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EDITED BY
Marta Solé,
BarcelonaTech (UPC), Spain

REVIEWED BY
Steve Whalan,
Southern Cross University, Australia
Carly J. Randall,
Australian Institute of Marine Science
(AIMS), Australia

*CORRESPONDENCE
Josh W. Pysanczyn
✉ j.pysanczyn@exeter.ac.uk

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The role of acoustics within the sensory landscape of coral larval settlement

Josh W. Pysanczyn[1]*, Elizabeth A. Williams[1], Emelie Brodrick[1], Daniel Robert[2], Jamie Craggs[3], Kristen L. Marhaver[4] and Stephen D. Simpson[1,2]

[1]College of Life and Environmental Sciences, University of Exeter, Exeter, United Kingdom, [2]School of Biological Sciences, University of Bristol, Bristol, United Kingdom, [3]Horniman Museum and Gardens, London, United Kingdom, [4]CARMABI Foundation, Piscaderabaai z/n, Willemstad, Curaçao

Recruitment of coral larvae on reefs is crucial for individual survival and ecosystem integrity alike. Coral larvae can detect and respond to a wide range of biotic and abiotic cues, including acoustic cues, to locate suitable sites for settlement and metamorphosis. However, the acoustic ecology of coral larvae, including how they perceive auditory cues, remains poorly understood. In this mini-review we consider both *ex situ* physiology and behavior, and *in situ* ecological and behavioral studies, to first provide an updated overview of the abiotic and biotic cues used by coral larvae to guide settlement. We then explore in detail the use of acoustic cues and the current literature on behavioral responses to acoustic stimuli. Finally, we discuss gaps in our understanding of the mechanisms by which coral larvae detect acoustic cues, highlighting a novel application of technology to explore these sensory capabilities. We also address how larval phonotaxis, i.e., the ability to orient to a sound cue, can be applied to coral reef conservation. Current research suggests that acoustic cues are likely used at small spatial scales, and that coral larvae may have directional acoustic sensitivity enabling phonotactic behavior. Recruitment of coral larvae on reefs is significantly influenced by habitat-specific soundscape variation and likely affected by anthropogenic disturbance. We propose a novel application of the remote sensing technology, micro-scanning laser Doppler vibrometry (LDV), to quantify the micromechanical responses of putative acoustically sensitive epidermal microstructures. We then highlight the potential for incorporation of acoustic enrichment techniques in coral reef conservation and restoration interventions.

KEYWORDS

coral reefs, bioacoustics, phonotaxis, laser doppler vibrometry, restoration, acoustic enrichment, larvae

1 Introduction

Marine invertebrate larvae were once considered passive particles lacking the ability to detect or respond to their environment (G. Thorson, 1950; Chia et al., 1984) but it is now widely accepted that interactions between both environmental conditions and biologically-generated cues affect larval behavior and physiology across many marine invertebrate taxa, including corals (Rodriguez et al., 1993; Shanks, 2009; Gleason and Hofmann, 2011) (Table 1). The ocean was once described as 'The Silent World' by Cousteau and Dumas in 1953, but we now know that coral reefs are bioacoustically rich. Many reef inhabitants produce sound during a wide array of behaviors which together contribute to the ambient soundscape of the "choral" reef (Schmitz, 2002; Lobel et al., 2010; Lobel, 2013; Radford et al., 2014a). This ambient soundscape has been shown to act as an orientation cue for the pelagic larvae of many fish, decapod crustaceans and reef-building corals, assisting their orientation towards suitable settlement sites (Tolimieri et al., 2000; Tolimieri et al., 2002; Jeffs et al., 2003; Simpson et al., 2004; Leis and Lockett, 2005; Simpson et al., 2005; Montgomery et al., 2006; Vermeij et al., 2010; Radford et al., 2011).

Reef-building corals represent keystone species in coral reef ecosystems, providing valuable ecosystem goods and services to 100s of millions of people (Woodhead et al., 2019). However, the behavioral responses of coral larvae (planulae) to acoustic stimuli and the sensory mechanisms by which they detect acoustic cues remain poorly understood. Yet, these are of increasing importance, especially in the context of growing anthropogenic pressures on coral reefs, including climate change, overfishing, sewage and fertilizer runoff and noise pollution (Lecchini et al., 2018; Richmond et al., 2018; Jones, 2019; Duarte et al., 2021). Coral larvae can respond to an array of environmental cues that guide their settlement. We review these, with a particular emphasis on acoustics and soundscapes, the importance of which is just recently coming to light.

1.1 Environmental cues influencing coral larval settlement

1.1.1 Water flow and local currents

Local water currents play an extremely important role in the connectivity between coral reefs, influencing species diversity, dispersal and recruitment of coral larvae across local to regional spatial scales (Roberts, 1997; Veron, 2000; Veron, 2011; Veron et al., 2015; Hata et al., 2017). Currents connecting reefs seldom fall below 100 mms^{-1} (Baird and Morse, 2014). As coral larvae swim at speeds of <5 mms^{-1} (Szmant and Meadows, 2006; Gleason et al., 2009; Hata et al., 2017), directed swimming from the open ocean to reefs is limited. Nevertheless, modelling using data obtained from fish has shown that vertical migration of larvae during ontogeny reduces interactions with ocean currents, thus altering recruitment and connectivity among reefs (Paris et al., 2007). Wave action has also been shown to accelerate development in purple sea urchin (*Strongylocentrotus purpuratus*) and Pacific sand dollar (*Dendraster excentricus*), where increased turbulence, associated with shallower coastal waters, induced larval competence and enhanced larval settlement (Gaylord et al., 2013; Hodin et al., 2018).

1.1.2 Light intensity

Corals need sufficient levels of solar radiation to support the photosynthetic requirements of their symbionts (Chalker et al., 1988). Ambient light levels, spectral quality and substratum color significantly influence larval settlement across many species of coral larvae (Babcock and Mundy, 1996; Mundy and Babcock, 1998; Mason et al., 2011; Strader et al., 2015; Foster and Gilmour, 2016; Sakai et al., 2020). However, the strength and directionality of larval phototaxis varies with species, age, water temperature, light intensity and wavelength of light (Lewis, 1974; Bassim and Sammarco, 2003; Brooke and Young, 2005; Gleason et al., 2006; Sakai et al., 2020; Mulla et al., 2021).

During settlement experiments, coral larvae of many species preferentially settle onto the undersides of substrates in shallower water, altering their settlement preferences to vertical and upward facing surfaces at greater depths (Birkeland, 1977; Bak and Engel, 1979; Birkeland et al., 1981; Wallace and Bull, 1981; Rogers et al., 1984; Harriott, 1985; Wallace, 1985; Babcock and Mundy, 1996; Strader et al., 2015). Several species, however, aggregate in darker regions, representing a trade-off between required photosynthetically active radiation (PAR) and intensified levels of ultraviolet radiation (UVR). At irradiance levels found in near-surface waters, light has been shown to increase avoidance behaviour (Gleason et al., 2006), prolong settlement (Baker, 1995; Kuffner, 2001) and cause higher levels of mortality of larvae (Gleason and Wellington, 1995; Wellington and Fitt, 2003).

1.1.3 Hydrostatic pressure

Hydrostatic pressure causes directional changes in swimming orientation (barotaxis) in a range of aquatic invertebrate taxa (Forward, 1990; Kingsford et al., 2002; Goldsteins and Butler, 2009). However, to our knowledge, only one study on the brooding coral *Porites astreoides* (Stake and Sammarco, 2003) has examined barotaxis in cnidarians. In this study, booded larvae were exposed to pressures ranging from surface conditions (103.4 kPa) to those at ~40 m below the surface. When exposed to surface pressure, larvae displayed positive barotaxis and swam downwards, but at greater pressures, larvae swam upwards (Stake and Sammarco, 2003). Although evidence of barotaxis in coral larvae is limited, these findings reflect those demonstrated by other zooplankton (Morgan, 1984; Forward, 1989; Forward, 1990; Kingsford et al., 2002). Furthermore, barotaxis enables corals to sense and settle in their species-specific optimal irradiance environments, even when irradiance information is lacking, e.g., during diurnal/nocturnal shifts or periods of shading (Stake and Sammarco, 2003; Gleason and Hofmann, 2011).

