Biology of Damselfishes

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Sound Production in Damselfishes

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Introduction

The damselfishes (Pomacentridae) are one of the most thoroughly investigated and best understood family of acoustic reef fishes (Lobel et al. 2010). Scuba divers can easily hear damselfish sounds without the aid of a hydrophone, particularly when a male is aggressively defending his territory. These features of pomacentrid acoustic behavior make them easily accessible to bioacoustic study (Lobel et al. 2010). In this chapter, we review the different terms that have been used to describe the damselfish calls, summarize the behavior associated with sound production in different genera, and provide some additional information on species in which the sounds have not yet been described. In the next section, we focus on different acoustic characteristics and how they are important in damselfish communication and synthesize data on sound producing mechanisms. Lastly, we postulate about the origin of the sound production mechanism and its use in Pomacentridae.

Damselfishes are a well-known vocal species from the 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). Different terms (threatening, shaking, click, grunt, etc.) were given to differentiate these

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various sounds but "pops" and "chirps" were the most commonly used (Schneider 1964, Allen 1972). This terminology for sound is however inconsistent since these call nouns were not always supported by empirical descriptions of the physical characteristics of the sounds. Moreover, both terminologies were associated with different kinds of behavior (Amorim 2006), such as courtship, fights, chases or threat displays (Mann and Lobel 1998, Parmentier et al. 2010). The best-characterized sound in damselfishes is the "chirp", produced by the male of several species (e.g., *Abudefduf* spp., *Dascyllus* spp., *Stegastes* spp.) primarily during a stereotyped courtship swimming display called the "signal jump", "dip" or "gamboling". The courtship dip consists of a male rising in the water column and then rapidly swimming downwards near, or to the prospective spawning area, at the same time as making a pulsed sound (Myrberg 1972, Spanier 1979, Lobel and Mann 1995, Mann and Lobel 1998, Lobel and Kerr 1999) and adopting in some species a unique species-specific courtship coloration (Myrberg et al. 1978). "Pops" usually referred to single (less frequently, double) pulsed sounds, while chirps would correspond to multiple pulsed sounds. However, multiple-pulsed "pops" were described in *Stegastes partitus* (Myrberg 1972), *Plectroglyphidodon lacrymatus*, *Dascyllus aruanus* (Parmentier et al. 2006), *Amphiprion akallopisos* (Parmentier et al. 2005) and *A. frenatus* (Colleye and Parmentier 2012). The inconsistent use of the terms is probably due to human perception of the sound. Isolated pulses sound like pop, but a combination of these same pops in multiple-pulse sound like chirps. For example, the sounds made simultaneously to dips (= dip sounds) of *Dascyllus flavicaudus* sound like cooing pigeons but pulses that composed these chirps are physically identical to pops (Parmentier et al. 2010). In *Dascyllus albisella*, Mann and Lobel (1998) has also indicated that two types of aggressive sounds were produced: a popping sound that was composed of one or two pulses, and a multiple-pulse "chirp" resembling the signal jump sound. However, there was no significant difference between the aggressive pop and the aggressive chirp in average pulse duration, peak frequency or frequency bandwidth (Mann and Lobel 1998).

Despite this overlap, it is possible to differentiate two main kinds of sounds in damselfishes, especially when the same species is able to make both kinds of sounds. It is however quite difficult to provide quantitative and qualitative data for each of the sound types because the acoustic characteristics depend on the species. Both types of sounds can be multiple-pulsed. We propose to call pops, the sounds in which pulses have longer pulse duration, longer pulse period and fewer pulses than chirps (Fig. 1). Pops are made during teeth snapping (Parmentier et al. 2007, Colleye et al. 2012) mainly during aggressive behaviors (chase and defense of the territory), courtship or reproduction. These sounds are found in all the pomacentrids studied so far. Chirps are produced during head shaking and correspond to submissive behavior during agonistic interactions (Schneider 1964, Colleye and Parmentier 2012). The mechanism allowing "chirp" production is currently not known. They were recorded only in *D. aruanus* (Parmentier et al. 2006), *A. akallopisos* (Parmentier et al. 2005) and *A. frenatus* (Colleye and Parmentier 2012). The main reason for this poor list would be that chirps are usually less audible than pops and are more difficult to detect in field studies.

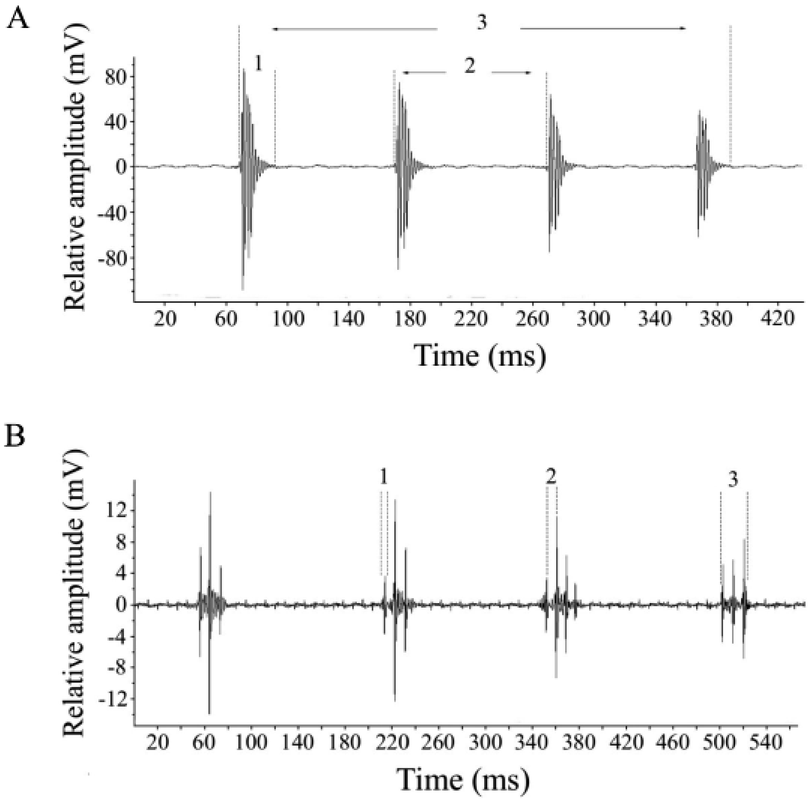

Fig. 1. Oscillograms comparing the temporal patterns between pops (A) and chirps (B) in *Amphiprion frenatus*. In A, there is only one call with four pulses. In, B there are four calls each having different pulses. Modified from Colleye and Parmentier (2012). Note the differences in pulse duration (1) and pulse period (2). The acoustic variable measured in (3) represents the sound duration in the case of submissive sounds (B), and the train duration in the case of aggressive sounds (A).

Details on the study of the sound parameters in teleosts were recently reviewed (Fine and Parmentier 2015). Three major tools used for describing fish sounds are (Fig. 2), an image showing frequency versus time, oscillograms, which depict amplitude against time (Fig. 1) and frequency spectra (Fig. 3), which show amplitude against frequency and indicate dominant frequencies within a sound. A sonogram is simply a series of frequency spectra from short time samples of a signal. Most pomacentrid sounds are a series of short-duration pulses and therefore present as vertical lines (a wide frequency band with a short duration) on a sonogram (Fig. 2). Since damselfish sounds include a series of pulses, 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 (an output of the amplitude, typically in dB, against frequency).

In this chapter, we will first focus on the ethological, physiological and morphological knowledge concerning the acoustic communication in damselfish.

