RESEARCH ARTICLE

Oyster larvae swim along gradients of sound

Brittany R. Williams ⓘ | **Dominic McAfee** ⓘ | **Sean D. Connell** ⓘ

Southern Seas Ecology Laboratories,
School of Biological Sciences, The
University of Adelaide, Adelaide, SA,
Australia

Correspondence
Sean D. Connell
Email: sean.connell@adelaide.edu.au

Abstract

1. Marine soundscapes provide navigational information for dispersing organisms, but with wide-scale habitat loss, these soundscapes are becoming muted. Consequently, dispersing larvae that use soundscapes for navigation may be lost at sea, limiting the success of restoration efforts that rely upon the recruitment of dispersing organisms to restore habitat. Where limited larval supply constrains restoration efforts, using speakers to create gradients in healthy soundscapes could provide the navigational cue that attract larvae and enhances recruitment.

2. Combining laboratory and field studies, we test whether broadcasting soundscapes might act as a directional cue for oysters targeted for national-scale reef restoration; the Australian flat oyster *Ostrea angasi*. In the laboratory, we tested whether settlement of larvae increases along a gradient of increasing sound intensity (8 m laboratory tank) versus a no sound control, and whether settlement increases with soundscapes that approximate healthy reefs.

3. In the field, we tested the context dependency and magnitude of using boosted soundscapes for restoration practice in areas of low, medium and high background noise, by observing the settlement rates of naturally recruiting oysters at three restoration sites when exposed to boosted reef sound relative to ambient conditions.

4. In the laboratory, we showed that 83% of larvae swim horizontally towards reef sound to settle in greater densities closer to its source, a near doubling of the larvae (44%) that dispersed in the no sound controls. Larval settlement increased by 300% in the presence of reef sound relative to controls in the laboratory. In the field, speakers increased larval settlement in localities of lower background noise. To our knowledge, this is the first evidence that oyster larvae can swim horizontally and choose to move towards a sound source.

5. *Synthesis and applications*. We discovered that oyster larvae can swim horizontally towards reef sound and then settle in higher densities, relative to controls. Importantly, this effect of sound on recruitment is enhanced in localities of lower background noise. We propose that where recruitment is limited, restoration practitioners best use acoustic technology in localities of lower background noise to guide larvae to boost recovery.

1 | INTRODUCTION

Dispersing animals orientate, navigate and then settle into suitable adult habitat using a combination of visual (McFarland, 1986), olfactory (Svane & Young, 1989) and acoustic cues across multiple scales (Kingsford et al., 2002). Without such cues, their navigational capacity is compromised and they are more likely to be lost at sea (Rossi, Connell, et al., 2016; Rossi, Nagelkerken, et al., 2016; Rossi et al., 2017). Sound is a vital source of navigational information for dispersing marine organisms and is comprised of ambient, geo-physical, biological and anthropogenic sounds called 'soundscapes' (Pijanowski et al., 2011). These soundscapes confer information to dispersers about habitat-type and the presence of conspecifics (Gordon et al., 2018).

With global habitat degradation and environmental change, sensory cues such as those provided by soundscapes are diminishing (Duarte et al., 2021; Rossi et al., 2017). These 'muted-scapes' carry less navigational information to dispersing organisms (Williams et al., 2021) in search for adult habitat. Hence, coastal restoration efforts that seek to restore habitat-forming species and their ecosystem functions, which in turn revive these sound-scapes (Lamont et al., 2021), may have low capacity for restoration where recruitment is limited. The most soniferous producers of biological noise in marine habitats are snapping shrimp (Johnson et al., 1947). The production and collapse of a cavitation bubble formed by the snapping shrimp (Versluis et al., 2000) produces a loud 'snap' (up to 210 dB re 1 mPa at point source; Schmitz, 2002), which forms a chorus of crackling sound when shrimp are aggregated (Nolan & Salmon, 1970). These sound-producing species are not only muted by human activity (i.e. shipping, pile-driving, seismic air guns, SONAR; Rossi, Connell, et al., 2016; Rossi, Nagelkerken, et al., 2016), making the habitats they occupy less attractive to navigating larvae (Gordon et al., 2018), but these species and their sounds are largely lost where their habitats have been extinguished (e.g. functionally extinct oyster reefs; Beck et al., 2011).

