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Replayed reef sounds induce settlement of *Favia fragum* coral larvae in aquaria and field environments[a)]

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Abstract: Acoustic cues of healthy reefs are known to support critical settlement behaviors for one reef-building coral, but acoustic responses have not been demonstrated in additional species. Settlement of *Favia fragum* larvae in response to replayed coral reef soundscapes were observed by exposing larvae in aquaria and reef settings to playback sound treatments for 24–72 h. Settlement increased under 24 h sound treatments in both experiments. The results add to growing knowledge that acoustically mediated settlement may be widespread among stony corals with species-specific attributes, suggesting sound could be one tool employed to rehabilitate and build resilience within imperiled reef communities. © *2024 Acoustical Society of America.*

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1. Introduction

The settlement of coral larvae is a process of critical importance for the growth and replenishment of reef communities, particularly, as the degradation of reef habitats has reduced coral brooding stocks around the globe (Hughes *et al.*, 2019). Coral larvae are capable of using multimodal sensory information from their environment to discriminate suitable habitats and correspondingly alter their vertical orientation in the water column in preparation for settlement (Kingsford *et al.*, 2002). However, coral larval behavioral responses to sensory cues can be highly variable depending on the characteristics of a given species (Ritson-Williams *et al.*, 2016), and large knowledge gaps remain regarding the responses of coral larvae to some lesser-studied cue types such as sound. As a result, our ability to accurately predict larval outcomes on reefs under rapidly shifting environmental regimes remains extremely limited. Studies of how different sensory inputs impact these complex settlement behaviors have potentially broad implications for coral management and restoration practices.

The role of the ambient sound environment in larval settlement has only recently begun to be investigated (Pysanczyn *et al.*, 2023). Coral reefs exhibit dynamic soundscapes containing sounds of local fauna, including territorial and mating calls of fishes (Lobel and Mann, 1995; Myrberg, 1997), shrimp snaps (Lillis and Mooney, 2018; Loye and Proudfoot, 1946), and scraping of feeding parrotfish and echinoids (Radford *et al.*, 2008; Tricas and Boyle, 2021). Along with natural patterns of spatiotemporal variation, differences in the soundscape characteristics of reefs have been linked to indicators of reef biodiversity and community assemblages (Elise *et al.*, 2019; Kaplan *et al.*, 2015), suggesting these acoustic cues can be ecologically informative to reef larvae.

Lillis *et al.* (2018) observed that larvae of the hard coral *Porites astreoides* exhibited higher rates of settlement when exposed to reef soundscapes rich with low-frequency fish sounds than larvae exposed to sounds from a degraded reef or sand patch. A subsequent experiment demonstrated that *P. astreoides* settlement can be increased in naturalistic settlings by broadcasting reef sounds using underwater speakers (Aoki *et al.*, 2024). These results suggest that enrichment of the acoustic environment could be used to encourage settlement in struggling coral populations (Williams *et al.*, 2021). However, a necessary next step is to investigate if acoustically mediated settlement occurs in additional coral species. Further, because larval seeding processes occur via *in situ* and *ex situ* methods, it is important to establish if acoustically induced settlement can occur in aquarium and field-based settings. As tank and free-field acoustics can differ substantially, characterizing the acoustic fields received by larvae under both conditions is essential.

In this study, we exposed larvae of the brooding coral species *Favia fragum*, or golfball coral, to continuous playback of reef sounds recorded from a healthy reef site and assessed whether the addition of this acoustic cue influenced

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settlement rates. Work was conducted at a long-term soundscape study site within the marine portion of the U.S. Virgin Islands (USVI) National Park (Kaplan *et al.*, 2015). We conducted field and aquarium experiments to approximate diverse larval seeding techniques. Settlement rates were evaluated as a function of sound treatment, exposure duration, and larval age with the intent of addressing how acoustic treatments impacted settlement over the course of the larval competency period.

