DECEMBER 20 2022

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J. Acoust. Soc. Am. 152, 3747–3755 (2022)
https://doi.org/10.1121/10.0016613

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JASA ARTICLE

Tank acoustics substantially distort broadband sounds produced by marine crustaceans

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ABSTRACT:
Marine crustaceans produce broadband sounds that have been mostly characterized in tanks. While tank physical impacts on such signals are documented in the acoustic community, they are overlooked in the bioacoustic literature with limited empirical comparisons. Here, we compared broadband sounds produced at 1 m from spiny lobsters (*Panulirus argus*) in both tank and *in situ* conditions. We found significant differences in all sound features (temporal, power, and spectral) between tank and *in situ* recordings, highlighting that broadband sounds, such as those produced by marine crustaceans, cannot be accurately characterized in tanks. We then explained the three main physical impacts that distort broadband sounds in tanks, respectively known as resonant frequencies, sound reverberation, and low frequency attenuation. Tank resonant frequencies strongly distort the spectral shape of broadband sounds. In the high frequency band (above the tank minimum resonant frequency), reverberation increases sound duration. In the low frequency band (below the tank minimum resonant frequency), low frequencies are highly attenuated due to their longer wavelength compared to the tank size and tank wall boundary conditions (zero pressure) that prevent them from being accurately measured. Taken together, these results highlight the importance of understanding tank physical impacts when characterizing broadband crustacean sounds.

https://doi.org/10.1121/10.0016613

(Received 22 September 2022; revised 5 December 2022; accepted 6 December 2022; published online 20 December 2022)

[Editor: Arthur N. Popper] Pages: 3747–3755

I. INTRODUCTION

Bioacoustic experiments with marine invertebrates and fishes often rely on observations made in tanks (Popper and Hawkins, 2018). These studies are necessary before performing *in situ* recordings because they permit isolation of the sounds produced by a species without ambiguity from other sources (Rountree *et al.*, 2006). Tanks are also useful to make visual observations to associate sounds with specific behaviors. However, performing acoustic recordings in such arenas presents many challenges since a tank is an enclosure that results in sound distortion. While tank complexities have been known for decades in the acoustic literature (e.g., Stanton and Beyer, 1978; Pierce, 1981; Schroeder, 1996; Novak *et al.*, 2018), they remain poorly described or overlooked in many bioacoustic studies.

The oldest articles discussing biological sound deformations in tanks were from Parvulescu (1964, 1967). Although widely cited in the bioacoustic literature, this transcript of a discussion that took place at a conference does not contain measurements or quantifications that permit understanding or quantification of tank acoustic impacts on biological sounds. Akamatsu *et al.* (2002) and Novak *et al.* (2018) more recently illustrated both theoretically and experimentally that tank resonant frequencies and reverberation distort narrowband fish sounds. The authors reviewed mathematical formulas to estimate the resonant frequencies of a particular tank using its dimensions. Additionally, the attenuation of low frequencies has also gained attention with some studies highlighting that sound exposure experiments in tanks are not suitable for performing fish hearing studies (Duncan *et al.*, 2016; Rogers *et al.*, 2016; Gray *et al.*, 2016). While these works are often a review of prior knowledge, these results are highly valuable for the bioacoustic community as they explain complicated phenomena in straightforward terms, thus, making such knowledge more accessible. However, it is noteworthy that all of the references reported here focused on narrowband fish sounds.

Crustaceans are among the most soniferous of marine animals (Schmitz, 2002). Tank impacts on broadband sounds produced by marine crustaceans have been largely undiscussed in the bioacoustic literature (e.g., Buscaino *et al.*, 2011; Coquereau *et al.*, 2016; Filiciotto *et al.*, 2019; Sal Moyano *et al.*, 2019; Flood *et al.*, 2019; Peixoto *et al.*, 2020; Buscaino *et al.*, 2021; Hamilton *et al.*, 2021; Ceraulo *et al.*, 2022). As such, data from these studies cannot be extrapolated to *in situ* environments because tank impacts on recorded signals were not assessed. Only a few studies have quantified tank impacts on crustacean broadband sounds. For example, Patek and Baio (2007) illustrated that reverberation extends the duration of tropical spiny lobster (*Panulirus interruptus*) sounds. Tank resonant frequencies distort the spectral shape of European spiny lobster sounds

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(*Palinurus elephas*; Jézéquel *et al.*, 2019). Moreover, low frequencies (i.e., *frequencies* below the tank resonant frequencies) are highly attenuated and cannot be measured properly in tanks (Jézéquel *et al.*, 2020b). Thus, broadband sounds should not be characterized in tanks without a full understanding of their physical impacts. Ideally, tank recordings should be complemented by *in situ* recordings, which mitigate tank acoustic issues, while introducing other experimental difficulties (e.g., visibility, ambient noise).