The restoration of native oyster reefs is a global enterprise (Bagget et al., 2014; McAfee et al., 2020), and in Australia, the revival of the native flat oyster (*Ostrea angasi*) has become a national focus after the discovery of the extent of its functional extinction (Alleway & Connell, 2015). Worldwide, overharvesting of oysters removed their hard-shell substrate from the seafloor (mid-1800s to early 1900s), with disease and declining water quality compounding this loss (Beck et al., 2011; McAfee & Connell, 2021). Natural recovery has been limited by the transition from hard-shell substrate needed for settlement to sedimentary seafloors. Current oyster restoration practice, including those in Australia, involves providing the foundations for recruitment and habitat

building through the construction of boulder reefs (Brumbaugh & Coen, 2009). For these restoration efforts to be repeatedly successful and scalable across the globe, a supply of oyster recruits is required. However, where there is a natural supply of recruits, they are lost at sea and reliance on natural recruitment is risky. Hence, common restoration practice is to seed reefs with hatchery-reared larvae (Brumbaugh & Coen, 2009) which may not be an efficient, cost-effective or scalable approach.

Using sound technology to lead larvae to restoration reefs may represent an alternative, scalable approach that attracts settlers over wide areas in a way that not only boosts recruitment, but can be done cost-effectively. Artificial playback of attractive sound-scapes (i.e. those dominated by snapping shrimp crackle) through underwater speakers may restore lost soundscapes at restoration reefs, helping larvae navigate to their source. Studies show that Eastern oyster larvae *Crassostrea virginica* settle in response to attractive habitat sounds (Lillis et al., 2014; Lillis et al., 2015), and that attraction to sound is well known across other marine and terrestrial animal groups (Williams et al., 2021). We now know oysters can respond and settle in response to attractive sounds by switching behaviour from hovering to sinking through the water column (Finelli & Wethey, 2003; Wheeler et al., 2015), achieving vertical speeds between 0.001 to 9.07 mm/s (Rodriguez-Perez et al., 2020). However, we do not know whether oyster larvae actively swim horizontally towards attractive sounds. Many questions remain surrounding the swimming capabilities of marine invertebrate larvae, however, larvae are likely behaving more actively in the water column as a function of their well-developed sensory capacity (Kingsford et al., 2002; Lillis et al., 2014; Rodriguez-Perez et al., 2020). If larvae are not only capable of choosing to sink, but also of actively swimming horizontally towards sound, then they may have far greater control over their use of sound as a cue to navigate currents. Here, we present laboratory and field data on how a habitat-forming species targeted for restoration in Australia, *Ostrea angasi*, actively responds to gradients in habitat-related sound and how the magnitude of boosted sound affects their natural settlement at restoration sites.

2 | MATERIALS AND METHODS

2.1 | Study system

Experiments were conducted in the University of Adelaide aquarium and at three oyster restoration sites in Gulf St. Vincent, South Australia. No permits or ethics approval were required to carry out this work. Gulf St. Vincent was characterised by reefs formed by *O. angasi* until these reefs were all lost to a 19th century oyster

fishery (Alleway & Connell, 2015), being replaced with sand flats with little of the hard substratum required for oyster settlement (Tanner, 2005). There is now great interest in reviving *O. angasi* reefs, and in 2017 and 2020, two boulder reef restorations were constructed approximately 1 km offshore in 8–10 m of water, Windara Reef (34°30.496′S, 137°53.953′E) and Glenelg Reef (34°58.38′S, 138°29.88′E), respectively. Additionally, in 2018, a reef restoration was constructed in a heavily urbanised estuary of Gulf St. Vincent, Port River (34°50.7′S, 138°29.88′E), in 4–6 m of water. Each of these sites have observed natural *O. angasi* settlement. *Ostrea angasi* is a brooding oyster that releases one to three million veliger larvae (170–189 μm; Crawford, 2016) during months where mean seawater temperatures exceed 17°C (McAfee & Connell, 2020). These larvae spend several days to 2 weeks in the water column, dispersing tens of kilometres (North et al., 2008), after which they can explore the benthos as pediveliger larvae, before permanently attaching to the substrate as 'spat'. Consequently, techniques that encourage the settlement of *O. angasi* at restoration sites are of interest.

In the laboratory, we aimed to determine the influence of marine soundscapes on the horizontal movement and settlement of pediveliger *O. angasi*, by experimentally testing: (a) whether settlement increases in the presence of soundscapes that approximate healthy reefs, and (b) whether distance of movement and ensuing settlement increases along an 8-metre gradient of increasing sound. Using independently replicated laboratory conditions and a field experiment, these experiments compared treatments of sound with controls of no sound.

