10 Sound Communication

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CONTENTS

10.1 INTRODUCTION

Today, fish acoustic communication is considered an important aspect of teleost social behavior across a wider taxonomic spectrum since fish sounds have been reported in many different unrelated taxa (Parmentier et al. 2021; Lobel et al. 2010). Acoustic signals mediate fish social interactions in a wide range of activities such as distress or alarm situations, conspecific identification, courtship and agonistic interactions, mate choice, mate quality assessment, and coordination of gamete release (Amorim et al. 2015).

Damselfishes are a well-known vocal species from coral reefs. Some species are not only able to make sounds; they can also emit different kinds of sounds that are produced in various behavioral contexts (Mann and Lobel 1998; Parmentier et al. 2010; Parmentier et al. 2016). To date, sounds have been recorded and analysed in various species from the genera *Abudefduf*, *Amphiprion*, *Chromis*, *Dascyllus*, *Plectroglyphidodon*, *Pomacentrus*, and *Stegastes* (Parmentier et al. 2016). Sounds were also reported but not analyzed in *Hypsypops* (Limbaugh 1964; Fish and Mowbray 1970), *Microspathodon* (Emery 1973), and *Chrysiptera* (Graham 1992). Most pomacentrid sounds are a series of short-duration pulses. In that kind of series, one can measure the duration and number of pulses in the series, pulse period (time between the start of one pulse and the next), the related pulse repetition rate (number of pulses per unit time), interpulse interval (the silent period between pulses), pulse duration, and the frequency or power spectrum (Myrberg et al. 1978; Spanier 1979; Lobel and Mann 1995). All these characters do not carry the same kind of information and the physical properties of the acoustic environment can affect the cues in different ways during sound propagation. Features such as pulse periods are the most important in order to discriminate the pomacentrid sounds (Mann and Lobel 1997). Other parameters may not be relevant for interspecific comparisons. For example, the dominant frequency and the pulse duration are only related to fish size (Colleye et al. 2009; Myrberg et al. 1993), not to the species. Moreover, the number of pulses in a sound could be simply owing to its motivational state (Parmentier et al. 2010).

10.2 PRODUCTION OF DIFFERENT TYPES OF SOUNDS

Collingwood (1868) was the first to report in a scientific textbook the unusual phenomenon of a fish living in association with tropical sea anemones. As this intimate relationship between anemonefishes and their invertebrate hosts is the more glamorous aspect of their general biology, the considerable emphasis placed on this topic has tended to obscure other equally interesting specificities about the behaviors of these fish. In recent years, attention has turned to other aspects of the life history of anemonefishes. Any diver that has attempted to approach an anemonefish has experienced how it can rush toward intruders, making rapid nodding movements with the head, opening and closing jaws with convulsive jerks. These movements are related to sound production, audible to human ears at a distance of a meter or more (Moyer and Sawyers 1973) showing that these fish can produce volitional sounds. The present chapter aims at synthesizing knowledge about acoustic communication in anemonefishes. Previous reviews can be found in the book entitled *Biology of Damselfishes* (Frédérich and Parmentier 2016).

Literature on sound production in anemonefishes can be traced back to as early as 1930 when Verwey stated that *A. akallopisos* and *A. polymnus* were able to produce sounds (Verwey 1930). The sounds, which were clearly audible to the human ear, were mainly associated with agonistic activity. They were emitted by the fish in conjunction with both threat and submissive postures. Then, Schneider studied sound production in *A. clarkii*, *A. polymnus*, *A. frenatus*, and *A. percula* (Schneider 1964). He documented three types of sounds: threatening, fighting, and shaking sounds. Threatening sounds were used to intimidate other fish from a large distance, while fighting sounds were produced when attacking other specimens. Both types of sounds are the same but fighting sounds usually possess a single unit. According to the author, shaking sounds are "by contrast very different and were produced by the attacked fish" (Schneider 1964).