1.1.4 Temperature variation

Stressful sublethal temperatures interfere with normal settlement behavior in coral larvae. In studies on two broadcast-spawning corals, warmer water temperatures negatively affected

TABLE 1 Collated research outlining the abiotic and biotic environmental factors and cues that induce behavioral, physiological and ecological changes associated with enhanced or disrupted settlement in coral larvae.

	Environmental Factor/Cue	Behavioural, Physiological & Ecological changes	References
Abiotic	Light Intensity	1. Step-down photophobic response (marked decrease in swimming speed in response to an attenuation of light intensity). 2. Determination of settlement orientation 3. Avoidance of biological harmful levels of UVR 4. Delay in settlement 5. Increase in mortality	1. Sakai et al., 2020 2. Birkeland, 1977; Bak and Engel, 1979; Birkeland et al., 1981; Wallace and Bull, 1981; Rogers et al., 1984; Harriott, 1985; Wallace, 1985; Babcock and Mundy, 1996 3. Gleason et al., 2006 4. Baker, 1995; Kuffner, 2001 5. Gleason and Wellington, 1995; Wellington and Fitt, 2003
	Hydrostatic Pressure	1. Barotaxis	1. Stake and Sammarco, 2003
	Sedimentation	1. Reduction in net settlement 2. Induction of settlement on suboptimal surfaces	1. Lewis, 1974; Hodgson, 1990; Gilmour, 1999; Goh and Lee, 2008; Perez et al., 2014; Humanes et al., 2017 2. Babcock and Davies, 1991; Gilmour, 1999; Babcock and Smith, 2000; Birrell et al., 2005; Ricardo et al., 2017
	Temperature	1. Increased mortality 2. Reduction of pre-competency period 3. Reduction in settlement success 4. Increased respiration 5. Reduced photosynthesis 6. Reduced number of algal symbionts 7. Reduced longevity 8. Interference with the detection of other cues	1. Edmunds et al., 2001; Bassim and Sammarco, 2003; Randall and Szmant, 2009a; Randall and Szmant, 2009b 2. Nozawa and Harrison, 2005; Randall and Szmant, 2009a; Heyward and Negri, 2010 3. Jokiel and Guinther, 1978; Bassim et al., 2002; Bassim and Sammarco, 2003; Randall and Szmant, 2009a; Ritson-Williams et al., 2016 4. Edmunds et al., 2001; Edmunds et al., 2005 5. Edmunds et al., 2001; Edmunds et al., 2005 6. Edmunds et al., 2001; Edmunds et al., 2005 7. Edmunds et al., 2001; Putnam et al., 2008 8. Bassim and Sammarco, 2003; Putnam et al., 2008; Winkler et al., 2015
	Water Current/ Flow	1. Increased dispersal and reef connectivity	1. Roberts, 1997; Veron, 2000; Gleason and Hofmann, 2011; Veron, 2011; Veron et al., 2015; Hata et al., 2017
Biotic	Biochemical cues	1. CCA-induced settlement/ metamorphosis 2. Species specific and generalist attraction to CCA 3. Biofilm induced settlement/ metamorphosis 4. Response to CCA-associated microbial communities 5. Avoidance of repellent chemical cues produced by coralline algae and epithelial sloughing	1. Morse et al., 1988; Morse and Morse, 1991; Morse et al., 1994; Heyward and Negri, 1999; Hadfield and Paul, 2001; Negri et al., 2001; Baird and Morse, 2004; Golbuu and Richmond, 2007; Erwin et al., 2008; Vermeij and Sandin, 2008; Hay, 2009; Ritson-Williams et al., 2009; Diaz-Pulido et al., 2010; Ritson-Williams et al., 2010; Ritson-Williams et al., 2014; Ritson-Williams et al., 2016; Gómez-Lemos et al., 2018 2. Harrington et al., 2004; Ritson-Williams et al., 2009; Ritson-Williams et al., 2010; Tebben et al., 2015; Gómez-Lemos et al., 2018; Jorissen et al., 2021 3. Negri et al., 2001; Erwin et al., 2008; Tebben et al., 2011; Tran and Hadfield, 2011; Siboni et al., 2012; Sneed et al., 2014; Gómez-Lemos et al., 2018; Dobretsov and Rittschof, 2020; Siboni et al., 2020; Jorissen et al., 2021 4. Harrington et al., 2004; Ritson-Williams et al., 2010; Gómez-Lemos et al., 2018; Jorissen et al., 2021 5. Masaki et al., 1984; Keats et al., 1997; Suzuki et al., 1998; Degnan and Johnson, 1999; Harrington et al., 2004
	Acoustic cues and Soundscape	1. Positive phonotaxis 2. Increased settlement due to louder acoustic levels and higher levels of low-frequency sound 3. Interference of anthropogenic noise on settlement choice	1. Vermeij et al., 2010 2. Lillis et al., 2016; Lillis et al., 2018 3. Lecchini et al., 2018

larval physiology, dispersal and settlement *via* increased larval mortality (Bassim and Sammarco, 2003; Randall and Szmant, 2009a), increased swimming/searching behaviors (Bassim and Sammarco, 2003), reduced pre-competency period (Nozawa and Harrison, 2005; Heyward and Negri, 2010) and reduced settlement success (Jokiel and Guinther, 1978; Bassim et al., 2002; Bassim and Sammarco, 2003). Similarly, in studies on brooding corals, as water temperatures dropped below or exceeded the ambient temperatures from where they were collected, planulae exhibited increased mortality (Edmunds et al., 2001; Randall and Szmant, 2009b; Ritson-Williams et al., 2016), reduced longevity (Edmunds et al., 2001; Putnam et al., 2008), reduced net settlement (Hartmann et al., 2013; Ritson-Williams et al., 2016), increased metamorphosis, reduced photosynthesis and diminished algal symbiont density (Edmunds et al., 2001; Edmunds et al., 2005).

1.1.5 Suspended and deposited sediment

Sedimentation has negative effects on both adult and larval-stage coral (Reviewed in Jones et al., 2015; Tuttle and Donahue, 2022). In observational studies of the brooding species *Favia fragum* (Lewis, 1974) and *Pocillopora damicornis* (Hodgson, 1990; Goh and Lee, 2008; Perez et al., 2014), net larval settlement was significantly reduced when suspended sedimentation was higher. Likewise, in field and laboratory studies, both high (~100 mg l^{-1}) and low (~50 mg l^{-1}) levels of suspended sediment adversely affected larval settlement and survival in the broadcast-spawning species *Acropora digitifera* and *A. tenuis* (Gilmour, 1999; Humanes et al., 2017). In both *in situ* and aquaria studies using larvae of the broadcast-spawning *A. millepora*, increased deposited sedimentation both reduced larval settlement and prevented larval settlement on upward facing substrates, with larvae settling only on vertical surfaces and the undersides of substrates (Babcock and Davies, 1991; Gilmour, 1999; Babcock and Smith, 2000; Birrell et al., 2005; Ricardo et al., 2017). Sedimentation most likely interferes with larval settlement by disrupting other sensory mechanisms, e.g., by masking chemical cues and impairing phototaxis (Ricardo et al., 2017). However, because it is difficult to track sediment dynamics on reef surfaces through time, it remains difficult to predict how the effects of sedimentation on short-term settlement will affect longer-term recruitment and survival.

