

Acoustic scaling in the European spiny lobster (*Palinurus elephas*)

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ABSTRACT:

Sound is an important cue for arthropods. In insects, sound features and sound-producing apparatus are tightly correlated to enhance signal emission in larger individuals. In contrast, acoustic scaling in marine arthropods is poorly described even if they possess similar sound-producing apparatus. Here, the acoustic scaling of the European spiny lobster is analyzed by recording sounds *in situ* at 1 m from a wide range of body sizes. The dimensions of associated sound-producing apparatus increased with body size, indicating sound features would also be influenced by spiny lobster size. Indeed, temporal sound features changed with body size, suggesting differences in calling songs could be used for spiny lobster acoustic communication. Source levels (peak–peak) ranged from 131 to 164 dB re 1 μ Pa for smaller and larger lobsters, respectively, which could be explained by more efficient resonating structures in larger animals. In addition, dominant frequencies were highly constrained by ambient noise levels, masking the low-frequency content of low intensity sounds from smaller spiny lobsters. Although the ecological function of spiny lobster sounds is not clear yet, these results suggest larger body sizes benefit because louder calls increase the broadcast area and potential interactions with conspecifics, as shown in the insect bioacoustic literature.

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I. INTRODUCTION

Sound communication is widely spread in terrestrial arthropods. Several studies have shown that sounds are under sexual selection to enhance signal emission, which is important in mate attraction (Simmons and Ritchie, 1996; Robinson and Hall, 2002). Hence, acoustic scaling with body size is broadly described in insects and is notably related to modifications of their sound-producing apparatus (Montealegre-Z, 2009). For example, intensity levels increase while dominant frequencies decrease with the body size in cicadas (Bennet-Clark and Young, 1994; Sanborn and Phillips, 1995). Such results are crucial for understanding the ecological role of sounds in their life history traits (Podos and Patek, 2015). Indeed, louder sounds associated with lower frequencies increase the broadcast area and, thus, potential interactions with conspecifics, such as during the reproduction period (Bennet-Clark, 1998; Römer, 1998). In marked contrast, acoustic scaling in marine arthropods is poorly known even if there are similarities in the sound-producing apparatus with terrestrial arthropods.

Among marine arthropods, the bioacoustics of spiny lobsters (*Palinuridae*) have been broadly studied due to their

intriguing sound-producing apparatus (Parker, 1878; Moulton, 1957; Meyer-Rochow and Penrose, 1976). Their sound-producing apparatus is located at the base of each second antenna and is constituted of two body parts that act as a friction analogous to crickets (Patek, 2001). The soft, ridged plectrum rubs posteriorly over the anterior part of the hard file-like surface covered with microscopic shingles (Meyer-Rochow and Penrose, 1974; Patek, 2001; Patek and Baio, 2007). This stick-and-slip movement generates a series of broadband pulses, called “antennal rasps” (AR), during each slip (Moulton, 1957; Hazlett and Winn, 1962; Patek *et al.*, 2009). Their ecological meaning has been mostly attributed to an anti-predator context (Bouwma and Herrkind, 2009), and there is no evidence yet on the potential use of AR for intra-specific communication. However, recent studies on the European spiny lobster (*Palinurus elephas*) showed that the AR recorded *in situ* have dominant frequencies below 1 kHz (Jézéquel *et al.*, 2019; Jézéquel *et al.*, 2020), which could be used for acoustic communication (Popper *et al.*, 2001). Understanding the acoustic scaling may further help to better understand the ecological role of AR for spiny lobsters.

Previous studies have already analyzed the scaling of AR with body size in tropical spiny lobsters (Meyer-Rochow and Penrose, 1976; Patek and Oakley, 2003; Patek *et al.*, 2009). While strong correlations have been found

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between sound-producing apparatus and body size (but without evidence of sexual selection), correlations between sound features and body size were minor (e.g., Patek *et al.*, 2009). This could be due to the fact that most of these studies were performed in tanks where sound reverberation and resonant frequencies strongly affect the shape of broadband sounds (Jézéquel *et al.*, 2018). For example, Jézéquel *et al.* (2019) recently showed that spectral features of AR produced by spiny lobsters cannot be accurately measured in tank. In addition, the range of sizes usually tested in the bioacoustic literature does not cover the wide range of sizes reported in these large marine decapods (Goni and Latrouite, 2005). Thus, it is now necessary to investigate acoustic scaling in spiny lobsters through direct *in situ* recordings from a wide range of body sizes.

The aim of this study was to investigate acoustic scaling with body size and sound-producing apparatus in the European spiny lobster (*Palinurus elephas*) during *in situ* recordings. First, we analyzed sounds recorded at 1 m from the spiny lobsters of a wide range of body sizes [from 2.6–13.5 cm of carapace length (CL)]. Then, we measured several morphological features (e.g., length, width) related to their sound-producing apparatus. Those results permitted us to apprehend the changes of temporal, intensity, and spectral features of AR with body size. They were then compared to the available bioacoustic literature on spiny lobsters, as well as on insects, and the ecological implications are discussed (see Sec. IV C).

II. MATERIALS AND METHODS

A. 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 (Animal research: Reporting in vivo experiments) 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 statuses were checked daily by the authors. No specimens were harmed during this study and there was no mortality. Except for larger lobsters, all spiny lobsters were released back into the environment where they were collected at the end of the study.

B. Animal collection, characteristics, and care

For this study, 24 *P. elephas* lobsters of a large range of sizes were used. Seventeen small spiny lobsters (3 males and 14 females), with a CL of 2.6–8 cm, were selected during scuba diving on the Bay of Perros Guirec (48°50′2.044″ N, 3°26′28.312″ W, France) on May 28, 2019. Seven large spiny lobsters (2 males and 7 females), with CL of 9.5–13.5 cm, were bought to local fishermen a few days after they were captured in the Iroise Sea on May 21, 2019. We defined small vs large lobsters based on previous data from Goni and Latrouite (2005). Only hard-shell lobsters with full sets of intact appendages were selected for this study.

