

# Multiple exaptations leading to fish sound production

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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) posits 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, Schleinzer, & 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 gratuitous 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 exaptations and adaptations were subsets of "*adaption*," 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 *adaption* 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 adaptations, one for the original function and subsequent ones for new functions, without any need to prove that the first adaptation 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, & Mathevon, 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 specific behaviours that have also coevolved for communication. The specific behaviour 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 (Lapiedra, 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 (Zelditch & 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 Ophidiiform (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, Manguit, & Parmentier, 2009; Rice & Lobel, 2003), gobiids (Parmentier *et al.*, 2013; Stadler, 2002), cottids (Colleye *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*, Serrasalminidae), 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 (Millot & 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 ceratomandibular 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, Frédérick, Spanopoulos-Zarco, Balart, & Parmentier, 2014). Further, cutting the ceratomandibular ligaments prevents both feeding and sound production.

Beside sound production, the function of the ceratomandibular ligament, a morphological novelty, provides a diversification in the

feeding mechanism (Frédérick, Olivier, Litsios, Alfaro, & Parmentier, 2014; Olivier, Frédérick, Herrel, & Parmentier, 2015). In the filamentous algae grazer Cortez damselfish (*Stegastes rectifraenum* 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 ceratomandibular ligament appears to be vital for feeding in the grazer, but not in the anemonefish 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 fighting 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. Secondarily, 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 hand-held (Ghahramani, Mohajer, & Fine, 2014; Heyd & Pfeiffer, 2000; Kaatz, Stewart, Rice, & Lobel, 2010; Ladich, 1997; Lechner, Wysocki, & Ladich, 2010) or during dyadic contests (Hadjiaghai & 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.

- In this review, the exaptation concept is focused on fishes using stridulatory mechanisms to produce sounds. As we noted above, exaptations also played a key role in the evolutionary history of mechanisms based on swim bladders and sound-producing muscles. It is therefore likely that exaptations 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 exaptation.

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## REFERENCES

- Aiken, R. B. (1985). Sound production by aquatic insects. *Biological Reviews*, 645, 163–211.
- Alexander, R. M. (1966). Physical aspects of swimbladder function. *Biological Reviews*, 41, 141–176.
- Bertucci, F., Attia, J., Beauchaud, M., & Mathevon, N. (2012). Sounds produced by the cichlid fish *Metriacroma zebra* allow reliable estimation of size and provide information on individual identity. *Journal of Fish Biology*, 80, 752–766.
- Bertucci, F., Ruppé, L., Wassenbergh, S. Van., Compère, P., & Parmentier, E. (2014). New insights into the role of the pharyngeal jaw apparatus in the sound-producing mechanism of *Haemulon flavolineatum* (Haemulidae). *The Journal of Experimental Biology*, 217, 1–8.
- Bosher, B. T., Newton, S. H., & Fine, M. L. (2006). The spines of the channel catfish, *Ictalurus punctatus*, as an anti-predator adaptation: An experimental study. *Ethology*, 112, 188–195.
- Boyle, K. S., Colleye, O., & Parmentier, E. (2014). Sound production to electric discharge: sonic muscle evolution in progress in *Synodontis* spp. catfishes (Mochokidae). *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 281, 1197.
- Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer Associates Inc.
- Burkenroad, M. D. (1930). Sound production in the Haemulidae. *Copeia*, 1930, 17–18.
- Colleye, O., Nakamura, M., Frederich, B., & Parmentier, E. (2012). Further insight into the sound-producing mechanism of clownfishes: what structure is involved in sound radiation?. *Journal of Experimental Biology*, 215, 2192–2202.
- Colleye, O., Ovidio, M., Salmon, A., & Parmentier, E. (2013). Contribution to the study of acoustic communication in two Belgian river bullheads (*Cottus rhenanus* and *C. perifretum*) with further insight into the sound-producing mechanism. *Frontiers in Zoology*, 10, 71.
- Colleye, O., & Parmentier, E. (2012). Overview on the diversity of sounds produced by clownfishes (Pomacentridae): Importance of acoustic signals in their peculiar way of life. *PLoS ONE*, 7, e49179.
- Colson, D., Patek, S., Brainerd, E., & Lewis, S. (1998). Sound production during feeding in *Hippocampus* seahorses (Syngnathidae). *Environmental Biology of Fishes*, 51, 221–229.