1.1.6 Biochemical cues

In numerous studies of both brooding and broadcast-spawning coral species, crustose coralline algae (CCA) and its cell wall-associated compounds have been widely found to attract coral larvae and induce coral larval attachment (Morse et al., 1988; Morse and Morse, 1991; Morse et al., 1994; Morse et al., 1996; Heyward and Negri, 1999; Hadfield and Paul, 2001; Negri et al., 2001; Baird and Morse, 2004; Harrington et al., 2004; Golbuu and Richmond, 2007; Erwin et al., 2008; Vermeij and Sandin, 2008; Hay, 2009; Ritson-Williams et al., 2009; Diaz-Pulido et al., 2010; Ritson-Williams et al., 2010; Ritson-Williams et al., 2014; Tebben et al., 2015; Ritson-Williams et al., 2016; Gómez-Lemos et al., 2018; Jorissen et al., 2021). While CCA has also been found to induce settlement and metamorphosis across many different invertebrate taxa (Pawlik, 1992; Hadfield and Paul, 2001; Whalan et al., 2012; Sneed et al., 2015), the inducing capacity of CCA is highly variable, with complex interspecific interactions between corals and CCA. In two critically endangered species of broadcast-spawning Caribbean Acroporids (*A. palmata* & A. *cervicornis*), different species of CCA each induce varied amounts of larval settlement, with two relatively rare species of CCA being the most effective (Ritson-Williams et al., 2010). Interestingly, the cosmopolitan encrusting coralline algae *Titanoderma prototypum*m, found across both Caribbean and Pacific reefs, appears to be more attractive to larvae of reef-building Acroporids, inducing greater rates of settlement compared with other, more common, co-inhabiting CCA species (Harrington et al., 2004; Ritson-Williams et al., 2010; Gómez-Lemos et al., 2018). Furthermore, *T. prototypumm* significantly promoted settlement on the CCA surface compared with neighboring dead coral or plastic surfaces (Jorissen et al., 2021). In addition, some studies have found that specific microbial biofilms can also induce larval settlement in the absence of the CCA (Negri et al., 2001; Erwin et al., 2008; Tebben et al., 2011; Sneed et al., 2014; Gómez-Lemos et al., 2018; Dobretsov and Rittschof, 2020; Jorissen et al., 2021). Marine microbial biofilms are composed of many species of bacteria, unicellular algae (including diatoms) and protozoa. These produce an array of extracellular polymeric substances and signaling proteins shown to impact larval settlement and metamorphosis (reviewed in Dobretsov & Rittschof, 2020). Several studies have identified *Pseudoalteromonas* spp., a marine bacterium found in both Caribbean and Pacific CCA species, as a strong inducer of metamorphosis in larvae from both brooding and broadcast-spawning corals, including the important reef-building families Acroporidae and Pocilloporidae (Negri et al., 2001; Tebben et al., 2011; Siboni et al., 2012; Tebben et al., 2015) as well as an inducer of complete settlement (i.e., attachment to the substrate and metamorphosis) (Tran and Hadfield, 2011; Sneed et al., 2014; Tebben et al., 2015). It is worth noting that many CCA species have also evolved strategies to deter or prevent larval settlement, such as allelopathy (Suzuki et al., 1998; Degnan and Johnson, 1999) and sloughing (shedding of upper epithelial layers) (Masaki et al., 1984; Keats et al., 1997).

Thus, it is likely that CCA-induced coral settlement results from cues produced both by the CCA itself and by the associated microbial biofilm (Webster et al., 2004; Gómez-Lemos et al., 2018; Jorissen et al., 2021).

2 Acoustic cues and soundscapes

The grinding and popping of foraging echinoids, grazing scarids, vocalizing fish and snapping shrimp all contribute to the biophony of coral reefs (Simpson et al., 2004; Simpson et al., 2008; Lobel et al., 2010; Lobel, 2013; McWilliam et al., 2017). Thus, higher quality, healthy coral reefs are significantly louder, richer in acoustic events and more acoustically complex than degraded reefs (Piercy et al., 2014; Bertucci et al., 2016; Freeman and Freeman, 2016; Gordon et al., 2018). Acoustic cues are particularly useful for aquatic animals as sound travels faster and further underwater relative to other sensory cues, irrespective of directional currents (Urick, 1983; Ainslie, 2010; Duarte et al., 2021). Many marine invertebrates, therefore, have evolved the ability to detect and respond to acoustic cues, most likely by using specialized receptors (Salmon and Horch, 1973; Popper et al., 2001; Schmitz, 2002; Kaifu et al., 2008; Mooney et al., 2010; Vermeij et al., 2010; Wilkens et al., 2012; Lillis et al., 2013; Edmonds et al., 2016; Lillis et al., 2016; Solé et al., 2016; Vazzana et al., 2016; Charifi et al., 2017; Wale, 2017; Jézéquel et al., 2018; Lillis et al., 2018), and many taxa demonstrate increased rates of larval settlement in the presence of acoustic cues and during louder levels of acoustic cues (Jeffs et al., 2003; Simpson et al., 2004; Simpson et al., 2005; Stanley et al., 2010; Simpson et al., 2011; Stocks, 2012; Stanley et al., 2012a; Stanley et al., 2012b; Lillis et al., 2013; Lillis et al., 2015; Hinojosa et al., 2016).

Acoustic cues can also influence the swimming orientation and settlement behavior of coral larvae. In an *in situ* settlement chamber experiment, larvae of the Caribbean scleractinian coral *Orbicella faveolata* (previously *Montastraea faveolata*) exhibited directed phonotaxis, with larvae moving towards the source of a broadcasted coral reef soundscape irrespective of chamber orientation (Vermeij et al., 2010). In a separate study, *O. faveolata* larvae exhibited higher settlement rates when exposed to soundscapes from louder, more diverse coral reefs when compared to soundscapes from two quieter reefs characterized by either sponges and coral rubble or industrial debris and algal growth. (Lillis et al., 2016). These findings imply that the elevated acoustic power associated with more diverse habitats, or the absence or presence of specific frequencies within healthier habitats, may lead to increased larval settlement. The same authors found that settlement rates in larvae of the reef-building coral *Porites astreoides* doubled in an acoustic environment with higher levels of low-frequency sound, which are typical of a healthier reef with higher coral cover and higher densities of fish (Lillis et al., 2018). This suggests that low-frequency sounds are the predominant drivers of response in this species, and that the absence of these low frequencies may reduce settlement.

High-frequency sounds attenuate more rapidly underwater, but lower-frequency sounds emanating from reefs are theoretically detectable to invertebrates within 500 m from the source (Rogers and Cox, 1988; Anderson et al., 2021). However, currents and fluid flows may limit the ability of larvae to successfully navigate to cues 500 m away; therefore in practice, the range of detection and successful response may be closer still to 10 – 100 m (Gleason and Hofmann, 2011). Although *O. faveolata* larvae exhibit directional phonotaxis *in situ* (Vermeij et al., 2010), the experimental confinement to an acrylic chamber likely restricted fluid flow, allowing larvae to move unimpeded by currents. Therefore, our understanding of the spatial scale at which coral larvae are able to detect acoustic stimuli in their natural environment is still limited. The difficulties associated with *in situ* settlement experiments in complex topographical and hydrodynamic environments both highlights the challenge of interpreting the ecological significance and restoration utility of experimental results (Hata et al., 2017; Mayorga-Adame et al., 2017; Randall et al., 2020; Levenstein et al., 2022) as well as the many considerations that must be made when deisgning future acoustic larval settlement experiments.

To date, most studies of phonotaxis in coral planulae have been conducted with larvae from broadcast spawners (but see Lillis et al., 2018), therefore larvae from brooding corals are relatively understudied. However, it is proposed that mechanosensory epidermal cilia are responsible for auditory perception in coral (Vermeij et al., 2010). Therefore, given the abundance of dense cilia found on their surface, brooded larvae are also expected to possess the sensory mechanisms to detect and respond to acoustic stimuli (Gleason and Hofmann, 2011). This hypothesis requires further testing.

3 Mechanisms for acoustic detection in coral larvae

Sonic vibrations in water have both pressure and particle motion components (Reviewed in Nedelec et al., 2016). In their adult stages, most aquatic invertebrates can detect the particle motion component of sound, using specialized organs such as mechanosensory setae, chordotonal stretch receptors between the joints of appendages and statocyst and statolith receptor systems (Popper and Fay, 1999; Popper and Lu, 2000; Popper et al., 2001; Bleckmann, 2004; Nedelec et al., 2016). Many invertebrate larvae, including those of cnidarians, have a diversity of cilia-based mechanosensory systems that function during feeding, locomotion, tactic response, predator–prey interactions and settlement (Chia and Crawford, 1977; Chia and Koss, 1979; Freeman and Ridgway, 1990; Marlow et al., 2009; Bezares-Calderón et al., 2020), with many of these systems sensitive to acoustic particle motion (Tranter et al., 1982; Rogers and Cox, 1988; Budelmann, 1992; Kennedy et al., 1996; Zhadan, 2005; Tran and Hadfield, 2013; Lillis et al., 2015).

The sensory mechanisms employed by coral larvae to detect acoustic stimuli, however, remain unknown. Early studies of the temperate reef-building coral-species *Balanophyllia regia* and the tropical coral species *Pocillopora damicornis* demonstrated that the larval ectoderm is primarily composed of flagellated collar cells - a single flagellum surrounded by a ring of microvilli (Lyons, 1973; Vandermeulen, 1975). While the main function of these cells are primarily thought to be calcification, phagocytosis of food particles and motility, it has been suggested that these cells may also have a sensory function. This assumption was based on their similarities with statocyst systems used in the detection of acoustic cues in other invertebrate taxa (Lyons, 1973).