2.2 | Handling of larvae and sound creation

For our laboratory experiments, hatchery-reared pediveliger oyster larvae, which displayed the swimming behaviour and actively searching foot that allows them to move and settle, were supplied by the South Australian Research and Development Institute and used within 2 days of arrival. Experiments ran throughout August and September 2020, and September 2021, which coincides with the ideal timing for *O. angasi* hatchery production. Larvae were fed a mix of *Isochrysis* sp. and *Chaetoceros calcitrans* algae, and their holding tanks had daily changes of filtered seawater.

To expose oysters to marine soundscapes, we recorded the soundscapes of a healthy reef habitat (Noarlunga Reef) and sedimentary habitats (described below) in Gulf St. Vincent (for details of recording, see Appendix S1: Section S1). We played these soundscapes in the laboratory using underwater speakers (25 W, 4 Ohm, full range resonance speaker, no flat frequency response, secured inside waterproof PVC housing; H × W: 10 × 12 cm) parameterised to replicate in-situ soundscape conditions (see Appendix S1: Section S2). These speakers represent low-cost speakers that researchers and practitioners can self-construct (see AusOcean Laboratories). To ensure playback of each soundscape was representative of the habitat-type, we composed playback files using recordings

from several different times and sites within the same habitat (see Appendix S1: Section S1).

2.3 | Settlement response to soundscapes

To test how different sounds influence settlement rates, we exposed oyster larvae to different soundscapes in the laboratory that we played in 20-litre buckets of seawater. For a 24 hr period, larvae were exposed to sound treatments that were either reef ('Reef') or sedimentary habitat ('Sedimentary') soundscapes (looped 15 min-long recordings), or a no sound control ('Ambient'; see Appendix S1: Section S1). The pediveliger larvae were in peak condition for a period of 10 days, after which their condition declined. Hence, on each of these 10 days, we ran six replicates of the 'Reef' and 'Sedimentary' treatments (*n* = 60 per treatment), and five replicates of the 'Ambient' treatment (total of *n* = 50). Adopting the methods of Lillis et al., 2014, sound treatments were created using a speaker placed inside a 20-litre bucket of seawater (21°C). Within each bucket, we placed a 70 ml specimen jar filled with seawater and containing a settlement tile (2.5 × 2.5 cm sanded PVC square) and approximately 45 pediveliger oyster larvae (3 ml pipette of larvae at 15 oysters/ml). Each bucket was soundproofed with acoustic foam (5 mm thick self-adhesive sound absorbing foam, Jaycar) to avoid sound crossover between buckets, and darkened with cloth (Grunt black builder's film) to maintain the darker conditions that are known to encourage oyster larvae to settle (Ritchie & Menzel, 1969; Shaw et al., 1970). Each bucket was randomly assigned a sound treatment for 24 hr, after which the specimen jars were removed and the number of oysters settled on the substrate counted under a dissecting microscope. Settled larvae were gently agitated using water from a pipette to ensure proper attachment. To ensure there were no experimental artefacts from individual buckets, we repositioned the speakers and randomly alternated sound treatments among buckets for each experimental run. Finally, significant differences among treatment means were assessed using ANOVA and S-N-K post-hoc tests in SPSS statistics.

2.4 | Response of movement and settlement to soundscape gradients

To test larval movement and settlement in response to a gradient of increasing 'Reef' sound, larvae were placed in a choice experiment where they could horizontally swim towards or away from the sound source. We placed larvae in the middle of an 8 m-long tank (800 × 15 cm PVC pipe, sealed at each end and centrally cut along the length of the pipe to create 2 × 8 m long flume tanks), with either a speaker (broadcasting 'Reef' sounds) or a control speaker ('Ambient') placed at one end. The 8-m length was chosen because we could parameterise our speakers to create a sound gradient that dissipated over 4 m, such that from 4–8 m from the

speaker sound was undetectable. This meant that larvae centrally positioned in the 8 m tank would experience increasing reef sound in one direction, or simply background (non-speaker) sound in the other direction. Over 7 days, seven trials of Reef and Ambient ($n = 7$) sound treatments were run whereby oyster larvae were exposed to treatments for 24 hr (using looped 15-min sound recordings). Each day, a speaker was assigned to a sound treatment and placed at one end of the 8 m tank filled with seawater (21°C). Along the length of the tank, removable settlement tiles (5 × 5 cm sanded PVC square) were placed at 25 cm intervals (0–800 cm, where '0 cm' contained the speaker). To ensure any larvae settled on the settlement tiles had swum rather than crawled to the tile, each settlement tile was elevated above the bottom of the tank using a pedestal (5 mm bolt) attached to the tile's underside. To preclude the influence of currents on the swimming behaviour of larvae, we prior confirmed a lack of current by observing food dye movement within each tank. As in the first experiment, tanks were soundproofed using acoustic foam and darkened to encourage settlement.

