Revisiting the bioacoustics of European spiny lobsters *Palinurus elephas*: comparison of antennal rasps in tanks and *in situ*

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ABSTRACT: Spiny lobsters (Palinuridae) are capable of emitting sounds called antennal rasps. In the bioacoustics literature, such broadband sounds have mostly been characterized from tank recordings where reverberation and resonant frequencies might strongly distort their features. Hence, in this study, we compared antennal rasps produced by European spiny lobsters *Palinurus elephas* in both tank and *in situ* conditions. We found significant differences in all sound features (temporal, intensity and spectral features) between tank and *in situ* recordings, confirming that antennal rasps — and broadband sounds generally — cannot be accurately characterized in tanks if sound reverberation is ignored. In recordings of antennal rasps made *in situ*, we show that the main acoustic power is located in the low frequency band (below 1 kHz), which was missed by all earlier studies done in tanks where such low frequencies cannot be properly measured. The hearing capacities of crustaceans suggest roles for intra-specific communication of these sounds, and their high levels indicate they could be heard above noise. Indeed, we outline that antennal rasps are among the loudest sounds known in the marine animal kingdom, with peak-to-peak sound pressure levels (calculated at 20 cm from the source) above 175.7 dB re 1 µPa^2, and peak-to-peak source levels (estimated at 1 m from the source) ranging from 154.2 to 160.6 dB re 1 µPa^2. These acoustic properties imply they could be detected *in situ* during passive acoustic monitoring. This study also highlights the importance of using appropriate measurement methods when characterizing sounds produced by marine invertebrates.

KEY WORDS: Passive acoustics · Spiny lobsters · Palinuridae · *Palinurus elephas* · Antennal rasp · Tank reverberation · Resonant frequencies

1. INTRODUCTION

Ecologists are looking for new environmental descriptors to monitor marine ecosystems. Among the different tools available to survey coastal ecosystems, passive acoustics seems promising, mostly because it is non-invasive and non-destructive (Rountree et al. 2006). Recent studies have highlighted the potential of passive acoustics to monitor tropical marine eco-systems by focusing on producers of specific sounds, such as snapping shrimps and fish (Lammers et al. 2008, Kaplan et al. 2015, Deichmann et al. 2018). In contrast, temperate marine ecosystems have received much less attention, and there is a growing interest to identify species producing sounds that can be detected and isolated among ecosystem soundscapes. In addition to accurately characterizing sounds emitted by these species, we also need to be able to asso-

ciate them with particular behaviors to understand their ecological meanings (Briffa et al. 2003, Ladich & Myrberg 2006). These steps are crucial before envisaging the use of biological sounds as potential marine ecosystem indicators. Crustaceans should be considered as having high potential for bioacoustics studies because they emit a large diversity of sounds (Staaterman 2016), particularly in temperate coastal waters (Coquereau et al. 2016).

Among marine crustaceans, tropical spiny lobsters have received attention for many decades in marine bioacoustics because they produce specific sounds (Moulton 1957, Meyer-Rochow & Penrose 1976, Patek et al. 2009). The mechanism of sound production is external, is located at the base of each second antenna and consists of 2 parts: the soft, ridged plectrum that rubs posteriorly over the anterior part of the hard file-like surface covered with microscopic shingles (Meyer-Rochow & Penrose 1974, Patek 2001, Patek & Baio 2007). This stick-and-slip movement generates a series of broadband pulses during each slip. The associated sound produced during a full movement is composed of many short pulses (the pulse train), and each pulse train is called an 'antennal rasp' (Moulton 1957, Hazlett & Winn 1962b, Patek et al. 2009). The ecological meaning of antennal rasps has mostly been attributed to an anti-predator context, such as helping clawless spiny lobsters to deter or escape from predators (Bouwma & Herrnkind 2009, Staaterman et al. 2010). However, far less is known about the bioacoustics of spiny lobsters living in temperate coastal waters (Buscaino et al. 2011a,b).

The European spiny lobster *Palinurus elephas* (Fabricius, 1787) inhabits European coastal waters from the Northeast Atlantic to the Mediterranean Sea (Ceccaldi & Latrouite 2000) and occurs from the shoreline down to about 200 m water depth (Hunter 1999). It is a large, mobile crustacean with an activity pattern characterized by diurnal sheltering and nocturnal foraging (Giacalone et al. 2015). Its life cycle is quite different from other benthic crustaceans, because it has an unusually long pelagic larval stage (between 6 and 12 mo) followed by benthic juvenile and adult stages, with growth happening through successive molts (Hunter 1999). Because of its high commercial value, *P. elephas* has been historically overfished in many European waters (Goñi & Latrouite 2005), which brought this species to its current status of 'Vulnerable' on the IUCN Red List (Goñi 2014). A striking example of population collapse is found in Brittany, France, where landings dropped from 1000 t in the 1950s to <20 t by the

2000s (Goñi & Latrouite 2005). In this context, it is critical to find new study tools, such as passive acoustics, to monitor this species in these areas.

Antennal rasps produced by spiny lobsters, including *P. elephas*, have mostly been investigated and characterized in tank experiments (e.g. Hazlett & Winn 1962a, Mulligan & Fischer 1977, Buscaino et al. 2011a; see Table S1 in the Supplement at www. int-res.com/articles/suppl/m615p143_supp.pdf). These studies in tanks are necessary before performing *in situ* recordings, because they permit isolating the sounds produced by the studied species, without ambiguity from other sources of sounds present in the oceans. Tank studies are also useful to make visual observations that are essential to associate sounds with behaviors. However, sound characterization in tanks presents many challenges, particularly for broadband sounds that are commonly produced by crustaceans. In a previous article, Jézéquel et al. (2018) illustrated that reverberation in small, constrained volumes like the tanks often used in marine bioacoustics studies, extends the sound duration. In addition, the resonant frequencies, which are specific to each tank's dimensions (Akamatsu et al. 2002), distort the spectral shape of broadband sounds so that their intensity and spectral features cannot be characterized properly (Jézéquel et al. 2018). Moreover, low-frequency sounds (i.e. with frequency below the first resonant frequency of the tank used) are highly attenuated and cannot be measured properly (Rogers et al. 2016). Thus, broadband sounds, such as antennal rasps produced by spiny lobsters, should not be characterized in tanks without a full understanding of the sound reverberation in the tanks. Ideally, tank recordings should be complemented by *in situ* recordings, which mitigate the reverberation issue, while introducing other experimental difficulties (e.g. visibility, ambient noise). Accurately characterizing a sound is important to be able to detect it among the myriad other biological sounds present in marine environments (e.g. Tricas & Boyle 2014, Putland et al. 2017), and is also critical for inferring its potential ecological role.

Here we characterized for the first time the antennal rasps emitted by the European spiny lobster *P. elephas* under *in situ* conditions. We first compared different features of these sounds calculated from both an experimental tank and *in situ*, and then compared them with the existing literature. We assessed the potential ecological roles of these sounds based on our results and determined the potential of such sounds for *in situ* passive acoustic monitoring.