After collection, all lobsters were immediately transferred in holding tanks located in an isolated, quiet room from the facilities of the Institut Universitaire Européen de la Mer (IUEM) in Plouzané (Brittany, France). Holding tanks were continuously supplied with the same sand-filtered seawater pumped from the Bay of Brest (temperature: 14.6 ± 0.6 °C, salinity: 34.7 ± 0.1). Abundant sections of rigid, polyvinyl chloride (PVC) pipes, associated with rocks, were provided as shelters in each tank. Animals were acclimatized at least 15 days in these holding conditions before they were used in the recording experiment.

C. Recording device

Sounds produced by spiny lobsters were recorded *in situ* by using one pre-amplified hydrophone (HTI-99-IF, High Tech, Long Beach, MS) with a sensitivity of -174.9 dB re 1 V μ Pa⁻¹ and a flat response from 0.002–50 kHz. The hydrophone was connected to a compact autonomous recorder (EA-SDA14, RTSys, Caudan, France) powered by battery. Recordings were made with a sampling frequency (F_s) of 156 kHz and a 32 bit resolution. The recording device was set with a gain of 0 dB which permitted us to characterize the powerful pulses without clipping the recorded sounds (i.e., *sound saturation*).

D. Experimental setup

Sound recordings were performed in the same experimental site described in Jézéquel *et al.* (2020). It is a shallow water area (depth during recordings: 9 m) with a flat sandy bottom located in the Bay of Brest (48°21′32.951″ N, 4°32′59.024″ W), just beneath the facilities of the IUEM. The experimental site was located about 100 m outside a marina hosting 120 recreational boats.

The day prior to the recording experiment, scuba divers transferred spiny lobsters into three galvanized steel cages (1 m × 1 m × 0.5 m) placed side by side on the experimental site. Abundant sections of rigid, PVC pipes were provided as shelters. The next day (June 14, 2019), scuba divers placed the recording device while scuba diving in front of the centered holding cage. The hydrophone was attached at 0.5 m above the bottom to a metal rod anchored with a concrete tube at 1 m from the point source delimited by a rope laid on the bottom. Sound recordings were performed during low tide to avoid tidal currents. Next, the scuba divers gently picked up each spiny lobster, handled them one by one, and positioned them at the source point. Each individual lobster was maintained at the same depth (0.5 m) as the hydrophone during recordings. During the manipulation, the spiny lobsters were held so that they faced the hydrophone at 1 m. We chose to handle spiny lobsters to elicit sound production as commonly described in the bioacoustic literature on spiny lobsters (Meyer-Rochow and Penrose, 1976; Patek *et al.*, 2009; Jézéquel *et al.*, 2019). Each sound recording for the different spiny lobsters lasted 20–30 s. During this time, the two scuba divers held their breath to avoid the emission of intrusive noise related to air bubbles. Once the

experiments were completed, all spiny lobsters were transferred back to their initial holding tanks. They were kept under the same conditions of acclimatization period described above, and rested for two additional months.

E. Sound recordings from small spiny lobsters in their natural habitat

A previous study performed in the same experimental site showed that AR produced by small-sized spiny lobsters ($CL < 3$ cm) did not present a low-frequency content (i.e., < 1 kHz) (Jézéquel *et al.*, 2020). Thus, we also recorded AR at 0.1 m from three same sized lobsters ($CL < 3$ cm) in a quitter site on September 29, 2018, using the same experimental protocol and sound recording device presented in Jézéquel *et al.* (2019). Although these sound recordings were made at a different distance from spiny lobsters compared to the experimental site (0.1 vs 1 m, respectively), we chose to use them to compare the spectral shape (but not the source levels) of the AR.

F. Morphological measurements of sound-producing structures

After sound recordings, all tested lobsters were returned to their initial holding tank and were kept under the same holding conditions described in Sec. II B. At the end of this holding period, all 17 small and medium-sized spiny lobsters used during *in situ* recordings molted. When a lobster molted, its carapace was immediately removed out from its holding tank and kept for morphological analysis. We extracted the sound-producing apparatus from the molts of each tested spiny lobster, which comprises the antennular plate with two symmetrical files, and two isolated plectrums (Meyer-Rochow and Penrose, 1976; Patek and Oakley, 2003). However, the seven large lobsters did not molt during the same period of time. Thus, they were killed by placing them on ice at -40°C for 1 h, and we dissected their structures of sound production with scalpels, scissors, and pincers.

All structures were stored individually and air-dried prior to morphological analysis (as in Meyer-Rochow and Penrose, 1976). Because the structures of sounds production in spiny lobsters are symmetrical, we analyzed randomly one side of each structure (i.e., either one left or right file and one left or right plectrum) per lobster (Meyer-Rochow and Penrose, 1976). The air-dried samples were first coated using gold-palladium with a thickness of 5 nm and then observed with a scanning electron microscope (SEM) (Hitachi S-3200N, Hitachi, Tokyo, Japan), operating at 15 kV.

We pictured three different parts of the sound-producing apparatus as follows:

- (1) The antennular plate was viewed from above [Figs. 1(A) and 1(D)]. We measured its length from posterior to anterior along the midline axis and its width between the most posterior edges of the two files.
- (2) The file was viewed laterally. We measured its length (curved line passing antero-posteriorly from the appearance of shingles) and its width (line passing ventro-

dorsally at the center of the file). We also pictured an image of the central portion of the file ($G = 500$; $248 \times 186 \mu\text{m}$ field of view with 1024×768 pixels [Figs. 1(B) and 1(E)]. From this image, we measured the medial-lateral length of 30 shingles per file. We also counted the number of shingles per window of $100 \times 100 \mu\text{m}$.