The laser Doppler vibrometry (LDV) method relies on the detection of the Doppler frequency shift that occurs when light is dispersed by a moving surface (Rothberg et al., 2017). In a study exploring particle motion detection in marine invertebrates, LDV was used to measure whole body vibrations (displacement, velocity and acceleration) as a putative stimulus of statocyst organs in cuttlefish (Family Sepiidae) and scallops (Family Pectinidae) (André et al., 2016). This experiment piloted the use of LDV techniques in an underwater bioacoustics study and highlights its potential value for use across other marine invertebrate taxa. LDV has also been successfully used to measure the mechanical response of microstructures such as antennae and sensory hairs to electrical and sound stimuli in several terrestrial invertebrates (Göpfert et al., 1999; Göpfert and Robert, 2002; Sutton et al., 2016). Although it is evident that coral larvae both respond to acoustic cues and possess the mechanosensory structures capable of detecting particle motion (Vermeij et al., 2010; Lillis et al., 2016; 2018) (Figures 1C, D), to date there have not been any attempts to measure the mechanical responses of their exterior cilia-based sensory systems to acoustic cues in a bioacoustics study, nor has this been done for the larvae of any marine invertebrate. We propose that laser Doppler vibrometry could be broadly applied to investigate the mechanosensory ability of coral larvae epidermal cilia, including quantifying both cilia beat dynamics and frequency-specific sensitivity to incident particle velocity. Using analytical signals capturing the spectral diversity of samples from coral reef sound recordings, and playbacks of the recordings themselves, it will be possible to determine the auditory sensitivity and bandwidth of coral larvae, offering a mechanistic basis for their phonotactic behavior (Figures 1A, B).

4 Ecological significance and applying acoustic enrichment to reef conservation and restoration

Coral reef soundscapes play an important role in coral larval orientation, habitat location, settlement and recruitment, ultimately affecting reef growth and resilience (Vermeij et al., 2010; Lillis et al., 2016; Lillis et al., 2018). However, with many coral reefs subject to degradation through climate change, overfishing and pollution, reef soundscapes are changing (Spalding and Brown, 2015; Hughes et al., 2017; Hughes et al., 2018; Duarte et al., 2021). For example, between 2012 and 2016, cyclones and intense bleaching meant the Great Barrier Reef experienced the most severe degradation period in recorded history (Hughes et al., 2017). As a result, soundscapes were negatively impacted across four complementary ecoacoustic indices; they were on average 15 dB SPL re 1 µPa quieter and had significantly reduced acoustic complexity, richness and rates of snapping shrimp (Family Alpheidae) snaps (Gordon et al., 2018).

In light of the ecological crisis on coral reefs, novel restoration techniques are becoming increasingly important in the conservation and restoration of these ecosystems. One promising new tool is acoustic enrichment, whereby recordings from relatively healthy coral reefs are played back through underwater speakers (Gordon et al., 2019). This approach has been demonstrated to improve metrics of fish community health in degraded coral reef habitat on an experimental scale (Gordon et al., 2019). Over the natural fish breeding season on the Great Barrier Reef (November-December), this study showed that reefs with acoustic enrichment had increases in fish recruitment across multiple trophic guilds, a doubling in overall fish abundance, and a 50% increase in species richness (Gordon et al., 2019). A subsequent study found that successful management and restoration of coral reefs leads to the recovery of the natural soundscape; maturing restoration projects in Sulawesi exhibited similar levels of acoustic richness to healthy reefs (Lamont et al., 2021).

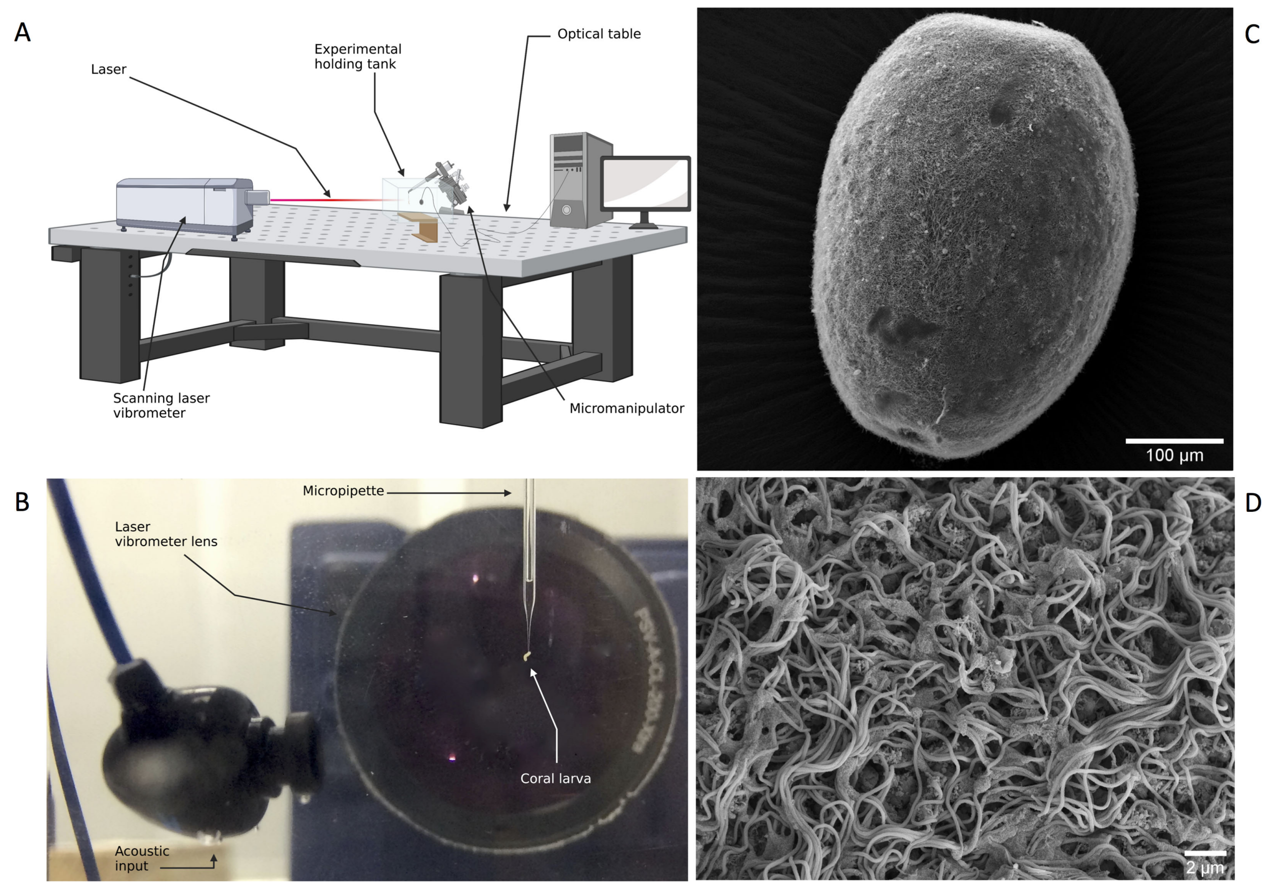

FIGURE 1
(A) Proposed set-up for coral larvae laser Doppler vibrometry experiment. **(B)** Close-up of set-up for tethering *Acropora millepora* larvae in laser Doppler vibrometry experiment **(C)** Scanning Electron Microscopy (SEM) image of an *Acropora millepora* planula larva. **(D)** Magnified larval epiderm highlighting cilia. SEM images: Emelie Brodrick. Laser Doppler Vibrometry schematic **(A)** created with BioRender.com.

Recent coral reef restoration efforts have focused on increasing population sizes, genetic diversity and the natural adaptive capacity of corals, for example, through fragment rescue, asexual propagation, *in situ* and *ex situ* coral nurseries and sexual propagation in order to mitigate reef degradation caused by climate change and local stressors (Heyward et al., 2002; Cruz and Harrison, 2017, dela Cruz and Harrison, 2020; Suzuki et al., 2020; Randall et al., 2020; Vardi et al., 2021; Harrison et al., 2021; Baums et al., 2019, 2022). In addition, coral breeding efforts in land-based facilities continue to scale up (Craggs et al., 2017; Craggs et al., 2020; O'Neil et al., 2021) while virtually all coral propagation programs seek more efficient ways to induce coral settlement in large numbers without introducing potentially detrimental competing organisms (Randall et al., 2020). Acoustic enrichment can be used in conjunction with all of these newer, breeding-based restoration techniques to help increase settlement rates, population growth and species diversity. By boosting coral settlement at restoration sites, short term acoustic enrichment will also help to restore natural acoustic complexity and phonic richness, thus further accelerating and reinforcing reef recovery.

