Broadening of acoustic repertoire in Pomacentridae: tonal sounds in the Ambon damselfish *Pomacentrus amboinensis*

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Abstract

Damselfish are prolific callers, identified as being able to produce different kinds of sounds (pops and chirps) associated with various behaviors. During courtship and chase behaviors, the coral reef damselfish *Pomacentrus amboinensis* produces a previously unknown additional kind of call that we have named the wiping sound. These calls have two to three long (54 ± 13 ms) units that do not show the usual percussive aspect of the pomacentrid sounds. Calls consist of a high-pitched (from 550 to 775 Hz) tonal sound in which the cycle repetition rate corresponds to the peak frequency. The high frequency of this tonal sound can be excluded as coming from the contraction of sound producing muscles. These sounds could be the result of a mechanism that drives the merging of successive pops. In the noisy environment of coral reefs and the resulting competition for acoustic space, the wiping sounds appear to be a good way to increase signal distinctiveness and opportunities for correct signal discrimination. This new kind of sound supports that acoustic communication is highly important in the biology of damselfishes and their diversification.

Introduction

Although there are numerous fishes producing many different kinds of sounds (Fine & Parmentier, 2015), the diversity of calls within a taxon is usually more restricted. A few taxa are, however, able to employ different mechanisms and can therefore emit completely different kinds of sounds. Some *Synodontis* catfish (Mochokidae), for example, produce sounds using swim bladder muscles or pectoral spines (Fine & Ladich, 2003; Parmentier *et al.*, 2010a; Boyle, Colleye & Parmentier, 2014).

Pomacentridae also includes fishes producing different kinds of sounds. Damselfishes (399 species, 28 genera) are one of the most thoroughly investigated families of acoustic reef fishes (Lobel *et al.*, 2010). To date, sounds have been recorded and analysed in various species from the genera *Abudefduf*, *Amphiprion*, *Chromis*, *Dascyllus*, *Plectroglyphidodon*, *Pomacentrus*, *Premnas* and *Stegastes* (Parmentier, Lecchini & Mann, 2016). Sounds were also reported but not analysed in *Hypsypops rubicundus* (Limbaugh, 1964; Fish & Mowbray, 1970), *Microspathodon chrysurus* (Emery, 1973), and *Chrysiptera leucopoma* (Graham, 1992).

Two kinds of sounds are currently recognized (Parmentier *et al.*, 2016). They can be both composed of one to many pulses. Pops are made through teeth snapping (Parmentier *et al.*, 2007; Colleye *et al.*, 2012; Olivier *et al.*, 2014), mainly during aggressive behaviors (i.e. chase and defense of territory), courtship or reproduction. Pops are found in all the pomacentrids studied so far (Parmentier *et al.*, 2016). Amongst the pop sounds, modifications at the level of the number of pulses or in the periods between consecutive pulses can create different calls corresponding to various behavioral contexts (Mann & Lobel, 1998; Parmentier *et al.*, 2010b, 2016). It is probably the case for the "grunts" described in *Stegastes partitus* (Myrberg, 1972; Kenyon, 1994). The second kind of sound, chirp, is accompanied by head-shaking movements and corresponds to submissive behavior during agonistic interactions. It has been recorded in some species only (Schneider, 1964; Parmentier *et al.*, 2006; Colleye & Parmentier, 2012), probably because the low acoustic intensity does not easily allow its detection in the field. In clownfish, they are always composed of several pulses, whereas pop sounds are composed of a single pulse unit that can be emitted alone or in series. Chirps also exhibit shorter pulse periods and shorter pulse durations than aggressive sounds (Colleye & Parmentier, 2012). The mechanism responsible for the production of chirps remains unknown.

The most conspicuous behavior associated with sounds in damselfishes concerns the courtship display known as the signal jump. This behavior is performed by males rising in a water column and then rapidly swimming downwards while producing a pulsed sound (Lobel & Mann, 1995). This behavior can be repeated many times during reproductive periods and it could be an indicator of male vigor (Mann & Lobel, 1997). For example, *Dascyllus* species are very prolific callers