2. Methods

2.1 Larval collection

Experiments took place in July 2022 in the National Park on the south side of St. John, USVI. We collected 12 colonies of *F. fragum* from Great Lameshur Bay at depths of 2–5 m, where colonies were separated by at least 3–5 m to distribute sampling effort across the collection area and increase the probability of incorporating diverse genets among parent colonies (Warner *et al.*, 2016). Colonies were housed in shaded outdoor raceways fed by unfiltered ambient seawater at the Virgin Islands Environmental Resource Station [VIERS; Fig. 1(a)]. Beginning six days after the new moon of June 28 (Goodbody-Gringley, 2010), corals were held in mesh-lined containers and examined each morning for newly released planulae. Larvae were maintained in containers of 0.22 μm-filtered seawater for no more than 48 h prior to experimental use. Between July 4 and July 11, 264 larvae were collected and used for the sound exposure studies. To test the effect of sound exposure on settlement behaviors, larvae were transferred into 140 ml polypropylene [a material exhibiting minimal acoustic attenuation values of 0.05–0.18 dB/mm (Selfridge, 1985)] cups containing 0.22 μm-filtered seawater and a conditioned (1 month in local seawater) ceramic kiln stilt (3.8 cm diameter). This allowed groups of larvae to be exposed to variable acoustic cues at reef sites and in aquaria while standardizing the available settlement surface and limiting the influence of currents and waterborne settlement cues (Lillis *et al.*, 2018). Following the experiments, all coral colonies were returned to Great Lameshur Bay.

2.2 Field sound exposure experiment

On July 7, 80 *F. fragum* larvae were pooled and divided into 4 cups containing 20 larvae each. Two cups were attached using cable ties to a rebar stake in Great Lameshur Bay (18.3182496° N, 64.722593° W) and two additional cups were placed in the neighboring Grootpan Bay [18.3097656° N, 64.717558° W; Fig. 1(a)]. The following morning two cups of ten newly spawned larvae were added to the stakes at both sites. All cups were removed from the experiment and analyzed for settlement on June 9; therefore, half of the cups ($n = 4$, 20 larvae per cup) were exposed to experimental conditions for 48 h while half of the cups ($n = 4$, 10 larvae per cup) were only exposed for 24 h.

Great Lameshur and Grootpan Bay are quiet, sandy sites with low levels of ambient sound (quantitative measures of particle motion at nearby sites in these bays during the same month are reported in Jézéquel *et al.*, 2023a). A Reef Acoustic Playback System (RAPS) was deployed at each site to enrich the local sound environment during the experiment. The RAPS is a solar-powered speaker system designed to allow automated autonomous underwater playback of sound files (Aoki *et al.*, 2024). Speakers (LL916; Lubell Labs Inc., Columbus, OH; frequency response 200 Hz–23 kHz) were attached to cinder blocks and placed on the benthos at 1 m distance from the larval cups [Fig. 1(b)].

At the Great Lameshur site, acoustic treatment consisted of 24-h continuous playback of the soundscape of a nearby site, Tektite Reef, known to be a relatively healthy reef habitat with elevated levels of snapping shrimp and

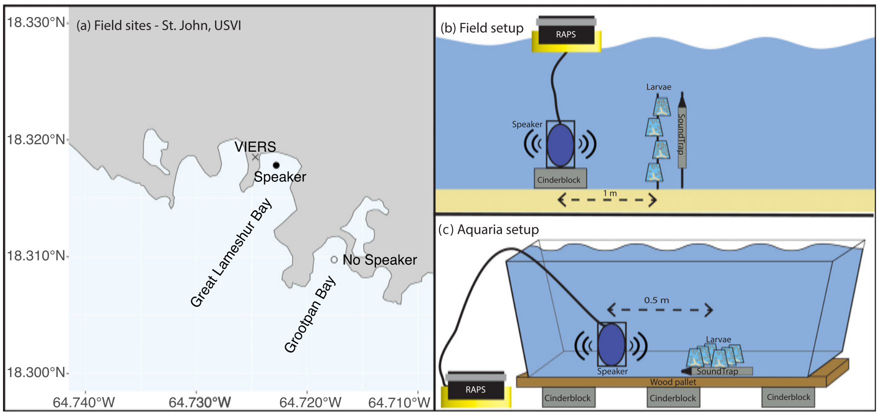

Fig. 1. Illustrations of experimental setup, showing (a) map of field sites in the USVI, where X = VIERS, where aquaria experiments took place, filled circle = sound enrichment site, white circle = control site; and (b) field setup for larval sound exposure experiment. Blue RAPS speaker is shown at left with larvae in cups and an acoustic recorder placed 1 m from the audio source. (c) Aquarium larval sound exposure experiment is displayed. Cups of larvae and the acoustic recorder are placed 0.5 m from the source.