- Connaughton, M. A. (2004). Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. *The Journal of Experimental Biology*, 207, 1643–1654.
- Courtenay, W. R. J. (1971). Sexual dimorphism of the sound producing mechanism of the striped cusk eel *Rissola marginata* (Pisces: Ophidiidae). *Copeia*, 259–268.
- Cullen, J. A., Maie, T., Schoenfuss, H. L., & Blob, R. W. (2013). Evolutionary novelty versus exaptation: Oral kinematics in feeding versus climbing in the waterfall-climbing Hawaiian Goby *Sicyopterus stimpsoni*. *PLoS ONE*, 8, e53274.
- Diogo, R. (2005). Osteology and myology of the cephalic region and pectoral girdle of *Pimelodus blochii*, comparison with other pimelodines, and comments on the synapomorphies and phylogenetic relationships of the Pimelodinae (Ostariophysi: Siluriformes). *European Journal of Morphology*, 42, 115–126.
- Dumont, E. R., Dávalos, L. M., Goldberg, A., Santana, S. E., Rex, K., & Voigt, C. C. (2012). Morphological innovation, diversification and invasion of a new adaptive zone. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 279, 1797–1805.
- Dumortier, B. (1963). Morphology of sound emission apparatus in Arthropoda. In R. G. Busnel (Ed.), *In acoustic behaviour of animals* (pp. 277–345). New York, NY: Elsevier Publishing Company.
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist*, 139, 125–153.
- Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 340, 215–225.
- Estramil, N., Bouton, N., Verzijden, M. N., Hofker, K., Riebel, K., & Slabbekoorn, H. (2014). Cichlids respond to conspecific sounds but females exhibit no phonotaxis without the presence of live males. *Ecology of Freshwater Fish*, 23, 305–312.
- Fine, M. L. (2012). Swimbladder sound production: The forced response versus the resonant bubble. *Bioacoustics*, 21, 5–7.
- Fine, M. L., Friel, J. P., McElroy, D., King, C. B., Loesser, K. E., & Newton, S. (1997). Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus*. *Copeia*, 1997, 777–790.
- Fine, M. L., King, T. L., Ali, H., Sidker, N., & Cameron, T. M. (2016). Wall structure and material properties cause viscous damping of swimbladder sounds in the oyster toadfish *Opsanus tau*. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 283, 20161094.
- Fine, M. L., King, C. B., & Cameron, T. M. (2009). Acoustical properties of the swimbladder in the oyster toadfish *Opsanus tau*. *The Journal of Experimental Biology*, 212, 3542–3552.
- Fine, M., King, C. B., Friel, J., Loesser, K. E., & Newton, S. (1999). Sound production and locking of the pectoral spine of the channel catfish. *American Fisheries Society Symposium*, 24, 105–114.
- Fine, M. L., & Ladich, F. (2003). Sound production, spine locking and related adaptations. In G. Arratia, B. G. Kapoor, M. Chardon & R. Diogo (Eds.), *Catfishes* (pp. 249–290). Enfield, New Hampshire: Science Publishers Inc.
- Fine, M. L., Lin, H., Nguyen, B. B., Rountree, R. A., Cameron, T. M., & Parmentier, E. (2007). Functional morphology of the sonic apparatus in the fawn cusk-eel *Lepophidium profundorum* (Gill, 1863). *Journal of Morphology*, 268, 953–966.
- Fine, M. L., Malloy, K. L., King, C., Mitchell, S. L., & Cameron, T. M. (2001). Movement and sound generation by the toadfish swimbladder. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology*, 187, 371–379.
- Fine, M. L., McKnight, J. W., & Blem, C. R. (1995). The effect of size and sex on buoyancy in the oyster toadfish. *Marine Biology* 123, 401–409.
- Fine, M. L., & Parmentier, E. (2015). Mechanisms of sound production. In F. Ladich (Ed.), *Sound communication in fishes* (pp. 77–126). Wien: Springer.

- Fish, M. P. (1953). The production of underwater sounds by the northern seahorse, *Hippocampus hudsonius*. *Copeia*, 1953, 98–99.
- Fish, M. P., & Mowbray, H. M. (1970). *Sounds of western north Atlantic fishes*. Baltimore, MD: The Johns Hopkins Press.
