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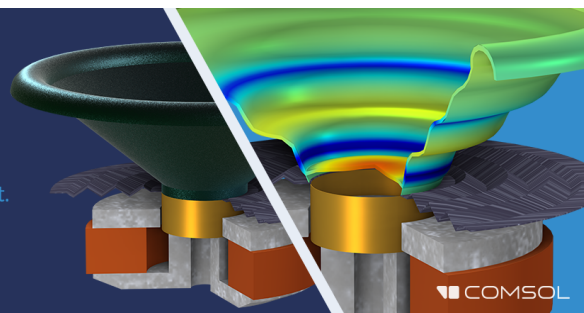
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Acoustic properties and shallow water propagation distances of Caribbean spiny lobster sounds (*Panulirus argus*)

Youenn Jézéquel,^{a)}  Nadège Aoki,^{b)}  and T. Aran Mooney 

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

ABSTRACT:

Marine crustaceans produce broadband sounds that are useful for passive acoustic monitoring to support conservation and management efforts. However, the propagation characteristics and detection ranges of their signals are poorly known, limiting our leveraging of these sounds. Here, we used a four-hydrophone linear array to measure source levels (SLs) and sound propagation from Caribbean spiny lobsters (*Panulirus argus*) of a wide range of sizes within a natural, shallow water habitat (3.3 m depth). Source level in peak-peak (SLpp) varied with body size; larger individuals produced SLpp up to 166 dB re 1 μ Pa. However, transmission losses (TL) were similar across all sizes, with a global fitted TL of 12.1 dB. Correspondingly, calculated detection ranges varied with body size, ranging between 14 and 364 m for small and large individuals (respectively). This increased up to 1612 m for large spiny lobsters when considering lower ambient noise levels. Despite the potential ease of tank studies, our results highlight the importance of empirical *in situ* sound propagation studies for marine crustaceans. Given the important ecological and economic role of spiny lobsters, these data are a key step to supporting remote monitoring of this species for fisheries management and efforts to acoustically quantify coral reefs' health. © 2023 Acoustical Society of America.

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I. INTRODUCTION

As marine ecologists seek to better estimate and track the health of imperiled coral reefs, passive acoustic monitoring (PAM), a method involving listening for and tracking soundscape cues, is a promising non-invasive tool (Mooney *et al.*, 2020). A diverse array of animals associated with coral reefs are acoustically active (Tricas and Boyle, 2014; Lillis and Mooney, 2018; Kügler *et al.*, 2020). Yet information on source levels and their detection ranges are needed to use biological sounds for monitoring of behaviors and spatial distributions in an ecosystem. While such data may be available for some marine mammals (e.g., Stafford *et al.*, 1998; Bonnel *et al.*, 2014) and fish species (e.g., Mann and Lobel, 1997; Locascio and Mann, 2011), empirical data on sound propagation and detection range for marine invertebrates such as crustaceans are scarce.

Sounds produced by marine crustaceans are mostly characterized as broadband pulses (Schmitz, 2002). Estimating their sound propagation ranges can be challenging as most crustacean species inhabit shallow coastal waters, often at depths less than tens of meters. These shallow environments contribute to complex sound fields due to physical constraints such as the boundaries created by the water surface and the seabed (Rogers and Cox, 1988; Bass and Clark, 2003). Without empirical transmission loss data,

it is consequently difficult to accurately model propagation of these biological sounds (Richardson *et al.*, 1995). Until now, detection ranges of crustacean sounds have relied on initial estimations of source levels performed using distant measurements that are then artificially back-propagated to 1 m by using theoretical propagation models (e.g., Radford *et al.*, 2011). Other studies have used transects to measure propagation of broadband sounds produced by marine invertebrates from coral reefs (Piercy *et al.*, 2014; Thilges *et al.*, 2019; Raick *et al.*, 2021). However, these calculations have been made using whole soundscapes without identifying individual sources.

Coral reef soundscapes are largely dominated by snapping shrimp snaps, particularly at frequencies above 1–2 kHz (Lammers *et al.*, 2008; Kaplan *et al.*, 2015; Lillis and Mooney, 2018). Some studies have sought to assess detection ranges of these snaps (e.g., Butler *et al.*, 2017). However, snapping shrimp colonies produce abundant and often overlapping signals, individuals are visually cryptic, and snap rates can be very low (1–2 snaps/h; Lillis *et al.*, 2017). Thus, it is difficult to verify localization by computing acoustic propagation models.

Spiny lobsters also inhabit coral reefs and can provide another important potential candidate for crustacean sound propagation studies. Their sound production mechanism is located at the base of each second antenna and consists of two parts: the soft, ridged plectrum that 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

^{a)}Electronic mail: yjezequel@whoi.edu

^{b)}Also at: MIT-WHOI Joint Program in Oceanography/Applied Ocean Science & Engineering, Cambridge, MA 02139, USA.

movement generates a series of broadband pulses during each slip. The associated sound produced during a full movement is composed of a series (or train) of short pulses, and each pulse train is called an “antennal rasp” (Moulton, 1957; Mulligan and Fischer, 1977; Patek *et al.*, 2009). These antennal rasps are described as broadband sounds with peak frequencies below 1 kHz (Jézéquel *et al.*, 2022a). 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 and Herrnkind, 2009; Staaterman *et al.*, 2010).

