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RESEARCH ARTICLE

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Soundscape enrichment enhances recruitment and habitat building on new oyster reef restorations

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Abstract

1. Marine soundscapes provide important navigational cues to dispersing larvae in search of suitable habitat. Yet, widespread habitat loss has degraded marine soundscapes and their functional role in recruitment. Habitat restoration efforts can provide suitable substrate for habitat regeneration, such as constructing reefs to facilitate recruitment and habitat growth by oysters, but typically occur where soundscapes are degraded and recruitment is limited. Enhancing marine soundscapes on newly constructed reefs using speaker technology may ensure sufficient recruitment to establish a trajectory of recovery for the desired habitat.
2. Across two of the largest oyster reef restorations in Australia, we deployed low-cost marine speakers at four sites and at three times throughout the recruitment season to test whether soundscape enrichment could boost recruitment and habitat formation by oysters. In the presence and absence of soundscape playback, we compared oyster recruitment rates to settlement panels across space and time, and oyster habitat cover and three-dimensional habitat building on newly constructed boulder reefs.
3. On the settlement panels deployed across the two reef restorations, soundscape playback significantly increased oyster recruitment at 8 of the 10 sites by an average ($\pm$1 SE) 5.1 $\pm$ 1.9 times (5281 $\pm$ 1384 more larvae per m^2), and by as much as 18 times.
4. On boulders atop newly constructed reefs, where the restoration goal is for oysters to form three-dimensional habitat, the surface area covered by oysters after 5 months did not differ between speaker and control treatments. However, soundscape playback appeared to influence the earlier recruitment of oysters, resulting in significantly more large oysters per boulder that formed significantly more three-dimensional habitat building by an average 4.3 $\pm$ 1.2 times relative to nonspeaker controls.
5. *Synthesis and applications*. Our results show that using speakers to enrich marine soundscapes at new restoration sites can boost oyster recruitment, resulting

in more larger oysters that form more three-dimensional habitat atop reef restorations. In accelerating the formation of these vertical growth forms, which provide the ecological functions that motivate restoration efforts, the early application of speaker technology on new reef restorations may help steer ecological succession on a trajectory of desired habitat recovery, potentially reducing the substantial cost of ongoing intervention.

KEYWORDS
acoustic technology, ecosystem restoration, marine soundscapes, recruitment, shellfish reef, underwater speakers

1 | INTRODUCTION

Ecological soundscapes provide important navigational cues that influence the movement and habitat selection of diverse animal groups (e.g. birds, fish, mammals, invertebrates; Gomes et al., 2021; Williams et al., 2021). Such acoustic cues, which are composed of the biological and physical components of an ecosystem (Pijanowski et al., 2011), confer information on the quality and location of habitats over spatial scales that can far exceed other cues (e.g. sight and smell in forests or oceans; McComb et al., 2003). Consequently, soundscapes can play a critical role in ecological recruitment, but are seldom utilised in conservation or restoration efforts. This is of concern because where ecosystems have been degraded, soundscapes are degraded (Butler et al., 2016; Gordon et al., 2018; Rossi et al., 2017), compromising the supply of new recruits that are foundational for habitat recovery and ecological function.

Applied soundscape ecology may be a particularly valuable tool in marine ecosystem restoration, which relies upon on natural recruitment to seed recovery but typically occurs where soundscapes are degraded (Williams et al., 2021). For example, on coral reefs, broadcasting healthy reef soundscapes using underwater speakers demonstrably enhances fish recruitment and retention (Gordon et al., 2019; Leis et al., 2003), a process that can counteract reef degradation and may accelerate recovery. Furthermore, soundscape enrichment can attract the primary habitat-formers that underpin ecological communities, such as coral and oyster larvae (Lillis et al., 2015; Vermeij et al., 2010). Such larvae are typically considered relatively passive dispersers. However, oyster larvae, for example, actively swim towards and settle in response to habitat-specific sounds (Lillis et al., 2013; Williams et al., 2022), with settlement rates increasing with the 'attractiveness' (health) of the soundscape (Williams et al., 2021). In this *Decade on Ecosystem Restoration* (2021–2030), soundscape enrichment may offer a technological solution to enhance a fundamental component of restoration success; a means for enhancing early successional processes to steer restorations on the desired trajectory of recovery.

Among the marine habitats to have experienced significant global decline (e.g. seagrasses, coral reefs, kelp forests), oyster reefs are considered among the most degraded (Beck et al., 2011). A desire to recover the ecological goods and services that oyster reefs provide society (McAfee et al., 2020) is fuelling a growing global restoration agenda (e.g. Hernández et al., 2018; McAfee, McLeod, et al., 2022; Pogoda et al., 2019). These restorations typically involve the provision of hard substrate to facilitate the recruitment and growth of oyster habitat. Yet, the soundscapes at restoration sites are typically degraded (Gordon et al., 2018) and increasingly altered by human activities (Duarte et al., 2021). Consequently, even where natural recruitment persists, restoration progress may be limited by insufficient settlement cues. Where this results in a lack of early recruitment by oysters to constructed reefs, the challenge of restoring oyster habitat may be compounded by rapidly colonising competitors, such as turf-forming algae that can spatially dominant hard substrate (Gorgula & Connell, 2004) to the exclusion of recruiting organisms such as oysters (McAfee et al., 2021). Therefore, techniques that enhance the recruitment of the organisms targeted for restoration, such as soundscape enrichment using speakers, may be important tools for ensuring early recruitment at restoration sites.

In this study, we deployed low-cost marine speaker technology across two of Australia's largest oyster reef restorations to test their capacity to enhance larval recruitment and early habitat formation on reef boulders. Using soundscape recordings collected from healthy reefs >20 km from the study sites, we enriched soundscapes at four sites across the two reef restorations, repeating this at three time periods throughout the oyster recruitment season (November to April; McAfee & Connell, 2020). In the presence and absence of soundscape playback, we anticipated that (1) oyster recruitment would be boosted by soundscape enrichment, and (2) that the early recruitment induced by soundscapes would result in more larger oysters that (3) would produce greater habitat cover and more of the three-dimensional growth forms that benefit associated ecological communities (McAfee et al., 2018). By demonstrating that soundscape enrichment can accelerate early biogenic habitat building on constructed reefs, we aim to investigate the potential value of adopting sound technology in the informative years of marine restoration projects.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted across two large oyster reef restorations in Gulf St. Vincent, South Australia: Windara Reef (34°30.604″ S, 137°53.949″ E), a 20-hectare reef constructed in 2017–2018, and Glenelg Reef (34°58.314″ S, 138°29.787″ E), a 3-hectare reef constructed in 2020 (Figure 1). These two restoration sites, which are approximately 80 km apart on opposite sides of Gulf St. Vincent, are each located ~1 km offshore in 7–10 m of water. Both sites consist of sandy seafloor atop which limestone boulder reefs (L: 10–30 m; W: 6–10 m; H: ~1 m) were constructed to facilitate the settlement of the Australian flat oyster *Ostrea angasi*. Both restoration sites were once characterised by seagrass meadows and/or flat oyster reefs but have transitioned to sedimentary seafloors following extensive loss of these habitats throughout the Gulf (i.e. 6200 ha of seagrass lost in the past 70 years, Tanner et al., 2014, while oyster reefs were completely lost about 100 years ago, Alleway & Connell, 2015). Despite the loss of oyster reefs *O. angasi* larvae can still recruit in the high numbers when provided with suitable settlement substrate (McAfee et al., 2021) during an observed recruitment window from mid-October to April (Austral summer; McAfee & Connell, 2020). Within weeks of the construction of Windara Reef (2018), a thick cover of filamentous turf algae had smothered all sunlit surfaces of the new reefs, excluding *O. angasi* larvae from settling atop the reef boulders (McAfee et al., 2021).