To begin, we gently pipetted 200 ml (~15 oysters/ml) of pediveliger larvae onto the surface water at the centre of the tank (4 m mark from the speaker, the 'entry' point). After 24 hr, settlement tiles were removed and the number of settled oysters counted on the top and bottom of the tiles following the methods described for the first experiment. For each experimental run, we alternated sound treatments among tanks and switched the direction of the sound source (by repositioning the speaker) to ensure there were no experimental artefacts from individual tanks.

To compare the distribution of settled oysters between the reef sound and control treatments, we performed a two-sample Kolmogorov–Smirnov test (K-S test) that compares whether the empirical distribution of two samples are different. The Friedman test was found to be an unsuitable method for analysing this data as the distribution of settled oysters naturally concentrated around the larval entry point (the middle of the tank), inevitably resulting in a significantly different distribution across length of the tank. To assess the influence of sound on the percentage of larvae dispersing towards the sound source, we used a two-sample t-test to detect significant differences in the number of settled oysters that had dispersed from the entry point towards the speaker (or speaker control). Additionally, as marine larvae likely interpret gradients in the particle motion component of sound (Popper & Hawkins, 2018), we calculated the particle acceleration (dB re 1 μm/s^2) along the length of each tank for each treatment (see Appendix S1: Section S2). We did this following methods in the literature (Lillis et al., 2014; MacGillivray & Racca, 2006) using the sound pressure levels obtained from two calibrated ST202 hydrophones (Ocean Instruments, flat frequency response 0.1–30 kHz, sensitivity −169 dB re 1 V/μPa), and the Euler equation, which states that a gradient in pressure (∇p) across a volume equals the density (ρ_o) of the medium multiplied by the change in particle acceleration $\left(\frac{\partial u}{\partial t} \right)$ (Popper & Hawksins, 2015)

$$- \nabla p = \rho_o \frac{\partial u}{\partial t}.$$

Many organisms, including invertebrates, are expected to sense the particle motion component of sound (Popper et al., 2001) so it must be parameterised in this domain (Nedelec et al., 2017). All tests were run using SPSS.

2.5 | Settlement response to soundscapes in the field

To provide evidence that gradients in healthy reef sound also influence natural oyster recruitment in the field, we conducted a playback experiment where underwater speakers either broadcast reef sound ('Reef') or no sound at all ('Ambient'). In April 2021, during the peak recruitment time for this species, we ran a 1-month experiment across multiple sites of different background noise levels in the Port River, Glenelg Reef and Windara Reef, where an underwater speaker (the same as used in the laboratory, but housed with batteries; H × W: 50 × 12 cm) continuously played the same healthy reef recording used in the laboratory (see Appendix S1: Section S1). Speaker playback was parameterised in the field to confirm that speakers created distinct gradients in reef sound relative to the ambient, background soundscape. To do this, hydrophones were positioned 1 m above the seafloor at 1, 10, 20 and 30 m away from the speaker at each site, recording the soundscapes in the presence ($n = 4$) and absence of speaker playback ($n = 4$; see Appendix S1: Section S3). At the Glenelg and Windara reef sites, speakers created a sound gradient that was detectable up to 10 m from the speaker, after which it diminished to background levels. The intensity of these sound gradients (i.e. the increase in sound pressure above the ambient noise) was greatest at the newly constructed Glenelg Reef ('low background noise') relative to Windara Reef ('medium background noise') as the reef soundscape has partially recovered at the latter (Williams et al., 2021). However, in the Port River ('high background noise'), speakers did not enhance the reef soundscape above the ambient sound due to persistent anthropogenic noise (i.e. this site is located in an urban waterway). Here, we define the term 'background noise' to mean any sound in the soundscape (i.e. anthropogenic, geophysical or biological) that interferes with the playback recording broadcast by our speakers. At each speaker location, a dummy control speaker was placed 50 m away to ensure no sound crossover between treatments, while limiting spatial variability in recruitment. Speakers were secured 0.5 m above the seafloor. Around each speaker, a vertically oriented settlement panel [15 × 15 cm concrete board that larval oysters can settle on (Goelze et al., 2020)] was attached to a plastic stake 0.3 m above the seafloor. Each stake was placed within 2 m of the speaker and at least 1 m apart from one another. Replication differed among the restoration sites as a function of their scale, whereby the smaller the site the more limited the spatial replication to avoid sound cross-over between speakers and controls: i.e. Port River ('high background noise'): $n = 8$ panels over the 0.0025 ha site; Glenelg Reef ('low background noise'): $n = 12$ over 3 ha; Windara Reef ('medium background noise'): $n = 18$ over 20 ha. After 1 month, a time chosen to avoid over-saturation by larvae, the