Previous studies of European spiny lobsters (*Palinurus elephas*) illustrated that antennal rasps are of relatively high amplitude and increases with body size, with larger individuals producing source levels (in peak-peak) up to 167 dB re 1 μ Pa (Jézéquel *et al.*, 2020). Sound production can be reliably induced by handling spiny lobster which aims to imitate a predation event (Jézéquel *et al.*, 2019). Hence, spiny lobsters are practical candidates for accurately measuring source levels (SLs) and sound propagation over different distances, while precisely controlling the animal’s position. A recent study used a 100 m linear array of hydrophones to empirically calculate sound propagation features from European spiny lobsters (Jézéquel *et al.*, 2020). The authors showed that under quiet ambient noise levels, sounds from the largest individuals could be detectable at the km scale, rendering a high potential for PAM of these sounds, and consequently, monitoring for individuals and populations. However, more studies are needed to verify these results at different water depths and examine whether such SLs and detection ranges are applicable to other spiny lobster species.

The Caribbean spiny lobster, *Panulirus argus*, is a tropical and sub-tropical species common in the western Atlantic Ocean and is a valuable economic, societal and cultural resource (Cruz and Bertelsen, 2008). Its distribution ranges from Bermuda and North Carolina to north-eastern Brazil. The Caribbean spiny lobster fishery directly employs 50 000 people, and helps support an additional 200 000 people working in related fields, generating more than US\$450 $\times$ 10⁶ per year (Winterbottom *et al.*, 2012). This industry is particularly important to small island states which may have limited economic options, but have developed infrastructure to access undersea habitats and facilitate natural population growth and exports (Higgs *et al.*, 2016). Yet increased consumer demand, higher market values, expanding fishing fleets, and perhaps, climate variability, have led to the *P. argus* resource being fully or over-exploited over much of its range (Cochrane and Chakalall, 2001). Like any slow growing marine population, monitoring of *P. argus* can be challenging. By characterizing acoustic signals and their propagation, passive acoustics offers a cost-effective means to monitor population sizes and distributions.

Here, we performed a field study to measure propagation features of broadband antennal rasps produced by Caribbean spiny lobsters (*P. argus*). We deployed a four-hydrophone linear array with sensors placed between 1 and

60 m from the animals and measured sounds from a wide size-range of spiny lobsters in a shallow water area near a coral reef. This habitat is a nighttime foraging ground for these lobsters. Using this setup, we measured sound pressure levels and transmission losses within the range of the array. Detection ranges were then assessed using different conditions of ambient noise levels and transmission loss models. Finally, we examined the spectral contents of the antennal rasps with increasing distance from the spiny lobsters and discussed their potential ecological implications.

II. MATERIALS AND METHODS

A. Study animals and holding conditions

A total of 12 *P. argus* individuals representing a wide range of sizes were hand-collected for the experiments on the 27th of June in St. John, US Virgin Islands (USVI). We caught eight juveniles with carapace lengths (CL) from 4.3 to 8.5 cm while snorkeling in Great Lameshur Bay (18°19′05.8″N, 64°43′27.1″W) at a depth of 0.5 m. Four adults (CL = 10.0–12.3 cm) were sampled while SCUBA diving on a reef off Reef Bay (18°18′49.1″N, 64°45′29.2″W) at a depth of 12 m. After capture, all individuals were transferred to a large holding tank (0.9 $\times$ 1.9 $\times$ 0.6 m) outside the marine laboratory facilities of the University of the Virgin Islands beside Great Lameshur Bay. The tank was provided with continuous seawater directly pumped from the nearby bay and shaded with a dark mesh to reduce direct sunlight. Polyvinyl chloride (PVC) tubes were supplied as shelters. Spiny lobsters were kept in these holding conditions for one-week prior to acoustic recordings. Two individuals molted during the holding period; thus ten spiny lobsters were used for this experiment.

B. Experimental setup

The experimental site was located in Great Lameshur Bay (18°19′06.2″N, 64°43′23.8″W), a relatively quiet, natural ocean environment free from vessel noise adjacent to the holding facilities [Figs. 1(A) and 1(B)]. It is a shallow water area (3.4 m depth) with a flat bottom of sand and seagrass patches and constitutes a nighttime foraging habitat for spiny lobsters (personal observations). The day prior to the recording experiment, all spiny lobsters were transferred to a steel cage (1.0 m $\times$ 1.0 m $\times$ 0.5 m) placed on the bottom of the bay via snorkel. A flap at the top facilitated the handling of the animals within the cage during the experiment. Spiny lobsters were then acclimatized for an additional 24 h to recover from the short transport from the seawater tank to the cage.

