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RESEARCH ARTICLE

Combining ecology and technology to kick-start oyster reef restoration

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Techniques that enhance the recruitment of foundation species to restoration sites can inform the ecological development of the restored habitat. However, techniques are often considered in isolation, potentially overlooking synergies from combining them. Native oyster reefs have been lost worldwide, resulting in restoration efforts in systems that are often recruitment limited, or where recruiting oysters must spatially compete with opportunistic species. Here, we present a field-based study that combines ecological knowledge on positive species interactions with novel acoustic technology, both of which are demonstrated to boost oyster recruitment in isolation, to test whether their interaction synergistically enhances the early larval recruitment that drives oyster reef development. At three sites across a 20 ha oyster reef restoration in southern Australia, we used self-made speakers to broadcast healthy reef soundscapes that attract oysters and combine this with artificial kelp that facilitates oyster recruitment by suppressing competitive species (turfing algae). The combination of acoustic enrichment and artificial kelp increased oyster recruitment to the topside of substrate (326.98% increase), whereas only acoustic enrichment increased recruitment to the underside of substrate (126.95% increase). Our findings suggest that the combination of multiple techniques and their interactive effects might boost the early stages of reef development, providing proof-of-concept that these approaches can help oysters to build and bind reefs (i.e. recruit to the topside and underside, respectively). By combining ecology with technology during the first stages of a developing reef restoration, we show the potential value of these novel approaches to kick-start the recovery of lost oyster reefs.

Key words: acoustic enrichment, artificial kelp, ecology, oyster reef, positive species interactions, recruitment, restoration, technology

Implications for Practice

- Restoring oyster reefs typically involves adding hard substrate to facilitate oyster recruitment. But many restorations occur where recruitment is limited, and where opportunistic species can rapidly monopolize new hard substrate.
- Techniques that can help oysters rapidly settle at new restoration sites, such as acoustic enrichment that attracts oysters or kelp canopies that suppress competitors, may help steer the initial development of restorations. Yet, combining these techniques may benefit early reef development beyond using each technique in isolation.
- By combining acoustic enrichment with artificial kelp mimics, we significantly boosted wild oyster recruitment to new reef restorations.
- Such synergies between techniques may offer a novel approach for informing the early ecological development of reef restorations.

Introduction

Ecosystem restoration is now a global enterprise yielding some notable successes (Saunders et al. 2020). However, there still exists considerable risk of project failure, especially for marine restorations. Current restoration practice in the marine environment largely relies upon natural recruitment processes, yet this can be variable or eroded (Caddy, 1986), limiting the success of restorations in places with an inadequate supply of larval recruits (e.g. shellfish reef restorations). In addition, spatial competition with opportunistic species can limit establishment of the target species. For example, turf-forming algae can rapidly colonize and monopolize hard substrates, forming a competitive barrier to larval recruits such as oysters (McAfee et al. 2021). Algae turfs can homogenize hard benthic habitats by trapping sediments that form a physical barrier to other recruiting organisms (Gorgula & Connell 2004; Gorman et al. 2009). Where these turfs smother the topside of substrates, there is a high risk that reef-building larvae will be unable to recruit in sufficiently high numbers during the early stages of reef restoration. In

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restorations where there are recruitment bottlenecks and competitive barriers to recruits, technology paired with ecological knowledge might offer a solution.

The combination of ecology and technology are emerging as a cultural norm for solution science to redress restoration risks and overcome environmental problems (Rhoten & Parker 2004). For example, drones can see through waves to identify suitable conservation sites (Chirayath & Earle 2016) and we can non-invasively track animal movements (Francisco et al. 2020). Technology is also known to replace lost environmental cues that are needed to guide dispersing animals to suitable habitat (e.g. biogenic soundscapes; Williams et al. 2021). Combining technology and ecological knowledge is still a relatively new idea, but may offer solutions to help protect and repair the environment (Pimm et al. 2015), such as overcoming factors that limit ecosystem establishment.

Acoustic enrichment has the potential to overcome recruitment bottlenecks. Healthy marine habitats have soundscapes filled with biological choruses produced by soniferous organisms (Johnson et al. 1947; Staaterman et al. 2011; Erbe et al. 2017). By contrast, unstructured habitats are often devoid of complex biogenic sounds (Butler et al. 2016; Gordon et al. 2018; Sueur et al. 2019). As a result of habitat degradation and rising anthropogenic noise (i.e. shipping, pile-driving, seismic airguns; Duarte et al. 2021), biological sounds and the navigational information they provide to dispersing animals are disappearing or being masked (Pine et al. 2016). In turn, larvae that use sound to navigate and select settlement habitat may be unable to use sound cues for orientation. But if acoustic technology can provide these navigational cues to places where they are lost, we could potentially steer the early stages of recruitment and reef development (McAfee et al. 2023).