- (3) The plectrum was viewed medially [Figs. 1(C) and 1(F)]. We measured its length as the maximum distance ventrodorsally and its width as the maximum distance antero-posteriorly. We also counted the number of ridges per plectrum, and measured the space inter-ridge.

The same point of view was made for each structure and each lobster. The magnification used with the SEM depended on the sample size, and ranged from $15\times$ to $25\times$. Except for smaller lobsters ($CL < 3$ cm), the sound-producing structures from larger lobsters (file and antennular plate) were too wide to be viewed entirely in one picture. Thus, we obtained 2–40 pictures of these samples using a 50% overlap. Then, the picture mosaics from each structure were assembled by merging them in Photoshop (version CS6, San Jose, CA). After this procedure, all measurements were made digitally after calibrating the pixel size according to the real image scale using the image processing and analysis software Image J [National Institutes of Health (NIH) Image].

G. Sound analysis

Recordings of sounds (in .wav format) were analyzed to confirm sound production by each tagged spiny lobster. Based on this annotation, each AR was extracted manually using the Audacity software[®] (version 2.1.1; Audacity Team 2015). AR were defined as pulse trains composed of at least several pulses separated by less than 20 ms from each other (Jézéquel *et al.*, 2019). Hence, any isolated pulses present in the recordings were not analyzed here. AR that overlapped were not analyzed here. We performed sound analysis on 20–30 pulse trains per spiny lobster. All sequences were processed using custom MATLAB scripts (version 9.1; The MathWorks, Natick, MA). AR were bandpass filtered between 0.005 and 50 kHz, and were characterized by examining three different types of sound features (see Jézéquel *et al.*, 2019 for details): temporal, intensity, and spectral features.

We calculated four different temporal features based on the time series: total duration of the pulse trains, number of pulses per train, time inter-pulse and pulse rate. The intensity feature was referred as the sound pressure level (SPL) calculated in peak-peak at 1 m from the spiny lobsters, and was thus referred as the source level (SL_{pp} , in dB re $1 \mu\text{Pa}$). When pulse trains were affected by low frequencies related to ambient noise, especially for small spiny lobsters (see results), we measured the SL_{pp} based on the pulse with the highest and lowest amplitude of the train to avoid overestimating their values. When pulse trains could not be isolated from the ambient noise, we did not calculate their SL_{pp} . Finally, the spectral feature was represented by the dominant frequency (DF) (in Hz), which was defined

as the frequency where the power spectral density (in dB re $1 \mu\text{Pa}^2 \text{Hz}^{-1}$) was maximal.

Recordings of ambient noise at the two sites (10 min each) without divers underwater were first visualized to ensure the absence of AR. Because anthropogenic activities affected the ambient noise recordings at the experimental site, sound sequences were both cut into 20 sequences of 30 s each, and we randomly selected 3 of 20 sequences from each recording. The sequences where anthropogenic noise (mainly shipping) was dominant were not considered in the analysis. We calculated the SPLs in root mean square (SPL_{rms}) of all selected 30 s long sequences in the 0.005–50 kHz frequency band. This provided a mean value for the ambient noise at each site, and was referred to as the ambient noise level (ANL).

H. Statistical analysis

We analyzed the relationships among the body sizes of spiny lobsters, sound-producing structures, and the sound features.¹ We first tested whether differences occurred between males and females of same sizes using Mann–Whitney tests. As no differences were found ($p > 0.05$), we regrouped these data for further statistical analysis. We then computed Akaike information criterion corrected by our small sample size (AICc) (Cavanaugh, 1997). The square-root transformations resulted in the best fit (i.e., lowest AICc) compared to linear and log-transformed models. Hence, all data (except for SL_{pp}) were square-root transformed prior analysis. The morphological shapes of sound-producing apparatus between small and

large spiny lobsters are similar (Fig. 1) (Meyer-Rochow and Penrose, 1976; Patek *et al.*, 2009). Hence, we used least squares linear regressions on the different datasets for *P. elephas*, as isometric relationships have been shown between the body size, the sound-producing structures, and the sound features in tropical spiny lobsters (Meyer-Rochow and Penrose, 1976; Patek *et al.*, 2009). A non-least squares linear regression was used with a simple logarithmic model for fitting the source level with body size, as $\text{SL}_{\text{pp}} = a + b \times \log_{10}(\text{CL})$, as it has been described in the literature with insects (e.g., Sanborn and Phillips, 1995). These different analyses were performed in MATLAB using the fitlm function.

Finally, a non-parametric Mann–Whitney test was used to determine whether DFs from small-sized spiny lobsters were identical between the experimental site characterized by high ANL and the second site with lower ANL (significance level, $\alpha = 0.05$).

III. RESULTS

A. Effects of body size on sound-producing structures

The dimensions of the different morphological features of the sound-producing apparatus all changed significantly according to the body size of the spiny lobsters (Figs. 1 and 2). The length and width of the antennular plate, file, and plectrum continue to increase throughout life, with significant linear relationships found between carapace length and size of the sound-producing components. While the length and the number of shingles per file increased, their density decreased with body size. The space inter-ridges as