number of oysters settled on the outer facing side of the panel were enumerated under a dissection microscope. For each site, we calculated the effect size means and standard errors of larval settlement between treatments and of the boosted sound, using the standardised mean difference (Cohen's *d*) and the 'bootstrap' procedure (see Efron & Tibshirani, 1993). All analyses were performed in R (v.4.0.5).

3 | RESULTS

3.1 | Response of settlement to soundscape gradients

Analysis of *O. angasi* settlement across an intensifying sound gradient with proximity to the speaker indicated that larvae can choose to swim towards the source of the sound and settle more in its presence, compared to no sound (Figure 1). The two-sample K-S test indicated that the distribution of settled oysters in the Reef and Ambient treatments significantly differed ($D[231] = 0.475$, $p < 0.001$), with a greater frequency distribution in the presence of Reef sound than the control. Particle acceleration along the length of the tank remained at constant in the Ambient treatment, however in the Reef treatment it gradually dissipated from the speaker to near background levels at the entry point mark (4 m), after which it remained relatively stable (from 4.25–8 m) and reflected that of the Ambient treatment (Figure 1).

Of the settled oyster larvae that had dispersed from the entry point towards the speaker, we observed $82.7 \pm 3.4\%$ (mean ± 1 *SE*) of settled larvae dispersing in the sound treatment, which was significantly greater than the $44.0 \pm 13.9\%$ (± 1 *SE*) observed in the absence of sound (two-sample t-test; $t[7] = 1.89$, $p = 0.015$; Figure 2). This observation indicates that not only do oyster larvae prefer to settle in the presence of sound over no sound, but that they can choose to actively swim towards the source of the sound.