Conspecific and habitat-related sounds are known to be attractants for animals across both terrestrial and marine groups (DeJong et al. 2015; Williams et al. 2021). For example, oyster larvae preferentially settle in the presence of habitat-related reef sounds (Lillis et al. 2014*a*, 2015; McAfee et al. 2023) and are demonstrated to navigate toward these sounds in the laboratory via horizontal swimming behavior (Williams et al. 2022). Marine sound can travel over great distances to convey information to dispersing organisms. This is in contrast to visual cues that operate at small scales (meters to tens of meters; Kingsford et al. 2002; Leis & McCormick 2002) and olfactory cues which rely on water movement to disperse (Atema 1988; Leis & McCormick 2002). Acoustic enrichment shows promise in overcoming limited recruitment for restoration outcomes. However, several knowledge gaps remain surrounding how we can harness underwater speaker technologies for restoration, including the translatability of acoustic enrichment to realistic restoration scenarios, and whether combining this technique with other restoration tools might be effective.

Another technique for managing the early stages of reef restorations, one that could be paired with acoustic enrichment, is facilitating the positive species interactions that support recruitment processes. Positive interactions among foundation species can enhance the stability and emergent function of ecosystems (Loreau et al. 2002; Angelini et al. 2011) and enhance restoration outcomes (Angelini et al. 2015; Derksen-Hooijberg et al. 2017; Gagnon et al. 2020). The co-occurrence of foundation species can also reduce environmental stress and biotic competition (e.g. predation, spatial competition) among species (Bruno et al. 2003) to the benefit of at least one species and the detriment of none (Bulleri et al. 2018). These facilitations are highly diverse, playing key roles in ecological community structure which can maintain conditions that benefit conservation outcomes (Bruno et al. 2003). For example, kelp can facilitate oyster recruitment by reducing competition from turf-forming algae (Shelamoff et al. 2019; McAfee et al. 2021). However, kelp and oysters might be able to overcome these issues together. For example, kelp might facilitate understory recruitment of larval oysters by removing algal turf via frond abrasion (Irving & Connell 2006) or via reduced understory light that inhibits turf growth (Connell 2003), or by providing refuge from predators (Tedford & Castorani 2022). Meanwhile, oysters may provide hard substrata for kelp to grow upon and filter the surrounding seawater. Consequently, prioritizing positive species interactions in restoration efforts, and how they might interact with acoustic enrichment, may help maintain the conditions required to facilitate the recovery of the target ecosystem.

In Australia, restoration of the native flat oyster (*Ostrea angasi*) is underway to revive a functionally extinct ecosystem. These oysters once carpeted the coastline of Australia's Southern Ocean (Alleway & Connell 2015; Gillies et al. 2020), supplying a variety of ecosystem services. However, where these shellfish reefs once thrived, there now exist barren sand flats of little biological complexity (Tanner 2005). Although work to restore Australia's lost shellfish reefs is underway (McAfee et al. 2022), many of these restorations face the major challenge of ensuring sufficient natural recruitment of oysters along coastlines where algal turf can rapidly monopolize newly constructed reef substrata. Following the construction of reef restorations, the early success (the initial weeks and months) of organismal colonization and growth can inform the ecological trajectory of the project. Consequently, techniques for enhancing early recruitment of target organisms may benefit restoration practice.

Here, we present an experimental test at three sites across a 20 ha restoration reef of how acoustic enrichment (using novel speaker technology), and positive species interactions (using artificial kelp that mimics the understory frond abrasion and light reduction of natural kelp), can increase the first stages of recruitment by oysters to newly constructed reef restorations. We assessed the recruitment of oysters among treatments of acoustic enrichment, artificial kelp mimics, and their combination; and how influencing recruitment patterns may contribute to reef-building (i.e. recruitment to the topside of rocky substrate) and reef-binding (i.e. recruitment to the underside of the rocky substrate) within our experimental units.