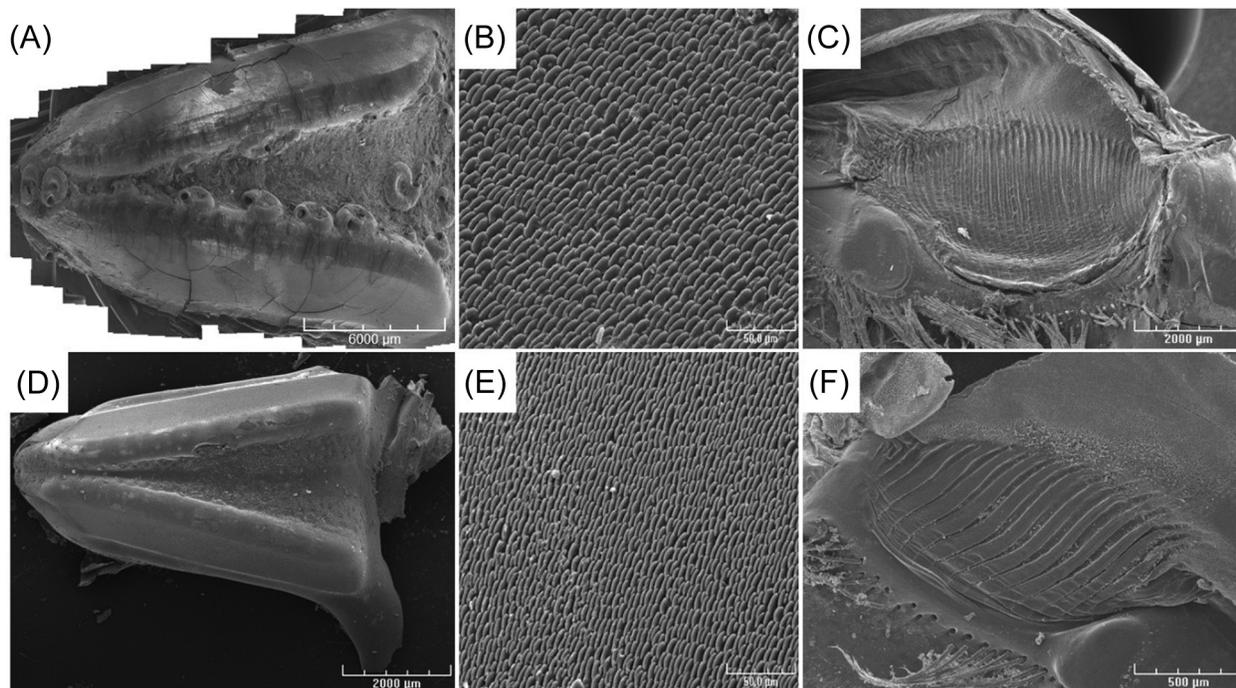


FIG. 1. SEM photography of the sound-producing apparatus from a large (top; CL = 12 cm) and a small (bottom; CL = 2.6 cm) spiny lobster. (A)–(D) Antennular plates viewed from above with the two files visible. (B)–(E) Zoom of the right files, showing the shingles. (C)–(F) Plectrum with the ridges. Note that the morphological shapes are analogous between the two different-sized lobsters.

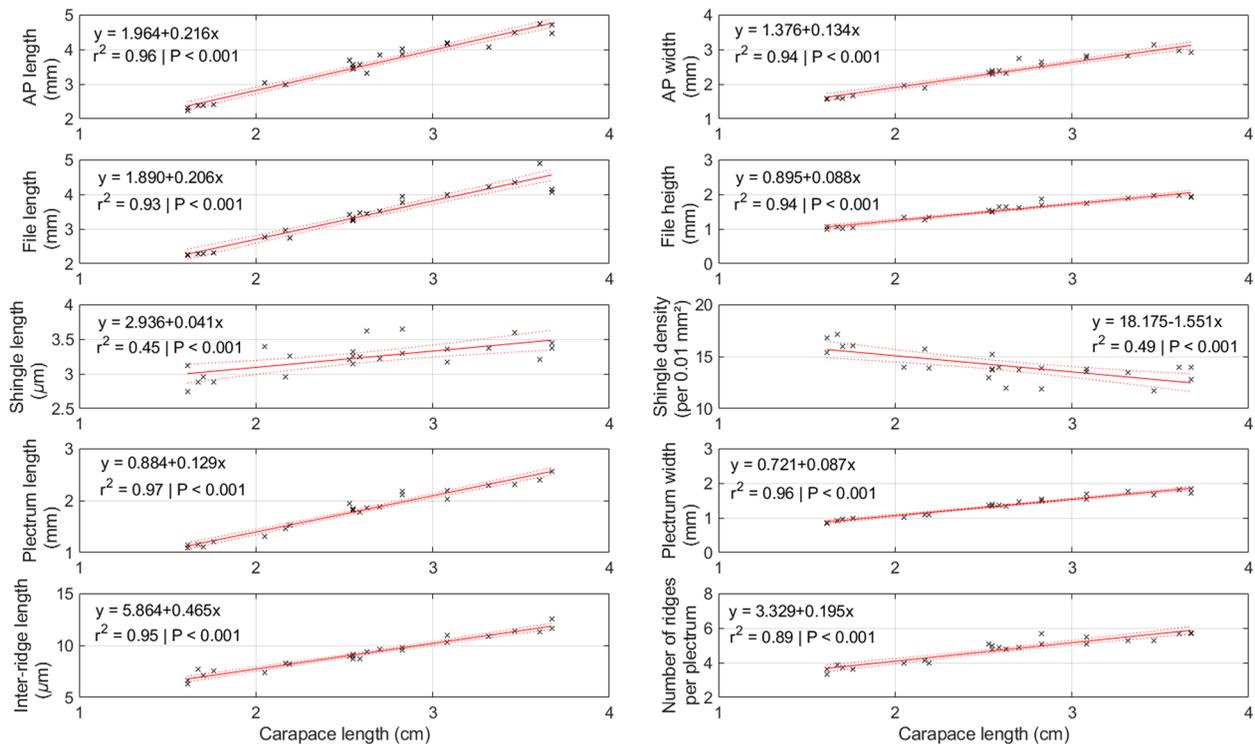


FIG. 2. (Color online) Linear relationships between the different structures of the sound-producing apparatus (square-root transformed) with spiny lobster body sizes. Each datapoint represents the mean value for an individual lobster. Dashed red lines show 95% confidence intervals around the models.

well as the total number of ridges per plectrum followed the same linear growth pattern so that large spiny lobsters have more ridges than smaller ones. By considering the changes in morphological features of sound-producing apparatus, we expect the sounds features to be also influenced.