The next day (4th July), SCUBA divers built a linear array of hydrophones in front of the holding cage. The array used four Soundtraps (ST600, Ocean Instruments, Auckland, NZ) set with a frequency sampling of 192 kHz and powered with Panasonic NCR18650B Lithium-Ion batteries. We deployed the four acoustic recorders along a line of increasing distances (i.e., 1, 5, 10, and 60 m) away from the spiny lobsters [Figs. 1(B) and 1(C)]. The frequency

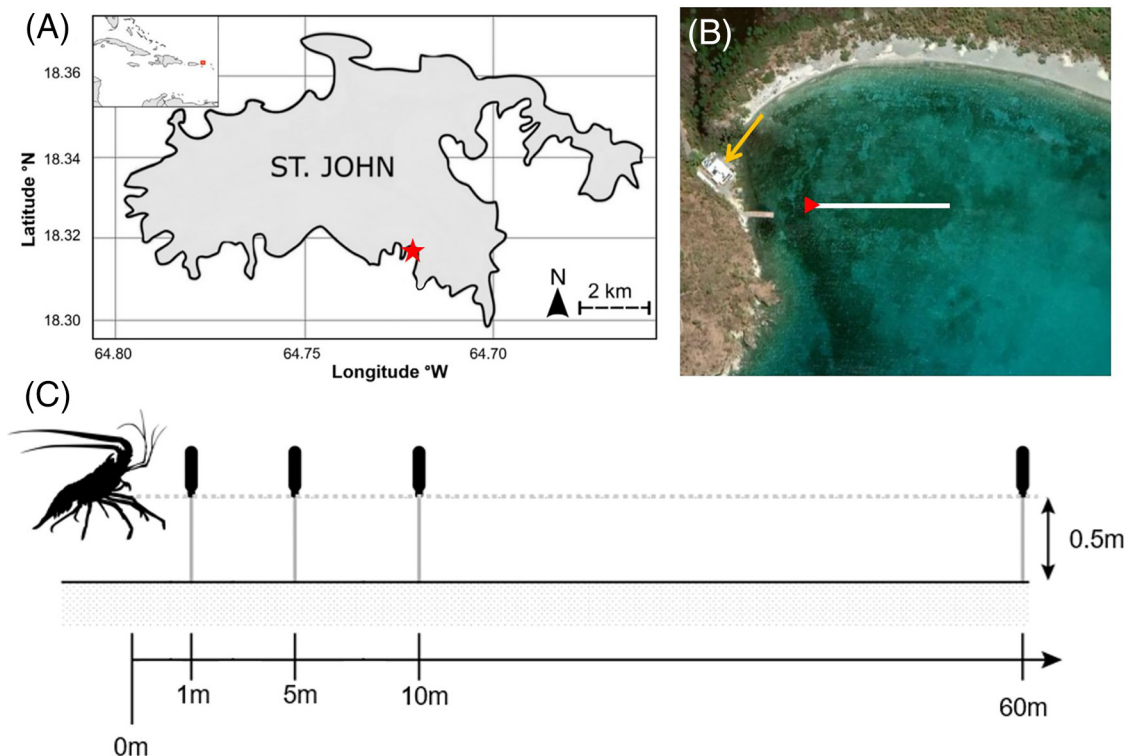


FIG. 1. (Color online) (A) St. John, US Virgin Islands, with Great Lameshur Bay noted by the red star. (B) The red triangle is the source point (i.e., 0.0 m) where spiny lobsters were handheld to record their sounds in front of the four-hydrophone array (white line, 60 m long). The holding facilities are noted by the orange arrow. (C) The linear array of hydrophones was built underwater while SCUBA diving with four different hydrophones that were placed between 1 and 60 m from the spiny lobster. Note that the hydrophone located at 1 m recorded the source level. Individuals were handheld while they produced sounds in front and the same axis of the linear array.

response of the hydrophones was ± 3 dB between 0.02 and 60 kHz, and sensitivities ranged between -175.1 and -176.4 dB re $1 \text{ V } \mu\text{Pa}^{-1}$. The closest hydrophone (1 m) was set with the ST600 low gain option to allow us to characterize spiny lobster sounds without clipping (i.e., sound saturation). Hydrophones were attached 0.5 m above the bottom using rebar stakes previously hammered vertically into the substrate. Distances were carefully checked with two 30 m-long transect tapes.

All ten spiny lobsters were held in the cage at the same time. Antennal rasps were clearly audible, even to the diver, and these were only detected when individuals were handheld in front of the linear array of hydrophones. Next, each spiny lobster was gently picked up, positioned at the source point (i.e., 0 m) and handled one by one [Fig. 1(C)]. The source point was defined as the point where spiny lobsters were placed and handled. This was located at the beginning of the transect tape, 1 m from the first hydrophone. Each individual was maintained at the same distance above the bottom (0.5 m) as the hydrophones during recordings, and the spiny lobsters were held so that their bodies faced the linear array of hydrophones. Thus, the body of the animals was aligned along the same axis as the array of hydrophones. We chose to handle spiny lobsters to elicit their sound production, as this method is commonly described in the bioacoustic literature on spiny lobsters (e.g., Jézéquel *et al.*, 2019). This permitted us to compare our results with a

previous study that used a similar recording set up to assess sound propagation of European spiny lobsters in 10 m water depth (Jézéquel *et al.*, 2020). The sound recording period for each spiny lobster lasted between 20 and 30 s. During this time, the divers paused their breathing to avoid the emission of intrusive noise related to air bubbles. In total, the recording experiment lasted 40 min. After each spiny lobster sound recording, we measured its carapace length and placed it in a catch bag away from the cage to avoid recording it another time. In the end of the recordings, five sharp rasps were made against the cage walls which permitted us to synchronize both hydrophones.