Methods

Site Description

Our study took place at Windara Reef, a shellfish reef restoration in Gulf St Vincent, South Australia. Windara Reef was constructed in 2017–2018 in 8–10 m of water approximately 1 km offshore of the Yorke Peninsula (34°30.496′S, 137°53.953′E; see map in McAfee et al. 2023). The restoration consists of 159 individual reefs constructed from limestone rocks across 20 ha. Although natural reefs of the native oysters are no longer present, scattered individuals are present and high rates of natural spat recruitment have been observed across Windara Reef during months where mean seawater temperature exceeds 17°C (McAfee & Connell 2020). The native flat oyster is a brooding oyster that can release up to 3 million veliger larvae (170–189 μm; Crawford 2016) which can disperse tens of kilometers riding ocean currents (North et al. 2008). After spending up to two weeks floating in the water column, these larvae explore the seafloor as pediveliger larvae, before permanently attaching to a substrate as spat. Oysters are typically observed to actively recruit to the underside of surfaces (Medcof 1955; Gillespie 2009; Poirier et al. 2019). Techniques that can encourage the recruitment of oyster larvae and help them to establish a foothold on reefs are therefore of interest to restoration efforts.

Experimental Design and Data Collection

In the field, we set out to test the recruitment response of *Ostrea angasi* larvae to acoustic enrichment, positive species interactions, their combination, and how these influence the first stage of reef development. This first recruitment phase can heavily influence reef development as it can determine the primary habitat on the rocky substrate that steers the ecological trajectory (McAfee et al. 2023). Recruitment to the topside of rock substrate facilitates the "reef-building" component where oysters form three-dimensional habitat for colonization by associated species. Meanwhile, the underside facilitates the "reef-binding" component that acts to bind individual reef rocks together. This binding is akin to the crustose coralline algae that is prevalent throughout coral reefs, which glue loose sediments together to build and stabilize reefs (Bosence 1983; Bjork et al. 1995; Payri & Cabioch 2004; Tierney & Johnson 2012).

Our experiment was performed during a 1-month study from February to March 2021. The short duration of this study was intended to capture the first recruitment event to the rocky substrate prior to the emergence of turfing algae that forms over the juvenile oysters, making it unfeasible to identify or count them. In addition, previous acoustic enrichment work shows that longer deployments can obscure treatment effects due to recruits saturating the substrata (Lillis et al. 2015; McAfee et al. 2023). Consequently, this study did not collect data on turfing algae; though its emergence seems inevitable based on prior observations of the hundreds of reefs constructed in this area.

To test the effect of acoustic enrichment and positive species interactions, we used underwater speakers playing healthy reef habitat sounds and artificial kelp mimics, respectively (described below). Artificial kelp was used rather than live kelp transplants because they can effectively mimic the natural functions of live kelp like shading and scouring (Russell 2007; McAfee et al. 2021), and because they avoid denuding local kelp forests for a short-term experiment. We observed the rates of recruitment of oysters to the topside and underside of substrate comprised of limestone rocks when exposed to four treatments; acoustic enrichment ("Sound"), artificial kelp ("Artificial Kelp"), acoustic enrichment combined with artificial kelp ("Sound + Artificial Kelp"), and no acoustic enrichment or artificial kelp ("Control"). These treatments were tested at three sites ("sites 1–3") across Windara Reef, each spaced at least 200 m apart.

Enriching Acoustic Cues

Soundscapes were enriched using underwater speakers playing recordings made from a local healthy reef habitat (Noarlunga Reef, Gulf St Vincent, South Australia). Because we were interested in using sound as a settlement cue, sound recordings were made during the loudest time of day for the primary sound producers, snapping shrimp, which is within 1 hour of sunrise for our local reefs (Rossi et al. 2017; Williams et al. 2021) and across other reef systems (Radford et al. 2010; Lillis et al. 2014*b*; Bohnenstiehl et al. 2016). Hour-long recordings were made during the Austral summer (December) at high tide (4–8 m of water) using four calibrated ST202 hydrophones (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, 48 kHz sampling frequency, data digitized using a 16-bit resolution) suspended 1 m above the seafloor using a subsurface buoy.

To broadcast the reef soundscape, we used underwater speakers (5 × 3 cm vibration loudspeaker [25 W, 4 Ohm, omnidirectional sound, frequency response 0.3–20 kHz; unbranded], an audio amplifier [MAX9744 amplifier; Adafruit], a 64-bit processor [Raspberry Pi 3 Model B+] and four rechargeable batteries [12 V SLA; RS Components Pty Ltd], secured inside waterproof PVC housing; H × W: 10 × 12 cm; Supplement S1). These speakers were designed with our technology collaborators at the Australian Ocean Lab for approximately $400 AUD (for design plans, see Supplement S1). To continuously broadcast the reef soundscape for the 1-month duration of the experiment, we played a 1-minute-long looped sound file of our dawn recordings. Whereas this continuous broadcasting of the dawn soundscape is not representative of real-world conditions, our aim was to enhance larval recruitment through acoustic enrichment, hence we used the most biologically active time of the day which is demonstrated to stimulate the greater rates of larval settlement (Williams et al. 2021). Our speakers boosted the local soundscape relative to controls and was shown to match some of the broadband snaps seen in the original reef soundscape (Supplement S3). We parameterized this sound in the field at one of the three sites (site 1) and compared its spectral characteristics to those of the original reef recording to ensure it provided a sound boosting effect relative to the control treatment and matched the original recording as closely as possible (see below). We used a dummy speaker for the control treatments, and attached a speaker or dummy speaker to an experimental unit (35 cm × 35 cm × 35 cm) which we elevated 0.5 m from the seafloor and attached to a subsurface buoy.