Current examples of acoustic enhancement in reef restoration include 'The Reef Song Project', an Australian Coral Reef Resilience Initiative (ACRRI) undertaken in association with the Australian Institute of Marine Science (AIMS). This project is the first to investigate the efficacy of acoustic enrichment *in situ*. Using healthy reef recordings to attract fish communities to sixty patch reefs made of coral rubble and live fragments at Ningaloo Reef and the Great Barrier Reef in Australia, this five-year initiative is primarily exploring the roles of fish husbandry and herbivory on coral growth and reef recovery. Using photogrammetry, coral growth will be monitored over time (Australian Institute of Marine Science, 2023). Additionally, the Woods Hole Oceanographic Institute (WHOI) have developed the 'Reef Solutions Initiative'. Following the discovery by WHOI scientists that coral larvae are attracted to the soundscapes of healthy reefs (Lillis et al., 2016; Lillis et al., 2018), this initiative seeks to incorporate acoustic enrichment into intervention strategies to help corals repopulate degraded reefs (Woods Hole Oceanographic Institute, 2023). To improve our understanding of the reef recovery process and the impact of reef restoration, the application of low-cost, low specification passive acoustic monitoring in combination with machine-learning analysis may be applied to improve the analysis of ecoacoustic indices and successfully track coral reef restoration (Lamont et al., 2022; Williams et al., 2022).

In sum, acoustic enrichment is a promising tool for coral reef restoration due to its demonstrated efficacy across multiple taxa, yet its potential is still largely untested. Restoring keystone species and re-establishing complex interspecific interactions can promote successful management and restoration of coral reef ecosystems. Reef-building scleractinian corals are keystone species and it is their three-dimensional structure on which all coral reef life forms depend for food, sanctuary and survival. In order to fully assess the potential of acoustic enrichment and effectively apply this method as a reef restoration tool, we must continue to explore how different coral taxa respond to acoustic cues while gaining a better understanding of the mechanisms by which coral larvae sense their acoustic environment. This will also allow us to effectively place acoustics within the hierarchy of sensory cues that coral larvae integrate to locate an optimal site for settlement and recruitment to the reef.

Author contributions

JP, EW and SDS conceived the idea for this mini-review. JP wrote the manuscript. All authors listed made substantial contribution to the discussion of ideas outlined in the work and the development of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Ainslie, M. (2010). *Principles of sonar performance modelling*. Berlin: Springer. doi: 10.1007/978-3-540-87662-5

Anderson, E. R., Butler, J., and Butler, M. J. (2021). Response of fish and invertebrate larvae to backreef sounds at varying distances: Implications for habitat restoration. *Front. Mar. Sci.* 8, 697. doi: 10.3389/FMARS.2021.663887/BIBTEX

André, M., Kaifu, K., Solé, M., van der Schaar, M., Akamatsu, T., Balastegui, A., et al. (2016). Contribution to the understanding of particle motion perception in marine invertebrates. *Adv. Exp. Med. Biol.* 875, 47–55. doi: 10.1007/978-1-4939-2981-8_6

Australian Institute of Marine Science (AIMS). (2023). Australian Coral Reef Resilience Initiative. Available at: https://www.aims.gov.au/research-topics/environmental-issues/climate-change/australian-coral-reef-resilience-initiative. (Accessed 21 February 2023).

Babcock, R., and Davies, P. (1991). Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* 9, 205–208. doi: 10.1007/BF00290423

Babcock, R., and Mundy, C. (1996). Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. *J. Exp. Mar. Biol. Ecol.* 206, 179–201 doi: 10.1016/S0022-0981(96)02622-6

Babcock, R., and Smith, L. (2000). Effects of sedimentation on coral settlement and survivorship. *Mar. Biol.* 137 (4), 663–676. doi: 10.1007/s002270000374

Baird, A. H., and Morse, A. N. C. (2004). Induction of metamorphosis in larvae of the brooding corals *Acropora palifera* and *Stylophora pistillata*. *Mar. Freshw. Res.* 55, 469–472. doi: 10.1071/MF03121

Bak, R. P. M., and Engel, M. S. (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* 54, 341–352. doi: 10.1007/BF00395440

Baker, A. C. (1995). "Solar UV-a inhibition of planula larvae in the reef-building coral *Pocillopora damicornis*. In: D. Gulko and P. Jokiel (Eds.), *Ultraviolet radiation and coral reefs*, (Hawaii: Hawaii Institute of Marine Biology Tech Rep) 41, 149–163.

Baums, I. B., Baker, A. C., Davies, S. W., Grottoli, A. G., Kenkel, C. D., Kitchen, S. A., et al. (2019). Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecological Applications* 29 (8), e01978.

Baums, I. B., Chamberland, V. F., Locatelli, N. S., and Conn, T. (2022). Maximizing Genetic Diversity in Coral Restoration Projects. In *Coral Reef Conservation and Restoration in the Omics Age* (pp. 35–53). Cham: Springer International Publishing.

Bassim, K. M., and Sammarco, P. W. (2003). Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral (*Diploria strigosa*). *Mar. Biol.* 142, 241–252. doi: 10.1007/s00227-002-0953-z

Bassim, K. M., Sammarco, P. W., and Snell, T. L. (2002). Effects of temperature on success of (self and non-self) fertilization and embryogenesis in *Diploria strigosa* (Cnidaria, scleractinia). *Mar. Biol.* 140, 79–88. doi: 10.1007/s00227-001-0722-4

Bertucci, F., Parmentier, E., Lecellier, G., Hawkins, A. D., and Lecchini, D. (2016). Acoustic indices provide information on the status of coral reefs: An example from moorea island in the south pacific. *Sci. Rep.* 6, 33326. doi: 10.1038/srep33326

Bezares-Calderón, L. A., Berger, J., and Jékely, G. (2020). Diversity of cilia-based mechanosensory systems and their functions in marine animal behaviour. *Philos. Trans. R. Soc. B: Biol. Sci.* 375, 20190137. doi: 10.1098/rstb.2019.0376

Birkeland, C. (1977). "The importance of rate of biomass accumulation in early succession stages of benthic communities to the survival of coral recruits," in *Proc. 3rd Int. Coral Reef Symp*. 16–21.

Birkeland, C., Rowley, D., and Randall, R. H. (1981). Coral recruitment patterns at Guam. In *Proc. 4th Int. Coral Reef Symp*. 2, 399–344.

Birrell, C. L., McCook, L. J., and Willis, B. L. (2005). Effects of algal turfs and sediment on coral settlement. *Mar. pollut. Bull.* 51, 408–414. doi: 10.1016/j.marpolbul.2004.10.022

Bleckmann, H. (2004). 3-d-orientation with the octavolateralis system. *J. Physiol. Paris* 98, 149–171. doi: 10.1016/j.jphysparis.2004.03.015

Brooke, S., and Young, C. M. (2005). Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*. *Mar. Biol.* 146, 735–747. doi: 10.1007/s00227-004-1481-9

Budelmann, B. U. (1992). Hearing in nonarthropod invertebrates. *The Evolutionary Biology of Hearing*. 141–155. doi: 10.1007/978-1-4612-2784-7_10

Chalker, B. E., Barnes, D. J., Dunlap, W. C., and Jokiel, P. L. (1988). Light and reef-building corals. *Interdiscip. Sci. Rev.* 13, 146–154. doi: 10.1179/isr.1988.13.3.222

Charifi, M., Sow, M., Ciret, P., Benomar, S., and Massabuau, J. C. (2017). The sense of hearing in the pacific oyster, *Magallana gigas*. *PloS One* 12 (9), e0185353. doi: 10.1371/journal.pone.0185353

Chia, F. S., Buckland-Nicks, J., and Young, C. M. (1984). Locomotion of marine invertebrate larvae: a review. *Can. J. Zool.* 62, 1205–1222. doi: 10.1139/z84-176

Chia, F.-S., and Crawford, B. (1977). Comparative fine structural studies of planulae and primary polyps of identical age of the sea pen, *Ptilosarcus gurneyl*. *J. Morphol.* 151, 321–342. doi: 10.1002/jmor.1051510108

Chia, F.-S., and Koss, R. (1979). Fine structural studies of the nervous system and the apical organ in the planula larva of the sea anemone *Anthopleura elegantissima*. *J. Morphol.* 160, 179–196. doi: 10.1002/jmor.1051600303

Cousteau, J. Y., and Dumas, F. (1953). *The silent world*. Ed. J. Dugan (New York: Harper and Brothers).