B. Acoustic scaling at the experimental site

Although the different temporal features highly varied within lobsters, their means showed significant linear relationships regarding to body size (Fig. 3). Temporal features were also significantly correlated with anatomical features such as the maximum space inter-ridges and the number of ridges (Fig. S1).

In addition, the SL_{pp} increased with body size, larger lobsters producing louder AR compared to smaller lobsters (Fig. 4). The relationship was strong with a r-squared equal to 0.95. Similar trends were found with anatomical features, where larger spiny lobsters with larger sound-producing apparatus generated higher SL_{pp} (Fig. S2).

Finally, we found a significant decrease in DFs with body size. Smaller spiny lobsters ($CL < 3$ cm) had DFs above 1 kHz whereas larger spiny lobsters ($CL > 3$ cm) had DFs below 1 kHz (Fig. 5).

C. Acoustic masking in spiny lobsters

Interestingly, AR recorded from small-sized lobsters ($CL < 3$ cm) in the spiny lobster habitat showed DFs below 1 kHz, similar to those in larger lobsters in the experimental site (Figs. 5 and 6). There was a significant difference in

DFs between the two sites (MW, $p < 0.001$); the AR recorded from small-sized animals in the spiny lobster habitat showing lower DFs (< 1 kHz) compared to the experimental site (Fig. 7). This result was likely due to acoustic masking by ambient noise levels in the low-frequency band in the experimental site. Indeed, the ANL in the experimental site was 109.2 ± 0.6 dB re $1 \mu Pa$ with most energy below 1 kHz, whereas it was 93.4 ± 1.2 dB re $1 \mu Pa$ in the spiny lobster habitat (Fig. 6).

IV. DISCUSSION

This study shows a strong influence of spiny lobster body size on sound-producing structures and changes in sound features, which is similar to the bioacoustic literature in insects. While the low-frequency content of the AR is strongly affected by ANL at all sizes, larger lobsters may benefit because louder calls would increase broadcast area and potential interaction with conspecifics.

A. Influence of body size on sound-producing structures

Overall, sound-generating structures in *P. elephas* scaled with body size. Indeed, the isometric relationships between all anatomical parts (except shingle density) with body size were positively significant (Figs. 1 and 2). These results are fully consistent with the literature available on tropical spiny lobsters (Meyer-Rochow and Penrose, 1976; Patek, 2002; Patek and Oakley, 2003; Patek and Baio, 2007; Patek et al., 2009). Meyer-Rochow and Penrose (1974)

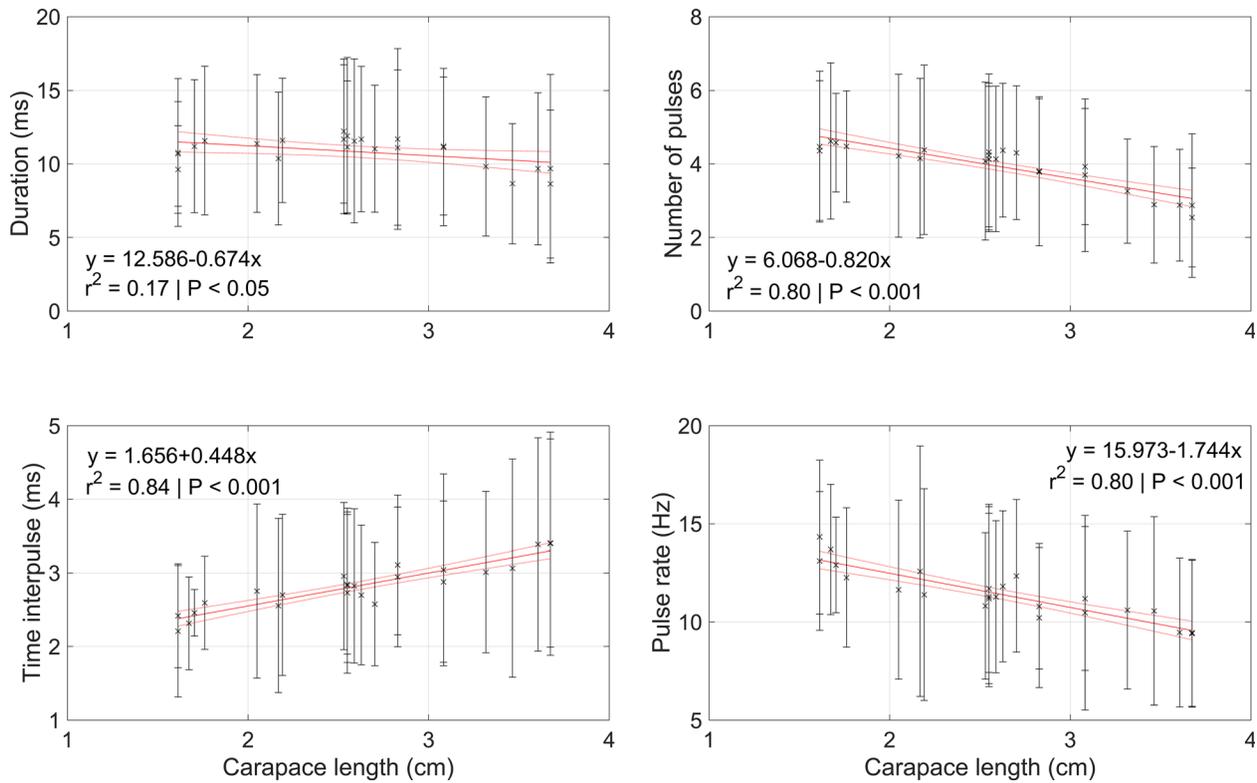


FIG. 3. (Color online) Linear relationships between the different temporal features (square-root transformed) of AR with spiny lobster body sizes. Each data-point represents the mean value (\pm standard deviation) for an individual lobster. Dashed red lines show 95% confidence intervals around the models.

notably found that the sound-producing apparatus becomes fully functional after the postpuerulus larvae settle into the substrate, and remains similar throughout the spiny lobster’s life (see also Fig. 1). Following this metamorphosis, the file and plectrum grow in length, and the teeth increase in number. However, while the size of the shingles increases, their densities decrease.