Understanding tank impacts on biological sounds is critical. Ignoring these phenomena can lead to misunderstanding data and overlooking signal components that can provide insights into their potential ecological roles. This is especially true for the low frequency content that marine crustaceans detect (Popper and Hawkins, 2018). Accurately characterizing a sound is also crucial to be able to detect it among the myriad other biological sounds present in marine environments (e.g., Tricas and Boyle, 2014; Putland *et al.*, 2017). This is particularly relevant when developing worldwide libraries characterizing biological sounds using common sound features, such as duration, power, and frequencies (Parsons *et al.*, 2022), that are modified by tank acoustics. There is, therefore, a clear need to empirically address how tanks impact broadband sounds produced by marine crustaceans.

In this study, we characterized the broadband sounds emitted by Caribbean spiny lobsters (*P. argus*) in both tank and *in situ* conditions. By comparing different sound features calculated at the same distance (1 m) with the same animals, we empirically highlighted the differences between tank and field-based recordings. In light of these results, we then discussed the three main tank physical impacts that distort crustacean broadband sounds in order to provide a practical guide to future recordings for the bioacoustic community.

II. MATERIALS AND METHODS

A. Study animals and holding conditions

For the purpose of this study, we hand collected ten *P. argus* individuals of a wide range of sizes on June 27, 2022 in St. John, U.S. Virgin Islands within the Virgin Islands National Park. Seven small spiny lobsters [carapace length (CL) = 4.3–8.5 cm] were caught via snorkeling in Great Lameshur Bay (18°19′05.8″ N, 64°43′27.1″ W). Three larger adult spiny lobsters (CL = 10.0–12.3 cm) were captured via scuba diving on a reef off Fish Bay (18°18′49.1″ N, 64°45′29.3″ W). All individuals were then transferred to one large holding tank ($1.9 \times 0.9 \times 0.7\,\mathrm{m}^3$) outside the facilities of the University of the Virgin Islands, in Great Lameshur Bay. The rectangular holding tank was composed of fiberglass-sided walls (thickness = 0.5 cm) and was isolated from the ground using a dense wooden table that rested on cinderblocks [Fig. 1(A)]. The tank was continuously supplied with seawater pumped from the nearby bay and was shaded with dark mesh to reduce direct sunlight. Spiny lobsters were kept in these holding conditions for 1 week prior to acoustic recordings. The study was permitted by National Parks Service (NPS) Permit No. VIIS-2022-SCI-005.

B. Sound recordings

We recorded sounds produced by spiny lobsters both in a tank and *in situ* using the same acoustic recorder (Fig. 1). To enable accurate comparisons between the two different physical environments, we recorded sounds from same spiny lobsters both in the holding tank and *in situ*. To do so, spiny lobsters were gently handheld 1 m from the acoustic recorder. This procedure has been widely used in the bioacoustic literature to elicit sound production in spiny lobsters (e.g., Patek *et al.*, 2009; Jézéquel *et al.*, 2019). It also permitted us to record sounds by accurately controlling the distance between individuals and the acoustic recorder, which enabled comparison between tank and *in situ* recordings. Recordings were made in an otherwise identical way. Sound recordings were first performed in the holding tank 24 h after spiny lobster collection. A calibrated SoundTrap (ST600, Ocean Instruments, Auckland, NZ) with a sampling rate of 192 kHz was attached to a rebar and positioned at 0.5 m from the bottom in both physical environments (Fig. 1). Then spiny lobsters were handheld one-by-one to elicit sound production in front of and at 1 m facing the hydrophone. Sound recordings lasted 30 s for each individual.

The field site was located in the Great Lameshur Bay (18°19′06.2″ N, 64°43′23.8″ W), adjacent to the holding facilities. It is a shallow water area (3.4 m depth) with a flat

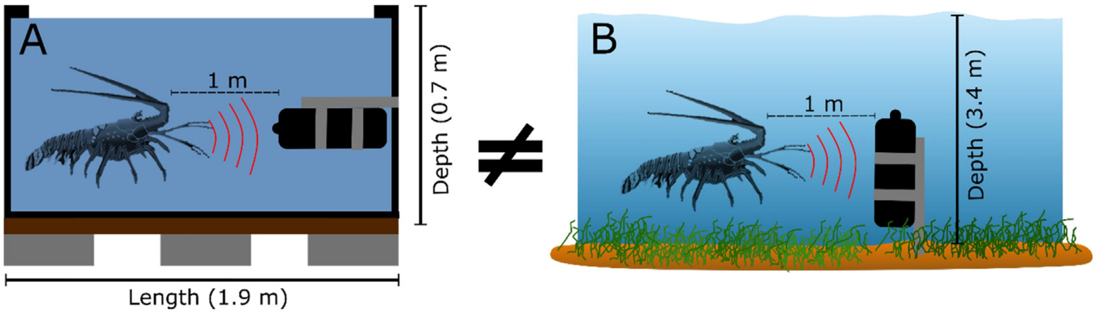

FIG. 1. (Color online) Spiny lobster sounds were recorded in two different physical environments: a rectangular tank (A) and *in situ* (B). Figures are not drawn to scale.