3.2 | Response of settlement to soundscapes

Comparisons of *O. angasi* settlement to different sound treatments indicate that larvae recruit in greater densities to 'Reef' sound compared to those exposed to 'Sedimentary' soundscapes or 'Ambient' controls (Figure 3). 'Reef' playback (mean settlement 1.2 ± 1 *SE*) received four times the number of settling larvae than 'Sedimentary' (mean 0.3 ± 1 *SE*) and 'Ambient' treatments (mean 0.3 ± 1 *SE*), a significant increase of 300% (one-way ANOVA: $F_{2,167} = 12.755$, $p = 0.001$) compared to 'Sedimentary' and 'Ambient' treatments ($p > 0.05$), which were statistically indistinguishable. This indicates that 'Reef' sounds are more attractive to oyster larvae.
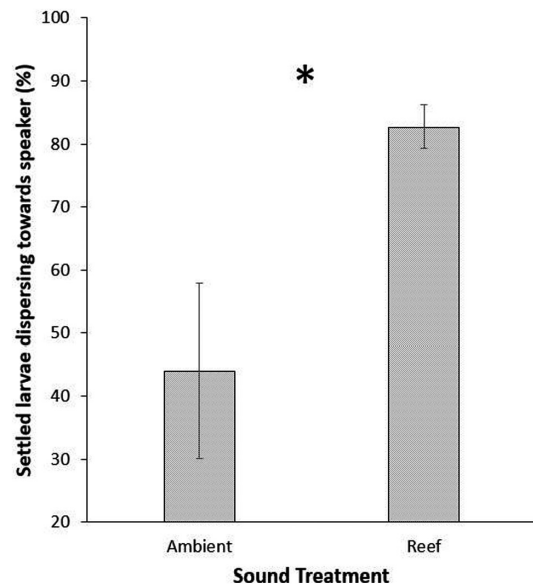
FIGURE 2 The percentage of oyster larvae that dispersed from the entry point (4 m) towards the speaker (Reef) or control speaker (Ambient). '*' denotes a significant difference between treatments ($n = 7$ replicates)
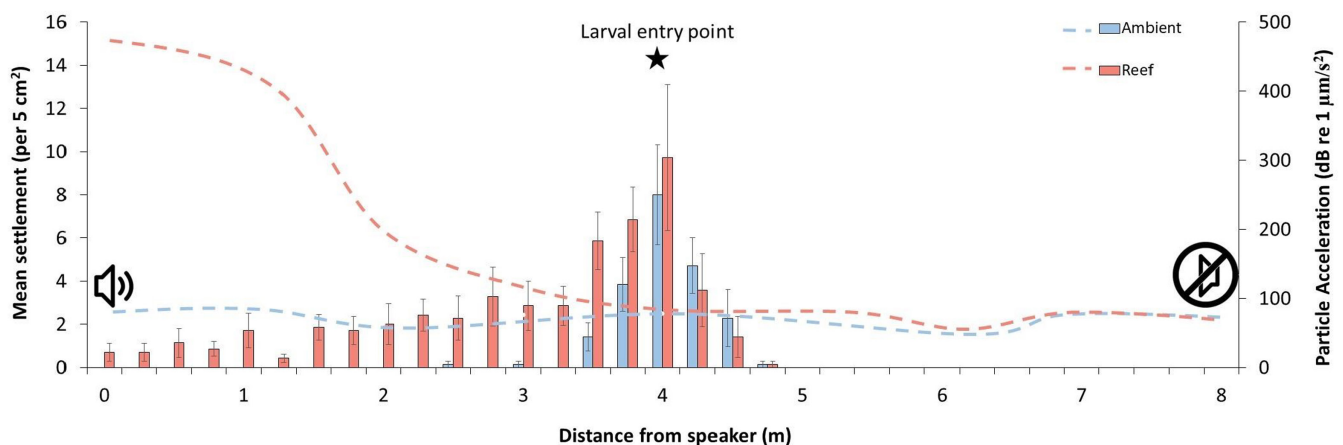
FIGURE 1 Across an 8 m gradient of increasing sound (right to left), oysters settled across the sound gradient in greater densities (Reef, $n = 7$) relative to no sound (Ambient, $n = 7$). In the Ambient treatment, the particle acceleration of sound was consistent across the 8-m length of the tank, whilst in the Reef treatment, there was a gradient in acceleration, with it decreasing from the speaker at '0' metres until the entry point at 4 m, whereby it reached ambient levels
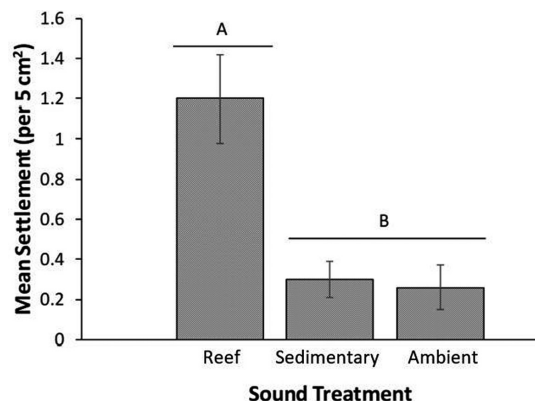
FIGURE 3 Mean larval settlement (± 1 *SE*) with exposure to playback of 'reef' ($n = 60$), 'Sedimentary' ($n = 60$) and 'Ambient' ($n = 50$) sound in the laboratory. Letters and lines above columns denote significant differences between treatments

FIGURE 4 Effect sizes of larval settlement (mean ± 1 *SE*) and boosted sound (mean ± 1 *SE*; log10, obtained from sound pressure level data) between 'Reef' and 'Ambient' sound treatments in the field at 'high background noise' ($n = 8$), 'medium background noise' ($n = 18$) and 'low background noise' ($n = 12$) restorations

3.3 | Response to gradients in soundscapes in the field

Analysis of natural recruitment in the field indicated that larval recruitment increased exponentially where gradients in reef soundscape were most elevated above the background soundscape (Figure 4). At the 'low background noise' site, the effect sizes of each larval settlement ($d = 3.452 \pm 1.89$) and boosted sound ($d = 31.912 \pm 4.73$) were greater than that at the 'medium background noise' site ($d = 0.7 \pm 1.06$ and $d = 2.36 \pm 0.98$, respectively). Whereas the 'high background noise' site had the lowest effect size of settlement ($d = 0.025 \pm 0.49$) and boosted sound ($d = 0.203 \pm 0.05$). This indicates that acoustic enrichment of reef sounds are more attractive to oyster larvae in situations where the sound broadcast boosts the soundscape relative to the ambient conditions.