The shape of the sound-producing apparatus in spiny lobsters is closely related to the stridulating mechanisms in insects, such as crickets (Fig. 1) (Walker and Carlyle, 1975; Desutter-

Grandcolas, 1995; Montealegre-Z and Mason, 2005). These singing species have modified forewings (tegmina) which are rubbed together; during closing, the plectrum from one tegmen strikes the teeth file of the opposite tegmen. Several authors have found positive allometric relationships between body size and the dimensions of the sound-producing apparatus. For example, the number and the spacing of the ridges, as well as the dimensions of both plectrum and file, increase with body size (Montealegre-Z, 2009; Anichini *et al.*, 2017). In addition, larger crickets have wider, but fewer teeth, that are further parted (Anichini *et al.*, 2017). Overall, our study shows close

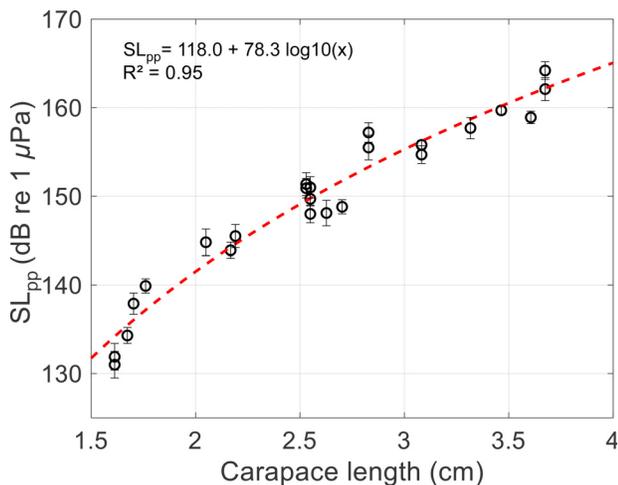


FIG. 4. (Color online) Evolution of source levels (SL_{pp} , in peak-peak) measured at 1 m from spiny lobsters with body size at the experimental site.

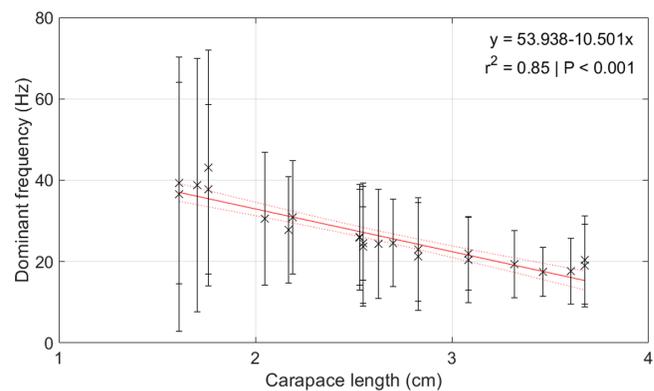


FIG. 5. (Color online) Linear relationships between the dominant frequency (square-root transformed) of AR with spiny lobster body sizes. Each data-point represents the mean value (\pm standard deviation) for an individual. Dashed red lines show 95% confidence intervals around the models.

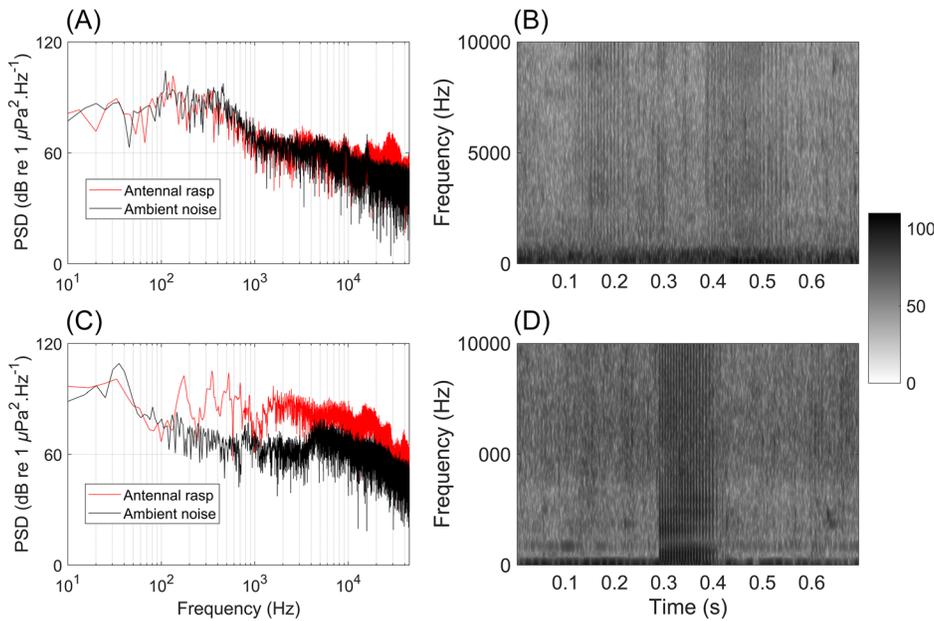


FIG. 6. (Color online) Examples of power spectral densities (PSDs) in red (left) and spectrograms (right) of AR produced by two small-sized spiny lobsters (CL = 2.6 cm for both lobsters) in two different environmental conditions: a high ANL (top) and a low ANL (bottom). The ANLs are presented in black in the PSDs. Note that the AR analyzed in the higher ANL was recorded at 1 m, while the AR analyzed in the lower ANL was recorded at 10 cm.

similitudes in the evolution of sound-producing structures in spiny lobsters compared to insects (Rebrina *et al.*, 2020).

