



# Acoustic behaviour of the European spiny lobster *Palinurus elephas*

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**ABSTRACT:** The acoustic behaviour of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) was examined in the absence or presence of predators or conspecifics. Observations were conducted in a tank equipped with digital video and acoustic monitoring and recording systems using 25 adult lobsters and 5 common octopuses *Octopus vulgaris*. Single lobsters or groups of 4 lobsters were studied for 2 h. These were left alone during the first hour and exposed to a single specimen of the common octopus during the second hour. The lobsters' signals were acoustically analysed. Signal duration, number of pulses per signal, pulse rate, bandwidth, peak intensity, and peak frequency were measured. Single lobsters emitted a higher number of signals than lobsters belonging to a group. The signal (rasp) was audible to humans only in the presence of a predator and was always associated with specific behavioural events. In the absence of a predator, the lobsters produced ultrasound signals (screech) having lower duration, number of pulses per signal, bandwidth, and peak intensity and higher pulse rate and peak frequency. Audible rasps were produced in an anti-predator context, whereas the ultrasound screeches were also emitted under non-stressful conditions. Thus, these signals may play a role in intraspecific communication.

**KEY WORDS:** Acoustic behaviour · *Palinurus elephas* · Intraspecific communication · Antipredator behaviour

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## INTRODUCTION

Spiny lobsters (Palinuridae), like other arthropods, produce acoustic signals (Moulton 1957, Meyer-Rochow & Penrose 1974, Patek 2002, Patek & Oakley 2003, Patek & Baio 2007, Bouwma & Herrnkind 2009, Patek et al. 2009). The sound is produced by a specialised stridulating organ composed of 2 parts: a movable plectrum attached to the last segment of the antennal peduncle and a rigid file (Meyer-Rochow & Penrose 1974, 1976, Patek 2002, Patek & Oakley 2003, Patek & Baio 2007). This organ is located at the

base of the long second antenna, which is also the lobster's primary defensive weapon (Patek 2002). The lobster draws the plectrum up the file by moving the antenna base posteriorly to produce sound. Friction between the soft underside of the plectrum and the anteriorly projecting scales of the file causes the moving plectrum to alternately stick and slip, producing a pulse of sound with each slip (Meyer-Rochow & Penrose 1974, 1976, Patek 2001, 2002). Some authors have assumed that lobsters only produce sounds in an anti-predator context (Lindberg 1955, Moulton 1957, Hazlett & Winn 1962, Takemura

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1971, Meyer-Rochow & Penrose 1974, 1976, Smale 1974, Mulligan & Fischer 1977, Patek 2001, 2002, Bouwma & Herrnkind 2009, Patek & Oakley 2003, Patek et al. 2009, Staaterman et al. 2010). Although various functional hypotheses for distress calls in other animals in anti-predator contexts have been suggested (Smith 1986, Driver & Humphries 1988, Klump & Shalter 1984), the role of lobsters' stridulation and the potential receivers remain unclear.

The European spiny lobster *Palinurus elephas* (Fabricius, 1787) is common along the Mediterranean and northeastern Atlantic coasts (Hunter 1999, Ceccaldi & Latrouite 2000). This species, which is primarily active at night, lives between the shore and a depth of 200 m on rocky and coralligenous substrates where micro-caves, crevices and natural holes are available (Ceccaldi & Latrouite 2000).

*Palinurus elephas* emits acoustic signals termed rasps (Patek & Oakley 2003). The rasp duration, number of pulses per rasp and pulse rate have only been assessed after stress caused by human manipulation, and the spectral characteristics of the rasp were not studied (Patek & Oakley 2003). Moreover, studies on the production of sound by spiny lobsters have primarily focussed on the audible range, and information on acoustic emissions under different ecological conditions remains rare and fragmentary (Patek & Oakley 2003, Buscaino et al. 2011, Staaterman et al. 2010). Information about the context in which lobsters emit acoustic signals is important because it allows improved knowledge of the ecological role of these signals. Moreover, the acoustic parameters that characterise the signals could provide valuable information. For example, the energy distribution at different frequencies could indicate species that are potentially able to perceive the signals if the audiogram of these species is known. The power of the signal reveals its spatial range before it is lost in the undersea background noise. Moreover, if the signals are emitted in the absence of predators, a wider role for these signals could be hypothesised in addition to an anti-predator function.