4 | DISCUSSION

Pioneering research into larval dispersal initially recognised ocean currents as 'highways' (sensu Garth, 1966) to convey larvae to adult habitat. Today, we recognise this larval transport to be far more than passive conveyance, as assumed until the 1990s (Leis, 2015). Larvae that regulate their movement vertically and horizontally over fine scales can interact with large- and small-scale currents in the pursuit of adult habitat (Pearce & Phillips, 1988). As sound travels over distances [e.g. reef-related sounds of snapping shrimp (Butler et al., 2017)], it might signal to larvae that they are in the presence of conspecifics, prompting them to simultaneously navigate currents and sound gradients. Such considerations might help our thinking about the dynamics of recruitment. For example, early attention to recruitment dynamics was prompted by the mere consideration of the potential consequences of variable larval supply (Underwood & Denley, 1984), and later, the reconsideration of the distances at which they disperse (Jones et al., 1999).
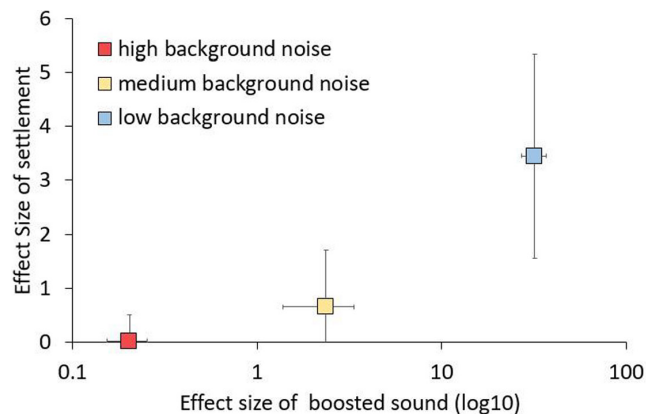
4.1 | To swim or not to swim?

We found that *O. angasi* larvae alter their behaviour to actively swim horizontally towards the source of habitat-related sounds, from at least 4 m away, and move downwards to settle onto substratum in greater densities where the sound is more closely associated to reef-related sounds. This ability allows them to recruit in greater numbers in the field. That oyster larvae can detect and settle preferentially in the presence of sound has been shown previously (Lillis et al., 2014), but to our knowledge, this is the first evidence that oyster larvae can swim horizontally and choose to move towards a sound source.

Until now, oyster larvae were only known to actively sink or swim downwards in response to sound (Wheeler et al., 2015). These earlier findings of vertical control were important, because they suggested that settlement was more nuanced than the widespread view that larvae had little control over settlement and were instead governed by large-scale physical processes such as ocean currents (Leis, 2015; Marliave, 1986). Our finding builds on this recognition of fine scale capacity for control, which in combination with ocean currents, suggests that larvae have the capacity to influence their dispersal more than current thinking allows.

4.2 | Mechanisms

The specific mechanism by which oyster larvae detect sound is still unknown, yet the literature points to invertebrates detecting the particle motion component of underwater sound (Budelmann, 1989; Budelmann, 1992; Nedelec et al., 2017). Where marine mammals have ear structures to detect sound pressure (Popper & Fay, 1993), marine invertebrates and fish tend to detect the particle motion component of underwater sound (Budelmann, 1992; Popper & Fay, 1993) with sensory structures that can detect particle vibration. For example, epidermal cells covered in cilia, or statocyst

structures that work similar to accelerometers (Budelmann, 1989; Budelmann, 1992; Popper & Hawkins, 2018). As some crustacea and molluscs use statocysts to detect sound, it is generally believed that oyster larvae would use statocysts too (Fuchs et al., 2013; Lovell et al., 2005). Such receptors enable invertebrates to detect and orientate towards sources of sound which acts as one of the most highly directional cues for marine navigation.

