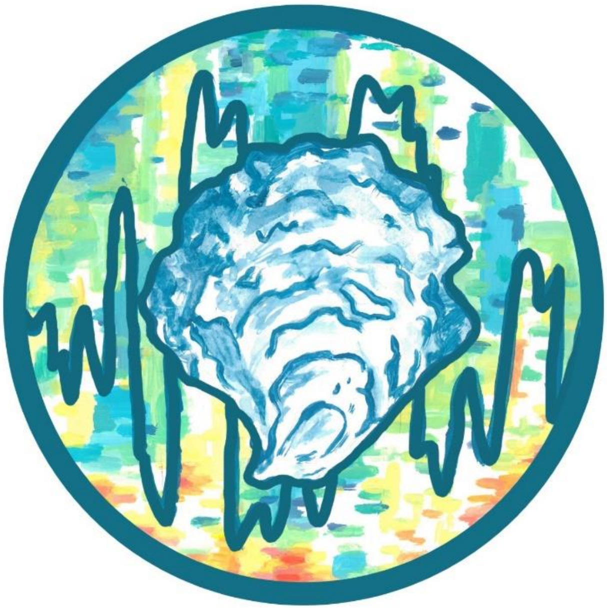
Enriching Marine Soundscapes to Restore Australia's Lost Native Oyster Reefs



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ABSTRACT

Australia’s native flat oyster reefs (*Ostrea angasi*) are considered functionally extinct, which has prompted ambitious restoration efforts that aim to revive this lost ecosystem and deliver ecological and economic returns on investment. However, many of these restorations are occurring in systems where oysters are recruitment limited and where larvae must compete with opportunistic species to establish a foothold on reefs. These challenges combine to limit the success of restorations. Consequently, there are calls for novel solutions that can overcome these limitations and boost the recovery process. Healthy, habitat-related soundscapes can provide navigational information for dispersing life-stages. However, these biological signals are being muted by the loss of habitat from which they originate and masked by rising anthropogenic noise. Subsequently, dispersing larvae that rely on acoustic cues for navigation are lost at sea, limiting the success of restorations that rely upon a steady supply of recruits. This thesis presents a novel solution for restoring lost oyster reefs: acoustic enrichment of healthy, habitat-related sounds using marine speakers. By reprovisioning the sounds of healthy reefs that have been lost, we might guide oyster larvae towards new restorations and kick-start the early successional stages of reef development which are critical to their success. In this thesis, I combine aquarium and field experiments to present new evidence for acoustic enrichment as a tool that can convey navigable information for dispersing oysters in search for adult habitat. I demonstrate that acoustic cues tend to be silenced as habitat is lost, creating negative feedbacks that hinder restoration efforts. In the aquarium and field, I demonstrate that oyster larvae have increased recruitment in the presence of playback of healthy, habitat-related reef sounds. I also discover that larval recruitment increases along a gradient of sound intensity associated with healthy reefs, with larvae being capable of horizontal swimming behaviour to navigate towards this sound. Furthermore, I reveal that anthropogenic noise might not only reduce the effectiveness of acoustic enrichment for restoration by masking biological signals, but that it might also disrupt recruitment patterns. Finally, I reveal the value of combining ecology and technology,

using artificial kelp and acoustic enrichment, to boost oyster recruitment to the reef-building and binding components of oyster reefs. On coasts in which habitats and their biological soundscapes have been eliminated, combining ecology with acoustic technology could provide signals that attract larvae from passing currents and repair recruitment processes. However, as I demonstrate, there appears to be context dependency in the success of acoustic enrichment enhancing recruitment, having limited value in noisy locations. The idea that habitat degradation is global and the resulting ‘muted-scapes’ have dampened navigational cues for their replenishment, suggests that acoustic enrichment could be used to recreate gradients of sound needed to boost ecosystem restoration and recovery.

STATEMENT OF CANDIDATE

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

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GENERAL SUMMARY

Australia's native flat oyster reefs have been functionally extinct for over 100 years, with no sign of natural recovery. Restoration of this lost ecosystem is now underway to recover the multitude of services they can provide to society and the environment. However, the success of this ambitious project relies upon innovative solutions that can maximise returns on restoration investment. Currently, restoration practice falls short of these ambitions.

Here, I examine whether acoustic enrichment of the marine soundscape is an effective technique for the recovery of Australia's native flat oyster. The biological components of many marine soundscapes have been denuded or masked due to habitat degradation and rising anthropogenic noise. This is concerning as many marine organisms utilise this component of the marine soundscape during their early life-stages to help them establish and grow in suitable habitat. Bringing these sounds back into the soundscape using acoustic technology could potentially reprovision these lost acoustic cues for organisms like the oyster.

This thesis: (1) considers how organisms respond to sound for the purposes of developing and applying acoustic technology to boost restoration outcomes, (2) tests the recruitment and swimming response of larval oysters to acoustic enrichment in the laboratory and field, (3) explores the value of acoustic enrichment in boosting the recruitment of larval oysters in the presence of anthropogenic noise and (4) examines how combining positive species interactions (through artificial kelp) and acoustic enrichment (through speaker technology) can boost the early stages of reef restorations.

This research took place predominately across two restoration shellfish reefs in South Australia and found that depending on the context, acoustic enrichment can repair recruitment processes and boost the recovery of Australia's lost oyster reefs. Overall, it appears that acoustic enrichment offers a promising solution to revive extinct shellfish ecosystems and maximise returns on investment.

CHAPTER ONE

GENERAL INTRODUCTION

For millennia, our ecosystems have been extensively degraded, yet the drivers of this are only recently being understood (MEA, 2005; Mazor et al., 2018). The marine environment has suffered particularly great losses, largely due to climate change, unsustainable fishing, pollution and shipping activity (Halpern et al. 2019). With human populations growing along coastal areas (Neumann et al. 2015), pressures within estuarine and nearshore environments are exacerbating. Activities like coastal development, pollution and nutrient run-off (Daidu et al. 2019) decrease biodiversity and in turn degrade ecosystem function (Loreau et al. 2001; Worm et al. 2006; Cardinale et al. 2012), disrupt primary production (Tilman et al. 1996; Hooper et al. 2005) and alter trophic interactions (Cardinale et al. 2002; Duffy 2003). Nearly every country has experienced deleterious changes to their coastal ecosystems (Halpern et al. 2019), resulting in the need for solutions that will aid in habitat restoration. However, for habitat restoration to be successful, it is critical that target organisms recruit to restoration sites. Underwater sound may aid in the recruitment process, as it holds great functional value for marine animals.

1.1 Underwater sound

Sound is created by the quick variation in pressure or density of a sound wave’s molecules moving through a medium (i.e., through water). It has two components, particle pressure and particle motion (Rogers and Cox 1988; Montgomery et al. 2006). Particle pressure is the change in pressure caused by the particles compressing and rarefacting as a sound wave moves. It dominates the acoustic farfield (greater than 1-2 wavelengths from a sound source) and decreases slowly (proportional to the inverse of distance) (Montgomery et al. 2006). Meanwhile, particle motion is the back-and-forth movement of particles that transfers vibratory energy to other particles through a medium. Particle motion dominates the acoustic nearfield (within around 1-2 wavelengths of a sound source) and decays rapidly (proportional to the inverse of the distance squared) (Montgomery et al. 2006).

In the ocean, sound propagates irrespective of currents. In deep water, it travels faster and further due to the high density of the water (Fine and Lenhardt, 1983). Furthermore, low frequency sounds travel farther than high frequency sounds, as the wavelength of a sound increases as its frequency decreases (Urick, 1983; Montgomery and Radford, 2017). Compared to other mediums like air, sound in the ocean experiences very little sound loss and can travel distances up to 100 kilometres (Rogers and Cox, 1988). This is because the density of water makes it a good conductor of sound, enabling it to travel up to five times faster in water than in air. Whilst sound can be altered due to non-biological agents like salinity, temperature and landscape features (i.e., canyons), it still remains the ideal sensory cue for marine organisms at large scales. This is because other cues cannot travel as far underwater. Visual cues are restricted by the availability of light that can penetrate into the ocean and the seeing ability of the organism, whilst olfactory cues can only travel far if they are carried by moving water (i.e., currents). Such cues are more important at the small-scale. There are many types of underwater sound that combine to form the “soundscape”.

1.2 Marine soundscapes

A ‘soundscape’ is the set of sounds emanating from an environment and was conceptualised in 2009 by Bryan Pijanowski and Almo Farina. Soundscapes are rich with a combination of sounds from ambient, geophysical, biological and anthropogenic origins. Sounds of a geophysical nature are well documented, encompassing those that come from waves, wind, precipitation, breaking ice and the formation of carbonic acid (Rodgers and Cox, 1988; McDonald et al. 2006; Etter, 2012). These sounds occur across a broad range of frequencies, constituting the majority of ambient sound (Erbe et al. 2015; Lindesth and Lobel, 2018). Meanwhile, anthropogenic sound originates from people and is ever increasing in our oceans. Shipping and seismic exploration dominate the low frequencies (10-500 Hz) whilst sonar and small vessels dominate the higher frequencies (500 Hz-25 kHz) (Hildebrand, 2009). Activities like offshore pile-driving produce high levels of underwater sound (up to

220 dB re 1 µPa at 1 metre) (Reinhall and Dahl, 2011), with the accumulated evidence showing these activities to have deleterious effects on marine life (Holles et al. 2013; Fahlman et al. 2014; Jones et al. 2018).

Biological sounds are highly diverse and are produced by mammals, fish and invertebrates during processes like feeding, mating and navigation (Knowlton and Moulton, 1963; Ladich, 1997; Amorim, 2006). These sounds can vary latitudinally, diurnally, seasonally and with lunar cycles (Mok and Gilmore, 1983; Farina, 2015). Whales and dolphins produce a myriad of sounds including whistles, clicks, squeaks, pulses and moans (Farina, 2014). Meanwhile pinnipeds produce an assortment of sounds from barks, grunts and trills to yelps, bells and bellows (Schusterman and Van Parijs, 2003). These animals generate sounds using air movement (Montgomery and Radford, 2017) and detect it using hair-like or membranous receptors, depending on how far away the sound is (Farina, 2014).

Fish predominately produce sound in the lower frequencies (Loye and Proudfoot, 1946; Lobel, 1992; Lindseth and Lobel, 2018). Accumulating observations have shown that fish have a broad vocal repertoire of growls, roars, barks, honks, chirps, drums, knocks, sirens and pops, amongst other descriptions. These sounds are generated in a variety of ways such as stridulation of swim bladder muscles, pectoral fins or girdles, as well as through pharyngeal teeth grating, hydrodynamic movement of fins, tendon vibration, air release and using muscles to vibrate the gas-filled swim bladder (Lobel, 1992; Ladich et al. 2006; Montgomery and Radford, 2017). Whilst some species can detect the particle motion component of sound using sensors like the lateral line, majority are known to detect the pressure component using an enclosed gas bubble, like the swim bladder that most fish possess (Popper and Fay, 1999). This gas bubble vibrates with the pressure component of sound and converts this into motion, essentially acting as a transducer (Montgomery et al. 2006). This vibratory motion then radiates within the fish’s body, indirectly stimulating the otolith situated within the fish’s inner ear. Another mode of detection is via hair cells that can respond to hydrostatic pressure changes, as seen in the dogfish (*Scyliorhinus canicular*) (Fraser and Schelmerdine 2002).

Some of the most pervasive biological sound producers in the ocean are invertebrates like snapping shrimp, sea urchins and spiny lobsters. These dominate the higher frequencies (2-15 kHz) with snaps, cracks and rasps (Everest et al. 1948; Buscaino et al. 2011; Rossi et al. 2016*b*, 2017). To stun and kill prey, snapping shrimp have a large, modified claw that creates and collapses a cavitation bubble that shoots out a high-velocity water jet when it closes (Versluis et al. 2000; Hess et al. 2013). The collapse of this bubble also produces a snap sound that can exceed 190 dB re 1 µPa at source point (Au and Banks, 1998; Chitre et al. 2003). When large aggregations of snapping shrimp snap, it produces a cacophonous crackling sound. Snapping crackle was first characterised by the US navy in World War II when it was detected by sonar and mistaken to be jamming by the enemy (Johnson, 1947). The crackling was so loud that the navy started to conceal their submarines amongst snapping shrimp populations to mask themselves from the enemy's sonar (Johnson, 1947). Being a universal source of marine sound, shrimp crackle is a key component of ambient noise, peaking in loudness during the dusk and dawn choruses (Everest et al. 1948; Lillis and Mooney, 2016; Lillis et al., 2017).

Invertebrates tend to detect the particle motion component of sound (Fay, 1984; Budelmann, 1992*a*, *b*; Lu et al. 1996), likely through superficial hearing receptors on the organism's body, or internal statocyst systems (Frings and Frings, 1967; Budelmann, 1988; Budelmann, 1992*a*, *b*). Statocysts are organs that essentially operate as accelerometers that detect differences in density. Inside the statocyst is a statolith which has a density higher than that surrounding the organism. Due to this, the statolith moves less than the organism does when subjected to sound. From the statolith are connected a group of mechanosensory cilia (fine hair-like structures) that can sense the changes in motion between the statolith and the surrounding tissue of the organism (Montgomery et al. 2006). Scallops are known to use abdominal sense organs to detect vibrations (Zhadan, 2005), whilst the pediveliger stage of several bivalve species utilise statocysts to detect the particle motion component of sound (Gragg and Nott, 1977; Kennedy et al. 1996; Gosling, 2003). Whilst some invertebrates do not appear to have a system to detect sound, this does not imply an inability to detect it (Montgomery et al. 2006).

It is the various combinations of these sounds over space and time that give rise to the multitude of soundscapes we record in our oceans. However, attention has started to focus on how climate change and human activities are silencing the ocean's natural sounds. Ocean acidification is changing the sound production mechanisms of soniferous organisms (Rossi et al. 2016*a*) and community structure and species distributions are being altered (Rossi et al. 2016*b*; Sueur et al. 2019). With habitat destruction comes a loss of the soniferous organisms associated with these habitats. Due to this, the oceans are transitioning from having healthy, soniferous soundscapes to those of 'muted-scapes' with little biological sound and diversity, or to those filled with anthropogenic noises. This is concerning as healthy soundscapes are critical for the functioning and survival of marine organisms.

1.3 The importance of underwater sound to animals

Both the larvae and adults of many marine animals respond to sound. Studies using light traps have shown that fish are attracted to different frequencies of reef sound (Leis et al. 2003; Tolimieri et al. 2004; Simpson et al. 2008) and alter their swimming behaviour and navigation in response to it (Leis et al. 2002; Radford et al. 2011). Additionally, reef fish increase their settlement in response to habitat-related sounds (Simpson et al. 2004; Gordon et al. 2019; Suca et al. 2020). Meanwhile, cephalopod adults can detect low frequency vibrations (Packard et al. 1990) and crab larvae are not only attracted to habitat-related sound (Montgomery et al. 2006), but settle and metamorphose more in its presence (Stanley et al. 2010, 2011, 2012). Furthermore, coral larvae settle in response to reef sounds (Lillis et al. 2016) and mussels exposed to loud vessel noise biofoul more (Wilkens et al. 2012). Lastly, adults of the Pacific oyster (*Crassostra gigas*) can detect low frequency sounds (Charifi et al. 2017), whilst larvae of the Eastern oyster (*Crassostrea virginica*) settle more in the presence of oyster reef sounds (Lillis et al. 2014*a*, *b*, 2015). These studies demonstrate that habitat-related sounds are important for marine animals. If this ubiquitous underwater property can be utilised, we may be able to harness it as a cost-effective restoration tool.

1.4 The global loss of shellfish reefs

Shellfish reefs are a particularly imperilled coastal ecosystem. Once spreading throughout the world's temperate estuaries and coastlines (Drake, 1875; Blake and zu Ermgassen, 2015), they served as the equivalent of coral reefs to tropical climates. In the North Sea alone, oyster beds carpeted an impressive 24 000 Km^2 of the seafloor (Olsen, 1883). Now, 85% of oyster reefs are lost (Lotze et al., 2006; Ogburn et al., 2007; Beck et al., 2011). These hard-shelled habitats were rapidly desertified into soft sediment containing little biological diversity and little ecological function (McAfee and Connell, 2020*a*). Based on available data, the only continent with over 50% of its native reefs remaining is South America (McAfee and Connell, 2020*a*). Large shell middens indicate that the exploitation of shellfish reefs dates back tens of thousands of years (Bailey and Flemming, 2008), such as the middens in Ertebølle (Denmark), which contain some 50 million shells (McAfee and Connell, 2020*a*).

Early interpretations reveal that the most intense declines in shellfish occurred throughout a fifty year period (1840-1890), where over 1100 Km of reef were denuded each year (McAfee and Connell, 2020*a*). The key drivers of this were unsustainable bivalve extraction and dredging (Nehring, 1999; Hall-Spencer et al., 2010; Cook et al., 2013). This harvesting commenced in estuaries close to developing areas, spread down the coast to each successive site and then eventually collapsed (Kirby, 2004). Dredging is particularly destructive because it indiscriminately removes hard-shell substrate from the seafloor to the extent that it cannot naturally recover (Bergquist et al. 2006; Powell and Klinck 2007). Meanwhile, trawling can exploit and destruct deeper, subtidal shellfish reefs (McAfee and Connell, 2020*a*). Australia's native oyster reefs were not exempt from these extensive losses.

1.5 Australia's native flat oyster

Australia's native flat oyster, *Ostrea angasi* (Sowerby, 1871), also called the mud or Port Lincoln oyster, once covered Australia's southern coastline. In South Australia alone, they extended over 1500 Km of seafloor (Alleway and Connell, 2015). This subtidal oyster grows up to 18 cm in length, can weigh up to 400 grams (Mitchell et al., 2000; Jones and Gardner, 2016) and reaches sexual maturity after two years. During spawning events, females retain eggs in the mantle cavity until inflowing seawater carrying sperm fertilises them (Crawford, 2016; Gillies et al, 2017). This initial brooding means that they have the highest larval survival rate of all oysters (Crawford, 2016). After a week, the larvae inside the mantle cavity reach 170-189 µm in size and become 'veligers'. These are released into the water by vigorous movements of the adult's shell, with between 1 to 3 million veligers being released per adult per spawning event (Crawford, 2016). The veligers drift in currents for some two weeks after which they settle onto a substrate using their byssus gland (Crawford, 2016). It is at this stage that the veligers metamorphose onto their chosen substrate into 'spat', where they grow and remain for the duration of their lives (Crawford, 2016). This spawning occurs from mid-spring and throughout summer, when ocean temperatures reach 18°C (O'Sullivan 1980; Alleway and Connell 2015).

Between 1886-1946, Australia's native oysters experienced large declines (Alleway and Connell, 2015). Where hard, complex structures once carpeted the seafloor, now only expanses of sand, mud, turf-forming algae and seagrass patches remain (Grove-Jones 1986; Tanner, 2005; Bryars et al. 2008). Apart from Indigenous shell middens providing evidence of the historical distribution of *O. angasi* in Australia (Radford and Campbell, 1982; Godfrey, 1989), there exists little other documentation. This is due to the small emphasis that was historically placed on their economic value and importance (McAfee and Connell, 2020*a*).

Consistent with the IUCN Red List of Ecosystems, *O. angasi* is critically endangered and in need of rapid intervention for its recovery (Gillies et al. 2020).

1.6 The value of oysters

Oyster reefs gift a suite of benefits to society and the environment, at a value of up to $99, 000 per hectare per year (Grabowski et al., 2012). As ecosystem engineers, they can modify, maintain and create habitat for other organisms (Jones et al., 1994). Their composition of live and dead shell foundations form complex aggregated and three-dimensional structures which increase species richness and abundance by providing organisms with sites for shelter, nesting, refuge and reproduction (Jones et al,. 1994, 1997; Bertness et al., 1999; Coen and Humphries, 2017). Furthermore, many recreationally and commercially important fish species (i.e., the blue cod) rely upon these reef foundations (Cranfield et al. 2001; Airoldi et al. 2008). The structure of an oyster reef also provides climate refuge for organisms by ameliorating stressful conditions (i.e., extreme temperatures) (Silliman et al., 2011; McAfee et al., 2016).

Furthermore, by extensively filtering seawater, oysters remove particulates from the water column to improve its quality (Underwood and Fairweather, 1989; Dame, 1996; Newell, 2004). This reduces turbidity and allows light to penetrate the water, which encourages seagrass growth and limits that of phytoplankton (Newell, 2004). Oysters also cycle nutrients back to the seafloor via their nutrient-rich faeces and pseudofaeces (Newell, 2004; Coen and Humphries, 2017; Ray and Fulweiler, 2020). Furthermore, they have a negligible greenhouse gas footprint as they can remove excess nitrogen by simulating denitrification (Ray and Fulweiler, 2020). Additionally, oysters regenerate local water alkalinity by dissolving and precipitating calcium carbonate from their shells. This reduces corrosive conditions that oyster larvae are adverse to (Green et al., 2009; Waldbusser et al., 2013).

Finally, oyster reefs are at times the only hard structures in soft-sediment environments (Stephens and Bertness, 1991; Seed, 1996; Beck et al., 2011). This means that reefs can lessen the energy that reaches shorelines from storm surges and wave action, inhibiting coastal erosion (Scyphers et al., 2011; Safak et al., 2020). Unsurprisingly, the loss of these shellfish reefs have resulted in a loss of the ecosystem services provided by them. Fortunately, restoration has the potential to cost-effectively and sustainably transition degraded shellfish reefs back into healthy, functioning ecosystems (Byers et al., 2006).

1.7 Restoration underway

Coastal restoration is a burgeoning field, with several projects yielding returns to ecological function (Grabowski et al., 2012; Dillon et al., 2015). Such restorations are in favour of rebuilding habitat, cleaning coastal waters, stabilising shorelines, increasing broodstock and providing an educational outreach (Coen et al., 2007; Grabowski and Peterson, 2007; Brumbaugh and Coen, 2009). These ventures are well established in North America, with Europe, East Asia and Australia now also restoring shellfish reefs (Laing et al., 2006; Beck et al., 2011; Gillies et al., 2018). In Pamlico Sound (North Carolina) constructed oyster reefs have been rapidly colonised by unique fish species (Pierson and Eggleston, 2014), whilst restoration along the Great Wicomico River (Virginia) has seen thriving populations of 185 million oysters return (Shulte et al., 2009).

Numerous techniques are used to restore oyster reefs. The most common is seeding the degraded site with larvae and providing hard substrate for the larvae to attach to (Blomberg, 2008; zu Ermgassen et al., 2020). Seeding is where larvae are attached to oyster shells and transplanted onto a reef (Brumbaugh and Coen, 2009; ORET, 2009). This shell closely mimics a natural reef's structure, chemistry and interstitial space, however, other materials like limestone are often used due to a limited supply of shell (Chatry et al., 1986; Brumbaugh and Coen, 2009; George et al., 2015). Another technique is to increase the height of a restored reef's structure to reduce sedimentation, increase dissolved oxygen and increase water flow (Coen and Humphries, 2017), each of which increases the chances of oyster larvae surviving.

Further considerations when restoring a reef are the choice of location, size and timing of construction. Areas that can be naturally restocked by larvae in the water column are preferable, especially if this location also provides connectivity to other habitats (Grabowski et al., 2005; Gilby et al. 2018). Sites that historically had shellfish populations are usually considered (Gillies et al., 2018), however, these sites may no longer be suitable if they have experienced changes in water quality, salinity, substrate availability and recruitment. In terms of size, reefs on the scale of kilometres to tens of kilometres seem to be most effective (Gilby et al. 2018). Lastly, the timing of reef seeding and substrate provision can make or break restoration efforts. Oysters have temporal variations in food webs and biomass of organisms across different trophic levels (Xu et al., 2020). Furthermore, when substrate is provided to oyster reefs before oysters naturally spawn, turf-forming algae may outcompete larvae for this settlement space (McAfee et al. 2020). This highlights the importance of synchronising reef building with times when there are more oysters naturally spawning in the water and when there is more oyster food available.

To restore native oysters to South Australian waters, the South Australian Government and the Nature Conservancy have initiated its ‘Great Southern Seascapes Program’. This began in 2017 with ‘Windara Reef’, a 20-hectare reef made of concrete structures and limestone boulders which was seeded with more than seven million oysters (Fig 1.). More reefs have now been established on Adelaide’s metropolitan coastline. However, a challenge to these restorations is limited larval recruitment, despite oyster larvae being observed in these places. Recruitment in the marine environment is the process by which juvenile individuals of a species move and settle into the habitat of their adult conspecifics. A lack of recruits puts the early successional stages of reef development at risk from being unable to grow into healthy, functioning ecosystems. To meet the ambitious goals of the world’s ‘Decade on Ecosystem

Restoration' (2021-2030, United Nations, *General Assembly resolution* 73/284), we need restorative solutions that are innovative and can tackle problems like limited recruitment. A potential solution for native flat oysters may be acoustic enrichment of the ocean's soundscape.

Fig. 1. Construction of Windara Reef in 2017, showing A) the limestone boulders used to construct the reef, B) construction vessel *MPV Andrew Wilson* constructing the reef and C) a custom-designed concrete structure used to construct the reefs. *Images taken by*: Department of Primary Industries and Regions, the Government of South Australia, 'Shellfish reef construction', sourced on 25th of January 2022, https://www.pir.sa.gov.au/fishing/recreational_fishing/windara_reef/shellfish_reef_construction

1.8 Research aims:

The degradation of marine ecosystems and their associated soundscapes mean that organisms that rely upon acoustic cues are likely unable to locate suitable healthy sites during recruitment and other key processes. With the loss of Australia's native oyster reefs and their soundscapes, larval oysters may be lost at sea. Can we restore these oyster reef soundscapes using underwater speaker technology? If we can, it may lead larval oysters looking for a place to settle away from silent, barren-scapes in the ocean towards soniferous sites targeted for oyster reef restoration. My thesis investigates how gradients of recreated sound could be a novel technique to encourage the recruitment of larval oysters to restoration reefs to boost their recovery. The four data chapters comprising this thesis address key knowledge gaps surrounding; 1). the potential that acoustic enrichment has for restoration, 2). the response and swimming behaviour of *O. angasi* in response to sound and its gradients, 3). the feasibility of using acoustic enrichment in places containing background anthropogenic noise and 4). whether acoustic enrichment and multispecies restoration can boost the recruitment of *O. angasi* larvae to restoration reefs.

Whilst it is clear that animals do respond to sound and that it can be used for conservation and restoration purposes, no review of this literature has occurred. In Chapter Two, I consider how organisms respond to sound for the purposes of developing and applying acoustic technology to boost restoration outcomes. The findings of this paper will help researchers and restoration practitioners to realise the importance of marine sound in the recruitment processes of organisms in habitats targeted for restoration.

Furthermore, we know that larval oysters are attracted to sound in some cases, however, much remains to be learnt about the species *O. angasi* and whether larval oysters can swim towards the source of a sound. In Chapter Three, I use aquarium experiments and a field experiment to investigate whether *O. angasi* can not only detect habitat-related sounds and use it during settlement, but whether they can also swim towards the source of habitat-related sounds along a gradient of sound. This research has large implications for restoration, as current thinking assumes that larval oysters can only change their position in the water column vertically, being unable to swim horizontally as they are at the whim of ocean currents. These findings will change perspectives surrounding the degree of control larval oysters have and how they have a greater ability to interact with large-scale processes than previously thought.

Increasingly, shellfish restorations are occurring in localities of rising anthropogenic noise, such as along metropolitan coastlines and in urbanised waterways. In Chapter Four, I explore the context dependency surrounding acoustic enrichment for restoration, to determine whether it still has restorative value in localities containing background anthropogenic noise.

The outcomes of this paper suggest that not only is acoustic enrichment context dependent, having little value in the presence of anthropogenic noise, but that anthropogenic noise may even disrupt recruitment processes of oyster larvae.

In many sites targeted for oyster restoration, larval recruitment is not only limited, but turf-forming algae often outcompete larvae for substrate space. In Chapter Five, I investigate how combining ecology and technology might kick-start the early stages of reef development by increasing recruitment to the reef-binding underside and reef-building topside of boulders substrates. I do this by using artificial kelp mimics that simulate positive interactions between kelp and recruiting oysters, and acoustic enrichment which works to overcome recruitment bottlenecks. The outcomes of this research highlight for restoration practitioners the importance of combining ecology with technology to boost restoration during the early stage of reef development.

In my final chapter (Six), I synthesise the outcomes of my four data chapters. I discuss how acoustic enrichment is a novel solution for habitat restoration with great potential, followed by the value in knowing that oyster larvae can detect sound and actively navigate towards its source. I then discuss the context dependency surrounding this technique, to guide restoration scientists and practitioners in how they might upscale their restoration efforts. Lastly, I discuss how combining ecology with technology, through acoustic enrichment and multispecies restoration, might work to maximise the success of oyster restoration efforts.

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CHAPTER TWO

Repairing recruitment processes with sound technology to accelerate habitat restoration

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Contribution to the Paper	Concept and design Data collection Analysis and interpretation First draft Critical revision		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate’s stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate’s stated contribution.

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2.1 Abstract

Humanity’s ambitions to revive ecosystems at large scales requires solutions to move restoration efforts beyond the small-scale. There are increasing calls for technological solutions to reduce costs and facilitate large-scale restoration through the use of emerging technologies using an adaptive process of research and development. We show how technological enrichment of marine soundscapes may provide a solution that repairs the recruitment process to accelerate the recovery of lost marine habitats. This solution would solve the problems of current practice that largely relies upon natural recruitment processes, which carries considerable risk where recruitment is variable or eroded. By combining the literature with laboratory experiments, we describe evidence for “highways of sound” that convey navigable information for dispersing life stages in search for adult habitat. We show that these navigational cues tend to be silenced as their habitat is lost, creating negative feedbacks that hinders restoration. We suggest that reprovisioning soundscapes using underwater technology offers the potential to reverse this feedback and entice target organisms to recruit in greater densities. Collective evidence indicates that the application of soundscape theory and technology may unlock the recruitment potential needed to trigger the recruitment of target organisms and the natural soundscapes they create at large scales.

Key words: bioacoustics; conservation; ecosystem restoration; habitat loss; soundscape enrichment; supply-side ecology

2.2 Introduction

Our “Decade on Ecosystem Restoration” (2021-2030, United Nations, *General Assembly resolution* 73/284) signifies humanity’s growing hope that restoration can help achieve our sustainability goals. This goal requires substantial global commitments to large-scale restoration (e.g., the Bonn Challenge) but the scale of current restoration practice often falls short of our ambitions (e.g., restoring 350 million hectares of forest by 2030). To address this shortfall, technological solutions are needed to reduce the cost per unit area of restoration and facilitate its up-scaling (Perring et al. 2018).

There is optimism that technology may rise to this challenge. Rapid advancements and reduced costs are allowing technology to play a greater role in environmental management and conservation, often successfully solving specific needs (reviewed by Stuart et al. 2015). For example, aerial drones can now see through waves, allowing precise reef mapping to identify suitable sites for restoration (Chirayath and Earle 2016). Such technological advancements provide opportunities to reduce planning costs and up-scale restoration efforts. The utility of acoustic technology in marine ecosystem restoration is also emerging, with small-scale studies and successes on oyster and coral reef habitats (Lillis et al. 2014*a*, 2015, Gordon et al. 2019).

Our oceans are full of noises that provide functional cues for dispersing organisms. Recent attention to the rich sensory information conveyed by soundscapes, alongside marine technology, allows researchers to identify and reproduce certain functional components of soundscapes that attract target species. However, this can be difficult as the marine soundscape and its sensory information is variable through time and space, and the extent to which technology can attract target species is unknown. Though knowledge gaps also remain on the generality and scale at which soundscape manipulation may benefit conservation, early research suggests that applied soundscape ecology may be a new frontier for marine ecosystem restoration.

2.3 The evolution of soundscape ecology research

Soundscape ecology is defined as the biological, geophysical and anthropogenic sources that form a “soundscape”, and how this varies and interacts with the environment over space and time (Pijanowski et al. 2011*a*, *b*). It emerged as a research field from the study of terrestrial forests, being first described by Traux (1978). Since its inception, soundscape research has continually improved due to (1) rapidly advancing recording technology (Allan et al. 2018); (2) improved acoustic data storage and processing (Sueur et al. 2014); and (3) informative ecological theories (Urban et al. 1987, Kirchhoff et al. 2012). Field studies have characterised the geophysical sources of sound (Swanson et al. 1988) and how animals produce (reviewed by Bradbury et al. 1988, Fletcher 2007) and behaviourally respond to sound (Marten et al. 1977). Recently, research on the impacts of anthropogenic noise has shown broadly negative impacts on terrestrial and marine animals (Jerem and Matthews 2021, Duarte et al. 2021).

To assess the potential for applied soundscape research, we reviewed literature on applied soundscape ecology published over the past 80 years (Supporting information A: Section S1). Our search identified 67 studies that manipulated sound either as a tool for habitat restoration or to examine animal attraction to broadcast sound (i.e., orientation, movement and settlement: Supporting information A: Table S1). These studies show that animals perceive, behaviourally respond to and are attracted by sound (Fig. 1). About half of these studies are terrestrially focused, with birds, amphibians and mammals the focus groups (37.21%, 7.45% and 6.09% of all studies, respectively). Marine studies were dominated by fish (33.59% of all studies) and to a lesser extent, bivalves, crustaceans and corals (7.15%, 7.15% and 1.35%, respectively). To identify the primary aim of these studies, we categorised them as those investigating organismal responses to sound in “orientation, movement and settlement” (67.65%), “response rate” (14.71%), “vocal or alarm response” (8.82%) and those focused on "habitat restoration" (8.82%; Fig. 1). To our knowledge, the first study to apply soundscape ecology for habitat restoration was Kress (1983), who amplified the social vocalisations of Arctic Terns to attract them to a former nesting site, re-establishing breeding grounds within three years. In the marine environment, Gordon et al. (2019) effectively doubled fish settlement and retention on degraded coral reefs by playing healthy reef sounds. In the laboratory, settlement of oyster larvae (*Crassostrea virginica*) near doubled when exposed to playback of oyster reef soundscapes relative to no playback (Lillis et al. 2014*a*), with similar observations (1.4 times increase) recorded in the field (Lillis et al. 2015). These studies suggest that acoustic enrichment of marine soundscapes may boost the key process of habitat recovery: the recruitment of species of conservation value.