To understand the ecological meaning of the production of sound by spiny lobsters, we conducted outdoor arena experiments to examine the acoustic signals under different conditions (alone, in the presence of conspecifics, or in the presence of a predator). The goals of the study were to characterise the acoustic signals emitted by European spiny lobsters and to determine whether their number and structure depended on the presence of conspecifics, the presence of a predator (*Octopus vulgaris*), or the ongoing behaviour of the lobster.

## MATERIALS AND METHODS

### Collection and housing of animals

The study was performed at the Capo Granitola/CNR laboratory (SW Sicily) from May through June 2009. Twenty-five adult European spiny lobsters *Palinurus elephas* (17 males and 8 females) weighing  $193 \pm 55$  g and  $183 \pm 26$  mm in total length (mean  $\pm$  SD), respectively, and 5 adult common octopuses *Octopus vulgaris* weighing  $1656 \pm 168$  g (mean  $\pm$  SD) were used. All animals were captured between January and February 2008. The European spiny lobsters were captured at a depth of 20 to 25 m near Isola delle Femmine (NW Sicily) by fishermen using a commercial trammel net (54-mm inner-panel mesh size, 1200 m length). The individuals were transferred to 2 shaded outdoor PVC circular tanks (3.0 m diameter) supplied with a thin layer of sand approx. 1 cm deep. The common octopuses were caught using trammel nets by a commercial fishery at the same location and depths used to capture the lobsters. In the laboratory, the octopuses were kept in an outdoor PVC circular tank (3.0 m diameter) supplied with a thin layer of sand approx. 1 cm deep. The temperature and salinity levels were monitored using a multiparametric probe (EC300, VWR International) and were kept constant, at  $19.3 \pm 0.78^\circ\text{C}$  (mean  $\pm$  SD) and  $35.4 \pm 0.81$  ppt (mean  $\pm$  SD), with a constant flow of seawater provided at a rate of  $25 \pm 3.7$  l min<sup>-1</sup> (mean  $\pm$  SD). The tanks were covered with a dark cloth to reduce the light intensity. The lobsters were fed crabs and frozen shrimps ad libitum. The octopuses were fed shrimps and frozen fish (*Boops boops*) ad libitum. The lobsters and the octopuses were deprived of food for 5 d before the start of the experimental trials. All animals were kept under natural photoperiods.

The protocols of animal husbandry and experimentation were reviewed and approved in accordance with recommended standards (NRC 1996) and EEC Directive 86/609.

### Rationale and experimental procedures

We carried out all the experiments in the afternoon (at approx. 17:00 h), and completed them before sunset (20:00 h). The lobsters, individually or in groups of 4 individuals, were randomly collected from the holding tanks, assigned to the trials and used in one experiment only to meet the assumption of experimental independence. Each individual predator was

used twice. The lobsters (individually or in groups) were released into the centre of the experimental tank. No shelter was present in the tank. The trial started after 1 h of habituation. After this habituation period and in the absence of any predator, the lobster's acoustic signals were monitored and recorded for 1 h (no-predator trials). A predator was then released into a small cylindrical tank (80 cm diameter, 40 cm height) in the centre of the arena. After 10 s, the tank was removed, leaving the predator in the arena. The lobster's acoustic behaviour (individually or in groups) was monitored and recorded for an additional 1 h (predator trials).

To assess the differences in the number and in the characteristics of the acoustic signals emitted by *Palinurus elephas*, we analysed the acoustic behaviour of lobsters under different conditions. Overall, we performed 20 trials: a single lobster (no stimuli/stress:  $n = 5$  trials), grouped lobsters (only conspecific stimuli/stress:  $n = 5$  trials), a single lobster with a predator (predation stimuli/stress:  $n = 5$  trials), and grouped lobsters with a predator (conspecific stimuli/stress and predation stress:  $n = 5$  trials). The synchronised audio-video system also recorded the behaviour of the lobsters visually (Buscaino et al. 2011) and permitted us to characterise and define the acoustic signals produced in association with particular behavioural events.