2.2 | Enriching marine soundscapes

To locally enrich marine soundscapes at multiple sites across each restoration, we deployed self-constructed underwater speakers at two sites across each of Windara Reef and Glenelg Reef (Figure 1). Soundscapes were enriched using the same speaker technology at all sites (5 × 3 cm vibration loudspeaker [25 W, 4 Ohm, omni-directional sound, frequency response 0.3–20 kHz; unbranded], an audio amplifier [MAX9744 amplifier; Adafruit] and a 64-bit processor [Raspberry Pi 3 Model B+] encased inside watertight PVC housing) but were powered using different solutions designed to suit each location. At Glenelg Reef, a solar-powered rig (pontoon) was anchored above the reef restoration where it powered two waterproofed speakers (via cables) positioned 60 m apart on the seafloor. This solar-powered rig allows for continual speaker operation and is suited to Glenelg Reef because it is located on Adelaide's metropolitan coast where the rig can remotely communicate with operators on shore (via broadband) and be readily accessed for maintenance. These speakers and the rig were conceived by our technology partners AusOcean, who designed and constructed the technology and whose designs are open-source (e.g. AusOcean Underwater Speaker Guide, 2019; www.ausocean.org/technology). In contrast to Glenelg, Windara Reef is on a more remote coastline with sporadic broadband access unsuited to the rig's operation. Therefore, we modified the speaker units to encase all the electronics inside water-tight PVC piping (Diameter × Length: 15 × 50 cm) with 3 × 12 V

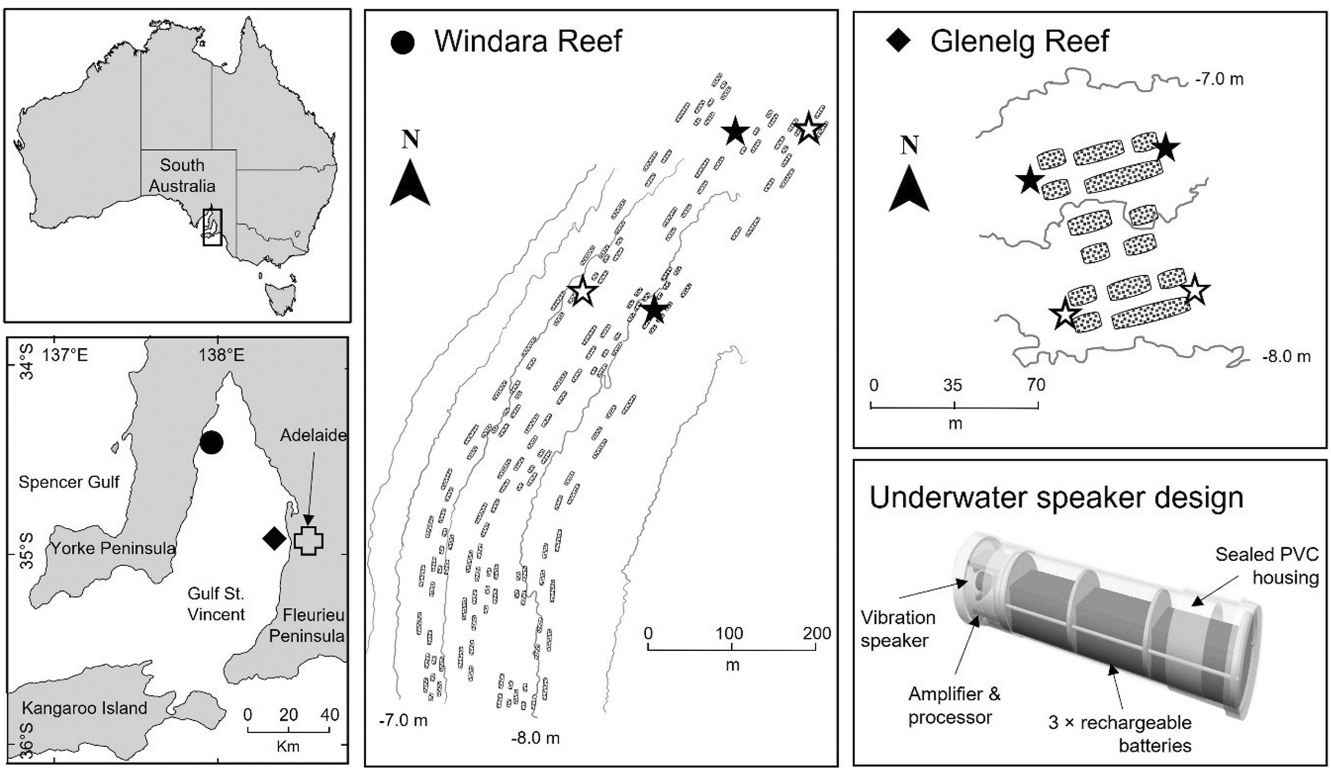

FIGURE 1 Two reef restoration sites in Gulf St. Vincent, South Australia (bottom left): the 20-ha Windara Reef (circle) composed of 159 boulder reefs (dotted rectangles), and the 3-ha Glenelg Reef (diamond) composed of 14 reefs. Stars denote sites for the speaker (black stars) and control (white stars) treatments. Diagram of the self-constructed, low-cost speakers (bottom right) used to enrich soundscapes.

SLA rechargeable batteries (RS Components Pty Ltd) that powered speakers for ~7 days. This self-contained, mobile speaker unit (Figure 1) allowed us to position our two speaker sites more broadly at Windara Reef relative to Glenelg Reef, but required speakers to be exchanged every 6 days.