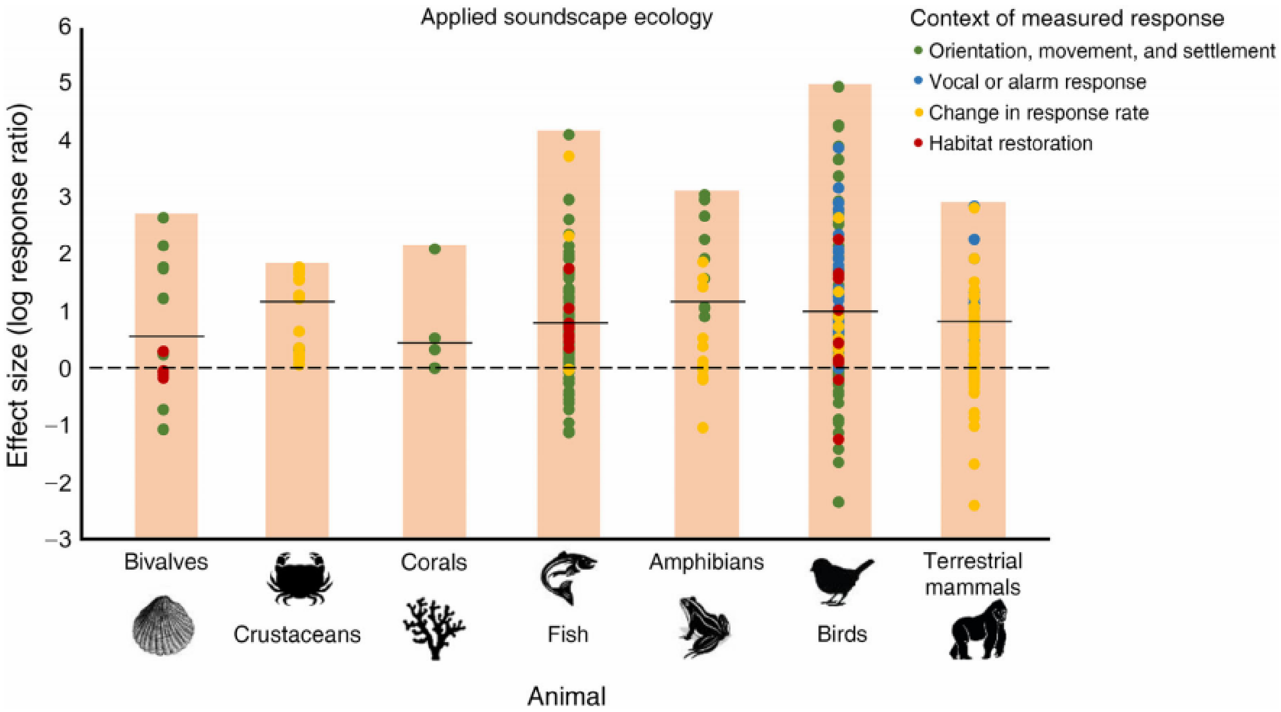

Fig. 1. Effect sizes (log response ratio) of positive and negative effects of sound playback among studies testing the attraction of animals (e.g., to restoration of habitat). The context for these studies is grouped into four categories that assess change to "orientation, movement and settlement," "response rate" of a response, "vocal or alarm response" and "habitat restoration", which assess restoration potential. Horizontal black lines across each bar represent mean effect sizes per animal group.

2.4 Marine soundscapes

2.4.1 The discovery of sound in the sea

Though research on marine sound is relatively new to western science, fishing communities worldwide have listened to underwater animals for hundreds of thousands of years (e.g., by listening through paddling oars pressed against their ears; Winderen 2018). In the 20th century, underwater warfare serendipitously initiated the scientific study of the ocean's biological soundscape. During World War I, submarine activity required research on sonar, hydrodynamics and echolocation to detect torpedoes and reduce drag on torpedoes and submersibles (Johnson et al. 1947, Hastings and Au 2012). The crackling chorus of benthic habitats interfered with this sonar performance and was initially interpreted by the United States military as enemy radar jamming (Johnson et al. 1947, Hasting and Au 2012). Recognising the biological origins of this noise (snapping shrimp) revealed a dynamic and noisy ocean, rather than a silent one.

2.4.2 Marine soundscapes

A diversity of sounds orchestrate marine soundscapes. Mammals vocalise squeaks, squeals, moans and groans (reviewed by Erbe et al. 2017), fish bark, honk, drum and knock (reviewed by Kasumyan 2008) and invertebrates contribute pervasive snaps, cracks, rasps and rumbles (Johnson et al. 1947, Staaterman et al. 2011). There are also abiotic processes like ambient noise (Farina 2014), geophysical sounds like waves (Lindseth and Lobel 2018), and increasingly anthropogenic sounds from activities like shipping and pile driving (Hildebrand 2009). The snapping shrimp (family Alpheidae) are the most ubiquitous soniferous animals in coastal systems (Johnson et al. 1947). They produce high-level snap sounds (up to 210 dB re 1 mPa at 1 m; Schmitz 2002) that are second in loudness only to sperm whale clicks (up to 236 dB re 1 mPa at 1m; Møhl et al. 2003). The shrimps' loud snaps are created by the formation and collapse of cavitation bubbles upon rapid closure of a modified claw (Versluis et al. 2000). The chorus created by aggregated shrimp provides a broadband background crackling sound that can propagate long distances offshore (Nolan and Salmon 1970).

2.4.3 Functional relevance of marine soundscapes

Marine larvae interpret a diversity of sensory cues to locate suitable settlement sites, including visual (Thorson 1964, McFarland 1986), olfactory (Sweatman 1983, Svane and Young 1989) and auditory cues. Visual cues tend to be limited to scales of metres to tens of metres (Kingsford et al. 2002, Leis and McCormick 2002), while olfactory cues can travel far but are dictated by currents and tides (Atema 1988, Leis and McCormick 2002). By contrast, audio cues disperse independently of ocean currents and can therefore convey information to dispersing animals over distances that exceed or rival visual or chemical cues.

Many marine animals are attracted to sound, both as larvae and adults. Several studies have used light traps to observe fish attraction to different types of sound (Simpson et al. 2004, 2008, Tolimieri et al. 2004). Cephalopods respond to low-frequency vibrations by changing their breathing and jetting activity (Packard et al. 1990) and crab larvae orientate toward and settle more in the presence of reef sound (reviewed by Montgomery et al. 2006, Stanley et al. 2011). When exposed to loud vessels, mussels increase their rates of biofouling of hulls (Wilkens et al. 2012). At low acoustic frequencies (10 to <1,000 Hz) adult oysters (*Crassostrea gigas*) close their valves (Charifi et al. 2017). The ubiquity of animal sound production and behavioural responses to sound suggest that acoustic cues play a foundational role in marine ecosystem function (reviewed by Kasumyan 2008).

Researchers have reported varying distances across which sound propagates underwater; from hundreds of metres (Lillis et al. 2014*b*) to several kilometres (McCauley 1997). The distance over which researchers measure sound propagation can vary as a function of which of its components are measured; i.e., sound pressure vs. particle motion (Nedelec et al. 2021). While the majority of studies observe the pressure component, which is relevant for mammals, which use ears for hearing, the particle motion component is uncommonly observed, but represents the component used by the majority of marine animals: fish and invertebrates (Budelmann 1992, Popper and Fay 1993, Popper and Hawkins 2018). The relationship between sound pressure and particle motion are directly related under specific circumstances, yet the technology available to measure particle motion has only recently become commercially available, and their use in aquaria and costal observations remain in their infancy (Nedelec et al. 2021).

The actual distance of detection of sound by animals, however, depends on the hearing ability of the recipient (Kaplan and Mooney 2016) and abiotic factors, such as coastal morphology, depth, salinity and temperature, as well as sound intensity at its source (Radford et al. 2011). Lower frequency sounds propagate across greater distances from their source and understanding the relative sensitivities of animals to this spectrum is a fundamental area of future research. Broadly, fish are known to have peak sensitivity at the lower frequency range (<1.5 kHz), but can hear up to >100 kHz (Popper and Fay 1993, Popper and Hastings 2009, Fay and Popper 2012). Marine invertebrates are potentially sensitive to these low ranges and higher frequencies, including those created by snapping shrimp (2-23 kHz). The gaps in knowledge signal the enormity of future research, including the hearing capabilities and structures that remain unknown for most species and life stages of fish and invertebrates (Mann et al. 2007).

2.5 From soundscapes to muted-scapes

2.5.1 Silencing marine soundscapes

Research suggests that natural marine soundscapes are gradually silencing due to changing climate and intensifying human activities. Ocean acidification is altering the sound production mechanisms of soniferous species (Rossi et al. 2016*a*) and altering community structure and species distributions (Rossi et al. 2016*b*, Sueur et al. 2019). These changes not only influence sound-producing organisms, but also the organisms that use these acoustic cues to navigate to suitable habitat (Sueur et al. 2019).

In some cases, this change is not gradual, but rapid (Indeck et al. 2015, Butler et al. 2016, Gordon et al. 2018). The biological impacts of noise pollution are also becoming clear. Anthropogenic noise masks the acoustic cues used by marine animals, alters vocalisations, interrupts larval settlement, disrupts fish behaviours, alters predator-prey relationships and can cause injury (Clark et al. 2009, Holles et al. 2013). For example, whales have increased risk of gas bubble embolism when they reduce swimming and reduce resurfacing due to naval sonar noise (Fahlman et al. 2014). Whilst some animals are adapting to anthropogenic disturbances (e.g., killer whales increase their vocalisations by 1 dB for every decibel increase in background noise; Holt et al. 2009), other animals are unable to respond (McCauley et al. 2003, Jones et al. 2018). Ongoing environmental and anthropogenic changes to marine ecosystems will likely continue to diminish the acoustic function of marine soundscapes (Rossi et al. 2016*a*, 2017). And in many cases, the historical extraction of marine habitat-forming species (e.g., oyster reefs) would have transitioned soniferous marine habitats into sedimentary barrens centuries ago (McAfee and Connell 2021). With wholesale habitat loss, the function of marine soundscapes is also lost, potentially limiting the capacity of these habitats to naturally recover.

Early research on the utility of soundscape manipulation to boost processes that aid habitat recovery shows potential (Lillis et al. 2014*a*, 2015, Gordon et al. 2019). However, the value of soundscape manipulation to restoration efforts will be context dependent and there is little knowledge on the effect of soundscapes across gradients of recruitment. Furthermore, studies to date have been small in space and time, so we do not know if soundscape manipulation can aid habitat recovery at large spatial scales. And knowledge gaps remain on what constitutes a healthy soundscape and how to best parameterise it over space and time.

2.5.2 Reviving marine soundscapes and function: Oyster restoration case-study

To assess whether habitat restoration can transform degraded soundscapes (“muted-scapes”) back to functional soundscapes, we first compared the soundscapes of natural, partially restored and degraded marine habitats and then assessed how these differences alter recruitment processes. First, we recorded soundscapes associated with three distinct marine habitats of Southern Australia (Gulf St. Vincent, South Australia): a temperate rocky reef ecosystem, a sedimentary barren where oyster reefs historically existed but were lost to dredge fishing (Alleway and Connell 2015), and a large restoration site (20 ha) on which lost oyster reefs are being restored (McAfee et al. 2021; Supporting information B: Section S1). Based on sound pressure levels and snapping shrimp snap counts, we found that acoustic characteristics increased from degraded to healthier habitats; the sedimentary habitat was the quietest, the rocky restoration site louder and natural rocky reef the loudest and contained the most snapping shrimp snaps (Supporting information B: Figs. S2-S4). The restored reef site (3 years old) had intermediate snap counts and volume, indicating that early successional processes on constructed reefs can at least partially restore soundscapes, but technological may be required to speed up the restoration of soundscapes.

In the laboratory, we assessed whether these soundscapes influence the rate of recruitment of Australia’s flat oyster larvae (*Ostrea angasi*), the main reef-building organism targeted for restoration (Supporting information B: Section S2). Our analysis revealed a higher proportion of larval settlement in response to Restoration Reef soundscape playback compared to that of the Lost Reef and no sound control treatments (Fig. 2). These responses point to the value of determining whether oysters recruit in greater densities to natural soundscapes of increasing volume. It is possible that a maximum density of recruitment might be induced, after which increasing volume no longer increases recruitment. Despite these critical questions for developing technology, our results suggest that the historical transformation of reefs to bare sand has degraded the functional role that sounds play in facilitating recruitment.

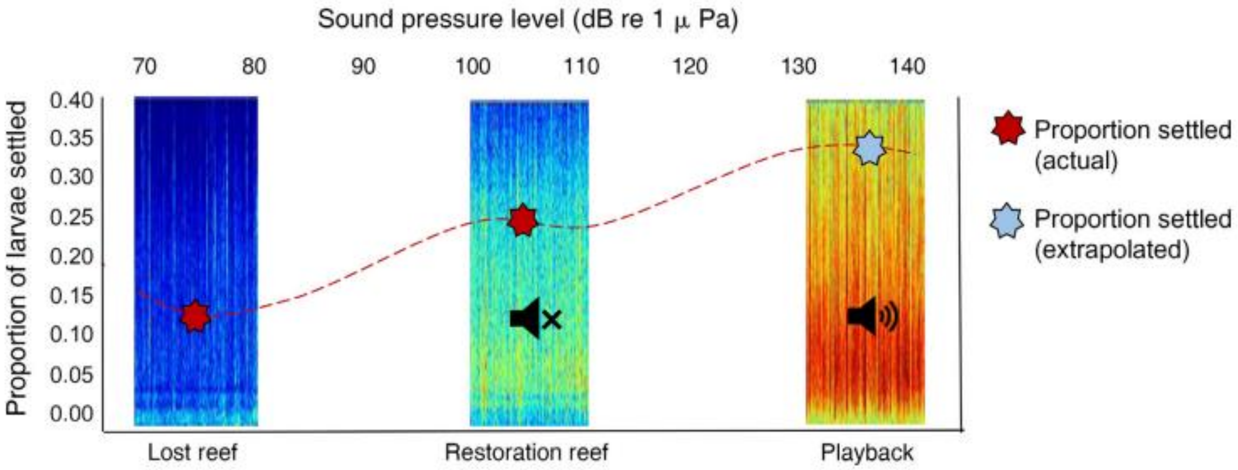

Fig. 2. Diagram conceptualising historical through future soundscapes. Two centuries ago, Australia had extensive native oyster reefs (Alleway and Connell 2015) that were extracted to functional extinction (Lost reef) for which early restoration shows signs of recovering soundscapes (Restoration reef) that could benefit from soundscape enhancement to attract more oysters (Playback). Red stars represent actual proportion of oyster larvae that settle in the presence of sound playback, whilst blue stars represent the hypothetical potential for boosting settlement with sound playback. Spectrograms show recordings from a lost reef, a newly restored reef (3 years old), and an amplified natural reef recording (Supporting information B: Section S2).

By artificially enhancing soundscapes, speaker playback has the potential to boost the early successional stages of reef development. If soundscape playback can increase recruitment of the species targeted for restoration, sound technology appears set to become a useful tool for accelerating restoration projects. The best use of this technology may centre on synchronising its use with other restoration strategies that aim to provide conditions (e.g., settlement substrate) that maximise recruitment. For example, synchronising soundscape enrichment with the timing of recruitment or interventions to provide competitor-free substratum (McAfee and Connell 2020, McAfee et al. 2021) may increase the success of restoration initiatives.

2.6 Conclusion

Returning the function of sound to habitats where it was lost has the potential to kick start restoration projects on a trajectory for recovery. In the marine realm, where the main reef-building species respond to sound, technology for enriching soundscapes has the potential to change the way we restore marine habitats worldwide. However, large technical and biological gaps remain in knowledge and expanding the evidence base for soundscape enrichment over greater temporal and spatial scales is needed to build confidence in this technological solution. Yet, the demonstrated potential to accelerate key restoration processes by orders of magnitude suggest potential for applied soundscape ecology.

Through the use of emerging technologies, there are increasing calls for technological solutions to reduce the cost of restoration and facilitate large-scale restoration (Perring et al. 2018) using an adaptive process of research and development (Anthony et al. 2017). While the role of sound for attracting animals has long been known, acoustic technologies are emerging for use by restoration ecologists and practitioners. We anticipate that technological development will be rapid and fill the current inadequacies of instrumentation and biologists will be open to discovering how the diversity of sounds evoke responses in the animals they seek to save or revive. It is these types of technological innovations that are required if we are to save or revive ecosystems at the scale of our growing ambitions.

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2.9 Supporting information A

Section S1: Literature review

We conducted a systematic literature search of peer-reviewed applied soundscape ecology literature spanning over 80 years (1940 and 2021) using ‘Web of Science’. We considered applied ‘soundscape ecology’ papers as those assessing the capacity of sound playback to enhance behavioural responses to sound cues among target animal groups in both terrestrial and marine realms. Our search criteria considered papers belonging to one of four categories: 1) those papers using speaker playback to stimulate processes for habitat restoration (category ‘habitat restoration’), 2) papers testing the attraction, settlement, or redistribution of animals to playback of sounds (category ‘orientation, movement and settlement’), 3) papers that demonstrate vocal or alarm responses (category ‘vocal or alarm response’), and 4) papers that demonstrate a change in behaviour response rate (category ‘response rate’). Papers were not included that only documented physiological responses with no clear ecological outcomes. Papers were included if they used broadcast sound including natural soundscapes, ambient sound, conspecific/heterospecific calls and artificially generated sounds. We excluded papers using playback of predator and anthropogenic sounds with the intent of seeing deleterious responses, as these have been proven to have deleterious effects rather than ‘attraction/encouragement’ effects. Papers were included that provided animal response to both control and sound treatments, from which we calculated effect sizes in the form of log response ratios. Both significant and non-significant responses to sound were included. In ‘Web of Science’, we ran our search terms for the categories: biology, ecology, zoology, biodiversity conservation, environmental sciences, marine freshwater biology, fisheries and biophysics. Our specific search terms were:

> TI=((sound* OR acoustic* OR soundscape* OR noise* OR auditory*) AND (enhanc* OR enrich* OR restor* OR manip* OR settl* OR recruit* or attract* OR respon* OR orient* OR relocat*))

This search returned 965 possibly relevant papers. Papers that met our search criteria were reviewed in full and references therein were followed to find a total of 67 relevant papers, that encompassed 91 individual studies (Table S1). Of the 67 papers, 33 were marine and 34 were terrestrially focused. These papers were sorted by animal group and into the four categories described above for graphical presentation (Fig. 1, manuscript proper).

Table S1. Papers on applied soundscape ecology, from 1940 to 2021. Effect size are logged response ratios between the control and sound treatment. '*' indicates a significant result from a study.

Author, year	**Paper, journal**	**Group/Species**	**Country**	**Experiment Aim**	**Effect size (logged response ratio)**
Ahlering et al., 2006	Conspecific attraction in a grassland bird, the Baird's sparrow, *Journal of Field Orinthology*	Baird's sparrow (*Ammodramus bairdii*)	North Dakota, USA	Role of playback of conspecifics in attracting sparrows to suitable breeding habitat	1.7918*
Allen 1977	Response of willow grouse chicks to auditory-stimuli 1. Preference for hen grouse calls, *Behavioural Processes*	Willow grouse (*Lagopus lagopus lagopus*)	Karlsøy, Norway	Response of willow grouse to playback of grouse hen calls	2.1972* 2.5649* 2.5649*
Andrews et al., 2015	When to use social cues: conspecific attraction at newly created grasslands, *The Condor*	Grasshopper sparrow (*Ammodramus savannarum*)	Illinois, USA	Influence of playback of conspecific in attracting sparrows to newly created habitat	0.6311* -0.0645 0.1782
Anich and Ward, 2017	Using audio playback to expand the geographic breeding range of an endangered species, *Biodiversity Research*	Kirtland's warbler (*Setophaga kirtlandii*)	Wisconsin, USA	Extending the geographic breeding range of warblers using playback of conspecifics	1.3863* 1.7047*
Buxton and Jones, 2012	An experimental study of social attraction in two species of storm-petrel by acoustic and olfactory cues, *The Condor*	Leach's storm-petrel (*Oceanodroma leucorhoa*) Fork-tailed storm-petrel (*Oceanodroma furcata*)	Aleutian Islands, Alaska, USA	Effectiveness of playback of conspecifics in encouraging recolonisation of storm-petrels	0.3365* 0.6931* 0.8755* 2.0015* 2.6254* 2.9716* 3.4012* 3.6889* 3.9318* 4.9767* -2.3026 0.2877 0.4055 0.6931

Buxton et al., 2015	Use of chorus sounds for location of breeding habitat in 2 species of anuran amphibians, *Behavioural Ecology*	American toad (*Anaxyrus americanus*) Cope's gray tree frog (*Hyla chrysoscelis*)	Indiana, USA	Use of acoustic cues in attracting toads and frogs to new breeding ponds	1.9459* 3.0991*
Carey et al. 1997	Comparison of the attractiveness of acoustic and visual stimuli for brushtail possums	Brushtail possum (*Trichosurus vulpecula*)	Hamilton, New Zealand	Whether playback of a beep sound attracts possums into traps	1.1787*
Clark et al. 2012	Increasing breeding behaviors in a captive colony of northern bald ibis through conspecific acoustic enrichment, *Zoo Biology*	Northern bald ibis (*Geronticus eremita*)	Bronx Zoo, New York, USA and Austria	Whether playback of conspecific breeding vocalisations increases reproductive behaviours in the ibis	0.1076* 0.1466* 0.2320* 0.2378* 0.3448* 0.3448* 0.4082* 0.4292* 0.5550* 0.7631* 0.9269*
DeJong et al., 2015	Attracting songbirds with conspecific playback: a community approach, *Behavioural Ecology*	Ovenbird (*Seiurus aurocapillus*) Black-throated green warbler (*Setophaga virens*) Rose-breasted grosbeak (*Pheucticus ludovicianus*) Eastern wood-pewee (*Contopus virens*) Great-crested flycatcher (*Myiarchus crinitus*) Hermit thrush (*Catharus guttatus*)	Michigan, USA	Use of multispecies playback in establishing nesting territories in migratory songbirds	0.1431* 0.1484* 0.3254* 0.3677* 0.4274* 0.9163* 0.9163* 0.9808* 1.5041* 1.6094* 1.7636* 2.1972* 2.8332* -2.3026 -2.3026 -1.6094 -1.3863 -1.3863 -1.0986 -0.9163 -0.8473 -0.8473 -0.6931 -0.5596 -0.4055 -0.3567 -0.1355 -0.1330 -0.0800 -0.0741 -0.0690 -0.0645 -0.0488 -0.0408 -0.0364 -0.0180 -0.0047 0.0000 0.0000 0.0077 0.0165 0.0235 0.0351 0.0645 0.0690

					0.0741 0.0800 0.0953 0.1000 0.1009 0.1018 0.1054 0.1178 0.1484 0.1542 0.1823 0.1823 0.1823 0.4055 0.4055 0.5108 0.5596 0.8755 1.2993
Eggleston et al. 2015	Soundscapes and larval settlement: larval bivalve responses to habitat-associated underwater sounds, *Advances in Experimental Medicine and Biology*	Eastern oyster (*Crassostrea virginica*) Hard clam (*Mercenaria merceneria*)	-	Settlement of bivalves when exposed to habitat associated underwater sounds	0.1512* 0.1719* -0.1542
Eriksson and Wallin, 1986	Male bird song attracts females: a field experiment, *Behavioural Ecology and Sociobiology*	Pied flycatcher (*Ficedula hypo- leuca*) Collared flycatcher (*Ficedula albicollis*)	Oland and Hosjön, Sweden and	Attraction in birds to playback of singing birds	1.0986* 1.7918* 2.1972*
Evans, 1973	Differential responsiveness of young ring-billed gulls and her- ring gulls to adult vocalizations of their own and other species, *Canadian Journal of Zoology*	Ring-billed gulls (*Larus delawarensis*)	Manitoba, Canada	Effect of bird calling on individual call recognition	0.2766* 0.3945* 0.6751* 0.8362* 0.9163* 1.2417* 1.2879* 1.3584* 1.4469* 1.6681* 1.7164* 1.7663* 1.8506* 1.9588* 1.9600* 2.1446*
Gordon et al. 2018	Habitat degradation negatively affects auditory settlement behaviour of coral reef fishes, *Proceedings of the National Academy of Sciences*	Coral reef fishes	Lizard Island, Queensland, Australia	Attraction of fish to post degradation and pre-degradation reef sounds	0.5000* 3.0000*
Gordon et al., 2019	Acoustic enrichment can enhance fish community development on degraded coral reef habitat, *Nature Communications*	Coral reef fish	Lizard Island, Queensland, Australia	Use of playback of healthy reef sound in increasing fish settlement and retention to degraded habitat	0.7324* 0.6061* 0.6031* 0.5108* 0.6286* 0.5754* 0.8267* 0.7621* 0.8362* 0.4055*

					1.0986* 1.0986* 1.7918*
Hahn and Silverman, 2007	Managing breeding forest songbirds with conspecific song playbacks, *Animal Conservation*	Black-throated blue warbler (*Dendroica caerulescens*)	Michigan, USA	Whether conspecific playback influences settlement patterns of blue warblers	0.6140*
Huijbers et al. 2012	A test of the senses: fish select novel habitats by responding to multiple cues, *Ecology*	French grunt (*Haemulon flavolineatum*)	Curaçao, the Carribean	Response of fish to auditory cues	0.6712* 0.8978* -0.4055 -0.2162 0.0282 0.3773
Impekoven, 1976	Responses of laughing gull chicks (*larus-atricilla*) to parental attraction-calls and alarm-calls, and effects of prenatal auditory experience on responsiveness to such calls, *Behaviour*	Laughing gull (*Larus atricilla*)	New Jersey, USA	Response of laughing gull chicks to adult calls	1.3863* 2.0794* 3.2189* 3.9120*
James et al., 2015	Investigating behaviour for conservation goals: conspecific call playback can be used to alter amphibian distributions within ponds, *Biological Conservation*	Green and golden bell frog (*Litoria aurea*)	Ash Island, New South Wales, Australia	Whether conspecific calls can manipulate distributions of frogs to ponds areas	1.0986* 1.6094*
Jeffs et al. 2003	Crabs on cue for the coast: the use of underwater sound for orientation by pelagic crab stages, *Marine Freshwater Research*	Hermit crab (*Pagurus* spp.) Porcellanid crab (*Petrolisthes elongatus*) Grapsid crab (*Helice crassa*)	Omaha Bay, New Zealand	Light traps with a sound treatment and control treatment to attract crustacea.	0.6187* 0.6725* 0.9762*
Kress, 1983	The use of decoys, sound recordings, and gull control for re-establishing a tern colony in Maine, *Colonial Waterbirds*	Arctic tern (*Sterna paradisae*)	Maine, USA	Re-establish breeding populations of Arctic terns using decoys and acoustic attractants	0.4868* 1.6094*
Leis and Lockett, 2005	Localisation of reef sounds by settlement-stage larvae of coral-reef fishes (*Pomacentridae*), *Bulletin of Marine Science*	Damselfish (*Pomacentridae*)	Lizard Island, Queensland, Australia	Ability or fish larvae to hear and localise reef sounds in linear selection chambers	0.2231* 1.0609* 2.0209*
Leis et al. 2003	Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some	Damselfish (*Pomacentridae*) Goatfish (*Mullidae*) Emperors (*Lethrinidae*) Cardinalfish (*Apogonidae*)	Lizard Island, Queensland, Australia	Effect of light traps with broadcast reef sound on fish catches	0.1726* 0.3209* 0.3644* 0.7191* 0.8020* 0.9390* 0.9491*

	times, *Journal of Fish Biology*	Combtooth blennies (*Blenniidae*)			1.2738*
Lenske and La, 2014	White-throated sparrows alter songs differentially in response to chorusing anurans and other background noise, *Behavioural Processes*	White-throated sparrows (*Zonotrichia albicolis*)	Ontario, Canada	Playback of choruses, car noise and wind to see short term changes in sparrow singing behaviour	0.0438* 0.0580* 0.1495*
Lillis et al., 2014	Oyster larvae settle in response to habitat-associated underwater sounds, *PLOS ONE*	Eastern oyster (*Crassostrea virginica*)	North Carolina, USA	Investigate the effect of habitat-associated estuarine sound on the settlement patterns of oysters	0.1857* 0.0504* 0.6109*
Lillis et al., 2015	Soundscape manipulation enhances larval recruitment of a reef-building mollusc, *PeerJ*	Eastern oyster (*Crassostrea virginica*)	North Carolina, USA	How settlement of oyster larvae is affected by replayed habitat-related sounds	0.3392* 0.3392* 0.3392* 0.3392* -0.1178 -0.0572 -0.018 -0.0053
Lillis et al. 2018	Soundscapes influence the settlement of the common Caribbean coral *Porites astreoides* irrespective of light conditions, *Royal Society Open Science*	Common Carribean coral (*Porites astreoides*)	Tektite reef and Cocoloba reef, US Virgin Islands	Settlement of coral to soundscapes of different sound levels and frequencies	0.7577* 0.9555* -0.1054 0.1431
Lugli et al. 1996	The importance of breeding vocalizations for mate attraction in a freshwater goby with a composite sound repertoire, *Ethology Ecology and Evolution*	Goby (*Padogobius martensii*)	-	Effect of sound playback on mate attraction	0.452* 1.3863*
MacDonald et al. 2019	Manipulating social information to promote frugivory by birds on a Hawaiian island, *Ecological Applications*	Red-billed leiothrix (*Leiothrix lutea*) Japanese white-eye (*Zosterops japonicus*) Red-whiskered bulbul (*Pycnonotus jocosus*) Red-vented bulbul (*Pycnonotus cafer*)	O'ahu, Hawaii, USA	Whether playback of bird vocalisations increases visitations and frugivory on fruiting plants	1.3626* 2.6835*
Moskát and Hauber, 2019	Sex-specific responses to simulated territorial intrusions in the common cuckoo: a dual function of female acoustic signalling, *Behavioural Ecology and Sociobiology*	Common cuckoo (*Cuculus canorus*)	Apaj, Hungary	Responses or common cuckoo to playback of calls	0.8824* 1.4065* 2.7726* 3.7044* -0.0572

Myrberg et al. 1969	Shark attraction using a video-acoustic system, *Marine Biology*	Sharpnose shark (*Rhizoprionodon*) Caribbean reef shark (*Carcharhinus springeri*) Silky shark (*Carcharhinus falciformis*) Nurse shark (*Ginglymostoma cirratum*)	Bimini, Bahamas	Attraction of sharks to sound playback	4.1352*
Myrberg et al. 1972	Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source, *Bulletin of Marine Science*	Silky shark (*Carcharhinus falciformis*)	Straits of Florida, Florida, USA	Playback of different signals to attract sharks	1.2186*
Nelson and Johnson, 1972	Acoustic attraction of Pacific reef sharks: effect of pulse intermittency and variability, *Neuroscience and Behaviour*	Silky shark (*Carcharhinus menisorrah*) (*Carcharchinus albimarginatus*) (*Carcharhinus melanopterus*) Whitetip reef shark (*Triaenodon obesus*) Sicklefin lemon shark (*Hemigaleops fosteri*)	Eniwetok atoll, Marshall Islands	Response of sharks to low frequency pulsed sounds	1.3863* 1.4469* 1.6094* 1.7346* 1.7492* 1.7492* 1.7918* 1.9661* 2.3979*
Podolsky, 1990	Effectiveness of social sitmuli in attracting Laysan albatross to new potential nesting sites, *The Auk*	Laysan albatross (*Diomedea immutabilis*)	Kuaui, Hawaii, USA	Whether the sight and sound of established albatross breeders encourage first-time breeders to join existing colonies	0.7288* 0.7813*
Podolsky and Kress, 1992	Attraction of the endangered dark-rumped petrel to recorded vocalisations in the Galapagos Islands, *The Condor*	Dark-rumped petrel (*Pterodroma phaeopygia*)	Galapagos Islands	Whether playback of conspecifics attracts petrels to habitats	0.1829* 1.6818* 1.7111* -1.2040 -0.1542
Radford et al. 2007	Directional swimming behaviour by five species of crab postlarvae in response to reef sound, *Bulletin of Marine Science*	Red rock crab (*Guinusia chabrus*) Seaweed crab (*Notomithrax ursus*) Smooth shore crab (*Cyclograpsus lavauxi*) Common shore crab (*Hemigrapsus edwardsii*) Hermit crab (*Pagurus spp.*)	Omaha Bay, New Zealand	Orientation of crab postlarvae to underwater sound playback in a binary choice chamber	0.7770* 1.2879*
Radford et al. 2011	Juvenile coral reef fish use sound to locate habitats, *Coral Reefs*	Coral reef fish	Lizard Island, Queensland, Australia	Nocturnal movement of juvenile reef fish to reefs in response to broadcast habitat-specific acoustic cues	0.3952* 0.5878* 0.6396* 0.7577* 1.2528 1.3863 1.7918 1.9459 2.1972
Robbins and Margulis, 2014	The effects of auditory enrichment on gorillas, *Zoo Biology*	Western lowland gorillas (*Gorilla gorilla gorilla*)	Buffalo Zoo, New York, USA	Effectiveness of naturalistic sounds, classic music and rock music on reducing stereotypical behaviour in gorillas	0.4700* 0.7538* 0.7885* 0.9163* 1.3863* 1.5488*