soniferous fish sounds (Kaplan *et al.*, 2015). A broadband 25 dB amplification was applied to these recordings using Adobe Audition (Adobe Inc., San Jose, CA) to maximize levels of low-frequency fish calls without clipping, and files were synced to play at the same local time as when they were recorded. Grootpan Bay served as the control site, where the RAPS played a silent file during the first 24 h of the experiment. After observing that silent file playback produced a small amount of electrical sound from the RAPS, the speaker at the control site was modified for the second experimental day to continuously play an unamplified 30-min recording of the Grootpan Bay soundscape made by a SoundTrap ST-600 STD recorder (Ocean Instruments, Auckland, New Zealand) placed next to the larvae and sampling at 48 kHz. Thus, larvae in Great Lameshur Bay received an enriched soundscape treatment, including amplified fish sounds recorded from a more active reef while control larvae were exposed to the relatively quieter and less biologically active ambient sounds of Grootpan Bay. Sound levels throughout the experiment were monitored using ST-600 STD acoustic recorders mounted adjacent to the settlement cups at 1 m distance from the speakers.

Calibration measurements of the acoustic field produced 1 m from the RAPS during playback in Great Lameshur Bay were recorded using an orthogonal array of four hydrophones (HTI-96-MIN/3V/Low Noise; High Tech Inc., Long Beach, MS; nominal sensitivity, −165 dB re 1 V/μPa; frequency response, 2 Hz–30 kHz) connected to a four-channel SoundTrap ST-4300 recorder (Ocean Instruments, Auckland, New Zealand). Measurements of particle motion across three axes were then calculated from the pressure gradients between individual hydrophones in the array (Nedelec *et al.*, 2021).

2.3 Aquarium sound exposure experiment

Aquarium sound exposures were conducted in two identical rectangular fiberglass tanks ($1.9 \times 0.9 \times 0.7\ \mathrm{m}^3$) mounted on wooden planks over a set of cinder blocks to reduce ground vibrations [Fig. 1(c)]. Tanks were supplied with unfiltered local seawater and shaded with dark mesh. On July 11, 144 larvae were pooled and divided into 12 cups containing 12 larvae each. Six cups were placed in the control tank and six cups were placed in the experimental tank; a small piece of ceramic tile was attached to the cups to prevent floating. A speaker was placed on the bottom of each tank 0.5 m from the larval cups and between 0.45 and 0.5 m from the tank walls on all other sides. The experimental aquarium received the same 24-h reef sound treatment played via the RAPS as the experimental field site. In the control aquarium, the RAPS was powered on, but the speaker did not play any sound files, which is a slight difference from the field control treatment. Larval settlement was assessed after 24 h and 72 h of sound exposure (3 cups of 12 larvae per treatment and timepoint).

Sound pressure within the aquaria was recorded during the experiments using two ST-600 STD recorders (Ocean Instruments, Auckland, New Zealand). Particle motion within the experimental tank was measured at the location of the cups using a neutrally buoyant triaxial ICP accelerometer (Model W356B11, PCB Piezotronics Inc., Depew, NY). The signal from the accelerometer was first passed through a signal conditioner (Model 480B21, PCB Piezotronics Inc.) and an analog filter (Model 3382, Krohn-Hite Corporation, Brockton, MA) and, subsequently, digitized by a laptop running a custom MATLAB script (MathWorks. Inc, Natick, MA). We were unable to fully remove all sources of background noise in the aquaria as continuous action of a nearby water pump was a necessity for our field site. A small amount of ambient noise was, therefore, present in our aquaria recordings in addition to elevated bands of sound centered on 1.7 kHz, an artifact corresponding to the first minimum resonant frequency of the tank. Sounds below this minimum resonant frequency, including most relevant reef fish sounds, were not expected to be distorted during playback (Jézéquel *et al.*, 2022).