bottom constituted of thin sand and seagrass patches. One day prior to the recording experiment, all spiny lobsters were transferred into one steel cage (1.0 m × 1.0 m × 0.5 m, 0.5 m^3) placed on the sandy bottom. A door was located at the top to facilitate handling the animals in the cage. Spiny lobsters were allowed to acclimate for 24 h to recover from the short (200 m) transport. The next day (4 July), the acoustic recorder was attached 0.5 m (depth of the hydrophone) above the bottom using a rebar stake previously hammered vertically into the substrate. The recorder was located 1 m in front of the holding cage.

C. Sound analysis

Sound recordings (in .wav format) were first visually analyzed to confirm sound production by each spiny lobster. Each sound was then manually extracted using the software Audacity (version 3.1.3). We analyzed a total of 10 sounds per spiny lobster in the tank and *in situ* (20 sounds analyzed per individual). All sequences were processed using custom MATLAB scripts (version 2021a; MathWorks, Natick, MA). Sounds from tank and *in situ* recordings were characterized by examining three different types of sound features: temporal, power, and spectral. These metrics were chosen as they are useful for passive acoustic monitoring studies (Mooney *et al.*, 2020) and to assess communication (Popper *et al.*, 2001).

We calculated two different temporal features: total duration (in ms) and number of pulses per sound. Total duration was calculated as the duration between the first "rise" of the first and the last pulses of each sound (Jézéquel *et al.*, 2019). When pulses from a sound could not be clearly isolated from each other (i.e., because the reverberation of one pulse overlapped with the next one or because two sounds occurred simultaneously), we did not calculate its temporal features.

We computed two different power features based on source levels (SLs; in dB re 1 μPa). As spiny lobster sounds are pulse trains characterized by short and transient sounds, we chose to calculate the SL in peak-to-peak ($\mathrm{SL}_{\mathrm{pp}}$), which is the most representative power feature for these types of sounds (Erbe, 2011). We also calculated the SL in root mean square ($\mathrm{SL}_{\mathrm{rms}}$), which 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 (here, a window of 1 s was used).

Finally, we determined the spectral feature of spiny lobster sounds by calculating the peak frequency where the power spectral density (PSD; in dB re 1 $\mu\mathrm{Pa}^2\ \mathrm{Hz}^{-1}$) was maximal.

D. Tank resonance

Peak frequencies from spiny lobster sounds recorded in the tank were compared with the resonant frequencies of the tank. The resonant frequencies ($f_{\mathrm{rectangular}}$, in Hz) of our rectangular tank with the dimensions length (L), width (W), and height (H) were calculated using the formula for normal modes in a rectangular enclosure that is commonly used in room acoustics (Long, 2005; Kuttruff, 2016; Pierce, 2019),

$$f_{\mathrm{rectangular}} = \frac{c}{2}\sqrt{\left(\frac{l}{L}\right)^2 + \left(\frac{m}{W}\right)^2 + \left(\frac{n}{H}\right)^2}, \tag{1}$$

where c is the sound velocity in seawater (1500 m s^{-1}); l, m, and n represent integers ($\geq$1); and the combination of these is called the "mode number." The minimum resonant frequency is then defined at mode (1, 1, 1) for a particular tank dimension. To our knowledge, this was first introduced to the bioacoustic community in Akamatsu *et al.* (2002).

The equation above is based on the assumption that the tank walls, tank bottom, and water surface are all pressure release interfaces. This is a usual assumption for bioacoustic tanks. The vertical (bottom) pressure release boundary condition is justified here since the bottom of the tank is not in direct contact with the ground [Fig. 1(A)]. This leads to a simple formula that depends exclusively on the tank size and the water sound speed. It is, thus, very convenient and usually accurate enough for bioacoustic purposes (Jézéquel *et al.*, 2018; Jézéquel *et al.*, 2019); it will thus be used in this paper. Still, it is interesting to know that a more realistic model that accounts for leakage through tank walls has been proposed by Novak *et al.* (2018). Its use requires further knowledge about the acoustic properties (sound speed and density) of the tank wall material.

Also, note that shallow water *in situ* environments act as waveguides, 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 (see Ainslie, 2010). Because our sound recordings were performed at 1 m, which was well below the water depth (~3.4 m), we expected our sound recordings to be mostly free of waveguide effects.

E. Statistical analysis

The different sound features are presented as mean ± standard deviation (SD). The three sound features described above were tested to determine whether significant differences in means were evident by comparing sounds from the same spiny lobsters recorded between tank and *in situ* recordings. 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 whether their probability distributions were equal (significance level, $\alpha = 0.05$) using custom made MATLAB scripts.