2. MATERIALS AND METHODS

2.1. Ethical statement

Experiments with European spiny lobsters are not subject to restriction for animal scientific research according to the French legislation and the European Community Council Directive of September 2010 (2010/63/UE). However, we followed the ARRIVE guidelines (Kilkenny et al. 2010) to ensure that all experiments were performed under good conditions. Animals were handled with care during the study, and their health status was checked daily by the authors and the aquariology staff of the public aquarium Océanopolis in Brest, France, where the laboratory experimental work was done. No specimens were harmed during this study and there was no mortality. At the end of the study, all specimens were released back into the environment where they were collected.

2.2. Antennal rasp recordings and video

Sounds were recorded using 1 pre-amplified hydrophone (HTI-96-MIN, High Tech), with a sensitivity of -163.7 dB re 1 µPa^{-1} and a flat response from 2 Hz to 50 kHz. This hydrophone was connected to a Wildlife Acoustics Song Meter (Model SM2) recorder with a gain of 0 dB, and was powered by cell batteries. Recordings were made with a sampling frequency of 48 kHz at a 16-bit resolution. The HTI-96-MIN / Wildlife SM2 recording device had the capacity to record sounds with sound pressure levels in peak-to-peak up to 185 dB re 1µPa^2. This is crucial to characterize powerful pulses without clipping the recorded sound (i.e. sound saturation).

Video recordings were made during laboratory and *in situ* experiments using 2 GoPro® HERO3 cameras at a recording rate of 29.97 frames s^{-1}. The videos permitted confirmation of antennal rasp production by the spiny lobsters tested.

2.3. Laboratory experiment

2.3.1. Animal collection, characteristics and care

The laboratory work was carried out at the Océanopolis public aquarium in Brest. For these experiments, a total of 13 *Palinurus elephas* juveniles (7 males and 6 females) were used. Specimens had a carapace length (CL), as measured from the anterior tip of the rostrum to the medial point of the posterior carapace margin, between 4.2 and 7 cm. They were collected carefully by hand while scuba diving in the Bay of Brest, at depths of between 15 and 25 m during 2 diving sessions on 18 and 19 July 2018. Only inter-molt individuals with full sets of intact appendages were selected for this study. After capture, they were immediately transferred randomly to 4 glass-sided rectangular holding tanks (0.6 × 0.5 × 0.35 m, length × width × effective height; seawater volume = 0.105 m^3), with 2 to 4 individuals per holding tank. Each individual was described (size, sex) and given an identification number.

Holding tanks were continuously supplied with sand-filtered, UV-sterilized seawater pumped from the Bay of Brest. Temperature, salinity and animal conditions were controlled twice a day. During the holding period, temperature varied between 17.08 and 18.15°C, and salinity between 34.84 and 35.05. All animals were fed with fresh pieces of fish (mackerel) and cephalopods (squid) ad libitum. They were kept under a 12:12 h light:dark photoperiod; daylight conditions (from 08:00 to 20:00 h) were simulated using fluorescent light tubes above the holding tanks. Several sections of rigid PVC pipe were provided as shelters in each tank. The bottom of each holding tank was supplied with a layer of sand 5 cm deep to provide a suitable foothold surface for the animals. Animals were acclimatized at least 1 mo in these holding conditions before they were used in experiments.

2.3.2. Experimental set-up and conditions of antennal rasp recordings

For the laboratory recordings, we used a plastic-sided rectangular tank (1.13 × 0.73 × 0.5 m; 0.4 m^3) which was placed in a quiet room. During the experiments, it was continuously supplied with the same seawater as the holding tanks, and the bottom was also covered with clean sand. One video camera (same model GoPro® as mentioned above) was placed on the bottom of the tank along the center of the short wall, and a second one was placed 50 cm above the center of the tank, looking down (i.e. plan view). During recordings, the tank was lit with 2 LED strips placed 50 cm above the water surface.

Before antennal rasp recordings, the flow of seawater in the room was cut off. The ambient noise of the experimental tank was recorded for at least 10 min without the animals to check for any additional electrical or other transient sounds. Spectrum analysis of

the ambient noise in the experimental tank showed the absence of any peak frequencies compared to those that were present during sound recordings made with animals. At low frequencies (≤50 Hz), peaks present corresponded to electrical noise from the recorder. These peaks were excluded from the analyses of biological sounds.

Next, we carefully transferred 1 spiny lobster from its holding tank to the experimental tank and waited for the individual to stop exploring and assume a resting position (about 5 min). The animal was then gently picked up and held at distances of between 20 and 30 cm from the hydrophone and about 20 cm off the substrate to elicit antennal rasps, as is commonly described in the bioacoustics literature on spiny lobsters (Moulton 1957, Meyer-Rochow & Penrose 1976, Patek et al. 2009). Antennal rasp recordings lasted about 30 to 60 s (individuals stopped emitting antennal rasps after this period), and all individuals were tested once during the study. After recordings were complete, each individual was returned to its holding tank, and sound files were archived for analysis.

2.4. *In situ* recordings

2.4.1. Site description

For comparison, we also recorded antennal rasps from spiny lobsters *in situ*, in the Bay of Perros Guirec, Brittany, France, where small groups of juveniles have been observed by recreational divers. Three different spots were selected in the bay, within 3 km of each other, where small groups of individuals were present. Juveniles were observed to be in typical habitats (similar to habitats described in the Mediterranean Sea; Díaz et al. 2001) of vertical, rocky outcrops (approximately 5 to 10 m high), with less than 12 m seawater depth at low tide. They were covered with colonies of jewel anemones (genus *Corynactis*) and colonial gorgonians (*Eunicella verrucosa*) just below the kelp belt (*Laminaria digitata*). These outcrops have many crevices inhabited by juvenile spiny lobsters. Because these areas are often subject to strong water currents (>2 knots), we performed antennal rasp recordings 30 min before and after low tide, when tidal currents were lowest.

2.4.2. *In situ* recordings of antennal rasps

Antennal rasp recordings were made on 29 September, and again on 21 October 2018 at the sites described above. We deployed the recording device about 2 m from the rock face and at 2 m above the substrate, in front of the crevices where spiny lobsters were visible. First, the ambient noise at each site was recorded for 10 min. Just before sounds were recorded, 2 experienced divers free-dived to explore the vertical rocky outcrops and note the different locations where spiny lobsters were found. This permitted us to observe and determine individually the different spiny lobsters that could be tested, to avoid testing the same lobster twice. After this, we first filmed and then carefully collected an individual spiny lobster and brought it quickly to within 20 to 50 cm of the hydrophone, and 10 m below the seawater surface. During the manipulation, the spiny lobster was held so that it faced the hydrophone, and pointed away from the rocky face. The individual was then gently released back into its crevice. All individuals that were successfully caught were tested once, and each antennal rasp recording session lasted around 30 to 60 s. Carapace length and sex for each tested individual were both noted. Because the antennal rasp recordings were performed while free-diving, background noise from the diving activity was minimal in the vicinity of the recording device.