2.4 Analysis

Surfaces of the ceramic stilts and cups were scanned for settled larvae using a dissecting microscope (40× magnification) within 3 h of collection from treatment sites. The percentage of settled larvae per cup in the sound and control treatments at each time point were compared employing student's *t*-tests for the field and aquarium trials (de Winter, 2013), using a standard 0.05 level of significance. To examine the effect of larval age on responses to acoustic cues, we pooled data between the field and aquarium trials and tested for differences in responses across both experiments between larvae exposed to treatments for 24 h and larvae exposed for >24 h. The larval competency period in *F. fragum* is known to peak between 8 and 36 h post release (Goodbody-Gringley, 2010), therefore, we expected larvae exposed to 24 h treatments to still be within a "peak competency" window on analysis, whereas larvae exposed for 48–72 h were likely "post competency."

Acoustic data were analyzed using custom MATLAB scripts (MathWorks. Inc, Natick, MA) to generate spectrograms and power spectra to compare field and tank recordings. Power spectral densities (PSDs) in the pressure domain for control and sound treatments in the field and tanks were calculated for 144 1-min clips sampled every 10 min over 24 h of the experiment using Welch's method. Median PSD values for each treatment were then used for comparison between treatments.

Acoustic analyses focused on frequencies below 2000 Hz, corresponding to the known auditory sensitivity ranges of most reef fishes and invertebrates. Analysis of field recordings of sound pressure and estimated particle motion followed methods outlined in Jones *et al.* 2022). Values of root-mean-squared sound pressure levels (SPLrms) and particle acceleration levels (PALrms) across three axes and the vector norm (the square root of the sum of squares of linear acceleration of each axis) in the 10–1000 Hz frequency band were calculated for thirty 10-s segments clipped from 5 min of continuous

RAPS playback audio at the field experimental site. Correlations between the SPLrms and PALrms values were then analyzed using an ordinary least squares regression.

Analysis of the aquarium accelerometer recordings also followed previously described methods (Jézéquel *et al.*, 2023b). Values of PALrms from 10 to 1000 Hz were calculated for ten 1-min clips of audio recorded from a continuous playback session in the experimental tank. Because pressure and particle motion calibration recordings in the tanks were conducted at different times, direct correlations between these values were not calculated.

3. Results

3.1 Larval settlement results

In the field, zero settlement was observed at the control site after 24 h while larvae settled at the sound-enriched site at substantially greater rates [30% ± 28% – mean ± standard deviation [SD; Fig. 2(a)]. Despite this observation of higher settlement in the sound treatment, no statistical difference between the sound and control treatments in the field was observed ($p > 0.05$) as a result of the small number of available replicates and, thus, limited statistical power for these trials. After 48 h of sound exposure, the mean settlement rates had increased to 85% ± 21% at the control site and 73% ± 39% at the sound-enriched site, again, with no significant differences between treatments.

In aquaria, larvae that received 24 h of acoustic enrichment settled at significantly higher rates compared to the no-sound control tank (49% ± 2% treatment vs 11% ± 13% control, $p < 0.05$). After 72 h of acoustic enrichment in tanks, significant differences in settlement between the treatment and control tanks were no longer observed, although the treatment tank showed less variability (lower SD) than the control [38% ± 3% treatment, 39% ± 13% control; Fig. 2(b)].

Looking at trends across field and tank trials, larvae exposed to acoustic cues within the “peak competency” window of less than 36 h post release settled in significantly higher proportions ($p < 0.05$; 41% ± 18%) compared with quiet controls [7% ± 11%; Fig. 2(c)]. However, when exposure durations were extended into the “post competency” window, there were no significant differences between settlement in the sound treatment cups (52% ± 27%) compared to the controls (57% ± 29%).

3.2 Acoustic enrichment impacts

The RAPS playback in the aquaria and field experiments elevated the soundscape above ambient levels [Figs. 3(a)–3(d)] primarily in the frequency range of 500–2000 Hz, as evidenced by elevation in the median PSD in this range at the treatment sites compared to that at the controls [Figs. 3(e) and 3(f)]. Compared to the *in situ* treatment, *ex situ* playback in aquaria showed evidence of expected noise levels and distortions [Figs. 3(a)–(d)], including a constant level of ambient noise at frequencies below 50 Hz that was observed only in the aquarium recordings.