III. RESULTS

A. Tank recordings

Waveforms of the spiny lobster sounds consisted of pulse trains that were difficult to isolate because of sound reverberation [Fig. 2(A)]. The effects of sound reverberation were also seen in spectrograms where all pulses

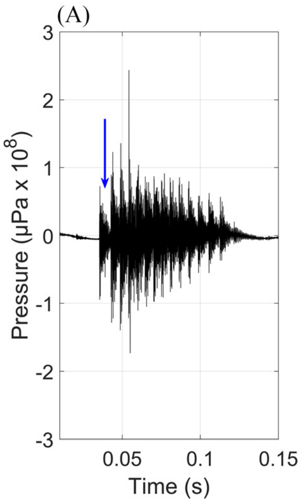

FIG. 2. (Color online) Waveforms of sounds produced by the same *P. argus* individual (CL = 8.5 cm) at 1 m in the experimental tank (A) and *in situ* (B). Note that scales of *y* axes are different. The blue arrow highlights the smear of noise following the pulses, which is due to tank sound reverberation.

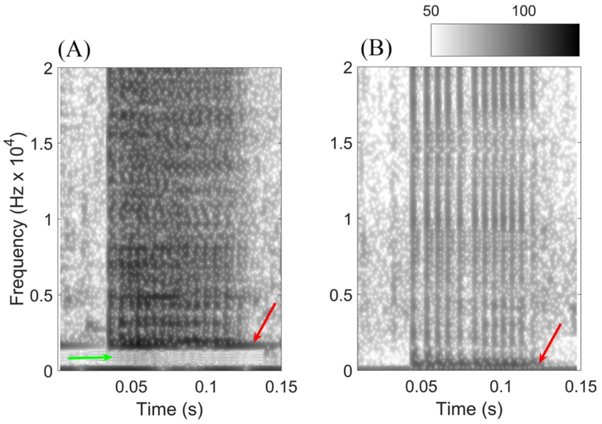

FIG. 3. (Color online) Spectrograms (fast Fourier transform length: 4024; Hamming window: 1001 points; 99% overlap) of sounds produced by the same *P. argus* individual (CL = 8.5 cm) at 1 m in the experimental tank (A) and *in situ* (B). Red arrows indicate the peak frequency of each sound. Notice that the peak frequency of the sound recorded in the tank corresponds to the minimum resonant frequency calculated for the experimental tank (1.7 kHz). The green arrow shows the large gap of acoustic energy below the tank minimum resonant frequency that is due to attenuation of low frequencies in tanks. The color scale bar is in dB re 1 $\mu\mathrm{Pa}^2\ \mathrm{Hz}^{-1}$.

(dark vertical lines) were followed by a "smear" [dark horizontal lines; Fig. 3(A)]. When taking this into account, we concluded that temporal features could not be accurately calculated.

Power features were high, with a mean $\mathrm{SL}_{\mathrm{pp}}$ of 163.8 ± 5.8 dB re 1 μPa (range: 149.5–173.6 dB re 1 μPa), and mean $\mathrm{SL}_{\mathrm{rms}}$ was 141.6 ± 6.0 dB re 1 μPa (range: 124.4–151.5 dB re 1 μPa).

The first and second minimum resonant frequencies calculated for the experimental tank ranged between 1.7 and 2 kHz and strongly influenced the spectral shape of the spiny lobster sounds. Indeed, 82% of these sounds had their first peak frequencies within this frequency range, which was clearly seen in both the PSDs [Fig. 4(A)] and spectrograms [dark horizontal line at 2 kHz; Fig. 3(A)]. Below 2 kHz, a relatively large energy gap of more than 40 dB was found in all recorded sounds [Figs. 3(A) and 4(A)]. However, low frequency background noise was still present [i.e., <100 Hz; see Fig. 4(A)] and corresponded to a water pump system outside the tank.

In contrast, above 2 kHz, high energy peaks were present [Figs. 3(A) and 4(A)]. These higher frequencies corresponded to other resonant frequencies associated with the experimental tank and caused highly variable dominant