that can repeat their sounds hundreds to thousands of times a day (Lobel & Mann, 1995; Parmentier *et al.*, 2010b). It is possible that a female could sample many calls before making a decision to spawn with a given male (Parmentier *et al.*, 2016) since female mate choices are related to the courtship rate (Oliver & Lobel, 2013). Among the different acoustic characteristics used by the conspecifics, the number of pulses in a call in combination with the period between successive pulses would be the most reliable features allowing species identification (Myrberg, Spanier & Ha, 1978; Spanier, 1979; Mann & Lobel, 1997). Frequency spectrum and call amplitude do not appear to be critical for species recognition (Ha, 1973) but they could be useful to identify the size of the emitter within species (Myrberg, Ha & Shamblott, 1993; Colleye *et al.*, 2009, 2011). In this study, we aim to present a third kind of sound that is produced by the Ambon damsel *Pomacentrus amboinensis* Bleeker, 1868. This sound differs remarkably from the pops and chirps because it is not pulsed. In addition, we hypothesize about the related sonic mechanism.

Materials and methods

The Ambon damselfish, *P. amboinensis*, is common within coral reef fish communities in the Indo-Pacific. This species is generally associated with small reef patches in shallow areas and males defend their territories throughout the year (Siebeck, 2004). Field recordings of sound production by *P. amboinensis* were made at Dongsha Atoll National Park (20°41′56.5″N 116°43′06.9″E, Taiwan). Recording sessions, each lasting from 1 to 4 h, were made from April to May 2015 at a depth of between 1 and 3 m in a lagoon close to the seagrass beds. Videos were carried out in five different sites that were separated by at least 20 meters. Sea water in the lagoon was on average 29°C. Recordings of sounds produced by *P. amboinensis* were made using a SONY HDD video camera placed in a housing (HC3 series, Ocean Images, Cape Coral, FL, USA) and coupled with an external hydrophone HTI – 96 (High Tech. Inc., Long Beach, MS, USA) with a flat response of 20 Hz to 20 kHz and having a nominal calibration of -164dBV lPa-1 (Loggerhead Instruments Inc., Sarasota, FL). Recordings were made by placing the housing in front of the coral patches. A total of 6 different patches were filmed and sounds were recorded from *c.* 15 specimens.

The sounds were extracted as WAV files using the AoA audio extractor setup freeware (version 1.2.5). They were digitized at 44.1 kHz (16-bit resolution), low-pass filtered at 1 kHz and analysed, using AvisSoft-SAS Lab Pro 4.33 software (Avisoft Bioacoustics, Glienicke, Germany). Only the sounds with a good signal to noise ratio were used in the analyses. Temporal features were measured from oscillograms, and frequency parameters were obtained from power spectra. The following sound parameters were measured: sound duration (ms); number of units in a sound; unit period (measured as the average peak-to-peak interval between consecutive unit in the entire sound (ms); unit length (measured as the time from the beginning of one unit to its end). Peak frequencies were obtained from logarithmic power spectra (Hamming window, Fast Fourrier Transform, resolution 11 Hz).

After the recordings, 10 fishes having a total length between 8 and 12.5 cm were caught using hand nets. It allowed the assessment of the approximate size of the specimens that were video recorded, but we cannot claim the caught specimens were the video recorded specimens. All caught fish were euthanized in MS-222, measured to the nearest mm and placed in 5% formalin fixative solution. They were dissected and examined with a Wild M10 (Leica Camera, Solms, Germany) binocular microscope equipped with a camera lucida to assist in the illustration process.

Results

When analysed, certain sounds made by *P. amboinensis* were not similar to any of the other sounds recorded in pomacentrids (Fig. 1). They were made either during courtship dips or during conspecific chases. To the human ear, these calls can be compared to the sound of a windscreen wiper on a dry glass, meaning that these sounds do not show the usual percussive aspect of other pomacentrid sounds. Calls comprised one ($n = 43$), two ($n = 36$) or three ($n = 8$) units. In calls having two to three units, the period duration was (mean ± SD) 146 ± 30 ms ($n = 53$). Each unit consisted of long suites of 15–58 sound cycles. Unit duration was on average 54 ± 13 ms ($n = 141$), defining the unit duration (Fig. 2). Moreover, the peak repetition rate corresponds to the peak frequency, which strongly suggests that these calls are tonal sounds. This peak frequency is also the fundamental frequency.

The mean fundamental frequency of the tonal sounds varied from 550 to 775 Hz among individuals and averaged 645 ± 45 Hz ($n = 144$). An additional characteristic was found at the level of the power spectrum. In pomacentrids, the power spectrum can show different frequency peaks with similar energies meaning it is not always comfortable to distinguish the dominant frequency (Parmentier *et al.*, 2010a,b; Colleye *et al.*, 2011, 2012). In *P. amboinensis*, a single frequency formed a narrow important peak exceeding all other frequencies (Fig. 1c).