Rollo et al. 2007	Attraction and localisation of round goby (*Neogobius melanostomus*) to conspecific calls, *Behaviour*	Round goby (*Neogobius melanostomus*)	Presque Isle Bay, Pennsylvania, USA	Response to playback of low frequency pulsed sounds	0.3712* 0.4700* 0.5557* 0.6131* 2.1203* -0.0247 0.0513
Sabet et al. 2016	Behavioural responses to sound exposure in captivity by two fish species with different hearing ability, *Animal Behaviour*	Zebrafish (*Danio rerio*) Lake Victoria cichlids (*Haplochromis piceatus*)	-	Effect of sound exposure on fish swimming speeds	2.3514* 3.7376* 0.0000 0.0000
Schepers and Proppe, 2016	Song playback increases songbird density near low to moderate use roads, *Behavioural Ecology*	Black-throated green warbler (*Setophaga virens*) Eastern wood-pewee (*Contopus virens*) Great crested flycatcher (*Myiarchus crinitus*) Hermit thrush (*Catharus guttatus*) Ovenbird (*Seiurus aurocapilla*) Rose-breasted grosbeak (*Pheucticus ludovicianusi*)	Michigan, USA	Whether playback of song from migratory birds increased territory establishment along roads	-0.3030* -0.3090* -0.3420* -0.3540* -0.621* 0.3160* 0.4690* 0.5760* 1.1640* 1.2490* 1.7470* 1.8830* 3.6190* 4.5380* -0.2330 -0.2220 -0.2170 -0.1540 -0.0510 -0.0420 -0.0400 -0.0320 0.0430 0.0880 0.1060 0.1405 0.2340 0.8380
Schwarzkopf and Alford, 2007	Acoustic attractants enhance trapping success for cane toads, *Wildlife Research*	Cane toad (*Rhinella marina*)	Queensland, Australia	Whether playback of conspecific mating calls attracts cane toads	0.9555* 1.0986* 1.118*
Shepherdson et al. 1989	Auditory enrichment for Lar gibbons *Hylobates lar* at London Zoo, *International Zoo Yearbook*	Lar gibbon (*Hylobates lar*)	London zoo, London, USA	Response of gibbons to broadcast gibbon vocalisations	0.7655* 1.0704* 1.0986* 1.3863* 1.3863* 1.9459*
Siegel et al., 2018	Using conspecific broadcast for willow flycatcher restoration, *Avian Conservation and Ecology*	Willow flycatcher (*Empidonax traillii*)	California, USA	Effectiveness of acoustic cues in restoring flycatchers to suitable but unoccupied restored habitat	1.6094*
Simpson et al. 2004	Attraction of settlement-stage coral reef fishes to reef noise, *Marine Ecology Progress Series*	Coral reef fish	Lizard Island, Queensland, Australia	Whether light traps with loudspeakers broadcasting reef sound attract settlement stage reef fishes	0.1749* 0.7082*
Simpson, 2005	Homeward sound, *Science*	Cardinalfish (*Apogonidae*)	Lizard Island, Queensland, Australia	Settlement behaviour of fish in the presence of reef sounds	0.1178* 0.5878* 0.6931*

		Damselfish (*Pomacentridae*)			0.6931* 0.7059* 0.7419* 0.7655* 1.3863* 0.0645 0.2231 0.2231
Simpson et al. 2008a	Settlement-stage coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef noise, *Animal Behaviour*	Coral reef fish	Lizard Island, Queensland, Australia	Which components of broadcast reef sounds alongside light traps evoke behavioural responses in larval fish	0.3087* 0.6385* -1.0531 -1.0296 0.2877
Simpson et al., 2008b	Nocturnal relocation of adult and juvenile coral reef Fishes in response to reef noise, *Coral Reefs*	Cardinalfish (*Apogonidae*) Goby fish (*Gobiidae*) Sandperches (*Pinguipedidae*)	Lizard Island, Queensland, Australia	Whether sound is used by adult and juvenile reef fishes as an orientation cue in nocturnal movements	0.2231* 0.4568* 0.6506* 0.9445* 1.0068* -1.0986 -1.0986 -0.9163 -0.6931 -0.693 -0.5596 -0.5108 -0.4055 -0.3567 -0.2231 -0.2076 -0.1335 -0.1335 -0.1335 -0.1335 -0.1178 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0408 0.0953 0.1054 0.1398 0.1542 0.1542 0.3185 0.4055 0.4055 0.4418 0.6931 0.6931 0.6931 0.6931 1.3863 1.3863 2.0794
Simpson et al. 2010	Behavioural plasticity in larval reef fish: orientation is influenced by	Ambon damsel (*Pomacentrus amboinensis*)	Lizard Island, Queensland, Australia	Using acoustic conditioning and binary choice chambers to determine whether responses to acoustic	0.3747* 0.4055* 0.5108* 0.2336 0.3747

	recent acoustic experiences, *Behavioural Ecology*	Charcoal damsel (*Pomacentrus brachialis*) Lemon damsel (*Pomacentrus moluccensis*) Blue-scribbled damsel (*Pomacentrus nagasakiensis*)		cues are fixed behaviours or influenced by recent acoustic experience	0.3878
Soltis et al. 2002	Squirrel monkey chuck call: vocal response to playback chucks based on acoustic structure and affiliative relationship with the caller, *American Journal of Primatology*	Gothic arch squirrel monkeys (*Saimiri sciureus*)	-	Observing behaviours to playback of vocalisations	0.1054* 0.2666* 0.4055* 0.5108* 0.6061* 0.7985* 0.9383* 1.0986* 1.0986* 1.0986* 1.1701* 1.2528* 1.3863* 1.3863* 1.9459* 1.9459* 2.3026* 2.8904*
Sosa-López et al. 2017	Sexual differentiation and seasonal variation in response to conspecific and heterospecific acoustic signals, *Ethology*	White-bellied wren (*Uropsila leucogastra*)	Jalisco, Mexico	Examining of territorial behaviour with playback of conspecific and heterospecific songs	0.6931* 1.0986* 1.3863* 1.3863* 1.6094* 2.0794* 2.3979* 2.7081* 2.8332* 2.9444* 2.9444* 2.9444*
Sperry et al., 2019	Conspecific attraction as a management tool for endangered and at-risk species on military lands, *Construction Engineering Research Laboratory and Engineer Research and Development Center*	Grasshopper sparrow (*Ammodramus savannarum*) Savannah sparrow (*Passerculus sandwichensis*), Golden-winged warbler (*Vermivora chrysoptera*) Upland sandpiper (*Bartramia longicauda*) Prairie warbler (*Setophaga discolor*) Eastern towhee (*Pipilo erythrophthalmus*) Northern bobwhite (*Colinus virginianus*) Blue grosbeak (*Passerina caerulea*) Brown thrasher (*Toxostoma rufum*) Painted bunting (*Passerina ciris*)	Wisconsin, Louisiana, USA	Whether conspecific attraction can encourage colonisation of restored habitats by birds and amphibians	1.0498* 2.3026* 0.1335 0.1576
Stanley et al. 2010	Induction of settlement in crab megalopae by ambient underwater reef sound, *Behavioural Ecology*	Shore crab (*Grapsidae*) Common rock crab (*Hemigrapsus sexdentatus*) Smooth shore crab (*Cyclograpsus lavauxi*) Stalk-eyed mud crab (*Macrophthalmus hirtipes*)	Lizard Island, Queensland, Australia	Settlement behaviour and time to metamorphose with exposure to reef sound	1.3000* 1.6000* 1.8000*

Stanley, 2011	Behavioural response thresholds in New Zealand crab megalopae to ambient underwater sound, *PLOS ONE*	Common rock crab (*Hemigrapsus sexdentatus*) Smooth shore crab (*Cyclograpsus lavauxi*) Purple rock crab (*Leptograpsus variegatus*) Tunnelling mud crab (*Austrohelice crassa*)	-	Behavioural responses of crab megalopae to playback or reef sounds in the lab	1.2500* 1.3000* 1.5600* 1.6800* 1.7500*
Stanley et al. 2012	Location, location, location: finding a suitable home among the noise, *Proceedings of the Royal Society B: Biological Sciences*	Common rock crab (*Hemigrapsus sexdentatus*) Smooth shore crab (*Cyclograpsus lavauxi*) Hairy coral crab (*Cymo andreossyi*) Common decorator crab (*Schizophrys aspera*) Thin-shelled rock crab (*Grapsus tenuicrustatus*)	Leigh Marine Laboratory, New Zealand and Lizard Island, Queensland, Australia	Effect of sound playback on time to metamorphose in crabs	0.1006* 0.1749* 0.2253* 0.3023* 0.3655* 0.6733*
Stobutzki and Bellwood 1998	Nocturnal orientation to reefs by late pelagic stage coral reef fishes, *Coral Reefs*	Cardinalfish (*Apogonidae*) Damselfish (*Pomacentridae*)	Lizard Island, Queensland, Australia	Nocturnal orientation of reef fish to natural sound cues	0.1795* 0.6381* 0.8071*
Stocks et al. 2012	Response of Marine Invertebrate Larvae to Natural and Anthropogenic Sound: A Pilot Study, *The Open Marine Biology Journal*	Pacific Oyster (*Magallana gigas*)	-	Response of invertebrate larvae to different sound playback	0.3285* -0.0200 0.3102
Suca et al. 2020	Variable and spatially explicit response of fish larvae to the playback of local, continuous reef soundscapes, *Marine Ecology Progress Series*	Blenny (*Labrisomidae*) Damselfish (*Pomacentridae*) Lizardfish (*Synodontidae*) Snapper (*Sparidae*)	St John, US Virgin Islands	Response of fish to playback of reef sounds	0.6931* 0.9808*
Testud et al. 2020	Acoustic enrichment in wildlife passages under railways improves their use by amphibians, *Global Ecology and Conservation*	Spiny toad (*Bufo spinosus*) Fire salamander (*Salamandra salamandra*) Agile frog (*Rana dalmatina*) Edible frog (*Pelophylax* kl. *esculentus*) Pool frog (*Pelophylax* kl. *Lessonae*) Alpine newt (*Ichthyosaura alpestris*) Marbled newt (*Tirturus marmoratus*) Northern crested newt (*Triturus cristatus*)	Pays-de-la-Loire, France	Whether broadcast mating calls makes amphibians cross passages more quickly and complete the crossings	0.4140* 0.5416* 1.4553* 1.6051* 1.8740* -1.0116 -0.1823 -0.1335 -0.1335 -0.1252 0.0000 0.0632 0.1355
Tolimieri et al. 2000	Ambient sound as a cue for navigation in reef fish larvae,	Triplefin (Tripterygiidae) Pilchard (*Clupeidae*)	Omaha Bay, New Zealand	Attraction of fish to light traps with underwater speakers broadcasting reef sounds	0.2950* 1.8281* 2.6799* 0.2630 0.2950

	Marine Ecology Progress Series				
Tolimieri et al. 2004	Directional orientation of pomacentrid larvae to ambient reef sound, *Coral Reefs*	Damselfish (*Pomacentridae*)	Lizard Island, Queensland, Australia	Attraction of larval reef fish to reef sound playback in a binary choice chamber	1.1111*
Vélez et al. 2017	The signal in noise: acoustic information for soundscape orientation in two north American tree frogs, *Behavioural Ecologyi*	Green tree frog (*Hyla cinerea*) Cope’s gray tree frog (*Hyla chrysoscelis*)	-	Orientation response of frogs to natural and artificial sounds	2.3026* 2.7081* 2.9957*
Villain et al. 2016	Songbird mates change their call structure and intrapair communication at the nest in response to environmental noise, *Animal Behaviour*	Zebra finch (*Taeniopygia guttata*)	Saint-Etienne, France	Playback of wind noises and silent control to see changes in duets	0.6931* 0.9343*
Virzi et al., 2012	Effectiveness of artificial song playback on influencing the settlement decisions of an endangered resident grassland passerine, *The Condor*	Cape sable seaside sparrow (*Ammodramus maritimus mirabilis*)	Florida, USA	Influence of conspecific song playback on attraction of sparrows to suitable breeding habitat	2.3026*
Wallace et al. 2013	An investigation into the use of music as potential auditory enrichment for moloch gibbons (*Hylobates moloch*), *Zoo Biology*	Moloch gibbon (*Hylobates moloch*)	Kent, UK	Playback of classical music to see response behaviour in gibbons	0.2754* 0.6790* 0.9110* 2.8526* -2.3910 -1.6610 -0.9843 -0.8473 -0.7415 -0.400 -0.3854 -0.2785 -0.2253 -0.1731 -0.1304 -0.0824 -0.0693 -0.0567 -0.0323 0.0374 0.0374 0.0680 0.1484 0.1598 0.1611 0.1611 0.2231 0.2789 0.3712 0.3747 0.5741 0.5857 0.5910 0.6143

					0.7055 0.7161 0.8771 1.0033 1.0213 1.2875 1.2928
Ward and Schlossberg, 2004	Conspecific attraction and the conservation of territorial songbirds, *Conservation Biology*	Black-capped vireo (*Vireo atricapilla*)	Texas, USA	Whether conspecific attraction in vireos occurs when exposed to playback of vocalisations	4.2905* 4.3175*
Wilkens, 2012	Induction of settlement in mussel (*Perna canaliculus*) larvae by vessel noise, *Biofouling*	Green-lipped mussel (*Perna canaliculus*)	Leigh Marine Laboratory, Auckland, New Zealand	Biofouling response of mussels to underwater vessel sounds	1.2500* 1.2900* 1.6700* 2.6700*
Wilson and Dill, 2002	Pacific herring respond to simulated odontocete echolocation sounds, *Canadian Journal of Fisheries and Aquatic Sciences*	Herring (*Clupea pallasii*)	Bamfield, British Columbia, Canada	Response of herring to broadband bisonar sounds	0.3185* 1.4500* 1.7000*

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2.10 Supporting information B

Section S1: Methods for soundscape data

Site description

Acoustic sampling for soundscape characterisation for this study was undertaken in Gulf St Vincent, South Australia (Fig. S1). In the mid-19th century, Gulf St Vincent was characterised by gulf-wide oyster (*Ostrea angasi*) reefs that were extirpated by an oyster dredged fishery by the early 20th century (Alleway and Connell 2015). In the mid-20th century, extensive populations of *Heterozostera* seagrass, scallops, bryozoans, and *Malleus* and *Pinna* bivalves were still present throughout the Gulf (Shepherd and Sprigg 1976). However, surveys in the early 2000s revealed only some *Posidonia* and *Amphibolis* spp. seagrass meadows (Bryars et al. 2008), with extensive barren sedimentary flats characterising much of the Gulf. This suggests a loss of habitat complexity attributed, at least in part, to increased water turbidity and nutrient input (Connell et al. 2008, Gorman et al. 2009), and damage from trawling (Tanner 2005).

To characterise the soundscapes of habitats that are indicative of how the Gulf has changed, we sampled three different habitat types; 1) sedimentary habitats at locations where oyster reefs were historically lost (‘Lost Reef’), 2) boulder reefs constructed in sedimentary habitats to restore lost oyster reefs (‘Restoration Reef’) and 3) a natural rocky reef system (‘Natural Reef’) (Fig. S1). These were chosen because they represent a gradient in physical and biological complexity that may equate to a gradient in sound production. All acoustic samples were made during the ‘dawn chorus’ (within one hour of sunrise) at high tide. Sites within each habitat type were positioned 100-350 metres apart, and all were in 4-8 m of water. The Restoration Reef recordings were recorded on Windara Reef, Australia’s largest oyster reef restoration project constructed where native reefs were historically lost. Along the 1.1 km Windara Reef, we sampled n = 3 restoration reef sites, each of which were sampled at two time points (Table S1). The Lost Reef recordings were taken from n = 4 sedimentary habitat sites, each sampled at two time points. This sedimentary site was chosen because is it similar to the Windara Reef site (12 km away) but lacks constructed reefs, and is devoid of vegetation or epifaunal bivalves (e.g. *Pinna bicolor*). Our Natural Reef recordings were taken from $n = 4$ locations along Edithburgh's coastline, each sampled at two time points. This rocky reef habitat was chosen because it is considered relatively 'natural', having not been dredged or intensively fished, and is the closest rocky reef habitat on the same coastline as the other two habitat types (Fig. S1). It is characterised by a mosaic of predominately *Ecklonia radiata* kelp forests, *Cystophera* and *Sargassum*, which are the species associated with rocky reef habitat in the Gulf St Vincent (Connell and Irving, 2008) (See table S1 for site details).

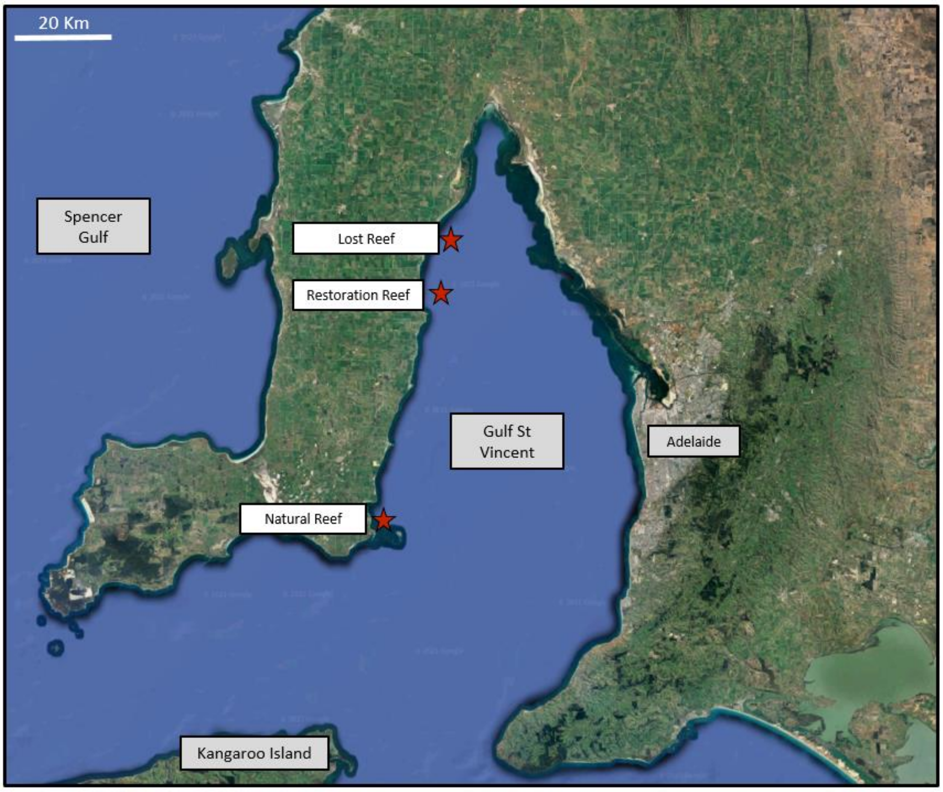

Fig. S1. Map showing the study sites (red stars) in Gulf St Vincent, South Australia, where we recorded soundscapes of three habitat types: sedimentary habitat where oyster reefs were historically lost ('Lost Reef'), sedimentary habitat where reefs have been constructed to restore lost oyster reefs ('Restoration Reef'), and a natural rocky reef habitat ('Natural Reef').

Table S1. Summary of our study sites for soundscape data, including GPS coordinates, habitat type, month and lunar phase during which the recordings were taken. All recordings were made during the 'dawn chorus' (within one hour of sunrise), at high tide in 4-8 metres of water.

Location/Site	**GPS Coordinates**	**Habitat Type**	**Month/ Lunar Phase**
Lost Reef, Site A	-34.406948, 137.945561	Sedimentary	April (new) June (new)
Lost Reef, Site B	-34.403853, 137.947220	Sedimentary	April (new) June (new)
Lost Reef, Site C	-34.408358, 137.940493	Sedimentary	April (new) June (new)
Lost Reef, Site D	-34.404463, 137.946173	Sedimentary	April (new) June (new)
Restoration Reef, Site A	-34.511444, 137.897750	Restoration Oyster Reef	April (new) June (new)
Restoration Reef, Site B	-34.508528, 137.899583	Restoration Oyster Reef	April (new) June (new)
Restoration Reef, Site C	-34.507306, 137.901861	Restoration Oyster Reef	April (new) June (new)
Natural Reef, Site A	-35.080599, 137.748447	Natural Reef	April (new) June (new)
Natural Reef,, Site B	-35.081116, 137.748708	Natural Reef	April (new) June (new)
Natural Reef, Site C	-35.081523, 137.748608	Natural Reef	April (new) June (new)
Natural Reef, Site D	-35.080922, 137.749289	Natural Reef	April (new) June (new)

Data collection

To characterise and compare the acoustic characteristics of the Lost Reef, Restoration Reef and Natural Reef sites, we recorded their ambient soundscapes. At each of our selected sampling sites, we deployed calibrated ST202 hydrophones (Ocean Instruments, flat frequency response 0.1-30 kHz, sensitivity −169 dB re 1 V/μPa) set to a sampling frequency of 48 kHz (24 bit), and set to record for two minutes every fifteen minutes. Hydrophones were anchored one metre above the seafloor and remained suspended using a sub-surface buoy. Recordings were made at dawn in order to capture one of the snapping shrimp’s most bioacoustically active periods (Radford et al. 2010, Lillis et al., 2014a, Bohnenstiehl et al., 2016). For each of the two time periods (April and June 2019), recordings among sites were made over two days with the order of site recordings randomised for each period.

Soundscape processing and analysis:

We used the program Audacity to process each recording and filter out unwanted anthropogenic (e.g. boat) noise. Similar to the methods in the literature (Bohnenstiehl et al. 2016, Lillis and Mooney 2016, Ricci et al. 2016), we used 30 second-long samples from each site for our spectrogram analysis, sound pressure level calculations, and snap counts. For visual comparison of soundscape differences between habitats, we created spectrograms (Fig. S2) using the Short-Time Fourier transform in MATLAB® (Natick, MA, USA). These were made using the Hann window (length 1 s, 50% overlap).

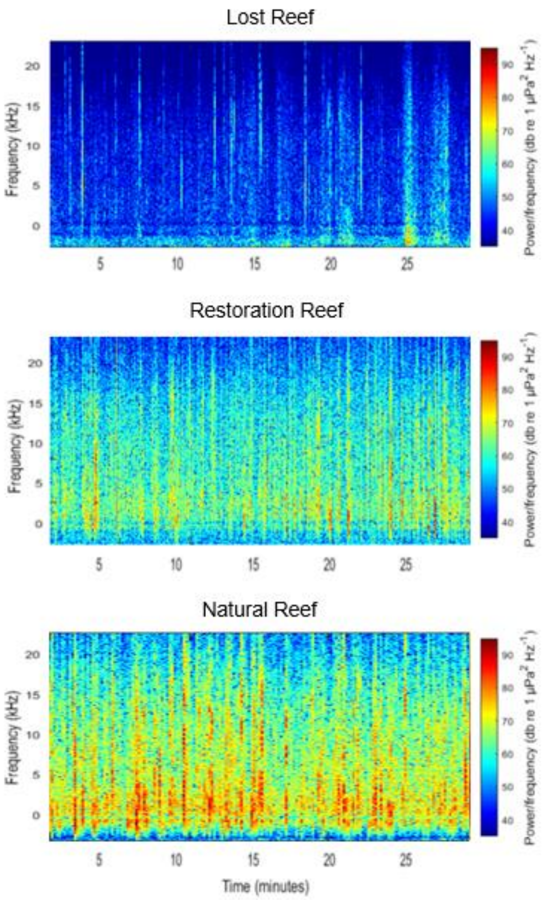

Fig. S2**.** Spectrograms for the dawn, new moon soundscape recordings (30 seconds) of ‘Lost Reef’, ‘Restoration Reef’, and ‘Natural Reef’ soundscape samples taken in June. Spectrograms were produced using 1 s windows with 50% overlap.

To calculate the mean sound pressure levels for each habitat, we used the package ‘PAMGuide’ in MATLAB® (Merchant et al., 2022) by applying a high pass filter at 2 kHz to each recording, and by entering a Hann window (length 1 s, 50% overlap) into the package’s settings. To compare sound pressure levels between habitat types, we ran a one-way ANOVA that showed habitats significantly differed ($F_{2,19} = 44.154$, $p < 0.001$). Post-hoc Tukey’s tests showed sound pressure levels significantly increased from Lost, to Restoration, to Natural Reef habitats (Fig. S3A). To count the number of snapping shrimp snaps in each recording, we used the program Avisoft SASlab lite (Avisoft Bioacoustics, Berlin, Germany). We did this by firstly applying a high-pass filter to the recordings to remove all frequency signals below 2 kHz, because snapping shrimp snaps peak between 2-5 kHz (Lillis et al., 2014b). We then used the pulse-train analysis tool in the program to count the mean number of snaps above a set amplitude threshold of 100. To assess habitat differences in the number of snaps, we ran a one-way ANOVA that showed significant differences among habitats ($F_{2,19} = 75.778$, $p < 0.001$). Post-hoc Tukey’s tests confirmed that snaps increase from Lost, to Restoration, to Natural reefs (Fig. S3B). To confirm that our spectrogram ‘snapshot’ data (Fig. S2) is representative of their respective habitats during the sampling periods, we created simple plots that show that each habitat’s sound pressure level and snap counts do not overlap in space or time with those of other habitat types (Fig. S4).

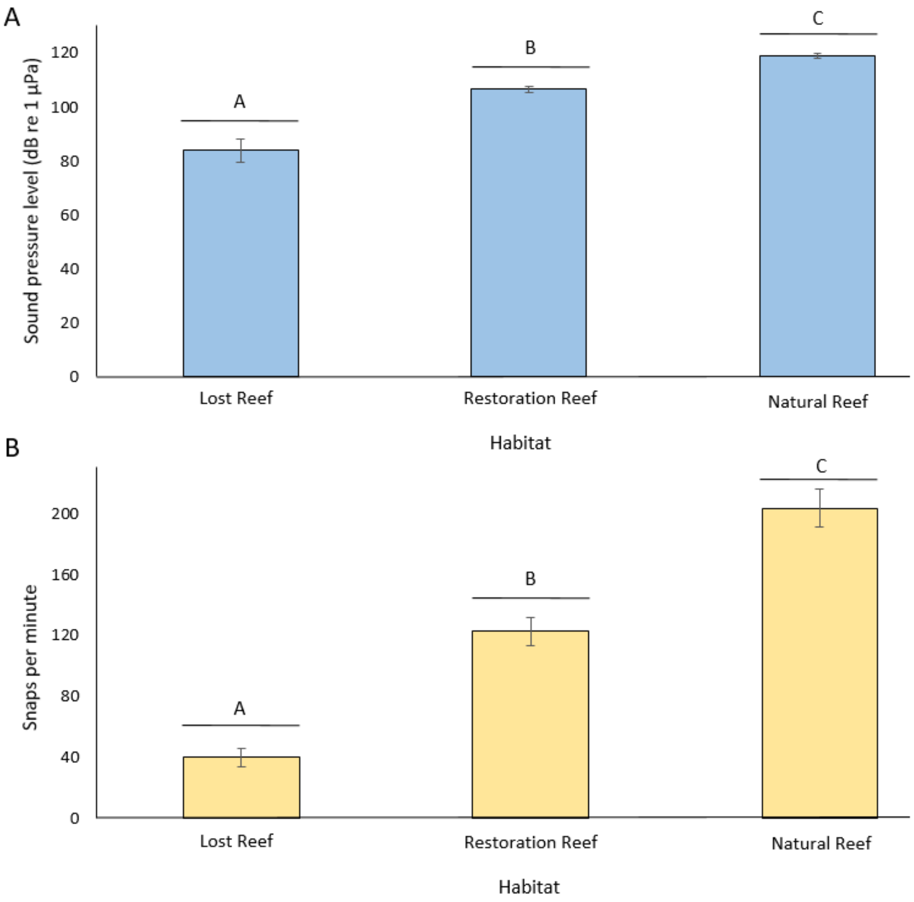

Fig. S3. (A) Sound pressure levels (mean ± 1 S.E.) and (B) snapping shrimp snaps per minute (mean ± 1 S.E.) for Lost Reef (*n* = 8), Restoration Reef (*n* = 6) and Natural Reef (*n* = 8) soundscape recordings. Significant differences (*p*<.05) denoted by letters and lines above columns, tested using one-way ANOVA and Tukey post hoc tests.

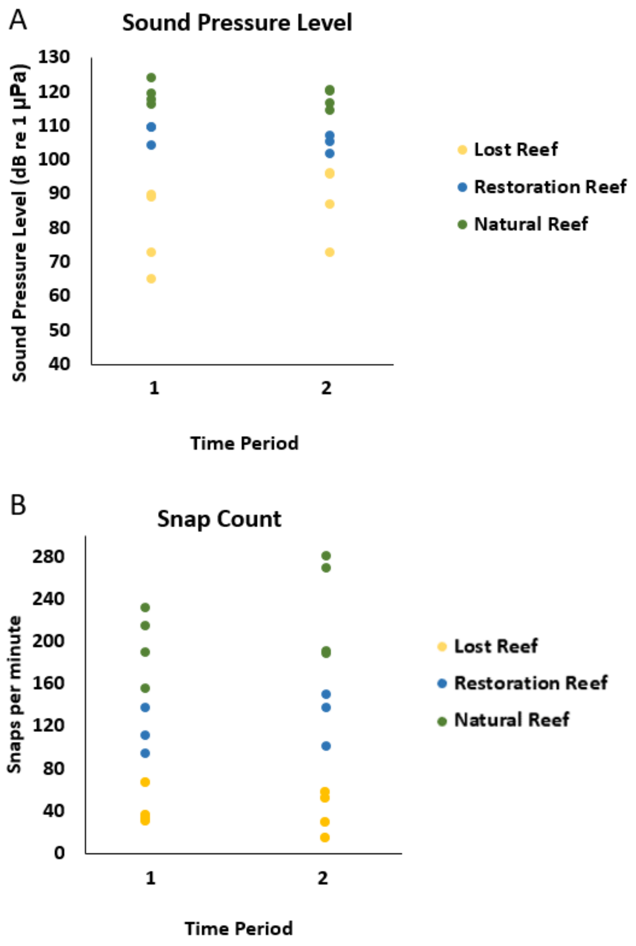

Fig. S4. (A) Sound pressure levels and (B) snapping shrimp snaps per minute randomly sampled for two time periods, for each habitat (Lost Reef *n* = 8, Restoration Reef *n* = 6 and Natural Reef *n* = 8) during dawn and the new moon.

Section S2: Methods for laboratory playback experiments

Experimental design and data collection

To see how altered soundscapes may influence the rate of oyster settlement, we conducted laboratory experiments where the settlement of pediveliger oyster larvae (*Ostrea angasi*) was observed when exposed to no sound ('Ambient'), sedimentary habitat ('Lost Reef') sounds, and restoration reef ('Restoration Reef') sounds. Soundscapes played were 15 minute-long recordings of Lost Reef, Restoration Reef and Ambient sounds; we ran 10 trials, each of which had 5 replicates of no sound control (*n* = 50) and 6 replicates for each Lost Reef and Restoration Reef (*n* = 60). Each trial ran for 24 hours. To ensure soundscape playback was representative of each habitat type, each habitat recording consisted of snippets of recordings from the different sites within each habitat and the different recording times. In Fig. 3 (manuscript proper), the ‘Playback’ spectrogram was created by amplifying the Natural Reef recordings from Edithburgh to represent what a manipulated soundscape might look like using underwater speaker. The settlement value for Playback has, therefore, been extrapolated from the oyster settlement results we observed from the other habitat soundscapes.

Our sound recordings were played using underwater speakers (25W, 4 Ohm, full range resonance speaker, no flat frequency response, secured inside waterproof PVC housing; H × W: 10 × 12 cm) that we parameterised in the laboratory to replicate in-situ soundscape conditions. To do this, we used hydrophones to record the playback sounds of each treatment, using this data to create acoustic spectra, sound pressure levels and particle acceleration values. We produced root mean square (rms) acoustic spectra to determine how acoustic power in our playback treatments changed in relation to in-situ recordings, in the frequency range that has the highest biological influence and the low frequency peak of snapping shrimp snaps (around 2-5 kHz; Au and Banks 1998, Campbell et al. 2019) (Fig. S5). We calculated this in PAMGuide in MATLAB® (Merchant et al. 2022) using the Hann window (length 1 s, 50% overlap). Lastly, we calculated the particle acceleration for each playback treatment and in-situ recordings. We did this following the methods of Lillis et al. (2013) and others (Macgillivray and Racca 2006; Wahlberg et al. 2008) using the sound pressure levels obtained from our two calibrated hydrophones in the laboratory, and the Euler equation (Fig. S6). Many organisms are expected to sense sound in the particle motion domain (Popper et al. 2001; Kaifu et al. 2008), and so it is important to parameterise sound in this manner (Nedelec et al. 2021).

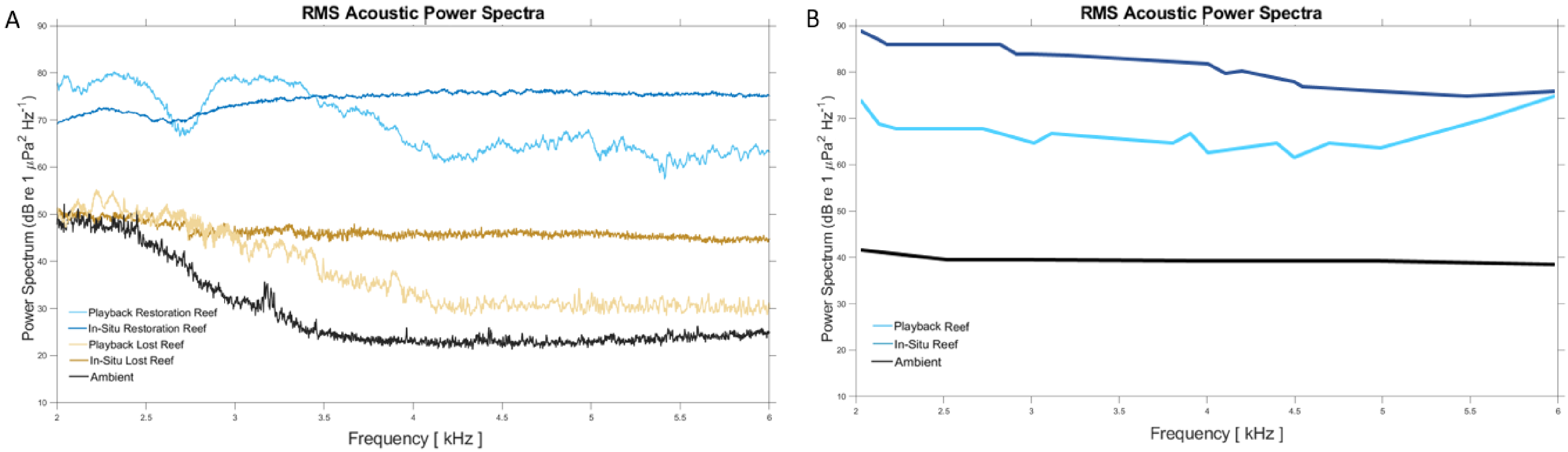

Fig. S5. Acoustic spectra (rms) for laboratory playback sound recordings compared to in-situ recordings. For the purpose of understanding generality, we provide (A) our recordings (South Australia, Australia) and (B) the only other known sound playback recordings (North Carolina, USA) for oyster spat in the laboratory, replotted after Lillis et al. (2013). Ambient refers to the background sound present in the experiment without playback. In-situ refers to the raw soundscape recordings from the field. Playback refers to the recorded soundscapes played back in the laboratory.