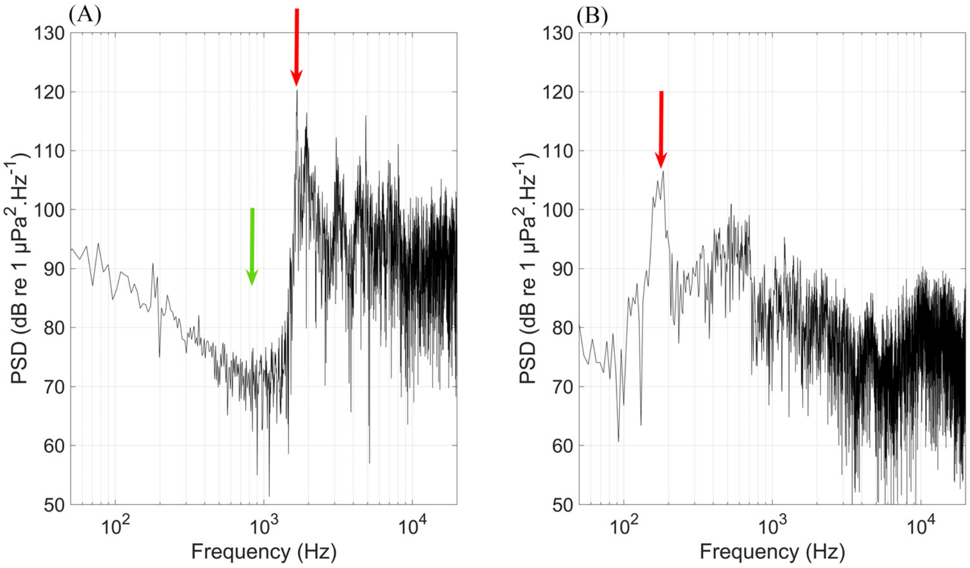

FIG. 4. (Color online) PSDs of sounds produced by the same *P. argus* individual (CL = 8.5 cm) at 1 m in the experimental tank (A) and *in situ* (B), with the *x* axis in logarithmic scale. Red arrows indicate the peak frequency of each sound. Notice that the peak frequency of the sound recorded in the tank corresponds to the minimum resonant frequency calculated for the experimental tank (1.7 kHz). The green arrow shows the large gap of acoustic energy below the tank minimum resonant frequency that is due to the attenuation of low frequencies in tanks.

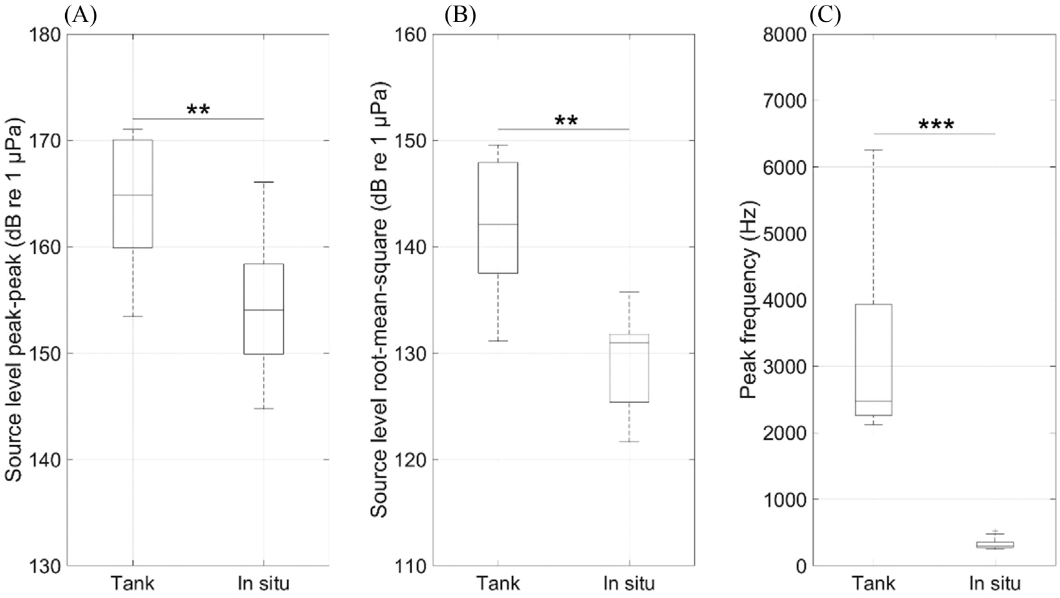

FIG. 5. Boxplots showing significant differences (*U*-test) of sound features (SL_{pp}, SL_{rms}, and peak frequencies) calculated from *P. argus* spiny lobsters in the experimental tank and *in situ*. Asterisks highlight significant differences between the two environments (**, $p < 0.01$; ***, $p < 0.001$).

frequencies with a mean of 3.3 ± 1.6 kHz [range: 1.7–24.8 kHz; Figs. 3(A) and 4(A)].

B. *In situ* recordings

Compared to spiny lobster sounds recorded in the experimental tank, sounds recorded *in situ* presented clear waveforms with pulses that could be easily isolated [Fig. 2(B)]. This was also highlighted in the spectrograms, which did not have the smearing seen in the tank recordings [Fig. 3(B)]. Thus, temporal features could be calculated for all recorded sounds emitted by the ten spiny lobsters tested. Mean total duration was 48.8 ± 16.5 ms (range: 15–151 ms), with a mean number of pulses per sound of 8.2 ± 3.3 (range: 3–26) and mean pulse rate of 173.7 ± 41.0 Hz (range: 62.5–407.4 Hz).