Speaker treatments enriched soundscapes by continuously playing a looped recording of a healthy reef soundscape recorded from a rocky reef habitat located 20 km south of Glenelg Reef (Port Noarlunga Reef). This rocky reef was selected because no flat oyster reefs remain in mainland Australia, and because previous soundscape monitoring throughout Gulf St. Vincent (e.g. Rossi et al., 2017; Williams et al., 2021) showed this site to be among the most bio-acoustically active. Recordings of the reef soundscape were made using four hydrophones (Sound Trap 202, Ocean Instruments, frequency response 0.1–30 kHz, set to high gain sensitivity [−169 to −169.8 dB re 1 V/μPa], −3 dB bandwidth of 21.6 kHz, with a sampling frequency of 48 kHz and data digitised using a 16-bit resolution) distributed across the 1.6 km reef at depths between 5 and 8 m, and suspended 0.7 m above the reef on a sub-surface buoy. Recordings were made within an hour of sunrise because this time is often the most bio-acoustically active period of the day (Bohnenstiehl et al., 2016; Radford et al., 2011), a phenomenon that has been locally observed (unpublished data from the sites surveyed by Williams et al., 2021). The recorded reef soundscape is dominated by high-density, broadband snapping shrimp snaps (Appendix S1, Figure S1) that characterise temperate reef soundscapes world-wide (Lillis et al., 2014; Nolan & Salmon, 1970). For the sound treatment, speakers played a looped 1-min recording composed of snippets recorded by each of the four hydrophones. Our low-cost, self-constructed speakers were shown to not replicate the recorded soundscape perfectly (Appendix S1, Figure S1). Nevertheless, these speakers (1) enriched soundscapes relative to ambient controls (i.e. increased the root-mean-square sound pressure level [SPL_{rms}] and snaps per minute, discussed below), (2) broadcast a clean snapping shrimp soundscape to the human ear (on land and in water) and (3) demonstrably influenced larval oyster swimming and settlement behaviour in the laboratory (Williams et al., 2022).

Each speaker was positioned 2 m from a boulder reef where they were secured 40 cm above the seafloor on a metal fencing post secured in the ground. Control treatments were established between 50 and 60 m from each speaker dependent on the distance between the constructed reefs, and were created using dummy speakers (sand-filled speaker units) similarly secured next to a reef. Prior to commencing the experiment, the volume of the speakers was parametrised at each site to enrich the SPL_{rms} up to 10 m from the speaker. To quantify this, hydrophones were positioned at distances of 1, 10 and 20 m from each speaker to record soundscapes before and after speakers were turned on (n = 4 recordings at each of the four sites). Speakers increased the SPL_{rms} at 10 m distance by an average 4.5 and 3.2 dB re 1 μPa at Glenelg and Windara Reef, respectively, but did not influence the SPL_{rms} at 20 m relative to the ambient soundscape (Appendix S1, Figure S2). This indicates that the omni-directional speakers enriched a circular area at least 20 m in diameter but no more than 40 m, ensuring no sound crossed-over between or within the speaker and control treatments. At each restoration, soundscapes were simultaneously recorded at each speaker and control site by hydrophones positioned 1 m from each speaker or dummy control, with speakers turned off and on to measure enrichment. Recordings were made for an hour after sunrise at each restoration site, with the two restorations recorded 2 days apart due to the limited number of hydrophones. After recordings were processed (methods in Appendix S1), two sample t-tests were used to determine whether speakers significantly enriched soundscape's SPL_{rms} and snaps per minute relative to the ambient soundscape.

2.3 | Experimental set-up

To test the impact of soundscape enrichment on oyster settlement and habitat formation, we assessed oyster recruitment to settlement panels and oyster habitat formation on limestone boulders in the presence and absence of speaker playback. At each site, six plastic crates (40 × 40 × 40 cm) were positioned 2 m apart and 2 m from a speaker (or dummy control) such that they encircled the speaker. These crates provided attachment points for vertical settlement panels and to house limestone boulders. To assess oyster recruitment in space and time, we deployed standardised settlement panels (15 × 15 cm fibreboard) at each site for 1 month to avoid over-saturation by recruits (observed during longer deployments), and repeated these deployments three times throughout the recruitment season (November, January and March; McAfee & Connell, 2020). For each time period, divers attached two vertical settlement panels to the outside of each crate, securing them 30 cm above the seafloor using cable ties. After 1 month, settlement panels were removed, and the number of recruited oysters counted from the central 7 × 7 cm area (an area shown to be representative of the entire panel) of the outer surface of the settlement panel under dissection microscope. The number of larvae per tile was calculated per m^2 and averaged between the two tiles per crate to provide n = 6 replicate crates per treatment, per site, for each time. At Windara Reef, storms prevented the exchange of speakers to maintain our sound treatments through March, and therefore these data were excluded from the analysis.

To assess how soundscape enrichment influences habitat formation on new boulder reefs, we quantified attributes of the habitat formed by oysters on boulders 5 months after the construction of Glenelg Reef. This component was only run at Glenelg Reef because (1) the rig provided continuous speaker playback (which was not feasible at Windara Reef for 5 months), and because (2) Glenelg Reef was constructed just prior to our experiment beginning (December 2020). Within a week of reef construction, we placed eight boulders (diameter: 15–30 cm) inside each of the n = 6 crates per site to form independent replicate reefs that reached 30 cm above the seafloor (although we did not run this experimental component at Windara Reef, we similarly placed clean boulders in the crates at Windara Reef to ensure comparable conditions for the settlement panels among restoration sites). At the end of the recruitment season (early May 2021), after 5 months of continual exposure to either speaker or nonspeaker control treatments, the top three boulders were removed per crate for analysis in the laboratory. The recruitment of oysters over the 5 month period saturated the exposed boulder surfaces (38,222 ± 2380 recruits m^{-2}; mean ± 1 SE oyster density from subsamples of 10 boulders across treatments; see Appendix S1), such that counts of total oyster density were not informative. Instead, on the exposed upper surface of each boulder, we measured the (1) percentage cover of oyster habitat on each boulder, (2) the number of oysters that were >25 mm in height (the largest size class: Appendix S1; Figure S3) as an indication of the earliest recruits to reef boulders and (3) the percentage of early three-dimensional habitat growth (hereafter 'habitat building') that was >5 mm above the boulder surface (a height above which no solitary oyster grew, but represented habitat formed by the converging growth of multiple oysters). Boulder surface area and percentage cover was measured in ImageJ (Schneider et al., 2012) from photos taken in the plane of boulder's upper surface. Three-dimensional habitat over >5 mm was manually measured (using a measuring probe) and marked on the boulder surface, after which the percentage cover was measured from photos in ImageJ. Data were averaged across the three boulders per crate ($n = 6$ per treatment, per site).

2.4 | Biological data analysis

To assess whether oyster recruitment to the settlement panels was boosted by soundscape enrichment, we ran separate three-way ANOVAs for Windara Reef and Glenelg Reef with the factors Sound (two levels: speaker vs. control), Time (two levels at Windara Reef; three levels at Glenelg Reef) and site (two levels). To assess differences in the percentage of oyster habitat cover, the density of large oysters (>25 mm) and habitat building (three-dimensional growth) on reef boulders, we ran two-way ANOVAs between the factors Sound (two levels) and site (two levels). All analyses were run using the raw data that satisfied the assumptions of normality and homoscedasticity (assessed using Levene's test). Significant differences were assessed using Tukey's HSD post-hoc tests to identify the source of variation. Finally, the relationship between the number of large oysters and three-dimensional habitat building was assessed using linear regression on all the individual boulders across sites (i.e. each of the three boulders per replicate).

