CLOWNFISH TRIGGERS PLASTICITY IN THE ACOUSTIC COMMUNICATION OF THE THREE-SPOT DAMSELFISH

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ABSTRACT

The concept of Acoustic Niche plasticity refers to the plasticity of acoustic resources allocation within a species. Few studies have focused on this adaptability in fish species. The relationship between anemones and clownfish is one of the best-known symbioses in coral reefs. However, other fishes also use anemones for shelter. The three-spot damselfish (*Dascyllus trimaculatus*) can inhabit the same sea anemone as the orange-fin clownfish (*Amphiprion chrysopterus*) in French Polynesia. Because both Pomacentridae species communicate acoustically through the same sound production mechanism, their sounds are very similar. We have demonstrated that *D. trimaculatus* produces shorter sounds when it shares its anemone with the clownfish. In addition, the daily sound production cycle of *D. trimaculatus* changes in the presence of the clownfish. It decreases sound production during the day and produces more sounds at sunset. These modifications should reduce the acoustic overlap of the signals produced by both species and differentiate the acoustic niche of *D. trimaculatus* from that of *A. chrysopterus*, thereby minimizing competition. This study supports the concept of Acoustic Niche plasticity, showing differences in the three-spot damselfish sound production when it cohabits with another vocal species (*Amphiprion chrysopterus*).

Introduction

Acoustic communication is crucial for many animal species. To avoid acoustic interference and competition, vocal species living in complex and noisy environments have developed different strategies (Allen-Ankins and Schwarzkopf 2022). Sympatric vocal fish species have shown their ability to partition their signal space, e.g., emitting sounds at distinct locations or times of day with different spectral or temporal features (Ruppé et al. 2015; Bertucci et al. 2020; Wilson et al. 2020; Bolgan et al. 2022). These studies support the concept of Acoustic Niche plasticity, i.e., the allocation of acoustic resources (e.g., call temporal features, call spectral features, and diel timing of calling activity) is not fixed within a fish species as the same species can adapt its use of acoustic resources (Bolgan et al. 2022).

Clownfish are especially well-known for their symbiosis with sea anemones (Allen 1972; Fautin and Allen 1997; Ollerton et al. 2007; Ricciardi et al. 2010). Clownfish groups form obligate associations with sea anemones that provide fish with spawning sites and protection from predators (Allen 1972; Fautin 1991; Buston 2003). However, this is not the only fish taxon with close relationships with sea anemones (Fautin and Allen 1992; Hayashi et al. 2020). *Dascyllus trimaculatus*, the three-spot damselfish, is widely distributed in western Indo-Pacific coral reefs (Randall and Allen 1977). Although adults of this species usually do not associate with anemones (Randall and Allen 1977), juveniles generally live in symbiosis with large sea anemones or branching corals (Randall and Allen 1977; Fautin 1986; Fautin and Allen 1992). Large sea anemones harboring *D. trimaculatus* may also have concurrent symbiotic relation-ships with *Amphiprion* clownfish (Randall and Allen 1977; Fautin 1986; Hayashi et al. 2020). In French Polynesia, the sea anemone *Heteractis magnifica* can harbor both *D. trimaculatus* and *A. chrysopterus*, inducing competition between both species (Holbrook and Schmitt 2004; Hayashi et al. 2020). *Amphiprion chrysopterus*, the dominant competitor of this relationship, has a direct negative effect on the density of *D. trimaculatus*, the dominated competitor (Holbrook and Schmitt 2004).

Both species belong to the Pomacentridae, a family wellknown for its ability to produce sounds (Parmentier et al. 2016). The sound production mechanism has been described in *Amphiprion clarkii* (Parmentier et al. 2007). It involves the cerato-mandibular ligament connecting the lower jaw to the hyoid bar, at the level of the ceratohyal (Parmentier et al. 2007). Upon simultaneous neurocranium elevation and hyoid depression, this ligament acts as a rope, forcing rapid closure of the mouth (Parmentier et al. 2007). Sounds are produced at teeth snapping (Parmentier et al. 2007; Olivier et al. 2015, 2016). Because this ligament is a synapomorphic character in the Pomacentridae (Stiassny 1980; Olivier et al. 2016), the sounds emitted by the genera *Amphiprion* and *Dascyllus* are produced by the same mechanism (Olivier et al. 2015, 2016; Parmentier et al. 2016). Although both *A. chrysopterus* and *D. trimaculatus* produce similar pulsed sounds (Luh and Mok 1986; Colleye et al. 2009; Parmentier et al. 2009), the main challenge of their cohabitation is that the sounds are not produced in the same behavioral context. Sounds are only made during aggressive behaviors in *Amphiprion* species (Colleye and Parmentier 2012), whereas *Dascyllus* species also communicate vocally during reproduction and courtship behaviors (Lobel and Mann 1995; Mann and Lobel 1998;