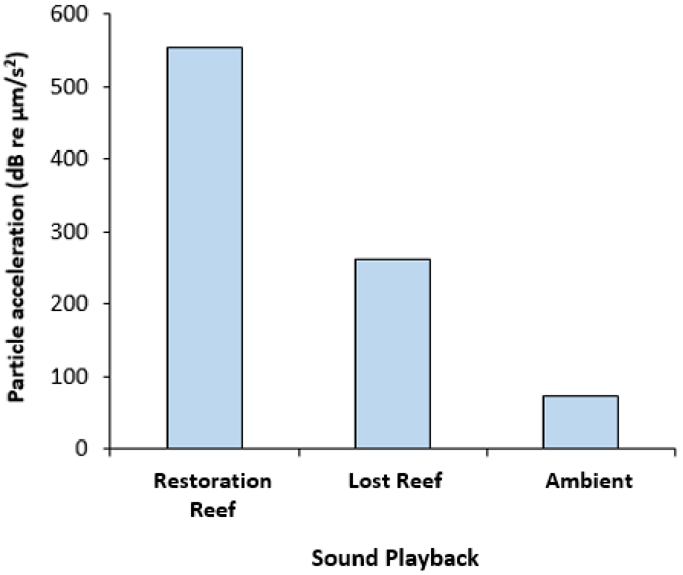

Fig. S6. Comparison of full spectrum particle acceleration values for playback of sound treatments in the laboratory.

We assigned each speaker to a sound treatment and then placed it in a 20-litre bucket filled with seawater (21°C). Experimental buckets were soundproofed with dampening foam to avoid sound crossover between buckets, and darkened with shade cloth as oyster larval settlement has been shown to increase in darker conditions (Ritchie and Menzel, 1969; Shaw et al. 1970). Using the experimental design developed by Lillis et al. (2013), we placed a piece of settlement substrate (2.5 cm x 2.5 cm sanded PVC square) inside 70 mL specimen jars filled with seawater, and then pipetted 3 mL (at 15 oysters/mL) of pediveliger oyster larvae into each specimen jar (pediveligers provided by the South Australian Research and Development Institute and used within two days of arrival). One specimen jar was placed into each bucket treatment and exposed to sound treatments for 24 hours. After 24 hours, we removed the jars and counted the number of oysters settled onto the substrate using a dissecting microscope. We gently agitated the larvae using water from a pipette to ensure they were properly attached to the substrate. For each experimental run, we repositioned the speakers and alternated sound treatments among buckets to ensure there were no experimental artifacts from individual buckets. Fig. 3 in the main manuscript uses these values of the proportions of larvae settled in each of the Lost Reef and Restoration Reef treatments. Using these proportions, we then performed an ANOVA which showed significant differences among treatments ($F_{2,167}$=12.755, p=.001). A post hoc S-N-K test showed that the Restoration Reef treatment was significantly different to the other treatments (at p>.05) and that the Ambient and Lost Reef treatments were statistically indistinguishable from one another.

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CHAPTER THREE

Oyster larvae swim along gradients of sound

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Contribution to the Paper	Concept and design Data collection Analysis and interpretation First draft Critical revision		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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By signing the Statement of Authorship, each author certifies that:

iv. the candidate's stated contribution to the publication is accurate (as detailed above);

v. permission is granted for the candidate in include the publication in the thesis; and

vi. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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3.1 Abstract

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. 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. In the field, we test 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. 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. 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.

Key words: soundscapes; recruitment; marine larvae; settlement cue; noise pollution; restoration; oyster reef; shellfish

3.2 Introduction

Dispersing animals orientate, navigate and then settle into suitable adult habitat using a combination of visual (McFarland 1986), olfactory (Svane and 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 et al. 2016*a*, *b*, Rossi et al. 2017). Sound is a vital source of navigational information for dispersing marine organisms and is comprised of ambient, geophysical, 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 like those provided by soundscapes are diminishing (Rossi et al. 2017, Duarte et al, 2021). 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 soundscapes (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 and Salmon 1970). These sound-producing species are not only muted by human activity (i.e., shipping, pile-driving, seismic air guns, SONAR) (Rossi et al. 2016*a*, *b*), 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 and Connell 2015). Worldwide, overharvesting of oysters removed their hard-shell substrate from the seafloor (mid1800s to early 1900s), with disease and declining water quality compounding this loss (Beck et al. 2011, McAfee and Connell 2021). Natural recovery has been limited by the transition from hardshell 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 and 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 and 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 soundscapes (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, 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 and 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.

3.3 Methods

3.3.1 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 and 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 and Connell 2020). These larvae spend several days to two 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 aim to determine the influence of marine soundscapes on the horizontal movement and settlement of pediveliger *O. angasi*, by experimentally testing: (1) whether settlement increases in the presence of soundscapes that approximate healthy reefs, and (2) 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.

3.3.2 Handling or 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 two 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 Supporting information: Section S1). We played these soundscapes in the laboratory using underwater speakers (25W, 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 Supporting information: 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 Supporting information: Section S1).

3.3.3 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-hour period, larvae were exposed to sound treatments that were either reef (‘Reef’) or sedimentary habitat (‘Sedimentary’) soundscapes (looped 15 minute-long recordings), or a no sound control (‘Ambient’) (see Supporting information: 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 (5mm 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 and Menzel 1969, Shaw et al. 1970). Each bucket was randomly assigned a sound treatment for 24 hours, 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.

3.3.4 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 seven days, seven trials of Reef and Ambient (n = 7) sound treatments were run whereby oyster larvae were exposed to treatments for 24 hours (using looped 15-minute 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 hours, 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 and Hawkins 2018), we calculated the particle acceleration (dB re 1 μm/s2) along the length of each tank for each treatment (see Supporting information: Section S2). We did this following methods in the literature (Lillis et al. 2014, MacGillivray and 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 ($\frac{\partial u}{\partial t}$) (Popper and Hawkins 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. 2021). All tests were run using SPSS.

3.3.5 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 one-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 Supporting information: 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 metres away from the speaker at each site, recording the soundscapes in the presence (n = 4) and absence of speaker playback (n = 4) (Supporting information: 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 x 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 one 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 and Tibshirani 1993). All analyses were performed in R (v.4.0.5).

3.4 Results

3.4.1 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 (Fig. 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 (Fig. 1).

Of the settled oyster larvae that had dispersed from the entry point towards the speaker, we observed 82.7 ± 3.4% (mean ± 1 S.E.) of settled larvae dispersing in the sound treatment, which was significantly greater than the 44.0 ± 13.9% (± 1 S.E.) observed in the absence of sound (two-sample t-test; $t(7) = 1.89$, $p = .015$) (Fig. 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.

3.4.2 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 (Fig. 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: $F_{2,167} = 12.755$, $p = .001$) compared to ‘Sedimentary’ and ‘Ambient’ treatments ($p > .05$), which were statistically indistinguishable. This indicates that ‘Reef’ sounds are more attractive to oyster larvae.

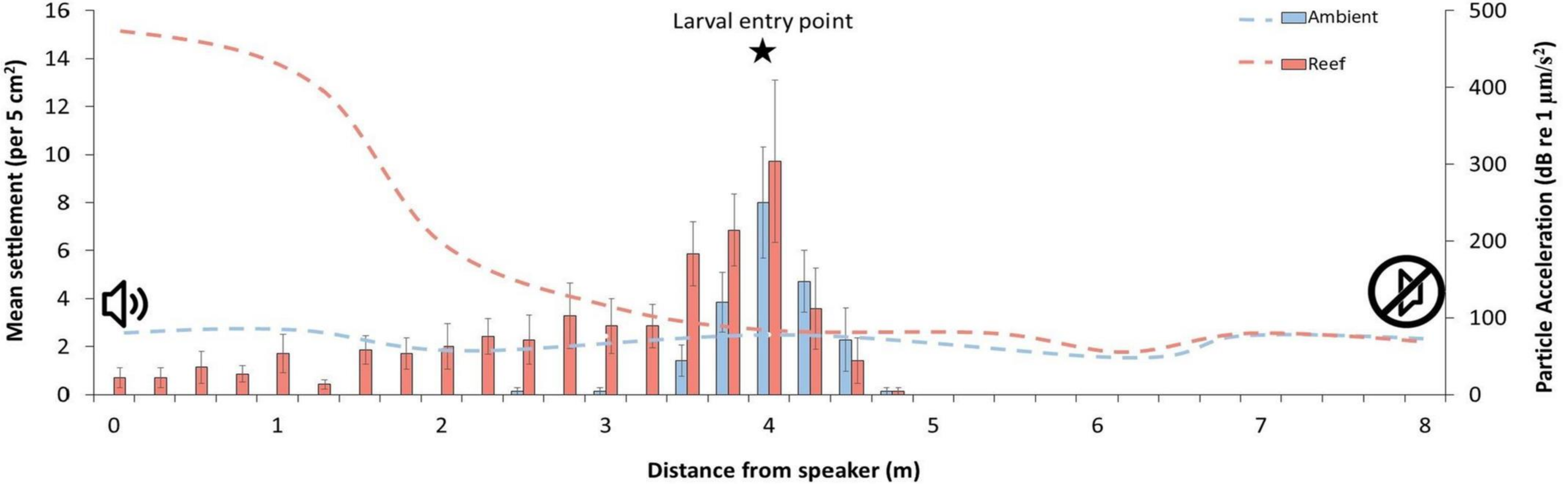

Fig. 1. Across an 8 m gradient of increasing sound (right to left), oysters settled across the sound gradient in greater densities (Reef, *n* = 7) relative to no sound (Ambient, *n* = 7). In the Ambient treatment, the particle acceleration of sound was consistent across the 8-m length of the tank, whilst 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.

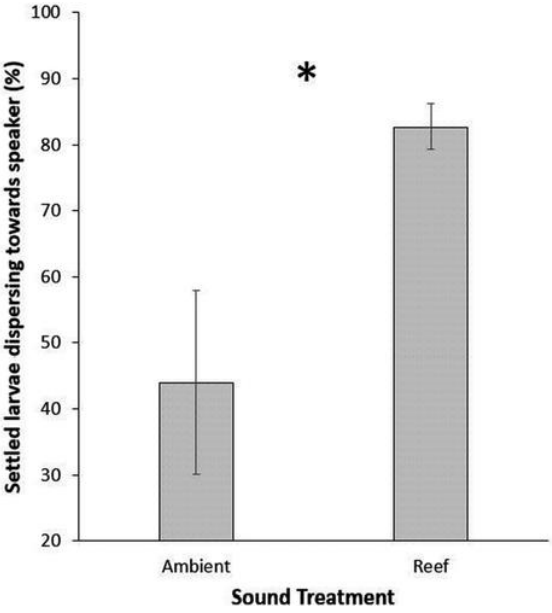

Fig. 2. The percentage of oyster larvae that dispersed from the entry point (4 m) towards the speaker (Reef) or control speaker (Ambient). '*' denotes a significant difference between treatments (*n* = 7 replicates).

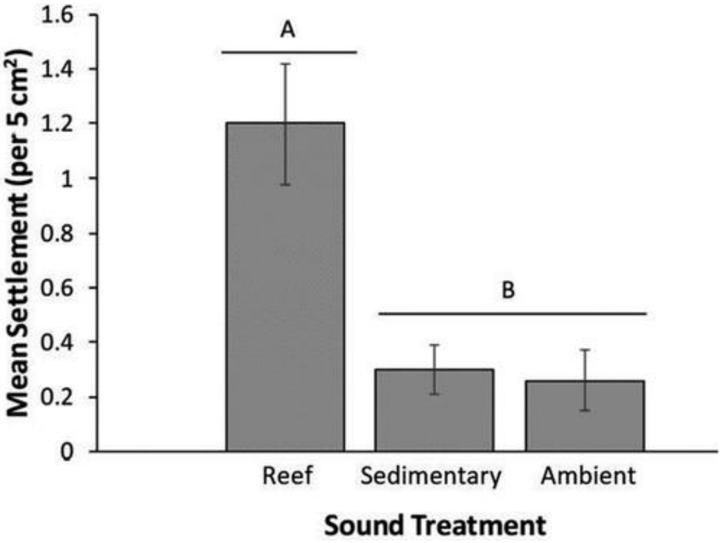

Fig. 3. Mean larval settlement (±1 SE) with exposure to playback of 'reef' (*n* = 60), 'Sedimentary' (*n* = 60) and 'Ambient' (*n* = 50) sound in the laboratory. Letters and lines above columns denote significant differences between.

3.4.3 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 (Fig. 4). At the 'low background noise' site, the effect sizes of each larval settlement (*d* = 3.452 ± 1.89) and boosted sound (*d* = 31.912 ± 4.73) were greater than that at the 'medium background noise' site (*d* = 0.7 ± 1.06 and *d* = 2.36 ± 0.98, respectively). Whereas the 'high background noise' site had the lowest effect size of settlement (*d* = 0.025 ± 0.49) and boosted sound (*d* = 0.203 ± 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.

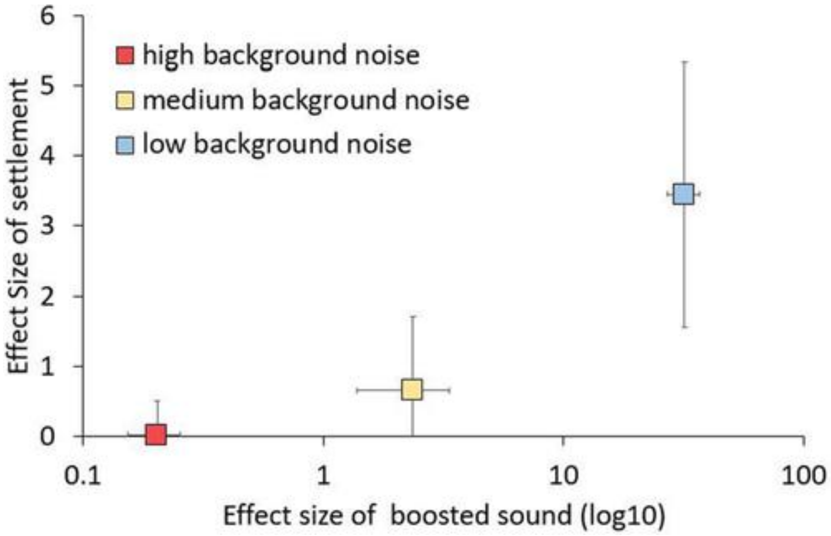

Fig. 4. Effect sizes of larval settlement (mean ± 1 SE) and boosted sound (mean ± 1 SE; log10, obtained from sound pressure level data) between 'Reef' and 'Ambient' sound treatments in the field at 'high background noise' (*n* = 8), 'medium background noise' (*n* = 18) and 'low background noise' (*n*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

3.5 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 and 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 and Denley 1984), and later, the reconsideration of the distances at which they disperse (Jones et al. 1999).

4.5.1 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 metres 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 (Marliave 1986, Leis 2015). 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.

4.5.2 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, 1992, Nedelec et al. 2021). Where marine mammals have ear structures to detect sound pressure (Popper and Fay 1993), marine invertebrates and fish tend to detect the particle motion component of underwater sound (Budelmann, 1992, Popper and

Fay 1993) with sensory structures that can detect particle vibration. For example, epidermal cells covered in cilia, or statocyst structures that work like accelerometers (Budelmann, 1989, 1992, Popper and Hawkins 2018). As some crustacea and molluscs use statocysts to detect sound, it is generally believed that oyster larvae would use statocysts too (Lovell et al. 2005, Fuchs et al. 2013). 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.

4.5.3 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.

4.5.4 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 which 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 (Simpson et al. 2004, Montgomery et al. 2006, Gordon et al. 2019), which could result in sound technology creating recruitment sinks, whereby predators consume new recruits at rates that rival their settlement rates. Lastly, 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 (Pimm 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.

3.6 Conclusion

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.

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3.9 Supporting information

*Note: All raw data material and sound files can be found on figshare (https://figshare.com/s/b3a744924fa647631748)

Section S1: Soundscape playback recordings

The soundscape playback recordings used in each of our soundscape gradient and preference experiments, and our field experiment, came from two habitat types in the Gulf St Vincent, South Australia, taken in 2019 across April and June. The 'Reef' playback recording came from snippets of soundscapes across three sites at Windara Reef, Australia's largest shellfish restoration project constructed where native reefs once stood. Windara Reef consists of 60 concrete structures and 10, 000 tonnes of limestone covered in Pacific oyster shells and juvenile native oysters, that make up 159 reef segments across 20 hectares. Surveys in 2019 revealed that the average density of oysters at Windara Reef was at 488 individuals/m^2 (Reeves et al. 2019). The 'Sedimentary' playback recording came from snippets of soundscapes across four sedimentary sites with similar characteristics to Windara Reef but lacking constructed reefs, or epifaunal bivalves (e.g. *Pinna bicolor*). These recordings were each taken during the 'dawn chorus' (within one hour of sunrise) at high tide, in 4-8 metres of water. This dawn chorus is one of the snapping shrimp's most bioacoustically active periods (Radford et al. 2010, Lillis et al. 2014, Bohnenstiehl et al. 2016). To record these soundscapes, we used calibrated ST202 hydrophones (Ocean Instruments, flat frequency response 0.1-30 kHz, sensitivity −169 dB re 1 V/μPa) set to a sampling frequency of 48 kHz (24 bit), and set to record for two minutes every fifteen minutes. These were anchored one metre above the seafloor and remained suspended using a sub-surface buoy.

Section S2: Parameterisation of soundscape playback recordings in the laboratory

To ensure soundscape playback in each the soundscape gradient and preference experiments was representative of in-situ soundscape recordings, we used calibrated ST202 hydrophones (Ocean Instruments, flat frequency response 0.1-30 kHz, sensitivity −169 dB re 1 V/µPa) set to a sampling frequency of 48 kHz (24 bit) to record the playback of sounds in each treatment and compared these to the original field recordings. This data was used to create acoustic spectra and calculate particle acceleration values for our experimental tanks. We produced root mean square (rms) acoustic spectra to determine how acoustic power in our playback treatments changed in relation to in-situ recordings, in the frequency range that has the highest biological influence and the low frequency peak of snapping shrimp snaps (around 2-5 kHz) (Au and Banks 1988, Campbell et al. 2019) (Fig. S1-S2). We calculated this with the package 'PAMGuide' in MATLAB® (Merchant et al. 2022) using the Hann window (length 1 s, 50% overlap). Finally, we calculated the particle acceleration for each playback treatment to show how it changed between sound treatments (Fig. S3). We did this following the methods in the literature (Lillis et al. 2014, MacGillivray and Racca 2016, Wahlberg et al. 2008) using the sound pressure levels obtained from our two calibrated hydrophones in the laboratory, and the Euler equation. Many organisms, including invertebrates, are expected to sense the particle motion component of sound (Popper et al. 2001, Kaifu et al. 2008) so it must be parameterised in this domain (Nedelec et al. 2021).

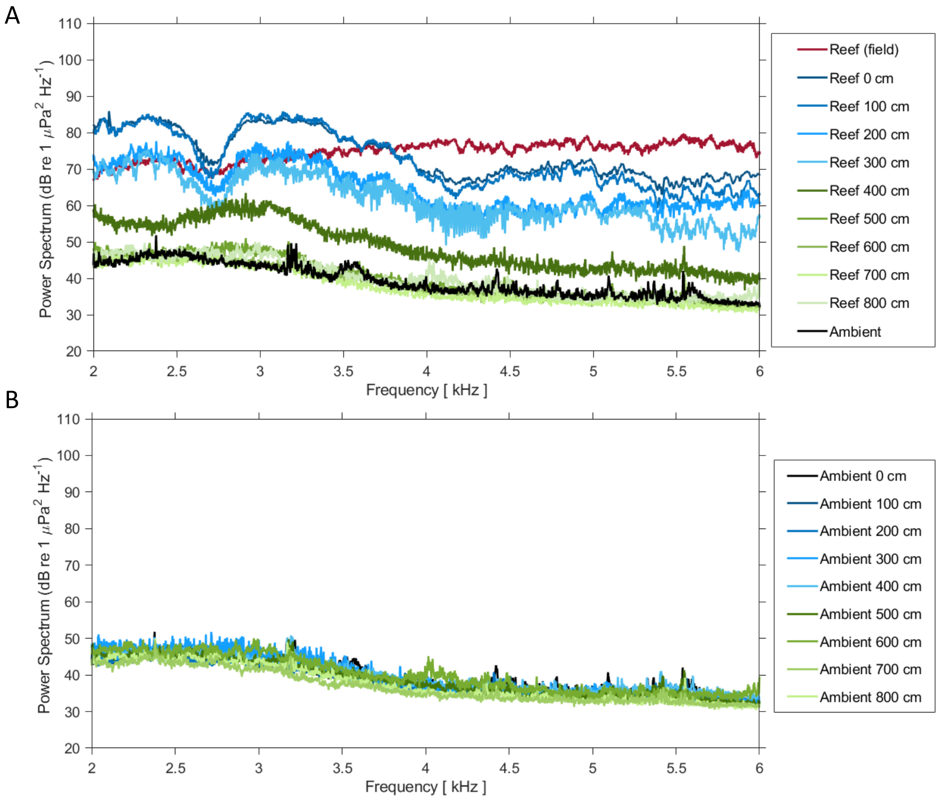

Figure. S1. Acoustic spectra (rms) of sound files played in soundscape gradient experiments for (A) the 'Reef' sound treatment compared to the in-situ reef recording and (B) the 'Ambient' treatment, along the experimental gradient in sound.

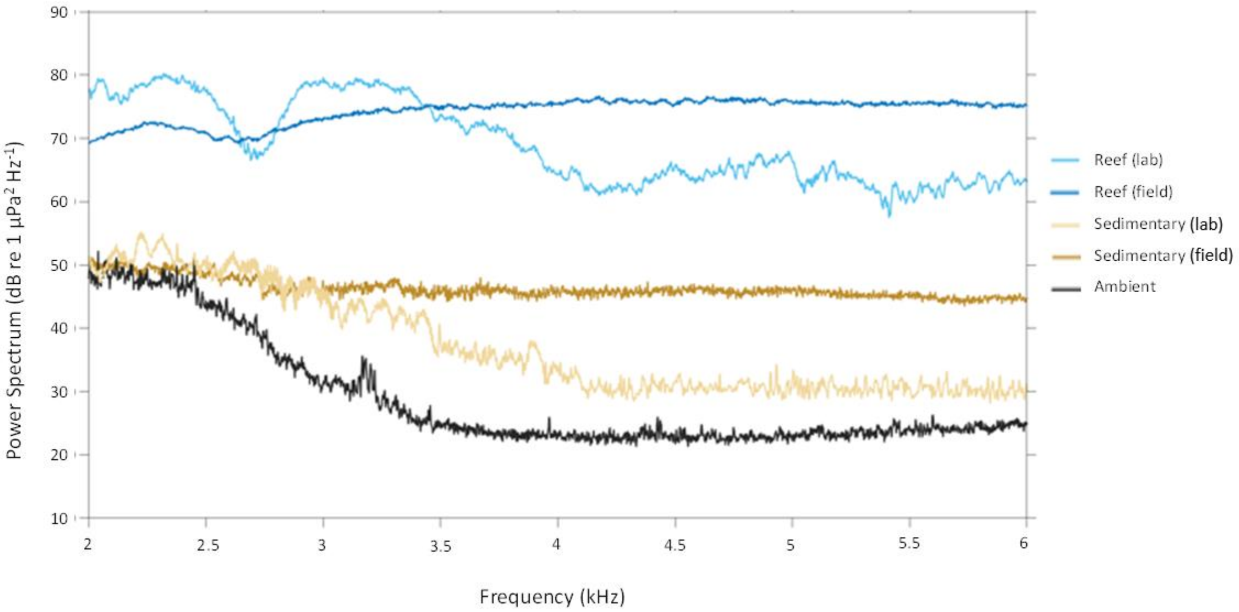

Figure. S2. Acoustic spectra (rms) of sound files ('Reef', 'Sedimentary', 'Ambient') used in soundscape preference experiments, compared to in-situ recordings. 'Ambient' refers to the background sound present in the experiment without playback. 'Field' refers to the raw soundscape recordings from the field. 'Lab' refers to the recorded soundscapes played back in the laboratory.

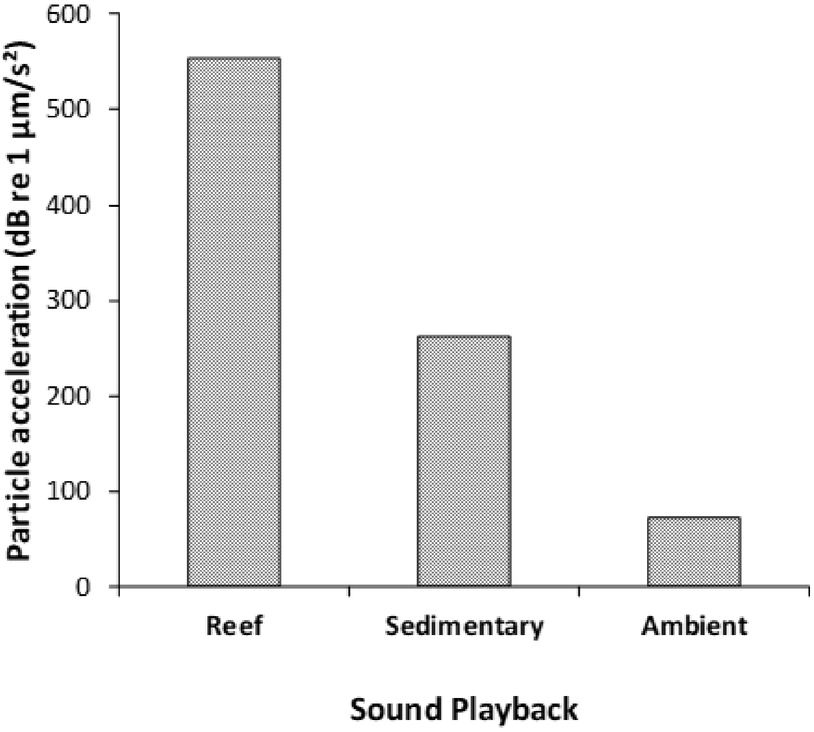

Figure. S3. Particle acceleration values for ‘Reef’, ‘Sedimentary’ and ‘Ambient’ treatments in soundscape preference experiments.

Section S3: Parameterisation of soundscape playback recordings in the field

To test whether the soundscape playback in our field experiments had greater sound intensity along a gradient than that of the ambient soundscape, we recorded the playback of sound at each ‘high background noise’, ‘medium background noise’ and ‘low background noise’, and compared this to the ambient soundscape. To do this, we used calibrated ST202 hydrophones set to a sampling frequency of 48 kHz (24 bit) and set to record continuously. We anchored hydrophones 1 metre from the seafloor at 1, 10, 20 and 30 metres away from the speaker, suspending them with a subsurface buoy. We then recorded the soundscapes when the speaker was playing (*n* = 4) against when it was not playing (*n* = 4). From this data, we created acoustic spectra and calculated the mean sound pressure levels (SPL) and snaps per minute for each treatment, across each distance. We used the package ‘PAMGuide’ in MATLAB® (Merchant et al. 2022) to calculate root mean square (rms) acoustic spectra to determine how acoustic power in each treatment changed over the full spectrum frequency range (0 to 22 kHz) across the distances (Fig. S4). We used a Hann window for this (length 1 s, 50% overlap). To calculate the mean sound pressure levels for each treatment across distance, we used the package ‘PAMGuide’ in MATLAB® (Merchant et al. 2022) by applying a high pass filter at 2 kHz to each recording, and by entering a Hann window (length 1 s, 50% overlap) into the package’s settings (Fig. S5). To count the number of snapping shrimp snaps in each recording per treatment at each distance, we used the program Avisoft SASlab lite (Avisoft Bioacoustics, Berlin, Germany) (Fig. S6). We did this by firstly applying a high-pass filter to the recordings to remove all frequency signals below 2 kHz, because snapping shrimp snaps peak between 2-5 kHz (Lillis et al. 2014*b*). We then used the pulse-train analysis tool in the program to count the mean number of snaps above a set amplitude threshold of 100. We then ran two-sample t-tests to determine whether there were any significant differences between the SPL and snap counts in each treatment along each distance in the soundscape gradient.

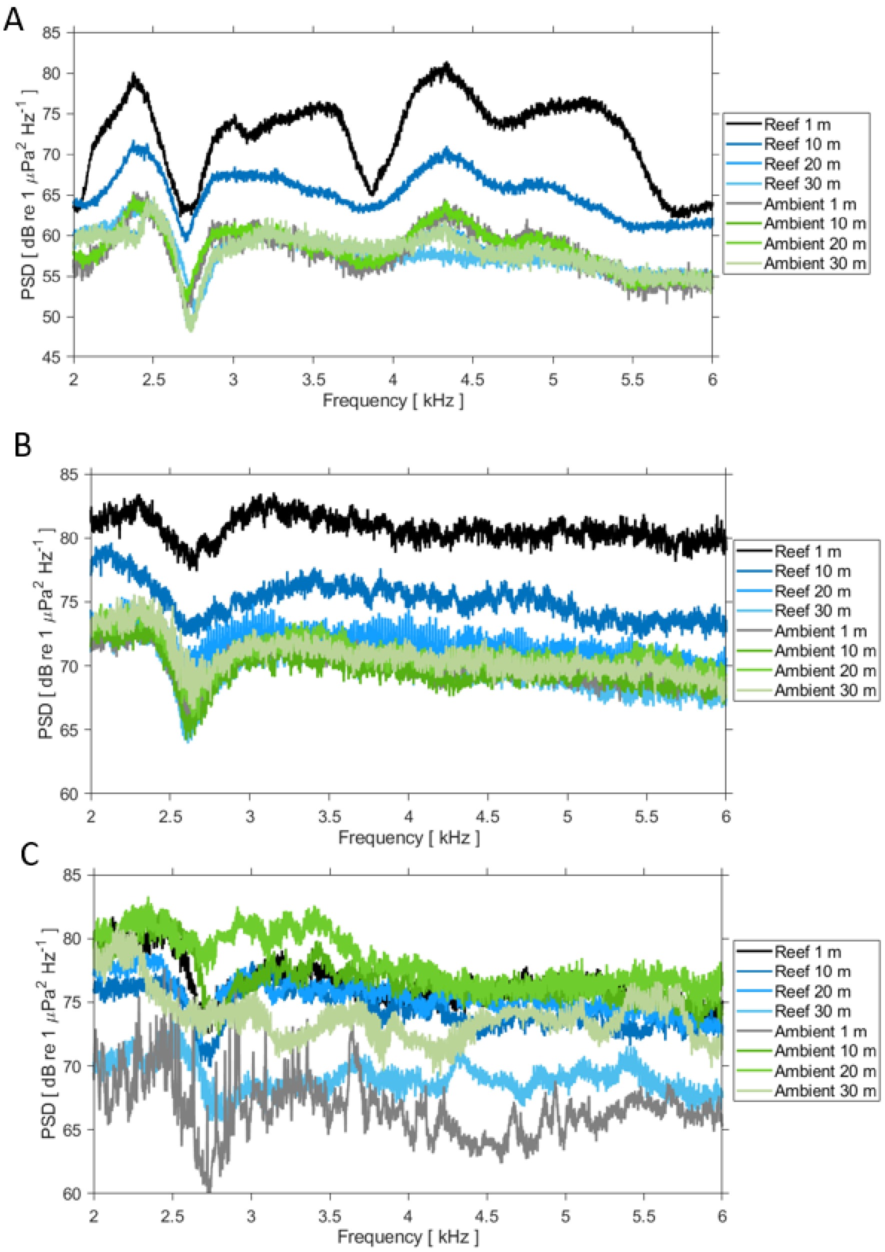

Figure. S4. Acoustic spectra (rms) for sound (‘Reef’) versus control (‘Ambient’) treatments at A). ‘low background noise’, B). ‘medium background noise’ and C). ‘high background noise’, along a gradient of 30 metres from the speaker.