3 | RESULTS

3.1 | Soundscape enrichment

Spectrograms of the enriched and ambient soundscapes demonstrate that the speakers visibly enhanced the spectral characteristics of the soundscape (Figure 2). When speakers were turned off, speaker and control sites were visibly homogenous with only minimal variation in SPL_{rms} (Figure 2). By contrast, when speakers were turned on, they significantly enriched the localised soundscape's SPL_{rms} by 8.9 dB re 1 μPa (two-sample t-test: $t[6] = 45.13$, $p = 0.001$) at Glenelg Reef, and by 4.2 dB re 1 μPa ($t[6] = 4.69$, $p = 0.018$) at Windara Reef (Figure 2). Similarly, snapping shrimp snap counts significantly increased from (mean ± 1 SD) 112 (±9) to 547 (±82) per minute when speakers were turned on at Glenelg Reef ($t[6] = 9.87$, $p = 0.002$), and from 369 (±42) to 763 (±32) per minute when speakers were turned on at Windara Reef ($t[6] = 14.91$, $p = 0.001$).

3.2 | Oyster recruitment in space and time

Across all sites and times, soundscape enrichment increased the recruitment of oyster larvae to settlement panels by, on average, 4.4 ± 1.6 times (mean ± 1 SE) compared to control treatments, and by as much as 18.1 times (at Glenelg Reef in March; Figure 3). Oyster recruitment was generally very high across sites and times, with an average 3425 ± 378 and 7882 ± 918 oysters m^{-2} observed on settlement panels from the control and speaker treatments respectively. At both restoration sites, the effect of speakers on oyster recruitment varied as a function of time and site (significant Sound × Time × Site interaction at Windara Reef [$F_{1,47} = 6.30$, $p = 0.016$] and Glenelg Reef [$F_{2,71} = 3.17$, $p = 0.049$]; Appendix S1). At Windara Reef, soundscape enrichment significantly increased recruitment at three of the four sites (across times) by an average 2.8 ± 0.6 times, an increase of 3985 ± 1028 oysters m^{-2} per settlement panel. And at Glenelg Reef, recruitment was significantly increased at five of the six sites by 6.6 ± 3.0 times, equating to an increase of 6228 ± 981 oysters m^{-2} per settlement panel (Figure 3).

3.3 | Oyster habitat formation

Oyster habitat cover was generally high on the reef boulders across sites, covering (mean ± 1 SE) 69.4% ± 6.0 and 80.1% ± 4.1 of the upper surfaces of boulders in the control and sound treatments respectively. Two-way ANOVA did not detect any significant interaction (Sound × Site: $F_{1,23} = 2.04$, $p = 0.169$) or main effect of sound ($F_{1,23} = 2.76$, $p = 0.112$) on habitat cover between control and sound treatments (Figure 4). The influence of soundscape enrichment on the largest size class (Appendix S1; Figure S3) of oysters was not dependent on site (Sound × Site: $F_{1,23} = 0.30$, $p = 0.590$), but rather, a significant influence was detected for the main effect of soundscape enrichment (Sound: $F_{1,23} = 17.82$, $p < 0.001$). Soundscape enrichment significantly increased the number of large oysters (>25 mm) by, on average, 2.4 ± 0.3 times (and up to 4.2 times) compared to control treatments (Figure 4), with a maximum of 352 large oysters m^{-2} in sound treatments compared to 175 m^{-2} among controls. Similarly, the impact of soundscape enrichment on three-dimensional habitat building was not dependent on site (Sound × Site: $F_{1,23} = 2.5$, $p = 0.129$), but on the main effect of sound (Sound: $F_{1,23} = 42.1$, $p < 0.001$) that significantly increased habitat

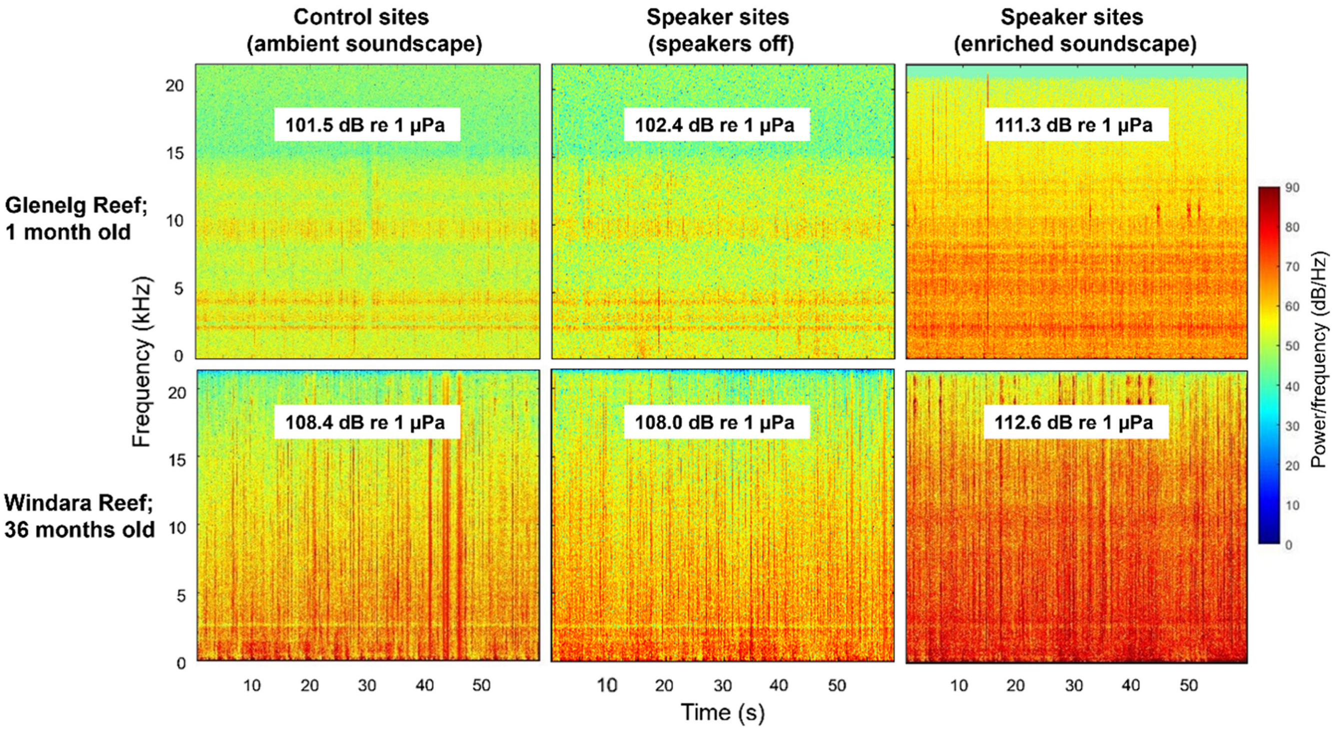

FIGURE 2 Spectrograms recorded at control sites (ambient soundscapes) and the speaker sites before and after the speakers were turned on. Within sites, control and speaker sites were recorded simultaneously within an hour of sunrise. Root-mean-square sound pressure levels are provided for each habitat recording.