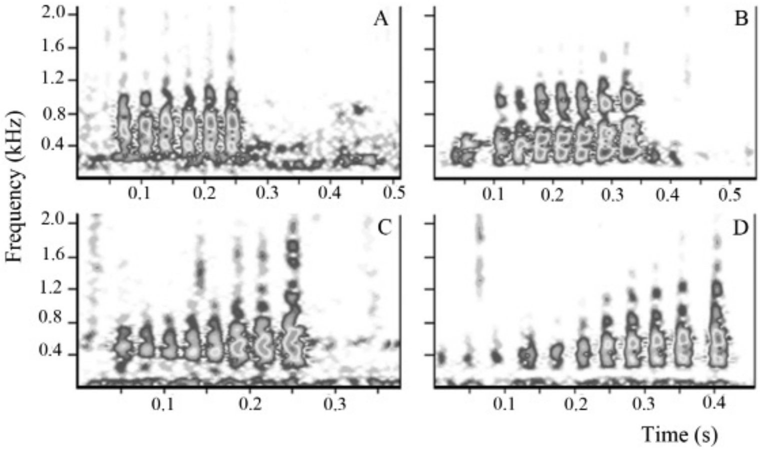

Fig. 2. Spectrogram of dip sounds in *Dascyllus albisella* (A), *D. flavicaudus* (B), *D. aruanus* (C) and *D. trimaculatus* (D). Despite the figure, note that the species do not show a species-specific distribution of the pulses in a call. Each spectrogram shape could apply to any of the four *Dascyllus* species. Modified from Parmentier et al. (2009b).

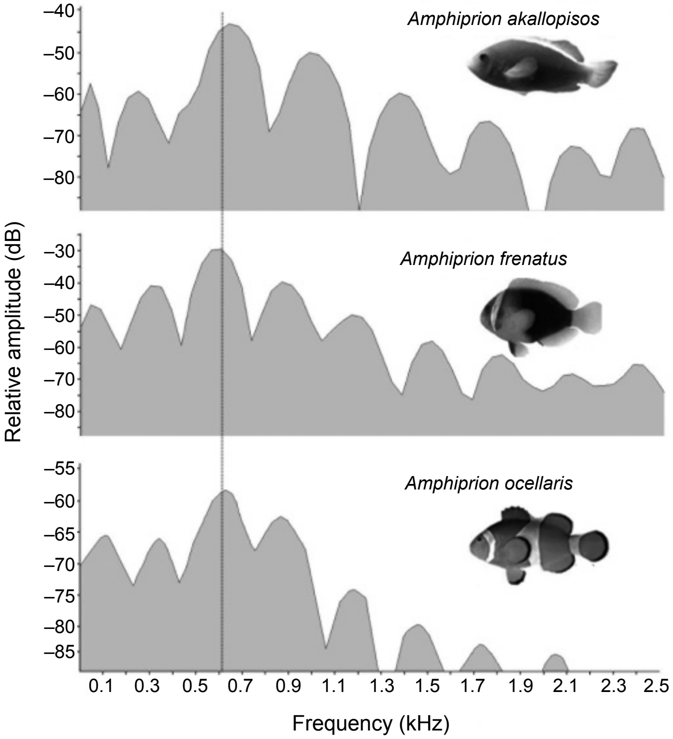

Fig. 3. Power spectrum in *Amphiprion akallopisos*, *A. frenatus* and *A. ocellaris*. Sound comparisons of these three species based on three specimens having the same size (61–63 mm SL) revealed that their dominant frequency is not significantly different. See Colleye et al. (2011) for further details.

In the second part of the chapter, we will provide additional information concerning the sound production of some species and review the different species for which the sounds are (at least) partly analyzed.

Signal Characters

Acoustic signals may carry much information. Generally speaking, sounds in fishes consist of trains of pulses that can be characterized by different parameters such as: sound duration (ms), pulse duration (ms), number of pulses in a train, pulse period (ms), the interpulse interval (measured as the time from the end of one pulse to the beginning of the next one) and dominant frequency (Hz). 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.

Among all studied parameters, pulse period is least affected by propagation when compared to peak frequency, pulse duration, interpulse interval, and the coefficient of variation of pulse amplitudes within a call (Mann and Lobel 1997). Pulse period varied by only 2% compared to its mean value, whereas the interpulse interval varied by about 10% and the other parameters by 40%. These results suggest that the pulsed sound functions over short distances and that the pulse period provides the most reliable basis for signal identification because it degrades the least with propagation through the environment (Mann and Lobel 1997). On the other hand, frequency spectrum and amplitude do not appear to be critical for species recognition (Ha 1973). This hypothesis is supported by different studies concerning different clades: *Stegastes*, *Dascyllus* and *Amphiprion*.

The bicolor damselfish *Stegastes partitus*, the beaugregory damselfish *Stegastes leucostictus*, the dusky damselfish *Stegastes dorsopunicans* and the threespot damselfish *Stegastes planifrons* are sympatric damselfishes from the coral reefs of southern Florida and the Caribbean. These species appear to have a common reproductive season, and congeners often maintain residences and territories within a few meters of each other (Myrberg et al. 1978). It is not unreasonable to assume that the sounds produced by the members of each species can be heard by the members of all others, based on the remarkable similarity of their hearing abilities (Myrberg and Spires 1980). In such conditions, sounds could be important for purposes of species recognition in order to avoid misidentification during courtship. The characteristics of the sounds of these *Stegastes* species showed that pulse period was different between species, with significant overlap of other metrics (Table 1; Spanier 1979).

Table 1. Acoustic characteristics of the dip sounds in four sympatric species of *Stegastes* (Spanier 1979).

	Number of pulses	**Pulse length (ms)**	**Pulse period (ms)**	**Frequency range (Hz)**
S. partitus	2–4	9.8	38	300–1200
S. leucostictus	3–6	15	31.9	180–1080
S. planifrons	3–6	11.6	42.1	200–900
S. dorsopunicans	4–9	11.7	40.4	200–1100

It was discovered that the males of these species would respond to playbacks of their sounds by performing courtship dips and producing sound (Myrberg et al. 1978, Spanier 1979). To study whether different species discriminated between the calls of other species, calls that varied in the number of pulses and the pulse period were played back to each species (Myrberg and Spires 1972, Myrberg et al. 1978, Spanier 1979). Two sets of calls were used. The first contained those calls having the most prevalent number of pulses for each species (Table 1). The second type contained 4-pulse calls from all species. The effectiveness of sounds was ascertained by counting the number of dips the male made in response to the sound playbacks. Species showed different abilities in recognizing their specific sounds.

The realization of signal jumps in reaction to playbacks indicated that each species was able to respond to the sounds of heterospecifics. However, they all responded significantly more to their own typical dip calls than to those of the other species when the typical number of pulses and pulse period were used, showing the species-specificity of the call. However, having responses to heterospecific sounds also indicate that there is an overlap in call structure between the species. The species-specific nature of the call was confirmed in an additional experiment (Spanier 1975) where the pulse period of the beaugregory (*S. leucostictus*) was artificially increased by 9 ms to produce a pulse interval equivalent to that of the dusky damselfish (*S. dorsopunicans*). This change was sufficient to cause the dusky damselfish to respond to the modified sound.

Another way to study which characters may be important in identification is to determine in closely related species which parameters are clearly different. The sounds of the four species of *Dascyllus* were first compared in 2009 (Parmentier et al. 2009b). The temporal characteristics of *D. aruanus* sounds differed widely from those of the other three species (*D. albisella*, *D. flavicaudus* and *D. trimaculatus*) and allowed the formation of two groups, corresponding to the phylogenetic branching (Bernardi and Crane 1999, McCafferty et al. 2002). For the purpose of this chapter, sounds in *Dascyllus carneus* and *D. reticulatus* were also analyzed (see further in the text). This comparison is based only on the pulse period (Fig. 4) because this character is least affected by signal propagation and thus would be a reliable carrier of information.