2.5. Sound analysis

2.5.1. Sound features of antennal rasps

Synchronized recordings of sounds (in .wav format) and videos were analyzed to confirm antennal rasp production by the spiny lobsters tested. Based on this annotation, each antennal rasp was extracted manually using the Audacity software® (version 2.1.1; Audacity Team 2015). Antennal rasps were defined as pulse trains composed of several pulses separated by less than 20 ms from each other. Hence any isolated pulses (mostly present in the *in situ* recordings) were not analyzed here. All sequences were then processed using custom MATLAB scripts (version 9.1; The MathWorks). Antennal rasps from tank recordings were analyzed between 60 Hz and 24 kHz to exclude electrical noise; frequencies below 60 Hz were ignored but not filtered. On the other hand, antennal rasps from *in situ* recordings were analyzed between 0 Hz and 24 kHz. No infra-sounds related to electronic self-noise from recording devices used were present during *in situ* recordings.

Antennal rasps from tank and *in situ* recordings were characterized by examining 3 different types of sound features: temporal, intensity and spectral fea-

tures. The different sound features are presented as mean ± SD.

For tank and *in situ* recordings, we calculated 3 different temporal features: total duration (in ms), number of pulses per antennal rasp and pulse rate (in Hz). Total duration was calculated as the duration between the first 'rise' of the first and the last pulses of each antennal rasp (Jézéquel et al. 2018). This allowed us to avoid some of the effects of reverberation that extended each single pulse duration in the experimental tank. The pulse rate was defined as the number of pulses per train divided by the total duration. When pulses from an antennal rasp could not be clearly isolated from each other (i.e. because the reverberation of one pulse overlapped with the next one, or because 2 antennal rasps occurred simultaneously), we did not calculate its temporal features.

We also calculated 2 different intensity features based on sound pressure level (SPL, in dB re 1 µPa^2). As antennal rasps are pulse trains characterized by short and transient sounds, we chose to calculate the SPL in peak-to-peak (SPL$_{pp}$) which is the most representative intensity feature for these types of sounds (Erbe 2010). We also calculated the SPL as a root mean square (SPL$_{rms}$) that can be applied to pulse trains if they are homogeneous in time and long enough, so that they look like continuous signals at the scale of the analysis window.

In addition, for antennal rasps recorded *in situ*, source levels were estimated as peak-to-peak (SL$_{pp}$) at 1 m from the spiny lobsters, based on SPL$_{pp}$ and a model of transmission loss (TL). As the hydrophone was located near the sound source (i.e. <1 m from the spiny lobsters), we assumed the antennal rasps propagate uniformly in all directions, permitting the use of a simple spherical spreading loss model to account for TL (Erbe 2010). Thus, SL$_{pp}$ was estimated as follows: SL$_{pp}$ = SPL$_{pp}$ + TL, with TL = $20\log_{10}(r)$ where r indicates the distance (in meters) between the spiny lobster and the hydrophone. Because it was difficult to maintain spiny lobsters underwater at a constant distance from the hydrophone during antennal rasp recordings while free-diving, we estimated the r from the videos as a minimum and maximum distance between the individual tested and the hydrophone. We estimated these distances between the spiny lobster held by the first diver and the hydrophone through the video recordings done by the second diver, and by knowing the dimensions of the recording device. The second diver filmed perpendicular to the direction of the spiny lobster held near the hydrophone, so that the Pythagorean theorem could be applied to calculate these distances. We then obtained 2 different peak-to-peak source levels: SL$_{pp}$ min and SL$_{pp}$ max. Note that in this study, the *in situ* SL$_{pp}$ estimates ignored any near-field effect. Because the use of more complex models of TL should be applied for antennal rasps recorded in the experimental tank, and because those models require a very accurate estimation of the source–receiver distance (Rogers et al. 2016), we did not estimate their SL$_{pp}$.

We also calculated 3 different spectral features: The first and second peak frequencies (Fp$_1$ and Fp$_2$, respectively; in kHz) represent the 2 frequencies where the power spectral density (PSD, in dB re 1 µPa^2 Hz^{-1}) was maximal. These frequencies for antennal rasps recorded in the experimental rectangular plastic tank were compared with the minimum resonant frequency of the tank. This minimum resonant frequency (in kHz) was calculated using the theoretical equation from Akamatsu et al. (2002) for a rectangular glass-sided tank with mode (1, 1, 1). Finally, the frequency bandwidth (*B*, in kHz) was estimated as the spread (i.e. standard deviation) of the PSD around Fp$_1$.

2.5.2. Ambient noise characterization

Recordings of ambient noise (10 min each) from the 5 *in situ* spots were first visualized to ensure the absence of antennal rasps. Next, they were both cut into 10 sequences of 1 min each, and we randomly selected 3 of 10 sequences from each recording per site. Ambient noise is characterized as a continuous sound (Erbe 2010); we thus calculated the SPL$_{rms}$ of each selected, 1 min long sequence. This provided a mean value of the SPL$_{rms}$ for the ambient noise at each spot. We also generated the sets of theoretical Wenz curves (Wenz 1962) for boat traffic noise (ranging from index 1 to 7) and wind noise (ranging from 0 to 30 knots) using custom MATLAB scripts. They were used as a comparison for the PSDs of the ambient noise calculated at each spot.

2.6. Statistical analysis

We first tested whether differences in means between the carapace length of individuals tested between the 2 groups (tank and *in situ*) were significant. As these data were normally distributed in both groups (Shapiro-Wilk test, p < 0.05), Student's *t*-test was applied (α = 0.05).

All sound features described above (except for the SL$_{pp}$ that was only calculated for antennal rasps re-

corded *in situ*) were then tested to determine whether significant differences in means were evident between the 2 groups. We aimed to compare tank and *in situ* recordings of antennal rasps produced by *P. elephas* using the same handling protocol. Thus, no variability among antennal rasps produced by a single individual, nor between individuals could be considered from the data collected. Considering the small number of sound recordings, and assuming that calculated variables for each individual can be assimilated to a random distribution, the non-parametric Mann-Whitney *U*-test was used to determine if their probability distributions were equal (α = 0.001). All statistical analyses were performed using R version 3.5.1 (R Core Team 2018).

3. RESULTS

3.1. Sound features of antennal rasps

In both tank and *in situ* recordings, all spiny lobsters tested produced audible antennal rasps during episodes of stress generated while handling. These were mostly accompanied by visible, vigorous contractions of their abdominal regions.

3.1.1. Tank recordings

A total of 387 antennal rasps from the 13 individuals tested (21–34 rasps ind.$^{-1}$) were recorded in the experimental tank. Waveforms consisted of pulse trains that were sometimes difficult to isolate because of sound reverberation (Fig. 1A). The effects of sound reverberation were also seen in spectrograms where all pulses (dark vertical lines) were followed by a 'smear' (dark horizontal lines; Fig. 1C). When taking this into account, temporal features could be calculated in 94% of the antennal rasp events. Their mean total duration was 120.5 ± 25.9 ms (range: 60–225 ms), with a mean of 15.0 ± 3.3 pulses per antennal rasp (range: 7–28) and a mean pulse rate of 127.9 ± 21.1 Hz (range: 78.4–226.7 Hz) (Table 1).