Unfortunately, this first study by Schneider revealed few detailed data about the acoustic features of vocalizations. Later, Allen recorded sounds for *A. chrysopterus* and *A.*

perideraion, both in the field and in the laboratory (Allen 1972). He differentiated two distinct sounds he called "clicks" and "grunts". Allen postulated clicks probably correspond to threatening sounds and can be emitted alone or in series of three to 15 pulses. However, he also noted that grunts are emitted in conjunction with threat postures by resident fish after new *Amphiprion* specimens were released in the tank. He did not record grunts in the field and did not detect the shaking sound observed by Schneider. His description and sonagraph do not provide enough data to distinguish grunts and clicks. We suspect the clicks and grunts reported by Allen are the same sounds because recordings made in a tank can distort sounds (Parmentier et al. 2014; Akamatsu et al. 2002). In *A. clarkii* and *A. frenatus*, Chen and Mok (1988) noted shaking sounds corresponded to submissive displays with the belly facing the dominant recipient. In a detailed study on *A. frenatus*, submissive sounds were produced when subordinates displayed submissive posture as a reaction to charge and chase by dominants, which means that these sounds were never recorded from dominant females (Colleye and Parmentier 2012). From all these studies, there are two types of sounds produced by the anemonefishes. Threatening and fighting sounds form the first group. The sound-producing mechanism of these sounds is most probably the same way because the major difference between them is only the number of pulses. In different pomacentrid species, a lower number of pulses is usually found during fighting than during threatening behaviors (Parmentier et al. 2010; Mann and Lobel 1998; Parmentier et al. 2021). The shaking sounds constitute the second group of sounds and correspond to a submissive behavior. In *A. frenatus*, a comparative study between threatening and shaking sounds allows to better distinguish them (Colleye and Parmentier 2012). In comparison to aggressive sounds, shaking sounds are always composed of several pulses forming a unit that can be produced alone or in series, whereas aggressive sounds are composed of a single pulse that can be emitted alone or in series (Figure 10.1). Consequently, aggressive sounds can be made of a single pulse which is not the case for submissive sounds (Figure 10.1). In *A. frenatus*, shaking sounds also exhibit significantly shorter pulse periods (12 ms versus 106 ms) and shorter pulse durations (8 ms versus 14 ms) than aggressive sounds (Colleye and Parmentier 2012). However, the frequency range of both kinds of sounds is equivalent. Although we do not have data from calibrated hydrophones to support our claims, shaking sounds clearly possess a lower amplitude than aggressive sounds. Aggressive sounds can be easily recorded in the field but shaking sounds are quite hard to distinguish from background noise and have never been recorded in situ. These sounds (and corresponding submissive behavior) were recorded only in tanks with low background noise conditions.

10.3   RELATIONSHIPS BETWEEN SOUNDS AND BEHAVIORS

The implication of acoustic signals in agonistic interactions may be a simple strategy to avoid conflicts, which otherwise might escalate to a severe outcome (Colleye and Parmentier 2012). In fact, in tank experiments, where specimens cannot escape, confrontations always start with sound production and charges before physical attacks that can lead to death. Between conspecifics, aggressive sounds are mainly produced by dominant individuals during charges, chases, and threat displays during agonistic interactions (Takemura 1983; Colleye et al. 2009). They can be produced by individuals of different sexual statuses (females, males, and non-breeders) during charge-and-chase displays when another con- or heterospecific (including humans!) approaches the sea anemone in which they dwell (Colleye et al. 2009). These sounds were first attributed to territory defence against hetero- or conspecifics (Schneider 1964; Allen 1972). The reason sounds are produced could however be more complex. In the fight against heterospecifics, the intruder can be deterred. However, in the fight between conspecifics, the confrontation does not always end with the departure of one antagonist since specimens can share the same host. In this case, the aggressive behavior does not correspond to physical territory defence.