building by 4.3 ± 1.2 times relative to controls (Figure 5). In the presence of sound, oysters formed three-dimensional habitat on 70% of boulders that reached up to 20 mm (mean: 10.6 ± 0.7 mm) above the boulder surface, as opposed to control treatments where just 10% of boulders exhibited three-dimensional growth up to 9 mm high (mean: 7 ± 0.5 mm). Linear regression showed that as the number of large oysters m^{-2} increased, so did the amount of three-dimensional habitat building ($F_{1,64} = 13.13$, $p = 0.001$), with the abundance of large oysters explaining $r^2 = 17.3\%$ of the variation in habitat building (Figure 5). Other than oysters, the only commonly observed animal on boulders were Serpulidae tube worms (primarily *Pomatoceros taeniata* and *Salmacina australis*) that typically provided <1% of habitat, and occasional Bryozoa (*Hornera foliacea*).

4 | DISCUSSION

Ensuring sufficient natural recruitment by the organisms targeted to seed ecological recovery is among the most important components of successful restorations (Vanderklift et al., 2020). And ensuring that this recruitment occurs rapidly may be particularly important where restoration efforts introduce hard substratum into the marine environment, which provides competitor-free substratum that opportunistic species can rapidly colonise and dominate (e.g. turf algae, Connell et al., 2014; Filbee-Dexter & Wernberg, 2018). Indeed, at one of the two restoration sites in this study, we previously witnessed turf algae monopolise restoration reefs within weeks of their construction, carpeting the reef boulders to the exclusion of recruiting oyster larvae (McAfee et al., 2021). Therefore, strategies that maximise the ability of the target organism to locate and settle at new restoration sites may be crucial to steer the ecological trajectory towards the desired habitat.

Our results suggest that the enrichment of natural soundscapes using underwater speakers may provide an efficient solution for boosting early recruitment and habitat building by oysters. At 80% of our study sites, soundscape enrichment significantly increased oyster recruitment by as much as 18.1 times (and on average, by 5.1 ± 1.9 times; mean ± 1 SE). This rapid recruitment in the presence of enriched soundscapes resulted in significantly greater densities of the largest size class of oysters; the first cohort to recruit to the newly constructed reefs. Recruitment was generally very high throughout the experiment, and it was therefore little surprise that oyster habitat cover did not significantly differ between sound and control treatments after 5 months. However, importantly, the presence of more large oysters in the sound treatments resulted in more of the three-dimensional habitat building that is a key outcome of oyster reef restoration (i.e. to facilitate associated communities via habitat provision and stress amelioration; Grabowski, 2004; McAfee et al., 2018). And notably, despite the arrival of turf algae within 4–8 weeks of reef construction, the early recruitment of oysters allowed them to form primary habitat irrespective of the presence of turf algae.

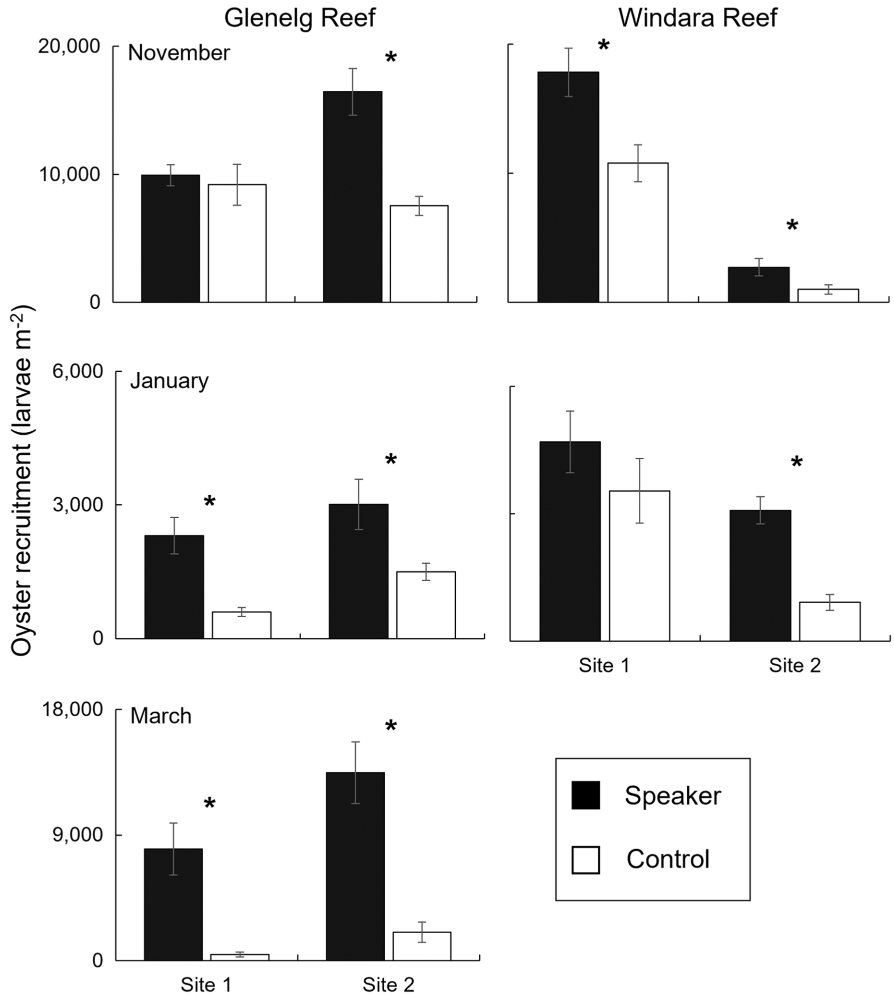

FIGURE 3 Oyster recruitment (mean ± 1 SE) to settlement panels positioned across two large reef restorations in the presence (black) and absence (white) of speakers playing healthy reef soundscapes. Settlement panels were exposed to treatments in the field for 1 month ($n = 6$). Significant differences ($p < 0.05$) between treatments are marked with an asterisk.