### Acoustic and video monitoring system and analysis

To avoid disturbing the animals inside the experimental tank, a laboratory enclosure was placed 5 m from the tank and the equipment required for audio-video monitoring and recording installed there. The acoustic signals emitted by the lobsters were recorded using a calibrated hydrophone (model 8104, Bruel & Kjer) with a sensitivity of  $-205.6$  dB re  $1\text{V}/\mu\text{Pa} \pm 4.0$  dB in the 0.1 Hz to 80 kHz frequency band. The hydrophone was used with a preamplifier (VP1000, Reson), 1 MHz bandwidth single-ended voltage, with the high-pass filter set at 10 Hz with a 32-dB gain. The equipment was connected to a digital acquisition card (USGH416HB, Avisoft Bioacoustics, septate with no gain) managed by dedicated Avisoft Recorder USGH software (Avisoft Bioacoustics).

The signals were acquired at  $300$  kilosamples  $\text{s}^{-1}$  at 16 bits and analysed by the Avisoft-SASLab Pro software (Avisoft Bioacoustics). The digital acquisition card was calibrated with pure tone sine waves at different frequencies (0.2, 1, and 50 kHz) with different

intensities (peak-to-peak 0.1 and 0.5 V) produced by a signal generator (AGILENT 33220) using the SASLab Pro software.

Signals from another hydrophone (Model 8104, Bruel & Kjer) connected to a preamplifier (VP1000, Reson, 1 MHz bandwidth single-ended voltage) and from 2 cameras were synchronised, digitised, and stored using a DAQ card (Model DV-RT4 Real Time, D-Vision) managed by custom-written software (Model DSE, D-Vision). This audio-video system was used to monitor the lobsters' and predators' behaviour and was synchronised with the system used to record the acoustic signals.

Owing to the reverberation produced by the walls of the tank and by the water surface, we conducted some additional acoustic measurements in open water to assess the possible influence of reverberation on the acoustic parameters. After the end of the trials, we recorded the acoustic signals of 2 lobsters, both in the tank and in a sea cage located in a circular natural harbour (with a diameter of approx. 200 m and a depth of 3 m). A stick was used to deliver a stressful stimulus. We measured the signal duration, pulse duration, number of pulses per signal, pulse rate, peak frequency, peak amplitude and bandwidth for the 'sea signals' and the 'tank signals'. The analysis revealed that the pulse duration, peak amplitude and bandwidth differed between the sea signals and the tank signals (Fig. 1). The reverberation in the tank prolonged the duration of the pulse and increased the peak intensity and bandwidth (Fig. 1b,c; see the area enclosed in a red rectangle).

The pulse duration could not be measured adequately in the tank because the reverberation of the first pulse overlapped with the second pulse. The pulse duration was therefore omitted from further analysis. We included measurements of the peak intensity and the bandwidth because we expected that these parameters would be affected much less strongly by reverberation than by the experimental conditions (the presence or absence of stimuli produced by a conspecific or a predator). These parameters would therefore offer additional information on the acoustic behaviour of the lobster. The analysis therefore included the rasp duration, number of pulses per rasp, pulse rate, peak frequency (the frequency of the maximum of the power spectrum), peak amplitude (the amplitude of the peak frequency) and the bandwidth (the difference between the maximum and the minimum frequencies, calculated relative to the level of the background noise and the inconspicuous signal-frequency limits appearing on the spectrogram).