Positive Interactions

To test the effect of positive species interactions, we used artificial kelp that we attached to experimental units

(35 cm × 35 cm × 35 cm black plastic crate; Supplement S1). As mentioned, these units can mimic the understory conditions of live kelp (shading, frond abrasion; Russell 2007) without denuding local kelp stocks. Our kelp mimics were achieved by fitting a galvanized wire mesh lid (30 cm × 30 cm; mesh size 5 cm × 5 cm) to the top of the unit, from which we attached a square of nylon shade cloth (dark green, 70% UV, Colaroo, 30 cm × 30 cm). From this square, we suspended nine strips of shade cloth (15 cm × 5 cm) inside the unit to mimic the substrate scraping of kelp fronds and their understory shading (Supplement S1). As the shade cloth was positively buoyant, a lead weight (0.3 cm diameter) was attached to the end of each strip to ensure contact with the rocks in the presence of water flow, thereby replicating the action of kelp fronds. The resulting experimental units were open on all faces except the top that the shade cloth covered. For the treatments without artificial kelp, experimental units had a galvanized wire mesh lid attached without any shade cloth.

At each of the three sites, we used three replicates per treatment (total of $n = 9$ per treatment), each signified by an experimental unit. Each unit was filled with limestone rocks (ranging from 101 to 175 cm^2 in size) to replicate the structure and hydrodynamics of a mini reef. We placed these rocks upon a galvanized wire mesh (mesh size 5 cm × 5 cm) platform that was secured inside the unit and elevated 12 cm from the seafloor to reduce the risk of sediment burial. At each site, we placed a speaker and dummy speaker on the seafloor, at least 50 m away from one another to avoid sound crossover between treatments, and because we were targeting larvae that likely cannot respond over large distances. We then placed three experimental units of each artificial kelp treatment (artificial kelp or no kelp) in a circle around the speaker or dummy speaker, each 1 m away from one another, and 2 m away from the speaker. At each site, experimental units containing these rocks were left within each treatment for a month. At the conclusion of the trial, the three top rocks in each unit (those exposed to kelp scour) were removed for enumeration in the laboratory.

Data Analysis

To compare the recruitment of larvae between treatments, the number of oysters recruited to the topside and underside of rocks was calculated as the average of the three rocks from each unit, thereby providing a solitary value per experimental unit; that is, nine topside and nine underside values per treatment across the three sites. Using these values, we calculated the average recruitment of larvae per treatment, and their standard errors, for each of the topside and underside of rocks. For each orientation, we initially performed three-way analysis of variances (ANOVAs) to test for the effects of "Sound" and "Artificial Kelp" (fixed factors, orthogonal) and "Site" (random factor). Prior to these tests, the data were square transformed to reduce left skewness, to satisfy assumptions of ANOVA. For greater clarity we also performed site-by-site analyses (Supplement S2). Finally, to assess whether variation in rock size influence patterns of oyster recruitment, we measured the surface areas of each rock by contouring aluminum foil to them, which we flattened and then measured the two-dimensional surface area in "ImageJ" (Schneider et al. 2012). One-way ANOVA using "Surface Area" as the predictor and "Recruitment" as the response variable (topside and underside recruitment of rocks combined) showed there were no significant differences in recruitment based on rock size. We performed all analyses in R (v.4.0.5).

Soundscape Parameterization

To ensure the playback of our experimental recording had greater sound intensity than that of the control treatment and to determine the area that our speakers were enriching, we needed to record its playback and compare it to the ambient soundscape and original healthy reef recording. To do this, we used calibrated ST202 hydrophones (as described above) set to record continuously. At site 1, we anchored hydrophones 1 m from the seafloor at 1, 10, 20, and 30–m intervals away from the speaker or dummy speaker, suspending them with a subsurface buoy. We then recorded the soundscape when the speaker was turned on against when it was turned off, four times per sound treatment. From this data, we created acoustic spectra and calculated the mean root-mean-square sound pressure levels (SPL_{rms}), the mean snapping shrimp snaps per minute (snaps) and the particle acceleration levels (PALs) for each treatment (Supplement S3). We also created spectrograms for each sound treatment at 1-m away from the speaker or dummy speaker, and for the original reef recording (Fig. 1). Given the logistical constraints of working at this remote outshore location, these spatial recordings of our speaker playback were only taken from one site (site 1). Therefore, it is possible that measurements of source transmission with distance from the speaker varied among sites, as sound propagation underwater can be impacted by the physical characteristics of the environment (i.e. seafloor, water depth, background noise). Nevertheless, our three sites were all similar in depth and proximity to constructed reefs.