C. Sound analysis

Each recorded antennal rasp was manually extracted using the software Audacity (version 3.1.3). We analyzed a total of ten antennal rasps per spiny lobster and per distance. The same sounds were analyzed at four different distances for each spiny lobster. All sequences were processed using custom MATLAB scripts (version 2021a; The MathWorks, Natick, MA).

We first chose to calculate the peak-to-peak SPL (SPL_{pp}), which is the most representative and practical amplitude feature for pulsed sounds (Erbe, 2011). The SPL_{pp} calculated at 1 m was referred to as the source level (SL_{pp}). When pulse trains could not be isolated from the

ambient noise, we did not calculate their SPLpp. We then averaged the SPLpp calculated per distance and per individual for further analysis. The SPLpp and SLpp were used for biological sound characterization. We chose to regroup the averaged values per group of size-matched individuals for a better overall description and for a comparison to data from Jézéquel *et al.* (2020). Three different groups of body sizes were defined and termed as follows: large ($10.0 < CL < 12.3$ cm, $n = 3$), intermediate ($7.1 < CL < 8.5$ cm, $n = 4$), small ($4.3 < CL < 6.8$ cm, $n = 3$).

We also calculated the SPL and SL as root mean square (SPLrms and SLrms, respectively) between 100 and 1000 Hz, which was the bandwidth with the highest energy peaks (see Sec. III). We calculate them for each pulse inside the pulse trains over a 1 ms window length (fast Fourier transform size, 192 points) centered on the pulse. Each value was then averaged over all pulses present in an antennal rasp to obtain its mean SPLrms and SLrms. The SPLrms and SLrms values were used to estimate transmission losses (TL), as well as to compute the passive sonar equation to estimate detection ranges (Ainslie, 2010). At 60 m, sounds from smaller spiny lobsters were lost in the ambient noise while looking at the time domain signals, their SPLpp and SPLrms were thus not computed.

Finally, we calculated the dominant frequency (in Hz) of each antennal rasp at the four distances (except at 60 m for small spiny lobsters, see Sec. III), represented as the frequency where the power spectral density (PSD) was maximal.

D. Ambient noise characterization

Sound recording sequences from the four hydrophones without antennal rasps were also used to characterize ambient noise levels (ANLs). We calculated the SPLrms in three randomly selected 30 s long sequences from the original sound recordings over the same frequency band as the antennal rasp SPLrms and SLrms (100–1000 Hz). This provided a mean ANL value at each hydrophone placement.

E. Evaluation of transmission losses

The datasets of the averaged SPLrms for each spiny lobster and each distance were fitted with nonlinear least squares regressions using custom-made scripts in MATLAB using the same procedure as in Jézéquel *et al.* (2020). The slope of the regressions permitted us to obtain transmission losses (TL, in dB) per spiny lobster, which represent the losses of intensity due to the geometrical spreading of sounds in a physical medium (Ainslie, 2010).

We obtained ten different TL models using this method on the dataset generated by each animal. We further estimated a global fitted TL coefficient by merging the sounds from all spiny lobsters into a global dataset. We compared this global fitted TL with other theoretical models of TL commonly used in the bioacoustic literature (Bass and Clark, 2003).

F. Estimations of detection ranges

For the purposes of this study, we assumed that signal detection by the hydrophones was primarily limited by the TL (previously calculated) and the ANL. Here, the low frequency absorption at 100–1000 Hz was considered insignificant even at the km scale (i.e., below 0.1 dB per km; Fisher and Simmonds, 1977). Using the previous results, we estimated the detection ranges of the antennal rasps by resolving the passive sonar equation (in the frequency domain) for all ten spiny lobsters (Ainslie, 2010),

$$Detection\ range = 10^{[(SL_{rms} - ANL - SNR)/TL]}. \quad (1)$$

With

- SLrms is the source level in dB re 1 μ Pa (averaged over ten measurements per spiny lobster), calculated in the 100–1000 Hz frequency band.
- ANL is the ambient noise level in dB re 1 μ Pa calculated over the 100–1000 Hz frequency band. We used two different values of ANL. First, we reported the mean ANL recorded by our hydrophones during the study. Second, we used one theoretical (but still realistic) value of ANL based on Wenz curves and calculated with a wind speed of 5 knots in the same frequency band as the *in situ* ANL (Wenz, 1962).
- SNR is the signal-to-noise ratio that corresponds to the minimum threshold needed for the hydrophones to detect the sound above the ANL. We used two different SNRs of 5 and 10 dB widely accepted for sonar systems (Ainslie, 2010).
- TL is the global coefficient of TL previously calculated for spiny lobsters. We also used the three theoretical TLs commonly used in the bioacoustic literature (Coates, 1989).

G. Cutoff frequency of the experimental site

Shallow water *in situ* environments acts as a waveguide, with sounds being distorted during propagation. An important waveguide effect is the presence of a cut-off frequency which leads to acoustic duct high pass behaviors, and was computed using the equation available in Ainslie (2010),

$$f_c = (\pi - \rho_{sed}/\rho_w)/(2\pi \sin \psi_c)(c/H), \quad (2)$$

where p_{sed} = sediment density (estimated at 2.14), p_w = water density, $\psi_c = \arccos(c/c_{sed})$, c = sound speed in water (1540 m.s^{-1}), c_{sed} = speed of sound in the sediment (1700 m.s^{-1}), and H = water depth (3.4 m).