Anemonefishes live in social groups composed of a breeding pair accompanied by no or several non-breeders. Group members are not related and non-breeders do not provide alloparental care (Buston 2004a; 2004b; Buston et al. 2007). Within each group, there is a size hierarchy: the female is the largest individual, the male is the second largest, and non-breeders get progressively smaller (Buston 2003). The size hierarchy represents the queue to become a breeding member: if the female of the group dies, then the male changes sex (Casadevall et al. 2009; Casas et al. 2016) and becomes the new female; the largest non-breeder becomes the new male (Buston 2004). As all individuals grow, the smallest individual is always the last recruit. In this system, without predation, individuals are thought to wait peacefully to inherit breeding positions following the death of the breeders (Branconi et al. 2020). In *A. percula*, individuals adjacent in rank are separated by body size ratios: the growth of individuals is regulated so that each dominant ends up being about 1.26 times the size of its immediate subordinate (Buston and Cant 2006). The same kind of ratio (< 1.30) is observed in the different groups of *A. frenatus* (Colleye and Parmentier 2012). In this small society, numerous agonistic interactions occur and appear to play an important role in maintaining these observed size differences between individuals that are adjacent in rank (Fricke 1979; Buston 2003). Larger fishes chase smaller ones, which means that the smallest one is the recipient of numerous charges (Fricke 1979). These chasing behaviors are accompanied by sound production. In anemonefish species, the size hierarchy is perfectly mirrored in the acoustic features. In aggressive sounds, pulse duration and dominant frequency are highly correlated with standard length ($r=0.97$): smaller individuals produce higher frequency and shorter duration pulses than larger individuals (Figure 10.2), irrespective of the sexual status (Colleye et al. 2009). Consequently, these sonic features might be useful
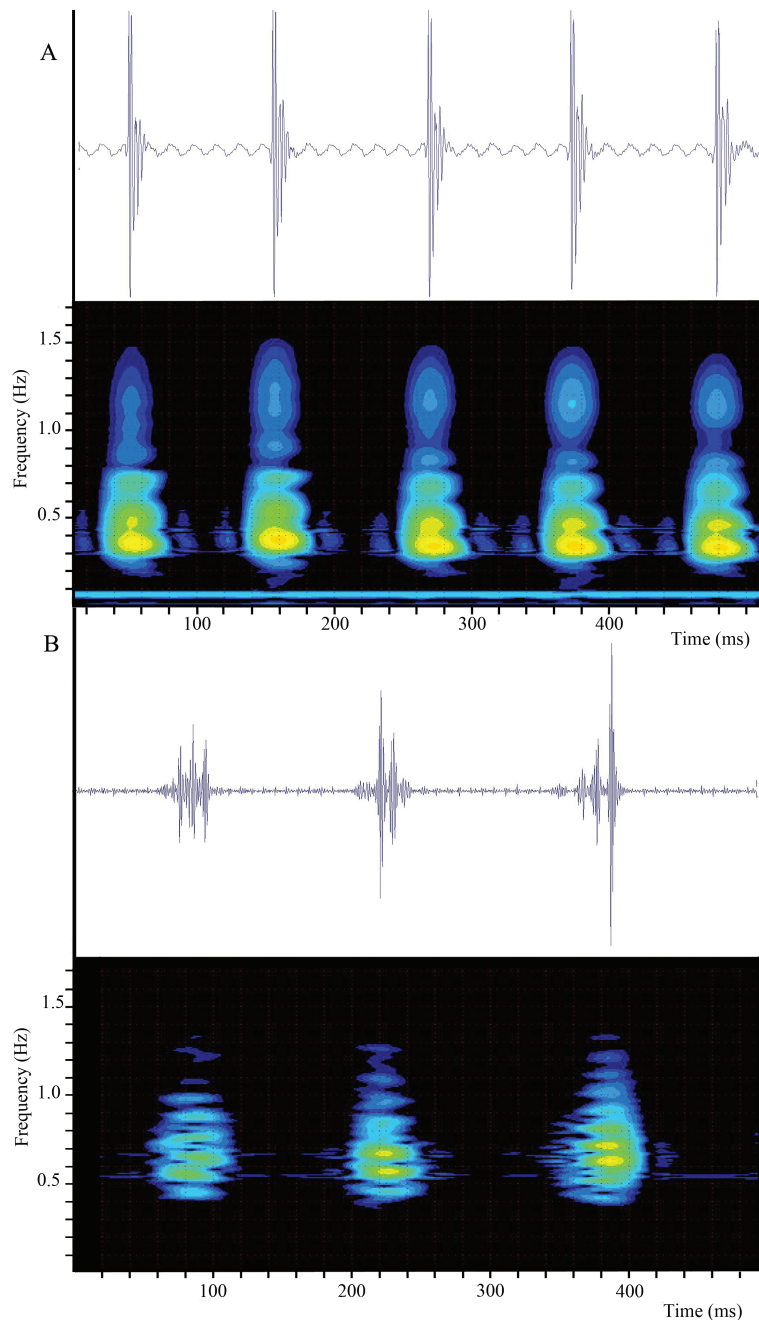
FIGURE 10.1 Oscillograms and spectrograms illustrating agonistic (A) and submissive (B) sounds produced by *Amphiprion frenatus* during interactions. Panels were placed at the same time scale to allow comparison. Note submissive sounds show a group of pulses with short periods whereas agonistic sounds possess longer periods between pulses. Redrawn from Colleye and Parmentier (2012).