Crabbe, J., Rodriguez-Martinez, R., Villamizar, E., Goergen, L., Croquer, A., and Banaszak, A. (2022). *Acropora cervicornis. The IUCN Red List of Threatened Species 2022*. Available at: https://www.iucnredlist.org/species/133381/165860142 (Accessed 21 February 2023).

Craggs, J., Guest, J. R., Davis, M., Simmons, J., Dashti, E., and Sweet, M. (2017). Inducing broadcast coral spawning ex situ: Closed system mesocosm design and husbandry protocol. *Ecol. Evol.* 7, 189–198. doi: 10.1002/ece3.3538

Craggs, J., Guest, J., Davis, M., and Sweet, M. (2020). Completing the life cycle of a broadcast spawning coral in a closed mesocosm. *Invertebr. Reprod. Dev.* 64, 189–198. doi: 10.1080/07924259.2020.1759704

Cruz, D. W. D., and Harrison, P. L. (2017). Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. *Sci. Rep.* 17 (1), 1–13. doi: 10.1038/s41598-017-14546-y

Degnan, B. M., and Johnson, C. R. (1999). Inhibition of settlement and metamorphosis of the ascidian *Herdmania curvata* by non-geniculate coralline algae. *Biol. Bull.* 197, 298–307. doi: 10.2307/1542787

dela Cruz, D. W., and Harrison, P. L. (2020). Enhancing coral recruitment through assisted mass settlement of cultured coral larvae. *PloS One* 15 (12), e0242847. doi: 10.1371/JOURNAL.PONE.0242847

Diaz-Pulido, G., Harii, S., McCook, L. J., and Hoegh-Guldberg, O. (2010). The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29, 203–208. doi: 10.1007/s00338-009-0573-x

Dobretsov, S., and Rittschof, D. (2020). Love at first taste: Induction of larval settlement by marine microbes. *Int. J. Mol. Sci.* 21, 731. doi: 10.3390/ijms21030731

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., et al. (2021). The soundscape of the anthropocene ocean. *Science* 371 (6529), eaba4658. doi: 10.1126/science.aba4658

Edmonds, N. J., Firmin, C. J., Goldsmith, D., Faulkner, R. C., and Wood, D. T. (2016). A review of crustacean sensitivity to high amplitude underwater noise: Data needs for effective risk assessment in relation to UK commercial species. *Mar. pollut. Bull.* 108, 5–13. doi: 10.1016/j.marpolbul.2016.05.006

Edmunds, P., Gates, R., and Gleason, D. (2001). The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. *Mar. Biol.* 139, 981–989. doi: 10.1007/s002270100634

Edmunds, P. J., Gates, R. D., Leggat, W., Hoegh-Guldberg, O., and Allen-Requa, L. (2005). The effect of temperature on the size and population density of dinoflagellates in larvae of the reef coral *Porites astreoides*. *Invertebrate Biol.* 124, 366–373. doi: 10.1111/j.1744-7410.2005.00018.x

Erwin, P. M., Song, B., and Szmant, A. M. (2008). "Settlement behavior of *Acropora palmata* planulae: Effects of biofilm age and crustose coralline algal cover," in *Proceedings of the 11th International Coral Reef Symposium*, Florida, 1219–1223.

Forward, R. B. (1989). Depth regulation of larval marine decapod crustaceans: test of an hypothesis. *Mar. Biol.* 102, 397–404. doi: 10.1007/BF00428280

Forward, R. B. (1990). Responses of crustacean larvae to hydrostatic pressure: Behavioral basis of high barokinesis. *Mar. Behav. Physiol.* 17, 1–17. doi: 10.1080/10236249009378773

Foster, T., and Gilmour, J. P. (2016). Seeing red: Coral larvae are attracted to healthy-looking reefs. *Mar. Ecol. Prog. Ser.* 559, 141–153. doi: 10.3354/meps11902

Freeman, L. A., and Freeman, S. E. (2016). Rapidly obtained ecosystem indicators from coral reef soundscapes. *Mar. Ecol. Prog. Ser.* 561, 1–14. doi: 10.3354/meps11938

Freeman, G., and Ridgway, E. B. (1990). Cellular and intracellular pathways mediating the metamorphic stimulus in hydrozoan planulae. *Roux's Arch. Dev. Biol.* 199, 357–365. doi: 10.1007/BF02029553

Gaylord, B., Hodin, J., and Ferner, M. C. (2013). Turbulent shear spurs settlement in larval sea urchins. *Proc. Natl. Acad. Sci. U.S.A.* 110, 6901–6906. doi: 10.1073/pnas.1220680110

Gilmour, J. (1999). Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Mar. Biol.* 135, 217–225. doi: 10.1007/s002270050645

Gleason, D. F., Danilowicz, B. S., and Nolan, C. J. (2009). Reef waters stimulate substratum exploration in planulae from brooding Caribbean corals. *Coral Reefs* 28, 391–398. doi: 10.1007/s00338-009-0480-1

Gleason, D. F., Edmunds, P. J., and Gates, R. D. (2006). Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral *Porites astreoides*. *Mar. Biol.* 148, 503–512. doi: 10.1007/s00227-005-0098-y

Gleason, D. F., and Hofmann, D. K. (2011). Coral larvae: From gametes to recruits. *J. Exp. Mar. Biol. Ecol.* 408, 42–57. doi: 10.1016/j.jembe.2011.07.025

Gleason, D. F., and Wellington, G. M. (1995). Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Mar. Biol.* 123, 693–703. doi: 10.1007/BF00349112

Goh, B. P. L., and Lee, C. S. (2008). "A study of the effect of sediment accumulation on the settlement of coral larvae using conditioned tiles," in *Proceedings of the 11th International Coral Reef Symposium*. (Florida: Ft. Lauderdale) 7–11.

Golbuu, Y., and Richmond, R. H. (2007). Substratum preferences in planula larvae of two species of scleractinian corals, *Goniastrea retiformis* and *Stylaraea punctata*. *Mar. Biol.* 152, 565–572. doi: 10.1007/s00227-007-0717-x

Goldsteins, J. S., and Butler, I. V. M. J. (2009). Behavioral enhancement of onshore transport by postlarval Caribbean spiny lobster (*Panulirus argus*). *Limnol. Oceanogr.* 54, 1669–1674. doi: 10.4319/lo.2009.54.5.1669

Gómez-Lemos, L. A., Doropoulos, C., Bayraktarov, E., and Diaz-Pulido, G. (2018). Coralline algal metabolites induce settlement and mediate the inductive effect of epiphytic microbes on coral larvae. *Sci. Rep.* 8, 16590. doi: 10.1038/s41598-018-35206-9

Göpfert, M. C., Briegel, H., and Robert, D. (1999). Mosquito hearing: Sound-induced antennal vibrations in male and female *Aedes aegypti*. *J. Exp. Biol.* 202, 2727–2738. doi: 10.1242/jeb.202.20.2727

Göpfert, M. C., and Robert, D. (2002). The mechanical basis of drosophila audition. *J. Exp. Biol.* 205, 1199–1208. doi: 10.1242/jeb.205.9.1199

Gordon, T. A. C., Harding, H. R., Wong, K. E., Merchant, N. D., Meekan, M. G., McCormick, M. I., et al. (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. *Proc. Natl. Acad. Sci. U.S.A.* 115, 5193–5198. doi: 10.1073/pnas.1719291115

Gordon, T. A. C., Radford, A. N., Davidson, I. K., Barnes, K., McCloskey, K., Nedelec, S. L., et al. (2019). Acoustic enrichment can enhance fish community development on degraded coral reef habitat. *Nat. Commun.* 10, 5413. doi: 10.1038/s41467-019-13186-2

Hadfield, M. G., and Paul, V. J. (2001). "Natural chemical cues for settlement and metamorphosis of marine-invertebrate larvae," in *Marine Chemical Ecology*, ed. J. B. McClintock and B. J. Baker (Boca Raton, FL: CRC Press).