Parmentier et al. 2009, 2010, 2022). During courtship, *Dascyllus* males perform a display (called the signal jump) to attract females (Myrberg and Spires 1972; Lobel and Mann 1995). This courtship dip involves the male rising into the water column and then swimming rapidly downward while emitting a pulsed sound (Lobel and Mann 1995; Parmentier et al. 2009, 2010). Because both species may share the same host and produce similar sounds with different meanings, it can result in misinterpretation. The courtship behavior of *D. trimaculatus* could be misinterpreted as aggression by the clownfish, leading to conflicts. Acoustic communication within the sea anemone host could be conflicting. We hypothesize that competition should result in signal diversification and/or modification to minimize interference (Krause 1993; Bolgan et al. 2022).

The present study aims at determining the impact of acoustic competition between *A. chrysopterus* and *D. trimaculatus* when living together. Firstly, we compared the acoustic parameters associated with the signal jump sounds between *D. trimaculatus* living alone in the sea anemones and specimens found cohabiting with *A. chrysopterus*. Secondly, since both species share the same host, we hypothesized that *D. trimaculatus* could change its daily sound production cycle. Consequently, we determined the daily

sound production cycle of *D. trimaculatus* alone and the cycle when the two species share the same anemone.

Materials and methods

STUDY SITE

This study was conducted in the lagoon at Temae, in Moorea (17° 29' 54" S, 149° 45' 19" W, French Polynesia). Recording sessions were made from February to May 2021, between 1 and 3 m depth. The average water temperature in the lagoon was 29 °C. Ten colonies of *D. trimaculatus* were recorded. They were composed of 8-77 individuals, inhabiting one or several juxtaposed sea anemones *Heteractis magnifica*. Five host colonies were found to be exclusively inhabited by *D. trimaculatus* while the other five colonies were inhabited by both *A. chrysopterus* and *D. trimaculatus*.

RECORDINGS

Behaviors associated with sound production in *D. trimaculatus* were recorded with two types of instruments: a GoPro7 (GoPro, San Mateo, CA, USA), placed in a housing (Spyfish, Liège, Belgium) and directly connected to an HTI-96-Min external hydrophone (sensitivity: — 170 dBV μPa-1, flat frequency response range: 20 Hz-20 kHz, a sampling rate of 44.1 kHz, 16-bit resolution; High Tech Inc, Long Beach, MS, USA); and a cyclops, composed of an HD video camera (Loggerhead Instruments, Sarasota, FL, USA) directly connected to an identical HTI-96-Min external hydrophone (sensitivity: — 170 dBV μPa-1, flat frequency response range: 20 Hz-20 kHz, a sampling rate of 44.1 kHz, 16-bit resolution; High Tech Inc, Long Beach, MS, USA). Both cameras were placed either on the

bottom or on some dead coral, about 1 m from each studied colony. Continuous recording sessions lasted up to 2 h, between 08:30 and 11:30. This time slot was chosen after a quick analysis of the daily sound production cycle had designated it as the richest in acoustic behaviors. The sounds associated with signal jumps were analyzed with the Avisoft-SASLab Pro software 5.2.13 (Avisoft Bioacoustics, Glienicke, Germany). Each file was previously down-sampled at 4 kHz with Adobe Audition (Adobe, San Jose, CA, USA) to ease the analysis by reducing the calculation time. The following sound parameters were measured: sound duration (in ms); number of pulses in a sound; pulse period (measured as the average peak-to-peak interval between consecutive pulses in the entire sound, in ms); interpulse interval (measured as the time from the end of one pulse to the beginning of the next one, in ms), pulse duration (measured as the time from the beginning of one pulse and its end, in ms) and dominant frequency (frequency component with the most energy, in Hz). Temporal features were measured from oscillograms while the dominant frequency was obtained from power spectra.

Recordings of the daily sound production cycle were made with a Snap underwater acoustic recorder (Loggerhead Instruments, Sarasota, FL, USA) directly connected to a HIT-96-Min external hydrophone (sensitivity: - 164 dBV µPa-1, flat frequency response range: 20 Hz-20 kHz, a sampling rate of 44.1 kHz, 16-bit resolution; High Tech Inc, Long Beach, MS, USA). Placed next to each of the ten colonies in the lagoon, the system was scheduled to record each colony for 15 min every 60 min for 24 h. Those audio recordings were made between February 16 and March 8, 2021. The soundtracks were analyzed using Raven Lite 2.0.1 (Cornell Lab of Ornithology, Ithaca, NY, USA). The sounds produced by *D. trimaculatus* or *A. chrysopterus* that contained a minimum of three pulses were manually counted for each 15-min recording per hour for the 24-h cycle of each colony.