H. Statistical analysis

We examined the correlations between SLpp and TL values with spiny lobster body sizes using Pearson tests ($\alpha = 0.05$) using custom MATLAB scripts. A one-way measure analysis of variance (ANOVAs, $\alpha = 0.05$) was used to

determine the potential effects of distance on the ambient noise levels.

III. RESULTS

During the experiment, the wind state ranged between 0 (calm) and 2 (light breeze) on the Beaufort scale, corresponding to speeds between 1 and 6 knots. The seawater temperature was 29 °C and the depth was 3.3 m. The ANL in the low frequency band from 100 to 1000 Hz varied slightly across the different hydrophones with a mean of 94.4 ± 1.7 dB re 1 μ Pa, and no statistical differences were found (one-way analysis of variance, ANOVA, $F_{1,10} = 1.903$, $p = 0.2$). No boat noise was present in the experimental recordings. The cutoff frequency of the experimental site was 0.17 kHz.

Antennal rasps from smaller individuals ($n = 3$) could not be analyzed at 60 m because the SNR was too low (i.e., the signals were below the ambient noise; Fig. 2). In marked contrast, all sounds from intermediate and large spiny lobsters ($n = 7$) were recorded on all the hydrophones, with distance up to 60 m (Fig. 2). The SLpp varied significantly and positively according to the body size of spiny lobsters (Pearson: $r = 0.614$, $t = 3.914$, $n = 10$, $df = 8$, $p < 0.01$; Fig. 3). We calculated a maximum difference of 20 dB between the smallest (SLpp = 146 dB re 1 μ Pa; CL = 4.3 cm) and the largest (SLpp = 166 dB re 1 μ Pa; CL = 12.3 cm) spiny lobsters (Figs. 2 and 3).

The TL models estimated as $\alpha \times \log_{10}(r)$ from the dataset of SPLrms vs distance did not significantly vary with

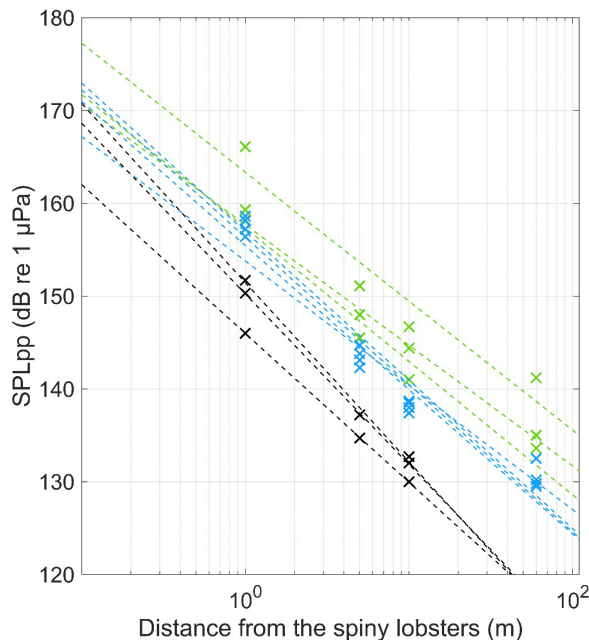


FIG. 2. (Color online) Evolution of SPLpp (crosses) recorded at different distances from the spiny lobsters (between 1 and 60 m) and their calculated fit curves using logarithmic models (dashed lines). Each point represents the mean SPLpp averaged on ten sounds. Note that the x -axis is in logarithmic scale. Each value calculated at 1 m corresponds to the SLpp of each spiny lobster. The colors are related to the body size of the spiny lobsters (green, large; blue, intermediate; black, small).

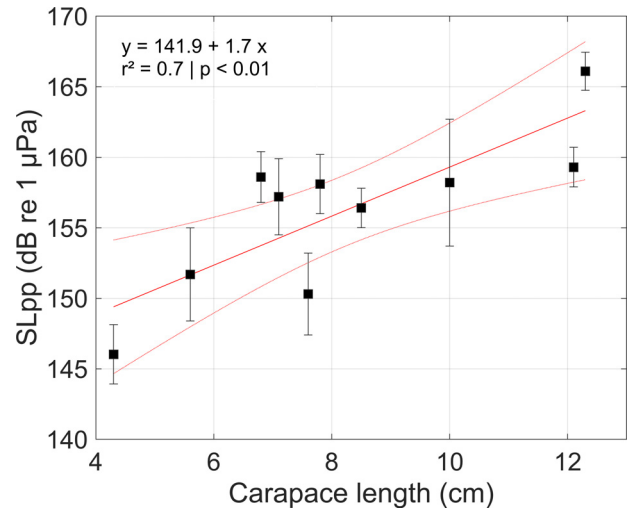


FIG. 3. (Color online) Evolution of SLpp (in peak-peak) measured at 1 m from spiny lobsters with body size at the experimental site. Data are presented as mean $\pm$ standard deviation, SD.

body size (Pearson: $r = -0.086$, $t = -0.533$, $n = 10$, $df = 8$, $p = 0.609$; Fig. 4). The estimated TL parameter α ranged between 11.40 and 13.89 (Fig. 5). By fitting the results among all individuals, the global fitted TL parameter α was 12.1, which is between the theoretical models of cylindrical ($\alpha = 10$) and practical ($\alpha = 15$) TL (Fig. 5).