- Frédérich, B., Olivier, D., Litsios, G., Alfaro, M. E., & Parmentier, E. (2014). Trait decoupling promotes evolutionary diversification of the trophic and acoustic system of damselfishes. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 281, 20141047.
- Futuyma, D. J. (1986). *Evolutionary biology*, 2nd edn. Sunderland, MA: Sinauer Associates Inc.
- Galeo, A. J., Fine, M. L., & Stevenson, J. A. (1987). Embryonic and larval development of the sonic motor nucleus in the oyster toadfish. *Journal of Neurobiology*, 18, 359–373.
- Gerald, J. W. (1971). Sound production in six species of sunfish (Centrarchidae). *Evolution*, 25, 75–87.
- Ghahramani, Z. N., Mohajer, Y., & Fine, M. L. (2014). Developmental variation in sound production in water and air in the blue catfish *Ictalurus furcatus*. *The Journal of Experimental Biology*, 217, 4244–4251.
- Gould, S. J. (2002). *The structure of evolutionary theory*. Cambridge, MA: Harvard University Press.
- Gould, S. J., & Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, 8, 4–15.
- Hadjiaghai, O., & Ladich, F. (2015). Sex-specific differences in agonistic behaviour, sound production and auditory sensitivity in the callichthyid armoured catfish *Megalechis thoracata*. *PLoS ONE*, 10, e0121219.
- Hagedorn, M., Womble, M., & Finger, T. E. (1990). Synodontis catfish: A new group of weakly electric fish. *Brain Behavior and Evolution*, 35, 268–277.
- Hawkins, A. D. (1993). Underwater sound and fish behaviour. In T. J. Pitcher (Ed.), *Behaviour of teleost fishes*, 2nd edn (pp. 129–169). London: Chapman & Hall.
- Heard, S. B., & Hauser, D. L. (1995). Key evolutionary innovations and their ecological mechanisms. *Historical Biology*, 10, 151–173.
- Heyd, A., & Pfeiffer, W. (2000). Über die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihren Zusammenhang mit der Phylogenese und der Schreckreaktion. *Revue Suisse de Zoologie*, 107, 165–211.
- Hill, G. L., Fine, M. L., & Musick, J. A. (1987). Ontogeny of the sexually dimorphic sonic muscle in three sciaenid species. *Copeia*, 3, 708–713.
- Holt, D. E., & Johnston, C. E. (2014). Sound production and associated behaviours in blacktail shiner *Cyprinella venusta*: A comparison between field and lab. *Environmental Biology of Fishes*, 97, 1207–1219.
- Johnston, C. E., & Johnson, D. L. (2000). Sound production in *Pimphales notatus* (Rafinesque) (Cyprinidae). *Copeia*, 2000, 567–571.
- Kaatz, I. M., Stewart, D. J., Rice, A. N., & Lobel, P. S. (2010). Differences in pectoral fin spine morphology between vocal and silent clades of catfishes (Order Siluriformes): Ecomorphological implications. *Current Zoology*, 56, 73–89.
- Kratochvil, H. (1985). Beiträge zur Lautbiologie der Anabantoidei—Bau, Funktion und Entwicklung von lauterzeugenden Systeme. *Zoologische Jahrbücher Physiologie*, 89, 203–255.
- Ladich, F. (1988). Sound production by the gudgeon, *Gobio gobio* L.; a common European freshwater fish (Cyprinidae, Teleostei). *Journal of Fish Biology*, 32, 707–715.
- Ladich, F. (1989). Sound production by the river bullhead, *Cottus gobio* L. (Cottidae, Teleostei). *Journal of Fish Biology*, 35, 531–538.
- Ladich, F. (1997). Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. *Bioacoustics*, 8, 185–208.
- Ladich, F. (2014). Diversity in hearing in fishes: Ecoacoustical, communicative, and developmental constraints. In C. Köppl, G. A. Manley, A. N. Popper & R. R. Fay (Eds.), *Insights from comparative hearing research. Springer handbook of auditory research*, Vol. 49 (pp. 289–321). New York, NY: Springer.
- Ladich, F., & Bass, A. H. (1998). Sonic/vocal motor pathways in catfishes: Comparisons with other teleosts. *Brain Behavior and Evolution*, 51, 315–330.