cues for individual recognition within a group and may convey information on the social rank of the emitter within the group (Colleye et al. 2009; Colleye and Parmentier 2012). Additional studies should be conducted to determine experimentally whether a fish can use sounds to infer the size and establish the social hierarchy of conspecifics. Interestingly, the relationship between peak frequency and size is equivalent across the different clownfish species (Figure 10.3), supporting that the size-related vocal message should be the same within the taxa. A recent experimental study has used different sensory cues (mechanosensory [pressure and/or touch], auditory, chemosensory, and/or visual) to show that juvenile anemonefish likely require the use of mechanosensory (pressure and/or touch) cues to assess the size of conspecifics (Desrochers et al. 2020). However, the experimental design of these authors did not indicate if sounds were produced during the duration of the experiment. The function of the sound can thus be hardly assessed.

Sound production abilities are not restricted to anemonefish since they can also be found in many different pomacentrid taxa (Parmentier et al. 2016). In *Dascyllus* species, up to six different types of sounds have been described
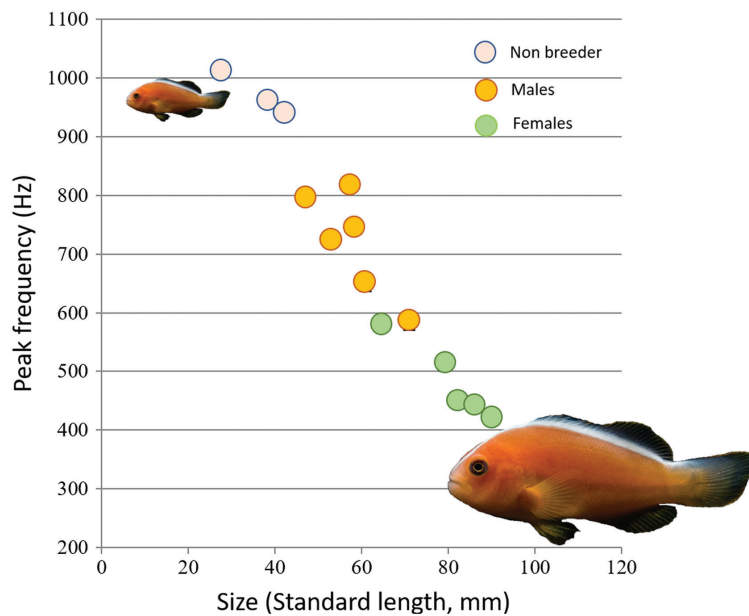
FIGURE 10.2 Relationships between standard length and peak frequency in *Amphiprion akallopisos*. The size ratio between both shown fish is respected. Redrawn from Colleye et al. (2009).