It is worth noting that we recorded only one popping call made of three pulses. Pulses within this pop had the same kind of power spectrum than those described in other damselfish species (Parmentier *et al.*, 2016), but the low *n* value did not allow us to make firm conclusions. It does at least suggest that *P. amboinensis* is able to make trains of pulses similar to other pomacentrids.

The morphological examination principally concerned structures that are known to be associated with sound production in damselfishes (Parmentier *et al.*, 2007; Colleye *et al.*, 2012). As in other pomacentrids, *P. amboinensis* possesses the ceratomandibular ligament between the ceratohyal and the lower jaw. At the level of the mandible, this ligament is divided into two parts (Fig. 3): the first inserts on the top of coronoid process of the articulo-angular whereas the second is enlarged and inserts on the dentary. At the level of the branchial basket, the anatomy of the pharyngeal jaw does not differ from other pomacentrids (Galis & Snelderwaard, 1997) and contains an arrangement of teeth typical of an omnivorous pomacentrid (Frédérich, Cooper & Aguilar-Medrano, 2016). The
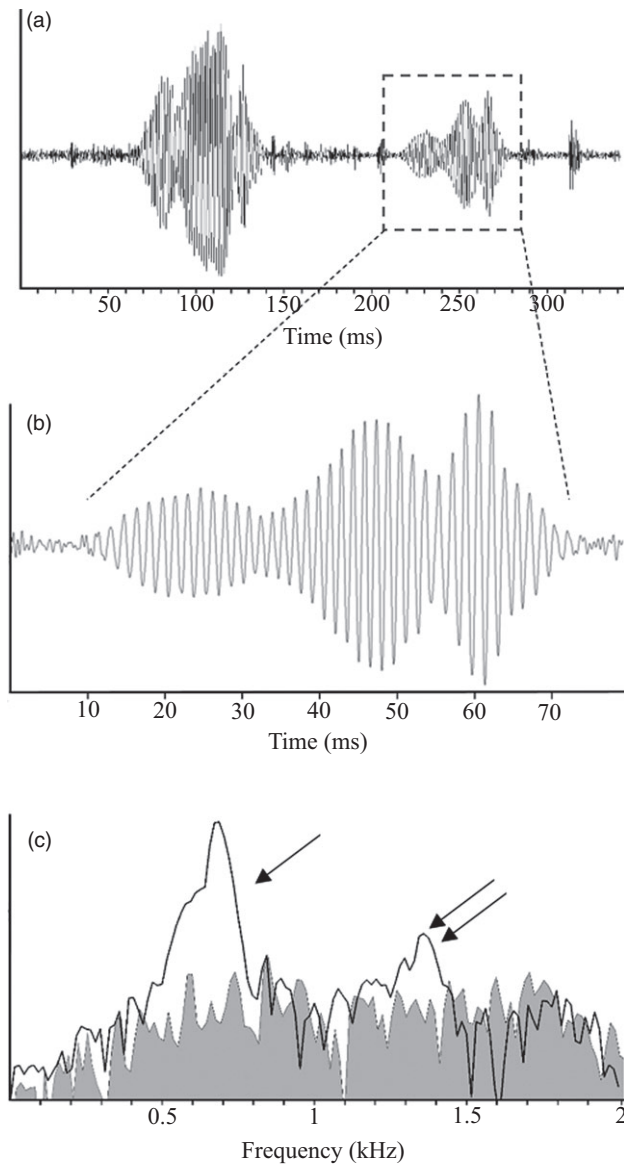
Figure 1 Oscillograms showing the sinusoid-like wave (a, b) and power spectrum (c) of wiping sounds in *Pomacentrus amboinensis*. In the power spectrum, the grey zone corresponds to the background noise. The main peak (arrow) is the fundamental frequency and the second peak (double arrow) corresponds to the 1st harmonic. This harmonic was seen in 50% of the analysed sounds (*n* = 87).

Figure 2 Relation between the number of cycles and unit duration in *Pomacentrus amboinensis* (*n* = 112). *y* = 1.52*X* + 2.15, *r*² = 0.89, *P* < 0.001.