As seen in Fig. 3, even if some SL_{pp} and SL_{rms} values were high (up to 168.6 and 137.7 dB re 1 μPa, respectively), their mean values were significantly lower than those measured in the experimental tank (*U*-test, $p < 0.001$). *In situ* SL_{pp} and SL_{rms} were 10 and 13 dB lower compared to tank recordings, although they were calculated at the same distance from the spiny lobsters (i.e., 1 m; Fig. 5).

As the spiny lobster sounds recorded *in situ* were not affected by tank acoustics, we could calculate their natural spectral features. Peak frequencies were found to be spread in the low frequency band [i.e., below 1 kHz; Figs. 3(B) and 4(B)]. The mean peak frequency was 0.33 ± 0.09 kHz (range 0.15–0.71 kHz) and was significantly lower than the tank recordings (*U*-test, $p < 0.001$; Fig. 5). This is vastly different from what was seen in the tank recordings, where peak frequencies were only found from 1.7 kHz (Figs. 3 and 4).

IV. DISCUSSION

All acoustic features (temporal, power, spectral) calculated from spiny lobster broadband sounds produced in a tank were significantly different from *in situ* field-based recordings. Although such results were to be expected and followed a well-known theory (e.g., Duncan *et al.*, 2016), we believe that their empirical illustration is an important reflection of this physical phenomenon on "typical" biological signals. The results underscore that broadband sounds, such as the ones produced by crustaceans, cannot be characterized properly in tanks. We detail below the three physical phenomena that are responsible for the distortion of tank-recorded broadband sounds, respectively known as resonant frequencies, sound reverberation, and low frequency attenuation.

A. Resonant frequencies

Each constrained volume (i.e., tank) has its own set of resonant frequencies. If a particular sound has a bandwidth overlapping with the resonant frequencies of the tank used, the energy at those resonant frequencies will be substantially modified in the received signal depending on observer position (Stanton and Beyer, 1978; Akamatsu *et al.*, 2002; Novak *et al.*, 2019). This results in a distortion of the spectral shape of the recorded sound, with visible individual peaks around the minimum resonant frequency [using small l, m, and n indices in Eq. (1)]. At higher frequencies, the number of resonant frequencies increases, and their density is such that individual resonance cannot be resolved anymore, a feature that also leads to a distorted spectral shape (Schroeder, 1996).

In our study, peak frequencies of spiny lobster sounds recorded *in situ* showed significantly different patterns compared with those recorded in the experimental tank. More than 82% of the peak frequencies calculated in the tank matched the first and second tank minimum theoretical frequencies [i.e., 1.7–2 kHz; see Figs. 3(A) and 4(A)]. The other peak frequencies corresponded to higher tank resonant frequencies. This distribution of energy toward high frequencies in our recordings is in accordance with the bioacoustic literature on spiny lobsters (e.g., Hazlett and Winn, 1962; Mulligan and Fischer, 1977; Buscaino *et al.*, 2011). For example, sounds produced in a tank by the same species as in our study showed first peak frequencies between 2 and 5.5 kHz (Mulligan and Fischer, 1977), which should have been described as being associated with the tank resonant frequencies. In contrast, all peak frequencies from sounds recorded *in situ* were calculated below 500 Hz [see Figs. 3(B) and 4(B)]. This is representative of the true spiny lobster sounds, as our *in situ* recordings were not affected by tank resonant frequencies and were recorded at short enough range to be free of waveguide distortion. Overall, our results are fully consistent with previous field-based studies on European (*P. elephas*; Jézéquel *et al.*, 2019; Jézéquel *et al.*, 2020a) and tropical spiny lobsters (*P. interruptus*; Patek *et al.*, 2009). These broadband sounds should, thus, be characterized as being mainly dominated by low rather than high frequencies.

Despite these findings, several papers reported only high peak frequencies in broadband sounds produced by other crustacean species that were similar to resonant frequencies of the tanks used (e.g., Filiciotto *et al.*, 2019; Sal Moyano *et al.*, 2019; Peixoto *et al.*, 2020; Hamilton *et al.*, 2021; Ceraulo *et al.*, 2022). As an example, Coquereau *et al.* (2016) showed peak frequencies of spider crab (*Maja brachydactyla*) feeding sounds that matched the tank minimum resonant frequency (i.e., 2.7 kHz). Flood *et al.* (2019) calculated peak frequencies in paddle crab (*Ovalipes catharus*) rasps only above the minimum resonant frequency of their tank (i.e., >1.6 kHz). Hence, the peak frequencies calculated for crustacean broadband sounds in tanks correspond mostly to resonant frequencies and do not illustrate the true frequency content of the same sounds recorded *in situ*.