Detection ranges of the antennal rasps produced by all spiny lobsters were estimated per body size group by considering the calculated SLrms and global fitted TL ($\alpha = 12.1$; Table I) for a water depth of 3.3 m. Under the experimental ANL conditions, we estimated that large individuals could be recorded at distances up to 364 m (Table I). In contrast, the estimated detection ranges for smaller individuals were less than 60 m (the maximum range encompassed by our array). These estimated values were consistent with the values observed on our *in situ* recordings; smaller spiny lobsters ($n = 3$) could not be recorded at 60 m (Fig. 2), matching our estimations of their detection

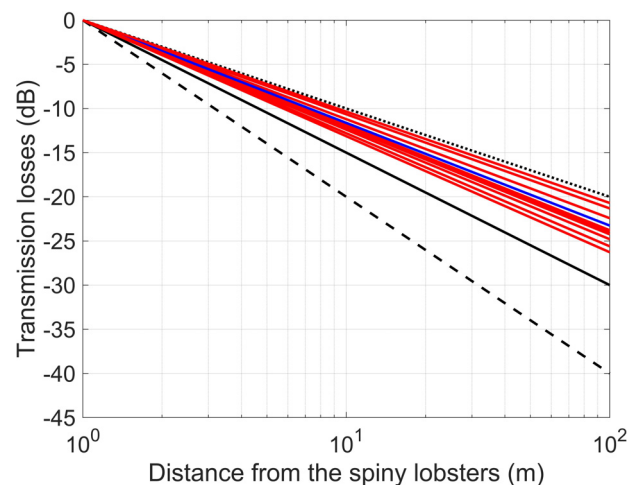


FIG. 4. (Color online) TL estimated for ten spiny lobsters (red lines) based on the dataset SPLrms vs distance, and the global fitted TL (blue line, $\alpha = 12.1$). Black lines represent theoretical models of TL, dotted is cylindrical ($\alpha = 10$), continuous is practical ($\alpha = 15$), and dashed is spherical ($\alpha = 20$).

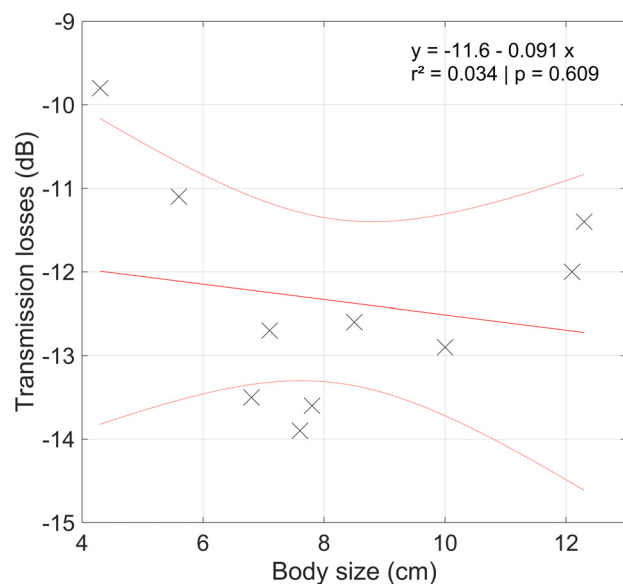


FIG. 5. (Color online) Linear relationship between spiny lobster transmission losses (dB) and body sizes.

ranges (see Table I). In a theoretical lower (but still realistic) ANL, larger individuals could be detectable at the km scale, with estimated detection ranges up to 1612 m (Table I). However, when considering other TL models typically used for deeper water depths, detection ranges were drastically reduced, with larger individuals being detectable only below 100 m (Table I).

Finally, the spectral content of recorded antennal rasps did not change with increasing distance. Sounds were dominated by low frequencies (< 1 kHz) at both short (1 m) and long distances (60 m) from spiny lobsters (Figs. 6 and 7).

IV. DISCUSSION

Understanding sound propagation and detection ranges is crucial to infer the potential of an acoustically active species for PAM applications. This study showed that

Caribbean spiny lobster sounds can be detectable over hundreds of meters in shallow waters with the potential to be detected at distances greater than 1 km. These results can contribute to the development of passive acoustic detectors to detect lobster presence within reefs and adjacent habitats.

Although SLs have been reported for marine mammals and fishes, data on SL measurements of marine crustaceans are rare. Our results were consistent with a previous study that measured SLpp from similarly sized European spiny lobsters (Jézéquel *et al.*, 2020). For example, large European spiny lobsters (CL = 13.5 cm) produced SLpp up to 167 dB re 1 μ Pa (Jézéquel *et al.*, 2020), while the largest Caribbean spiny lobsters (CL = 12.3 cm) in this study produced SLpp at a similar 166 dB re 1 μ Pa (Fig. 2). In addition, we also found that Caribbean spiny lobster SLpp is tightly correlated with body size with, larger individuals producing higher SLpp compared to smaller animals (Fig. 3). Ontogenetic variations of SLpp have been also described in European spiny lobsters, and such a trend could be explained by more efficient resonating structures in larger animals (Jézéquel *et al.*, 2020; Jézéquel *et al.*, 2022b).