Intensity features were high, with a mean SPL_{pp} of 171.0 ± 3.1 dB re 1 μPa^2, including some antennal rasps recorded at 20 cm from the spiny lobsters of up to 175.7 dB re 1 μPa^2 (Table 1). The mean SPL_{rms} was 151.2 ± 4.2 dB re 1 μPa^2 (Table 1).

The minimum resonant frequency calculated for the experimental tank was 1.94 kHz, and strongly influenced the spectral shape of the antennal rasps. Indeed, 268 out of the 387 (69%) antennal rasps had

their first peak frequencies at 2 kHz, which was clearly seen in both the PSDs (Fig. 1B) and spectrograms (dark horizontal line at 2 kHz; Fig. 1C). Below 2 kHz, a relatively large acoustic power gap was found in all antennal rasps (Fig. 1B,C). In contrast, above 2 kHz, high acoustic power was present up to 23 kHz (Fig. 1B,C). These higher frequencies corresponded to other resonant frequencies associated with the experimental tank and caused a highly variable Fp_1 and Fp_2, with means of 3.99 ± 3.68 kHz (range: 1.82–17.74 kHz) and 5.34 ± 4.27 kHz (1.82–17.83 kHz), respectively (Table 1). Because acoustic power was mainly focused around the minimum resonant frequency of the tank, the resulting bandwidth was limited, with a mean of 5.13 ± 2.51 kHz (0.42–11.70 kHz) (Table 1).

3.1.2. *In situ* recordings

During *in situ* recordings, 9 spiny lobsters (6 females, 3 males) were successfully caught and their antennal rasps recorded in the 3 different spots described above. Their mean CL was 5.1 ± 0.4 cm (SD) and did not differ significantly from the mean CL of spiny lobsters used for the laboratory experiments (*t*-test, p = 0.32). A total of 233 antennal rasps were recorded from all 9 spiny lobsters (range: 17–32 rasps ind.$^{-1}$).

Compared to antennal rasps recorded in the experimental tank, antennal rasps recorded *in situ* presented clear waveforms with pulses that could be easily isolated (Fig. 1D). This was also highlighted in the spectrograms, which did not have the smearing seen in the tank recordings (Fig. 1C,F). Thus, temporal features could be calculated for all 233 recorded antennal rasps emitted by the 9 individuals tested. Mean total duration was 147.0 ± 29.7 ms (53–266 ms), with a mean number of pulses per antennal rasp of 16.9 ± 4.7 (6–33) and a mean pulse rate of 115.9 ± 27.2 Hz (59.4–208.9 Hz; Table 1). Mean temporal features from antennal rasps recorded *in situ* were all significantly different from the antennal rasps recorded in the tank; the mean total duration and mean number of pulses per antennal rasp were higher (*U*-test, p < 0.001), whereas the mean pulse rate was lower (*U*-test, p < 0.001).

As seen in Table 1, even if some SPL_{pp} and SPL_{rms} values were also high (up to 175.7 and 146.4 dB re 1 μPa^2 at 20 cm from the spiny lobsters, respectively), their mean values were significantly lower than those measured in the experimental tank (*U*-test, p < 0.001). The mean values of SL_{pp} estimated at 1 m
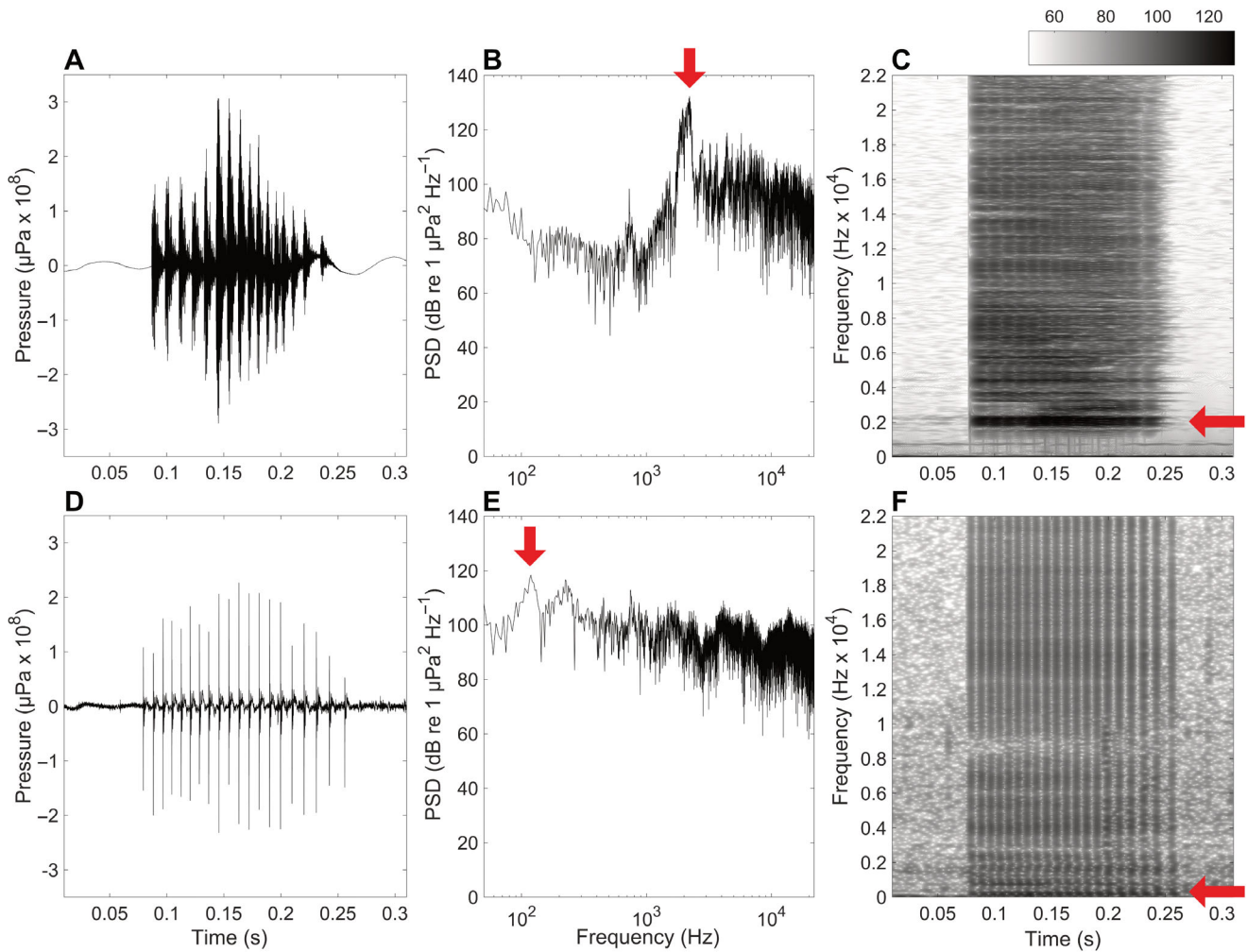
Fig. 1. Examples of typical antennal rasps produced by 2 *Palinurus elephas* juveniles and recorded at the same distance from the hydrophone (20 cm) in the experimental tank (top row) and *in situ* (bottom row). (A,D) Waveforms. (B,E) Acoustic spectra (Fast Fourier Transform length: 13 640), with the *x*-axis in logarithmic scale. (C,F) Spectrograms (Fast Fourier Transform length: 2024; Hamming window: 1001 points; 99% overlap). Red arrows indicate the first peak frequency of each antennal rasp. Notice that the first peak frequency of the antennal rasp recorded in the tank (top row) corresponds to the minimum resonant frequency calculated for the experimental tank alone (2 kHz); there is also a large gap of acoustic power below 2 kHz. The color scale bar is in dB re 1 µPa² Hz⁻¹. PSD: power spectral density

from the spiny lobsters in the field ranged between 154.2 ± 4.5 (SL_{pp} min) and 160.6 ± 4.4 (SL_{pp} max) dB re 1 µPa² (Table 1).