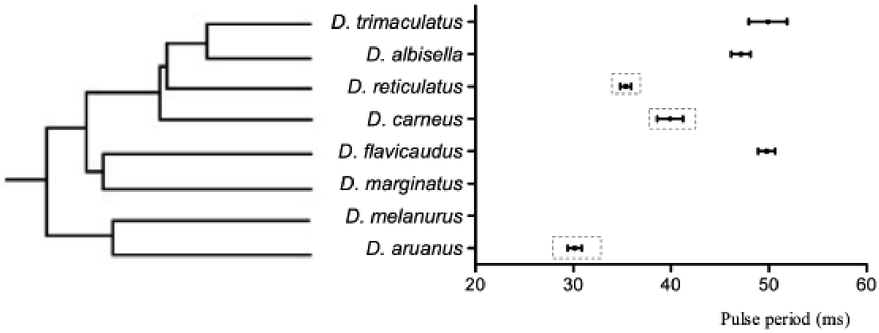

Fig. 4. Confrontation between the *Dascyllus* phylogeny (simplified figure from Bernardi and Crane 1999) and the variation of pulse period in 6 *Dascyllus* species (data from Parmentier et al. 2009b and from analysis made for the purpose of this chapter). Results are represented as means ± 95% confidence intervals. Dotted line rectangles show that the pulse periods of some species are completely isolated from the rest of the taxa.

According to Mann and Lobel (Mann and Lobel 1997), pulse period in *D. albisella* varied by only 2% as compared to its mean value, whereas other parameters (pulse length, frequency) varied by 40% or more of their mean values. Interestingly, the pulse period of *D. carneus* and *D. reticulatus* is significantly (Kruskal Wallis, $p < 0.05$) shorter than that of *D. trimaculatus*, *D. albisella* and *D. flavicaudus* and longer than that of *D. aruanus* (Fig. 4). It means that this character (pulse period) is sufficient to discriminate calls of both these fish species from the other previously studied *Dascyllus* species.

The courtship dip mating display associated with sound production in *Dascyllus aruanus* differs from other species. In *D. aruanus*, the male stops swimming, makes a forward rotating movement by raising its caudal fin, and then swims rapidly downward. In successive signal jumps, the fish stops swimming between each dip, and rises in the water column at the same time as raising its tail before the next jump. The movement resembles a sinusoidal curve. In the other three species, the swimming fish turns abruptly at a right angle and begins the dive to the side and not forwards as in *D. aruanus*. In all four species, the sounds are made not only during the descent, but also during the rise (Parmentier et al. 2009b). Based on an analysis of the sound parameters, *D. trimaculatus* groups with *D. albisella* (McCafferty et al. 2002), rather than one or both these fishes grouping with *D. flavicaudus*. This grouping of acoustic characteristics matches the phylogenetic relationships among these species (Parmentier et al. 2009b).

In the comparison of *D. trimaculatus*, *D. aruanus* and *D. flavicaudus*, significant differences in temporal characteristics (pulse period and interpulse interval) were also found between populations of sympatric species from Moorea in French Polynesia (*D. trimaculatus*, *D. aruanus*, and *D. flavicaudus*) and from Toliara in Madagascar (*D. trimaculatus* and *D. aruanus*) supporting the existence of dialects (Parmentier et al. 2009b). For example, the pulse period and pulse length of *D. trimaculatus* and *D. aruanus* are longer in Moorea than in Tulear. Playback experiments are however required in order to test the fish behavior and know if these statistically supported differences are important for the fish identification.

Interestingly, the temporal acoustic parameters concerning the fourth species (*D. albisella*), that lives in Hawaii and does not co-occur with other *Dascyllus* species, overlap all other *Dascyllus* and cannot be clearly distinguished. In the regions where they live in sympatry, it appears that *Dascyllus* species restrict the variability in their sounds. This could be evidence of adaptation with character displacement of sonic characteristics where different species co-occur (Parmentier et al. 2009b). Next to the sounds, the difference in the courtship dance during sound production can also aid species discrimination between sympatric species. In *D. carneus*, *D. albisella*, *D. flavicaudus* and *D. trimaculatus*, the swimming fish turns abruptly at a right angle and begins the dive to the side. In *D. aruanus*, the male stops swimming, makes a forward rotating movement by raising the caudal fin, and then swims rapidly downward (Parmentier et al. 2009b). In contrast to *D. aruanus*, these species change their coloration during the jump: the anterior part of their body becomes chocolate brown. However, the large white band behind the eye can become greyish in the biggest *D. aruanus* during the dips (pers. com.). Other modalities, such as vision (i.e., recognition of species-specific postures and coloration), probably augment any discrimination process in reproduction.

Another way to avoid any overlap in the communication channel would be to produce sounds at different periods of the day (Fig. 5). Study of the daily cycle in *D. flavicaudus* showed that this species made sounds mainly during the day with a

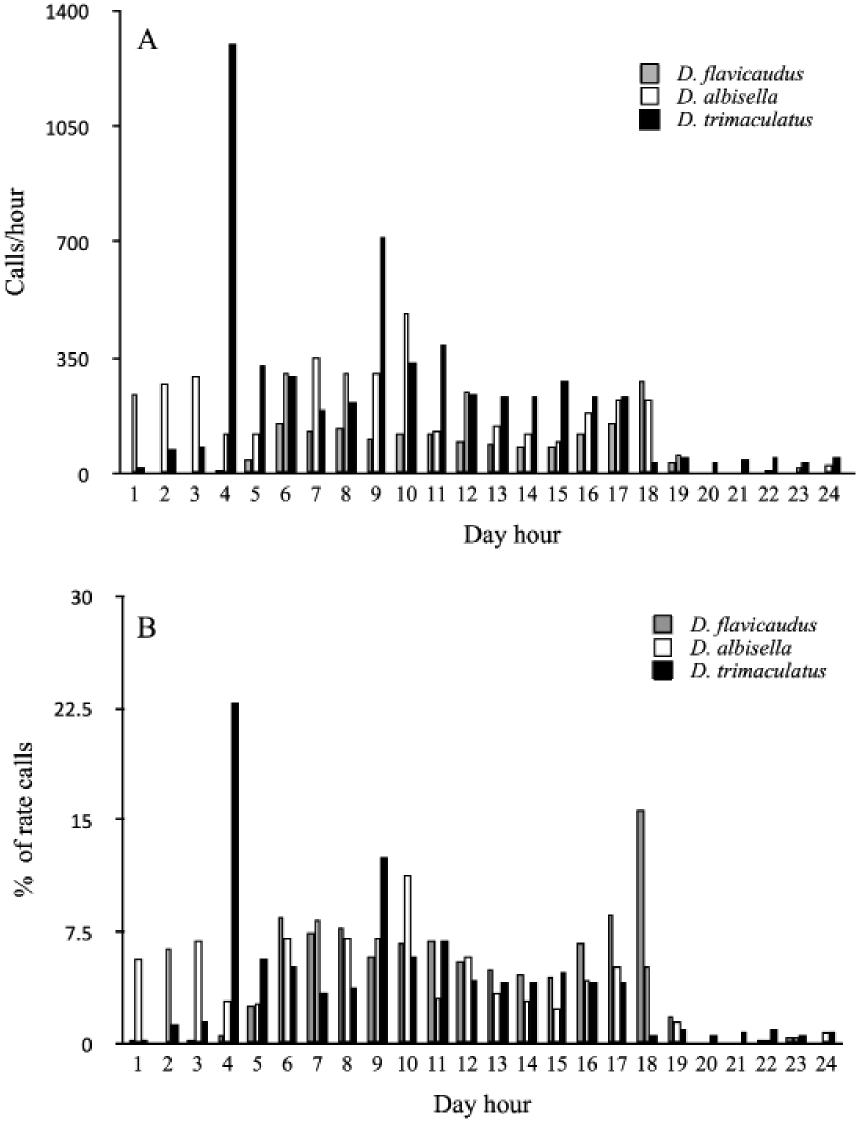

Fig. 5. Daily activity of sound production in three species of Pomacentridae. (A) Mean number of calls produced by hour and (B) ratio of the acoustic activity along the day. Data for *Dascyllus flavicaudus* are from Parmentier et al. (2010) and data for *Dascyllus albisella* are from Mann and Lobel (1997). Data concerning *D. trimaculatus* were acquired during November 2013 in Moorea. The number of recorded specimens is not the same, meaning we cannot assert from this graph that a species is calling more or less than another one.