- Ladich, F., Bischof, C., Schleinzner, G., & Fuchs, A. (1992). Intra- and interspecific differences in agonistic vocalization in croaking gouramis (Genus: *Trichopsis*, Anabantoidei, Teleostei). *Bioacoustics*, 4, 131–141.
- Ladich, F., & Fine, M. L. (2006). Sound-generating mechanisms in fishes: A unique diversity in vertebrates. In F. Ladich, S. P. Collin, P. Moller & B. G. Kapoor (Eds.), *Communication in fishes*, Vol. 1 (pp. 3–34). Enfield, NH: Science Publishers.
- Lagardère, J. P., & Ernande, B. (2004). Émissions sonores enregistrées en marais salé et attribuées à l'anguille européenne. *Comptes Rendus Biologies*, 327, 353–359.
- Lanzing, W. J. R. (1974). Sound production in the cichlid *Tilapia mossambica* Peters. *Journal of Fish Biology*, 6, 341–347.
- Lapiedra, O., Sol, D., Carranza, S., & Beaulieu, J. M. (2013). Behavioural changes and the adaptive diversification of pigeons and doves. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 280, 20122893.
- Larson, G., Stephens, P. A., Tehrani, J. J., & Layton, R. H. (2013). Exapting exaptation. *Trends in Ecology & Evolution*, 28, 497–498.
- Lauder, G. V. (1996). The argument from design. In M. R. Rose, & G. V. Lauder (Eds.), *Adaptation* (pp. 187–220). San Diego, CA: Academic Press.
- Lechner, W., Wysocki, L., & Ladich, F. (2010). Ontogenetic development of auditory sensitivity and sound production in the squeaker catfish *Synodontis schoutedeni*. *BMC Biology*, 8, 10.
- Lim, A. C. O., Chong, V. C., Chew, W. X., Muniandy, S. V., Wong, C. S., & Ong, Z. C. (2015). Sound production in the tiger-tail seahorse *Hippocampus comes*: Insights into the sound producing mechanisms. *The Journal of the Acoustical Society of America*, 138, 404–412.
- Longrie, N., Van Wassenbergh, S., Vandewalle, P., Mauguit, Q., & Parmentier, E. (2009). Potential mechanism of sound production in *Oreochromis niloticus* (Cichlidae). *The Journal of Experimental Biology*, 212, 3395–3402.
- Mann, D., & Lobel, P. S. (1998). Acoustic behaviour of the damselfish *Dascyllus albisella*: Behavioural and geographic variation. *Environmental Biology of Fishes*, 51, 421–428.
- Mayr, E. (1989). *Histoire de la biologie. Diversité, évolution et hérédité*. Paris: Fayard.
- McLennan, D. (2008). The concept of co-option: Why evolution often looks miraculous. *Evolution*, 1, 247–258.
- Millot, S., & Parmentier, E. (2014). Development of the ultrastructure of sonic muscles: A kind of neoteny? *BMC Evolutionary Biology*, 14, 1–9.
- Millot, S., Vandewalle, P., & Parmentier, E. (2011). Sound production in red-bellied piranhas (*Pygocentrus nattereri*, Kner): An acoustical, behavioural and morphofunctional study. *Journal of Experimental Biology*, 214, 3613–3618.
- Mohajer, Y. J., Ghahramani, Z. N., & Fine, M. L. (2015). Pectoral sound generation in the blue catfish *Ictalurus furcatus*. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology*, 201, 305–315.
- Moulton, J. M. (1958). The acoustical behavior of some fishes in the Bimini area. *Biological Bulletin*, 114, 357–374.
- Moulton, J. M. (1960). Swimming sounds and the schooling of fishes. *Biology Bulletin*, 119, 210–223.
- Myrberg, A. A. Jr. (1981). *Sound communication and interception in fishes*. In W. N. Tavolga, A. N. Popper & R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 395–426). New York, NY, USA: Springer-Verlag.
- Myrberg, A. A. J. (1997). Underwater sound: Its relevance to behavioural functions among fishes and marine mammals. *Marine and Freshwater Behaviour and Physiology*, 29, 3–21.
- Myrberg, A. A., Spanier, E., & Ha, S. J. (1978). Temporal patterning in acoustic communication. In E. S. Reese & F. Lighter (Eds.), *Contrasts in behaviour* (pp. 137–179). New York, NY: Wiley and Sons.