As no effects of reverberation were detected for the antennal rasps recorded *in situ*, we could calculate their natural spectral features for the first time. Acoustic power peaks were found to be spread in the low frequency band (below 1 kHz; Fig. 1E,F). Indeed, mean values of Fp_1 and Fp_2 were respectively 0.77 ± 0.24 kHz (0.12–1.66 kHz) and 0.96 ± 0.40 kHz (0.22–1.62 kHz) (Table 1). These were both significantly lower than the tank recordings (*U*-test, p < 0.001). This is the contrary to what was seen in the tank recordings where acoustic power was only found

from 2 kHz (Fig. 1B,C). However, these low peak frequencies did not include all the acoustic power contained in antennal rasps, with some acoustic power also found in higher frequencies (up to 23 kHz). This gave a mean bandwidth of 16.99 ± 5.38 kHz (4.90–23.00 kHz; Table 1) that was significantly larger than that of the tank recordings (*U*-test, p < 0.001).

3.2. Comparison of ambient noise and antennal rasps recorded *in situ*

During *in situ* recordings, the sea state was between 1 (Calm) and 2 (Smooth) on the Douglas scale,

Table 1. Sound features (temporal, intensity and spectral features) calculated for the European spiny lobster antennal rasps recorded in the experimental tank and *in situ*. Results are presented as means ± SD with ranges (minimum–maximum). A Mann-Whitney test was used to compare means of sound features between the tank and *in situ* recordings. **Bold** values highlight sound features that were significantly different (*U*-test, p < 0.001) between tank and *in situ* recordings. SL_{pp} (SPL_{rms}): peak-to-peak (root mean square) sound pressure level, SL_{pp}: peak-to-peak source level, Fp_1 (Fp_2): first (second) peak frequency, *B*: frequency bandwidth, NA: not applicable

Sound features	Antennal rasps	
	Tank	*In situ*
Temporal		
Total duration (ms)	**120.5 ± 26.0** (60–225)	**147.0 ± 29.7** (53–266)
Number of pulses per antennal rasp	**15.0 ± 3.3** (7–28)	**16.9 ± 4.7** (6–33)
Pulse rate (Hz)	**127.9 ± 21.1** (78.4–226.7)	**115.9 ± 27.2** (59.4–208.9)
Intensity		
SPL_{pp} (dB re 1 μPa^2)	**171.0 ± 3.1** (160.4–175.7)	**167.3 ± 3.9** (156.0–175.7)
SPL_{rms} (dB re 1 μPa^2)	**151.2 ± 4.2** (139.7–159.6)	**139.2 ± 3.0** (132.0–146.4)
SL_{pp} min (dB re 1 μPa^2)	NA	154.2 ± 4.5 (142.0–165.3)
SL_{pp} max (dB re 1 μPa^2)	NA	160.6 ± 4.4 (150.0–169.7)
Spectral		
Fp_1 (kHz)	**3.99 ± 3.68** (1.82–17.74)	**0.77 ± 0.24** (0.12–1.66)
Fp_2 (kHz)	**5.34 ± 4.27** (1.82–17.83)	**0.96 ± 0.40** (0.22–1.62)
B (kHz)	**5.13 ± 2.51** (0.42–11.70)	**16.99 ± 5.38** (4.90–23.00)

corresponding to wave heights of between 0 and 0.5 m. Wind state ranged between 0 (Calm) and 4 (Light breeze) on the Beaufort scale, corresponding to speeds between 1 and 18 knots. Seawater temperature was 16.5 ± 0.2°C and salinity was 35.4 ± 0.1.

Two different groups of ambient noise were distinguished among the 5 different spots where sound recordings were made. Two spots were directly subject to more energetic sea conditions (high wind speeds and waves), resulting in mean SPL_{rms} values of 121.0 ± 0.5 and 124.2 ± 1.0 dB re 1 μPa^2. In contrast, the 3 other locations were calmer, which was reflected in a lower mean SPL_{rms} of 109.5 ± 1.6 dB re 1 μPa^2. During ambient noise recordings, no antennal rasps were detected.

The PSD of the loudest ambient noise had its main acoustic power peaks at more than 100 dB re 1 μPa^2 Hz^{-1} below 25 Hz that was attributed to the friction of the hydrophone with water due to the waves (Fig. 2). The ambient noise levels at all 5 locations were within Wenz curves of between 25 Hz and 2 kHz. Above 2 kHz, acoustic power peaks were always found around 3 and 4 kHz that were almost 20 dB re 1 μPa^2 Hz^{-1} above Wenz curves (Fig. 2). This contribution was associated with isolated broadband pulses from unknown sources (no snapping shrimps were observed at the spots during the recordings). Despite these observations, PSDs of all antennal rasps recorded at the 5 spots were always above the PSDs of the ambient noise recorded at the same time and over the entire frequency range (except at frequencies below 25 Hz). For example, the PSD of a typical antennal rasp at its first peak frequency (0.125 kHz) was 30 dB re 1 μPa^2 Hz^{-1} above the PSD of the loudest ambient noise, and almost 50 dB re 1 μPa^2 Hz^{-1} above the quietest (Fig. 2). This pattern was also seen in the higher frequencies up to 23 kHz (Fig. 2).
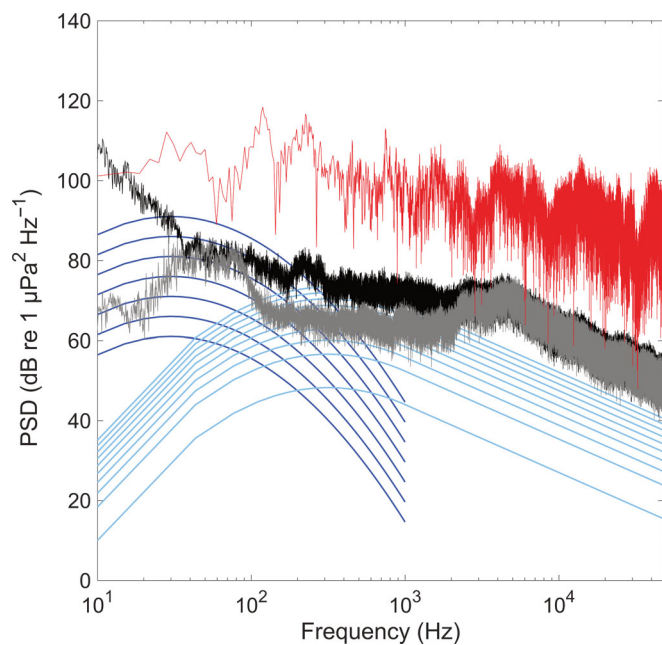