Harrington, L., Fabricius, K., De'Ath, G., and Negri, A. (2004). Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85, 3428–3437. doi: 10.1890/04-0298

Harriott, V. J. (1985). "Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reef," in *Proceedings Of The Fifth International Coral Reef Congress*. Tahiti, 27 May -1 June 1985. Symposia and Seminars (B), ed. R. H. Richmond (Miami, FL: International Society for Reef Studies) 4, 367–372.

Harrison, P. L., dela Cruz, D. W., Cameron, K. A., and Cabaitan, P. C. (2021). Increased coral larval supply enhances recruitment for coral and fish habitat restoration. *Front. Mar. Sci.* 8, 1786. doi: 10.3389/FMARS.2021.750210/BIBTEX

Hartmann, A. C., Marhaver, K. L., Chamberland, V. F., Sandin, S. A., and Vermeij, M. J. A. (2013). Large Birth size does not reduce negative latent effects of harsh environments across life stages in two coral species. *Ecology* 94, 1826–1837. doi: 10.1890/13-0161.1

Hata, T., Madin, J. S., Cumbo, V. R., Denny, M., Figueiredo, J., Harii, S., et al. (2017). Coral larvae are poor swimmers and require fine-scale reef structure to settle. *Sci. Rep.* 7, 1–10. doi: 10.1038/s41598-017-02402-y

Hay, M. E. (2009). Marine chemical ecology: Chemical signals and cues structure marine populations, communities, and ecosystems. *Ann. Rev. Mar. Sci.* 1, 193–212. doi: 10.1146/annurev.marine.010908.163708

Heyward, A. J., and Negri, A. P. (1999). Natural inducers for coral larval metamorphosis. *Coral Reefs* 18, 273–279. doi: 10.1007/s003380050193

Heyward, A. J., and Negri, A. P. (2010). Plasticity of larval pre-competency in response to temperature: Observations on multiple broadcast spawning coral species. *Coral Reefs* 29, 631–636. doi: 10.1007/s00338-009-0578-5

Heyward, A. J., Smith, L. D., Rees, M., and Field, S. N. (2002). Enhancement of coral recruitment by *in situ* mass culture of coral larvae. *Mar. Ecol. Prog. Ser.* 230, 113–118. doi: 10.3354/MEPS230113

Hinojosa, I. A., Green, B. S., Gardner, C., Hesse, J., Stanley, J. A., and Jeffs, A. G. (2016). Reef sound as an orientation cue for shoreward migration by pueruli of the rock lobster, *Jasus edwardsii*. *PloS One* 11, e0157862. doi: 10.1371/journal.pone.0157862

Hodgson, G. (1990). Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. *Coral Reefs* 9, 41–43. doi: 10.1007/BF00686720

Hodin, J., Ferner, M. C., Ng, G., and Gaylord, B. (2018). Sand dollar larvae show within-population variation in their settlement induction by turbulence. *Biol. Bull.* 235, 116–127. doi: 10.1086/699827

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543, 373–377. doi: 10.1038/nature21707

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., et al. (2018). Global warming transforms coral reef assemblages. *Nature* 556, 492–496. doi: 10.1038/s41586-018-0041-2

Humanes, R., Ricardo, G. F., Willis, B. L., Fabricius, K. E., and Negri, A. P. (2017). Cumulative effects of suspended sediments, organic nutrients and temperature stress on early life history stages of the coral *Acropora tenuis*. *Sci. Rep.* 7, 44101. doi: 10.1038/srep44101

Jeffs, A., Tolimieri, N., and Montgomery, J. C. (2003). Crabs on cue for the coast: The use of underwater sound for orientation by pelagic crab stages. *Mar. Freshw. Res.* 54, 953–956. doi: 10.1071/MF03007

Jézéquel, Y., Bonnel, J., Coston-Guarini, J., Guarini, J. M., and Chauvaud, L. (2018). Sound characterization of the European lobster *Homarus gammarus* in tanks. *Aquat. Biol.* 27, 195–202. doi: 10.3354/ab00692

Jokiel, P., and Guinther, E. (1978). Effects of temperature on reproduction in the hermatypic coral *Pocillopora damicornis*. *Bull. Mar. Sci.* 28, 728–734. doi: 10.1007/978-3-030-16663-7_68

Jones, N. (2019). The quest for quieter seas. *Nature* 568 (7751), 158–161.

Jones, R., Ricardo, G. F., and Negri, A. P. (2015). Effects of sediments on the reproductive cycle of corals. *Mar. pollut. Bull.* 100, 13–33. doi: 10.1016/j.marpolbul.2015.08.021

Jorissen, H., Galand, P. E., Bonnard, I., Meiling, S., Raviglione, D., Meistertzheim, A. L., et al. (2021). Coral larval settlement preferences linked to crustose coralline algae with distinct chemical and microbial signatures. *Sci. Rep.* 11, 20931. doi: 10.1038/s41598-021-94096-6

Kaifu, K., Akamatsu, T., and Segawa, S. (2008). Underwater sound detection by cephalopod statocyst. *Fisheries Sci.* 74, 1261–1268. doi: 10.1111/j.1444-2906.2008.01589.x

Keats, D. W., Knight, M. A., and Pueschel, C. M. (1997). Antifouling effects of epithallial shedding in three crustose coralline algae (Rhodophyta, coralinales) on a coral reef. *J. Exp. Mar. Biol. Ecol.* 213, 281–294. doi: 10.1016/S0022-0981(96)02771-2

Kennedy, V. S., Newell, R. I. E., and Eble, A. F. (1996). *The eastern oyster: Crassostrea virginica* (Maryland Sea Grant: College Park), 467, p.513.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G., and Pineda, J. (2002). Sensory environments, larval abilities and local self-recruitment. *Bull. Mar. Sci.* 70, 309–340. doi: 10.5343/bms.2002.1076

Kuffner, I. B. (2001). Effects of ultraviolet (UV) radiation on larval settlement of the reef coral *Pocillopora damicornis*. *Mar. Ecol. Prog. Ser.* 217, 251–261. doi: 10.3354/meps217251

Lamont, T. A. C., Chapuis, L., Williams, B., Dines, S., Gridley, T., Frainer, G., et al. (2022). HydroMoth: Testing a prototype low-cost acoustic recorder for aquatic environments. *Remote Sens Ecol. Conserv.* 8, 91–102. doi: 10.1002/rse2.249

Lamont, T. A. C., Williams, B., Chapuis, L., Prasetya, M. E., Seraphim, M. J., Harding, H. R., et al. (2021). The sound of recovery: Coral reef restoration success is detectable in the soundscape. *J. Appl. Ecol.* 58 (3), 742–756. doi: 10.1111/1365-2664.14089

Lecchini, D., Bertucci, F., Gache, C., Khalife, A., Besson, M., Roux, N., et al. (2018). Boat noise prevents soundscape-based habitat selection by coral planulae. *Sci. Rep.* 8, 10552. doi: 10.1038/s41598-018-27674-w

Leis, J. M., and Lockett, M. M. (2005). Localization of reef sounds by settlement-stage larvae of coral-reef fishes (Pomacentridae). *Bull. Mar. Sci.* 76, 59–74. doi: 10.4319/2005.76.3.12

Levenstein, M. A., Gysbers, D. J., Marhaver, K. L., Kattom, S., Tichy, L., Quinlan, Z., et al. (2022). Millimeter-scale topography facilitates coral larval settlement in wave-driven oscillatory flow. *PloS One* 17 (9), p.e0274088. doi: 10.1371/journal.pone.0274088

Lewis, J. B. (1974). The settlement behaviour of planulae larvae of the hermatypic coral *Favia fragum* (Esper). *J. Exp. Mar. Biol. Ecol.* 15, 191–203. doi: 10.1016/0022-0981(74)90042-2

Lillis, A., Apprill, A., Suca, J. J., Becker, C., Llopiz, J. K., and Mooney, T. A. (2018). Soundscapes influence the settlement of the common Caribbean coral *Porites astreoides* irrespective of light conditions. *R Soc. Open Sci.* 5 (12), 181358. doi: 10.1098/rsos.181358

Lillis, A., Bohnenstiehl, D. W. R., and Eggleston, D. B. (2015). Soundscape manipulation enhances larval recruitment of a reef-building mollusk. *PeerJ* 3, e999. doi: 10.7717/peerj.999

Lillis, A., Bohnenstiehl, D. W., Peters, J. W., and Eggleston, D. (2016). Variation in habitat soundscape characteristics influences settlement of a reef-building coral. *PeerJ* 4, e2557. doi: 10.7717/peerj.2557

Lillis, A., Eggleston, D. B., and Bohnenstiehl, D. R. (2013). Oyster larvae settle in response to habitat-associated underwater sounds. *PloS One* 8, e79337. doi: 10.1371/journal.pone.0079337

Lobel, P. S. (2013). The "Choral Reef": The ecology of underwater sounds. In *Joint International Scientific Diving Symposium*. 179–185.