A linear array of hydrophones allowed us to empirically determine the TLs based on SPLrms measurements between 1 and 60 m from Caribbean spiny lobsters. The global fitted TL model coefficient was 12.1 (Fig. 4), a value consistent with other sound propagation studies in shallow waters (Rogers and Cox, 1988; Richardson *et al.*, 1995; Bass and Clark, 2003), but different from the fundamental models that are often used in the bioacoustic literature. This result clearly demonstrates the importance of empirically assessing sound propagation in shallow waters to study crustaceans' sounds and suggests that propagation models should be carefully considered when applying those models to other shallow water taxa.

Notably, our global TL is different from the global TL of 17.6 estimated for European spiny lobsters (Jézéquel *et al.*, 2020). This difference can be partially accounted for

TABLE I. Average detection ranges (in m) of the antennal rasps produced by groups of size-matched spiny lobsters. The different TL coefficients correspond to the global TL ($\alpha = 12.1$) calculated from this study, and the theoretical models of cylindrical, practical, and spherical TLs. Min is SNR = 10 dB and max is SNR = 5 dB. ANL were computed in the 100–1000 Hz frequency band. Bold values highlight empirical results from the experimental site.

Group size	TL	This study		Wenz 5 knots		In situ distance of detection (m)
		Min ANL = 104.5	Max ANL = 99.5	Min ANL = 95	Max ANL = 90	
Small ($n = 3$)	10	24	77	146	461	10
	12.1	14	36	61	159	
	15	8	18	27	59	
	20	5	9	12	21	
Intermediate ($n = 4$)	10	154	487	928	2934	60
	12.1	65	168	286	743	
	15	29	61	94	203	
	20	15	24	36	56	
Large ($n = 3$)	10	390	1235	2352	7438	
	12.1	140	364	621	1612	
	15	53	115	177	381	
	20	20	35	48	86	

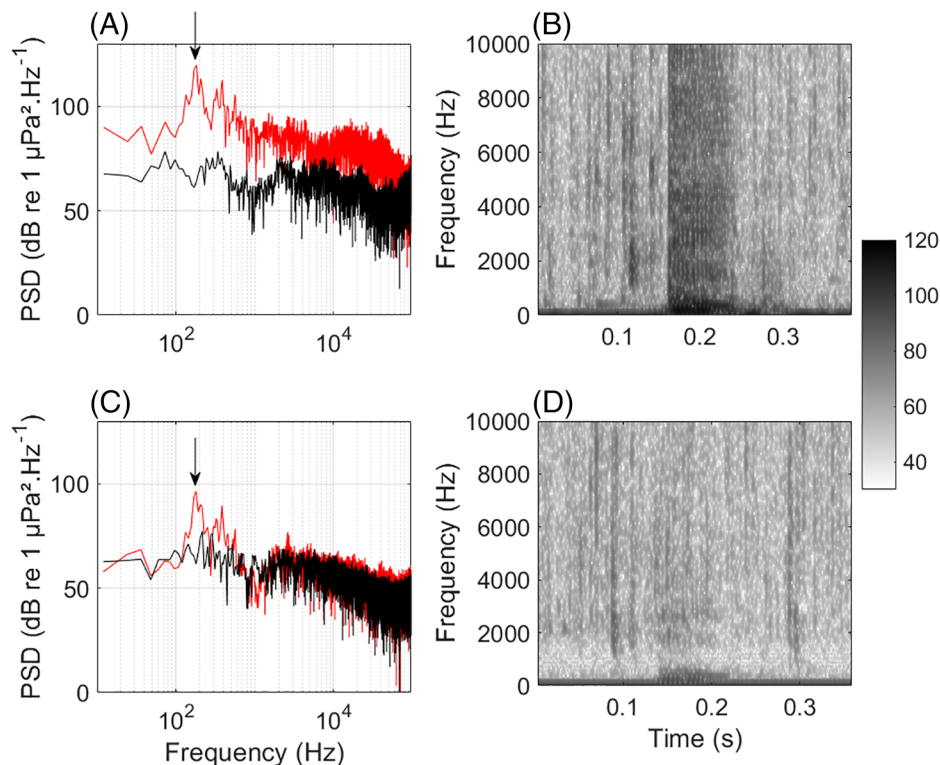


FIG. 6. (Color online) PSD (A and C) and spectrograms (B and D) of an antennal rasp produced by a large spiny lobster (CL = 12.1 cm) at 1 m (left) and 60 m (right). The black lines are the ambient noise levels recorded at the same distances. Black arrows show the dominant frequencies of the two signals that were calculated at 190 Hz at both distances.

the frequency band used to assess TL (this study: 0.1–1 kHz; Jézéquel *et al.*, 2020: 10–78 kHz). In addition, the study from Jézéquel *et al.* (2020) was performed at 10 m depth, while our recordings were made at 3.3 water depth, thus placing the physical environment closer to the cylindrical spreading model. It is noteworthy that TLs also strongly depend on bottom characteristics (see Ainslie, 2010). Finally, while we found that SLpp (and SLrms) varied with body size, there were no significant relationships between TL and body sizes (see Fig. 5), a similar result to Jézéquel *et al.* (2020). These results underscore that the physics of

sound propagation does not depend on the sound source, and it is thus independent from the animal body size. Thus, understanding the physical environment is crucial when trying to compare acoustic propagation studies.