Fig. 2. Acoustic spectrum of a *Palinurus elephas* antennal rasp recorded *in situ* (red), with the loudest ambient noise (black) and the quietest ambient noise (grey) recorded from the 5 different spots. The *x*-axis is in logarithmic scale. Thin lines indicate Wenz's traffic noise curves ranging from index 1 to 7 (dark blue) and Wenz's wind noise curves ranging from 0 to 30 knots (light blue). PSD: power spectral density

4. DISCUSSION

In this study of *Palinurus elephas* antennal rasps, we emphasize 2 important results. First, all sound features calculated between antennal rasps recorded in an experimental tank and *in situ* were significantly different. Secondly, this is the first time that *P. elephas* antennal rasps have been characterized *in situ*. We have shown that they are very loud, with SPL_{pp} values (calculated at 20 cm from the source) being higher than 175.7 dB re 1 μPa^2 and SL_{pp} values (estimated at 1 m from the source) ranging from 154.2 to 160.6 dB re 1 μPa^2, and with important acoustic power spread in low frequencies (below 1 kHz). These new results suggest possible ecological roles for these sounds and a strong potential for them to be detected *in situ*.

4.1. Temporal features of the antennal rasps

Sound reverberation in the experimental tank did affect the waveform of antennal rasps by extending the duration of single pulses (Fig. 1A,C). This phenomenon was absent in antennal rasps recorded *in situ* (Fig. 1D,F). Our results for temporal features are consistent with antennal rasps previously reported for *P. elephas* in the bioacoustics literature. Our mean total durations of 120.5 and 153.1 ms (tank and *in situ* recordings, respectively) were within an order of magnitude of other studies (Patek & Oakley 2003: 101 ms; Buscaino et al. 2011a: 90 ms; de Vincenzi et al. 2015: 70 ms), and are similar to antennal rasp total durations previously published for tropical spiny lobsters (Mulligan & Fischer 1977: *Panulirus argus*, 154 ms; Patek & Oakley 2003: *Panulirus japonicus*, 155.1 ms). In our study, the mean numbers of pulses per antennal rasp recorded in the experimental tank and *in situ* are in the same range as reported for studies done on *P. elephas* (Patek & Oakley 2003: 13.5; Buscaino et al. 2011a: 9.5; de Vincenzi et al. 2015: 8) and other tropical spiny lobsters (Patek & Oakley 2003: *Linuparus trigonus*, 17.9; Kikuchi et al. 2015: *Panulirus japonicus*, 11). Finally, our mean pulse rates of antennal rasps recorded in the experimental tank and *in situ* are close to other studies on *P. elephas* (Patek & Oakley 2003: 138.5 Hz; Buscaino et al. 2011a: 118.2 Hz; de Vincenzi et al. 2015: 134 Hz), and other species of tropical spiny lobsters (Patek & Oakley 2003: *L. trigonus*, 118.5 Hz; *Justitia japonica*, 131.4 Hz; *Panulirus homarus*, 120.6 Hz).

Even though we recorded and compared 2 groups of juveniles with similar sizes by using the same protocol, we found significant differences in all temporal features between tank and *in situ* recordings. This was surprising, as the temporal features we calculated are not impacted by tank reverberation. This variability could be attributed to differences between individuals and also between antennal rasps produced by the same individual or even the behavioral context (handling); however, these were not investigated for this explanatory study. For example, long-legged spiny lobsters *Panulirus longipes* show fatigue after producing antennal rasps for more than 30 s (Meyer-Rochow & Penrose 1976). Fatigue or exhaustion would be expected to lower the rates of antennal rasps and change their temporal features (e.g. pulse rate reduced; Meyer-Rochow & Penrose 1976).

Several authors working on tropical spiny lobsters have examined the scaling of antennal rasp temporal features with body size and even the mechanism of sound production. For example, Patek & Oakley (2003) found positive correlations between pulse rate and the number of pulses with file length, while antennal rasp total durations were negatively correlated with file length for *Panulirus argus*. Meyer-Rochow & Penrose (1976) and Patek et al. (2009) found a positive correlation between body size and antennal rasp total durations, while there was a negative correlation between size and pulse rate for *Panulirus longipes* and *Panulirus interruptus*, respectively. In this study, we used only similar-sized individuals. Performing additional sound recordings using a wider size range could permit verification of antennal rasp temporal features and the importance of inter-individual variability.

4.2. Intensity of antennal rasps

This is the first time that such high SPL values for antennal rasps have been reported in the bioacoustics literature on spiny lobsters. We calculated antennal rasp SPL_{pp} values at more than 175.7 dB re 1 μPa^2 in the tank and *in situ* at 20 cm from the specimens tested. In addition, because we recorded antennal rasps *in situ*, we could estimate for the first time their SL_{pp}. We found the SL_{pp} estimated at 1 m from the spiny lobsters ranged between 154.2 and 160.6 dB re 1 μPa^2. However, 2 different intensity features (SPL_{pp} and SPL_{rms}) were significantly lower in the *in situ* recordings compared to tank recordings. For example, the mean SPL_{rms} of antennal rasps *in situ* was 10 dB re 1 μPa^2 lower than in the tank recordings. This difference in SPL_{rms} is explained by

the 'smear of noise' accompanying each pulse in all antennal rasps recorded in the tank that increased sound intensity (see Fig. 1A,C), and this phenomenon was absent in antennal rasps recorded *in situ* (see Fig. 1D,F). In addition, due to the low-frequency sampling of our recording device (48 kHz), these intensity features might be underestimated if there is acoustic power spread at higher frequencies.

Several articles have reported SPLs in decibels for spiny lobsters (Latha et al. 2005, Patek et al. 2009, Buscaino et al. 2011a, de Vincenzi et al. 2015); the numerical values in the literature range from 50 to 150. Unfortunately, these results are not comparable because they were obtained with different signal-processing methods, and these earlier studies do not provide enough information to be able to re-estimate the values. For example, calculating an SPL on a frequency representation produces different numerical results depending on the method applied (e.g. power spectrum or PSD) and on the calculation parameters (e.g. sampling frequency, Fast Fourier Transform length). It should also be noted that antennal rasps are short, transient sounds. Fourier-based methods are poorly adapted for such signals, for the reasons previously discussed. As stated in ANSI (2005) and demonstrated by Erbe (2010), it is preferable to use time-domain metrics such as the SPL_{pp} and SPL_{rms} calculated in our study. Thus, here we chose to compare our results with other studies that also reported intensity features in SPL and SL from sounds emitted by other marine species.