B. Acoustic scaling

1. Temporal features

Scaling of temporal features with body size has been examined previously in several spiny lobster species and across the family as a whole (Meyer-Rochow and Penrose, 1974; Meyer-Rochow and Penrose, 1976; Patek, 2002; Patek and Oakley, 2003; Patek and Baio, 2007; Patek *et al.*, 2009). While the standard deviation is important within and across lobsters, all temporal features were significantly

influenced by body size (Fig. 3). Some of these trends differ from other tropical spiny lobsters, e.g., duration (Patek and Oakley, 2003), which could be associated with inter-species differences, although the decrease in pulse rate with body size is consistent with previous studies (Meyer-Rochow and Penrose, 1976; Patek *et al.*, 2009). However, this result is quite surprising, as the duration and number of pulses per AR should increase with body size, considering that the number of plectrum ridges and both plectrum and file lengths increase with body size (Figs. 3 and S1). Indeed, the number of pulses per AR in smaller lobsters usually exceeded the number of plectrum ridges by a factor two, as opposed to larger lobsters. Curiously, manual stridulations showed that tropical spiny lobsters do not use of the entire length of the file (Meyer-Rochow and Penrose, 1976). This result could be explained by a control of spiny lobsters to emit sounds from a specific number of pulses.

Interestingly, many studies on insects highlighted the amazing diversity of their calling songs composed by different numbers of pulses (Alexander, 1960; Robinson and Hall, 2002; Baker *et al.*, 2019), which are used for several types of intra-specific communication (Pollack, 2017). In our study, spiny lobsters were handled to elicit sound production to imitate their catch by a predator, as commonly done in the bioacoustics literature (Meyer-Rochow and Penrose, 1976; Patek *et al.*, 2009; Jézéquel *et al.*, 2019). While sound production may vary in other ecological context, to our knowledge, there is no evidence yet on intra-specific acoustic communication in marine invertebrates based on different temporal sound features.

Larger animals may also possess limited mechanical dexterity, thus obstructing the production of rapid or temporally complex acoustic patterns (Podos and Patek, 2015). Given the same closing speed, a larger file system presumably allows greater time between impacts and thus a greater inter-pulse duration compared to smaller files (Montealegre-Z, 2009).

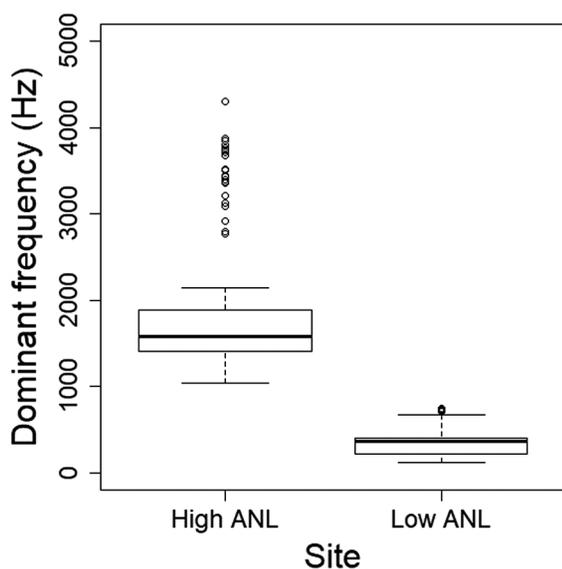


FIG. 7. Comparison of dominant frequencies from small-sized spiny lobsters producing AR in two different marine environments: the main experimental site with high ANL (left) and the spiny lobster habitat with low ANL (right).

Finally, temporal features may be related to physical stress, which is difficult to assess individually. For example, tropical spiny lobsters show fatigue after producing AR for more than 30 s (Meyer-Rochow and Penrose, 1976). Fatigue or exhaustion would be expected to lower the rates of AR (Meyer-Rochow and Penrose, 1976). Even if we acclimatized spiny lobsters in holding tanks before the experiments, we did not characterize their state of fatigue or exhaustion post-catch.

2. Intensity

The SL_{pp} recorded *in situ* showed a clear tendency to rise with increasing carapace length and the size of sound-producing apparatus (Figs. 4 and S2). Thus, larger spiny lobsters produce louder calls compared to smaller spiny lobsters. To our knowledge, this is the first relationship ever found in marine invertebrates, and is fully consistent to the bioacoustic literature available in insects (Villet, 1987; Sanborn and Phillips, 1995). This trend can actually be explained by two different mechanisms. A first possible explanation may be the existence of more efficient resonating structures in larger lobsters, with a greater ability to match the resonance of the sound-producing apparatus, as in crickets (Bennet-Clark, 1970; Michelsen and Nocke, 1974; Bennet-Clark, 1999). In addition, muscles used for stick-and-slip mechanisms in spiny lobsters are larger and have more power in bigger sized lobsters (Josephson and Young, 1979; Patek, 2002). Thus, the increase in available muscle energy in larger animals can be converted to a greater acoustic energy (Villet, 1987; Bennet-Clark, 1999).