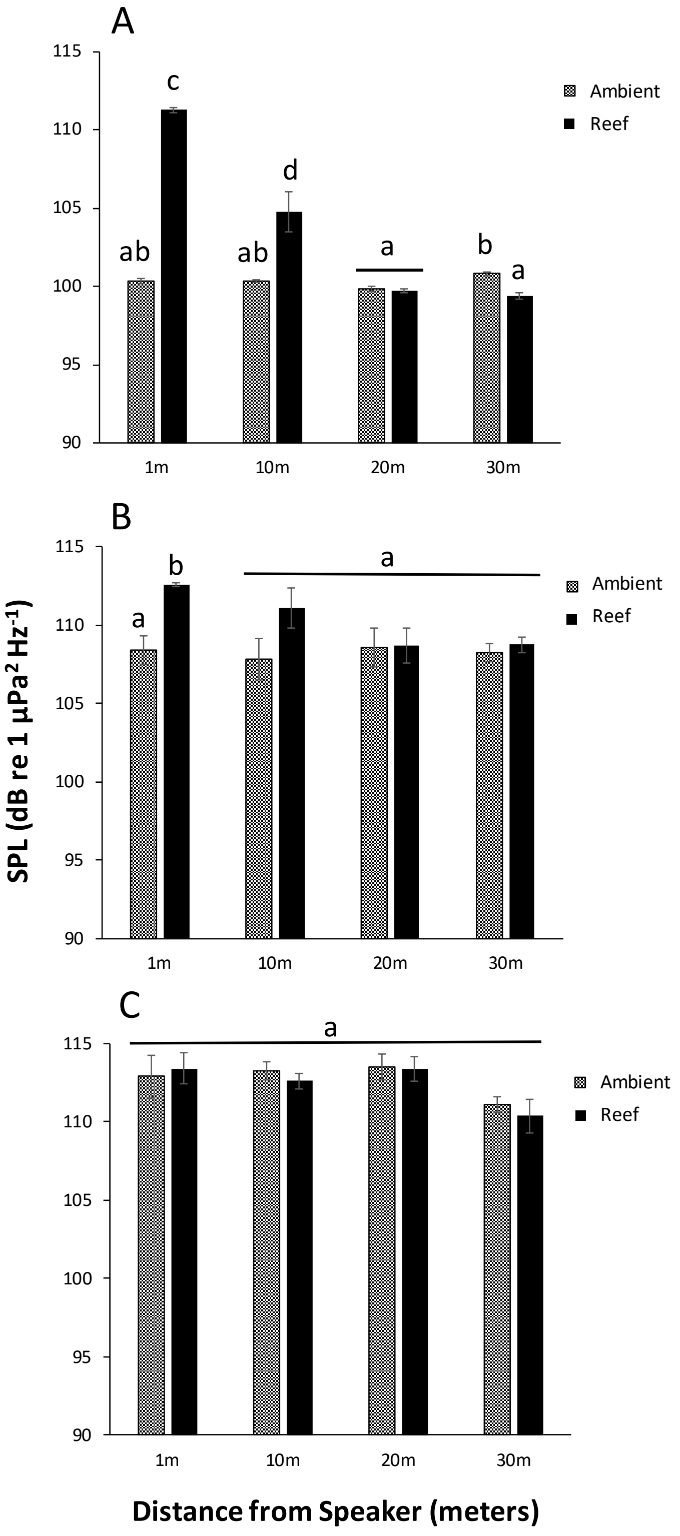

Figure. S5. Mean sound pressure level (±1 SE) for sound (‘Reef’) versus control (‘Ambient’) treatments at A). ‘low background noise’, B). ‘medium background noise’ and C). ‘high background noise’, along a gradient of 30 metres from the speaker.

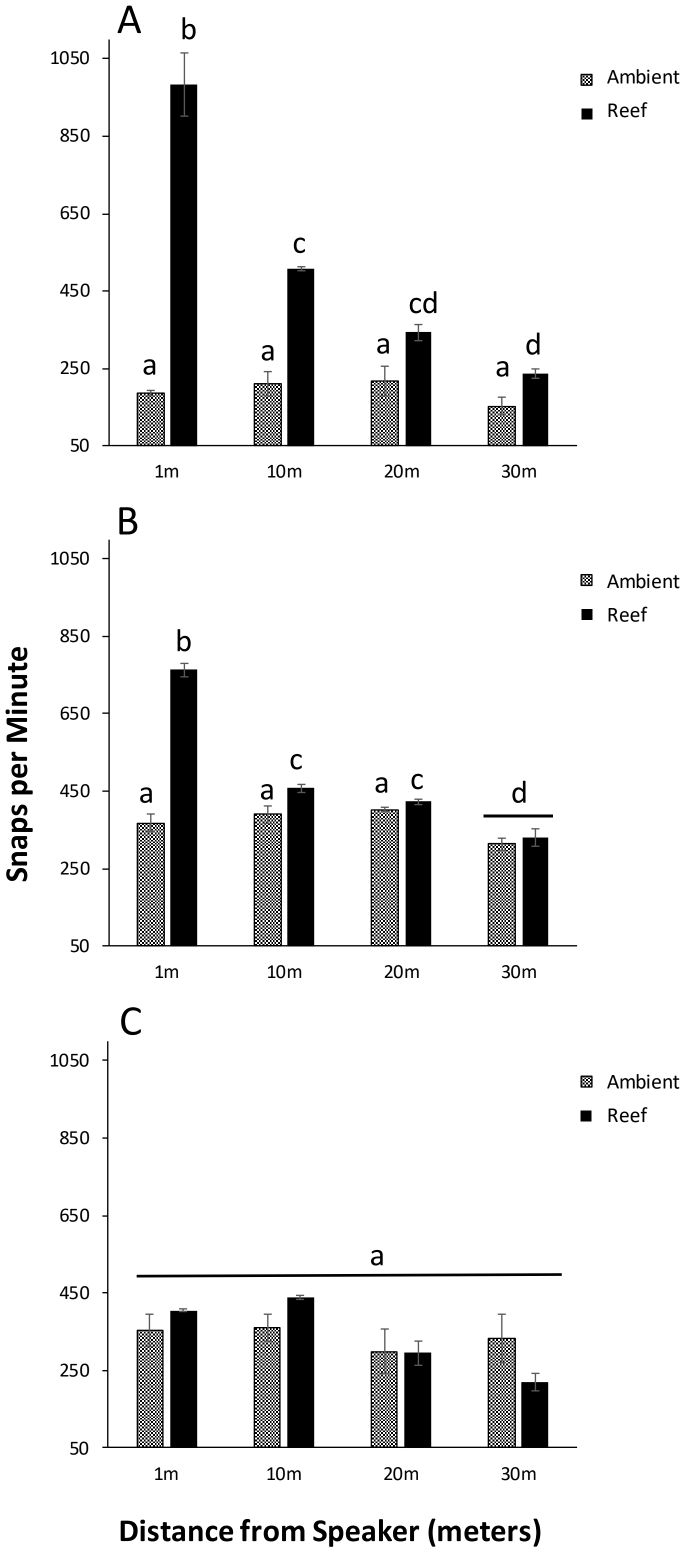

Figure. S6. Mean snaps per minute (±1 SE) for sound (‘Reef’) versus control (‘Ambient’) treatments at A). ‘low background noise’, B). ‘medium background noise’ and C). ‘high background noise’, along a gradient of 30 metres from the speaker.

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CHAPTER FOUR

Anthropogenic noise disrupts recruitment processes

Statement of Authorship

Title of Paper	Anthropogenic noise disrupts recruitment processes		
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Publication Details	Proceedings of the Royal Society B: Biological Sciences		

Principal Author

Name of Principal Author (Candidate)	Brittany Williams		
Contribution to the Paper	Concept and design Data collection Analysis and interpretation First draft Critical revision		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	3/3/2023

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

vii. the candidate's stated contribution to the publication is accurate (as detailed above);

viii. permission is granted for the candidate in include the publication in the thesis; and

ix. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	12.5% Concept and design Analysis and interpretation Critical revision		
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4.1 Abstract

Globally, anthropogenic noise is on the rise and is interfering with the natural acoustic cues used by organisms. The playback of natural soundscapes using speakers (i.e., acoustic enrichment) can provide navigational cues to boost recruitment of target organisms at restoration sites. But, can acoustic technology boost recruitment in noise-polluted sites? First, we used replicated aquarium experiments to test whether acoustic enrichment could boost oyster recruitment affected by anthropogenic noise. We show that whilst acoustic enrichment boosted recruitment by 2.57 times in the absence of anthropogenic noise (157% increase), this enrichment had no boosting effect in the presence of anthropogenic noise. We then predicted that acoustic enrichment should yield strong natural oyster recruitment within a relatively quiet, natural soundscape and weak responses within a site of anthropogenic noise. At the site of low anthropogenic noise, acoustic enrichment increased larval recruitment by 3.33 times (233% increase), whereas at the site of high anthropogenic noise, it provided no boost in recruitment. Our findings indicate that not only does anthropogenic noise reduce the opportunity for using acoustic enrichment for shellfish restoration, but that it also disrupts recruitment patterns, which play a critical role in maintaining ecosystem health and function.

Keywords: acoustic enrichment; anthropogenic noise; ecosystem restoration; oyster; recruitment

4.2 Introduction

The global nature of human activity is increasing anthropogenic noise in the world’s natural ecosystems. Noises from shipping and industrial trade, for example, are pervasive and pose serious environmental change that affects both terrestrial and marine animals. Marine organisms appear particularly vulnerable to the intensification of anthropogenic noise (Duarte et al. 2021) because sound travels faster underwater and is attenuated more slowly than sound in air (Hildebrand 2004; Ainslie 2010, Slabbekoorn et al. 2010). The duration, broad frequency range and intensity of these anthropogenic noises are dominating a large part of the soundscape that was once filled with the biophony (sound production) of fish and invertebrates (Pijanowski et al. 2011). Shipping, motor boating, SONAR and seismic exploration have the potential to mask the biological signals that marine animals use for conspecific communication, navigation and recruitment. This is because they overlap with the hearing ranges of animals (Erbe et al. 2014; Merchant et al. 2020). Such noises are often detrimental to marine mammals, inducing physiological and behavioural changes (Risch et al. 2012; Skeate et al. 2012; Pirotta et al. 2015), as well as stress, injury and mortality (Rolland et al. 2012; Fahlman et al. 2014; Duarte et al. 2021).

Anthropogenic noises also affect marine invertebrates, inducing physiological changes and organ damage, as well as influencing behaviour and communication (André et al. 2011; Day et al. 2017, 2019; Jézéquel et al. 2021). For example, boat noise disrupts settlement processes of coral and barnacle larvae (Lecchini et al. 2018; Branscomb and Rittschof, 1984) and the orientation of juvenile crabs (Sal Moyano et al. 2021). In extreme cases, the noise of seismic air guns can lead to developmental abnormalities in bivalve larvae (Aguilar de Soto et al. 2013). On the other hand, mussel larvae exhibit enhanced recruitment in the presence of vessel noise (Wilkens et al. 2012; Jolivet et al. 2016). Despite these documented impacts, large knowledge gaps remain on how anthropogenic noise affects invertebrate larvae, especially during recruitment processes. To date, there is little confidence surrounding how larval and adult bivalves perceive and use habitat-related sounds, let alone how anthropogenic noise may impact them during this important life stage (Duarte et al. 2021). Anthropogenic noise may disrupt recruitment patterns that have a large role in the maintenance and health of an ecosystem (Peng et al. 2015). This is of concern because rising anthropogenic noises increasingly overlap with habitats formed by animals (e.g., bivalves) that use natural soundscapes. Additionally, many ecosystem restorations are occurring along urbanised waterways and metropolitan coastlines where anthropogenic noise is prevalent (Pine et al. 2016; Kaplan and Solomon 2016).

Ecosystem restoration is particularly challenging in the marine environment. The inherent difficulties of working on or in the water mean that sites can only be accessed briefly and intermittently. To overcome these issues, restoration practice requires affordable and scalable solutions. For marine conservation, acoustic enrichment using underwater speakers can reprovision degraded biogenic sounds that diverse animal groups use as a navigational cue (Williams et al. 2021), with great potential for improving restoration outcomes (Gordon et al. 2019, Mcafee et al. 2023). However, its restorative value in the presence of anthropogenic noise is currently unknown.

Restorations of oyster reefs are increasingly occurring in noisy places. In Australia, the flat oyster (*Ostrea angasi*) is being restored from functional extinction. Acoustic enrichment can replace lost environmental cues that are needed to guide dispersing animals to suitable habitat (e.g., biogenic soundscapes; Williams et al. 2021). By acting as a navigable cue, playback of reef sound can guide oyster larvae to sites targeted for restoration (Lillis et al. 2014a, b; Williams et al. 2022; McAfee et al. 2023). However, we do not yet know how acoustic enrichment in the presence of anthropogenic noise may impact oyster recruitment. Anthropogenic noise could potentially mask the signal produced by acoustic enrichment and disrupt recruitment processes. If we are to use this technique to boost restoration efforts, we need to discern whether it can yield positive restoration outcomes in places associated with anthropogenic noise. Here, we assess the context-dependency by which acoustic enrichment can overcome a major challenge to ecosystem restoration; achieving sufficient natural recruitment of oyster larvae to restore shellfish reefs.

4.3 Methods

We performed aquarium and field experiments to determine the value of using acoustic enrichment for oyster reef restoration in localities associated with anthropogenic noise. In the aquarium, we tested whether acoustic enrichment, with or without anthropogenic noise, could boost recruitment of oysters relative to controls. In the field, we tested the effectiveness of acoustic enrichment on the recruitment of wild oysters across two restoration sites, one associated with a relatively quiet, natural soundscape, and one polluted by anthropogenic noise.

4.3.1 Reef soundscape playback recordings

For the acoustic enrichment playback recordings in each the aquarium and field experiments, we used soundscape recordings captured from a natural rocky reef in the Gulf St Vincent, South Australia (Port Noarlunga Reef). We recorded this reef soundscape because no flat oyster reefs remain on mainland Australia’s coastline, and because this reef is one of the healthiest soundscapes in the Gulf (Williams et al. 2021). Soundscape recordings were made during December (Austral summer) at high tide in 4-8 metres of water, within one hour of sunrise. Recordings were made at this time because it is one of the most bio-acoustically active periods of the snapping shrimp (Radford et al. 2010; Lillis et al. 2014a; Bohnenstiehl et al. 2016), and the time of day that has the loudest shrimp chorus locally (from previous soundscape surveying in the Gulf St. Vincent by Rossi et al. 2017; Williams et al. 2021). We took recordings continuously for an hour, using four calibrated Sound Trap 202 hydrophones (Ocean Instruments, frequency response 0.1-30 kHz, set to high gain sensitivity [-169 to -169.8 dB re 1 V/µPa], -3dB bandwidth of 21.6 kHz, 48 kHz sampling frequency, data digitised using a 16-bit resolution). Hydrophones were anchored one metre above the seafloor using a sub-surface buoy to suspend them. For the playback experiments, we created a looped

1-minute-long sound file that consisted of snippets of sound recorded by each of the four hydrophones. We then analysed the spectral characteristics of this recording (for details see Supporting information, Section S3).

4.3.2 Aquarium experiments

We performed our aquarium experiments at the University of Adelaide aquarium using hatchery-reared pediveliger oyster larvae (*O. angasi*) supplied by the South Australian Research and Development Institute. These larvae were used within two days of arrival and displayed swimming behaviour and an actively searching foot that enables them to move and settle. This species 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 (Austral summer, McAfee and Connell 2020). These larvae spend several days to two weeks in the water column, dispersing tens of kilometres (North et al., 2008), after which they can explore the seafloor as pediveliger larvae, before permanently attaching to substrate as ‘spat’.

To test the effectiveness of acoustic enrichment for oyster recruitment in the presence of anthropogenic noise, we exposed oysters to four sound treatments: (1) a healthy reef soundscape (“Reef”); (2) a healthy reef soundscape in the presence of anthropogenic noise (“Reef + Noise”); (3) a soundscape filled with anthropogenic noise (“Noise”); and (4) a no sound control (“Control”). Our healthy reef soundscape was recorded from Noarlunga Reef (described above). For the anthropogenic noise recording, we used a combination of shipping, motor boating, pile-driving and urban noises as recorded underwater. Each of these sound recordings came from ‘Freesound’, a collaborative repository of creative commons licensed audio samples, which we combined into a looped 1-minute-long sound file in the program Audacity.

We played our recordings using underwater speakers that we built with our technology collaborators at the Australian Ocean Lab (5 x 3 cm vibration loudspeaker [25W, 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 one rechargeable battery for power [12V SLA; RS Components Pty Ltd], secured inside waterproof PVC housing; H × W: 10 × 12 cm; www.ausocean.org/technology). For the "Reef + Noise" treatment, we used two speakers, one to play the reef soundscape recording, and one to play the anthropogenic noise recording. For the "Control", "Reef" and "Noise" treatments, we used a single speaker, accompanied by an additional dummy speaker which represented the second speaker used in the "Reef + Noise" treatment. We played all recordings at the highest volume on the amplifier and parameterised the sound treatments to replicate *in-situ* soundscape conditions (for details see Supporting information, Section S1).

Our oyster larvae were in peak condition (i.e., actively searching foot) for a period of two days, after which their condition declined. Therefore, we ran three trials (total *n* = 3 per treatment) across these two days, where we exposed larvae to our sound treatments by randomly assigning and placing the speakers into 9-litre plastic tubs filled with seawater (L x H x W: 31 x 22 x 18 cm; 20ºC). To limit background noise, these tubs were sound-proofed using acoustic foam (5mm thick self-adhesive sound absorbing foam, Jaycar). To generate the darker conditions that encourage oysters to settle, we covered the tubs in cloth (Grunt black builder's film; Ritchie and Menzel, 1969; Shaw et al., 1970). Within each tub, we placed three 70 mL specimen jars filled with seawater and containing a settlement tile (2.5 × 2.5 cm sanded PVC square) and approximately 300 pediveliger oyster larvae (18 mL pipette of larvae at approximately 16.67 oysters/mL). We ran trials for two hours, after which we removed the specimen jars and counted the number of oysters that had recruited onto each tile using a dissecting microscope. We gently agitated the larvae using water from a pipette to ensure proper attachment and discounted any crushed larvae. To ensure there were no experimental artefacts from individual tubs or speakers, between each experimental run we repositioned the sound treatments in the aquarium and switched the speakers between sound treatments.

To analyse our data, we firstly calculated the mean recruitment across the three settlement tiles within each tub to provide a solitary value per tub, per trial (*n* = 3 replicates per treatment). We used these three values to calculate the mean recruitment and standard error per treatment across all trials. We performed one-way ANOVAs to assess any significant differences in recruitment between treatments, ensuring the model assumptions were met. Firstly, we compared the “Reef” and “Control” treatments, which signified natural reef conditions. Secondly, we compared the “Reef + Noise” and “Noise” treatments, which signified anthropogenic conditions. Lastly, we calculated the effect size and standard errors of boosted recruitment between the “Reef” and “Control” treatments, and then the “Reef + Noise” and “Noise” treatments, using the standardised mean difference (Cohen’s *d*) and the bootstrap procedure (see Efron and Tibshirani, 1993). All analyses were performed in R (v.4.1.2).

4.3.3 Field experiments

We conducted our field experiments at two flat oyster restoration sites in Gulf St. Vincent, South Australia. This gulf once contained native oyster reefs which have now been lost to an oyster dredging fishery in the late 19th century (Alleway and Connell, 2015) and replaced by barren sand flats (Tanner, 2005). Flat oysters are now the focus of a nation-wide reef restoration program in Australia (McAfee et al. 2022). Our field sites included two oyster restorations with different ambient soundscapes: (1) “Natural Soundscape” (Glenelg Reef, 34˚58.38’ S, 138°29.88’ E), a relatively quiet, natural soundscape characterised by low-intensity snapping shrimp snaps and periodic boating activity during the day, is located off Adelaide’s metropolitan coastline and was constructed in November 2020; (2) “Anthropogenic Soundscape” (Port River Reef, 34˚50.7’ S, 138°29.88’ E), an urbanised soundscape characterised by frequent shipping, boating and relatively constant traffic noises, is the site of a 2018 restoration in a heavily urbanised river (for map see Supporting information; Section S2). Each of these restorations are located in 4-8 meters of water where natural recruitment of native oysters have been observed in high numbers in cases where sufficient substrate has been provided for them (McAfee et al. 2023). Our experiments were performed throughout the oyster recruitment season (i.e., October 2020 to March 2021; McAfee and Connell, 2020).

We observed the rates of wild *O. angasi* larval recruitment across these two sites when exposed to ambient conditions (“Control”) and with playback of a natural reef soundscape (“Enriched”). Here, we define the term ‘acoustic enrichment’ as the full level of sound produced by our marine speakers, and the term ‘signal’ as the proportion of acoustic enrichment that is received. Finally, we define the term ‘masking’ as the amount of interference that anthropogenic noise has upon acoustic enrichment. We quantify this reduction as a function of the difference between the sound pressure levels between treatments associated with natural ambient soundscapes versus treatments with ambient soundscapes containing anthropogenic noise. In the “Enriched” treatment, we used underwater speakers to play the reef soundscape (larger version of the speaker described above, including 4 rechargeable batteries for power, secured inside waterproof PVC housing; H × W: 10 × 12 cm). In the “Control” treatment, we used dummy control speakers that consisted of the waterproof PVC housing without the encased electronics.

The natural reef recording we played was the same as described in our aquarium experiments. To determine the acoustic characteristics of the ambient background noise at each site relative to the playback treatments, and to the natural reef recording, we recorded and analysed the soundscapes of each treatment at each of the reef locations (Figure 1; for more details see Supporting information, Section S3). At the “Natural Soundscape” reef, this revealed “Enriched” to substantially enrich sound pressure levels and snapping shrimp snap counts relative to “Control” (8.90 dB/Hz increase, 435 snaps per minute increase). By contrast, “Enriched” at the “Anthropogenic Soundscape” reef did not substantially enrich sound levels or snapping shrimp snaps relative to “Control”. The ambient soundscape at this site did contain a larger number of snapping shrimp snaps than “Natural Soundscape”, possibly due to it being an older restoration, however, it was also associated with frequent shipping, boating and urban noises (0.01-10 kHz). Finally, our self-constructed speakers could only partially recreate the acoustic characteristics of our natural reef recording (for more details see Supporting information, Section S3), but was still able to enrich the ambient soundscape at the sites associated with natural sounds. Of note, these speakers have previously demonstrated their ability to influence oyster swimming and settlement behaviour in the aquarium and field (Williams et al. 2022; McAfee et al. 2023).

At "Natural Soundscape", we had two replicate sites per "Control" and "Enriched" treatment and performed experiments across three trials ($n = 6$). At "Anthropogenic Soundscape", we had two replicate sites per treatment and performed experiments across two trials ($n = 4$). At each of the two locations, each speaker and dummy control were separated by at least 50 metres to avoid sound crossover between treatments. These were secured 0.5 metres above the seafloor. To provide a substrate for larvae to recruit to, we secured a vertically oriented panel (15 x 15 cm; concrete board in which larval oysters can settle; Goelz et al. 2020) to the top of a plastic stake, which we inserted 0.3 metres above the seafloor. We placed six of these stakes (four for "Anthropogenic Soundscape") two metres away from each speaker or dummy control, with each stake spaced at least 1 metre apart from one another. Our speakers played the sound recording looped continuously for a month, as the early stages of reef development are crucial to the success of shellfish restorations (McAfee et al. 2023). At the end of each trial, we removed the panels and counted the number of oysters that had recruited onto the outward facing side of the panel using a microscope.

We calculated the mean recruitment and standard errors per treatment across each of the two restoration sites, and then tested for significant differences between treatments using the Welch *t*-test, after ensuring the data met the assumptions for this test. Furthermore, we calculated the effect size means and standard errors of recruitment and of boosted root-mean-square sound pressure levels (SPL_{rms}) between treatments. We did this using the standardised mean difference (Cohen's *d*) and the bootstrap procedure. All analyses were performed in R (v.4.1.2).

4.4 Results

4.4.1 Aquarium experiments

Analysis of the aquarium experiments revealed a significant effect upon recruitment of acoustic enrichment relative to controls in conditions associated with natural sounds (Fig. 2A; 1-way ANOVA; $F_{1,4} = 8.158$, $p = 0.046$). "Reef" (mean recruitment per 2.5 cm^2 [± 1 SE], 15.44 ± 5.70) received 2.57 times the density of larvae than "Control" (mean recruitment per 2.5 cm^2 [± 1 SE], 6.00 ± 0.58), a significant increase by 157.33%. There was no significant effect upon recruitment of acoustic enrichment relative to controls in the presence of anthropogenic noise. "Reef + Noise" (mean recruitment per 2.5 cm^2 [± 1 SE], 14.67 ± 1.76) received no significant increase in density of larvae relative to "Noise" (mean recruitment per 2.5 cm^2 [± 1 SE], 15.11 ± 3.53) (Fig. 2A). Furthermore, the effect size of boosted recruitment between "Reef" and "Control" in conditions associated with natural soundscapes (Cohen's *d* [± 1 SE], 2.33 ± 1.10) was 14.56 times greater than that between "Reef + Noise" and "Noise" in conditions associated with anthropogenic soundscapes (Cohen's *d* [± 1 SE], 0.16 ± 0.39) (Fig. 2B).

4.4.2 Field experiments

Analysis of recruitment in the field revealed higher recruitment in "Enriched" than "Control" at "Natural Soundscape", but not at "Anthropogenic Soundscape". At "Natural Soundscape", the effect size of boosted recruitment between "Control" and "Enriched" (Cohen's *d* [± 1 SE], 3.452 ± 1.89) was 138.08 times greater (13,708% increase) than that at "Anthropogenic Soundscape" (Cohen's *d* [± 1 SE], 0.025 ± 0.49) (Fig. 3B). At "Natural Soundscape", the effect size of boosted sound (derived from SPL_{rms}) between "Control" and "Enriched" (Cohen's *d* [± 1 SE], 26.180 ± 4.73) was 128.97 times greater (12,796.6%

increase) than that at “Anthropogenic Soundscape” (Cohen’s *d* [± 1 SE], 0.203 ± 0.05) (Fig. 4B).

At “Natural Soundscape”, “Enriched” boosted recruitment by 3.33 times (mean recruitment per 15 cm^2 [± 1 SE], 49.89 ± 6.08) relative to “Control” (mean recruitment per 15 cm^2 [± 1 SE], 15.02 ± 2.87), a significant increase by 233% (*t*-test: $t(49.90) = -5.19$; $p = 0.001$) (Fig. 3A). At “Anthropogenic Soundscape”, there was no difference in recruitment between “Enriched” (mean recruitment per 15 cm^2 [± 1 SE], 28.90 ± 7.53) and “Control” (mean recruitment per 15 cm^2 [± 1 SE], 29.20 ± 10.53) (*t*-test: $t(27.16) = 0.02$; $p > 0.05$) (Fig. 3A).

At “Natural Soundscape”, there was a significant difference in mean sound levels (SPL_{rms}) and mean snaps per minute (snaps) between “Enriched” (mean SPL_{rms} [± 1 SE], 111.25 ± 0.17; mean snaps [± 1 SE], 547 ± 40.90) and “Control” (mean SPL_{rms} [± 1 SE], 102.35 ± 0.39; mean snaps [± 1 SE], 112 ± 4.43) (SPL_{rms} *t*-test: $t(6) = 45.13$; $p = 0.001$; snaps *t*-test: $t(6) = 9.88$; $p = 0.002$) (Fig. 4A; Supporting information, Section S3). At “Anthropogenic Soundscape”, the mean SPL_{rms} and mean snaps were statistically indistinguishable between “Enriched” (mean SPL_{rms} [± 1 SE], 112.83 ± 1.00; mean snaps [± 1 SE], 405.50 ± 3.60) and “Control” (mean SPL_{rms} [± 1 SE], 113.34 ± 1.37; mean snaps [± 1 SE], 353.80 ± 42.40) (Fig. 4A; Supporting information, Section S3).

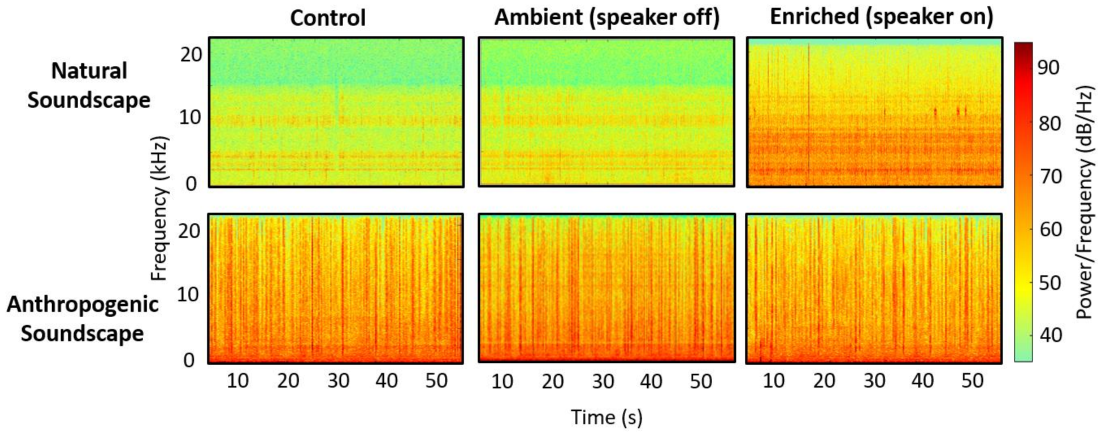

Figure 1. Spectrograms in the field for the “Control” and “Enriched” treatments, and the background ambient soundscape (60 second-long recordings) across two restoration sites; “Natural Soundscape” and “Anthropogenic Soundscape”. Spectrograms were produced using 1 s windows with 50% overlap.

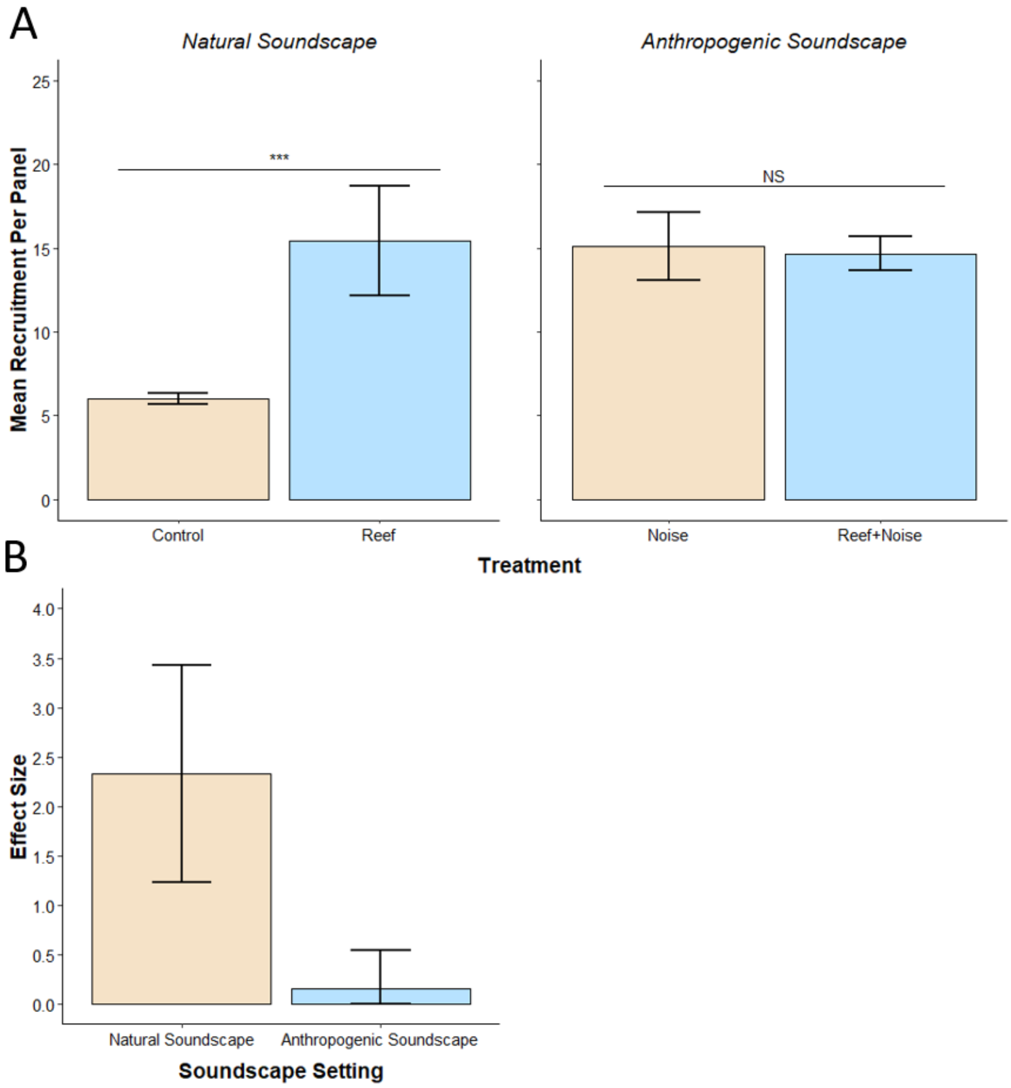

Figure 2. Oyster recruitment (mean recruitment per 2.5 cm^2 panel ± 1 SE) (A) in the aquarium between “Control” and “Reef” treatments (*n* = 3) in a natural soundscape setting (left) and between “Noise” and “Reef + Noise” treatments (*n* = 3) in an anthropogenic soundscape setting (right). Letters ‘NS’, ‘***’, and lines above columns indicate non-significance or significance, respectively, between treatments. Also shown are the effect sizes (Cohen’s *d* ± 1 SE) of (B) boosted larval recruitment between the “Control” and “Reef” treatments (“Natural Soundscape”) and the “Noise” and “Reef + Noise” treatments (“Anthropogenic Soundscape”).