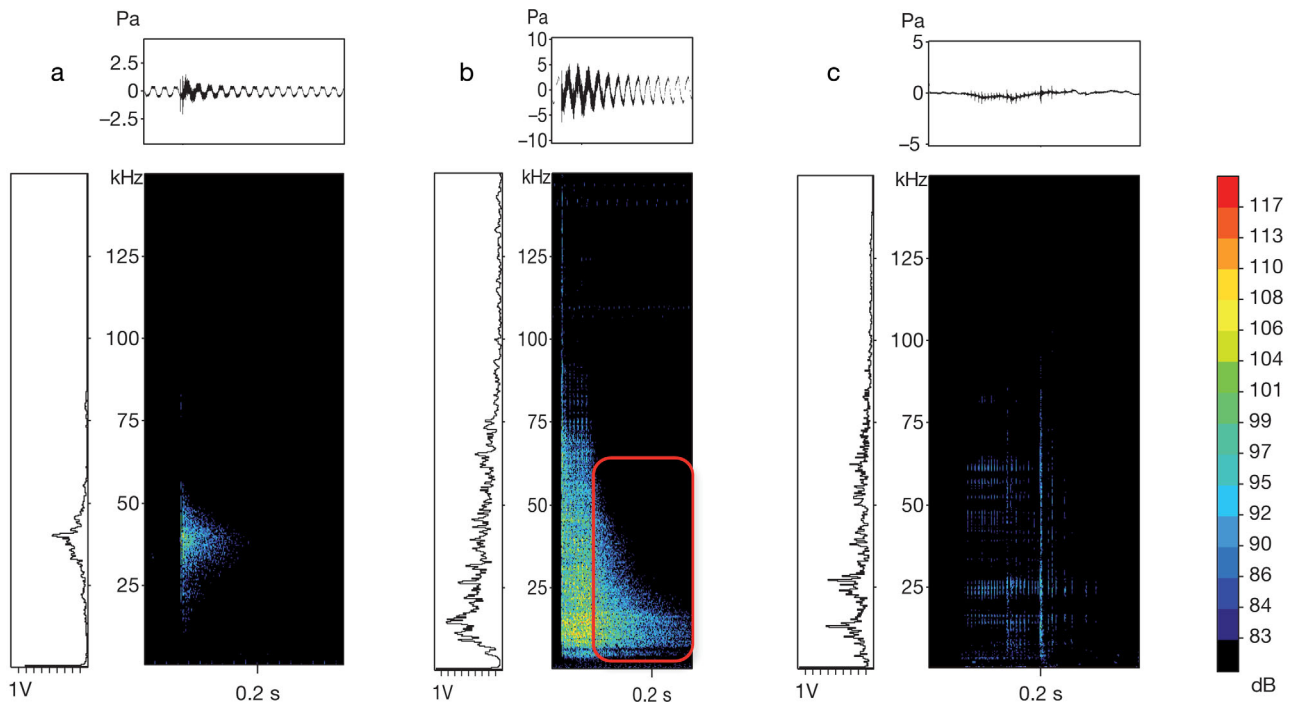


Fig. 1. *Palinurus elephas*. (a) Ultrasound screech (tank recording). (b) Audible rasp (tank recording). (c) Audible rasp (open-harbour recording). Oscillogram (top), maximum power spectrum (left), and spectrogram (right) of spiny lobster signals emitted 1 m from hydrophone. Oscillograms show pressure (Pa) vs. time (s). Maximum power spectra show frequency (kHz) vs. relative amplitude (V). Spectrograms show frequency (kHz) vs. time (s), with intensity in dB re 1  $\mu$ Pa on colour scale, 1024-sample Hanning window

We used the Kruskal-Wallis test to assess the differences between the numbers of acoustic signals emitted by the lobsters under different conditions (1—a single lobster, 2—grouped lobsters, 3—a single lobster with a predator, 4—grouped lobsters with a predator). We used the Mann-Whitney *U*-test to detect differences between the parameters of the acoustic signals emitted by the lobsters in association with anti-predator behaviour and in the absence of anti-predator behaviour.

## RESULTS

Overall, 452 signals were recorded during the trials. The mean numbers of the lobsters' acoustic signals under different conditions are shown in Table 1. In the presence of an octopus, the lobsters, both individually and in groups, produced more signals than in the trials without an octopus (Kruskal-Wallis,  $p < 0.05$ ). In the trials without an octopus, no significant difference was observed between the mean numbers of signals produced by the grouped lobsters and by a single lobster (Kruskal-Wallis,  $p > 0.05$ ). However, in the grouped lobsters, the mean number of signals

Table 1. *Palinurus elephas*. Mean number ( $\pm$  standard deviation) of acoustic signals produced by the lobsters under different conditions

Condition	No. of acoustic signals	
	Without an octopus	With an octopus
Single lobster	12.8 ( $\pm$ 7.7)	21.8 ( $\pm$ 10.5)
Grouped lobster	8.4 ( $\pm$ 2.9)	47.4 ( $\pm$ 12.2)
Per individual in group	2.1 ( $\pm$ 0.7)	11.9 ( $\pm$ 3.1)

produced per lobster was lower than that found for a single lobster (Kruskal-Wallis,  $p < 0.05$ ). In the trials with an octopus, no differences were found between the number of signals emitted by the grouped lobsters and by a single lobster (Kruskal-Wallis,  $p > 0.05$ ).