STATISTICS

Descriptive statistics (mean and standard deviation) were calculated for colonies with and without clownfish. Shapiro-Wilk normality tests were used to test the normality of the data. The homoscedasticity of the variances was checked with F tests of equality of variances (n = 2) or Bartlett tests (n > 2). F-tests were also used to compare the variance of signal jump sounds of *D. trimaculatus* accompanied or not by *A. chrysopterus*. For each acoustic parameter, a Wil-coxon-Mann-Whitney test was used to compare signal jump sounds based on the presence or absence of *A. chrysopterus*. A principal component analysis (PCA) was run on the six acoustic parameters, from the correlation matrix, to give an overview of the potential acoustic differences between the two types of colonies (with and without *A. chrysopterus*). Student t tests were used to compare PC1 and PC2 between colonies with and without *A. chrysopterus*. Spearman's rank correlation coefficients (rS) were used to quantify the relationship between principal components and acoustic parameters. For the daily sound production cycle, the percentages of sounds per hour compared to the total number produced during 24 h were calculated for each colony. This analysis was carried out for *D. trimaculatus* and *A. chrysopterus*. Wilcoxon-Mann-Whitney test and Student t test were used to compare the percentages of sounds between colonies of *D. trimaculatus* with and without the clownfish, for every hour of the daily sound production cycle. The number of sounds produced by *D.*

trimaculatus was compared between colonies with and without *A. chrysopterus* using a Wilcoxon-Mann-Whitney test. In addition, a Kruskal-Wallis test was used to compare the number of sounds of *D. trimaculatus* depending on the number of *A. chrysopterus* present (i.e., zero, one, or two). It was followed by Dunn's multiple comparison tests for pairwise comparisons (with Bonferroni correction). All the statistics were carried out with R 4.1.0 (GNU General Public License), and the significance level was α = 0.05.

Results

NUMBER OF CLOWNFISH

In the anemones inhabited by clownfish, the number of clownfish varied between one and two. Before carrying out our analysis, we realized a preliminary investigation to assess the potential effect of the number of clownfish present (i.e., zero, one, or two) on the number of sounds produced by *D. trimaculatus*. There was no difference whether there were one or two clownfish (Kruskal-Wallis test, $\chi 2$ = 33.92, df=2, P < 0.001) (Dunn test, Z = 1.15, P = 0.74 when comparing one vs. two clownfish) (Dunn test, Z = 4.36 and 5.07, all P < 0.001 when comparing 0 vs. 1 or 2 clownfish). Therefore, we only considered the absence or the presence of the clownfish.

IMPACT ON THE SOUNDS

Dascyllus trimaculatus produced fast pulsed train sounds associated with signal jumps in six of the ten colonies, when alone (3) and in cohabitation with clownfish (3) (Table 1). However, *D. trimaculatus* sounds differed significantly between colonies having only *D. trimaculatus* and colonies sheltering both species (Table 1). When cohabiting with the clownfish, *D. trimaculatus* produced significantly shorter sounds (Wilcoxon-Mann-Whitney test, W = 3425, P < 0.001) because they were made of fewer pulses (Wilcoxon-Mann-Whitney test, W = 3071, P < 0.001) and had a shorter pulse duration (Wilcoxon-Mann-Whitney test, W = 3622, P < 0.001) (Table 1). However, the pulse period (Wilcoxon-Mann-Whitney test, W = 7710, P < 0.01) and the interpulse interval (Wilcoxon-Mann-Whitney test, W = 9198, P < 0.001) were significantly longer when *D. trimaculatus* were living with the clownfish (Table 1). When both species were together, the dominant frequency of signal jump sounds was also higher (Wilcoxon-Mann-Whitney test, W = 8038, P < 0.001) (Table 1). The variance associated with interpulse interval (F test, F = 1.61, df = 64 and 183, P = 0.015) and dominant frequency (F test, F = 1.96, df=64 and 183, P < 0.001) was significantly larger in sounds of *D. trimaculatus* accompanied by *A. chrysopterus* than those of the signal jump sounds produced by *D. trimaculatus* alone. It was not the case for the other features.