(Lobel and Mann 1995; Mann and Lobel 1998; Parmentier et al. 2010, 2021). As in anemonefish, other pomacentrid species also produce aggressive sounds during territory defence against conspecifics and heterospecifics, but also fighting sounds and submissive sounds. Moreover, they produce sounds during courtship. Many pomacentrid males produce signal jumps to attract females. In *Dascyllus* species, sounds are also emitted when females visit male nests. To date, sound production during reproductive periods has been reported in *A. ocellaris*, *A. frenatus*, and *A. sandaracinos* (Takemura 1983). However, these observations need to be carefully considered since, according to the author, these species are supposed to emit weak sounds with high-frequency components of more than 2 kHz during reproduction. Anemonefish are not able to hear these frequencies (Parmentier et al. 2009). Therefore, high frequencies (> 2 kHz) have never been reported in other studies on the same species. The preparation of the nest requires that the male and female peck up the surface of the rock to clean it for correct egg adhesion. These high-pitched sounds could be a by-product of the nest cleaning activities, corresponding to gratings of teeth on the rocks. Cleaning rocks for spawning could originate different incidental sounds but it is not communication. Moreover, Takemura (1983) noted also in his description "sounds were not so closely connected with spawning, because these sounds were not always heard and were the same as usual sounds". In other words, sounds produced during the reproductive period are probably not related to reproduction or spawning. In addition, spawning events were also observed and audio-recorded in *A. akindynos*, *A. clarkii*, *A. perideraion*, *A. melanopus*, and *A. percula*. No sound has been recorded during a total of 13 complete spawning events (Colleye and Parmentier 2012). The lack of sounds during spawning events is probably

an evolutionary outcome related to their peculiar way of life. In their restricted territory, partners do not need to make sounds to attract females. Within pomacentrids It is however very interesting to note that the same kind of sounds (=groups of pulses), produced with the same mechanism (Parmentier et al. 2016), can have different meanings in species from different genera (e.g., *Dascyllus* and *Amphiprion*). Additional studies using play-back experiments are however required to better understand how these sounds are used by these species.