3. Spectral content

Our main experiment demonstrated a decrease in DFs with body size, smaller spiny lobsters producing high frequencies (>1 kHz) while larger spiny lobsters produced low frequencies (<1 kHz) (Fig. 5). These results suggest high-frequency sounds emitted by small-sized spiny lobsters could not be detectable by conspecifics, even at 1 m from the animals (Popper *et al.*, 2001). However, these recordings were performed in an environment affected by low-frequency anthropogenic noise from a near marina (Jézéquel *et al.*, 2020; Jézéquel *et al.*, 2021b). In marked contrast, additional recordings in a spiny lobster natural habitat with a lower ANL showed that same small-sized lobsters presented a low frequency content similar to larger spiny lobsters (< 1 kHz) (Figs. 6 and 7). Here, we hypothesize that the smaller spiny lobsters always produce AR with low-frequency contents but that the SL_{pp} is low so that the signal can be masked by the ANL. Hence, our results highlight that all spiny lobster sizes possess a low-frequency content that could be detectable among conspecifics.

Interestingly, insects generate higher frequencies using the same type of sound-producing apparatus compared to spiny lobsters. For example, bush crickets emit ultrasonic frequencies (>20 kHz) (Montealegre-Z, 2009). The frequency content of a generated sound in insects depends mostly on the speed of the stridulation. A high rate at which

the shingles and ridges are contracted produces higher frequencies (Morris, 1970). When considering the physical properties of seawater, it is likely that the friction between the file and plectrum is reduced in spiny lobsters, thus decreasing the stridulation's rate and the frequency content compared to terrestrial arthropods.

There is also a considerable difference in size between spiny lobsters and insects. The small size of insects is such that the efficiency of sound radiation is greater at higher frequencies (Robinson and Hall, 2002). According to Bennet-Clark (1999), the sound source should have a diameter that is greater than one third of the wavelength of the sound produced to obtain a good impedance match. While this is not the case for smaller spiny lobsters (which would also explain their low SL_{pp}), larger animals would be suitable to produce low frequencies ~300 Hz.

C. Ecological implications

Previous studies showed that spiny lobsters mostly rely on chemical cues to communicate during reproduction (Raethke *et al.*, 2004) and to attract conspecifics in shelters for protection against predators (Nevitt *et al.*, 2000). While chemical communication is effective over short distances, long range distances heavily depend on the direction of the current (Atema, 2018). In our study, we found a strong correlation between body size and SLs, larger spiny lobsters producing louder calls. A louder call travels farther in the marine environment, which tends to promote low-frequency propagation. While the ecological function of AR is not clear yet (but see Staaterman *et al.*, 2010), our results suggest larger lobsters would be more suitable for acoustic communication, as in insects.

The dramatic frequency-dependent sound attenuation in the habitat can have important consequences for acoustic communication. For crickets, attenuation increases with increasing frequency, thus the information contained in the high-frequency components of a broadband song will not be available for a receiver except at short distances (Römer and Lewald, 1992). In contrast, ANL in the marine environment seems to be the most important constraint for spiny lobster low-frequency communication. Indeed, our results showed that high ANLs mask the low-frequency content of small-sized spiny lobsters. Acoustic masking can alter animal communication and orientation (Clark *et al.*, 2009). Hence, acoustic scaling may be important in spiny lobsters as larger lobsters produce louder calls that are less likely to be masked by ANL. Curiously, insects can tune their sounds in terms of frequency, using the burrow as a resonator to increase communication distances (Bennet-Clark, 1999). Small-sized spiny lobsters are known to be cryptic and to live in small crevices (Diaz *et al.*, 2001), which could be used as resonators to counter high ANL.

The acoustic behaviour of spiny lobsters during intra-specific interactions is not known yet. There are few studies mentioning the production of AR being used as a threat display during agonistic encounters during access to food

(Berrill, 1976; Mulligan and Fischer, 1977). However, sound detection in spiny lobsters has never been assessed, leaving uncertainties whether they could use AR for acoustic communication. Marine crustaceans lack gas-filled organs, like swim bladders in fish, required for pressure detection, but are still capable of detecting the low-frequency acoustic stimuli arising from particle motion (Breithaupt and Tautz, 1990; Popper *et al.*, 2001; Popper and Hawkins, 2018). 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; Jézéquel *et al.*, 2021a). Last, but not least, it is not known whether spiny lobsters could also detect substrate-borne vibrations, as these are widely used for communication in terrestrial arthropods (Roberts and Wickings, 2022).

In this study, we did not measure the particle motion arising from AR due to the limited access of calibrated vector sensors. However, the time features measured here (duration, number of pulses, time inter-pulse, rates) are directly related to time features of the source signal—they can equivalently be measured using either pressure or particle motion. The intensity feature, SL_{pp} , would show different absolute values if measured in terms of particle motion. However, its relative variation is fully driven by the source mechanism and can be equivalently measured using pressure or particle motion. In other words, if particle motion was used, the relationship $SL_{pp} = a + b \times \log_{10}(CL)$, may result to a different a , but b would be the same, so that the discussion in Sec. IVC would remain unchanged. Finally, the spectral feature measurements (DF) are used to qualitatively characterize the presence/absence of low-frequency content in the AR. The pressure measurements performed in this study demonstrate the presence of low-frequency acoustic energy for all spiny lobsters. Although quantitative low-frequency levels may differ if measured using particle motion instead of pressure, those levels are not used here, therefore the pressure measurements are good enough for our purpose. Additional studies are now required to measure and understand the potential directionality of sound (particle motion and/or pressure) generated by these AR *in situ* (Popper and Hawkins, 2018). There are also needs to quantify the sound detection bandwidth and thresholds (i.e., audiogram) in *P. elephas* through neurophysiological or behavioural studies to confirm acoustic communication (Goodall *et al.*, 1990; Jézéquel *et al.*, 2021a).

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¹See supplementary material at <https://www.scitation.org/doi/suppl/10.1121/10.0016363> for the relations between spiny lobster sound features and sound-producing apparatus sizes.

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