The acoustic diversity associated with signal jumps was summarized by a PCA based on the six acoustic features(Fig. 1). The first two principal components of the PCA explained cumulatively 68.2% of the variation, with PC1 and PC2 explaining 42.3% and 25.9% of the variation respectively. The sound duration (Spearman rank correlation, rS = 0.73, P < 0.001), the number of pulses

(Spearman rank correlation, rS = 0.74, P < 0.001), the pulse duration (Spearman rank correlation, rS = 0.64, P < 0.001) and the interpulse interval (Spearman rank correlation, rS = - 0.76, P < 0.001) mostly contributed to the first principal component, whereas the pulse period (Spearman rank correlation, rS = - 0.74, P < 0.001) was principally associated with the second principal component. The colonies of *D. trimaculatus* living with or without *A. chrysopterus* were easily distinguished within this acoustic space along PC1 (Fig. 1). PC1 supported significant differences between the signal jump sounds depending on whether or not the host anemone was shared between *D. trimaculatus* and *A. chrysopterus* (Student test, t = - 8.99, df = 247, P < 0.001) (Fig. 1). The second component did not allow to separate the two types of colonies (Student test, t = - 0.53, df = 247, P = 0.59) (Fig. 1).

Table 1. *Comparison of different acoustic parameters characterizing the signal jump sounds produced by Dascyllus trimaculatus (mean ± standard deviation), grouped according to whether or not Amphiprion chrysopterus is present in the anemone*

	Dascyllus tri-maculatus alone (n = 184)	*Dascyllus trimaculatus* with *Amphiprion chrysopterus* (n = 65)	Wilcoxon–Mann–Whitney test statistics and p-values
Duration (ms)	194 ± 55	153 ± 51	W = 3425, P < 0.001
Number of pulses	5 ± 1	4 ± 1	W = 3071, P < 0.001
Pulse duration (ms)	17 ± 6	13 ± 6	W = 3622, P < 0.001
Pulse period (ms)	51 ± 6	54 ± 7	W = 7710, P = 0.003
Interpulse interval (ms)	34 ± 7	41 ± 8	W = 9198, P < 0.001
Dominant frequency (Hz)	373 ± 104	457 ± 145	W = 8038, P < 0.001

Numbers between brackets correspond to the number of analyzed sounds

Figure 1. *Scatterplot of principal component PC1 versus PC2, performed with the six acoustic parameters of signal jump sounds for the colonies composed of Dascyllus trimaculatus only (pink triangle) and those with Amphiprion chrysopterus (blue circle). Ellipses correspond to 95% of the observations, and dots correspond to ellipse centers*
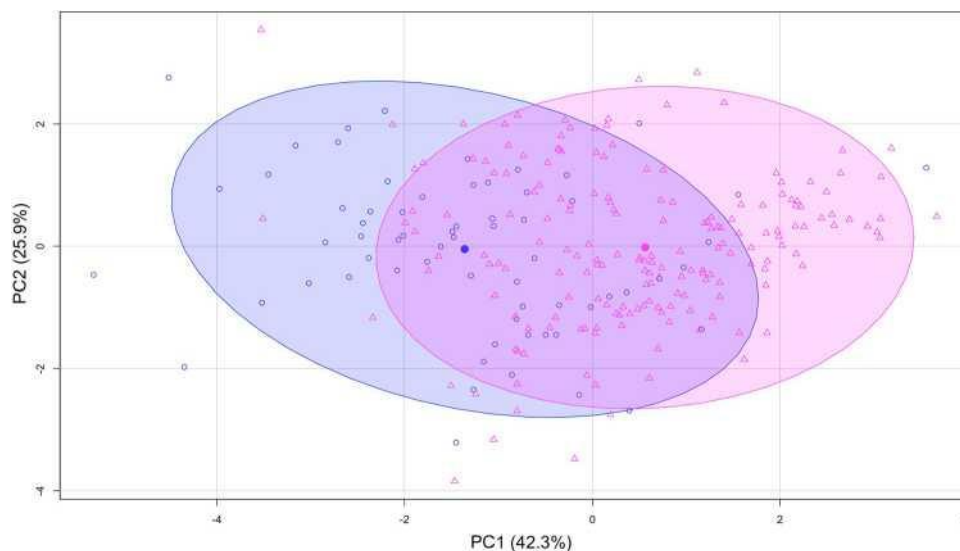
IMPACT ON THE NUMBER OF SOUNDS AND THE DAILY CYCLE

Alone within the sea anemones, *D. trimaculatus* produced significantly almost four times more sounds (Wilcoxon-Mann-Whitney test, W = 10,258, P < 0.001) than when in cohabitation with *A. chrysopterus*.

In anemones without clownfish, *D. trimaculatus* produced sound during both day and night (Fig. 2a). When this species was alone, the major peak of sound production (11.34% of the daily production) coincided with sunrise, which occurred between 05:54 and 06:00 in Moorea between February 16 and March 8, 2021 (Fig. 2a). Then, the sound production decreased gradually during the day (Fig. 2a) before a slight increase in sound production (5.44% of the daily production) after the sunset, i.e., between 18:19 and 18:32 (Fig. 2a). When *A. chrysopterus* was present, some modifications in the daily cycle should be noted. The peak of sound production (11.22% of the daily production) happened around 1 h before sunrise (Fig. 2b), and there was a second major peak (11.94% of the daily production) around sunset (Fig. 2b). In addition, it should be noted that there is some disparity in the daily cycle between the different colonies (Fig. 2a, b). *Dascyllus trimaculatus* produced more sounds at 06:00 when alone in the anemones (Student test, t = - 2.69, df = 8, P = 0.028). However, *D. trimaculatus* increased its sound production at 18:00 when the clownfish was present (Student test, t = - 2.69, df = 8, P = 0.028).