10.4   MECHANISM

The mechanism of sound production has been discussed since the first report on sound production in Pomacentridae. The hypotheses were sprawling and sometimes quite contradictory. Some authors claimed that sounds were produced by rapid up-and-down movements of the opercula and by movements of the mouth bones (Verwey 1930). In *Abudefduf luridus*, Santiago and Castro (1997) hypothesized that sound production involves a swim bladder mechanism, but extrinsic muscles attached to the swim bladder were never found in Pomacentridae species. Schneider (1964) noted "neither the gill-teeth nor the teeth on the upper and lower jaw are engaged in sound production" but other authors reported later that sounds could be produced by grating pharyngeal teeth and then be amplified by the swim bladder (Luh and Mok 1986; Rice and Lobel 2003). In all recorded anemonefishes, call duration is related to the number of pulses, suggesting there is a fixed mechanism with a motor pattern. Moreover, the peak frequency (between 350 and 1,100 Hz, according to the fish size) is too low for typical stridulatory mechanisms and too high for swim bladder sounds driven as a forced response to sonic muscle contraction.
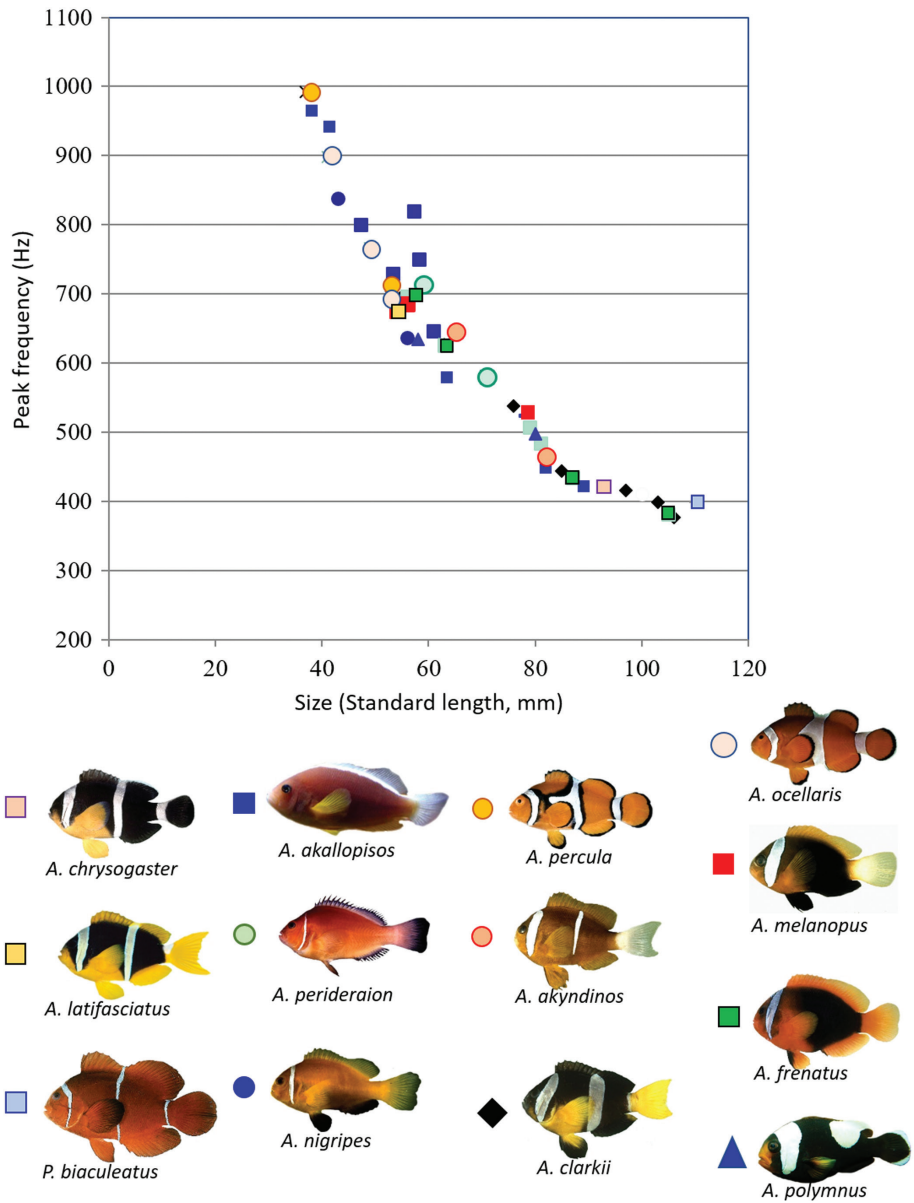
FIGURE 10.3 Correlation of peak frequency against fish size (SL) on acoustic variables in 13 clownfish species. Fishes ranged from 37 to 110 mm (n = 43). Results are expressed as mean values of 50 recorded pulses for each individual.

Using manipulations of freshly euthanized fish and high-speed videos coupled (or not) with X-rays and synchronized with sound recordings, it has been shown that aggressive sounds emitted by the yellowtail anemonefish *A. clarkii* result from the teeth collision induced by a fast jaw slam (Parmentier et al. 2007; Damien Olivier et al. 2015). This rapid mouth closing movement is caused by the cerato-mandibular (c-md) ligaments (right and left) joining the hyoid bars (at the level of the ceratohyal) to the medial sides of the mandibles (at the level of the coronoid process of the angular), a synapomorphic trait of the Pomacentridae (Stiassny 1981; Olivier et al. 2014). Consequently, Pomacentridae are the only known teleosts that use that kind of mechanism to close their mouth. According to the review of Olivier et al. (2016), the kinematic pattern during sound production in