Spectrograms of particle motion recordings of playback in the field and tank showed that low-frequency signals, including individual fish pulses, were resolvable in the particle motion domain below 2000 Hz [Figs. 4(a) and 4(b)]. For field recordings of the speaker playback made with the four-channel hydrophone array, SPLrms values ranged from 114 to 127 dB re 1 μPa and three-dimensional (3D) PALrms values ranged from 81 to 85 dB re 1 $\mu m/s^2$ during playback. These SPLrms and 3D PALrms values showed significant but weak correlations [Fig. 4(c); $R^2 = 0.511$, $p < 0.001$].

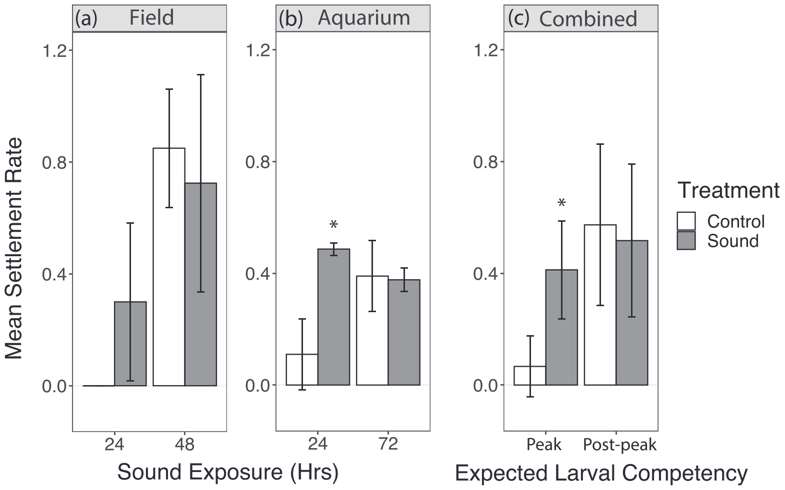

Fig. 2. Results of settlement experiments. Bar plots show mean per-cup settlement rate of *F. fragum* larvae following field (a) and aquarium (b) sound exposure, as well as the combined data grouped by larval age (c). Error bars = ±1 standard deviation (SD). “*” indicates significance between control and sound treatments, where $p < 0.05$. No settlement occurred in the field control treatment after 24 h.