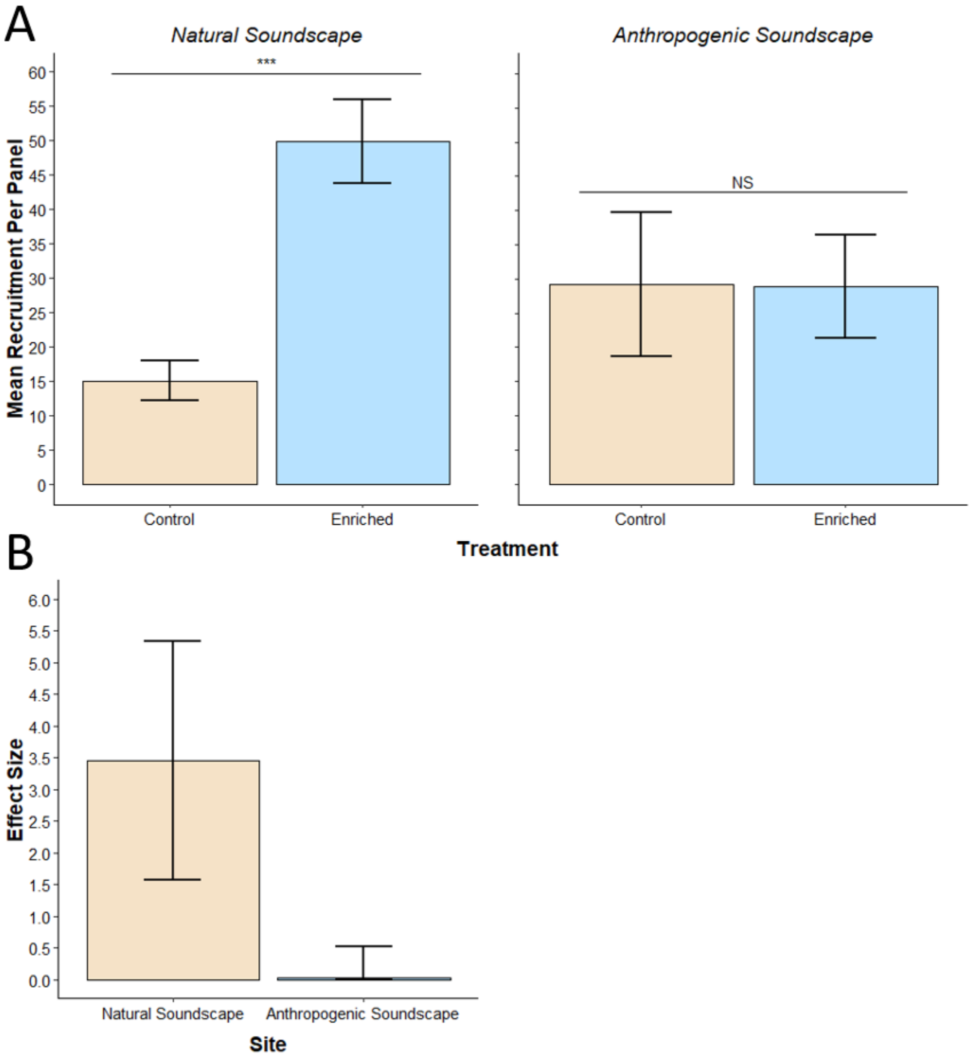

Figure 3. Oyster recruitment (mean recruitment per 2.5 cm^2 panel ± 1 S. E.) (A) in the field between “Control” and “Enriched” treatments across two restoration sites; “Natural Soundscape” (*n* = 6 per treatment) and “Anthropogenic Soundscape” (*n* = 4 per treatment). Letters ‘NS’, ‘***’ and lines above columns indicate non-significance or significance, respectively, between treatments. Also shown are the effect sizes (Cohen’s *d* ± 1 SE) of (B) boosted larval recruitment between the “Control” and “Enriched” treatments, across the two restoration sites.

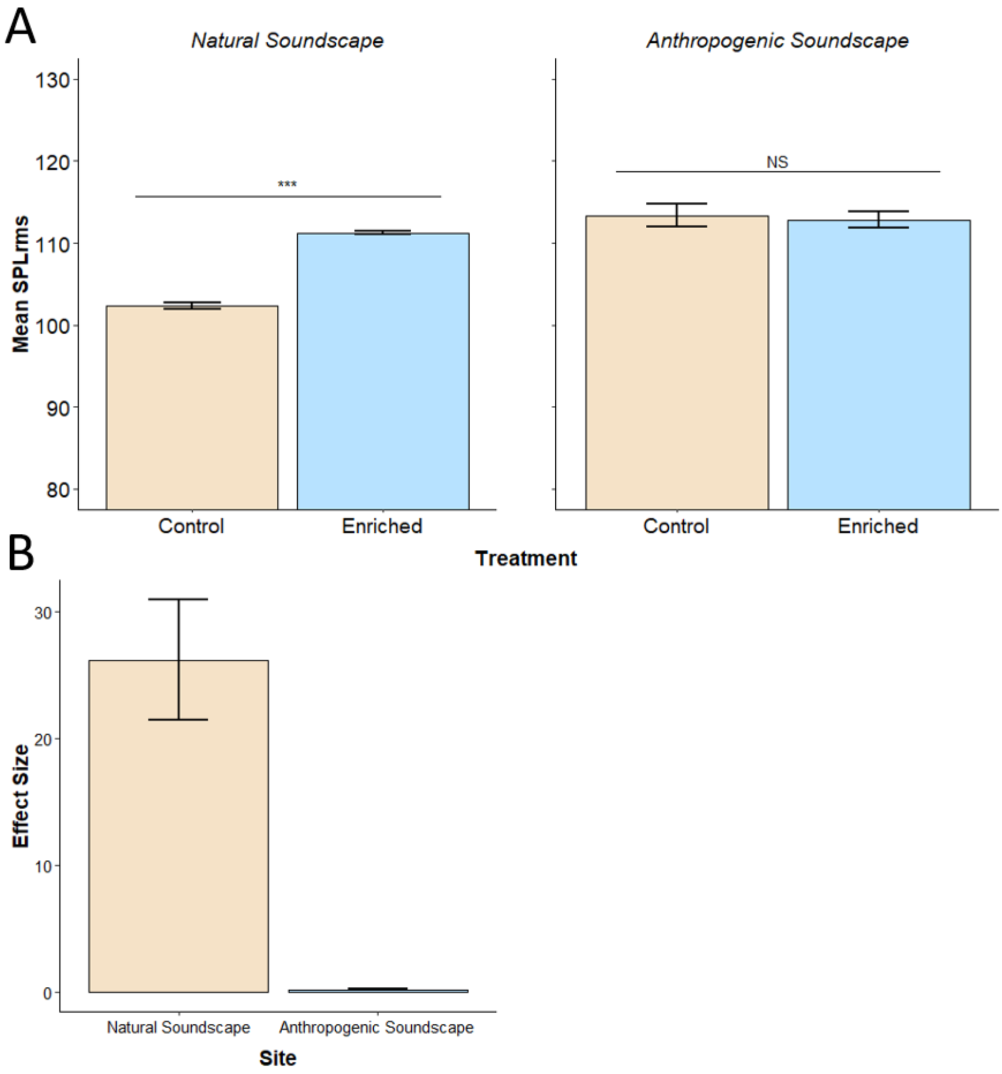

Figure 4. Mean SPL_{rms} (mean ± 1 S. E.) (A) in the field between “Control” and “Enriched” treatments across two restoration sites; “Natural Soundscape” (n = 4 per treatment) and “Anthropogenic Soundscape” (n = 4 per treatment). Letters ‘NS’, ‘***’ and lines above columns indicate non-significance or significance, respectively, between treatments. Also shown are the effect sizes (Cohen’s *d* ± 1 SE) of (B) boosted sound (derived from SPL_{rms}) between the “Control” and “Enriched” treatments, across the two restoration sites.

4.5 Discussion:

4.5.1 Applying acoustic enrichment in an Anthropocene Ocean

To upscale ecosystem restoration and receive positive economic and ecological returns on investment, innovative, affordable solutions are required. Acoustic enrichment may help restoration practitioners achieve this, but to our knowledge, its value in the presence of anthropogenic noise has not been examined. We show that high levels of anthropogenic noise appear to mask acoustic enrichment, which limits the effectiveness of using speakers to boost the recruitment of larval oysters to restoration reefs. Where acoustic enrichment works to enrich the ambient soundscape at restoration sites associated with relatively quiet, natural sounds like snapping shrimp snaps (i.e., our "Natural Soundscape" site), we observed a significant boost in larval recruitment. However, at sites associated with anthropogenic noise (i.e., our "Anthropogenic Soundscape" site), we observed a lack of oyster recruitment. This suggests that anthropogenic noise masks the acoustic signal the larvae are attracted to (i.e., natural habitat-related reef sounds).

Urbanised waterways are known to mask natural soundscapes (Duarte et al. 2021). This aligns with our findings, where playing healthy reef sounds only provided a significant boost to oyster recruitment in the absence of anthropogenic noise. Yet, in our laboratory experiment, comparable recruitment was observed between the anthropogenic noise treatment and the healthy reef treatment. This indicates that anthropogenic noise can still induce high settlement rates; a phenomenon that has also been observed with mussels (Wilkens et al. 2012; Jolivet et al. 2016). Yet, the omnipresent nature of anthropogenic noise in urbanised waterways likely reduces the navigational function of attractive marine sounds, such as those provided by our speakers (e.g., masking the direction of attractive sounds due to multiple anthropogenic sound sources [traffic, boating, coastal industry], as in this study). Shallow rivers, as in this study, generally have higher noise pollution due to the reflection of sound waves from the bottom and sides of the river (Urick 1983), with this reflection enhanced if the river is constructed with dense concrete material (Fediuk et al. 2021). From these findings, it appears that acoustic enrichment for oyster restoration is context dependent, with uncertain value in localities dominated by anthropogenic noise.

4.5.2 Disrupted recruitment processes

Not only does our work demonstrate that anthropogenic noise reduces the opportunity for using speakers for restoration, but it also adds to a growing body of research which suggests that anthropogenic noise disrupts recruitment processes. The recruitment process works to replenish populations and is intricately linked to the functioning and maintenance of a healthy ecosystem (Caley et al. 1996), especially where foundational, reef-building organisms are concerned (i.e., shellfish and coral). Successful recruitment requires larvae to distribute in the water column and select appropriate habitat by responding to visual, chemical and acoustic stimuli (Kingsford et al. 2002, Leis et al. 2011, Suca et al. 2020). Biological soundscapes can provide such directional and habitat quality information to animals, but where anthropogenic noise interference with these signals, recruitment may be disrupted. This is because many anthropogenic noises have high peak pressure levels which mask the biological soundscape (Stanley et al. 2012). Noise has serious implications for recruitment dynamics and is already known to affect many terrestrial and marine organisms (Kunc and Schmidt, 2019). For example, in choice experiments, boat noise in the presence of reef sounds cause coral reef fish larvae to move away from the sound, contrasting their attraction response in the presence of reef sounds alone (Holles et al. 2013). Future research might aim to elucidate whether this sort of behaviour is due to avoidance of noise, or perhaps an impaired ability to detect stimuli from reef sounds due to masking by noise. Regardless, the persistence and increase in pervasive anthropogenic noise across natural ecosystems, especially sites targeted for habitat restorations, are concerning. Joining the calls of others, we suggest that more regulation be introduced surrounding anthropogenic noise around our natural ecosystems. For example, there are suggestions that legislative bodies introduce legislation around noise in marine-protected areas and restoration sites (Chang and Zhang 2021, Williams et al. 2015). Furthermore, we might be able to manage noise production during peak recruitment periods of target organisms, to increase the likelihood of larvae that use natural soundscapes during recruitment to find settlement substrate (Lecchini et al. 2018). Understanding the role of healthy and anthropogenic noise during recruitment processes is key knowledge to inform, for example, where, when and how we manage and restore marine ecosystems.

4.5.3 Implications and opportunities for restoration

Following the construction of reef restorations, the recruitment patterns during the initial weeks and months of the restoration can inform the ecological trajectory of the project. At shallow depths, bare rocky substrate can be quickly dominated by opportunistic colonisers such as turf-forming algae that competitively excludes other organisms, such as oyster larvae (McAfee et al. 2021). Consequently, a priority for new reef restorations is to maximise recruitment during the early successional stages (McAfee and Connell 2020; Temmink et al. 2021; Vanderklift et al. 2020). From this and other work (Lillis et al. 2014a, b; Williams et al. 2022; McAfee et al. 2023), it appears acoustic enrichment could act as a cost-effective solution to boost recruitment and accelerate the recovery of the ecological goods and services that initially motivated the restoration, such as increased fish production (zu Ermgassen et al. 2016), improved water quality (Parker and Bricker, 2020) and shoreline stabilisation. Relative to other practices for seeding oyster recovery, such as hatchery production of oyster spat to plant on the reef (Geraldi et al. 2013), acoustic enrichment provides a relatively inexpensive strategy for maximising natural recruitment. For example, fish use sound to navigate and can be drawn to restoration sites (Gordon et al. 2019). However, noise pollution can also disorientate fish (Popper, 2003). With restorations increasingly occurring in noisy, metropolitan waterways, acoustic enrichment may have limited value. We therefore suggest that in the planning stages of reef restoration, the soundscapes of candidate sites be surveyed to establish whether acoustic enrichment can provide a sound-boosting effect relative to any anthropogenic noise. Where sites are characterised by high levels of noise pollution, they may be inappropriate sites to use this technique to enhance recruitment processes. However, if this noise can be mitigated, or if technological solutions in speakers can rise above this noise, then acoustic enrichment might provide a boosting effect to recruitment and yield positive ecological and economic returns on investment.

4.5.4 Future directions

Future research might aim to determine the sound detection mechanisms that enable larvae to detect and distinguish between sounds. For example, elucidating the role that particle motion and the statocyst play in larval recruitment, particularly in relation to anthropogenic noise, would be particularly valuable. For instance, we know that low frequency sounds can damage the statocyst of jellyfish, indicating potential trauma associated with exposure to noise pollution (Solé et al. 2016). Particle motion in relation to marine soundscapes and animal navigation is understudied compared to sound pressure (Nedelec et al. 2021). Marine invertebrates likely detect the particle motion component of sound through internal statocyst organs that detect differences in particle density created by sound waves (Frings and Frings, 1967; Budelmann 1992a, b). As shown elsewhere, larval oysters appear to detect and respond to healthy reef sounds (Lillis et al. 2014a, b; Williams et al. 2022; McAfee et al. 2023) which may have a particle motion range that is particularly attractive to them. Potentially, particle motion levels below this preferred range may not be detectable, and levels above it (e.g., created by anthropogenic noise pollution) may be confusing, unattractive, or even damaging (e.g., Solé et al. 2016). Statocysts have been described for the pediveliger stages of some bivalve species (Gragg and Nott, 1977; Morton, 1984; Kennedy et al. 1996; Gosling, 2003), including the European flat oyster, *Ostrea edulis* (Erdmann, 1934). With greater understanding of how organisms respond to the particle motion component of sound, we may be able to identify the sound frequencies and levels that are attractive or unattractive to target organisms (i.e., bivalves, fish). This might reduce uncertainty around observed variation in the attractiveness of sound among different species and the wide variety of environments in which they occur.

4.6 Conclusion

Reducing the bottlenecks to natural recruitment of target organisms represents a critical step towards achieving marine restoration success. In particular, the replenishment of reef-building populations are key to rebuilding the function of reef habitats. Innovative solutions like acoustic enrichment, when complemented with other restoration efforts, could maximise this key process of restoration, potentially reducing the risk of recruitment failure by ensuring a steady supply of recruits to seed recovery. However, we show that anthropogenic noise disrupts recruitment of a key reef-building organism, highlighting the context-dependency surrounding the use of acoustic enrichment. Where anthropogenic noise masks acoustic enrichment of healthy reef sounds and disrupts recruitment processes, the role of soundscape ecology may be reduced for restoration efforts. This masking is a concern because marine restoration efforts are increasingly occurring along noisy, metropolitan coastlines and urbanised waterways. But where there is little anthropogenic noise, acoustic enrichment appears to enhance the process of recruitment which is key to restoration success.

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4.9 Supporting information

**Note:* Raw data material and sound files can be accessed on figshare (https://figshare.com/s/a9cb6663f3a9418f2e0b).

Section S1: Aquarium playback parameterisation

To parameterise our aquarium playback treatments and ensure they represented *in-situ* conditions as closely as possible, we recorded the playback of the four treatments and compared them to *in-situ* recordings. To do this, we placed a speaker(s) or dummy speaker into the experimental tub and played each sound treatment. Firstly, we suspended calibrated Sound Trap 202 hydrophones (Ocean Instruments, frequency response 0.1-30 kHz, set to high gain sensitivity [-169 to -169.8 dB re 1 V/μPa], -3dB bandwidth of 21.6 kHz, 48 kHz sampling frequency, data digitised using a 16-bit resolution) directly next to the speaker and set them to record the broadcast sound of each treatment continuously for two minutes. We then attached an accelerometer (Monitran MTN/1100W submersible accelerometer) to the base of the transducer (using a mounting stud) and connected this to a data logger (DATAQ DI-4108-U high-speed data logger) to calculate the particle acceleration levels of the sound playback treatments continuously for two minutes. We ran each hydrophone and accelerometer recording four times per sound treatment. We then used this data to create acoustic spectra per treatment to compare them to *in-situ* conditions, and to calculate the mean root-mean-square sound pressure levels (SPL_{rms}) and mean particle acceleration levels (PALs) per treatment.

To determine how acoustic power in each treatment changed across frequencies relative to *in-situ* conditions, we calculated the root-mean-square acoustic spectra in the package 'PAMGuide' in MATLAB® (Natick, MA, USA) using a Hann window (length 1 s, 50% overlap) (Fig. 1). To calculate the SPL_{rms} for each treatment, we used the package 'PAMGuide' by applying a high pass filter at 2 kHz to each recording, and by entering a Hann window (length 1 s, 50% overlap) into the package's settings (Fig. 2). To calculate the mean PALs for each treatment, we used the package ‘paPAM’ (Nedelec et al., 2021) (Fig. 3). We then calculated the means and standard errors of SPL$_{rms}$ and PAL between the “Reef” and “Control” treatments in the natural soundscape setting, and then the “Noise” and “Reef + Noise” treatments in the anthropogenic setting. We then performed Welch’s t-tests to determine any significant differences between the SPL$_{rms}$ and PAL means in each treatment, having firstly ensured the assumptions for this test were met (Tables 1-2). These analyses were performed in R (v.4.1.2).

Acoustic spectra revealed each the “Reef” and “Noise” treatments to replicate the *in-situ* soundscape conditions well (Fig. 1). “Reef” and “Control” also had significantly different mean SPL$_{rms}$ and mean PALs (Fig. 2A-3A, Table 1), whilst “Noise” and “Reef + Noise” were statistically indistinguishable (Fig. 2B-3B, Table 2). Furthermore, to determine any relationship between the mean SPL$_{rms}$ and mean PAL, we performed a linear regression of the relationship per treatment. This revealed that as SPL$_{rms}$ increases, so too does PAL ($F_{1,\,2}$ = 43.301, $p < 0.022$), with increasing SPL$_{rms}$ explaining r^2 = 0.956% of the variation in PAL (Fig. 4).

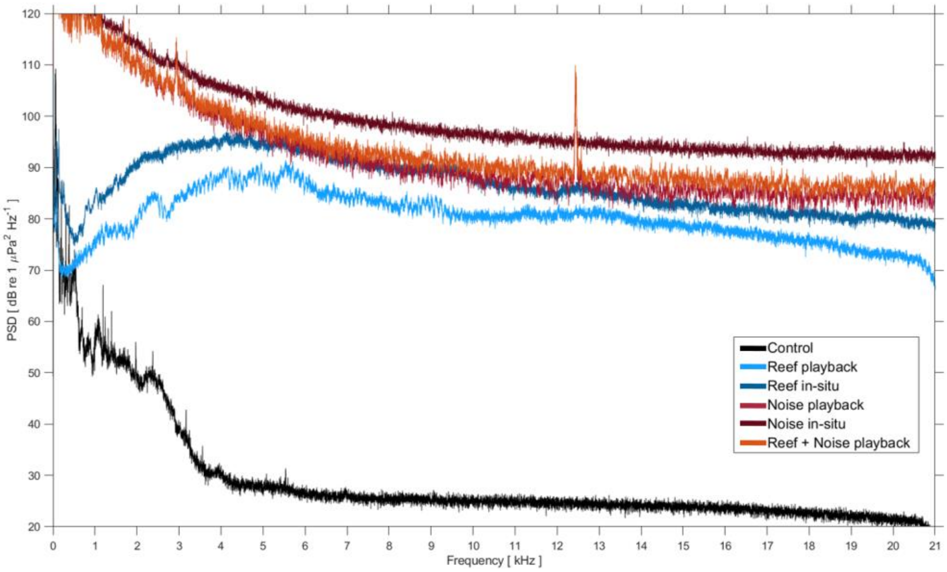

Figure 1. Root-mean-square acoustic spectra for “Control”, “Reef”, “Noise” and “Reef + Noise” playback recordings in the aquarium, compared against the *in-situ* reef soundscape and anthropogenic noise soundscape recordings.

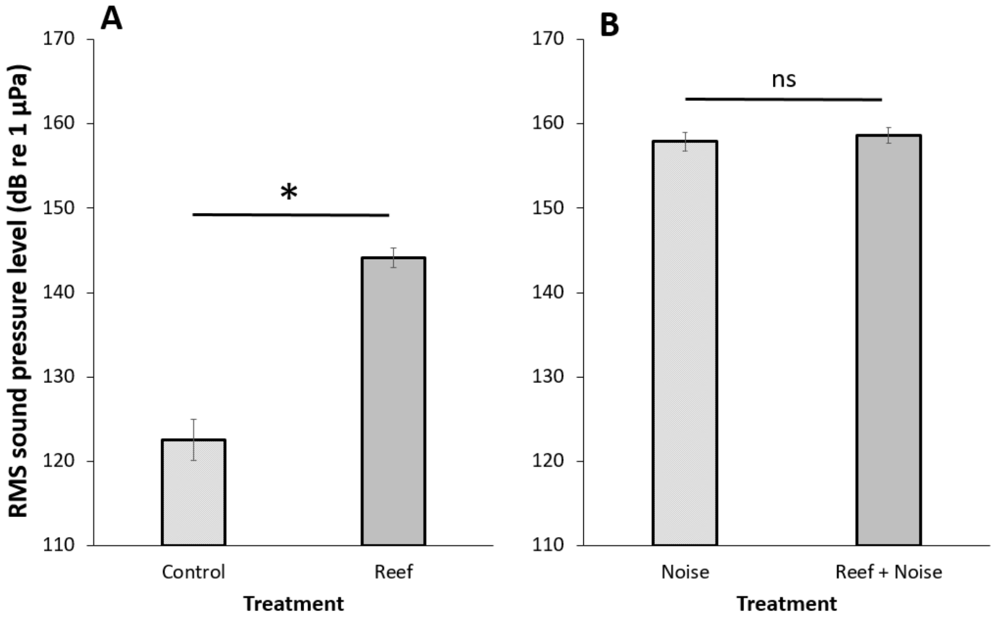

Figure 2. Mean root-mean-square sound pressure levels (SPL_{rms} ± 1 S. E.) for A) “Control” versus “Reef” soundscape treatments and B) “Noise” versus “Reef + Noise” soundscape treatments in the aquarium. “*” and “ns” above columns denote significant or non-significant differences between treatments, respectively.

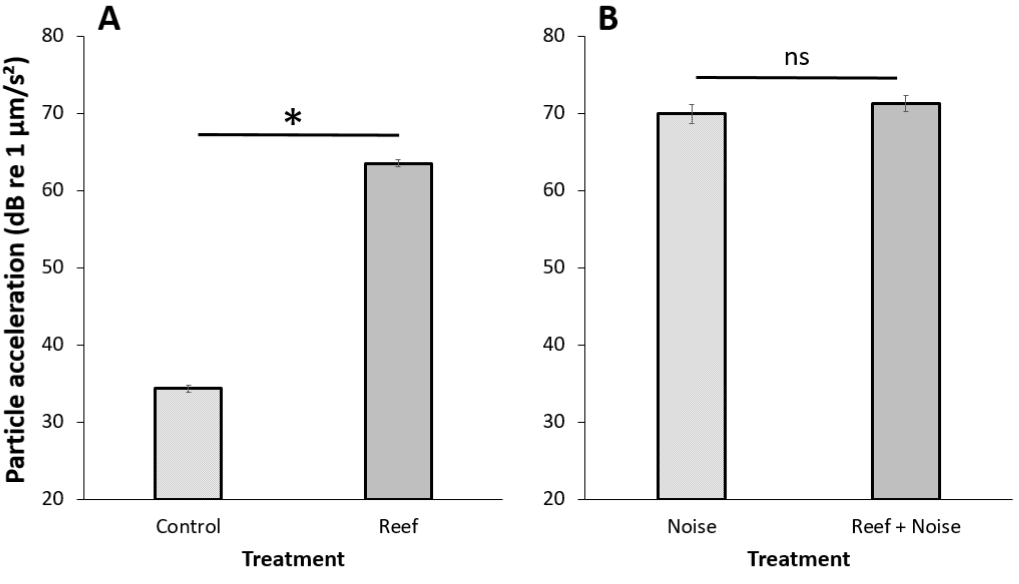

Figure 3. Mean particle acceleration levels (PALs ±1 S. E.) for A) “Control” versus “Reef” soundscape treatments and B) “Noise” versus “Reef + Noise” soundscape treatments in the aquarium. “*” and “ns” above columns denote significant or non-significant differences between treatments, respectively.

Table 1. Descriptive statistics and Welch's t-tests for mean SPL$_{\text{rms}}$ and mean PALs of "Reef" versus "Control" treatments in the aquarium.

Reef		**Control**		**Reef vs Control SPL$_{\text{rms}}$**		**Reef vs Control PAL**	
Mean SPL$_{\text{rms}}$ (± 1 S.E.)	**Mean PAL ± 1 (± 1 S.E.)**	**Mean SPL$_{\text{rms}}$ (± 1 S.E.)**	**Mean PAL ± (± 1 S.E.)**	**t-value (df)**	***P*-value**	**t-value (df)**	***P*-value**
144.13 (1.11)	63.54 (0.45)	122.55 (2.46)	34.33 (0.40)	15.993 (4.18)	<0.001	96.715 (5.93)	<0.001

Table 2. Descriptive statistics and Welch's t-tests for mean SPL$_{\text{rms}}$ and mean PALs of "Noise" versus "Noise + Reef" treatments in the aquarium.

Noise		**Reef + Noise**		**Noise vs Reef + Noise SPL$_{\text{rms}}$**		**Noise vs Reef + Noise PAL**	
Mean SPL$_{\text{rms}}$ (± 1 S.E.)	**Mean PAL (± 1 S.E.)**	**Mean SPL$_{\text{rms}}$ (± 1 S.E.)**	**Mean PAL (± 1 S.E.)**	**t-value (df)**	***P*-value**	**t-value (df)**	***P*-value**
157.90 (1.07)	69.95 (1.26)	158.60 (0.94)	71.31 (1.04)	-0.983 (5.91)	0.364	-1.661 (5.79)	0.150

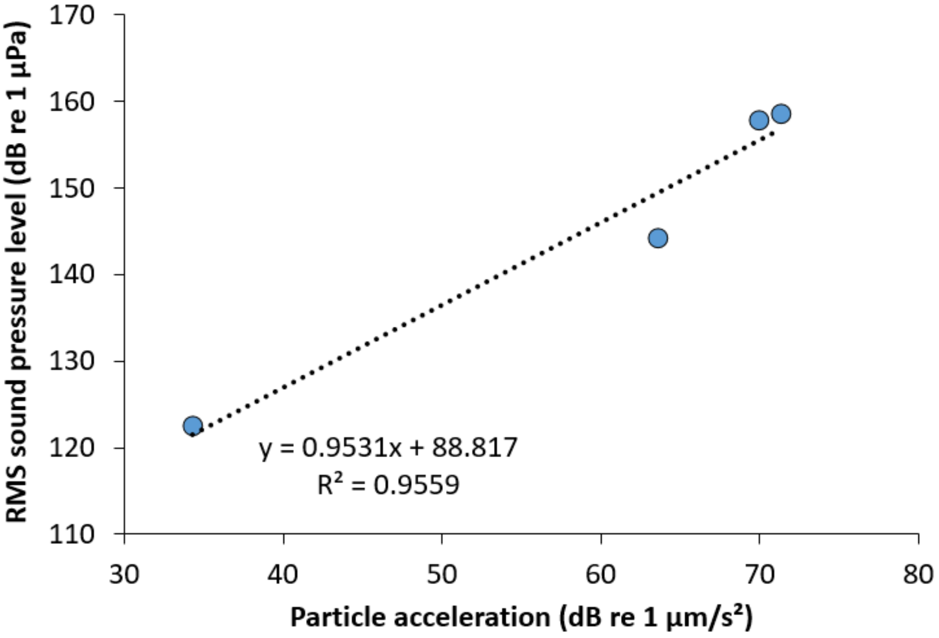

Figure 4. The relationship between mean root-mean-square sound pressure levels and mean particle acceleration levels for the different sound treatments (*n* = 4) used in the aquarium experiments.

Section S2: Map of field study sites

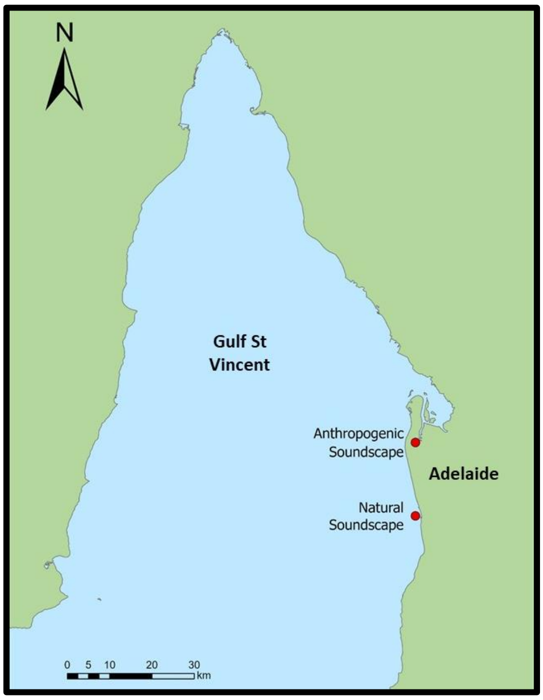

Figure 5. Map showing the study sites (red points) in Gulf St Vincent, South Australia, where we performed our field experiments.

Section S3: Field playback parameterisation

To determine whether the soundscape playback in our field experiments created a boost in sound relative to ambient noise levels, and to determine how well it reproduced the natural reef recording taken from Port Noarlunga, we recorded and analysed the playback of each sound treatment from each restoration reef. To do this, we used four calibrated hydrophones (as described above) and set them to record continuously. At each location, we anchored hydrophones 1 metre from the seafloor at 1, 10, 20 and 30 metres away from the speaker or dummy speaker, suspending them with a subsurface buoy. We then recorded the soundscapes when the speaker or dummy speaker was switched on against when it was switched off. From this data, we created mean root-mean-square acoustic spectra, calculated the mean root-mean-square sound pressure levels (SPL_{rms}) and mean snapping shrimp snaps per minute (snaps), and created spectrograms for each treatment.

We used the package ‘PAMGuide’ in MATLAB® to calculate the root-mean-square acoustic spectra to determine how acoustic power in each treatment across each distance changed over frequencies (Fig. 6). We used a Hann window for this (length 1 s, 50% overlap). To calculate the mean SPL_{rms} for each treatment across each distance, we used the package ‘PAMGuide’, entering a Hann window (length 1 s, 50% overlap) into the package’s settings (Tables 3, 5). To count the number of snapping shrimp snaps in each recording per treatment at each distance, we used the program Avisoft SASlab lite (Avisoft Bioacoustics, Berlin, Germany) (Tables 4, 6). We did this by firstly applying a high-pass filter to the recordings to remove all frequency signals below 2 kHz, because snapping shrimp snaps peak between 2-5 kHz (Lillis et al., 2014). We then used the pulse-train analysis tool in the program to count the mean number of snaps above a set amplitude threshold of 100. We then ran two-sample t-tests after ensuring the assumptions of this test were met, to determine whether there were any significant differences between the mean SPL_{rms} and mean snap counts in each treatment along each distance in the soundscape gradient (Tables 3-6). Finally, for visual comparisons of soundscape differences between treatments and the natural reef recording, we created spectrograms using the Short-Time Fourier transform in MATLAB®. These were made using the Hann window (length 1 s, 50% overlap) (Fig. 7).

Analysis of acoustic spectra at the “Natural Soundscape” restoration reef revealed the “Enriched” treatment to elevate sound levels across all frequencies up to 10 metres away from the speaker relative to the “Control” treatment, but to provide no such boost from 20 metres (Fig. 6). Meanwhile, at the “Anthropogenic Soundscape” restoration reef, there were no obvious differences between treatments across distance.

Analysis of the use of our speakers at the restoration reefs showed them to only partially reproduce the acoustic characteristics of the natural reef soundscape from Port Noarlunga. Our speakers created some of the broadband snaps seen in the natural reef soundscape, however, these were contained in the 0.3-10 kHz frequency range and did not extend above 10 kHz (Fig. 7). Taken from the four hydrophone recordings at Port Noarlunga, the natural reef's mean SPL_{rms} was 133.9 dB re 1µPa, and mean snaps was 920 snaps per minute. This is greater than those seen for the "Enriched" treatment at 1 m from the speaker at "Natural Soundscape" (mean SPL_{rms} = 111.3 dB re 1µPa; mean snaps = 547 snaps per minute; Tables 3-4) and "Anthropogenic Soundscape" (mean SPL_{rms} = 113.4 dB re 1µPa; mean snaps = 405.5 snaps per minute; Tables 5-6). These differences between the natural reef soundscape and our speaker may be the result of limitations in our speaker design and its housing, as well as the moderate volume at which the recording was played to ensure it did not crossover between treatments at each site. Despite this, our speakers were still able to enrich the soundscape at "Natural Soundscape" relative to ambient controls, produce clear shrimp snaps to the human ear and have demonstrated ability to influence the swimming and settlement behaviour of oyster larvae in the aquarium (Williams et al. 2022) and field (McAfee et al. 2023).