A. clarkii can be divided into three phases: initial, mouth-opening, and mouth-closing. (1) During the initial phase, the mouth is closed, the neurocranium is held at rest, and the hyoid apparatus is not depressed. At this moment, the cerato-mandibular ligament is loose and does not transmit any tension to the lower jaw. (2) During the mouth-opening phase, the neurocranium is elevated and the hyoid apparatus is depressed causing the downward rotation of the lower jaw. As a result, the insertion points of the c-md ligament are moved away from one another, causing tension in the ligament. With accentuated depression of the hyoid apparatus, the c-md ligament acts as a cord, forcing the lower jaw to rotate clockwise around its quadrate articulation. It induces the mouth to close within a few ms. Comparisons with available data in the literature show that the mechanism of

the c-md ligament provides the damselfish with one of the fastest mouth-closing mechanisms in teleosts (Olivier et al. 2015; Olivier et al. 2016). The transection of the c-md ligaments prevents sound production. This suite of events only explains the onset of the sounds. Using a combination of different approaches, further studies provided complementing explanations (Colleye and Parmentier 2012). In anemonefish, sound duration and frequency are known to be morphologically determined signals strongly related to fish size (Colleye et al. 2009; Parmentier et al. 2009; Colleye et al. 2011). This suggests that these acoustic features are subject to a morphological constraint. Considering the positive relationship existing between fish size and swim bladder volume, this organ could be the structure responsible for the size-related variations in acoustic features (Colleye et al. 2012). However, the swim bladder itself is too inefficient to act as a resonator. The walls of the swim bladder are rigidly attached to the articulated (and thus movable) ribs. The combination of ribs and swim bladder wall probably forms a structure analogous to a loudspeaker membrane. Vibrations of the rib cage could be the driver because they would provoke movements of this membrane, thus initiating sound production. The swim bladder wall is driven by bone movements. Experimental manipulation of the swim bladder confirmed its function related to sound production. Pulse duration and dominant frequency changed when filling the swim bladder with physiological liquid confirmed its function since it changes both the pulse duration and dominant frequency. Moreover, strikes of the rib cage with a hammer generated sounds with size-related variations in sound duration and frequency, suggesting that the vibrating properties of the rib cage might be responsible for the size-related variations observed in acoustic features (Colleye et al. 2012). Results of this kind were not found when striking the swim bladder wall, probably because this structure has high intrinsic damping (Fine 2012). All these experiments were mainly conducted using the anemonefish *A. clarkii*. However, since dominant frequency and pulse duration were strongly predicted by body size among 14 different anemonefish species, this highlights that all species use the same vocalization mechanism (Colleye et al. 2011). In conclusion to this part, we hypothesize that the pulse within a sound is initiated by a slam of the jaws. It provokes skeleton vibration at the origin of rib cage shaking. Close association of the rib cage with the swim bladder wall could constitute a structure analogous to a loudspeaker membrane causing the second part of the sound. The frequency and pulse duration are constrained by the size of the fish. Therefore, the only parameter that can be used to produce species-specific sounds has to be related to the motor pattern responsible for the fast mouth closing. It can vary at two levels: the number of slams and the speed (rhythm) between two slams, corresponding to the pulse period.

Lastly, because anemonefishes are confined to an anemone for habitat, and anemones are very sensitive to climate change (bleaching of its tissue due to thermal stress), the sound of anemonefish could be an indicator of coral reef health. Biodiversity assessment remains one of the most difficult challenges encountered by ecologists and conservation biologists, especially in hyper-diverse ecosystems such as coral reefs (Barnosky et al. 2011; Wilkinson et al. 2013). Biological sounds have been suggested as a means to quantify ecosystem health and biodiversity (Bertucci et al. 2015, 2016; Di Iorio et al. 2021; Mooney et al. 2021). By taking advantage of the sounds produced by clown species in healthy or bleached anemones, coral reef health could be monitored and surveyed.

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