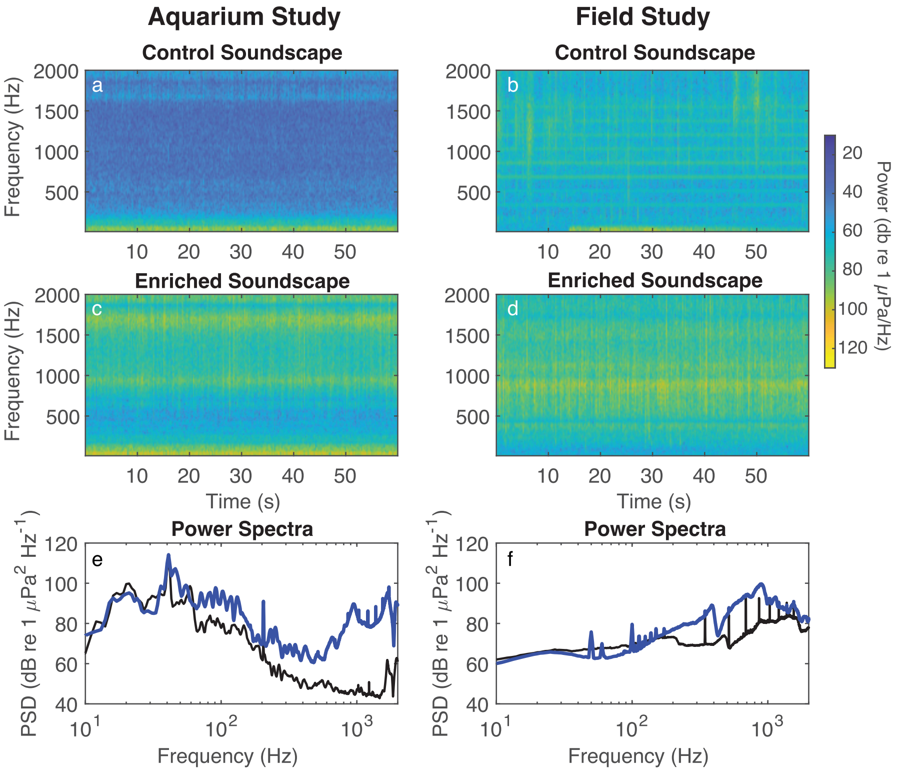

Fig. 3. Comparison of acoustic fields recorded during playback studies. Representative 1-min pressure spectrograms are displayed for (a) recording of the control tank, which received no sound playback; (b) recording of the control field site while an unamplified recording of the Grootpan Bay soundscape played from the speaker; (c) recording of replayed reef sounds during the aquarium trials; and (d) recording of the replayed Tektite reef sounds at the Great Lameshur Bay experimental site. Low-frequency median PSD values are shown for the (e) aquarium and (f) field studies. Control PSDs are depicted with thin black lines and playback treatment PSDs are shown with thick blue lines.

4. Discussion

These experiments show that acoustic enrichment using relatively healthy coral reef soundscapes can induce increased settlement in *F. fragum* coral larvae. Settlement rates were higher for larvae exposed to sound enrichment treatments in field and seawater-aquaria settings, suggesting transferability of these results to *in situ* and *ex situ* larval cultivation. This is the second species of hard coral that has been shown to settle in response to replayed sound stimuli; these results, therefore,

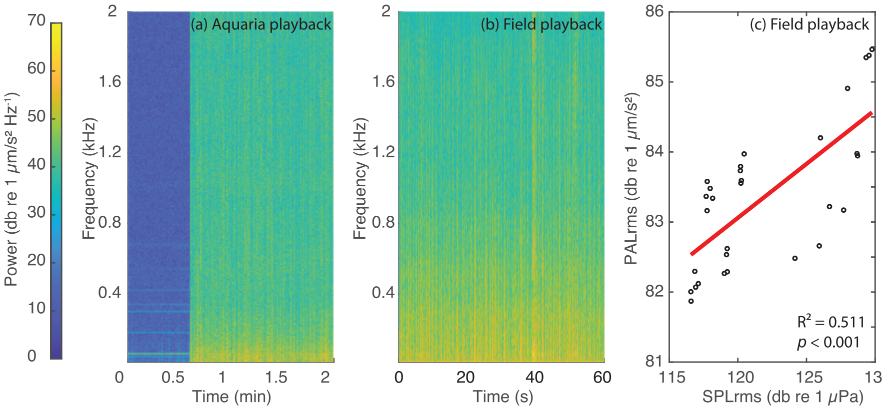

Fig. 4. Particle motion data. Spectrograms of three-dimensional (3D) vector norm particle acceleration are shown from (a) a 2-min portion of the aquaria playback recording (the speaker onset is visible at 0.6 min) and (b) a 1-min clip of field playback of reef sounds in Great Lameshur Bay. (c) PALrms values plotted against corresponding SPLrms values calculated from 10-s clips of speaker playback in Great Lameshur Bay are displayed. Red line shows the fitted linear model.

suggest that acoustically mediated settlement responses may be widespread among additional scleractinians. We acknowledge that low *F. fragum* spawning rates in the laboratory resulted in smaller than desired sample sizes for our study, yet, we observed similar trends in our tank and field studies despite this limitation.

Interestingly, significantly increased settlement rates were only observed during the first (24 h) analysis window; no differences were observed between treatment and control larvae after 48 or 72 h of acoustic enrichment in either the tank or field. This differs from previous work conducted with *P. astreoides* (Aoki *et al.*, 2024), which showed that benefits of acoustic enrichment persisted throughout at least 72 h of exposure. However, our results correspond with the biology of *F. fragum*, where larval searching and settlement behaviors peak between 8 and 36 h post release (Goodbody-Gringley, 2010). During this peak competency period, *F. fragum* larvae likely exhibit their highest degree of habitat selectivity to theoretically maximize their long-term survival and fitness. Outside of their competency window, larvae may become "desperate" (Knight-Jones, 1953) and respond to weaker or suboptimal settlement cues to conserve resources and lower their risk of mortality in the water column. *F. fragum* larvae contain fewer lipid reserves than other brooding coral larvae, a characteristic associated with shorter dispersal times and distances (Norström and Sandström, 2010). By contrast, although the maximal extent of the *P. astreoides* competency period has not been well described, this species is likely competent to settle as early as 3 h post release and for several subsequent days (Harrison and Wallace, 1990). These differing results imply that acoustic enrichment must take species characteristics and ecology into account to maximize effectiveness.