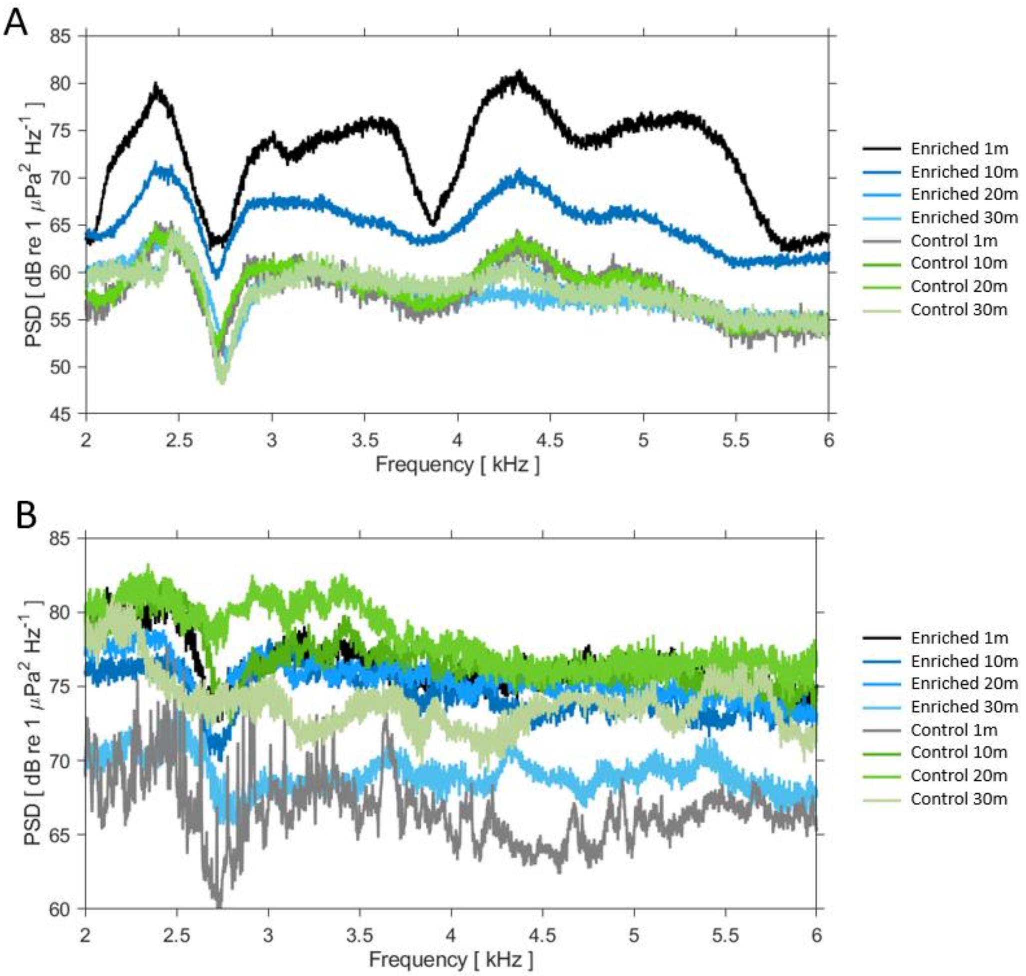

Figure 6. Root-mean-square acoustic spectra for sound (“Enriched”) versus control (“Control”) treatments at A) “Natural Soundscape” and B) “Anthropogenic Soundscape” restorations, along a gradient of 30 metres from the speaker.

Table 3. Descriptive statistics and two-sample t-tests for mean SPL_{rms} of “Enriched” versus “Control” treatments at “Natural Soundscape”, along a gradient of 30 metres from the speaker, where *a* = .05.

Distance from speaker (metres)	**Enriched**		**Control**		**Enriched vs Control**	
	Mean (Standard Deviation)	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
1	111.3 (0.34)	111.0-111.6	102.4 (0.79)	101.6-103.2	45.13(6)	.001
10	104.8 (2.59)	102.2-107.3	100.3 (0.22)	100.1-100.6	3.41(6)	.042
20	99.7 (0.31)	99.4-100.0	99.8 (0.29)	99.6-100.1	-0.62(6)	.561
30	99.4 (0.34)	99.0-99.7	100.8 (0.26)	100.5-101.1	-6.63(6)	.001

Table 4. Descriptive statistics and two-sample t-tests for snaps per minute of “Enriched” versus “Control” treatments at “Natural Soundscape”, along a gradient of 30 metres from the speaker, where *a* = .05.

Distance from speaker (metres)	**Enriched**		**Control**		**Enriched vs Control**	
	Mean (Standard Deviation)	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
1	547 (81.8)	465.2-628.8	112 (8.8)	103.1-120.9	9.88(6)	.002
10	507.75 (9.6)	489.1-517.4	211.0 (61.9)	149.1-272.9	9.47(6)	.002
20	344.3 (40.9)	303.4-385.1	217.8 (74.5)	143.2-292.3	2.98(6)	.031
30	237.0 (25.7)	211.4-262.7	153.3 (46.0)	107.2-199.3	3.18(6)	.024

Table 5. Descriptive statistics and two-sample t-tests for mean SPL_{rms} of “Enriched” versus “Control” treatments at “Anthropogenic Soundscape”, along a gradient of 30 metres from the speaker, where *a* = .05.

Distance from speaker (metres)	**Enriched**		**Control**		**Enriched vs Control**	
	Mean (Standard Deviation)	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
1	113.4 (2.0)	111.4-115.4	112.9 (2.7)	110.2-115.6	0.28(6)	.790
10	112.6 (1.0)	111.6-113.6	113.2 (1.2)	112.0-114.4	-0.78(6)	.467
20	113.4 (1.6)	111.8-114.9	113.5 (1.6)	111.9-115.1	-0.13(6)	.899
30	110.4 (2.1)	108.2-112.5	111.1 (0.9)	110.2-112.0	-0.62(6)	.569

Table 6. Descriptive statistics and two-sample t-tests for snaps per minute of “Enriched” versus “Control” treatments at “Anthropogenic Soundscape”, along a gradient of 30 metres from the speaker, where *a* = .05.

Distance from speaker (metres)	**Enriched**		**Control**		**Enriched vs Control**	
	Mean (Standard Deviation)	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
1	405.5 (7.2)	398.3-412.7	353.8 (85.0)	268.8-438.7	1.21(6)	.312
10	438.8 (12.0)	426.7-450.8	361.3 (70.5)	290.7-431.8	2.17(6)	.119
20	295.0 (64.7)	230.3-359.7	298.3 (115.1)	183.2-413.3	-0.05(6)	.963
30	221.3 (45.3)	175.9-266.6	331.0 (124.9)	206.1-455.9	-1.65(6)	.174

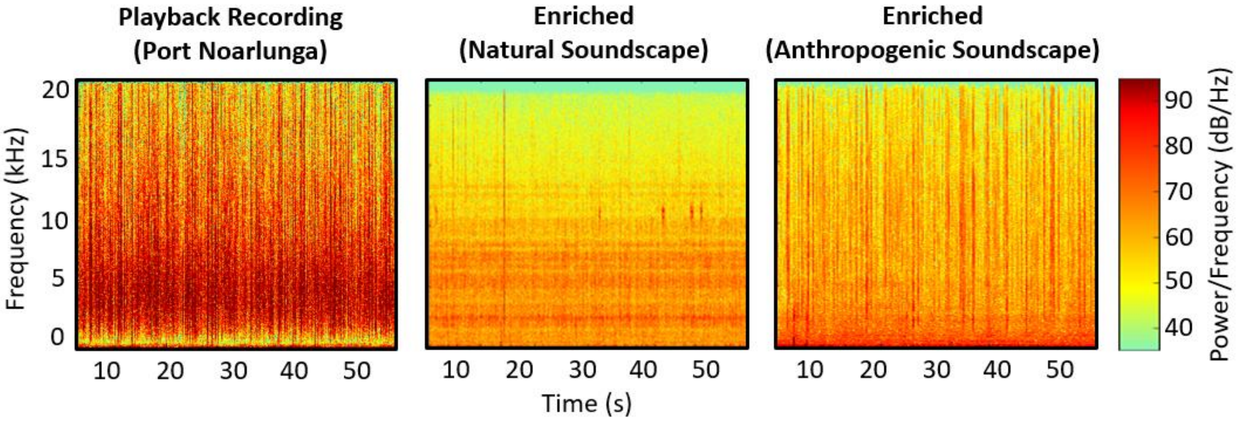

Figure 7. Spectrogram of the recording from Port Noarlunga reef used in the aquarium and field playback experiments, alongside spectrograms at 1m from the speaker of the “Enriched” treatments for each the Natural Soundscape and Anthropogenic Soundscape sites in the field (60 second-long recordings). Spectrograms were produced using 1 s windows with 50% overlap.

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CHAPTER FIVE

Combining ecology and technology to kick-start oyster reef restorations

Statement of Authorship

Title of Paper	Combining ecology and technology to kick-start oyster reef restorations		
Publication Status	✓ Published Submitted for Publication Accepted for Publication Unpublished and Unsubmitted work written in manuscript style		
Publication Details	A peer-reviewed version of Chapter 5 is now published as: “Combining ecology and technology to kick-start oyster reef restoration”, *Restoration Ecology*, e13975.		

Principal Author

Name of Principal Author (Candidate)	Brittany Williams		
Contribution to the Paper	Concept and design Data collection Analysis and interpretation First draft Critical revision		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	3/3/2023

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

x. the candidate’s stated contribution to the publication is accurate (as detailed above);
xi. permission is granted for the candidate in include the publication in the thesis; and
xii. the sum of all co-author contributions is equal to 100% less the candidate’s stated contribution.

Name of Co-Author	Dominic McAfee		
Contribution to the Paper	12.5% Concept and design Analysis and interpretation Critical revision		
Signature		Date	3/3/2023

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Contribution to the Paper	12.5% Concept and design Analysis and interpretation Critical revision		
Signature		Date	3/3/2023

5.1 Abstract

Techniques that can enhance the recruitment of foundation species are highly valued for instigating ecological restorations. Native oyster reefs have been lost worldwide, leading to restoration efforts in systems that are often recruitment limited, or where recruiting oysters must spatially compete with opportunistic species. Here, we combine ecological knowledge and acoustic technology to help drive the early successional processes on a large oyster reef restoration in southern Australia. Across three sites, we used self-made speakers to broadcast healthy reef soundscapes in order to attract naturally recruiting larvae to our reefs constructed of boulders. Additionally, we combine our sound treatments with artificial kelp that simulate positive synergies to boost recruitment of oysters. We show proof-of-concept that these approaches can boost recruitment of oysters towards building and binding reefs. Acoustic enrichment used in combination with artificial kelp increased the recruitment of oysters to reef-building (i.e., topside of boulders, 326.98% increase) and acoustic enrichment alone increased recruitment to reef-binding (i.e., underside of boulders, 126.95% increase). Our findings suggest that the combination of acoustic enrichment with artificial kelp might boost the early stages of reef development. By combining ecology with technology during the early stages of reef development, we show the potential value of these novel approaches in kick-starting the recovery of lost oyster reefs.

Keywords: acoustic enrichment; artificial kelp; ecology; oyster reef; positive species interactions; recruitment; restoration; technology

5.2 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. The combination of ecology and technology are emerging as a cultural norm for solution science to redress restoration risks and overcome environmental problems (Rhoten and Parker 2004). For example, drones can see through waves to identify suitable conservation sites (Chirayath and Earle, 2016) and we can non-invasively track animal movements (Francisco et al. 2020). Technology can also replace lost environmental cues that are needed to guide lost animals to suitable habitat (e.g., biogenic soundscapes; Williams et al. 2021). Using technology and ecological knowledge on species interactions may offer solutions to help protect and repair the environment (Pimm et al. 2015).

Acoustic enrichment has the potential to overcome restoration issues such as 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). Meanwhile, unstructured habitats are often void of these 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 (Williams et al. *in-review*). In turn, larvae that use sound during recruitment processes may be unsuccessful at reaching suitable adult habitat. Conspecific and habitat-related sounds are 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. 2014a, 2015; McAfee et al. 2023) and are demonstrated to navigate towards these sounds in the laboratory via horizontal swimming behaviour (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 (metres to tens of metres) (Kingsford et al. 2002; Leis and McCormick, 2002) and olfactory cues which rely on water movement to disperse (Atema, 1988; Leis and McCormick, 2002). If we can use acoustic technology to return these habitat-related sounds to places where they are lost, we could potentially steer the early stages of recruitment and reef development.

Another strategy for managing the early stages of reef restorations 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). At shallow depths, bare rocky substrate can be quickly dominated by opportunistic colonisers such as turf-forming algae that competitively excludes recruiting organisms like oyster larvae (McAfee et al. 2021). The algae traps sediment to form a barrier for new recruits, with this spatial dominance leading to homogenised coastlines (Gorgula and Connell, 2004; Gorman et al. 2009). However, kelp and oysters might be able to overcome these issues together. Kelp might assist larval oysters in settling onto substrates by removing algal turf via frond abrasion (Irving and Connell, 2006) and by inhibiting its growth by reducing understorey light (Connell, 2003). Meanwhile, oysters may provide hard substrata for kelp to grow upon and filter seawater surrounding it. Consequently, prioritising positive species interactions in restoration efforts 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 and Connell, 2015), 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). While work to restore Australia's lost shellfish reefs are 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 monopolise newly constructed reef substrata. Following the construction of reef restorations, the early success (the initial weeks and months) of organismal colonisation 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 of how acoustic enrichment (using speakers), and positive species interactions (using artificial kelp), can increase the initial recruitment stages of reef development by oysters. We assessed the recruitment of oysters among treatments of acoustic enrichment, artificial kelp, and their combination; and how these recruitment patterns contributed to reef-building topside and reef-binding underside of boulders.

5.3 Methods

5.3.1 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 in 8-10 metres of water approximately 1 km offshore of the Yorke Peninsula (34˚30.496' S, 137°53.953' E). The restoration consists of 159 limestone boulders reefs across 20 hectares. Although natural reefs of the native oysters are no longer present, scattered individuals are present and high rates of natural spat recruitment has been observed across Windara Reef during months where mean seawater temperature exceeds 17°C (McAfee and Connell, 2020). The native flat oyster is a brooding oyster that can release up to three million veliger larvae (170-189 µm) (Crawford,

2016) which can disperse tens of kilometres 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 1995; 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.

5.3.2 Experimental design and data collection

In the field, we set out to test the recruitment response of *O. angasi* larvae during the early stages of reef development to acoustic enrichment, positive species interactions, their combination, and how these relate to establishment of a reef. Recruitment to the topside of boulder substrate represents the “reef-building” component where oysters can form three-dimensional habitat for colonisation by associated species. Meanwhile, the underside represents the “reef-binding” component that acts to bind the reef together. This binding is akin to the crustose coralline algae that is prevalent throughout coral reefs, which glue loose sediments together to build and stabilise reefs (Bosence 1983; Bjork et al. 1995; Payri and Cabioch 2004; Tierney and Johnson 2012). Our experiment was performed during a one-month study from February to March 2021, as these early stages are critical in establishing a reef and determining its early ecological development. To test the effect of acoustic enrichment, we used underwater speakers playing healthy reef habitat sounds (described below). To test the effect of positive species interactions, we used artificial kelp designed to mimic the natural functions of kelp, a more sustainable experimental unit than denuding live kelp for a short-term experiment (described below). We observed the rates of recruitment of oysters to the topside and underside of limestone boulders when exposed to four treatments; acoustic enrichment (“Sound”), artificial kelp (“Kelp”), acoustic enrichment combined with artificial kelp (“Sound + Kelp”), and no acoustic enrichment or artificial kelp (“Control”). To cover as much spatial variation in larval recruitment as possible across Windara Reef, we tested this across three sites (“Site 1”, “Site 2”, “Site 3”).

5.3.3 Enriching acoustic cues

To test the effect of acoustic enrichment on recruitment, we used recordings that were sampled from a healthy reef habitat (Noarlunga Reef) in Gulf St Vincent, South Australia. To ensure this recording was representative of the habitat-type, we composed the playback file using recordings from several different times and sites within the same habitat during December (Austral summer). Sound recordings were made at high tide (4-8 metres of water) within one hour of sunrise, which is shown to be the loudest time of day for the snapping shrimp locally (Rossi et al. 2017; Williams et al. 2021) and across other reef soundscapes dominated by snapping shrimp (Radford et al. 2010; Lillis et al. 2014b; Bohnenstiehl et al. 2016). We took recordings continuously for an hour, 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], -3dB bandwidth of 21.6 kHz, 48 kHz sampling frequency, data digitised using a 16-bit resolution). Hydrophones were anchored one metre above the seafloor using a sub-surface buoy. A looped 1-minute-long sound file was then created using snippets of the recordings from each hydrophone. We used speakers (5 x 3 cm vibration loudspeaker [25W, 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 4 rechargeable batteries [12V SLA; RS Components Pty Ltd], secured inside waterproof PVC housing; H × W: 10 × 12 cm) to broadcast this reef recording, looping the sound file for the duration of the experiment. This was designed with our technology collaborators at the Australian Ocean Lab (AusOcean Underwater Speaker Guide, 2019; www.ausocean.org/technology). We parameterised this sound in the field 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 section 2.6 below). We used a dummy speaker for the control treatments, and attached a speaker or dummy speaker to a crate (35 cm x 35 cm x 35 cm) which we elevated 0.5 metres from the seafloor and attached to a sub-surface buoy.

5.3.4 Positive interactions

To test the effect of positive species interactions, we used artificial kelp that we attached to open experimental crates (35 cm x 35 cm x 35 cm). We did this by fitting a galvanised wire mesh lid (30 cm x 30 cm) to the top of the crate, from which we attached a square of nylon shade cloth (70% UV, Colaroo, 30 cm x 30 cm). From this square, we suspended nine strips of shade cloth (15 cm x 5 cm) inside the crate to mimic the substrate scraping of kelp fronds and their understorey shading. A lead ball weight (0.3 cm diameter) was attached to the end of each strip to ensure contact with the boulders in the presence of water flow, thereby replicating the action of kelp fronds as the cloth was positively buoyant. These units are a suitable substitute for live kelp as they can mimic the functions of live kelp fronds (i.e., shading and scouring) as previously shown (e.g., Russell 2007).

At each of the three sites, we used three replicates per treatment (total of n = 9 per treatment), each signified by an experimental crate. Each crate was filled with limestone boulders to replicate the structure and hydrodynamics of a mini reef, with only the three top boulders being collected for analysis per crate. We placed these boulders upon a galvanised wire mesh platform that was secured inside the crate and elevated 12 cm from the seafloor. At each site, we placed a speaker and dummy speaker on the seafloor, at least 50 metres away from one another to avoid sound crossover between treatments, and to represent as much of the spatial variability in recruitment in the restoration reef as possible. We then placed six experimental crates in a circle around the speaker or dummy speaker, each one-metre away from one another, and two metres away from the speaker. Three of these experimental crates contained artificial kelp, whilst three contained no artificial kelp. At the conclusion of the trial, the three top boulders were removed for enumeration in the laboratory.

5.3.5 Data analysis

To compare the recruitment of larvae between treatments, we first calculated the number of oysters on the topside and underside of three boulders in each crate, thereby providing an average value per crate. This yielded nine topside and nine underside averages for each treatment across boulders of uniform size (see below). Using these values, we calculated the average recruitment of larvae per treatment, and their standard errors, for each the topside and underside of boulders. For each orientation we performed three-way ANOVAs to test for the effects of ‘Sound’ and ‘Kelp’ (fixed factors, orthogonal) and ‘Site’ (random factor). Prior to these tests, the data was square transformed to satisfy assumptions of ANOVA. For greater clarity we also performed site-by-site analyses (Supporting information; Section S1; Fig. S1). Lastly, we measured the surface areas of each boulder by contouring aluminium foil to them, which we flattened and then measured the two-dimensional surface area in ‘ImageJ’ (Schneider et al. 2012) and performed a one-way ANOVA of Surface Area x Recruitment (topside and underside recruitment of boulders combined) for each treatment to determine any differences in recruitment based on boulder size. For each treatment, there were no significant differences in means based on boulder size. We performed all analyses in R (v.4.0.5).

5.3.6 Soundscape parameterisation

To ensure the playback of our experimental recording had greater sound intensity than that of the control treatment, and matched that of the original healthy reef recording as closely as possible, 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. We anchored hydrophones 1 metre from the seafloor at 1, 10, 20 and 30-metre 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 (see Supporting information; Section S2 for details). Lastly, we created spectrograms for each sound treatment at 1-metre away from the speaker or dummy speaker, and for the original reef recording (Fig. 1).

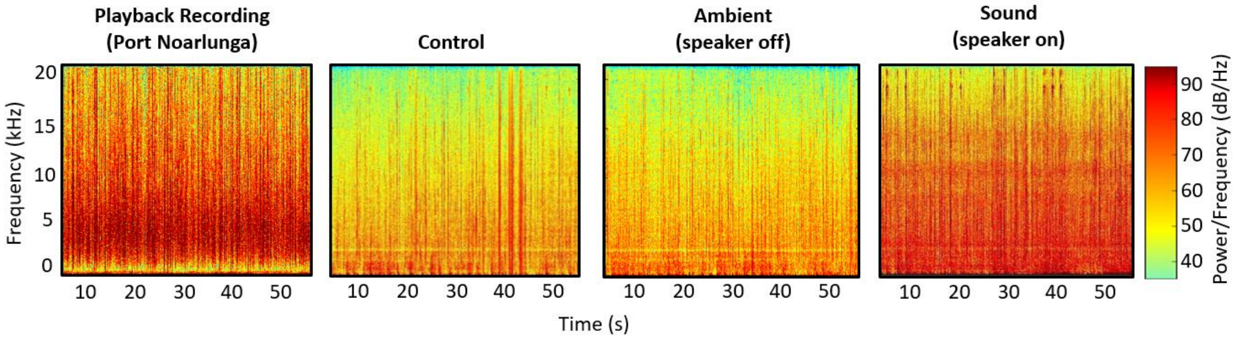

Figure 1. Spectrogram of the original reef soundscape recording from Port Noarlunga reef used in the playback experiments, alongside spectrograms at 1m from the speaker for the “Sound” and “Control” treatments, and the background ambient soundscape (60 second-long recordings). Spectrograms were produced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

5.4 Results

Across our three sites, we observed a total of 4628 oyster recruits, of which 26% recruited to the topside of boulders and 74% to the underside. On the topside, 16% of recruitment was in ‘Sound’ (13, 034/m^2), 24% in ‘Kelp’ (19, 448/m^2), 49% in ‘Sound + Kelp’ (40, 069/m^2) and 11% in ‘Control’ (9379/m^2). On the underside, 35% of recruitment was in ‘Sound’ (84, 138/m^2), 13% in ‘Kelp’ (29, 724/m^2), 35% in ‘Sound + Kelp’ (82, 000/m^2) and 17% in ‘Control’ (41, 379/m^2).

5.4.1 Reef-building

On the topside of boulders, there was a significant interactive effect on recruitment across all three sites (Sound x Kelp; Fig. 2; Supporting information; Section S3; Table S4; 3-way ANOVA; $F_{1,24} = 9.882$, $p = 0.004$). Pairwise tests showed that “Sound + Kelp” (mean recruitment per boulder [± 1 SE] 21.52 ± 3.01) received 4.3 times the density of larvae than “Control” (mean recruitment per boulder [± 1 SE] 5.04 ± 0.53), a significant increase by 326.98%. “Sound + Kelp” also received 2.9 times the density of larvae than “Sound” (mean recruitment per boulder [± 1 SE] 7.33 ± 0.77), a significant increase by 193.59%. Lastly, “Sound + Kelp” received 2.1 times the density of larvae than “Kelp” (mean recruitment per boulder [± 1 SE] 10.44 ± 1.22), a significant increase by 106.13%. Each “Sound”, “Kelp” and “Control” were statistically indistinguishable. ‘Site’ did not significantly influence the recruitment of oysters.

5.4.2 Reef-binding

On the underside of boulders, there was a significant effect of acoustic enrichment on recruitment (Fig. 2; Supporting information; Section S3; Table 5; 3-way ANOVA; $F_{1,27} = 20.350$, $p < 0.001$). “Sound” (mean recruitment per boulder [± 1 SE] 52.04 ± 8.32) received 2.3 times the density of settling larvae than “Control” (mean recruitment per boulder [± 1 SE] 22.93 ± 2.71), a significant increase by 126.95%. There were no detectable effects of artificial kelp. Lastly, ‘Site’ did not significantly influence the recruitment of oysters, even after pooling. These results indicate that acoustic enrichment combined with artificial kelp can boost the recruitment of oyster larvae to the reef-building topside of boulders, and that acoustic enrichment can do so to the reef-binding underside of boulders.

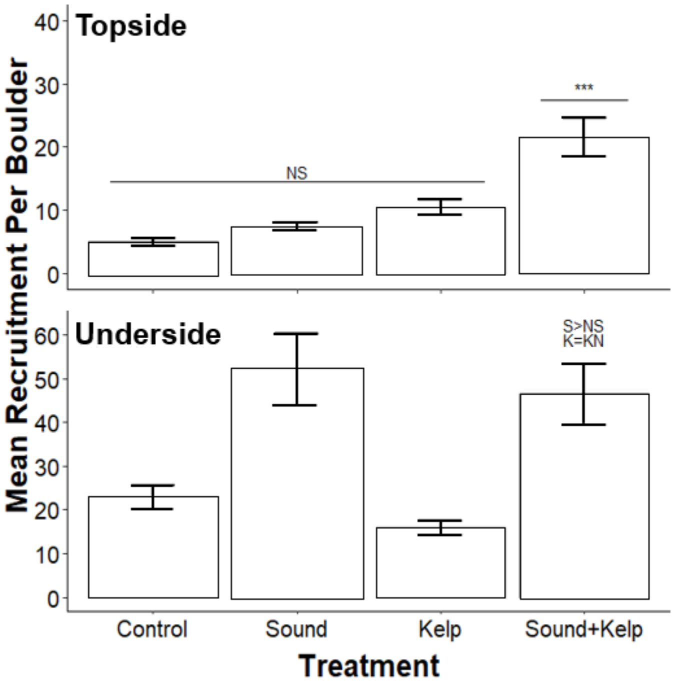

Figure 2. Acoustic enrichment used in combination with artificial kelp increases the recruitment potential of larvae to the topside of boulders. Acoustic enrichment can also increase the recruitment potential of larval oysters to the underside of boulders. Shown is the mean larval recruitment per boulder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

5.4.3 Soundscape parameterisation

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 metres away from the speaker relative to no sound controls, but to provide no such boost from 20 metres (see Supporting information; Section S2 for details). At 1 m from the speaker, "Sound" substantially enriched sound pressure levels and snapping shrimp snap counts relative to "Control" (4.2 dB/Hz increase, 394 snaps per minute increase) (see Supporting information; Section S2 for details). At source point, "Sound" also had a significantly higher particle acceleration level than "Control" (Welch t-test; $t_4 = 37.41$, $p < 0.001$; see Supporting information; Section S2 for details).

5.5 Discussion

Our findings show that we can boost oyster recruitment to the topside of boulders by over two-fold using acoustic enrichment and artificial kelp, and by over four-fold to the underside using acoustic enrichment. For restorations associated with recruitment bottlenecks, environmental suppressors and competitive barriers to recruitment, these techniques could give oysters the competitive advantage during recruitment and drive the early stages of reef development.

5.5.1. Acoustic enrichment

Current practice for shellfish reef restoration carries a high risk of recruitment and project failure. Furthermore, any larvae that are present in the water column and ready to recruit require navigational cues to locate suitable sites. We found that by re-creating lost soundscapes through acoustic enrichment, we can attract oysters to recruit in greater densities to both the topside and underside of boulders. In our study, provision of healthy soundscapes appeared to draw larvae to reefs, where they could then settle to eventually grow into complex, three-dimensional habitat. Our results are similar to increases in larval recruitment by the eastern oyster in the presence of reef sounds in both the laboratory (Lillis et al. 2014a) and field (Lillis et al. 2015). Likewise, oysters are shown to have increased recruitment in the presence of reef sound in the laboratory and field (Williams et al. 2022; McAfee et al. 2023). 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). As more affordable speakers emerge and become open-access (Pimm et al. 2015; Berger-Tal and Lahoz-Montfort 2018), acoustic enrichment might become a valuable tool to guide the informative stages of reef development, with substantial ecological and economic returns (zu

Ermgassen et al. 2016; Parker and Bricker, 2020). This could be an alternative to more costly restoration practices, such as hatchery production of oysters to seed reefs.

5.5.2. Positive species interactions

Positive species interactions are documented throughout the marine environment. For example, ribbed mussels can facilitate the growth of cordgrass in salt marshes (Bertness 1984) whilst blue mussels enhance eelgrass growth (Reusch et al. 1994). This is due to the bivalves depositing nutrient-rich faeces and pseudofaeces that assist in plant growth. Oysters can also increase the biodiversity of organisms like invertebrates by providing them with substrate, refugia from predators and amelioration of stressful environmental conditions via shading from high temperatures (McAfee & Bishop, 2019). In restorations where turf-forming algae smothers 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. If larvae are to overcome their recruitment bottlenecks, they need to outcompete algal turf for substrate space. We found that positive species interactions, through artificial kelp, used in combination with acoustic enrichment, provide oysters this competitive advantage to recruit in greater numbers to the topside of boulders. In our study, artificial kelp likely facilitated recruitment by maintaining boulders clear of turf through shading and abrasion by fronds. Our results are similar to others which also show native flat oysters to recruit in greater numbers in the presence of live (Shelamoff et al. 2019) and artificial kelp (McAfee et al. 2021). The kelp fronds likely provide a scraping mechanism to scour away algal turf and a shading mechanism to reduce understory light which inhibits algal growth, each enabling larvae to establish a foothold on the boulders. In shellfish restorations, the provision of substrate during inter-peak oyster recruitment will likely cause turf-forming algae to proliferate with no competition. This proliferation is enhanced where kelp has been lost (Filbee-Dexter and Wernberg, 2018) due to urbanisation and increased runoff of sediments and nutrients (Connell et al., 2008; Gorman et al. 2009). Implementing positive species interactions into restoration practice might inhibit this, creating synergies that establish reefs and later drive ecosystem productivity. Restoration still predominately consists of one species (McAfee et al. 2021), despite evidence showing bivalves and plants to have positive relationships together that enhance 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.

5.5.3. Knowledge gaps

These techniques show promise in encouraging the recruitment of oysters to reefs at high densities, however, they are not a panacea for the issues associated with shellfish restorations. Instead, we suggest synchronising acoustic enrichment and positive species interactions with pre-existing strategies, like the provision of appropriate substrate. Timing these techniques to occur during the peak recruitment season of the oyster will also likely give larval recruits the best chance of having competitor-free substratum (McAfee and Connell, 2020; McAfee et al. 2021). There also exist knowledge gaps on the application of these techniques before we can determine their translatability to habitats across space and time. For example, there is a paucity of data on the spatial extent from which larval oysters can be attracted (Rodriguez-Perez et al., 2020). We could gain this information by better understanding the swimming patterns of larvae in the field and the role that currents have in dictating their movement. Furthermore, there appears to be context dependency surrounding acoustic enrichment, with it having limited value in places associated with high anthropogenic noise (Williams et al., *in-review*). Another consideration is that in time, acoustic enrichment may no longer provide a boosting effect for larval recruitment. Once a reef's natural soundscape breaches a certain threshold in sound intensity, it may be able to attract larvae independent of acoustic enrichment. Likewise, once oysters have established a foothold and developed a complex reef structure, artificial kelp 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. A final consideration is that acoustic enrichment could attract predators (i.e., fish; Simpson et al., 2004; Montgomery et al., 2006; Gordon et al., 2019) that eat the larvae. Nuancing this is important to avoid fostering recruitment sinks for larvae, rather than increasing their recruitment.

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 towards restoration sites to increase recruitment to the underside of boulders. This technique can also boost recruitment to the topside of boulders when combined with artificial kelp that can shift the competitive advantage towards oysters, enabling them to establish a foothold on reefs. Combining these novel techniques offer a potentially valuable approach to enhance the recovery of oyster restorations, leading them on a trajectory of recovery.

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5.8 Supporting information

**Note:* All raw data material and sound files can be accessed on figshare (https://figshare.com/s/b4c51f61cd547211f5c6).

Section S1: Methods and results of site-by-site analysis in the field

Methods:

To compare the settlement of larvae between acoustic enrichment and artificial kelp unit treatments across each site, we firstly calculated the average number of topside and underside oysters that settled per three boulders in each crate at each site. This yielded three topside and three underside values per treatment at each site. Using these values, we calculated the average settlement of larvae per treatment at each site and their standard errors, for each the topside and underside of boulders. For each the topside and underside of boulders, we performed two-way ANOVAs to determine any significant effects of 'Sound', 'Kelp' (fixed factors, orthogonal) and the interaction of Sound x Kelp upon settlement of oysters. Prior to these tests, the data was square transformed to satisfy the model assumptions of normality, linearity and homoscedasticity.

Results:

At "Site 1" on the topside of boulders, there was a significant effect upon recruitment of artificial kelp (Fig. S1; 2-way ANOVA; $F_{1,8} = 7.266$, $p = 0.027$). "Kelp" (mean recruitment per boulder, [± 1 SE] 10.67 ± 2.34) received 2.18 times the density of larvae than "Control" (mean recruitment per boulder, [± 1 SE] 4.89 ± 0.4), a significant increase by 118.2%. There were no detectable effects of acoustic enrichment or the interaction. On the underside of boulders, there was a significant effect upon recruitment of acoustic enrichment (Fig. S1; 2-way ANOVA; $F_{1,8} = 23.759$, $p < 0.001$). "Sound" (mean recruitment per boulder, [± 1 SE] 64.56 ± 9.83) received 4.04 times the density of larvae than "Control" (mean recruitment per boulder, [± 1 SE] 16 ± 1.53), a significant increase by 303.5%. There were no detectable effects of artificial kelp or the interaction.