Results

Across our three sites, we observed a total of 4,628 oyster recruits, of which 26% recruited to the topside of rocks and 74% to the underside. On the topside, almost half the oysters recruited to the "Sound + Artificial Kelp" treatment (49% of recruits; equivalent to 40,069 spat/m^2), followed by the "Artificial Kelp" (24%; 19,448/m^2), "Sound" (16%; 13,034/m^2), and "Control" treatment (11%; 9,379/m^2). On the underside, the two sound treatments each supported 35% of all recruits ("Sound" [84,138/m^2]; "Sound + Artificial Kelp" [82,000/m^2]), with 17% observed in "Control" (41,379/m^2) and 13% in "Artificial Kelp" treatments (29,724/m^2).

Recruitment for Reef-Building

On the topside of rocks, ANOVAs on the recruitment of oysters did not detect any three-way interactions between "Site × Sound × Artificial Kelp" (Table S4). Instead, analyses revealed a significant two-way interaction between "Sound × Artificial Kelp" (Fig. 2; Table S4; two-way ANOVA; $F_{1,24} = 9.882$, $p = 0.004$). Pairwise tests showed

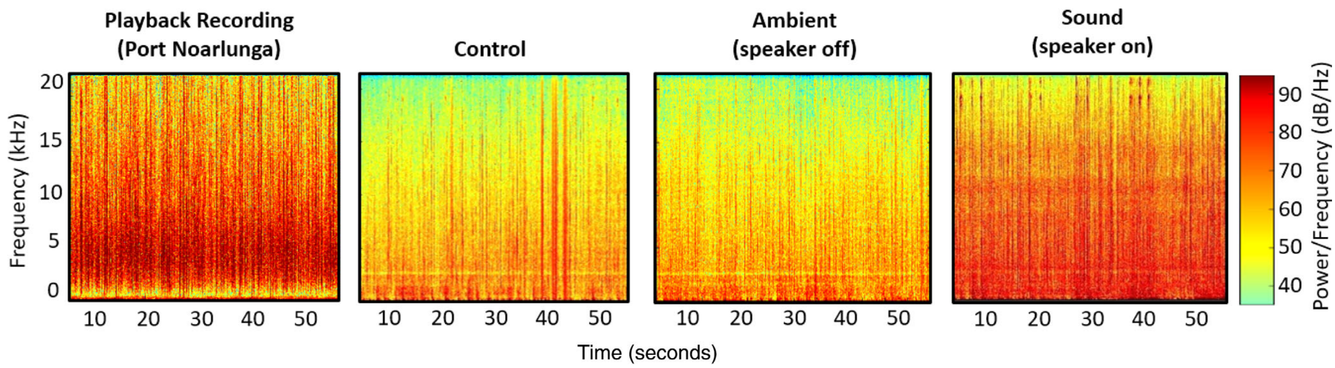

Figure 1. Spectrogram of the original reef soundscape recording from Port Noarlunga reef used in the playback experiments, alongside spectrograms at 1 m from the speaker for the "Sound" and "Control" treatments, and the background ambient soundscape (60 second-long recordings). Spectrograms were produced using 1-second windows with 50% overlap.

that "Sound + Artificial Kelp" (mean recruitment per rock [±1 SE] 21.52 ± 3.01) received 4.3 times the density of larvae than "Control" (mean recruitment per rock [±1 SE] 5.04 ± 0.53), a significant increase by 326.98%. "Sound + Artificial Kelp" also received 2.9 times the density of larvae than "Sound" (mean recruitment per rock [±1 SE] 7.33 ± 0.77), a significant increase by 193.59%. Finally, "Sound + Artificial Kelp" received 2.1 times the density of larvae than "Artificial Kelp" (mean recruitment per rock [±1 SE] 10.44 ± 1.22), a significant increase by 106.13%. Each "Sound," "Artificial Kelp," and "Control" were statistically indistinguishable. "Site" did not significantly influence the recruitment of oysters.