Few marine animals have been reported to emit such loud sounds. Some marine mammals, such as dolphin and whale species, have been shown to produce whistles and calls with SL_{pp} at 1 m that exceed 169 and 189 dB re 1 µPa^2, respectively (Janik 2000, Sirovic et al. 2007). Some fish have also been shown to emit very loud sounds, including large goliath groupers *Epinephelus itajara* with a maximum SPL_{rms} of 144 dB re 1 µPa^2 (distances from the fish not estimated; Mann et al. 2009), or black drums *Pogonias cromis* with highest SPL_{rms} calculated at 0.95 m exceeding 166 dB re 1 µPa^2 (Locascio & Mann 2011). In crustaceans, only snapping shrimps *Alpheus heterochaelis* have been shown to produce louder impulsive sounds (the 'snaps') compared to the antennal rasps of *P. elephas*. Snaps have been calculated to have SL_{pp} estimated at 1 m ranging from 145 to up to 215 dB re 1 µPa^2 (Cato & Bell 1992, Au & Banks 1998, Schmitz 2002). In the present study, we only recorded antennal rasps in juveniles (CL between 4 and 7 cm); larger adults (CL > 15 cm) may emit even louder antennal rasps if the earlier results of Meyer Rochow

& Penrose (1976) for the evolution of antennal rasp features with body size in *Panulirus longipes* can be generalized.

4.3. Spectral features

In our study, spectral features of antennal rasps recorded in the experimental tank were strongly affected by the tank resonant frequencies. Indeed, acoustic power was only present from 2 kHz (the minimum resonant frequency of our tank) to 23 kHz. This distribution of acoustic power toward high frequencies in our recordings is generally consistent with the bioacoustics literature on spiny lobsters. Buscaino et al. (2011a) and de Vincenzi et al. (2015) calculated both very high and variable first peak frequencies of 19.52 ± 6.70 and 22.93 ± 8.20 kHz, respectively, for *P. elephas* antennal rasps recorded in tanks. Other studies (also done in tanks) for species of tropical spiny lobsters also found high peak frequencies in antennal rasps (e.g. Hazlett & Winn 1962a, Mulligan & Fischer 1977, Patek et al. 2009; see Table S1). For example, antennal rasps produced by *Panulirus argus* in a tank of similar size to the tank used in the present study showed their first peak frequencies between 2 and 5.5 kHz (Mulligan & Fischer (1977), which should have been described as being associated with the tank resonant frequencies (Akamatsu et al. 2002, Jézéquel et al. 2018). Meyer-Rochow & Penrose (1976) were the first authors to mention the technical challenges of characterizing antennal rasps in tanks because of sound reverberation and resonant frequencies. They reported that antennal rasps were distorted by these phenomena, hence they did not calculate spectral features of the sounds (peak frequencies and bandwidth). These authors concluded that antennal rasps should contain acoustic power spread equally over their bandwidth (i.e. a white spectrum; Meyer-Rochow & Penrose 1976). In contrast, below 2 kHz, we found a large acoustic power gap that was present in all antennal rasps recorded in the experimental tank (Fig. 1B,C). This gap below the minimum resonant frequency of our experimental tank is explained by the high attenuation of low frequencies in such tanks because of their longer wavelength compared to the dimensions of the tank used (Rogers et al. 2016).

Not surprisingly, spectral features of antennal rasps recorded *in situ* showed significantly different patterns compared to antennal rasps recorded in the experimental tank. Indeed, the important acoustic power was present in the low frequency band (below

1 kHz; Table 1). These results are representative of the true antennal rasp sound, as our *in situ* measurements were not contaminated by tank reverberation. Thus, our results do not confirm the hypothesis of a white spectrum postulated by Meyer-Rochow & Penrose (1976). However, our results are consistent with the later work of Patek et al. (2009) using *Panulirus interruptus*, where these authors reported the Fp_1 in antennal rasps recorded *in situ* as 0.63 ± 0.37 kHz. In addition, Moulton (1957) described antennal rasps from *Panulirus argus* with peak frequencies of 0.80 kHz in a large naturalized aquarium. However, Kikuchi et al. (2015) recorded antennal rasps *in situ* from *Panulirus japonicus*, with mean values of peak frequencies of 10.00 ± 4.50 kHz. While we used the same protocol as in the existing bioacoustics literature in spiny lobsters to have comparable results, we did not take into account the potential effects of animal handling in the spectral features of antennal rasps. Further studies will be required to characterize antennal rasps without handling animals *in situ*. An interesting perspective is the use of fake predators, as described by Staaterman et al. (2010).

In addition, the bandwidths of our antennal rasps recorded *in situ* were significantly broader compared to antennal rasps recorded in the tank (Table 1). This is due to the minimum resonant frequency of the tank that concentrated the acoustic power, leading to distinct peaks in the PSDs (Fig. 1B). In contrast, spectra of antennal rasps recorded *in situ* had acoustic power spread much wider around peak frequencies (Fig. 1E). However, the bandwidth values reported here were limited by our system capacity. Because of the sampling frequency (48 kHz), we could not record frequencies higher than 24 kHz. Indeed, the estimated bandwidth (up to 23 kHz) actually covered the whole bandwidth of the recording device, and thus we concluded that the source bandwidth might be greater than 23 kHz. As a confirmation, Buscaino et al. (2011a) found acoustic power up to 100 kHz in antennal rasps produced by *P. elephas* in tanks.

4.4. Towards a new biological hypothesis concerning the potential ecological roles of antennal rasps in *P. elephas*

Accurately characterizing a sound produced by a particular species is not only crucial to be able to detect it *in situ* among other biological sounds, but also for inferring biological hypotheses about their potential ecological roles. In the next sections, we discuss the implications of our results.

4.4.1. Inter-specific communication

Most studies in the bioacoustics literature have proposed an anti-predator role for the antennal rasps (Moulton 1957, Meyer-Rochow & Penrose 1976, Staaterman et al. 2010). In this study, we elicited the production of antennal rasps in *P. elephas* by gently handling individuals, which is intended to imitate capture by a natural predator. In contrast with the clawed lobster *Homarus gammarus*, the clawless *P. elephas* relies on its spiny carapace and rigid antennas to defend itself against predators (Barshaw et al. 2003). Thus, being able to emit loud sounds could help individuals to deter potential predators. In contrast with previous studies (Buscaino et al. 2011a, de Vincenzi et al. 2015), we have demonstrated that most of the acoustic power contained in antennal rasps was spread into the low frequency band below 1 kHz. Interestingly, the sound sensitivity of some of their natural predators, namely cephalopods (including octopus), appears to be limited to the same band of low frequencies (Williamson 1988, Packard et al. 1990, Mooney et al. 2010). For example, a controlled experiment with *Panulirus argus* showed that stridulating individuals escaped more frequently from attacking octopuses than surgically muted individuals (Bouwma & Herrnkind 2009). In addition, Buscaino et al. (2011a) found that *P. elephas* produced more antennal rasps when exposed to an octopus than in the trials without an octopus in a tank. As the common octopus *Octopus vulgaris* is a well-known predator of the European spiny lobster (Barshaw et al. 2003) and is typically found in Brittany coastal waters in the same areas inhabited by *P. elephas* juveniles, these antennal rasps may indeed serve as a deterrent.