4.3 | Restoration

Our findings suggest there is merit in assessing whether such responses to sound gradients may be harnessed for conservation outcomes. Where larvae recruit in greater densities in the presence of attractive sounds, then sound playback may be used to enrich oyster reef restoration projects (Williams et al., 2021). Our field experiment shows that where speakers can amplify gradients in reef soundscapes above the background noise, these boosted soundscapes can attract more oyster larvae to settle in the proximity to the sound source. This experiment also inferred limitations to the application of this technique; localities of high anthropogenic noise (i.e. elevated background noise) may dampen such gradients. By broadcasting attractive sounds at sites people are trying to restore, we may be able to guide larvae through the 'muted-scapes' that carry little biological information, towards restoration reefs. To achieve human goals of restoring oyster reefs, sound technology may be able to overcome recruitment 'shadows' by signalling the presence of newly constructed or historically degraded reefs. By increasing larval settlement, restorers also have the capacity to reduce the risk of poor settlement during low recruitment periods; spatial and temporal variability of recruitment being notoriously variable in marine systems. Moreover, restoration may be accelerated if sound technology is used in tandem with times of natural peak recruitment and the provision of competitor-free substratum (Lipcius et al., 2021; McAfee et al., 2021). By putting sound back into currents, these gradients of larval transport (sensu Garth, 1966) may become more navigable, such that they represent gradients of sound to aid restoration.

4.4 | Knowledge gaps

Whilst the use of sound technology appears to be a promising tool for conservation technology, there are large knowledge gaps surrounding its application for restoration that need to be resolved. There is value in understanding the specific swimming patterns of larvae in response to sound and the extent to which currents dictate their movement, as these small- and large-scale interactions are likely to indicate the spatial extent from which oysters can be attracted (Rodriguez-Perez et al., 2020). Further field-based experiments are critical to establish whether sound technology is a feasible tool for restoration. It is likely that the technology is translatable to certain habitats in space and time, and of little value in others. For example, other environmental cues [e.g. physiochemical cues (Anderson, 1996; Xiujuan et al., 2008)] may

exert a stronger influence on larvae dispersal than sound, potentially overwhelming the influence of sound under certain circumstances. This may provide some explanation on why only a portion of the oyster larvae in these experiments settled. Additionally, if there are thresholds of sound intensity after which settlement no longer increases, then more mature habitats with soundscapes that breach such thresholds may no longer boost settlement using speaker playback. Sound technology may, therefore, only be useful in the early stages of restoration. Another consideration is that sound will not only attract oysters to a restoration site, but other species too, some undesirable. Fish are attracted to sound (Gordon et al., 2019; Montgomery et al., 2006; Simpson et al., 2004), which could result in sound technology creating recruitment sinks, whereby predators consume new recruits at rates that rival their settlement rates. Finally, marine sound technology is currently expensive. However, relative to hatchery production of oysters, it is inexpensive and may reduce overall restoration costs. In circumstances where soundscape playback enhances recruitment to the point that it saturates the restoration, then seeding would no longer be needed. Furthermore, where there is demand for this technology and with the rapid advancement of technology generally, we anticipate these techniques to become increasingly affordable and accessible (Stuart et al., 2015). If researchers can encourage engineers to develop affordable, restoration-specific technology alongside restorers, then soundscape playback has the potential to be a cost-effective restoration tool. We encourage expansion of this research and co-design with engineers to build confidence in this prospective technological solution.

5 | CONCLUSIONS

We show that oyster larvae can detect habitat-related sounds and navigate them to their source so that settlement increases along horizontal gradients of increasing sound. This observation shows that oysters have greater small-scale control over where they settle than simple use of vertical control, potentially allowing them to interact with larger scale agents of dispersal in the pursuit of adult habitat. As these findings are based on the early use of cost-effective technology, they point to the future potential of developing acoustic tools to guide larvae to restoration sites, something that would be particularly important to restoration success on coasts where recruitment is limited. Indeed, on coasts in which habitats have been eliminated along with their soundscapes, sound technology could provide signals to attract larvae from passing currents. The idea that habitat degradation is global and the resulting 'muted-scapes' have dampened navigational cues for their replenishment, suggests that sound technology could be poised to recreate gradients of sound needed to boost their restoration and recovery.

AUTHORS' CONTRIBUTIONS

B.R.W., D.M. and S.D.C. conceived the ideas and designed methodology; B.R.W. and D.M. collected the data; B.R.W., D.M. and S.D.C.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data are available via the Figshare Digital Repository https://figshare.com/s/b3a744924fa647631748 (Williams et al., 2022).

ORCID
Brittany R. Williams https://orcid.org/0000-0002-3618-2788
Dominic McAfee https://orcid.org/0000-0001-8278-8169
Sean D. Connell https://orcid.org/0000-0002-5350-6852

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