B. Sound reverberation

The soundfield in a tank is highly complex and can be described using various physical models. One solution is to use the modal view presented previously. As discussed above, it is convenient at intermediate frequencies because individual peaks (corresponding to individual resonant frequencies, which in turn coincide to individual modes) can be seen on the spectrum of the recorded signals. At higher frequencies, the modal density increases so much that individual resonance cannot be distinguished anymore (Schroeder, 1996). In such a regime, it becomes convenient to drop the modal view and turn toward a ray model: the acoustic field can be described as the sum of multiple reflections on the tank walls. Usually, there are so many reflections that individual echoes cannot be resolved (Schroeder, 1996). This phenomenon is usually called reverberation and can be seen as the persistence of a sound after its emission stops. Reverberation is a well-known effect of soundfields in enclosures and is described in detail in room acoustics literature (e.g., Long, 2005; Kleiner and Tichy, 2014; Kuttruff, 2016; Pierce, 2019). This results in a longer duration of the sound compared to the same sound recorded in an open field environment.

Sound reverberation in our experimental tank affected the waveform of spiny lobster sounds by extending the duration of single pulses, which could be seen as a smear of noise following pulses [Figs. 2(A) and 3(A)]. This phenomenon was absent from the *in situ* recordings [Figs. 2(B) and 3(B)]. Reverberation was so strong that individual pulses contained in spiny lobster sounds could not be isolated [Figs. 2(A) and 3(A)], which prevented us from calculating any temporal feature. Such a result is consistent with previous studies in European lobster (*Homarus gammarus*) and spiny lobster (*P. elephas*) broadband sounds recorded also in tanks (Jézéquel *et al.*, 2018; Jézéquel *et al.*, 2019). Interestingly, a study recorded sounds from another spiny lobster species (*P. interruptus*) using both acoustic and kinematic measurements in tanks (Patek and Baio, 2007). The authors showed that the mean pulse duration from acoustic recordings was twice as long compared to kinematic recordings.

Sound reverberation not only impacts the signal temporal length; it also affects the received levels. This aspect is quantified in our study by calculating SLs in rms. We found that SL_{rms} in tanks were significantly (13 dB) higher compared to *in situ* SL_{rms} (Fig. 5). This result was due to the extended duration of the pulses in tanks that increased sound power, as well as resulting in peak amplitudes that were higher in the tank. Hence, temporal features as well as SL_{rms} of broadband sounds cannot be accurately calculated in tanks.

C. Low frequency attenuation

Low frequencies (i.e., below the minimum resonant frequency of the experimental tank) are highly attenuated due to their longer wavelengths compared to the dimension of the tank, as well as tank wall boundary conditions (i.e., zero pressure; Duncan *et al.*, 2016; Rogers *et al.*, 2016; Gray *et al.*, 2016). As a result, low frequency sound does not propagate well and decays exponentially when traveling away from the source (e.g., see Duncan *et al.*, 2016). For example, a 100 Hz sound has a wavelength of approximately 15 m and is much larger than typical experimental tanks. Duncan *et al.* (2016) showed that, at the same distance from a sound source, the received level at 100 Hz is 10 dB lower in a tank compared to an open water environment. Note that this difference in received level depends on tank geometry as well as the distance between sound source and acoustic recorder. This phenomenon explains why previous bioacoustic studies that characterized crustacean (including spiny lobster) broadband sounds in tanks lack low frequency content (e.g., Buscaino *et al.*, 2011; Coquereau *et al.*, 2016; Filiciotto *et al.*, 2019; Sal Moyano *et al.*, 2019; Flood *et al.*, 2019; Peixoto *et al.*, 2020; Buscaino *et al.*, 2021; Hamilton *et al.*, 2021; Ceraulo *et al.*, 2022). Essentially, even if low frequencies are produced by an animal under study, they are so attenuated that they cannot be detected in the tank.

The attenuation of low frequencies was clearly noticeable in our tank recordings. The spectral shapes of the spiny lobster sounds presented an important energy gap of more than 40 dB below the minimum resonant frequency [i.e., <1.7 kHz; Figs. 3(A) and 4(A)]. In contrast, this low frequency energy gap was absent from our *in situ* recordings [Figs. 3(B) and 4(B)]. These results are in accordance with Jézéquel *et al.* (2019), which showed broadband sounds produced by European spiny lobsters (*Palinurus elephas*) in tanks lack low frequency content (<1 kHz), whereas it was present and largely dominant in an open water environment.

It is important to note that the *in situ* environment in this study cannot be considered as open water. Indeed, this water environment was shallow, in the sense that the water depth (~3 m) was small compared to the wavelength of the sound of interest (~1 m at 1.5 kHz). As a result, the *in situ* recordings embedded waveguide effects, in the same way that the laboratory recordings contained tank effects. However, because the *in situ* work was conducted in a natural spiny lobster habitat, the recorded signals are fully representative of what the animals may use for communication or what bioacousticians may detect when undertaking passive acoustic monitoring.