At “Site 2” on the topside of boulders, there was a significant effect upon recruitment of acoustic enrichment (Fig. S1; 2-way ANOVA; $F_{1,8} = 5.675$, $p = 0.044$). “Sound” (mean recruitment per boulder, [± 1 SE] 9 ± 0.88) received 1.72 times the density of larvae than “Control” (mean recruitment per boulder, [± 1 SE] 5.22 ± 0.95), a significant increase by 72.41%. There was also a significant effect upon recruitment of artificial kelp units (Fig. S1; 2-way ANOVA; $F_{1,8} = 10.638$, $p = 0.012$). “Kelp” (mean recruitment per boulder, [± 1 SE] 10 ± 1.76) received 1.92 times the density of larvae than “Control”, a significant increase by 91.57%. There was no detectable effect of the interaction. On the underside of boulders, there was a significant effect upon recruitment of acoustic enrichment (Fig. S1; 2-way ANOVA; $F_{1,8} = 9.208$, $p < 0.016$). “Sound” (mean recruitment per boulder, [± 1 SE] 38.5 ± 3.12) received 1.59 times the density of larvae than “Control” (mean recruitment per boulder, [± 1 SE] 24.22 ± 2.12), a significant increase by 58.99%. There were no detectable effects of artificial kelp units or the interaction.

At “Site 3” on the topside of boulders, there was a significant interactive effect upon recruitment (Sound x Kelp; Fig. S1; 2-way ANOVA; $F_{1,8} = 7.718$, $p = 0.024$). “Sound + Kelp” (mean recruitment per boulder, [± 1 SE] 24.56 ± 3.26) received 4.91 times the density of larvae than “Control” (mean recruitment per boulder, [± 1 SE] 5 ± 1.5), a significant increase by 391.2%. On the underside of boulders, there were no detectable effects of acoustic enrichment, artificial kelp units or the interaction.

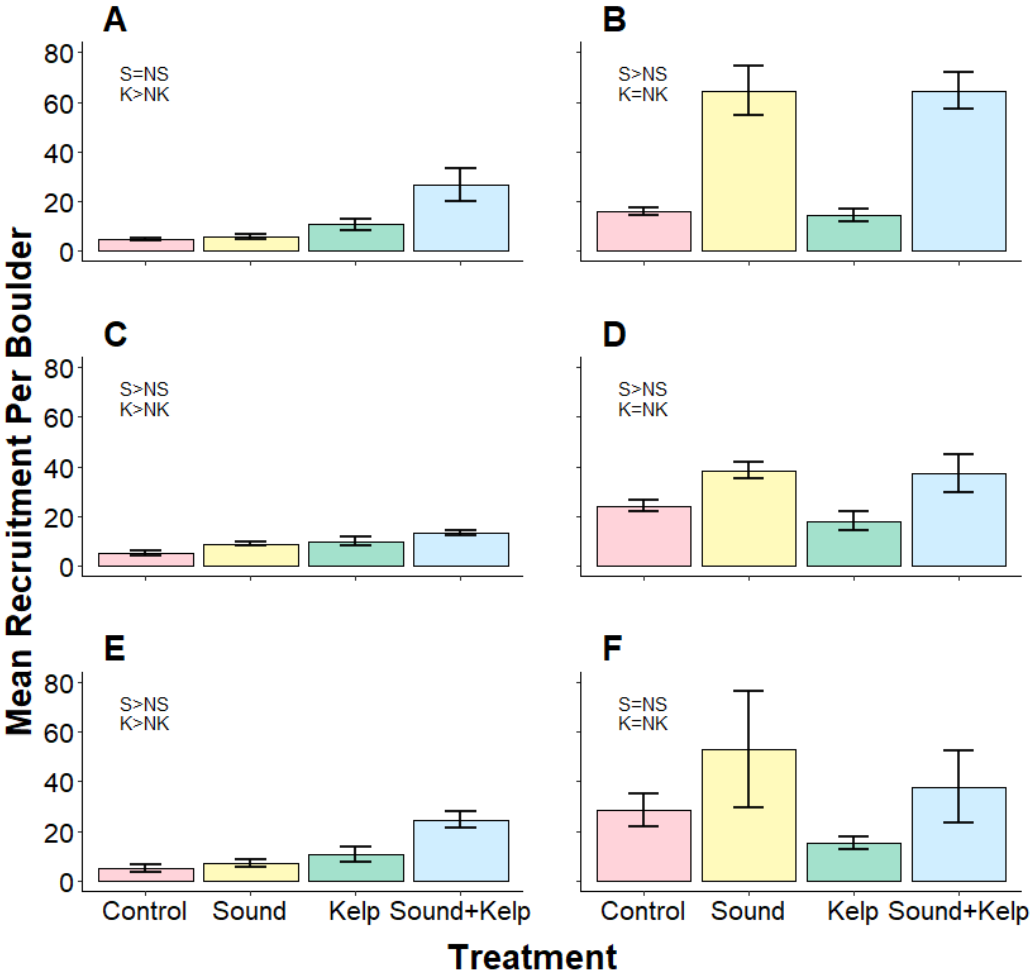

Figure S1. Plots showing the site-by-site analysis at Windara Reef of how ecology and technology can boost the recruitment of larval oysters to boulder substrates. Shown are the mean larval recruitment per boulder (±1 S.E.) per treatment of "Control", "Sound", "Kelp" and "Sound + Kelp" (*n* = 3) to the topside (left columns) and underside (right columns) of boulders across each site; "Site 1" (A, B), "Site 2" (C, D) and "Site 3" (E, F).

Section S2. Soundscape parameterisation in the field

Methods:

To ensure the playback of our experimental recording had greater sound intensity than that of the control treatment, and matched that of the original healthy reef recording as closely as possible, we used the package 'PAMGuide' in MATLAB® (Merchant et al. 2015) to calculate root-mean-square acoustic spectra to determine how acoustic power in each treatment changed over the full spectrum frequency range (0 to 22 kHz) across the distances. We used a Hann window to do this (length 1 s, 50% overlap). To calculate the SPL_{rms} for each treatment across distance, we used PAMGuide, applying a high pass filter at 2 kHz to each recording, and entering a Hann window (length 1 s, 50% overlap) into the package's settings. To calculate the snaps in each recording per treatment across each distance, we used the program Avisoft SASlab lite (Avisoft Bioacoustics, Berlin, Germany). We did this by firstly applying a high-pass filter to the recordings to remove all frequency signals below 2 kHz, because snapping shrimp snaps peak between 2-5 kHz (Lillis et al., 2014). We then used the pulse-train analysis tool in the program to count the mean number of snaps above a set amplitude threshold of 100. We then calculated the means and standard errors of each the SPL_{rms} and snaps for each treatment across each distance. After ensuring that the assumptions for this test were met, we ran two-sample *t*-tests to determine whether there were any significant differences between the SPL_{rms} and snaps. We then calculated the particle acceleration levels at source point of each the playback and ambient soundscapes, performing this four times per treatment. We did this using an accelerometer (MTN/1100W submersible accelerometer, Monitran) and data logger (DI-4108-U high speed data logger, DATAQ), analysing the data using 'paPAM' in MATLAB® (Nedelec et al. 2021). We then calculated the means and standard errors of the PALs per treatment. After ensuring that the assumptions for this test were met, we tested for significant differences between sound treatments using a Welch two-sample *t*-test. Finally, for visual comparisons of soundscape differences between treatments and the original reef recording, we created spectrograms using the Short-Time Fourier transform in MATLAB®. These were made using the Hann window (length 1 s, 50% overlap).

Results:

Our speakers created some of the broadband snaps seen in the original reef soundscape, however, these were contained in the 0.3-10 kHz frequency range and did not extend above 10 kHz (Main manuscript, Fig. 1). Taken from the four hydrophone recordings at Port

Noarlunga, the natural reef's mean SPL_{rms} was 133.9 dB re 1µPa, and mean snaps was 920 snaps per minute. This is greater than those seen for the "Sound" treatment at 1 m from the speaker (mean SPL_{rms} = 112.6 dB re 1µPa; mean snaps = 763 snaps per minute). These differences between the natural reef soundscape and our speaker may be the result of limitations in our speaker design and its housing, as well as the moderate volume at which the recording was played to ensure it did not crossover between treatments at each site. Despite this, our speakers were still able to enrich the soundscape relative to ambient controls, produce clear shrimp snaps to the human ear and have demonstrated ability to influence the swimming and settlement behaviour of oyster larvae in the aquarium (Williams et al. 2022) and field (McAfee et al. 2023).

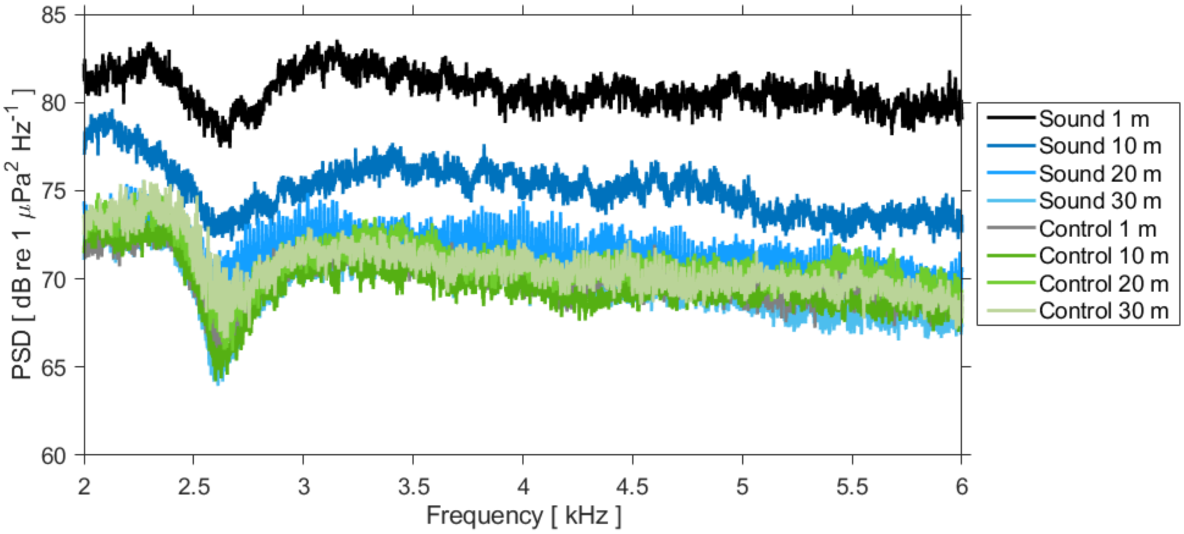

Figure S2. Acoustic spectra (rms) for "Sound" versus "Control" treatments, along a gradient of 30 metres from the speaker.

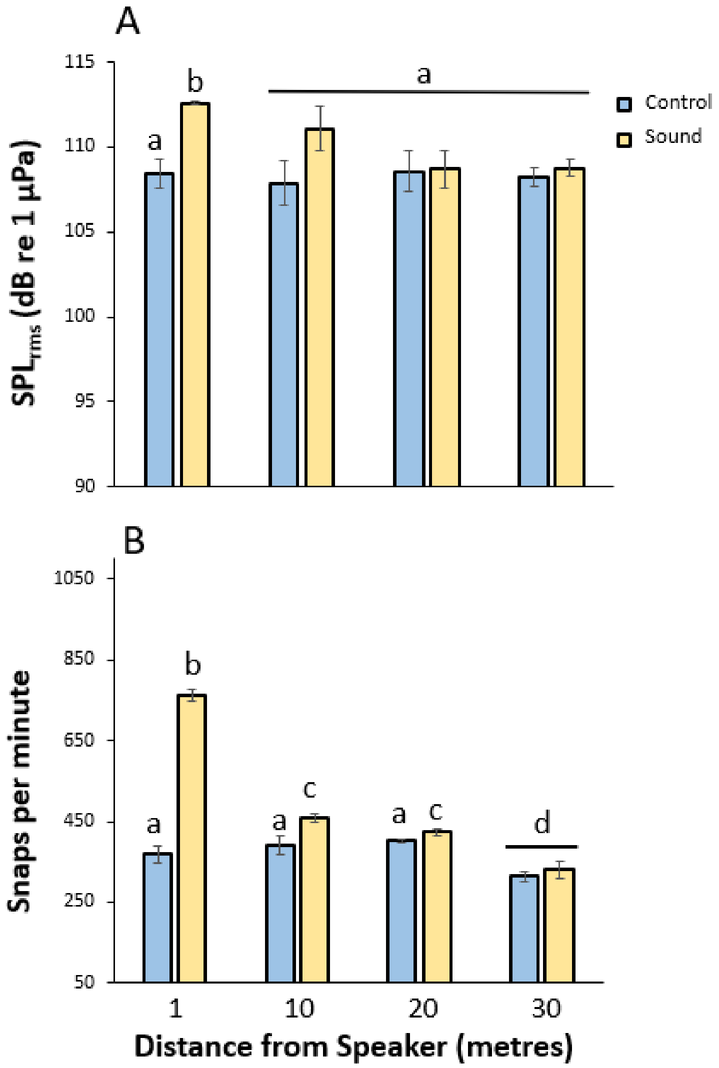

Figure S3. (A) Mean root-mean-square sound pressure levels (SPL$_{rms}$) (±1 S.E.) and (B) mean snaps per minute (snaps) (±1 S.E.) for “Sound” (n = 4) versus “Control” (n = 4) treatments, along a gradient of 30 metres from the speaker. Letters and lines above columns denote significant differences between treatments along each distance.

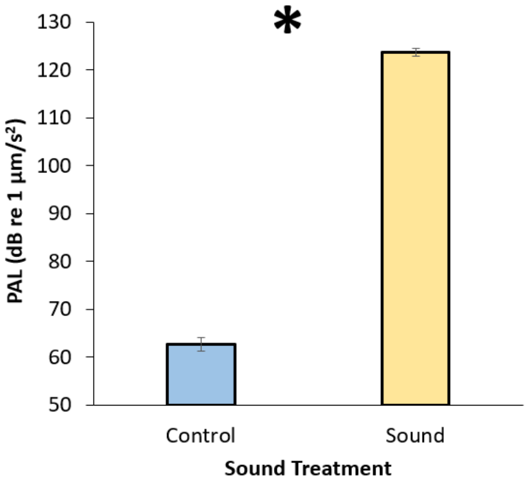

Figure S4. Mean particle acceleration (±1 S.E.) values for “Sound” (*n* = 4) versus “Control” (*n* = 4) treatments, at source point from the speaker or dummy speaker. ‘*’ denotes a significant difference between treatments.

Table S1. Descriptive statistics and Welch two-sample *t*-tests for mean SPL_{rms} of “Sound” versus “Control” treatments at Windara Reef, along a gradient of 30 metres from the speaker, where *a* = .05.

	Sound		**Control**		**Sound vs Control**	
Distance from speaker (metres)	**Mean (Standard Deviation)**	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
1	112.6 (0.2)	112.4-112.8	108.4 (1.8)	106.7-110.2	4.69(6)	0.018
10	111.1 (2.6)	108.5-113.7	107.9 (2.6)	105.3-110.5	1.76(6)	0.129
20	108.7 (2.3)	106.4-111.0	108.6 (2.4)	106.2-111.0	0.08(6)	0.942
30	108.8 (1.0)	107.7-109.8	108.2 (1.2)	107.1-109.4	0.68(6)	0.521

Table S2. Descriptive statistics and Welch two-sample *t*-tests for snaps per minute of “Sound” versus “Control” treatments at Windara Reef, along a gradient of 30 metres from the speaker, where *a* = .05.

	Sound		**Control**		**Sound vs Control**	
Distance from speaker (metres)	**Mean (Standard Deviation)**	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
1	762.8 (31.8)	730.9-794.6	368.8 (42.2)	326.6-410.9	14.91(6)	0.001
10	457.8 (22.5)	435.2-480.3	390.5 (45.8)	344.7-436.3	2.64(6)	0.058
20	423.0 (14.7)	408.3-437.7	402.5 (10.5)	392.0-413.0	2.27(6)	0.072
30	331.0 (43.5)	287.5-374.5	313.3 (29.0)	284.3-342.2	0.68(6)	0.527

Table S3. Descriptive statistics and Welch two-sample *t*-tests for particle motion levels of “Sound” versus “Control” treatments at Windara Reef, at source point of the speaker, where *a* = .05.

Sound		**Control**		**Sound vs Control**	
Mean (Standard Deviation)	**95% Confidence Interval**	**Mean (Standard Deviation)**	**95% Confidence Interval**	**t-value (df)**	***P*-value**
123.7 (2.8)	122.1-125.3	62.7 (1.6)	59.8-65.5	37.41(4)	0.001

Section S3: Tables for analysis of topside and underside recruitment

Table S4. ANOVA comparing the recruitment of oysters to the underside of boulders between acoustic enrichment and artificial kelp treatments at three sites.

Source	**df**	**MS**	**F**	**p**
Site	2	70406	2.103	0.144
Sound	1	446342	13.332	0.001
Kelp	1	731746	21.857	<0.001
Site x Sound	2	61989	1.852	0.179
Site x Kelp	2	94762	2.831	0.079
Sound x Kelp	1	330854	9.882	0.004
Site x Sound x Kelp	2	162435	2.426	0.110
Residual	24	803495		

Table S5. ANOVA comparing the recruitment of oysters to the underside of boulders between acoustic enrichment and artificial kelp treatments at three sites. Post-hoc pooling of the interaction terms ‘Site x Sound x Kelp’ and ‘Sound x Kelp’ with the residual provides a more powerful test of the factors “Sound” and “Kelp”, where appropriate (*p*>0.25; Winer et al. 1991).

Source	**df**	**MS**	**F**	**p**
Site	2	5051476	1.868	0.174
Sound	1	55032356	20.350	<0.001
Kelp	1	2369006	0.876	0.358
Site x Sound	2	7061731	2.611	0.092
Site x Kelp	2	1591757	0.589	0.174
Residual	27	2704413.48		

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CHAPTER SIX

Discussion

6.1 A novel solution for habitat restoration

For millennia, the health of our global ecosystems have been in decline. Rainforests like the Amazon have been denuded (Nobre et al. 1991; Matricardi et al. 2020), climate change has caused disease and bleaching in coral reef ecosystems (van Woesik & Kratochwill, 2022) and in many cases, fish stocks are depleted from industrial fishing (Hilborn et al. 2020). There no longer exists anywhere that is “pristine” and untouched by humans (Boivin et al. 2016). In response to this, the “Decade on Ecosystem Restoration” is underway to prevent, halt and reverse the degradation of ecosystems worldwide (2021-2030, United Nations, *General Assembly resolution* 73/284).

However, current restoration practice is often insufficient to meet these ambitious global commitments, as evident by many restorations having little to no success (Fuentes-Montemayor et al. 2011; Nilsson et al. 2015). This is the consequence of insufficient monitoring and goal setting in restoration projects, as well as improper links to ecological concepts and theory (Lindenmayer, 2020). Where such projects are costly, this inability to yield effective ecological outcomes is particularly detrimental. Such deficiencies in restoration therefore require innovative solutions to better deliver returns on ecological and economic investment (Brancalion and van Melis, 2017). Solutions that can reduce the risk of restoration failure, rapidly repair ecosystems and do so affordably and at large scales, are therefore highly valuable (Perring et al. 2018). This thesis has found that there is merit in using acoustic technology to revive degraded ecosystems. By broadcasting biological sounds to places where they have been removed or masked, recruitment processes can be enhanced to benefit the recovery of habitats.

By combining the fundamental theory with aquarium experiments, I have described evidence for “highways of sound” that can convey navigable information for dispersing life stages in search for adult habitat. By documenting the history of application of soundscape ecology for restoration outcomes, I have demonstrated that sound is used by a diversity of animal groups to navigate landscapes and seascapes to find a place to live. For example, sparrows fly to newly created habitats when conspecific calls are broadcast (Andrews et al. 2015), frogs and toads relocate to new breeding ponds (Buxton et al. 2015) and coral reef fish swim to degraded habitats when healthy reef sounds are broadcast (Gordon et al. 2019). By using this fundamental literature in an applied context, I highlight the potential use of habitat and conspecific-related sound. The generality and scale at which sound playback works to attract animals and encourage them to recruit in greater densities indicates its potential as a tool for restoration. Nonetheless, these findings indicate that there is a paucity of research surrounding soundscape playback for habitat restoration across animal groups. This thesis therefore encourages researchers to test this idea of acoustic enrichment in habitats and for species where it has yet to be studied, as it clearly has great potential for restoration outcomes.

Furthermore, I showed that the navigational cues embedded within biological soundscapes become muted as these habitats degrade or disappear. Through comparisons of natural temperate reef, partially restored reef and degraded reef soundscapes, I assessed whether the differences in sound in each habitat can alter recruitment processes. Where the natural temperate reef has the most biologically soniferous soundscape with the loudest levels of sound, the partially restored reef has intermediate levels and the degraded reef is relatively void of biological sound. This tells us that whilst marine soundscapes can change following large-scale habitat loss, they can at least be partially restored through reconstructed reefs that reprovision the shelter needed by animals who contribute to biologically soniferous soundscapes. If reefs are not reconstructed, then soniferous organisms are unlikely to return and the soundscape will remain muted. Findings concurrent to those in this thesis come from hard-bottom sponge habitats in Florida Bay (USA). In these studies, the soundscapes of degraded, hard-bottom habitats were restored through habitat restoration (Butler et al. 2016, 2017, 2022) because it increased the abundance of snapping shrimp which are key sound producers in these habitats. Furthermore, coral reef restoration in the Spermonde Archipelago

(Indonesia) led to the recovery of soundscapes in degraded tropical reefs (Lamont et al. 2021). Evidently, habitat restoration has the potential to transform degraded soundscapes back into those that are functional.

Acoustic enrichment may therefore be a new frontier for restoration of marine ecosystems like oyster reefs. The global removal of oyster reef habitat as a result of overharvesting, trawling and dredging (Beck et al. 2011; Cook et al., 2013; Alleway and Connell 2015), has left barren sandscapes in their wake (Grove-Jones 1986; Tanner, 2005; Bryars et al. 2008). As a result, these habitats no longer have soniferous biological soundscapes orchestrated by animals like the snapping shrimp. As snapping shrimp crackle is a known navigational cue for larval oysters as they recruit (Lillis et al. 2014, 2015), the loss of them means larvae may be unable to locate suitable places to settle in. Such muted-scapes of sand represent a loss that has persisted for over 100 years. This thesis therefore proposes that acoustic enrichment be used to recreate these lost biological soundscapes and entice larval oysters to restoration sites, thereby restoring these once extensive habitats.

6.2 Navigating highways of sound

The utility of restoring soundscapes to enhance restoration outcomes is emerging. In places where limited larval supply constrains restoration efforts, broadcasting healthy soundscapes using speakers could provide the navigational cue that attract larvae and enhances recruitment. However, there are knowledge gaps surrounding the response of marine larvae to different acoustic cues, and their swimming behaviour.

Through a series of aquarium experiments, I demonstrated that acoustic enrichment can be used to guide oyster larvae to restoration reefs. Previous studies demonstrate that larvae of the Eastern oyster can respond to reef sounds (Lillis et al. 2014, 2015). Furthermore, Eastern oyster larvae exhibit various swimming behaviours, with the ability to control their approach to the seafloor on the small scale (i.e., within 1-2 body lengths of the seafloor). They do this through vertical swimming behaviours, including diving behaviours where they rapidly accelerate downwards to make contact with the seafloor (Finelli and Wethey, 2003; Wheeler et al. 2015). In response to chemical cues, oyster larvae can also swim downwards, both in still water (Coon et al. 1990; Tamburri et al. 1992) and flowing water (Tamburri et al. 1996). In this thesis, I discovered that *O. angasi* larvae have the ability to move in more ways than we previously suspected. Not only can they respond to different habitat-related sounds and settle in higher densities in their presence, but that they can also actively navigate towards it, via lateral swimming behaviour.

Whilst pioneering research into larval dispersal recognised ocean currents as "highways" (*sensu* Garth, 1966), the predominant view until the 1990s was that larval settlement in the marine environment is relatively passive and relies on ocean currents for dispersal (Grosberg and Levitan, 1992; Leis, 2015). On the large scale (metres to kilometres), currents, tides and oceanographic features determine recruitment patterns as most invertebrate larvae are weak swimmers relative to the movement of water (Butman, 1987). Meanwhile, on small spatial scales (millimetres to centimetres), larvae have the ability to control settlement through various settlement cues (Butman, 1986; Pawlik 1992). Concurrent with current thinking that larvae can in fact interact with large and small-scale currents in the pursuit for adult habitat, I now show that larval oysters have the ability to navigate acoustic signals with far greater capacity than previously thought. By simultaneously interacting with sound gradients and ocean currents, they may be capable of accessing sites targeted for restoration. This tells us that there is promise in using soundscape playback to create "highways of sound" that can draw larval oysters in the water column to sites targeted for restoration. This is particularly exciting in the oceans where the dispersive stages are broadcast over very large areas and tend to be lost at sea if they cannot navigate to suitable habitat. Indeed, acoustic enrichment may be applied to a wide array of circumstances to entice target organisms to recreate populations and restore the functions of lost ecosystems.

However, large knowledge gaps remain before this technique can be applied. For example, we do not know the spatial extent that organisms, including the oyster, can be attracted (Rodriguez-Perez et al. 2020), nor the scale at which acoustic enrichment might work to attract organisms. This could be established through field-based experiments that test the swimming patterns of oyster and other types of larvae, the role that currents have in dictating their movement and how acoustic enrichment might influence these patterns. Another important consideration is that the use of this technique might attract unwanted organisms to the target site, like predators or invasive species. For example, fish are well-known to be attracted to reef soundscapes (Simpson et al. 2004; Montgomery et al. 2006; Gordon et al. 2019) and could predate upon larval recruits, fostering recruitment sinks instead.

Lastly, unravelling the sound-detection mechanisms that enable larvae to detect and distinguish between sounds is important. For invertebrates, particle motion and the statocyst organ that detects it are likely to play a key role in larval recruitment using acoustic enrichment. In relation to marine sound and animal navigation, this vibratory component of sound is understudied relative to sound pressure (Nedelec et al. 2021). Whilst statocysts have been described for some invertebrate larvae (Budelmann, 1989, 1992; Popper and Fay, 1993; Popper and Hawkins, 2018), including the European flat oyster (Erdmann, 1934) and pediveligers of other bivalves (Gragg and Nott, 1977; Morton, 1984; Kennedy et al. 1996; Gosling, 2003), they have not yet been described for the majority. By describing these organs and documenting how they respond to different frequencies and levels of particle motion, we may be able to identify the sounds and their ranges that are attractive or unattractive to organisms. This would help to clarify the observed variation in the attractiveness of sound among different species and the environments in which they occur.

6.3 Acoustic enrichment in a noisy world

If ecosystem restorations are to yield positive returns on investment, we require solutions that can enhance the processes key to restoration success. Whilst acoustic enrichment appears to tick this box, a knowledge gap remains surrounding its value in the presence of anthropogenic noise. Is it still effective in boosting larval recruitment in localities containing anthropogenic noise, or does this noise mask the signal? Filling this knowledge gap is critical, as many shellfish restorations are occurring along metropolitan coastlines and urbanised waterways of rising anthropogenic noise.

Through playback experiments in the field, I found that acoustic enrichment of healthy reefs sounds can boost oyster recruitment relative to more natural, quiet background controls. However, when acoustic enrichment is played at sites containing anthropogenic noise in the background, there is no boost in recruitment relative to background controls. This was also the case in the aquarium experiments, however, I observed comparable recruitment between the anthropogenic noise treatments and the healthy reef treatment. Anthropogenic noise can therefore still induce high settlement in oysters, as observed with mussels (Wilkens et al. 2012; Jolivet et al. 2016). However, the navigational function provided by biological sounds, like those broadcast by the speakers in this study, are likely reduced by anthropogenic noise in urbanised waterways due to its ubiquitous nature. The anthropogenic noises present in this field study came predominately from shipping, traffic and outboard motoring, which are known to mask biological soundscapes (Duarte et al. 2021). Furthermore, shallow rivers with dense concrete walls, as in this study, generally amplify this noise pollution due to the reflection of sound waves (Urick, 1983; Fediuk et al. 2021). In this thesis, I found that the value of acoustic enrichment for restoration might be context dependent. Importantly, in order to maximise returns on restoration investment, we should consider where we use acoustic enrichment. It may have little value in places that contain anthropogenic noise that masks the signal from the soundscape playback.

Lastly, anthropogenic noise and its impacts upon ecosystem restoration is a key area for future research. Many studies have shown that anthropogenic noise pollution negatively affects marine invertebrates by disrupting settlement processes, navigation, behaviour and physiology (Aguilar de Soto et al. 2013; Fewtrell and McCauley, 2012; Day et al. 2017). In regards to particle motion and anthropogenic noise, we also know that low frequency sounds can damage the statocyst of jellyfish, likely due to trauma associated with noise pollution exposure (Solé et al. 2016). However, we do not know how the particle motion levels created by anthropogenic noise affect the majority of marine invertebrates, including oysters. Particle motion levels that are too high might be confusing, unattractive or even damaging to larval and adult organisms. This could have serious ramifications for ecosystem restoration occurring in noisy places. If this noise disorientates reef-building larvae from being able to recruit to sites targeted for restoration and stresses already-established reef-builders, then reefs might be unable to function and provide ecosystem services at a high level. The rise of anthropogenic noise in places where restorations are occurring is therefore likely to affect future restoration efforts, both directly and indirectly.

6.4 Combining ecology and technology for restoration

Current restoration practice in the marine environment largely relies upon natural recruitment processes. However, recruitment can often be variable or eroded (Caddy, 1986), which carries considerable risk for restorations tasking place in recruitment-limited places. In the case of oyster restorations, turf-forming algae can also dominate and smother the substrates intended for oyster larvae to attach to, which means larvae are outcompeted for this space (McAfee et al. 2021b). This algae can trap sediment which creates a barrier to recruits and homogenises coastlines with algal turfs (Gorgula and Connell, 2004; Gorman et al. 2009). Several regions worldwide are beginning to restore reef habitats in places where biological soundscapes have been lost and where recruitment is limited (McAfee et al. 2022). It is therefore essential that restoration techniques be able to overcome these issues of limited recruitment and competition with smothering algal turf.

Positive species interactions are when species interact for the benefit at least one of the species, and to the detrimental of neither species (Bulleri et al. 2018). Such facilitations can maintain environmental conditions that benefit conservation outcomes, such as reducing predation and spatial competition among species (Bruno et al. 2003). Studies have found that oyster recruitment can be facilitated by kelp (Shelamoff et al. 2019; McAfee et al. 2021b), as the kelp removes algal turf via scraping mechanisms (Irving and Connell, 2006) and by reducing understorey light to inhibit algal growth (Connell, 2003). This thesis found that combining acoustic enrichment with positive species interactions might be a solution to cost-effectively sway the early succession of new reef systems towards restoration success.

By re-creating lost soundscapes with underwater speakers in the field, we showed that we can entice oysters to recruit in greater numbers on our restoration reefs by reef-binding (i.e., recruiting to the underside of boulders). Furthermore, by applying the ecological theory of positive species interactions (using artificial kelp) with speakers, we showed that we can entice oysters to recruit in greater numbers by reef-building (i.e., recruiting to the topside of boulders). This discovery indicates that by coupling marine science with acoustic technology, we might be able to create innovative solutions that can yield successful restoration outcomes.

However, it is important to consider that in time, acoustic enrichment and artificial kelp may no longer provide boosting effects for larval recruitment. Once a reef's soundscape breaches a certain threshold in sound intensity, it may be capable of attracting reef-building larvae independently of acoustic enrichment. Likewise, once oysters can establish footholds on reefs, artificial kelp may no longer be required. These present future research avenues that might help us to establish whether acoustic enrichment and artificial kelp are only valuable during the early stages of reef restorations. Lastly, these techniques alone will not be enough to restore reefs. It is critical that we work to synchronise acoustic enrichment and positive species interactions with the provision of appropriate substrate for larvae, and to time this during peak recruitment for oysters to enable more competitor-free substratum (McAfee and Connell, 2020; McAfee et al. 2021a).

Whilst technology has been the source of much environmental damage, it is now being harnessed as a solution to up-scale ecological restoration (Arts et al. 2015). This is because innovations in technology are becoming increasingly available and affordable. Furthermore, there is promise that technological development will be rapid to fill the current inadequacies of instrumentation required for biologists to unravel the intricacies of sound and how it evokes responses in organisms we seek to protect and revive. To our knowledge, no other studies have suggested using both acoustic enrichment and positive species interactions for shellfish restorations, despite the great potential that coupling this science and technology has. Returning the function of sound to habitats where it has been lost and using positive interactions to limit competition, might just kick-start restoration projects on a trajectory for recovery.

6.5 Final thoughts

Commitments to restore marine ecosystems are rapidly rising as we enter the decade on ecosystem restoration, yet marine restoration practice lags behind our ambition. Oyster reefs have been globally lost, along with their numerous ecosystem services. As a result, we urgently need novel solutions that can tackle the lack of recruitment limiting the success of restoration projects. Acoustic enrichment using underwater speakers could offer a cost-effective solution to upscale the restoration of lost shellfish reefs. However, we still need to see at which spatial scales this technique may be valuable. It will likely be most useful at broader spatial scales as sound travels great distances in the ocean relative to other sensory cues that operate on smaller scales (Atema, 1988; Kingsford et al. 2002; Leis and McCormick, 2002). On the small-scale, physiochemical and visual cues may exert a stronger influence on larval dispersal than sound and might overwhelm acoustic cues under some circumstances.

The outcomes of this thesis address several knowledge gaps surrounding acoustic enrichment as a novel tool for oyster reef restoration. I show that *O. angasi* can respond to healthy habitat sounds, and actively navigate towards the source of this sound via horizontal swimming behaviour. These findings indicate that oyster larvae have a greater capacity to navigate via active swimming behaviour during their dispersal than previous thinking allowed. Furthermore, we show that acoustic enrichment is context dependent and that when used with multispecies restoration, can provide a boosting effect in recruitment.

Whilst habitat restoration can restore biological soundscapes to a degree over time, technological intervention through acoustic enrichment might speed up the time it takes to reach our restoration goals. By turning barren-scapes into healthy reefs within a few years, acoustic enrichment can return the suite of benefits provided by oyster reefs sooner (i.e., fish habitat, food, tourism). This might result in greater impacts on policy and funding towards restoration projects (McAfee et al., 2021a). This thesis builds evidence for acoustic enrichment, a timely restoration solution that can boost the recruitment of larval oysters to shellfish reefs, reviving an ecosystem that has been extinct for over 100 years.

6.6. Literature cited

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