peak of activity at sunset and a second, higher one, at sunrise (Parmentier et al. 2010). This pattern differs from that of *Dascyllus albisella*, which produces sounds mainly in the morning (Mann and Lobel 1995). Sound production was also detected at night in this species and peaked just before spawning. *Dascyllus albisella* and *D. flavicaudus* are however not sympatric. In November 2013, we studied the daily rhythm of *D. trimaculatus* in order to compare it with its sympatric species *D. flavicaudus*. Recording of daily cycles in *D. trimaculatus* followed the method applied in *D. flavicaudus* (Parmentier et al. 2010). Recordings were made with a Digital Spectrogram Recorder (DSG, Loggerhead Instruments Inc.). The DSG recorder is a long-term, low-power recorder of acoustic signals. The system was scheduled to record for 10 min every 60 min. DSG had been placed during four days next to a group of 8 adult specimens. Sounds were digitized at 22 kHz (16-bit resolution), low-pass filtered at 2 kHz and analyzed using AvisSoft-SAS Lab Pro 4.33 software. Manual analysis consisted simply of identifying and counting the *D. trimaculatus* sounds. The question was to know if sympatric and closely related species share the acoustic daily activity in the same way or not. It appears that *D. trimaculatus* produced sounds mainly around 04:00 h, whereas the main peak of sound production was 18:00 h in *D. flavicaudus* (Fig. 5A). Both species produced few sounds during the night and called most during the day. *Dascyllus trimaculatus* produced more calls than *D. flavicaudus*. However, many factors (spawning, fish number in the colony, etc.) could affect the call rate (Oliver and Lobel 2013), so we also calculated the percentage of call rate during the day for each species (Fig. 5B). This confirms both peaks of calling activity, but it also shows that the time devoted to diurnal calls is roughly the same in the two species. It is worth mentioning that *Dascyllus* species are very prolific callers, they can repeat their sounds hundreds to thousands of times a day (Lobel and Mann 1995, Parmentier et al. 2010), so it is possible that a female could sample many calls before making a decision to spawn with a given male.

The next set of experiments supporting the importance of temporal parameters in sounds, and more precisely the pulse period, can be found in clownfish. Contrary to *Dascyllus* and *Stegastes*, fish from this taxa do not make sounds during courtship or reproduction but mainly during aggressive and concomitant submissive behaviors (Colleye and Parmentier 2012). Agonistic sounds were recorded and compared in fourteen clownfish species (Colleye et al. 2011). Pulse duration and dominant frequency did not help in differentiating the species, because there is a size-related intraspecific variation in dominant frequency and pulse duration: smaller individuals produce higher frequency and shorter duration pulses than larger ones, whatever the sexual status (Colleye et al. 2009). Surprisingly, the relationship between the fish size and both dominant frequency and pulse duration is not species-specific: all the specimens of the 14 species are situated on exactly the same slope. It means that the size of any *Amphiprion* can be predicted by both acoustic features and that the sound-producing mechanism is highly conservative. According to previously described methods (Colleye et al. 2011), we have analyzed the pulse period of an additional species (*Amphiprion sandaracinos*) for the purpose of this book chapter and it confirms this relationship. Such detailed data has not been collected for different species of the same genus in fishes. However, the same kind of relationship between size and dominant frequency was also found in *Dascyllus albisella* (Lobel and Mann 1995) and in *Stegastes partitus* (Myrberg et al. 1993). In the clownfish species, the number of pulses also broadly overlaps among species and does not help in differentiating between species. Once more, the pulse period appears to be useful because it displays the most variation between species and the least variability within species (Fig. 6), even if it shows overlap among sympatric species (Colleye et al. 2011). Again, these results have to be carefully considered because other environmental characteristics can help in differentiating between species: the different clownfish species live in different parts of the world, are not all found in the same sea anemone species, and can have different diet and different coloration patterns (see Chapter XIII). Interestingly, several species (*A. sandaracinos*, *A. akallopisos* and *A. perideraion*), that have lost their vertical bands, that are phylogenetically closely related (Santini and Polacco 2006, Litsios et al. 2012) and that can cohabit in individual sea anemones (i.e., *A. sandaracinos* with *A. chrysopterus* in the region of Madang, or *A. perideraion* with *A. clarkii* in the region of Okinawa) are all characterized by a smaller pulse period (Fig. 6) than other *Amphiprion* species. As previously stated, non-overlapping in this character may have been important in the taxon diversification. However, pulse period is not systematically significantly different among sympatric species: *A. clarkii*, *A. frenatus* and *A. ocellaris* have the same pulse period range (Colleye et al. 2011) while living in sympatry on the fringing reef around Sesoko island (Hattori 1991). These three species inhabit different host species, being *Heteractis crispa* for *A. clarkii*, *Entacmaea quadricolor* for *A. frenatus* and *Stichodactyla gigantea* for *A. ocellaris* (Hattori 1991, 1995), which suggests that overlap in pulse period among these species is of minor importance. Comparing *Dascyllus* and *Amphiprion* species (Figs. 4 and 6) shows that the shortest pulse period in anemonefishes is longer than the longest pulse period of *Dascyllus* species.

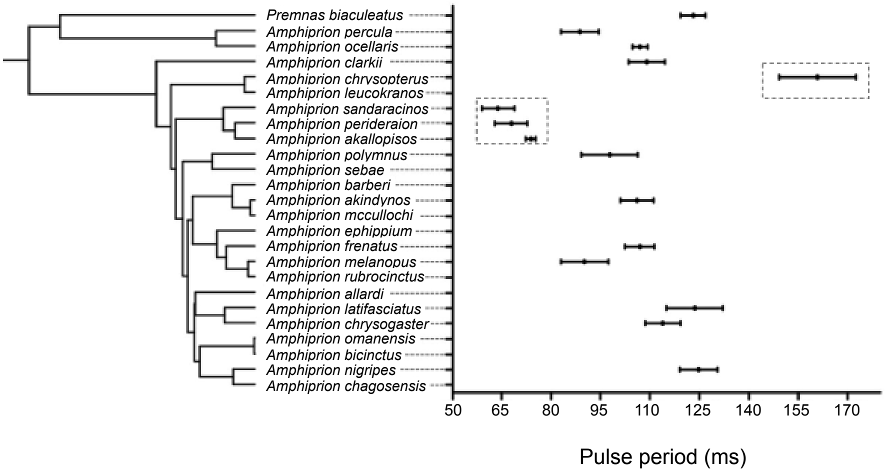

Fig. 6. Confrontation between the clownfish phylogeny (simplified figure from Litsios et al. 2012) and variation of pulse periods in 15 clownfish species (most data from Colleye et al. 2012). Results are represented as means ± 95% confidence intervals. Dotted line rectangles show that the pulse periods of some species are completely isolated from the rest of the taxa. Interestingly three closely related species have the shortest pulse period.

In the clownfish taxa, the dominant frequency of the calls could however be important at the intraspecific level. Within each clownfish species, the sex is controlled socially and there is a size-based dominance hierarchy: the breeding female is the largest individual, the breeding male is the second largest and the non-breeders get progressively smaller as the hierarchy descends (Fricke 1979, Buston 2003a, Buston and Cant 2006). The size hierarchy forms a queue to attain dominant status; individuals only ascend in rank when a higher rank individual disappears, and the smallest fish in the group is always the most recent recruit (Chapters IV and XII). The size-related variation in dominant frequency implies that smaller individuals produce higher frequency sounds than larger ones. Consequently, these sonic features might be useful cues for individual recognition within the group and may convey information on the social rank of the emitter within the group (Colleye et al. 2009, Colleye and Parmentier 2012).

Relationship between Sound Production and Spawning

Most of the sound production in *Dascyllus* is carried out by males during advertising and courtship behavior (Lobel and Mann 1995, Parmentier et al. 2010). The distance these calls are detectable is likely on the order of <15 m (Mann and Lobel 1997). Thus, it is a local communication signal and the receiving fish would have to be close by to detect the sound. *Dascyllus albisella* can make up to 3000 calls per day just prior to spawning (Mann and Lobel 1995). If each dip involves 1 m of swimming, this would mean that the fish would swim 3 km in one day. The rate of calling changes over the spawning cycle, with the highest levels occurring just before spawning (Mann and Lobel 1995). Since each of these sounds is accompanied by a courtship dip, these calls could act as an honest signal of male quality. This is an important assessment for females to make, since the males will guard their eggs in the nest for several days prior to their hatching into planktonic larvae (Oliver and Lobel 2013).