The optimal time and circumstances for deploying acoustic enrichment technologies are likely to vary based on differences in the life history traits of target species, therefore, it is critical to characterize these species-specific responses to sound. Extrapolation across species is challenging, especially from brooding corals to broadcast spawners with different breeding strategies, although notably the first observations of phonotaxis in scleractinians showed that *Montastraea faveolata*, a broadcast spawning coral, is also sound sensitive (Vermeij *et al.*, 2010). Investigating how responses to acoustic cues vary among additional species, including broadcast spawning corals, should be addressed in future studies. At a practical level, our demonstration of the relevance of acoustic cues to *F. fragum* alongside the *P. astreoides* results strengthens overall support for continued investigation of acoustic enrichment methods in corals.

Acoustically, replayed environmental sound cues can greatly differ from the natural soundscape, influenced by properties of the speaker, amplifier, and other system components. Compared to similar analyses made by Jones *et al.* (2022) of recordings of USVI reef soundscapes, playback from the RAPS during our field experiment produced pressure and particle motion fields at 1 m that are comparable to only the very highest ranges of naturally occurring sounds on nearby reefs. In tanks, sound cues are also distorted by resonance, reverberation, and attenuation effects (Jézéquel *et al.*, 2022; Rogers *et al.*, 2016).

Despite these limitations, the replayed reef sound cues produced by our speakers were sufficient to generate a significant biological settlement response in our laboratory experiments. This raises the question of what properties of the replayed soundscape (e.g., spectral vs contextual vs temporal) coral larvae are specifically responding to, particularly, as we consider what type of sound playback may be most effective for management and restoration purposes. Playback of ambient soundscapes containing reef fish calls may have unintended impacts on the broader reef community. Other invertebrate taxa have been shown to respond to unusual acoustic cues, such as vessel sounds, as they enact key behaviors such as metamorphosis (Stanley *et al.*, 2014). Whereas these types of behavioral discrimination experiments are challenging with invertebrates, one clear next step is to determine the minimum particle acceleration sound levels within particular low-frequency bands that induce significant increases in coral settlement rates; such data would then support the creation of a model of the effective range of acoustic enrichment for a given coral species (assuming propagation conditions and source levels are known) and a guide for using acoustic enrichment within a given aquarium environment. Our results suggest the potential of applying acoustic enrichment in a variety of restoration contexts, including encouragement of natural settlement, direct seeding to reefs, seeding within tents, and other structures, and doing so in confined, tank environments (Boström-Einarsson *et al.*, 2020).

It cannot be understated that particle acceleration, not sound pressure, is the essential acoustic variable of interest for studies of marine invertebrate acoustic responses (Popper and Hawkins, 2018). Consequently, particle motion measurement of replayed sound cues is vital for these and any future acoustic enrichment experiments. Future applications will require standard measures of the relevant cues (frequency and particle acceleration) to make biologically and ecologically relevant comparisons across taxa and environments. Data collection without such particle motion calibration measurements could lead to ill-informed conclusions on differences between species, sites, ecology, or other parameters.

Acoustic enrichment methods, while promising, are in their infancy, and effective applications will require considerable additional research. Although further investigation into the utility of acoustic enrichment for reef restoration is merited, no single tool is sufficient to address the range of stressors and environments in which practitioners are seeking to support coral reefs. A portfolio of viable restoration methods needs to be available to be tailored for specific local challenges (McLeod *et al.*, 2022). More broadly, for coral reefs to have a chance of persisting into the late 21st century, individual reef restoration campaigns must be accompanied by corresponding global actions to reduce carbon emissions and slow the accelerating deleterious effects of climate change on these vital ocean ecosystems.

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Author Declarations

Conflict of Interest

The authors have no conflicts to disclose.

Ethics Approval

Coral collection and handling was performed under National Parks Service Permit No. VIIS-2022-SCI-005.

Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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