Figure 2. *Daily sound production cycle of Dascyllus trimaculatus, when they were alone (a) and when Amphiprion chrysopterus was present (b). Daily sound production cycle of Amphiprion chrysopterus when Dascyllus trimaculatus was present (c). Each data represents the percentage of sounds produced in 15 min per hour over a 24-h day. The dotted lines represent each colony, and the solid lines represent their mean. Each color represents one colony. The yellow rectangles represent sunrise and sunset in Moorea between February 16 and March 8, 2021*
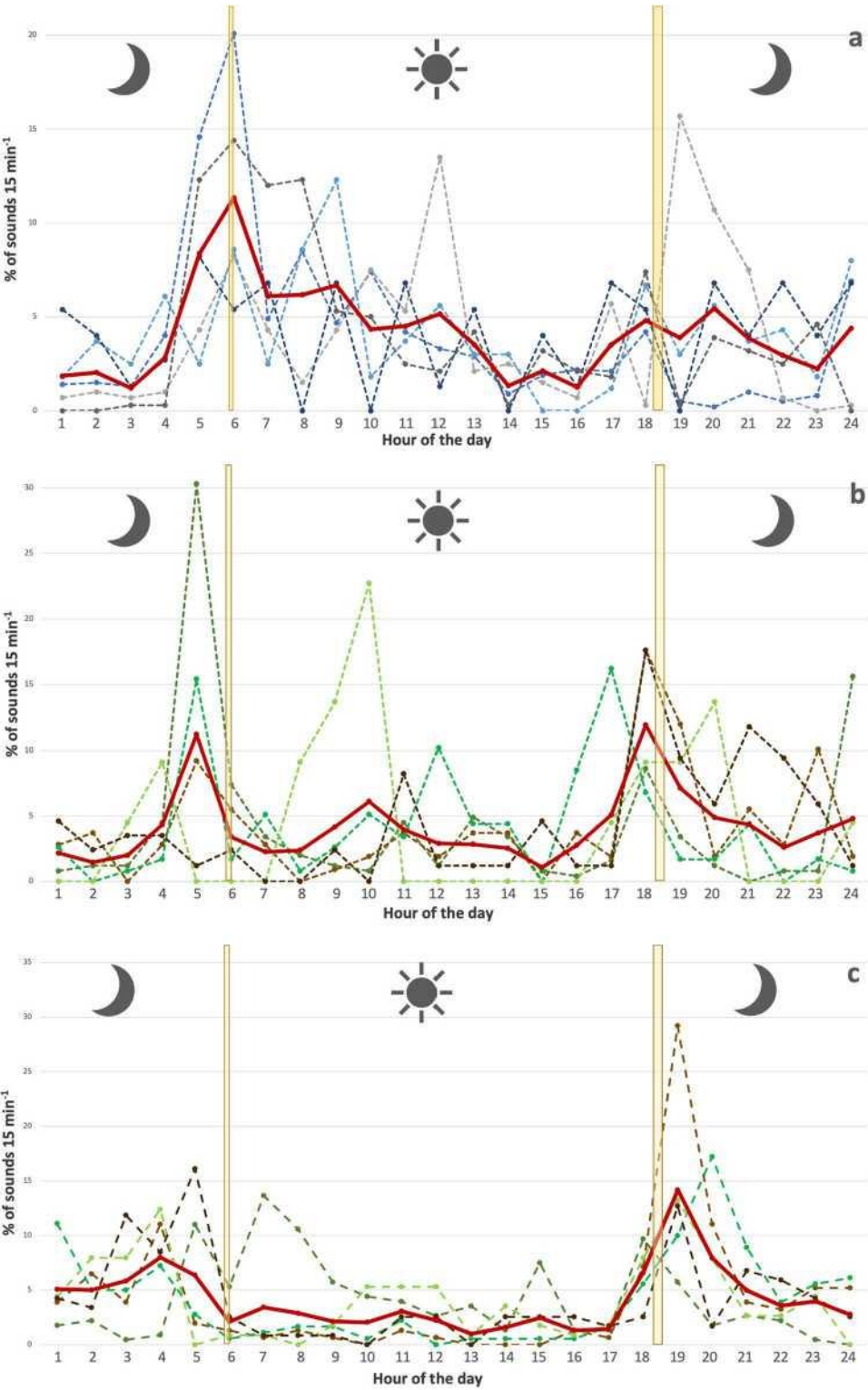
Discussion