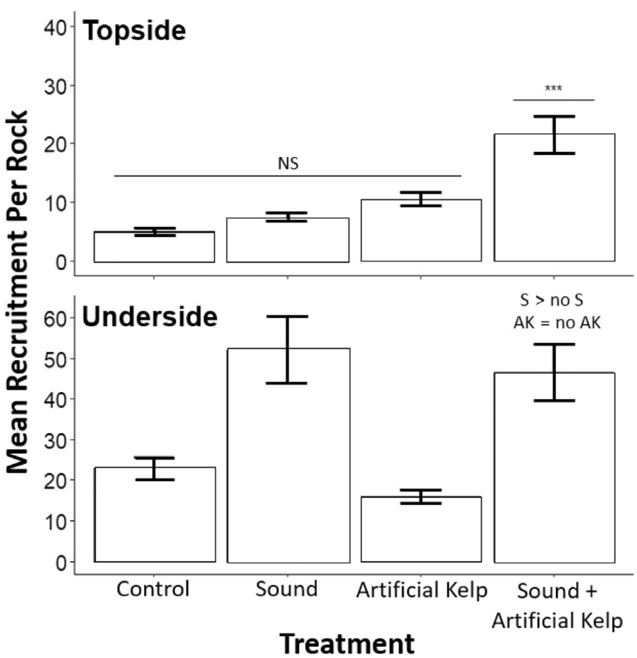

Figure 2. Acoustic enrichment used in combination with artificial kelp increases the recruitment potential of larvae to the topside of rocks. Acoustic enrichment can also increase the recruitment potential of larval oysters to the underside of rocks. Shown is the mean larval recruitment per rock (±1 SE) for each the "Control," "Sound," "Artificial Kelp," and "Sound + Artificial Kelp" treatments ($n = 9$) to the topside and underside of rocks.

Recruitment for Reef-Binding

On the underside of rocks, ANOVAs on the recruitment of oysters did not detect any effects of "Site," even after post hoc pooling of the interaction terms "Site × Sound × Artificial Kelp" and "Sound × Artificial Kelp" with the residual (Table S5). Instead, analyses revealed a significant effect of acoustic enrichment on recruitment (Fig. 2; Table S5; one-way ANOVA; $F_{1,27} = 20.350$, $p < 0.001$). "Sound" (mean recruitment per rock [±1 SE] 52.04 ± 8.32) received 2.3 times the density of settling larvae than "Control" (mean recruitment per rock [±1 SE] 22.93 ± 2.71), a significant increase by 126.95%. There were no detectable effects of artificial kelp. These results indicate that acoustic enrichment combined with artificial kelp can boost the recruitment of oyster larvae to the reef-building topside of rocks, and that acoustic enrichment can do so to the reef-binding underside of rocks.

Soundscape Parameterization

Our speakers created a boost in sound relative to controls that was detectable up to 10 m from the speaker, after which it diminished to background levels. Analysis of acoustic spectra revealed acoustic enrichment to elevate sound levels across all frequencies up to 10 m away from the speaker relative to no sound controls, but to provide no such boost from 20 m (Supplement S3). At 1 m from the speaker, "Sound" substantially enriched sound pressure levels and snapping shrimp snap counts relative to "Control" (7.9 dB/Hz increase, 402.5 snaps per minute increase; Supplement S3). At source point, "Sound" also had a significantly higher PAL than "Control" (Welch t-test; $t_4 = 37.41$, $p < 0.001$; Supplement S3).

Discussion

Our findings show that we can significantly boost the early recruitment of oysters to the topside of rocks by over 4-fold using acoustic enrichment and artificial kelp in combination, and by over 2-fold to the underside of rocks using acoustic enrichment. However, surprisingly, acoustic enrichment in isolation did not boost recruitment to the topside of rocks, while unsurprisingly, artificial kelp did not influence recruitment to the underside of rocks. Our findings provide proof-of-concept that using these techniques, either in combination or isolation, can boost oyster recruitment to help kick-start the building and binding of new reefs (i.e. recruit to the topside and underside, respectively). Where restoration projects experience limited recruitment or competitive barriers to recruitment, these techniques could give oysters a competitive advantage during recruitment and drive the early stages of reef development.