Other taxa could also be affected by this sound. Several fish species have been described as predators of tropical spiny lobsters, including triggerfish of the genus *Balistes* (Briones-Fourzán et al. 2006, Lavalli & Herrnkind 2009). The bioacoustics literature has shown that most fish hear best below 1 kHz (Ladich & Popper 2004). Thus, even though the triggerfish audiogram has not been described yet, it is likely that it could also hear in this low frequency band. Bouwma (2006) suggested that antennal rasps produced by *Panulirus argus* against triggerfish is aposematic, advertising the lobster's spiny defenses to predators. Interestingly, the tropical gray triggerfish *B. capriscus* is now a common species in Brittany coastal waters (Quéro et al. 2008) and would encounter *P. elephas*.

Finally, and by examining the spectral features of antennal rasps recorded *in situ*, the large bandwidth

(mean of 16.99 kHz) can provide a clear evolutionary advantage in clawless spiny lobsters. It seems possible that those types of broadband sounds could have been selected because they permit their emitters to target a maximum of different potential receivers (i.e. potential predators). Even molted spiny lobsters with a soft carapace can still produce antennal rasps, an observation which has also been reported for the buzzing sounds produced by the European lobster *H. gammarus* (Jézéquel et al. 2018). Thus, even when their protective carapace is weakened, the antennal rasps could still function as a deterrent (Patek 2001).

4.4.2. Intra-specific communication

Few studies have hypothesized a potential intra-specific communication of antennal rasps in spiny lobsters. This could be explained by our observation that most bioacoustics studies have characterized antennal rasps in tanks and reported that acoustic power is only present in high frequencies (above 10 kHz; e.g. Buscaino et al. 2011a), which could not be detected by crustaceans (Goodall et al. 1990, Popper et al. 2001, Lovell et al. 2005). Our findings now allow us to suggest how these sounds could be used as a means of intra-specific communication.

Crustaceans lack gas-filled organs, like swim bladders, required for pressure detection, but may be still capable of detecting low-frequency acoustic stimuli arising from the second component of acoustic energy, i.e. particle motion (Breithaupt & Tautz 1990, Popper et al. 2001, Popper & Hawkins 2018). For example, the Norway lobster *Nephrops norvegicus* responds *in situ* to particle motion over a frequency range of 20–200 Hz (Goodall et al. 1990). In addition, Lovell et al. (2005) found that common prawns *Palaemon serratus* in tanks are sensitive to particle motion generated by low-frequency sounds ranging from 100 Hz to 3 kHz. Diverse sensory receptors, adapted to detect particle motion from low-frequency sounds, have been described in crustaceans, including statocysts and sensory hairs (Popper et al. 2001, Radford et al. 2016). In this study, we did not measure the particle motion arising from antennal rasps *in situ*. However, as the pressure component associated with antennal rasps is very high, it is likely that the associated particle motion would also be elevated (Nedelec et al. 2016). Additional studies are now required to measure and understand the potential directionality of particle motion/sound generated by these antennal rasps *in situ* (Popper & Hawkins 2018). We also need to quantify the detection bandwidth and thresholds

(i.e. audiogram) in *P. elephas* through other means, such as behavioral studies (Goodall et al. 1990).

Spiny lobsters, and particularly juveniles such as those used in this study, are gregarious and generally live in high densities in shelters (Atema & Cobb 1980). Several studies have found that they use chemical and visual signals to maintain a social status inside a group of conspecifics through the use of aggressive agonistic encounters (Zimmer-Faust & Spanier 1987, Ratchford & Eggleston 1998, Shabani et al. 2009). Our results imply that antennal rasps may also be involved. Interestingly, Berrill (1976) showed that post-puerulus larvae of *Panulirus longipes* use agonistic encounters when competing for limited access to food and shelter, and that they use antennal rasps during these stressful events as a threat display.

4.5. Antennal rasp detection in underwater soundscapes

In contradiction with the existing bioacoustics literature, our study has highlighted the high acoustic potential of antennal rasps produced by spiny lobsters *in situ*. Our results clearly suggest that antennal rasps produced by *P. elephas* could be detected *in situ* above the ambient noise. Surprisingly, earlier studies carried out with tropical spiny lobsters *Panulirus interruptus*, using the same protocol of sound recordings as in this study, stated that antennal rasps recorded *in situ* are as loud as the ambient noise, so that they could not be detected (Patek et al. 2009, Staaterman et al. 2010). As discussed in Section 4.2, because the use of metrics to characterize sounds is not normalized (and sometimes missed), it is not possible to do a direct comparison of our results with those of Patek et al. (2009). Nonetheless, our ambient noise measurements (PSD, in dB re 1 uPa^2 Hz^{-1}) are fully consistent with other measurements performed in the same area (Mathias et al. 2016, Kinda et al. 2017).

Conversely, our hypothesis of antennal rasp detection *in situ* is consistent with the work of Kikuchi et al. (2015) who recorded *in situ* antennal rasps from *Panulirus japonicus*. These authors found a positive correlation between the frequency of detected antennal rasps and the number of spiny lobsters caught in nets, and also showed an increase in detected antennal rasps during night time. The European spiny lobster *P. elephas*, similar to *Panulirus japonicus*, has an activity pattern characterized by diurnal sheltering and nocturnal foraging (Giacalone et al. 2015). During nocturnal movements, *P. elephas* individuals could encounter other conspecifics or predators, leading to

the production of antennal rasps that would be detectable with hydrophones. However, further studies are needed to validate this potential method of detection and the distance of sound propagation at potential monitoring locations with high lobster densities.

5. CONCLUSIONS

We have revisited the bioacoustics of *Palinurus elephas* and more generally that of spiny lobsters as a group. First, we have confirmed that broadband sounds, such as the antennal rasps, cannot be accurately characterized in tanks (except for the temporal features used in this study) because of sound reverberation and tank resonant frequencies. Indeed, the tank properties distort shapes of broadband sounds. In contrast, antennal rasps from spiny lobsters can be characterized accurately when recorded directly in their natural environment (*in situ*). We have provided 3 different types of sound features: temporal, intensity and spectral features. Secondly, we have shown for the first time that antennal rasps are among the loudest sounds produced among marine animals. We have also highlighted that their acoustic power is present in a low frequency (below 1 kHz); such low-frequency content was missed in previous studies that were conducted in tanks. Using these new results, we could suggest a new biological hypothesis concerning their ecological roles, in particular for intra-specific communication, that has been overlooked in the bioacoustics literature. Finally, we clearly demonstrated that these sounds have suitable properties for *in situ* passive acoustic monitoring. This could contribute to additional *in situ* behavioral studies to better understand *P. elephas* movement patterns. This could also be developed as a tool for the management of *P. elephas* fisheries, especially to permit detection of areas with juveniles in order to protect them from destructive fishing practices (Goñi & Latrouite 2005).

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