Different metrics of male quality including dominant frequency, inter-pulse interval, pulse duration, pulse number or calling rate were correlated with the measure of mating success in *D. albisella* (Oliver and Lobel 2013). It showed that females would choose mates based on the courtship rate of males. These experiments concerned both visual (dips) and acoustic cue meaning playback experiments should determine the relative contributions of the acoustic and visual modalities to the success of the courtship display (Oliver and Lobel 2013). However, it remains that acoustic call structure does not seem implied in the mating success, meaning that the phenotypic differences between males cannot be clearly explained in the courtship behavior framework.

Mechanism and Hypothesis about Damselfish Sound Production

Despite the numerous studies on sound production in pomacentrids, the nature of the sound-producing mechanism has remained unresolved for a long time, only resting on few assumptions. Some authors claimed that sound was produced by rapid up-anddown movements of the opercula and by the movements of the mouth bones related to taking food (Verwey 1930, Takemura 1983). Others implied that sound was produced by grating pharyngeal teeth, and could then be amplified by the swimbladder (Luh and Mok 1986, Chen and Mok 1988, Rice and Lobel 2003). Sounds produced by *Abudefduf luridus* were thought to involve a swimbladder mechanism (Santiago and Castro 1997), but the authors do not specify whether they believe this mechanism involves extrinsic muscles attached to the swimbladder.

Aggressive sounds emitted by the clownfish *Amphiprion clarkii* result from rapid mouth closing movements (Parmentier et al. 2007). This fast jaw slam is enabled by the cerato-mandibular (c-md) ligament joining the lateral side of the hyoid bar to the medial side of the mandible (Chapter XIV). Briefly, once the mouth is opened, the ligament acts as a cord, forcing the mouth to close and the teeth to snap resulting in the production of sound.

The mechanism can be summarized in 4 phases and highlights that both opening and closing of the mouth can be produced through a single set of movements (Olivier et al. 2014). (1) In the initial phase, the mouth is closed, the neurocranium is lowered and the hyoid apparatus is not depressed. In this situation, the cerato-mandibular ligament is loose and cannot apply any traction on the lower jaw. (2) During the aperture phase, there is an elevation of the neurocranium which mechanically involves the lower jaw and branchial basket depression, a phenomenon well known in fish feeding (Osse 1969, Van Wassenbergh et al. 2005). (3) Rather than accentuating this movement, a higher amplitude elevation of the head actually forces the mandible to rotate around its quadrate articulation and the mouth to close rapidly (5 ms) in a slam. This movement is due to the backward movement of the branchial basket that causes the c-md ligament to tighten and the traction on the lower jaw (Parmentier et al. 2007). The teeth collisions caused by rapid jaw closure correspond only to the onset of the sound. (4) The swimbladder was shown to be a highly damped sound source prevented from prolonged vibrations and could not in this case be the resonator (Colleye et al. 2012). The acoustic radiator results probably from a vibrational wave due to buccal jaw snapping and is likely transferred to the rib cage via different functional units of the skeleton such as the suspensorium, the neurocranium and the vertebral column. Mobile ribs vibrate and drive the oscillations of the swimbladder wall (Colleye et al. 2012).

Since the c-md ligament is a synapomorphic trait of the damselfish family (Stiassny 1981) and because the sounds were recorded in basal clades (Lepidozyginae) such as in *Plectroglyphidodon lacrymatus* (Parmentier et al. 2006) and different *Stegastes* species (Myrberg and Spires 1972, Ha 1973, Spanier 1975, 1979, Myrberg et al. 1978, 1986, 1993), it was assumed all the pomacentrid species are able to make sounds. However, more than 120 species were dissected and some of them did not have the ligament. Stochastic mapping of this synapomorphic trait on a time-calibrated phylogeny of damselfishes suggests that the c-md ligament disappeared at least three times (within Chrominae, Abudefdufinae and Pomacentrinae). More surprisingly with regard to our hypothesis, some species lacking the c-md ligament are not muted and can produce pulsed sounds. Most of the time, the sound duration in pomacentrids is correlated to the number of pulses indicating that calls have a relatively constant pulse period (Lobel and Mann 1995, Parmentier et al. 2006) and that the mechanism of sound production can be repeated at regular intervals. Sound parameters were compared between

11 species having the c-md ligament and two species (*Chromis viridis* and *Chromis atripectoralis*) lacking the c-md ligament (Frédérich et al. 2014). Since all studied species displayed the same type of sound spectra and oscillograms, their sounds seem to be produced in a similar way. *Chromis viridis* and *C. atripectoralis* can generate pulsed sounds by mouth closing but they have to use a different motor pattern than clownfishes and the other species having the c-md ligament (Frédérich et al. 2014). Interestingly, both *Chromis* which do not possess the c-md ligament, show the highest standard deviation around the mean value of pulse period (SD > 36 ms) in comparison with all the other studied species (SD ≤ 30 ms). The inconstancy of pulse periods in *C. viridis* and *C. atripectoralis* seems to be related to the absence of the c-md ligament. Indeed, mouth opening and closing in these species could be achieved by different muscles (e.g., epaxial, sternohyoideus, adductor mandibulae muscles) complicating the synchronization and the temporal pattern. The coordination of such a system is expected to be more variable than the c-md ligament system allowing the opening and rapid closing of oral jaws by the lonely continuous backward movement of the hyoid bar (Parmentier et al. 2007). A high variation in the pulse period is also shown or suggested in different *Abudefduf* species (Santiago and Castro 1997, Lobel and Kerr 1999, Maruska et al. 2007). See for example Fig. 5 in Rice and Lobel (2003). We have dissected *Abudefduf sordidus*. In this species, there is no ligament between the hyoid bar and the lower jaw as is the case in most of pomacentrids. However, there is a tendon on the geniohyoideus that inserts on the angular of the lower jaw. This muscle could play a role in the production of sounds. Beyond the functional aspect of sound mechanism, this inconstancy in pulse period can be perceived as a species-specific acoustic cue in *Chromis* and *A. sordidus* as well as a more constant length of pulse period in others. This variation between species with and without the c-md ligament is a source of diversity in the acoustic repertoire of the family (Frédérich et al. 2014).

The teeth collision (with or without c-md ligament) mechanism that we have described should be the basic mechanism of dip and aggressive sounds of at least the species belonging to *Dascyllus*, *Stegastes*, *Pomacentrus*, *Chromis*, *Abudefduf*, *Plectroglyphidodon*. This mechanism is also used for the production of agonistic sounds in the *Premnas* and *Amphiprion* species.

Clownfish species are also able to produce another kind of sound (called submissive sounds) emitted when fish make head shaking movements (Parmentier et al. 2005, Colleye and Parmentier 2012). Generally speaking, submissive sounds are completely different from aggressive ones. They are always composed of several pulses forming units produced alone or in series, whereas aggressive sounds are composed of a single pulse unit that can be emitted alone or in series (Fig. 1B). They also exhibit shorter pulse periods and shorter pulse durations than aggressive sounds (Colleye and Parmentier 2012).

The importance of sound production in damselfish could be due to their way of life. Most of them establish permanent or temporary territories. Sounds generally occur simultaneously with aggressive actions either during pair-encounters or are produced by territorial residents as they encounter intruders. That vocalizations play an important role in territorial defense has been experimentally demonstrated in both avian and piscine species (Myrberg 1997). So long as territorial individuals could produce sounds, they maintained their territorial boundaries; however, muted individuals were unable to deter intruders from entering their shelter sites, despite appropriate visual displays (Myrberg 1997).