The presence of low frequencies (i.e., <1 kHz) in crustacean sounds is critical to assess whether associated species could use these sounds for acoustic communication (Popper *et al.*, 2001). Hence, the inability to properly measure low frequency sounds in tanks has largely biased acoustic communication studies with marine crustaceans, because those usually rely on the hypothesis that communication, if it exists, must rely on low frequencies (e.g., Jézéquel *et al.*, 2021; Dinh and Radford, 2021; Radford *et al.*, 2022). This study clearly demonstrates that low frequency content may propagate *in situ* even if not detected in tanks, despite the caveat that our *in situ* measurements were done in the near-field for the low frequency part of the signal. As a comparison, the spiny lobster CLs ranged between 4 and 12 cm, while the wavelength of the recorded sounds (~300 Hz) was 5 m. How this near-field impacted the estimated broadband SL values was not investigated.

D. Toward a practical guide for characterizing crustacean sounds in tanks

Based on the aforementioned measurements, we present a simple, yet practical, procedure for characterizing sounds produced by marine crustaceans in tanks.

(1) Measure the water depth, width, and length of the rectangular tank or diameter of the circular tank used.
(2) Compute the theoretical minimum resonant frequency using equations presented in Akamatsu *et al.* (2002). This value gives preliminary insights into the bandwidth from which the recorded sounds will be distorted.
(3) Record the sounds from the study species in the tank. Note that the behavioral contexts in which the sounds are produced can be accurately described with video recordings, potentially providing valuable ecological data.
(4) Sound characterization will depend on the recorded sound type:
(e) If it is a broadband pulse (i.e., encompassing tank resonant frequencies), temporal (e.g., pulse duration), amplitude, and spectral features are impacted by tank acoustics; hence, the recorded broadband sound cannot be characterized, and *in situ* recordings are needed for sound characterization. However, if the recorded sound is a pulse train, and if single pulses can be distinguished, inter-pulse duration can be computed [see Jézéquel *et al.* (2019) for a specific example].
(f) If the sound is low frequency and narrowband (i.e., below the tank minimum resonant frequency), temporal and spectral features can be computed. However, the power features (e.g., SL) are impacted by low frequency attenuation in the tank and must be computed *in situ*. Note that low frequency sounds produced by the study species may not be detectable in the tank because of high attenuation [see Jézéquel *et al.* (2020b) for a specific example].

V. CONCLUSION

We illustrated how broadband sounds, such as those commonly produced by marine crustaceans (including spiny lobsters), are strongly distorted by tank physical properties and, thus, cannot be representatively characterized in tanks. Overall, reverberation and resonant frequencies occur in the mid-to-high frequency band (i.e., from the minimum tank resonant frequency), while attenuation occurs in the low frequency band (i.e., below the minimum tank resonant frequency). In contrast, these broadband sounds can be characterized accurately when recording directly in their natural environment (*in situ*). While characterizing broadband sounds cannot be performed in tanks, preliminary experiments in these confined environments are still valuable to (1) assess the types of sound (i.e., narrow- vs broadband) produced by the study species isolated from the acoustically rich marine environment and (2) associate particular behaviors with produced sound. Understanding and correctly characterizing the *in situ* characteristics of a sound are particularly important as we increase passive acoustic monitoring for managed species such as spiny lobsters and other broadband acoustic signalers (Parsons *et al.*, 2022). Conversely, incorrectly describing an acoustic signal that is used in a management setting could lead to improper species management.

Other challenges due to tank acoustics can pose serious issues when performing bioacoustic studies. This is the case when measuring particle motion in tanks, which is the prevalent acoustic cue detectable by most fishes and marine invertebrates (Popper and Hawkins, 2018). Although such measurements were outside the scope of our study, particle motion in tanks cannot be estimated from sound pressure recordings but should rather be directly measured using specific devices such as accelerometers (Jones *et al.*, 2019). Further, if absolute particle motion levels are needed, it is of paramount importance for the sensor to be calibrated (at least in the frequency band of interest). Finally, studying behavior and hearing responses from an active source requires an accurate knowledge of the study animal position in a tank. Indeed, low frequency sounds, that are detectable by most marine fishes and marine invertebrates (<1 kHz), attenuate rapidly from a source in tanks (Duncan *et al.*, 2016). Local boundary conditions also matter, particularly the substrate composition (e.g., concrete vs soil). Hence, the study animal would show different responses depending on its distance from the source as it would be exposed to vastly different sound levels that are not representative of the same sound exposure levels in an open water environment. This is particularly important for highly mobile species, including fishes (Popper and Hawkins, 2018) and marine invertebrates (Jones *et al.*, 2020).

ACKNOWLEDGMENTS

The work was supported by two private foundations and National Science Foundation Ocean Technology and Interdisciplinary Coordination Grant Nos. 2024077 and 1736530 to T.A.M. We thank Amy Apprill, Ben Weiss, and Ciara Willis for their assistance in animal collection and the University of the Virgin Islands Center for Marine Science for use of their field station and the related support. We thank Seth Cones for drawing Fig. 1. The study was permitted by NPS Permit No. VIIS-2022-SCI-005 to T.A.M.; we thank the NPS for their logistical support.

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