Acoustic Enrichment

Current practice for shellfish reef restoration carries a high risk of recruitment and project failure. We demonstrate that such risk may be reduced by recreating lost soundscapes with underwater speakers either in combination with artificial kelp (to the topside of rocks) or in isolation (to the underside of rocks). Building upon previous work that demonstrates oyster larvae are actively attracted toward (Williams et al. 2022), dive (Wheeler et al. 2015), and settle in response acoustic enrichment in the laboratory (Lillis et al. 2014*a*) and field (Lillis et al. 2015; McAfee et al. 2023), this study found that soundscape enrichment resulted in higher numbers of recruited oysters that could, over the ensuing months, grow to form complex, three-dimensional habitat on the top of reef rocks and bind them together on the underside. However, on the topside of rocks, acoustic enrichment alone did not significantly boost recruitment. Although nonsignificant, the sound treatment did support 1.45 times more oysters than controls across sites. Of note, these results do not distinguish between the possibility that the recruited oysters actively dispersed towards our experimental units, or whether a greater proportion of the passing larvae were induced to settle in our sound treatments. Furthermore, oyster larvae use various environmental cues to navigate towards suitable settlement sites, and we did not test for the possibility that other cues (e.g. olfactory) varied among our study sites.

Many studies show that marine animals respond positively to playback of habitat-related and conspecific sounds (reviewed by Williams et al. 2021). For example, fish, crab, and coral larvae are attracted to and respond to reef sounds (Simpson et al. 2004; Montgomery et al. 2006; Stanley et al. 2010; Lillis et al. 2016; Gordon et al. 2018; Suca et al. 2020). Importantly, our study demonstrates the application of soundscape techniques in a realistic restoration scenario (i.e. reef habitats exposed to ocean currents), and identifies potential context dependencies of this technique; only enhancing topside recruitment when in combination with artificial kelp (discussed below). As more affordable speakers like the ones used here emerge and become open access (Pimm et al. 2015; Berger-Tal & Lahoz-Montfort 2018), acoustic enrichment could be an increasingly used tool to guide the informative stages of reef development, with substantial ecological and economic returns (zu Ermgassen et al. 2016; Parker & Bricker 2020). This could be an alternative to more costly restoration practices, such as hatchery production of oysters to seed reefs.

Positive Species Interactions

Positive species interactions are well documented throughout the marine environment. For example, bivalve mussels are demonstrated to enhance the growth of seagrasses and cordgrass in salt marshes (Bertness 1984; Reusch et al. 1994) via provision of various services (e.g. filtration of particles and biodeposition of nutrients, physical stability; Gagnon et al. 2020). Similarly, oysters enhance the recruitment and survival of biodiverse invertebrate communities by providing complex habitat that reduces biotic pressure (e.g. provision of predation refugia) and environmental stress (e.g. amelioration of high temperatures; McAfee & Bishop 2019). On modified coastlines, turf-forming algae is known to smother the topside of substrates to the exclusion of other recruiting organisms, and therefore presents a major challenge to reef restoration efforts (Gorman & Connell 2009; O'Brien & Scheibling 2018). This means that for recruiting larvae to form primary habitat on new substrate, they either need to recruit in high numbers before turf algae monopolizes the substrate, or access areas where spatial competitors are suppressed. We found that provisioning artificial kelp in combination with acoustic enrichment can provide the cues and conditions that enable oysters to rapidly recruit in greater numbers to the topside of rocks. As our experiment was concluded before turf algae could establish (to enable counting of oysters), it seems our artificial kelp units enhanced oyster recruitment by providing other conditions suitable for settlement, such as reduced light availability that is suggested to enhance oyster recruitment (Bayne 1969). Maintenance of reduced light conditions may also suppress turf algae when it establishes (Shelamoff et al. 2019). Yet, on the underside of rocks, artificial kelp had no influence on recruitment in either in isolation or combined with acoustic enrichment. This is not surprising as the artificial kelp had minimal interaction with the underside of rocks, which were already shaded and sheltered from frond abrasion.

In oyster reef restorations, the provision of substrate during periods of low or no oyster recruitment will likely enhance opportunity for turf-forming algae to spatially dominant the substrata. Indeed, this was observed at this restoration site when the first reef restorations were constructed outside the recruitment window for oysters (McAfee et al. 2021). In addition, the proliferation of turf algae is enhanced in environments where kelp has been lost (Filbee-Dexter & Wernberg 2018) due to coastal urbanization and increased runoff of sediments and nutrients (Connell et al. 2008; Gorman et al. 2009). However, although turf algae are a ubiquitous challenge for restorations in this region (based on observations across hundreds of constructed reefs), our study intentionally concluded before turf could establish (to aid oyster counting), and we used artificial kelp units that could produce unintended experimental artifacts. Therefore, mechanisms other than turf suppression would have driven the greater oyster recruitment beneath our kelp mimics, such as shading (discussed above) or the artificial kelp canopy excluding predators from accessing the recruited oysters. Predation is known to be a key factor limiting oyster recruitment to reefs (Tedford & Castorani 2022). But our structures would have only restricted access to larger fish that are unlikely to predate on newly settled oysters (i.e. <2 mm in size), while small and mesopredators could still access the experiment rocks via the sides of our artificial kelp units. In addition, our artificial kelp units may have altered hydrodynamic flow relative to the non-kelp units, which may have influenced recruitment. Regardless of the mechanism, our results build upon others which show that native flat oysters naturally recruit in greater numbers in the presence of live (Shelamoff et al. 2019) and artificial kelp (McAfee et al. 2021) in restoration scenarios. Implementing positive species interactions into restoration practice may create synergies that kick-start reef development to later drive ecosystem productivity. Restoration still predominately consists of single-species approaches (Silliman et al. 2015), despite evidence showing bivalves and plants positively interact to enhance their survival and ecosystem services, such as fish production (Gagnon et al. 2020; Reeves et al. 2020). By incorporating positive species interactions into our restoration plans alongside acoustic technology, we could increase the early succession of new reef systems and enhance the ecological services provided by oyster reefs.