4.1 | Implications for restoration practice

Healthy reef communities are maintained by the continual recruitment of numerous organisms that use various environmental cues (e.g. sound, sight, smell) to orient and recruit to suitable habitat (Kingsford et al., 2002). Given the diversity of organisms that use sound and the large spatial scales at which soundscapes can influence recruitment (Lillis et al., 2013; Simpson et al., 2005; Stanley et al., 2012; Vermeij et al., 2010), the recovery of functional soundscapes might be considered an important goal of restoration efforts. Several studies have shown that habitat restorations can restore soundscapes indicative of repaired habitat quality and function (e.g. restored oyster reefs, coral reefs, sponge habitat; Butler et al., 2022; Lamont et al., 2022; Lillis et al., 2014). However, new restorations typically occur where soundscapes are degraded, which can limit recruitment during the crucial early successional stages that inform community development. Planning to deploy substrate to coincide with known peaks in recruitment may provide a partial solution (Lipcius et al., 2021; McAfee & Connell, 2020), but this still relies on the relative chance encounter of sufficient larvae finding the new habitat, as opposed to their interaction with navigational cues (e.g. Williams et al., 2022). Building on previous observations that speakers can enhance the recruitment of diverse animal groups (reviewed by Williams et al., 2021), our results show that speakers can overcome the functional absence of natural soundscapes to help steer the initial weeks and months of rapid ecological succession on a trajectory towards the target habitat.

The greatest benefit of speakers will likely occur at the restoration's commencement, particularly where hard substratum is added to the marine environment. As mentioned, turf algae (hereafter 'turfs') previously monopolised boulder reefs within weeks of construction at one of our study sites (Windara Reef, 2017–2018), largely excluding oysters from settling atop the reefs (McAfee et al., 2021). Turf-dominated habitats are a global phenomenon that thrive on modified coastlines where structurally complex habitats have been degraded (e.g. kelp forests; Filbee-Dexter & Wernberg, 2018). This sees turfs forming primary habitat on hard-bottom surfaces that inhibit other organisms from accessing the hard substratum (Airoldi, 1998; Gorman & Connell, 2009). During this study, we similarly witnessed turf covering the new boulder reefs within 4–8 weeks of construction (Glenelg Reef), a time also characterised by high oyster recruitment (November 2020, Figure 3). While the turf appeared to monopolise the reef surface after 2 months, the rapid larval recruitment allowed oysters to settle prior to turfs establishing, after which the oysters formed encrusting habitat atop the reef boulders that eventually out-competed the thickening turf as primary habitat after 5 months.

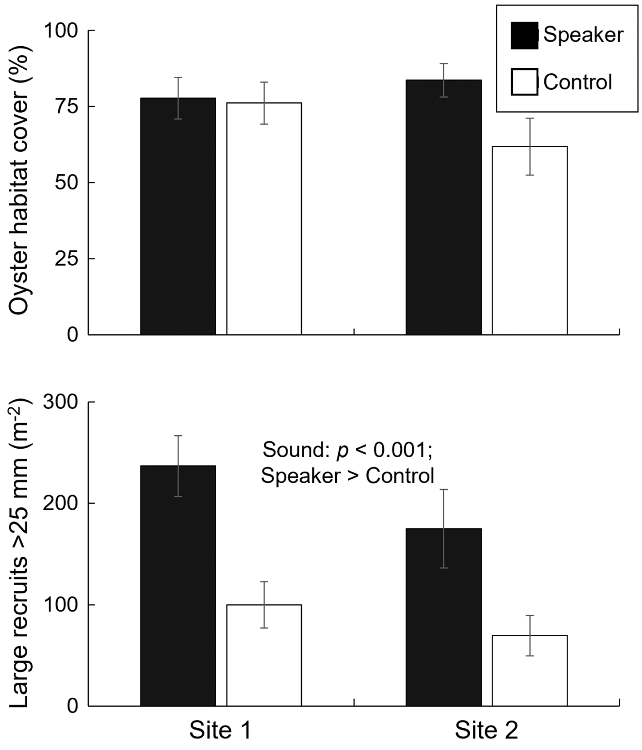

FIGURE 4 Oyster habitat cover (top; mean ± 1 SE) and the abundance of the largest size class of oyster (bottom) on the upper surface of reef boulders after 5 months in the presence (black) or absence (white) of soundscape enrichment ($n = 6$).

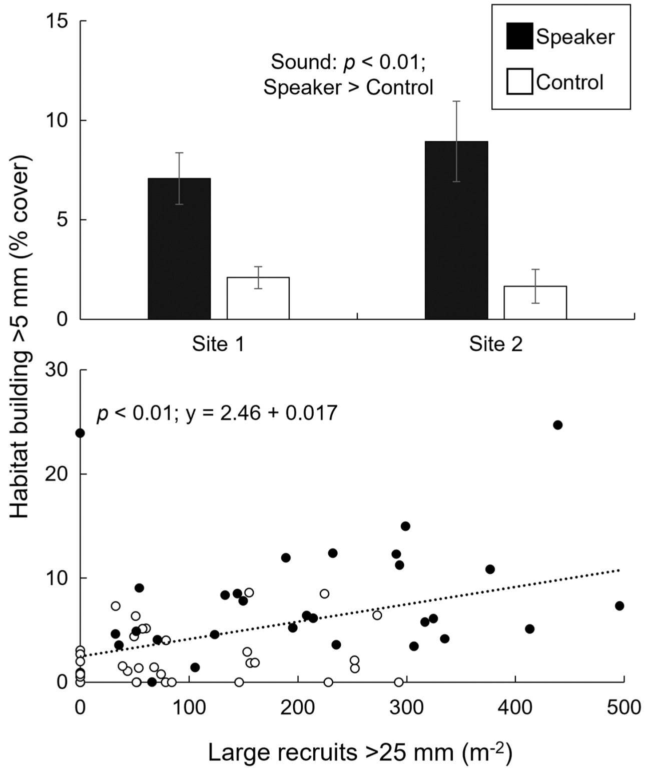

FIGURE 5 Three-dimensional habitat building (top; mean ± 1 SE) from the growth of converging oysters atop reef boulders ($n = 6$), and the relationship between the density of the largest oyster recruits and habitat building (bottom; across all boulders) in the presence (black bars and dots) and absence (white bars and dots) of soundscape enrichment.

The high oyster habitat cover was observed in both speaker and control treatments (Figure 4), likely due to the high natural recruitment in space and time (Figure 3). At locations where recruitment saturates the benthos, the benefits of speakers may be minimal or short-lived relative to recruitment-limited systems. For example, Lillis et al. (2015) found that soundscape enrichment increased early oyster settlement rates when recruitment was limited, but these benefits were overwhelmed as recruitment peaked. Similarly, our speakers enhanced the first cohort of recruits, but no different was detected in habitat cover after 5 months. Although the enhanced early recruitment resulted in more large oysters that formed more three-dimensional habitat, how long this enhanced habitat growth will persist remains uncertain. Such knowledge would be worth investigating across gradients in natural recruitment to identify the conditions under which speakers provide the greatest benefit to restorations. Certainly, the natural recovery of the restored soundscape will also determine how long speakers will benefit restoration efforts, and ambient soundscapes should therefore be monitored to identify when speaker enrichment becomes negligible.