This study supports the concept of Acoustic Niche plasticity by highlighting that the same species can exploit different acoustic resources depending on the surrounding

vocal species. It is a crucial adaptation that allows distinct species to coexist in the same habitat by partitioning the use of acoustic resources. Here, all acoustic parameters associated with signal jump sounds of *D. trimaculatus* can be distinguished depending on whether or not *A. chrysopterus* was present. During their cohabitation with *A. chrysopterus* , *D. trimaculatus* sounds were more "discrete" because they were shorter, having fewer pulses. Furthermore, *D. trimaculatus* produced statistically fewer sounds when accompanied by *A. chrysopterus*. This decrease in sound production attests to the dominance of *A. chrysopterus* in the relationship (Holbrook and Schmitt 2004). The various aggressions of this clownfish on *D. trimaculatus*, like those observed during this study, must undoubtedly limit its acoustic communication (Hayashi et al. 2020). These restrictions in the sound duration and the number of sounds of the three-spot damselfish could be related to the message meaning since sound production is usually associated with aggressive behavior for the clownfish. Sounds would aim at establishing the hierarchy in the clownfish community (Colleye and Parmentier 2012). It means that courtship sounds produced by *D. trimaculatus* could be considered aggressive sounds by the clownfish. In this case, the shift in acoustic parameters and production in *D. trimaculatus* could be an acoustic adaptation to avoid conflicts as much as possible.

These observations in the shift of acoustic features join the rare in situ studies showing an adaptation of fish communication according to the biocenosis (Lagardère et al. 2005). Indeed, Lagardère et al. (2005) had also shown that, within a sea cucumber, the Carapidae *Carapus boraborensis* and *C. homei* seemed able to modify their acoustic features if they were in the presence of conspecifics or heterospecifics. Interspecific acoustic interaction in anurans (Littlejohn and Martin 1969), birds (Popp et al. 1985; Brumm 2006), and insects (Greenfield 1988) showed that species adjust the frequency and the timing of their signals to avoid competition (Brumm and Slabbekoorn 2005). Moreover, it was also proven that sympatric species induce a shift in the number and types of calls in frogs (Schwartz and Wells 1983) and a shift in the rate and length of songs in birds (Popp and Ficken 1987). Those studies corroborate animal acoustic adaptability like the one found in the *Dascyllus* genus in this study.

The relationship between size and dominant frequency and the one between size and pulse duration have been shown in Pomacentridae species (Lobel and Mann 1995; Colleye et al. 2009, 2011). In this study, the dominant frequency was lower, and the pulse duration was longer when *D. trimaculatus* were alone. Although the size has not been measured in this study, it seems specimens living without clownfish were larger than their conspecifics which live with *A. chrysopterus*. In other words, the lower dominant frequency and the longer pulse duration

recorded in *D. trimaculatus* do not result from an adaptive process in sound production but are related to the fish size within populations.

In both types of colonies, *D. trimaculatus* had a peak of sound production around sunrise (Fig. 2a, b), as previously described by Parmentier et al. (2016). The greatest difference in the daily sound production cycle between *D. trimaculatus* alone and *D. trimaculatus* accompanied by *A. chrysopterus* stands at sunset (Fig. 2a, b) when the clownfish is present. When *A. chrysopterus* is present, *D. trimaculatus* decreases its sound production during the day and communicates more at sunset (Fig. 2a, b), the sound production increasing by 58% around 18:00. The clownfish seems to be the trigger for the *D. trimaculatus* sound production at sunset since no other difference exists between the two types of colonies. The reason for this shift remains obscure. Could the agonistic sounds of the clownfish stimulate the sound production in *Dascyllus* ?

Conclusion

The cohabitation of *D. trimaculatus* with the clownfish seems to correspond to modifications in *D. trimaculatus* sound production at different levels: the number of sounds, time of emission, and acoustic features. All these modifications are most probably used to minimize signal overlaps with *A. chrysopterus*, supporting the concept of Acoustic Niche plasticity due to biocenosis. It would be interesting to extend the study with experimentations, monitoring the evolution of acoustic features before introduction, during cohabitation, and after the removal of *Amphiprion* competitors.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007⁄s00227-023-04259-4.