By comparing in detail, the movements related to sound production and those related to biting in *Amphiprion* and *Stegastes*, we can reasonably postulate that sound production in pomacentrid results from the exaptation of feeding movements. Exaptation refers to a functional character previously shaped by natural selection for a particular function and that has been coopted for a new use (Gould and Vrba 1982, Larson et al. 2013). Pops are used in different combinations during different behaviors, but are constructed on the basis of the same mechanism involving the c-md ligament. The parsimony principle implies that this ancestral call was made of only one pulse.

Among the behaviors of all the species that we have examined, one is related to fighting and is mainly made of only one pulse, corresponding to a single jaw slam. The origin of the sound could be found in biting, because fighting sounds usually occur before the display of aggressive behavior with biting (Parmentier et al. 2010). Moreover, single pulse sounds can also be heard in *Plectroglyphidodon* and *Stegastes* species giving teeth strokes while simply grazing algae on their territories (Chapter XIV). This grazing activity also results from a mechanical single slam. We hypothesize that sounds in pomacentrids were first produced incidentally as a by-product of foraging and/or fighting activities. Single sounds were then selected because they resulted in successful territory and nest defense. Currently, one or two pulses are still used to deter conspecifics and heterospecifics. Because dip or visiting calls are made of trains of pulse, it is quite easy to postulate they should result from the repetition of the same motor pattern.

Sonic Behavior

Sounds can be used in different behavioral contexts that are not well defined in all damselfish. Here we review already studied species and we also include data concerning seven species that we have video recorded during field missions to Moorea Island (French Polynesia) and Madagascar. *Pomacentrus pavo*, *Plectroglyphidodon lacrymatus*, *Chromis viridis*, *Chromis atripectoralis*, *Stegastes nigricans* and *Stegastes punctatus* were recorded in Moorea during January and February 2009. *Dascyllus carneus* were recorded in Madagascar during June 2011. *Dascyllus reticulatus* were recorded in Dongsha atoll (Taiwan) during May 2015. The way we have recorded and analyzed the sounds follows the previous studies on *Dascyllus* and different clownfish species (Parmentier et al. 2010, Colleye and Parmentier 2012). Recording sessions, each lasting from 1 to 4 h, were made at a depth of between 1 and 5 m. Recordings of sound production were made using a SONY HDD video camera placed in a housing (HC3 series, Ocean Images, Cape Coral, Fl) and coupled with an external hydrophone (High Tech. Inc., HTI-96) with a flat response of 20 Hz to 20 kHz. Recordings were made by placing the housing in front of the coral patch. Sounds were extracted in .wav files using the AoA audio extractor setup freeware. Sounds were digitized at 44.1 kHz (16-bit resolution), low-pass filtered at 1 kHz and analyzed using AvisSoft-SAS Lab Pro 4.33 software. Only the sounds with a good signal to noise ratio were used in the analysis. The following sound parameters were measured: sound duration; number of pulses in a sound; pulse period (measured as the average peak-to-peak interval between consecutive pulses in the entire sound; pulse length (measured as the time from the beginning of one pulse and its end); dominant frequency.

Abudefduf

Abudefduf species produce aggressive sounds towards both conspecific and heterospecific intruders while nest guarding, preparing a nest substrate or during courtship while trying to attract a female for spawning. Sounds are mainly produced by males that can be distinguished by territorial behavior and by adoption of courtship/spawning coloration. *Abudefduf* also seem to differ from other genera in the way they form a nuptial parade. The male does not produce signal jumps but performs vigorous horizontal swimming, looping and then zigzags to motivate the female to follow him back to the nest (Lobel and Kerr 1999, Maruska et al. 2007). These courtship displays are not associated with sound production in *Abudefduf abdominalis* (Maruska et al. 2007) but they are in *A. sordidus* (Lobel and Kerr 1999, Lobel and Lobel 2013) and *A. luridus*[1] (Santiago and Castro 1997). In *A. abdominalis* and *A. vaigiensis*, two sounds produced during agonistic encounters with conspecific and heterospecific individuals were an aggressive short pulse (52–88 ms, <500 Hz) identified by 1 to 2 pulses per sound and longer pulse trains identified by more than 2 pulses (Maruska et al. 2007, Tricas and Boyle 2014). In both species, Tricas and Boyle (Tricas and Boyle 2014) described an additional agonistic high-frequency single pulse sound of short duration (18−23 ms) and high peak frequency (805–1162 Hz).

Circadian rhythms were only studied in *A. luridus*: the major proportion of sounds was recorded around sunrise and sunset (Santiago and Castro 1997). As in *Chromis viridis* and *C. atripectoralis*, *Abudefduf* species present a characteristic that allows distinguishing their calls easily from the other pomacentrids: their calls do not exhibit a consistent repeated pattern at the level of the pulse period (Lobel and Kerr 1999, Maruska et al. 2007). In *A. luridus*, it is not possible to establish a relationship between the number of pulses emitted and the pulse period (Santiago and Castro 1997).

Amphiprion and *Premnas*

Clownfishes live in social groups composed of a breeding pair and between zero to four non-breeders. Within each group, numerous agonistic interactions occur and they appear to play an important role by maintaining size differences between individuals adjacent in rank (Fricke 1979, Buston 2003b). Larger fishes chase smaller ones, which means that the smallest one is the recipient of numerous charges (Fricke 1979). All clownfish species have evolved ritualized threats and submissive postures that presumably serve to circumvent physical injury during intraspecific quarreling (Allen 1972). During threat postures, resident fish can face, charge and chase an intruder. Several authors (Schneider 1964, Allen 1972, Fricke 1974) have also highlighted the existence of a typical behavior (commonly called “head shaking”) as a reaction

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[1] According to the display description they give, we think these authors wrongly assume they observed aggressive behaviours.

to aggressive interactions. This behavior consists of a lateral quivering of the body that begins at the head and continues posteriorly. Clownfishes were also reported to produce sounds during both agonistic and submissive interactions (Schneider 1964, Allen 1972, Chen and Mok 1988, Parmentier et al. 2005).

Agonistic sounds are produced by individuals of different sexual status (females, males and non-breeders) who display charge-and-chase reactions when another hetero- or conspecific approaches the sea anemone in which they dwell (Colleye et al. 2009). Sound production in clownfishes can be traced back as early as 1930 when Verwey stated that *A. akallopisos* and *A. polymnus* could produce sounds (Verwey 1930). Studies were thereafter expanded to include different *Amphiprion*, and it has been noted that they produced sounds while swimming, feeding, associating with anemones, and particularly when fighting for an anemone (Schneider 1964, Takemura 1983, Parmentier et al. 2005). Further insight into the description of sounds was provided since two distinct sounds were differentiated based on their duration, frequency range and repetition of pulses (Allen 1972). Aggressive sounds are mainly produced by dominants during charges, chases and threat displays between conspecifics during agonistic interactions (Colleye et al. 2009), whereas submissive sounds (chirps) are always emitted when subordinates exhibit head shaking movements in reaction to aggressive displays by higher-ranking individuals (Colleye and Parmentier 2012). Therefore, both types of sounds seem to be an integral part of the agonistic behavior in clownfishes. Currently, 14 species (including *Premnas biaculeatus*) have been recorded and the sounds analyzed (Colleye et al. 2011). For the purpose of this chapter we have also recorded the sounds of *Amphiprion sandaracinos*.