Significant differences in all of the acoustic parameters were found when all signals emitted in the absence of an octopus were compared with signals emitted with a predator and associated with the anti-predator behavioural event (Mann-Whitney *U*-test,  $p < 0.01$  for all parameters) (see Table 2). We noted that in the trials without an octopus, the lobsters produced screeches that were barely audible (domi-

Table 2. *Palinurus elephas*. Comparison between the mean of the acoustic characteristics of the audible and ultrasound signals emitted by lobster. The Mann-Whitney *U*-test was used to compare all acoustics parameters (except for pulse rate); \**p* < 0.001

	Audible rasp Mean ± SD	Ultrasound screech Mean ± SD	Comparison		
			Difference between mean	<i>U</i>	p-value
Pulse rate, Hz	118.2 ± 54.4	298.9 ± 115.7	180.64		
Pulse number per signal, n	9.5 ± 4.5	3.4 ± 1.3	6.02	208	*
Signal duration, s	0.09 ± 0.05	0.013 ± 0.008	0.083	20	*
Bandwidth, kHz	122.9 ± 23.69	88.6 ± 23.9	34.3	317	*
Peak frequency, kHz	19.52 ± 6.7	34.71 ± 9.2	15.19	197	*
Peak amplitude, dB re 1 µPa	119.82 ± 8.44	114.11 ± 5.94	5.75	8919	*

nated by ultrasound frequencies) and without any association with a particular behavioural event. During the trials with an octopus, both the ultrasound screech and the audible rasp were recorded, and the latter were always associated with anti-predator behaviours: tail flip, lunge, parry, whip and point (Buscaino et al. 2011). As shown in Fig. 2, the signals associated with anti-predator events, relative to the other ultrasound signals, had a greater duration, number of pulses, peak amplitude and bandwidth as well as a lower peak frequency and pulse rate.

Fig. 1 shows examples of the ultrasound signal and of the audible rasps produced during the trials in the tank. Most of the energy of the ultrasound signals was concentrated in the 20–55 kHz range, whereas the energy of the more powerful audible rasps was concentrated in the 2–75 kHz range, with the peak frequency of 15 kHz.

## DISCUSSION

The acoustic signals of spiny lobster species from several areas of the world are known (Moulton 1957, Meyer-Rochow & Penrose 1974, 1976, Patek 2001, 2002, Patek & Oakley 2003, Bouwma & Herrnkind 2009). However, little information is available to characterise the rasps emitted by *Palinurus elephas*. Patek & Oakley (2003) assessed the duration, the number of pulses and the pulse rate for the rasp, but they provided no information about the spectral characteristics of the signal. The possible influence of different ecological conditions on the signals is not known because previous studies only focused on acoustic signals produced after the lobsters had been handheld (Patek & Oakley 2003, Patek et al. 2009).

The acoustic signals produced by *Palinurus elephas* under different conditions all consisted of a pulsatile rasp or screech with a variable number of pulses. These signals were similar in structure, but showed different acoustic characteristics. During the