4.2 | Considerations and future questions

While we demonstrated positive restoration outcomes from soundscape enrichment, restoration practitioners must consider the potential for negative impacts from speaker enrichment. For example, numerous organisms are attracted by soundscapes, such that speakers may also attract predators (e.g. fish) or invasive competitors (e.g. spatially dominant species) of the target species. In such circumstances, speaker sites could act as recruitment sinks that may denude other sites of the target species (a minor consideration in this study given there was no suitable neighbouring habitat for recruitment). Our ability to confine the experimental area impacted by our speakers (~10 m radius) would reduce such risks, but speakers used to fast-track restorations at the hectare-scale could enrich soundscapes over large areas (Lillis et al., 2014). Consequently, it is important to understand the diversity of organisms that respond to enriched soundscapes, and the variety of ways sound enrichment may impact trophic and ecological interactions on reef restorations. Our observation of recruited sessile organisms did not account for responding mobile species, and future studies that incorporate in situ observations of mobile species (e.g. underwater video, field surveys) are important to understand community-level responds and postsettlement processes.

Dispersing organisms in search of suitable habitat likely use a diversity of navigational cues that may vary in importance over space and time (Kingsford et al., 2002). For example, the importance of olfactory cues for navigation depends on the speed, direction and behaviour of the currents that carry those cues (Leis et al., 2011). Similarly, the influence of acoustic cues, which disperse independent of currents, can be affected by current activity and proximity to shore (Suca et al., 2020). Therefore, to make informed decisions on the value of manipulating environmental cues to enhance restorations, practitioners would benefit from studies that compare the effectiveness of various cues. For example, mixing crushed shell into sediment can enhance olfactory cues that boost bivalve recruitment (Green et al., 2013), and the physical structure of certain substrates can stimulate species-specific recruitment (e.g. mussels attaching to ropes; Temmink et al., 2021). Combining the investigation of diverse cues may reveal which cues complement or supersede the utility of soundscape enrichment, such that practitioners can prioritise the most effective recruitment cues.

5 | CONCLUSIONS

There is increasing hope that habitat restoration can reverse ecological damage and help humanity achieve its sustainability goals (e.g. United Nation's SDG 14). For marine restoration to fulfil this role, solutions are required to ensure restoration practices are efficient and require limited ongoing intervention. Utilising the diversity of environmental cues that marine organisms use to select suitable settlement sites (Kingsford et al., 2002) may enhance restoration efforts, among which marine soundscapes have largely been overlooked as a functional component of recruitment and reef maintenance (e.g. Gordon et al., 2019). Acoustic technology is becoming increasingly affordable and is likely to be significantly cheaper than the high cost of ongoing manual intervention. Our results add to the growing literature that shows the application of speakers can boost recruitment processes and extends this knowledge by demonstrating benefits to fast-tracked habitat formation. A notable observation of this work was the capacity for oysters to outcompete the turf algae, which rapidly smothered the reef within weeks of its construction but was replaced as the primary habitat by oysters over the ensuing months. This suggests that restoration efforts that use soundscape enrichment should prioritise its use at the beginning of projects to help steer the early ecological succession on a trajectory of desired habitat recovery.

AUTHOR CONTRIBUTIONS

Dominic McAfee and Sean D. Connell conceived the experiment and methodology; Lachlan McLeod, Brittany R. Williams, Andreas Reuter and Zak Wheaton conducted the fieldwork and collected the data; Dominic McAfee, Brittany R. Williams, Lachlan McLeod, Andreas Reuter and Zak Wheaton analysed the data; Dominic McAfee led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data for this publication are available through Dryad Digital Repository: https://doi.org/10.5061/dryad.xsj3tx9k0 (McAfee, Williams, et al., 2022).

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REFERENCES

Airoldi, L. (1998). Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology*, *79*(8), 2759–2770.

Alleway, H. K., & Connell, S. D. (2015). Loss of an ecological baseline through the eradication of oyster reefs from coastal ecosystems and human memory. *Conservation Biology*, *29*(3), 795–804.

Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., Defeo, O., Edgar, G. J., Hancock, B., Kay, M. C., Lenihan, H. S., Luckenbach, M. W., Toropova, C. L., Zhang, G., & Guo, X. (2011). Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience*, *61*(2), 107–116.

Bohnenstiehl, D. R., Lillis, A., & Eggleston, D. B. (2016). The curious acoustic behavior of estuarine snapping shrimp: Temporal patterns of snapping shrimp sound in sub-tidal oyster reef habitat. *PLoS ONE*, *11*(1), e0143691.

Butler, J., Stanley, J. A., & Butler, M. J. (2016). Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. *Journal of Experimental Marine Biology and Ecology*, *479*, 89–96.

Butler, J., Anderson, E., & Butler, M. J. (2022). Habitat restoration restores underwater soundscapes and larval recruitment. *Frontiers in Ecology and Evolution*, *10*.

Connell, S. D., Foster, M. S., & Airoldi, L. (2014). What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series*, *495*, 299–307.

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., Erbe, C., Gordon, T. A. C., Halpern, B. S., Harding, H. R., Havlik, M. N., Meekan, M., Merchant, N. D., Miksis-Olds, J. L., Parsons, M., Predragovic, M., Radford, A. N., Radford, C. A., Simpson, S. D., … Juanes, F. (2021). The soundscape of the Anthropocene ocean. *Science*, *371*(6529).

Filbee-Dexter, K., & Wernberg, T. (2018). Rise of turfs: A new battlefront for globally declining kelp forests. *Bioscience*, *68*, 64–76.

Gomes, D. G., Toth, C. A., Bateman, C. C., Francis, C. D., Kawahara, A. Y., & Barber, J. R. (2021). Experimental river noise alters arthropod abundance. *Oikos*, *130*(11), 2001–2014.

Gordon, T. A., Harding, H. R., Wong, K. E., Merchant, N. D., Meekan, M. G., McCormick, M. I., Radford, A. N., & Simpson, S. D. (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(20), 5193–5198.

Gordon, T. A., Radford, A. N., Davidson, I. K., Barnes, K., McCloskey, K., Nedelec, S. L., Meekan, M. G., McCormick, M. I., & Simpson, S. D. (2019). Acoustic enrichment can enhance fish community development on degraded coral reef habitat. *Nature Communications*, *10*(1), 1–7.

Gorgula, S. K., & Connell, S. D. (2004). Expansive covers of turf-forming algae on human-dominated coast: The relative effects of increasing nutrient and sediment loads. *Marine Biology*, *145*(3), 613–619.