Author contributions

EP contributed to the study's conception. EP, SL, and XR contributed to the study design. Data collection was performed by SL. Data analysis, visualization, and investigation were performed by SL and XR. Funding acquisition was performed by DL, SL, and XR. Resources were provided by EP and DL. EP supervised the study. The first draft of the manuscript was written by SL, EP, and XR. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

References

Allen GR (1972) The anemonefishes: their classification and biology. TFH Publ Inc, Neptune City

Allen-Ankins S, Schwarzkopf L (2022) Using citizen science to test for acoustic niche partitioning in frogs. Sci Rep 12:2447. https://doi. org/ 10. 1038/ s41598- 022- 06396-0

Bertucci F, Maratrat K, Berthe C, Besson M, Guerra AS, Raick X, Lerouvreur F, Lecchini D, Parmentier E (2020) Local sonic activity reveals potential partitioning in a coral reef fish community. Oecologia 193:125–134. https:// doi. org/ 10. 1007/ s00442- 020- 04647-3

Bolgan M, Di Iorio L, Dailianis T, Catalan IA, Lejeune P, Picciulin M, Parmentier E (2022) Fish acoustic community structure in Neptune seagrass meadows across the Mediterranean basin. Aquat Conserv Mar Freshw Ecosyst 32:329–347. https:// doi. org/10. 1002/ aqc. 3764

Brumm H (2006) Signalling through acoustic windows: Nightingales avoid interspecific competition by short-term adjustment of song timing. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 192:1279–1285. https:// doi. org/ 10. 1007/ s00359- 006- 0158-x

Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. In: Slater P (ed) Advances in the study of behavior. Academic Press, San Diego, pp 151–209. https:// doi. org/ 10. 1016/ S0065-3454(05) 35004-2

Buston P (2003) Social hierarchies: size and growth modification in clownfish. Nature 424:145–146. https:// doi. org/ 10. 1038/ 42414 5a

Colleye O, Parmentier E (2012) Overview on the diversity of sounds produced by clownfishes (Pomacentridae): importance of acoustic signals in their peculiar way of life. PLoS ONE 7:e49179. https://doi. org/ 10. 1371/ journ al. pone. 00491 79

Colleye O, Frederich B, Vandewalle P, Casadevall M, Parmentier E (2009) Agonistic sounds in the skunk clownfish *Amphiprion* akallopisos: size-related variation in acoustic features. J Fish Biol 75:908–916. https:// doi. org/ 10. 1111/j. 1095- 8649. 2009. 02316.x

Colleye O, Vandewalle P, Lanterbecq D, Lecchini D, Parmentier E (2011) Interspecific variation of calls in clownfishes: degree of similarity in closely related species. BMC Evol Biol 11:365. https:// doi. org/ 10. 1186/ 1471- 2148- 11- 365

Fautin DG (1986) Why do anemonefishes inhabit only some host actinians? Environ Biol Fishes 15:171–180. https:// doi. org/ 10. 1007/BF000 02992

Fautin DG (1991) The anemonefish symbiosis: what is known and what is not. Symbiosis 10:23–46

Fautin DG, Allen GR (1992) Field guide to anemonefishes and their host sea anemones. Western Australian Museum, Perth

Fautin DG, Allen GR (1997) Anemonefishes and their host sea anemones, revised. Western Australian Museum, Perth Greenfield MD (1988) Interspecific acoustic interactions among katydids Neoconocephalus: inhibition-induced shifts in dielperiodicity. Anim Behav 36:684–695.
https:// doi. org/ 10. 1016/S0003- 3472(88) 80151-9

Hayashi K, Tachihara K, Reimer JD (2020) Anemonefish aggressiveness affects the presence of *Dascyllus trimaculatus* co-existing with host anemones. Mar Biol 167:84.
https:// doi. org/ 10. 1007/s00227- 020- 03696-9

Holbrook SJ, Schmitt RJ (2004) Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. Ecology 85:979–985. https:// doi. org/ 10. 1890/ 03- 0406

Krause BL (1993) The Niche hypothesis: a virtual symphony of animal sounds, the origins of musical expression and the health of habitats. Soundscape Newsl 6:6–10

Lagardère JP, Millot S, Parmentier E (2005) Aspects of sound communication in the pearlfish *Carapus boraborensis* and Carapus homei (Carapidae). J Exp Zool A Comp Exp Biol 303A:1066–1074.
https:// doi. org/ 10. 1002/ jez.a. 230

Littlejohn MJ, Martin AA (1969) Acoustic interaction between two species of leptodactylid frogs. Anim Behav 17:785–791. https://doi. org/ 10. 1016/ S0003- 3472(69) 80027-8

Lobel PS, Mann DA (1995) Spawning sounds of the Damselfish, *Dascyllus* albisella (Pomacentridae), and relationship to male size. Bioacoustics 6:187–198. https:// doi. org/ 10. 1080/ 09524 622. 1995.97532 89

Luh HK, Mok HK (1986) Sound production in the domino damselfish, *Dascyllus trimaculatus* (Pomacentridae) under laboratory conditions. Jpn J Ichthyol 33:70–74