- Nguyen, T. K., Lin, H., Parmentier, E., & Fine, M. L. (2008). Seasonal variation in sonic muscles in the fawn cusk-eel *Lepophidium profundorum*. *Biology Letters*, 4, 707–710.



- Oliveira, T. P. R., Ladich, F., Abed-Navandi, D., Souto, A. S., & Rosa, I. L. (2014). Sounds produced by the longsnout seahorse: A study of their structure and functions. *Journal of Zoology*, *294*, 114–121.
- Oliver, S., & Lobel, P. (2013). Direct mate choice for simultaneous acoustic and visual courtship displays in the damselfish, *Dascyllus albisella* (Pomacentridae). *Environmental Biology of Fishes*, *96*, 447–457.
- Olivier, D., Frédérick, B., Herrel, A., & Parmentier, E. (2015). A morphological novelty for feeding and sound production in the yellowtail clownfish. *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology*, *323*, 227–238.
- Olivier, D., Frédérick, B., Spanopoulos-Zarco, M., Balart, E. F., & Parmentier, E. (2014). The cerato-mandibular ligament: A key functional trait for grazing in damselfishes (Pomacentridae). *Frontiers in Zoology*, *11*, 63.
- Ostrom, J. H. (1979). Bird flight: How did it begin? *American Scientist*, *67*, 46–56.
- Parmentier, E., Bouillac, G., Dragicevic, B., Dulcic, J., & Fine, M. (2010). Call properties and morphology of the sound-producing organ in *Ophidion rochei* (Ophidiidae). *The Journal of Experimental Biology*, *213*, 3230–3236.
- Parmentier, E., Colleye, O., Fine, M. L., Frédérick, B., Vandewalle, P., & Herrel, A. (2007). Sound production in the clownfish *Amphiprion clarkii*. *Science*, *316*, 1006.
- Parmentier, E., Fabri, G., Kaatz, I., Decloux, N., Planes, S., & Vandewalle, P. (2010). Functional study of the pectoral spine stridulation mechanism in different mochokid catfishes. *The Journal of Experimental Biology*, *213*, 1107–1114.
- Parmentier, E., & Fine, M. L. (2016). Fish sound production: Insight. In R. Suthers, F. Tecumseh, A. N. Popper & R. R. Fay (Eds.), *Vertebrate sound production and acoustic communication* (pp. 19–49). New York, NY: Springer.
- Parmentier, E., Fontenelle, N., Fine, M. L., Vandewalle, P., & Henrist, C. (2006). Functional morphology of the sonic apparatus in *Ophidion barbatum* (Teleostei, Ophidiidae). *Journal of Morphology*, *267*, 1461–1468.
- Parmentier, E., Kéver, L., Boyle, K., Corbisier, Y.-E., Sawelew, L., & Malavasi, S. (2013). Sound production mechanism in *Gobius paganellus* (Gobiidae). *The Journal of Experimental Biology*, *216*, 3189–3199.
- Parmentier, E., Kéver, L., Casadevall, M., & Lecchini, D. (2010). Diversity and complexity in the acoustic behaviour of *Dacyllus flavicaudus* (Pomacentridae). *Marine Biology*, *157*, 2317–2327.
- Parmentier, E., Lagardère, J.-P., Braquegnier, J.-B., Vandewalle, P., & Fine, M. L. (2006). Sound production mechanism in carapid fish: First example with a slow sonic muscle. *The Journal of Experimental Biology*, *209*, 2952–2960.
- Parmentier, E., Lecchini, D., & Mann, D. A. (2016). Sound production in damselfishes. In B. Frédérick & E. Parmentier (Eds.), *Biology of damselfishes* (pp. 204–228). Boca Raton, FL: CRC Press, Taylor & Francis.
- Patek, S. N., Baio, J. E., Fisher, B. L., & Suarez, A. V. (2013). Multifunctionality and mechanical origins: Ballistic jaw protrusion in trap-jaw ants. *Proceeding of the National Academy of Science of the United States of America*, *110*, 12787–12792.
- Pievani, T., & Serrelli, E. (2011). Exaptation in human evolution: How to test adaptive vs exaptive evolutionary hypotheses. *Journal of Anthropological Sciences*, *89*, 9–23.
- Popper, A. N., & Fay, R. R. (2011). Rethinking sound detection by fishes. *Hearing Research*, *273*, 25–36.