In addition to these behaviors, it was also reported that clownfishes might produce sounds during courtship. Courtship in clownfishes is generally stereotyped and ritualized, and is typically accompanied by different activities such as nest cleaning, spawning and nest care (Allen 1972). Basically, studies that describe the courtship sounds of clownfishes are limited in number. To date, sound production during reproductive periods has been reported in three clownfish species: *A. ocellaris*, *A. frenatus* and *A. sandaracinos* (Takemura 1983). However, these observations need to be carefully considered since, according to the author, the sounds were hardly heard and sometimes they do not seem to be directly related to spawning behavior. Moreover, the behavioral relevance of these data are somewhat doubtful since the three species would emit sounds with high frequency components of more than 2 kHz during reproduction, a frequency these fish cannot hear (Parmentier et al. 2009a). These sounds could just be a by-product of the nest cleaning activities. In addition, spawning events were observed and recorded in *A. akindynos*, *A. melanopus* and *A. percula* living in tank, in *A. clarkii* living in semi-natural condition and in *A. perideraion* living in the field. All these observations correspond to a total of 13 complete spawning events. Overall, the absence of sound production throughout all activities of the reproductive period was complete (Colleye and Parmentier 2012). Unlike other pomacentrids, sounds are not produced for mate attraction in clownfishes. It is likely an evolutionary outcome related to their peculiar way of life: these fishes form small social groups including only one mating pair, inhabit a restricted territory (the sea anemone), spend most of the time in close vicinity of their host and rarely interact with other species on the reef. On the other hand, sounds seem to be important in order to reach and to defend the competition for breeding status.

Chromis

Chromis damselfishes are planktivorous species that usually live in aggregations and schools (Pinnegar et al. 2007, Frédérich et al. 2009), but solitary fish can also be found defending small areas around rocky ledges and crevices. These territorial individuals chase away other *Chromis* and other species. The number of territorial individuals increases greatly during the spawning period (Myrberg et al. 1967). In different species, males spawn repeatedly with different females. They synchronously establish territories, prepare nests and court females through visual and acoustic display (Abel 1961, Picciulin et al. 2001, 2004). Females lay demersal eggs that are guarded and fanned by males until hatching. When eggs have concluded hatching, males abandon the nests and rejoin the feeding school (Picciulin et al. 2004).

In *Chromis chromis*, sounds are composed of a single pulse and are associated with aggressive behavior and the dip (Picciulin et al. 2001). Pulse train sounds were recorded for threespot chromis *Chromis verater* during agonistic interactions with a conspecific (Tricas and Boyle 2014).

Sounds with between 1 to 22 pulses (pulse duration 8 ms, pulse period 7 ms) were produced in tanks during agonistic interactions in *Chromis viridis* (Amorim 1996). The sounds of two sister-species, *Chromis viridis* and *Chromis atripectoralis* (Froukh and Kochzius 2008), were recorded in the field (Frédérich et al. 2014). Different behaviors were observed. Sounds associated with conspecific chases were recorded in *C. atripectoralis* but not in *C. viridis*. Sounds produced during conspecific chases had 4 to 6 pulses with a pulse period of 36 ± 7 ms. During conspecific fighting, both fish rotated around a common axis while attempting to bite the opponent. Sounds associated with chases were restricted to 1 to 2 pulses in both species in the majority of the cases. In *C. viridis*, sounds can be produced during the ascending or descending (81.3% of the cases) phases of the signal jump. During the signal jump, males become yellow, and black areas appear on the pectoral fins. Dip sounds have between 3 and 13 pulses (7 ± 3, n = 32) with a duration of 8 ± 3 ms (n = 196), and the period is highly variable (81 ± 51 ms, n = 183). In *C. atripectoralis*, the color pattern becomes dull during signal jumps. Dip sounds in this species have between 1 and 17 pulses (6 ± 5, n = 18) with a duration of 10 ± 8 ms (n = 103) and a highly variable pulse period (47 ± 20 ms, n = 183). The peak frequency was 661 ± 205 Hz (n = 196) in *C. viridis* and 790 ± 296 Hz (n = 107) in *C. atripectoralis*, but the fish sizes were not measured. Both species also have an unknown characteristic: dip sounds made during signal jumps can be composed of several pulse trains that are randomly emitted during the movements. These sequences appeared in 31% of the signals in *C. viridis* and 37.5% in *C. atripectoralis*. Pulse duration and peak frequency of sounds from *Chromis viridis* of Moorea were similar to sounds previously described from tank recordings (Amorim 1996). However, there is a large difference in the pulse period (81 vs. 8 ms) between both sets of data.

Sounds are also likely to be emitted by other *Chromis* species in which at least signal jumps have been observed: *C. multilineata* (Myrberg et al. 1967), *C. notata*

(Ochi 1985), *C. cyanea* (Albrecht 1969), *C. caeruleus*, *C. verater*, *C. ovalis* (Swerdloff 1970) and *C. iomelas* (pers. obs.). No signal jump was observed in *Chromis dispilus*. However, they have a comparable visual signal consisting of rapid alternate expansion and relaxation of the caudal fin, causing a distinctive flashing of the white margin along the inner edge of the tail (Russell 1971).

Dascyllus

Dascyllus species were the subject of numerous studies around the world and constitute probably one of the most complete descriptions of sounds related to different kinds of behavior. *Dascyllus albisella* was recorded in Johnston atoll and Hawaii (Lobel and Mann 1995), *D. flavicaudus* in Rangiroa and Moorea (Parmentier et al. 2009b, Parmentier et al. 2010), *D. aruanus* and *D. trimaculatus* in Rangiroa, Moorea and Madagascar (Parmentier et al. 2009b) and, finally, *D. carneus* in Madagascar (pers. obs.).

Different kinds of sounds were reported within the same *Dascyllus* species. In *D. albisella*, males produced pulsed sounds during the courtship behavior known as the signal jump, when visited by females (during pseudospawning), mating, and aggression towards heterospecifics and conspecifics, and nest preparation (Mann and Lobel 1998). Females made only aggressive sounds in this species. Sounds associated with fighting; mating/visiting, chasing and signal jumps were also recorded in *D. flavicaudus* (Parmentier et al. 2010). In both species, characteristics of the sounds related to different behaviors show significant differences (Lobel and Mann 1995, Mann and Lobel 1998, Parmentier et al. 2010), highlighting that acoustic features should be sufficient to infer the corresponding behavior.

Two studies provided data on the calling rate. In *D. flavicaudus*, daily recordings showed that sound production rates were higher at sunrise and sunset than during the day and that no sound was produced during the night (Parmentier et al. 2010). In *D. albisella*, sound production peaked each day at dawn. However, sound production was detected at night and was most intense just before spawning. The highest rates of sound production occurred on the day before and the day of egg-laying (Mann and Lobel 1995). In this species, sound production rates are also higher during their reproductive season (April) than during the non-reproductive season (October).

Specimens of *D. carneus* and *D. reticulatus* were recorded for the first time in Madagascar and Dongsha atoll respectively (see also above). In calling males we did not notice deep color changes in *D. reticulatus*, but it was marked in *D. carneus*: the anterior part of its body became chocolate brown during the signal jump. In *D. carneus*, the pulse length was (on average ± SD) 17 ± 4 ms (n = 185), the pulse period 40 ± 8 ms (n = 150) and mean dominant frequencies 753 ± 188 Hz. In *D. reticulatus*, the pulse length averaged 16 ± 3 ms (n = 110), the pulse period 35 ± 3 ms (n = 160) and the mean dominant frequency was 812 ± 110 Hz (n = 144).

Plectroglyphidodon

Plectroglyphidodon spp. are territorial species having a major influence on the algal communities within their territories through the exclusion of other herbivorous taxa from their territories (Brawley and Adey 1977) and/or farming activities corresponding to the selective removal of undesirable algae, active site selection, and fertilization (Ceccarelli et al. 2005, Hoey and Bellwood 2010, Emslie et al. 2012). To date, sounds have been recorded from *Plectroglyphidodon lacrymatus*, where sounds were originally recorded from three fish in an aquarium in Madagascar (Parmentier et al. 2006). Sounds were produced only when an observer approached the tank. The fish that was apparently responsible for making the sound faced the observer and spread its pectoral fins, showing an aggressive behavior, probably in relation to the defense of the territory. Sounds were produced in trains of two to five pulses (mean duration of each pulse: 56 ms), with a mean pulse period of 179 ms. Recordings of *P. lacrymatus* living in adjacent territories in Moorea enable the description of other sonic behaviors. Sounds were also recorded during signal jumps, conspecific chases and heterospecific fighting. During signal jumps, *P. lacrymatus* rise in the water column and then rapidly swim downwards while producing a pulsed sound. During chasing or fighting, calls are made consisting of one to two pulses. Dip sounds were composed of three to nine pulses with a pulse duration of 15 ± 3 ms (n = 137) and pulse periods of 75 ± 12 ms (n =107). The large difference in the pulse duration between both populations (Madagascar and Moorea) could be due to the resonating tank effect in Toliara. The difference between the pulse periods of both regions could be due to behavior (agonistic vs. signal jump) but is most probably related to geographic distribution (Parmentier et al. 2009b).