Gorman, D., & Connell, S. D. (2009). Recovering subtidal forests in human-dominated landscapes. *Journal of Applied Ecology*, *46*(6), 1258–1265.
Grabowski, J. H. (2004). Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. *Ecology*, *85*(4), 995–1004.
Green, M. A., Waldbusser, G. G., Hubazc, L., Cathcart, E., & Hall, J. (2013). Carbonate mineral saturation state as the recruitment cue for settling bivalves in marine muds. *Estuaries and Coasts*, *36*(1), 18–27.
Hernández, B. A., Brumbaugh, R. D., Frederick, P., Grizzle, R., Luckenbach, M. W., Peterson, C. H., & Angelini, C. (2018). Restoring the eastern oyster: How much progress has been made in 53 years? *Frontiers in Ecology and the Environment*, *16*(8), 463–471.
Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G., & Pineda, J. (2002). Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, *70*(1), 309–340.
Lamont, T. A., Williams, B., Chapuis, L., et al. (2022). The sound of recovery: Coral reef restoration success is detectable in the soundscape. *Journal of Applied Ecology*, *59*(3), 742–756.
Leis, J. M., Carson-Ewart, B. M., Hay, A. C., & Cato, D. H. (2003). Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some times. *Journal of Fish Biology*, *63*(3), 724–737.
Leis, J. M., Siebeck, U., & Dixson, D. L. (2011). How Nemo finds home: The neuroecology of dispersal and of population connectivity in larvae of marine fishes. *Integrative and Comparative Biology*, *51*(5), 826–843.
Lillis, A., Eggleston, D. B., & Bohnenstiehl, D. W. R. (2013). Oyster larvae settle in response to habitat-associated underwater sounds. *PLoS ONE*, *8*(10), e79337.
Lillis, A., Eggleston, D. B., & Bohnenstiehl, D. W. R. (2014). Estuarine soundscapes: Distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. *Marine Ecology Progress Series*, *505*, 1–17.
Lillis, A., Bohnenstiehl, D. R., & Eggleston, D. B. (2015). Soundscape manipulation enhances larval recruitment of a reef-building mollusk. *PeerJ*, *4*(3), e999.
Lipcius, R. N., Zhang, Y., Zhou, J., Shaw, L. B., & Shi, J. (2021). Modeling oyster reef restoration: Larval supply and reef geometry jointly determine population resilience and performance. *Frontiers in Marine Science*, *1395*.
McAfee, D., & Connell, S. D. (2020). Cuing oyster recruitment with shell and rock: Implications for timing reef restoration. *Restoration Ecology*, *28*(3), 506–511.
McAfee, D., Bishop, M. J., Yu, T. N., & Williams, G. A. (2018). Structural traits dictate abiotic stress amelioration by intertidal oysters. *Functional Ecology*, *32*(12), 2666–2677.
McAfee, D., McLeod, I. M., Boström-Einarsson, L., & Gillies, C. L. (2020). The value and opportunity of restoring Australia's lost rock oyster reefs. *Restoration Ecology*, *28*(2), 304–314.
McAfee, D., Larkin, C., & Connell, S. D. (2021). Multi-species restoration accelerates recovery of extinguished oyster reefs. *Journal of Applied Ecology*, *58*(2), 286–294.
McAfee, D., McLeod, I. M., Alleway, H. K., Bishop, M. J., Branigan, S., Connell, S. D., Connell, S. D., Copeland, C., Crawford, C. M., Diggles, B. K., Fitzsimons, J. A., Gilby, B. L., Hamer, P., Hancock, B., Pearce, R., Russell, K., & Gillies, C. L. (2022). Turning a lost reef ecosystem into a national restoration program. *Conservation Biology*, e13958. https://doi.org/10.1111/cobi.13958
McAfee, D., Williamsn, B., McLeod, L., Reuter, A., Wheaton, Z., & Connell, S. (2022). Data from: Soundscape enrichment enhances recruitment and habitat building on new oyster reef restorations. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.xsj3tx9k0
McComb, K., Reby, D., Baker, L., Moss, C., & Sayialel, S. (2003). Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, *65*(2), 317–329.
Nolan, B. A., & Salmon, M. (1970). The behavior and ecology of snapping shrimp (Crustacea: *Alpheus heterochelis* and *Alpheus normanni*). *Forma et Functio*, *2*, 289–335.
Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L., & Krause, B. L. (2011). What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, *26*, 1213–1232.
Pogoda, B., Brown, J., Hancock, B., Preston, J., Pouvreau, S., Kamermans, P., Sanderson, W., & von Nordheim, H. (2019). The Native Oyster Restoration Alliance (NORA) and the Berlin Oyster Recommendation: Bringing back a key ecosystem engineer by developing and supporting best practice in Europe. *Aquatic Living Resources*, *32*, 13.
Radford, C. A., Tindle, C. T., Montgomery, J. C., & Jeffs, A. G. (2011). Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. *Marine Ecology Progress Series*, *438*, 167–174.
Rossi, T., Connell, S. D., & Nagelkerken, I. (2017). The sounds of silence: Regime shifts impoverish marine soundscapes. *Landscape Ecology*, *32*, 239–248.
Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675.
Simpson, S. D., Meekan, M., Montgomery, J., McCauley, R., & Jeffs, A. (2005). Homeward sound. *Science*, *308*(5719), 221.
Stanley, J. A., Radford, C. A., & Jeffs, A. G. (2012). Location, location, location: Finding a suitable home among the noise. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3622–3631.
Suca, J. J., Lillis, A., Jones, I. T., Kaplan, M. B., Solow, A. R., Earl, A. D., & Mooney, T. A. (2020). Variable and spatially explicit response of fish larvae to the playback of local, continuous reef soundscapes. *Marine Ecology Progress Series*, *653*, 131–151.
Tanner, J. E., Irving, A. D., Fernandes, M., Fotheringham, D., McArdle, A., & Murray-Jones, S. (2014). Seagrass rehabilitation off metropolitan Adelaide: A case study of loss, action, failure, and success. *Ecological Management and Restoration*, *15*, 168–179.
Temmink, R. J., Angelini, C., Fivash, G. S., Swart, L., Nouta, R., Teunis, M., & van der Heide, T. (2021). Life cycle informed restoration: Engineering settlement substrate material characteristics and structural complexity for reef formation. *Journal of Applied Ecology*, *58*(10), 2158–2170.
Vanderklift, M. A., Doropoulos, C., Gorman, D., Leal, I., Minne, A. J. P., Statton, J., Steven, A. D. L., & Wernberg, T. (2020). Using propagules to restore coastal marine ecosystems. *Frontiers in Marine Science*, *7*, 724.
Vermeij, M. J., Marhaver, K. L., Huijbers, C. M., Nagelkerken, I., & Simpson, S. D. (2010). Coral larvae move toward reef sounds. *PLoS ONE*, *5*(5), e10660.
Williams, B. R., McAfee, D., & Connell, S. D. (2021). Repairing recruitment processes with sound technology to accelerate habitat restoration. *Ecological Applications*, *31*(6), e2386.
Williams, B. R., McAfee, D., & Connell, S. D. (2022). Oyster larvae swim along gradients of sound. *Journal of Applied Ecology*, *59*(7), 1815–1824. https://doi.org/10.1111/1365-2664.14188

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