- Price, T. D., Qvarnström, A., & Irwin, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, *270*, 1433–1440.
- Rauther, M. (1945). Über die Schwimmblase und die zu ihr in Beziehung tretenden somatischen Muskeln bei den Trigliden und anderen Scleroparei. *Zoologische Jahrbücher Anatomie*, *69*, 159–250.
- Rice, A. N., & Bass, A. H. (2009). Novel vocal repertoire and paired swimbladders of the three-spined toadfish, *Batrachomoeus trispinosus*: Insights into the diversity of the Batrachoididae. *The Journal of Experimental Biology*, *212*, 1377–1391.
- Rice, A. N., & Lobel, P. S. (2003). The pharyngeal jaw apparatus of the Cichlidae and Pomacentridae: Function in feeding and sound production. *Reviews in Fish Biology and Fisheries*, *13*, 433–444.
- Ripley, J. L., & Foran, C. M. (2007). Influence of estuarine hypoxia on feeding and sound production by two sympatric pipefish species (Syngnathidae). *Marine Environmental Research*, *63*, 350–367.
- Rome, L. C., & Lindstedt, S. L. (1998). The quest for speed: Muscles built for high-frequency contractions. *News in Physiological Sciences*, *13*, 261–268.
- Ruppé, L., Clément, G., Herrel, A., Ballesta, L., Décamps, T., Kéver, L., & Parmentier, E. (2015). Environmental constraints drive the partitioning of the soundscape in fishes. *Proceeding of the National Academy of Science of the United States of America*, *112*, 6092–6097.
- Schaefer, S. A. (1984). Mechanical strength of the pectoral spine/girdle complex in *Pterygoplichthys* (Loricariidae: Siluroidei). *Copeia*, *1984*, 1005–1008.
- Sismour, E. N., Nellis, S. C., Newton, S. H., Mays, D., & Fine, M. L. (2013). An experimental study of consumption of channel catfish *Ictalurus punctatus* by Largemouth Bass *Micropterus salmoides* when alternative prey are available. *Copeia*, *2013*, 277–283.
- Skoglund, C. R. (1961). Functional analysis of swimbladder muscles engaged in sound production of the toadfish. *The Journal of Biophysical and Biochemical Cytology*, *10*, 187–200.
- Stadler, J. M. (2002). Evidence for a hydrodynamic mechanism of sound production by courting males of the notchtongue goby, *Bathygobius curacao* (Metzlar). *Bioacoustics*, *13*, 145–152.
- Stiassny, M. L. J. (1981). The phyletic status of the family Cichlidae (Pisces, Perciformes): A comparative anatomical investigation. *Netherlands Journal of Zoology*, *31*, 275–314.
- Tavolga, W. N. (1971). Sound production and detection. In W. S. Hoar & D. J. Randall (Eds.), *Fish physiology. Vol. 5. Sensory systems and electric organs* (pp. 135–205). New York, NY: Academic Press.
- Tracy, H. C. (1961). Development of the spinal crest, nerves and muscles in the toadfish (*Opsanus tau*). *The Journal of Comparative Neurology*, *116*, 291–315.
- Vandewalle, P., Parmentier, E., & Chardon, M. (2000). The branchial basket in teleost feeding. *Cybiurn*, *24*, 319–342.
- Wahlberg, M., & Westerberg, H. (2003). Sounds produced by herring (*Clupea harengus*) bubble release. *Aquatic Living Resources*, *16*, 271–275.
- Wainwright, P. C. (1989a). Functional morphology of the pharyngeal jaw apparatus in perciform fishes: An experimental analysis of the haemulidae. *Journal of Morphology*, *200*, 231–245.
- Wainwright, P. C. (1989b). Prey processing in haemulid fishes: Patterns of variation in pharyngeal jaw muscle activity. *The Journal of Experimental Biology*, *141*, 359.
- Wcislo, W. T. (1989). Behavioral environments and evolutionary change. *Annual Review of Ecology and Systematics*, *20*, 137–169.
- Wilson, B., Batty, R. S., & Dill, L. M. (2003). Pacific and Atlantic herring produce burst pulse sounds. *Biology Letters*, *271*, 95–97.
- Zelditch, M. L., & Fink, W. L. (1996). Heterochrony: Stability and innovation in the evolution of form. *Paleobiology*, *22*, 241–254.

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