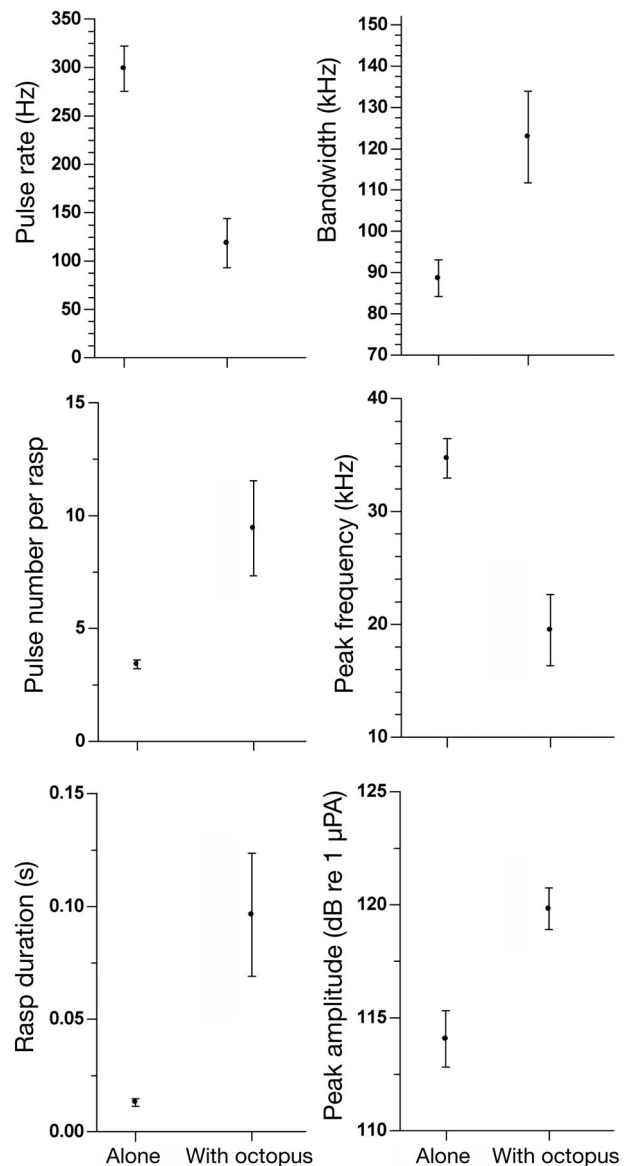


Fig. 2. *Palinurus elephas*. Means (error bar: 95% confidence interval) of the acoustic characteristics of the audible rasps emitted by lobsters in the presence of an octopus ('With octopus') and associated with anti-predator behaviour, and of the ultrasound screeches emitted in the absence of a predator ('Alone'; never associated with anti-predator behaviour)



trials without a predator, the lobster only produced ultrasound screeches, whereas in the presence of a predator, the lobster emitted both ultrasound and audible signals. The audible rasps were characterised by a higher duration, bandwidth, pulse number per rasp and peak amplitude as well as by a lower peak frequency and pulse rate.

We found that the pulse rate of the rasps of *Palinurus elephas* increased as the number of pulses decreased. These findings are consistent with the results of Patek et al. (2009) for *P. interruptus*. The mean numbers of pulses and the pulse rates for the ultrasound screeches and for the audible rasps were approx. 3 and 300 Hz, and 9 and 130 Hz, respectively. The latter values are similar to those found by Patek & Oakley (2003) (13 and 138 Hz, respectively). However, these authors analysed acoustic signals that were produced after the lobsters had been handheld.

The lobsters produced significantly more sounds in the presence of a predator. This result is in agreement with the findings of other authors (Lindberg 1955, Moulton 1957, Hazlett & Winn 1962, Meyer-Rochow & Penrose 1974, 1976, Patek 2001, 2002, Patek & Oakley 2003, Bouwma & Herrnkind 2009). These authors assumed that the lobsters only produced sounds in an anti-predator context. Moreover, Bouwma & Herrnkind (2009) demonstrated that spiny lobsters *Panulirus argus* with an experimentally disabled stridulating apparatus were attacked and killed by predators more frequently than intact spiny lobsters.

The audible rasp occurs in association with specific anti-predator behaviours (tail flip, lunge, parry, whip and point) (Buscaino et al. 2011) consisting of large-amplitude body movements that significantly affect the movements of the antennae. Various functional hypotheses have been offered as explanations for stridulation in lobsters. These hypotheses include calling for help from conspecifics, alerting conspecifics to danger, attracting another predator that might interfere with the attacker, aposematism, startling the predator, and a reduction in the kinetic friction between the antenna and the predator to facilitate escape (Smith 1986, Driver & Humphries 1988, Bouwma & Herrnkind 2009, Staaterman et al. 2010). According to these hypotheses, the lobster, the predator, or a second predator that can potentially interfere with the first predator may be potential targets of the signal. However, the receiver or receivers of the lobster's audible rasps have not yet been identified precisely. The kinetic friction hypothesis is only applicable to cases of direct contact between the predator and lobster. The other predator-related hypotheses seem unlikely

because the findings of our study suggest that the octopus is almost unable to hear the rasps. In fact, most of the energy of the rasp was distributed at frequencies higher than 1 kHz, whereas the hearing sensitivity of the octopus seems to be limited to lower frequencies (100–200 Hz) (Hanlon & Budelmann 1987, Williamson 1988, Packard et al. 1990).