In Hawaii, *Plectroglyphidodon johnstonianus* produce sounds directed towards neighboring conspecifics and heterospecifics (Tricas and Boyle 2014). Different kinds of sounds were described in this species. Single pulse sound or pulses produced in a train seem to correspond to sounds described in other damselfish species. The authors also reported for the first time “a half pulse sound waveform” corresponding to a distinctive single, strong, and rapid negative peak followed by a slower positive half cycle. These half pulses can be emitted in trains or not. Two kinds of growls are also described. They would occur as a series of contiguous pulses. Both growls can be distinguished on the basis of pulse rate and pulse amplitude (Tricas and Boyle 2014). Future studies are however required because few sounds were recorded.

Pomacentrus

Sounds were recorded in *Pomacentrus pavo* for the purpose of this chapter. These data however have to be considered carefully because the number of observations was limited, it concerned individuals coming from two different groups. *Pomacentrus pavo* live in small groups around coral patches but males cluster during the reproduction (pers. obs.). During reproduction, males isolate and defend small territories that are crevices within coral patches or shelters in the sand. In contrast to the nesting behavior of *Dascyllus* and *Amphiprion* which nest on the substrate, *P. pavo* nest in it. Courtship consists of signal jumps that can be accompanied by sounds in some cases. In this case, the sound is single pulsed and is made at the lower end of the signal jump. A second jump can directly follow and, in this case, the sound is again made at the lower end of the dive. Similar movements were observed in *Pomacentrus nagasakiensis* and grunting sounds were heard during female enticement (Moyer 1975). These sounds were however not described. Single pulses were also emitted during fights with conspecifics and sounds of two to three pulses were made during chases. There were two kinds of chases: males towards conspecifics, and males attempting to attract a female to their nests that chased and dipped in alternation. On three occasions, multiple-pulsed sounds (from 6 to 8 pulses) were emitted when the female entered and visited the nest. We could not observe the behavior inside the nest and do not know if it corresponds to spawning or to the visiting sound described in *Dascyllus albisella* (Mann and Lobel 1998) or in *Abudefduf abdominalis* (Maruska et al. 2007). We did not observe modifications of the color pattern during the signal jumps, the agonistic interactions or the female visit. The pulse duration was (mean ± SD) 17 ± 4 ms ($n = 89$). There was a difference between the pulse lengths of fighting (8 ± 2 ms, $n = 3$) and both signal jump (18 ± 4 ms, $n = 32$) and chases (17 ± 4 ms, $n = 31$). However, the small number of fighting pulses should prompt us to be cautious. Pulse periods from sounds produced during signal jumps were significantly longer (217 ± 58 ms, $n = 14$; Mann-Whitney $p < 0.05$) than during visiting (133 ± 37 ms, $n = 20$).

Stegastes

Stegastes species hold permanent territories and culture filamentous algae on dead corals. This farming involves selective weeding of algae in order to maintain algal communities that are distinct from the surrounding undefended substratum (Ceccarelli et al. 2005, Ceccarelli 2007). This taxon is particularly well known for active sound production in many different behavioral contexts such as courtship, territorial defense (against conspecifics and heterospecifics), chases and "keep-out" signals (Myrberg and Spires 1972, Ha 1973, Spanier 1975, 1979, Myrberg et al. 1978, Myrberg 1997). *Stegastes* have been used for different pioneering ethological experiments that were conducted on the Caribbean species *S. dorsopunicans*, *S. planifrons*, *S. leucostictus* and *S. partitus* (Spanier 1975, Myrberg et al. 1978, Spanier 1979). These experiments allowed the identification of signal characteristics that can help in species recognition. Different kinds of sounds have also been recorded in *Stegastes lividus* in Taiwan (Mok, pers. com.) and in the Hawaiian gregory *S. marginatus* during algal turf feeding and breeding territories (Tricas and Boyle 2014). In a tank, *S. rectifraenum* calls were also associated with shelter defense or biting filamentous algae. Pulse durations were significantly longer when biting filamentous algae but no significant difference was found between dominant frequency of calls and bites (Olivier et al. 2014). In the sympatric species *Stegastes nigricans* and *Stegastes punctatus* of French Polynesia, differences were also found in case of the Caribbean species. The sounds of *S. nigricans* were significantly (Mann-Whitney, $p < 0.01$) different from that of the *S. punctatus* on the basis of the pulse period (mean ± SD, 48 ± 11 ms, $n = 47$ vs. 63 ± 15 ms, $n = 51$) but not the pulse duration (Mann-Whitney, $p = 0.055$). Both species also significantly differed in the dominant frequency of sounds, probably because the specimens of *S. nigricans* (342 ± 160 Hz, $n = 76$) in Opunohu Bay (Moorea) were generally smaller than the *S. punctatus* (244 ± 21 Hz, $n = 67$).

Other Species

Sounds were also reported but not analyzed in *Hypsypops rubicundus* (Limbaugh 1964, Fish and Mowbray 1970), *Microspathodon chrysurus* (Emery 1973), and *Chrysiptera leucopoma* (Graham 1992). Few sounds were also recorded in *Dischistodus prosopotaenia* in Dongsha Atoll, Taïwan (pers. com.). In Rangiroa, we failed to record *Chrysiptera glauca*: we observed courtship behaviors but were unable to record any sounds. During courtship, males change coloration, their color pattern looking like the great white shark's color pattern: the back became darker and the belly brighter. The caudal fin forms a sail that seems to be used by the male to attract females to the nest.

Conclusion

Sound production in damselfish is probably used by all the species. The Pomacentridae provide a powerful model for the study of evolution of sound production, because there are so many extant species that produce sound and they live mainly in tropical and subtropical regions where the water is clear and behavior is readily observed. There is diversity in both intra and inter-specific calls, since some species are able to produce at least six different calls. Moreover, the association between the calls and the ability of some species to change their color pattern suggest a greater variety of messages than expected. Future studies should be conducted to describe sounds in more species in order to assess the role of acoustic communication in the evolutionary history of the taxa. It is important to note many factors such as temperature, size, and background noise can affect acoustic parameters in pomacentrids, making comparisons difficult (Demski et al. 1973, Mann and Lobel 1997, Feher et al. 1998, Connaughton et al. 2000, Colleye et al. 2009, Papes and Ladich 2011). Moreover, many other fundamental studies are needed on the sound production mechanism of chirps, the ability of inter-specific communication, and the use of call partitioning at the level of the reef.

We draw these general conclusions, but there is clearly a lot of room for more research:

1) All pomacentrids should be able to make sounds for communication purposes, but sounds are not produced during all behaviors in all species.
2) Sounds mainly consist of trains of pulses in which the number is higher when emitted towards conspecifics.
3) Courtship sounds are associated with stereotyped movements.
4) Dominant frequency (and most probably pulse duration) is related to the fish size in all species and more data should be collected to know if all the family species can be found on the same slope or not.
5) Sounds of sister species show many overlapping characteristics, indicating that this cue alone would not be sufficient to discriminate species.
6) Dialects are found within the same species.
7) Pop sounds result from jaw snapping, but another kind of mechanism has to be found for explaining the emission of chirps.
8) The call rate would be a determining factor in mating success, meaning sonic phenotypic differences related to size are not the evolutionary driving force.

We hypothesize that damselfish sound production originally evolved starting with the single pop associated with feeding/aggression. The coupling of sound production and exaggerated swimming could have evolved through sexual selection by females for male quality. In *Amphiprion* where there is one female per anemone, there is no exaggerated courtship dip associated with spawning.

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