Figure 3 Lateral view of the medial face of the left mandible in *Pomacentrus amboinensis* showing the double insertion of the cerato-mandibular ligament.

swimbladder wall is thin and intimately connected to both the ribcage and haemal spines of the first two caudal vertebrae. Ribs are articulated with the parapophysis of vertebral bodies and are analogous to tee beams, the horizontal bar being closely related to the swimbladder. Caudally, the crossing between the elongated haemal spines of the first caudal vertebrae and the anal fin pterygiophores constitutes a vertical sagittal wall that divides the posterior end of the swimbladder into two rounded parts. Fibres of hypaxial muscles insert medially on each rounded posterior extremity of the swimbladder.
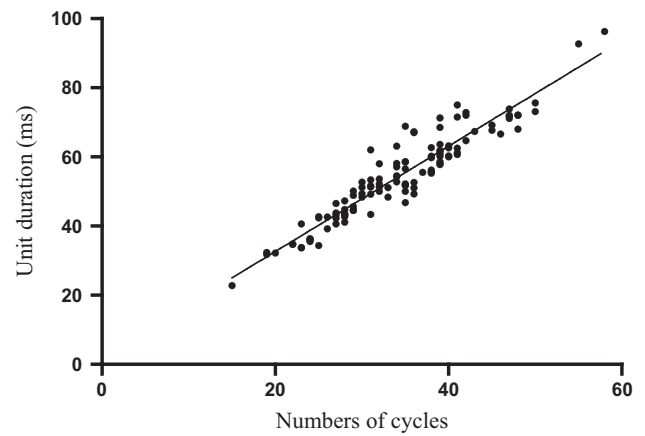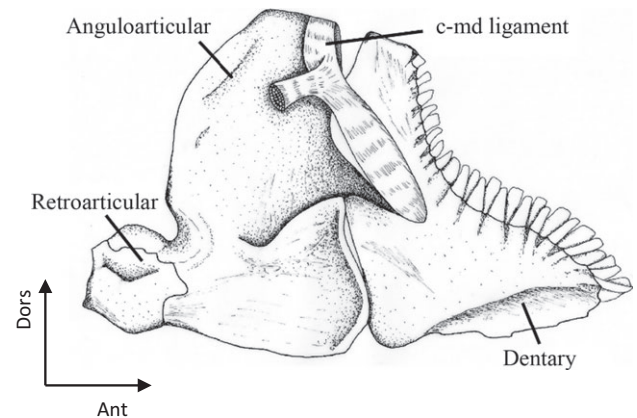
Discussion

Reef habitats house a large number of fish species that are able to communicate using sounds (Tricas & Boyle, 2014; Ruppé *et al.*, 2015). Different calling strategies can be used to increase the likelihood of being heard: increase in signal amplitude, call duration or call rate for example. This kind of variation does not, however, reduce the overlapping in acoustic characteristics that can be found between sounds of closely related species (Myrberg *et al.*, 1978; Spanier, 1979; Colleye *et al.*, 2011). In loud coral reef environments, the development of a new and different kind of sounds appears to be the best way to avoid misidentification. Damselfishes were already known for their ability to produce two kinds of sounds: pops and chirps. This study highlights that a wiping sound constitutes a third kind of clearly distinguishable sound, which underlines the importance of this communication channel in damselfishes.

Sounds of *P. amboinensis* show many common features with tonal sounds described in batrachoid toadfish (Fine, Bernard & Harris, 1993), gobiids (Lugli *et al.*, 1995, 1997; Lugli & Fine, 2007; Malavasi, Collatuzzo & Torricelli, 2008; Parmentier *et al.*, 2013), cottids or darters (Zeyl *et al.*, 2016): most of the energy is present at the fundamental frequency, the oscillogram corresponds to a sinusoidal-like wave and the peak frequency corresponds to the peak repetition rate (Lugli *et al.*, 1997; Lugli, Yan & Fine, 2003). The power spectrum peak is narrow, reinforcing the tonal quality (Tchernichovski *et al.*, 2000).