Analysis of the power of the signals could help to identify the potential receivers. The peak amplitude of the audible rasps was significantly higher than that of the ultrasound signals. The audible rasps could therefore cover a wider range in the sea and could potentially have receivers in addition to the predator attacking the lobster. These other receivers could be other lobsters or predators of predators. However, the hearing threshold of detection of the potential receivers should be compared to the level of the rasp at different distances from the source of the rasps.

Because the ultrasound screeches were produced without evident movements of the antennae, an additional mechanism to the stick and slip (Meyer-Rochow & Penrose 1974, 1976, Patek 2002, 2001, Patek & Oakley 2003, Patek & Baio 2007) could be speculated. However, a specific study should be carried out to confirm this hypothesis. The ultrasound screeches were produced both in the presence of the predator and with the predator absent, so that functions in addition to anti-predation could be hypothesised. It should be noted that ultrasound signals had a higher frequency distribution of energy (20–55 kHz) and that lower frequencies, <5 kHz, were not present. This is evidence against the possibility that these signals have lobster predators, such as fish or octopus, as receivers. Moreover, our study found that the number of ultrasound screeches produced was higher for single lobsters than for lobsters in groups. This result allows us to speculate on the potential for intraspecific acoustic communication, because a single lobster could use the ultrasound signal to recruit conspecifics.

The intraspecific communication of European spiny lobster is still hypothetical because the ability of these animals to perceive acoustic signals (including those emitted by conspecifics) has not yet been documented and even the sensitivity of lobsters to different frequencies remains unknown. The mechano-receptors of crustaceans, located in cuticular extensions of the exoskeleton, are called sensilla (Ali 1987) and are able to sense changes in pressure (Ali 1987). Decapod mechanoreceptors include setae (hair-like cells), chordotonal organs, and internal statocysts (Popper et al. 2001). In macruran decapods (crayfish), the hair

fans are sensitive to vibration (Breithaupt & Tautz 1990) and can respond to frequencies up to 100 Hz. According to Tautz (1979), hairs of different lengths may be tuned to different frequencies. In other crustaceans, e.g. *Palaemon serratus*, sensitivity to sounds with frequencies from 100 to 3000 Hz has been demonstrated (Lovell et al. 2005). *Hemisquilla californiensis* emitted rumbles for intraspecific communication, with the potential functions of maintenance of territory, or attraction of mates (Staaterman et al. 2011). Thus, the hypothesis that *Palinurus elephas* is able to perceive intraspecific acoustic signals appears reasonable. However, further studies of this topic should be conducted.

Some acoustic features of a signal could be different in a small tank. For example, Patek et al. (2009) found that the mean first dominant frequency of *Palinurus interruptus* signals was higher in a tank than in the field (1794 and 633 Hz, respectively). We found that the peak amplitude, the pulse duration, and the bandwidth of the signals were different in the tank, whereas the other parameters remained unchanged. The use of the tank, which is a completely controlled environment, allowed us to discover the previously unknown ultrasound screeches. In the sea, where all of the sources of acoustic signals cannot be known, these ultrasound pulses could not have been attributed to *P. elephas*. A larger tank lined with soundproofing materials would not be subject to reverberation and would allow full control of the experimental variables.

In this study, we characterised the audible rasp both in the frequency and in the time domain. Moreover, we indicated that the European spiny lobster emits the previously undescribed ultrasound screeches in the absence of stress caused by a predator. A single lobster unexposed to a predator produces more ultrasound if it is alone, compared with a lobster in a group. These data, together with the tendency of lobsters to cluster, e.g. during migration (Herrnkind 1969, Herrnkind et al. 1973, Lipcius & Herrnkind 1985, Herrnkind et al. 2001, Lavalli & Herrnkind 2009) or as an anti-predator tactic (Herrnkind et al. 2001, Nishimura 2002, Briones-Fourzán et al. 2006, Lavalli & Herrnkind 2009), could suggest that these animals use acoustic signals in addition to the chemical signals that spread slowly and for short distances (Nevitt et al. 2000, Briones-Fourzán 2009). Acoustic signals may allow lobsters to maintain contact with conspecifics and to use clustering and aggregation as anti-predator tactics (Herrnkind et al. 2001, Barshaw et al. 2003, Briones-Fourzán et al. 2006, Lavalli & Herrnkind 2009).

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