Based on these *in situ* SL and TL values, we were able to estimate detection ranges for each spiny lobster at our experimental site. As SLs varied with body size, detection ranges also changed. For example, the sounds produced by the three smallest individuals could not be detected by the hydrophone placed at 60 m; this was confirmed via the detection ranges estimated using the passive sonar equation (Fig. 2, Table I). Using the ANL recorded during the experiment, sounds from larger spiny lobsters could be detectable up to 364 m. Under a theoretical low (but still realistic) ANL (Wenz, 1962), all spiny lobster sounds could be detectable over 100 m, with sounds from larger individuals propagating at km scale (i.e., up to 1612 m; Table I). It is notable that the theoretical ANL used in our study is similar to SPLrms values recorded in coral reefs close to the current experimental site, and calculated in the same frequency band (100–1000 Hz; Jones *et al.*, 2022), hence showing consistency for our estimated detection ranges in natural spiny lobster habitats. However, under more conservative theoretical models of TL (spherical) that may be prevalent at higher water depths, detection ranges drastically decreased to less than 100 m for all spiny lobsters (Table I). Overall, our detection ranges were consistent with (Jézéquel *et al.*, 2020), showing the high potential for PAM of spiny lobster sounds in shallow waters over large spatial resolution. Considering the ecological importance of Caribbean spiny lobsters (Cruz and Bertelsen, 2008), the detection of their sounds could be used as indicators of animal presence,

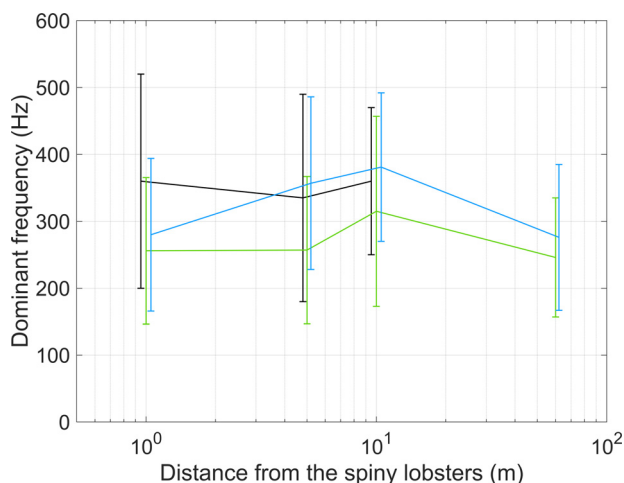


FIG. 7. (Color online) Averaged dominant frequencies calculated on the recorded antennal rasps as a function of the spiny lobster-hydrophone distance. The colors are related to the body sized groups of the spiny lobsters (green: large, blue: intermediate, black: small). Note that the x -axis is on logarithmic scale. Data are presented as mean $\pm$ SD.

which could in turn be used to identify areas of over-fishing and even assess the efficacy of marine protected areas.

We found that the spectral contents of spiny lobster sounds were dominated by low frequencies below 1 kHz up to 60 m from the animals (Figs. 6 and 7). The result differed from Jézéquel *et al.* (2020) that showed low frequency content was only present up to 10 m from European spiny lobsters. This difference can be explained by two factors. First, sound recordings in shallow waters (such as our experimental site) depend on cutoff frequencies that allow only certain modes to propagate at low frequencies (Ainslie, 2010). The nature of the bottom also plays a significant role in the waveguide. Second, ambient noise levels can mask some frequency bandwidth, especially low frequencies. Jézéquel *et al.* (2020) performed sound recordings near a marina, where shipping noise masked low frequency contents. In contrast, the present study was done in a quiet area without anthropogenic noise and where the dominant sounds in the area tend to be from snapping shrimp which are predominantly above 1.5 kHz (Kaplan *et al.*, 2015). Considering that crustaceans detect lower frequencies below 1 kHz (Jézéquel *et al.*, 2021; Dinh and Radford, 2021; Radford *et al.*, 2022), the TL results suggest that sound communication distances in spiny lobsters in quiet habitats could be much longer than previously thought. This also demonstrates a need for further studies to acquire spiny lobster audiograms and measurements of particle motion generated by antennal rasps underwater (Goodall *et al.*, 1990; Popper *et al.*, 2001; Song *et al.*, 2021).

V. CONCLUSIONS

We measured the propagation features of Caribbean spiny lobster sounds within *P. argus*' shallow water habitat. These data allowed us to estimate their detection ranges, and we notably found that sounds from larger individuals could be detectable at the km scale. These results provide key new data and underscore the potential efficacy of using PAM stations to examine the specific behaviors and habitat use of an important Caribbean fisheries species. With the proliferation of PAM applications in spiny lobster habitat (e.g., Staaterman *et al.*, 2014), and ongoing development of tools including real-time buoys (Mooney *et al.*, 2020), these data support the use of acoustic monitoring as an important cost-effective monitoring tool for managers and other coral reef stakeholders.

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