Mann DA, Lobel PS (1998) Acoustic behavior of the damselfish *Dascyllus* albisella: behavioral and geographic variation. Environ Biol Fishes 51:421–428. https:// doi. org/ 10. 1023/A: 10074 10429 942

Myrberg AA, Spires JY (1972) Sound discrimination by the bicolor Damselfish, Eupomacentrus partitus. J Exp Biol 57:727–735. https:// doi. org/ 10. 1242/ jeb. 57.3. 727

Olivier D, Frédérich B, Herrel A, Parmentier E (2015) A morphological novelty for feeding and sound production in the yellowtail clownfish: feeding and sound production in clownfish. J Exp Zool

Part Ecol Genet Physiol 323:227–238. https:// doi. org/ 10. 1002/jez. 1907

Olivier D, Frederich B, Parmentier E (2016) Cerato-mandibular ligament: a key trait in damselfishes? In: Frederich B, Parmentier E (eds) Biology of damselfishes. CRC-Press, Taylor & Francis, Boca Raton, pp 291–309

Ollerton J, McCollin D, Fautin DG, Allen GR (2007) Finding NEMO: nestedness engendered by mutualistic organization in anemonefish and their hosts. Proc R Soc B Biol Sci 274:591–598.
https:// doi.org/ 10. 1098/ rspb. 2006. 3758

Parmentier E, Colleye O, Fine ML, Frederich B, Vandewalle P, Herrel A (2007) Sound Production in the Clownfish *Amphiprion clarkii*. Science 316:1006–1006. https:// doi. org/ 10. 1126/ scien ce. 11397 53

Parmentier E, Lecchini D, Frederich B, Brié C, Mann D (2009) Sound production in four damselfish (*Dascyllus*) species: phyletic relationships? Biol J Linn Soc 97:928–940.
https:// doi. org/ 10. 1111/j.1095- 8312. 2009. 01260.x

Parmentier E, Kéver L, Casadevall M, Lecchini D (2010) Diversity and complexity in the acoustic behaviour of *Dascyllus* flavicaudus (Pomacentridae). Mar Biol 157:2317–2327. https:// doi. org/10. 1007/ s00227- 010- 1498-1

Parmentier E, Lecchini D, Mann DA (2016) Sound production in damselfishes. In: Frederich B, Parmentier E (eds) Biology of damselfishes. CRC-Press, Taylor & Francis, Boca Raton, pp 204–228

Parmentier E, Scalbert R, Raick X, Gache C, Frédérich B, Bertucci F, Lecchini D (2022) First use of acoustic calls to distinguish cryptic members of a fish species complex. Zool J Linn Soc 195:964–975. https:// doi. org/ 10. 1093/ zooli nnean/ zlab0 56

Popp JW, Ficken RW, Reinartz JA (1985) Short-term temporal avoidance of interspecific acoustic interference among forest birds. The Auk 102:744–748. http:// www. jstor. org/ stable/ 40867 11

Popp JW, Ficken RW (1987) Effects of non-specific singing on the song of the Ovenbird. Bird Behav 7:22–26. https:// doi. org/ 10.3727/ 01561 38877 91918 123

Randall HA, Allen GR (1977) A revision of the damselfish genus *Dascyllus* (Pomacentridae) with the description of a new species. Rec Aust Mus 31:349–385. https:// doi. org/ 10. 3853/j. 0067- 1975. 31.1977. 217

Ricciardi F, Boyer M, Ollerton J (2010) Assemblage and interaction structure of the anemonefish-anemone mutualism across the Manado region of Sulawesi, Indonesia. Environ Biol Fishes. https:// doi. org/ 10. 1007/ s10641- 010- 9606-0

Ruppé L, Clément G, Herrel A, Ballesta L, Décamps T, Kéver L, Parmentier E (2015) Environmental constraints drive the partitioning of the soundscape in fishes. Proc Natl Acad Sci 112:6092–6097. https:// doi. org/ 10. 1073/ pnas. 14246 67112

Schwartz JJ, Wells KD (1983) An experimental study of acoustic interference between two species of neotropical treefrogs. Anim Behav 31:181–190. https:// doi. org/ 10. 1016/ S0003- 3472(83) 80187-0

Stiassny MLJ (1980) The phyletic status of the family Cichlidae (Pisces, Perciformes): a comparative anatomical investigation.Neth J Zool 31:275–314. https:// doi. org/ 10. 1163/ 00282 9681X00013

Wilson KC, Semmens BX, Pattengill-Semmens CV, McCoy C, Sirović A (2020) Potential for grouper acoustic competition and partitioning at a multispecies spawning site off Little Cayman, Cayman Islands. Mar Ecol Prog Ser 634:127–146. https:// doi. org/ 10. 3354/meps13181