Knowledge Gaps

These very different techniques (acoustic enrichment and species interactions) show promise in encouraging the recruitment of oysters to reefs at high densities (McAfee et al. 2021, 2023); however, they are not a panacea for successful shellfish restorations. For example, many modified coasts where shellfish reefs have been lost are characterized by insufficient substrata, limited oyster recruitment, and prolific algal turf (Gorman et al. 2009). In such cases, combining acoustic enrichment and positive species interactions may be appropriate when combined with the provision of suitable hard substrate. Timing the deployment of these techniques to co-occur with peak recruitment of the target species will be important to maximize their chance of establishing on new substrate before spatial competitors (McAfee & Connell 2020). Although this study shows promise for applying these techniques to real reef restorations, knowledge gaps remain on their scalability for restoration practice. One key knowledge gap is understanding how often and for how long speakers effectively enrich acoustic cues during the recruitment season, and what the ramifications are of broadcasting sound over broader areas. In our study, we limited the transmission of our speaker playback ($\sim$10 m radius) to avoid sound crossover with controls and because we were targeting larvae that likely cannot respond over large distances. However, if applied for large-scale restoration work, loud commercial speakers could be used to alter soundscapes over large areas (hectare scales), which would attract a broader diversity of animals and predators that can respond over larger distances (i.e. fish; Simpson et al. 2004; Montgomery et al. 2006; Gordon et al. 2019). Understanding how predators of oyster larvae respond to acoustic enrichment is important to ensure this tool can facilitate oyster recruitment without also drawing predators, which could create recruitment sinks. In addition, as restorations mature and their natural soundscapes recover, they will attract larvae independent of acoustic enrichment. Understanding the acoustic thresholds to recruitment will inform when enrichment by speakers is no longer valuable for recruiting larvae. Similarly, once oysters have established a foothold and developed a complex reef structure, artificial kelp (or live kelp transplants) may not be required to overcome issues surrounding competition for space (i.e. algal turf). Addressing these knowledge gaps are important as they will determine whether acoustic technology and positive species interactions are only useful during the early stages of restoration.

There is also a paucity of data on whether oyster larvae are swept into the area by passive movement of currents and induced to settle by acoustic enrichment, or if they are attracted from afar (Williams et al. 2022). If they do actively disperse towards cues in the field, it remains unknown over what spatial scales larval oysters can be attracted (Rodriguez-Perez et al. 2020). Over large scales, currents and tides are known to drive recruitment patterns as most invertebrate larvae are weak swimmers relative to water currents (Butman 1987). However, on small spatial scales some larvae do have the ability to control settlement through various settlement cues (Butman 1986; Pawlik 1992). A better understanding of larval movement patterns in the field and the role of active movement relative to water currents could allow for more effective use of natural recruitment in restoration.

Ecosystem restoration is a global pursuit, working to protect and repair the environment. As such, approaches that can redress the risks associated with restorations beginning at their early stages are highly valued. We show that a key process for restoration success—oyster recruitment during the early stages of reef development—is enhanced by combining acoustic enrichment and positive species interactions. Where recruitment is variable or eroded, acoustic enrichment appears to act as an attractive cue that draws oysters from a broader area or encourage them to leave currents, and move toward restoration sites to increase recruitment to the underside of rocks. This technique can also boost recruitment to the topside of rocks when combined with artificial kelp that can create conditions suited to oyster recruitment, enabling them to rapidly establish a foothold on reefs. Combining these novel techniques offer a potentially valuable approach to enhance the recovery of oyster reef restorations, steering their early development on a trajectory of recovery.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Experimental units and underwater speaker.
Supplement S2. Methods and results of site-by-site analysis in the field.
Supplement S3. Soundscape parameterization in the field.
Supplement S4. Tables for analysis of topside and underside recruitment.

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