In male toadfish, the fundamental frequency of the boatwhistle advertisement is produced by the contraction rate of the intrinsic sonic muscles of the swimbladder (Fine *et al.*, 1993, 2001; Rice & Bass, 2009). A grunt-like phase can precede these tonal sounds. In Gobiidae, the mechanism of tonal sounds differs from Batrachoididae since swimbladder muscles are not found (Parmentier *et al.*, 2013), with some species not even possessing swimbladders (Lugli *et al.*, 1996). However, this taxa includes members that exemplify the continuum from trains of pulsed sounds to tonal sounds (Lugli *et al.*, 1995; Malavasi *et al.*, 2008; Zeyl *et al.*, 2016). In *Gobius paganellus*, sounds result from movements of the pectoral girdle (Parmentier *et al.*, 2013). As in toadfish, grunt sounds can be made before the tonal phase but not simultaneously. In both these taxa, it appears that clearly pulsed trains and tonal sounds are made by the same sound producing mechanism. Fishes produce these different calls by varying the rate of muscle contraction. In all fishes having tonal sounds, peak frequency is however well below 500 Hz because of physiological limitations at the level of vertebrate skeletal muscles (Rome & Lindstedt, 1998; Rome *et al.*, 1999). Consequently, it is not possible to consider the tonal sounds produced by *P. amboinensis* are due to fast contractions of muscles.

The pulsatile (pop) sounds of other pomacentrids and the wiping sounds of *P. amboinensis* are both produced during signal jumps meaning they probably have the same function. The recording of some isolated pulses and the presence of cerato-mandibular ligament at least confirm that *P. amboinensis* possesses the sonic mechanism usually found in Pomacentridae. For this reason, the mechanism of the wiping sound could be derived from this mechanism because it should be more parsimonious to adapt it than developing a new one. Movements related to sound production have been experimentally determined in the yellowtail clownfish *Amphiprion clarkii* (Parmentier *et al.*, 2007; Olivier *et al.*, 2015) and the Cortez damselfish *Stegastes rectifraenum* (Olivier *et al.*, 2014). Sound is initiated by teeth collisions caused by rapid jaw closure, which is attributed to a sonic ligament between the hyoid bar and the internal mandible. This mechanism explains, however, only the onset of the sound. The energy of the vibrating jaws resulting from the snapping jaw is probably transferred to the rib cage, the oscillation of which may excite the swimbladder walls (Colleye *et al.*, 2012). The interaction between rib cage and swimbladder may correspond to a beating diaphragm creating a sound wave. Therefore, the swimbladder itself does not act as a resonator; its wall seems to be driven by the oscillations of the rib cage (Colleye *et al.*, 2012). In damselfishes, the

dominant frequency ranges from 400 to 850 Hz according to fish body size (Lobel & Mann, 1995; Colleye *et al.*, 2011) but the power spectrum reveals their sounds can be made of two to three dominant frequencies (Colleye *et al.*, 2011). However, the most intense frequency is not systematically related to the same peak (Parmentier *et al.*, 2010b). In *P. amboinensis*, the wiping sound is within the usual frequency range of damselfish, but there is only one dominant frequency (around 650 Hz) that is related to a sinusoidal wave. This frequency is so high it cannot be sustained by high-speed sonic muscles.

In systems using a resonator, the vibration is excited by an impulse and it can be sustained by continued excitations that produce at best a single frequency. In pomacentrids, the sound is initiated by teeth collisions caused by rapid mouth closure and the resonator seems to be the swimbladder–rib cage interaction. In this case, prolonged sounds could result from a smaller resistive damping. *Pomacentrus amboinensis* has hypaxial bundles inserted on the swimbladder wall. They cannot be the driving force of the tonal sounds, but their contraction could stretch the swimbladder wall and act on the amplitude variation. Traction of these muscles would increase the swimbladder—rib cage stiffness and simultaneously decrease the damping.

Alternatively, the wiping sounds in *P. amboinensis* could result from the merging of different pulses emitted through the short realization of successive slams of the jaws. In this case, rapid series of pulses could be related to the lack of silent periods between consecutive pulses and eliminate the pulsating pattern of the sounds.

As a whole, our findings reinforce the importance of communication channels in damselfish. It has been shown that Ambon damselfish is able to use UV signals to perform species recognition (Siebeck *et al.*, 2010). This visual specialization coupled with the original kind of acoustic signal show how this species is largely invested with the task of identification. Further field experiments should help to understand how damselfish species use the different cues to discriminate individuals since the single use of sounds can provoke misidentification (Spanier, 1979; Parmentier *et al.*, 2009).

Conclusion

The present study highlights not only a new kind of high-pitched tonal sound in fishes but also the fascinating diversity of acoustic communication in damselfishes. Standardized studies on sound production in damselfishes should help to determine potential effects of acoustic communication on their diversification. Although explanations on the mechanism of tonal sound production in *P. amboinensis* are coherent, further examinations of living specimens remain to be done to test the validity of the proposed hypotheses.

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