustic communication based on pharyngeal jaws is not developed in all teleosts. In the case of haemulids, the co-opted function has been selected as these fish use it for communication. Furthermore, haemulids have complex pharyngeal jaws with developed teeth on ceratobranchials 4 that are usually not part of the lower pharyngeal jaw in other fishes (Vandewalle et al., 2000). These complex teeth scratch against the most external teeth of the upper pharyngeal jaw suggesting refinement for sound production.

The use of pharyngeal jaws in sound production has been mentioned in other taxa such as cichlids (Lanzing, 1974) and sunfishes (Gerald, 1971). However, more studies are needed because this mechanism has been assumed by some authors in the absence of strong empirical data.

3.4 | Syngnathidae: sound production from feeding movements

Sea horses and pipefishes (Syngnathidae) produce sounds during feeding competition, reproduction, male–male interaction and distress situations (Colson, Patek, Brainerd, & Lewis, 1998; Fish, 1953; Lim et al., 2015; Oliveira, Ladich, Abed-Navandi, Souto, & Rosa, 2014; Ripley & Foran, 2007). Once again, these taxa present strong similarities between the mechanism used during feeding and sound production. In both case, feeding strikes and sound clicks are generated when the head flexes rapidly backward provoking a strike between supraoccipital and post-cranial osseous plate(s), sometimes called the coronet (Colson et al., 1998). As in pomacentrids, clicks are detected simultaneously with feeding movements or are produced alone (Ripley & Foran, 2007). We infer that sound production was first a by-product of feeding strikes that was then selected for use in courtship and pair maintenance. This sonic mechanism may have contributed to the complex courtship behaviour found in many members of this family. Once the taxa entered into a new adaptive zone, minor morphological modifications have allowed diversification as differences in cranial bone morphology and cranial kinesis between species form unique acoustic signatures (Lim et al., 2015).

3.5 | Siluriformes: sound production utilizing pectoral structures

In catfishes, the armoured pectoral spine can be locked at a right angle against the pectoral girdle using skeletal specializations, and these structures function as antipredator adaptations (Fine & Ladich, 2003). The deployment of an enlarged spine provides some degree of protection, and the ability to lock increases the width of a catfish considerably and increases the difficulty of ingestion by predators (Bosher, Newton, & Fine, 2006; Sismour, Nellis, Newton, Mays, & Fine, 2013). However, the spine function does not seem limited to this function in all Siluriformes. Numerous catfish species use the dorsal process of the pectoral spine to stridulate, producing a series of pulses when grabbed by a predator (Bosher et al., 2006), when handled (Ghahramani, Mohajer, & Fine, 2014; Heyd & Pfeiffer, 2000; Kaatz, Stewart, Rice, & Lobel, 2010; Ladich, 1997; Lechner, Wysocki, & Ladich, 2010) or during dyadic contests (Hadjighaï & Ladich, 2015). The fused pectoral girdle, in addition to providing a rigid platform to anchor the spine (Schaefer, 1984), has secondarily become specialized as a sound radiator. Species capable of sound production have developed ridges, visible with scanning electron microscopy, on the under surface of the dorsal process (Fine et al., 1997; Parmentier, Fabri et al., 2010). Sounds are caused by a slip-stick mechanism: jerky movements of the pectoral spine correspond to the rubbing—of ridges against the cleithrum stimulate the pectoral girdle to vibrate. A discrete pulse is produced by each jerk movement (Ghahramani et al., 2014; Mohajer, Ghahramani, & Fine, 2015; Parmentier, Fabri et al., 2010). During the short rapid spine movement (jerk), the sound is of low amplitude. Amplitude increases following termination of the jerk motion when the spine is immobile, suggesting positive reinforcement of vibrations in the fused pectoral girdle (Mohajer et al., 2015).

Pectoral stridulation can be produced during spine abduction and adduction in many catfishes (Heyd & Pfeiffer, 2000; Kaatz et al., 2010; Ladich, 1997; Parmentier, Fabri et al., 2010). However, some species, including the channel catfish (Ictalurus furcatus, Ictaluridae), produce sounds only during the abduction movements (Ghahramani et al., 2014; Mohajer et al., 2015) that corresponds also to the defence system. Because erecting, locking and stridulation motions did not deter attacks (but complicated ingestions), associated sounds would function as a distress call (Bosher et al., 2006). From this stage, additional steps likely were added to develop the ability to stridulate during abduction and adduction and to use sounds in different behavioural contexts.

In summary, we suggest the complex mechanism catfish have developed to fully erect and lock the spines were co-opted to make sounds in most catfishes. Following use in movement, sound production was likely first related to defence functions, but was then further co-opted into agonistic and/or courtship signals (Fine & Ladich, 2003).

4 | CONCLUSION

Many fish species produce sounds employing a vast variety of sound-producing mechanisms. Sound-producing mechanisms evolved independently and sporadically in distantly related species, and therefore, their classification is based on analogies rather than the homologous systems of birds and mammals. Due to shared constraints, sound production tends to require the same organs (swim bladder, bone, teeth, etc.) for structural and functional reasons.

1. The concept of exaptation can be used as an entry to understand some of the myriad forms and solutions employed by sound-producing fishes. Existing anatomical structures are first
used in non-voluntary sound production, which probably provided advantages and later resulted in further selection and refinement into more sophisticated sonic organs.

2. In this review, the expatiation concept is focused on fishes using stridulatory mechanisms to produce sounds. As we noted above, expatiations also played a key role in the evolutionary history of mechanisms based on swim bladders and sound-producing muscles. It is therefore likely that expatiations have occurred in the evolutionary history of various other key macroevolutionary features throughout the animal kingdom. For instance a huge diversity of sound-producing structures in arthropods derives from the exoskeleton whose primordial role is in support and protection (Aiken, 1985; Dumortier, 1963). We hope the present essay will call attention to this often-neglected process and stimulate the search for other cases of expatiation.

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