Lobel, P. S., Kaatz, I. M., and Rice, A. N. (2010). "Acoustical behavior of coral reef fishes," in *Reproduction and sexuality in marine fishes: Patterns and processes*. 131–150. doi: 10.1525/california/9780520264335.003.0010

Lyons, K. M. (1973). Collar cells in planula and adult tentacle ectoderm of the solitary coral *Balanophyllia regia* (anthozoa eupsammiidae). *Z. für Zellforschung und Mikroskopische Anatomie* 145, 491–503. doi: 10.1007/BF00307189

Marlow, H. Q., Srivastava, M., Matus, D. Q., Rokhsar, D., and Martindale, M. Q. (2009). Anatomy and development of the nervous system of *Nematostella vectensis*, an anthozoan cnidarian. *Dev. Neurobiol.* 69, 235–254. doi: 10.1002/dneu.20698

Masaki, T., Fujita, D., and Hagen, N. T. (1984). The surface ultrastructure and epithallium shedding of crustose coralline algae in an "Isoyake" area of southwestern Hokkaido, Japan. *Hydrobiologia*, 116–117, 43–49. doi: 10.1007/BF00027669

Mason, B., Beard, M., and Miller, M. W. (2011). Coral larvae settle at a higher frequency on red surfaces. *Coral Reefs* 30, 183–191. doi: 10.1007/s00338-011-0739-1

Mayorga-Adame, C. G., Batchelder, H. P., and Spitz, Y. H. (2017). Modeling larval connectivity of coral reef organisms in the Kenya-Tanzania region. *Front. Mar. Sci.*. 4, 92. doi: 10.3389/fmars.2017.00092

McWilliam, J. N., McCauley, R. D., Erbe, C., and Parsons, M. J. G. (2017). Soundscape diversity in the great barrier reef: Lizard island, a case study. *Int. J. Anim. Sound its Recording* 27, 1–18. doi: 10.1080/09524622.2017.1344930

Montgomery, J. C., Jeffs, A., Simpson, S. D., Meekan, M., and Tindle, C. (2006). Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. *Adv. Mar. Biol.* 51, 143–196. doi: 10.1016/S0065-2881(06)51003-X

Mooney, T. A., Hanlon, R. T., Christensen-Dalsgaard, J., Madsen, P. T., Ketten, D. R., and Nachtigall, P. E. (2010). Sound detection by the longfin squid (*Loligo pealeii*) studied with auditory evoked potentials: Sensitivity to low-frequency particle motion and not pressure. *J. Exp. Biol.* 213, 3748–3759. doi: 10.1242/jeb.048348

Morgan, E. (1984). The pressure-responses of marine invertebrates: a psychophysical perspective. *Zool. J. Linn. Soc.* 80, 209–230. doi: 10.1111/J.1096-3642.1984.TB01974.X

Morse, D. E., Hooker, N., Morse, A. N. C., and Jensen, R. A. (1988). Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J. Exp. Mar. Biol. Ecol.* 116, 193–217. doi: 10.1016/0022-0981(88)90027-5

Morse, A. N. C., Iwao, K., Baba, M., Shimoike, K., Hayashibara, T., and Omori, M. (1996). An ancient chemosensory mechanism brings new life to coral reefs. *Biol. Bull.* 191, 149–154. doi: 10.2307/1542917

Morse, D. E., and Morse, A. N. C. (1991). Enzymatic characterization of the morphogen recognized by *Agaricia humilis* (Scleractinian coral) larvae. *Biol. Bull.* 181, 363–373. doi: 10.2307/1542493

Morse, D. E., Morse, A. N. C., Raimondi, P. T., and Hooker, N. (1994). Morphogen-based chemical flypaper for *Agaricia humilis* coral larvae. *Biol. Bull.* 186, 72–81. doi: 10.2307/1542051

Mulla, A. J., Lin, C. H., Takahashi, S., and Nozawa, Y. (2021). Photo-movement of coral larvae influences vertical positioning in the ocean. *Coral Reefs* 40, 1297–1306. doi: 10.1007/S00338-021-02141-7/FIGURES/5

Mundy, C. N., and Babcock, R. C. (1998). Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? *J. Exp. Mar. Biol. Ecol.* 223, 235–255. doi: 10.1016/S0022-0981(97)00167-6

Nedelec, S. L., Campbell, J., Radford, A. N., Simpson, S. D., and Merchant, N. D. (2016). Particle motion: the missing link in underwater acoustic ecology. *Methods Ecol. Evol.* 7, 836–842. doi: 10.1111/2041-210X.12544

Negri, A. P., Webster, N. S., Hill, R. T., and Heyward, A. J. (2001). Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. *Mar. Ecol. Prog. Ser.* 223, 121–131. doi: 10.3354/meps223121

Nozawa, Y., and Harrison, P. L. (2005). Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. *Coral Reefs* 24, 324–332. doi: 10.1007/s00338-005-0476-4

O'Neil, K. L., Serafin, R. M., Patterson, J. T., and Craggs, J. R. K. (2021). Repeated ex situ spawning in two highly disease susceptible corals in the family meandrinidae. *Front. Mar. Sci.* 8, 669976. doi: 10.3389/fmars.2021.669976

Paris, C. B., Chérubin, L. M., and Cowen, R. K. (2007). Surfing, spinning, or diving from reef to reef: Effects on population connectivity. *Mar. Ecol. Prog. Ser.* 347, 285–300. doi: 10.3354/meps06985

Pawlik, J. R. (1992). Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology: An Annual Review*, 30, 273–335.

Perez, K. III, Rodgers, K. S., Jokiel, P. L., Lager, C. V., and Lager, D. J. (2014). Effects of terrigenous sediment on settlement and survival of the reef coral *Pocillopora damicornis*. *Peer J.* 2, e387. doi: 10.7717/peerj.387

Piercy, J. J. B., Codling, E. A., Hill, A. J., Smith, D. J., and Simpson, S. D. (2014). Habitat quality affects sound production and likely distance of detection on coral reefs. *Mar. Ecol. Prog. Ser.* 516, 31–44. doi: 10.3354/meps10986

Popper, A. N., and Fay, R. R. (1999). The auditory periphery in fishes. *Comparative hearing: fish and amphibians*. 43–100. doi: 10.1007/978-1-4612-0533-3_3

Popper, A. N., and Lu, Z. (2000). Structure-function relationships in fish otolith organs. *Fisheries research*. 46 (1-3), 15–25. doi: 10.1016/S0165-7836(00)00129-6

Popper, A. N., Salmon, M., and Horch, K. W. (2001). Acoustic detection and communication by decapod crustaceans. *J. Comp. Physiol. A: Sensory, Neural, and Behavioral Physiology* 187 (2), 83–89. doi: 10.1007/s003590100184

Putnam, H. M., Edmunds, P. J., and Fan, T. Y. (2008). Effect of temperature on the settlement choice and photophysiology of larvae from the reef coral *Stylophora pistillata*. *Biol. Bull.* 215 (2), 135–142. doi: 10.2307/25470694

Radford, A. N., Kerridge, E., and Simpson, S. D. (2014). Acoustic communication in a noisy world: Can fish compete with anthropogenic noise? *Behav. Ecol.* 25 (5), 1022–1030. doi: 10.1093/beheco/aru029

Radford, C. A., Stanley, J. A., Simpson, S. D., and Jeffs, A. G. (2011). Juvenile coral reef fish use sound to locate habitats. *Coral Reefs* 30 (2), 295–305. doi: 10.1007/s00338-010-0710-6

Randall, C. J., Negri, A. P., Quigley, K. M., Foster, T., Ricardo, G. F., Webster, N. S., et al. (2020). Sexual production of corals for reef restoration in the anthropocene. *Mar. Ecol. Prog. Ser.* 635, 1–19. doi: 10.3354/MEPS13206

Randall, C. J., and Szmant, A. M. (2009a). Elevated temperature affects development, survivorship, and settlement of the elkhorn coral, *Acropora palmata* (Lamarck 1816). *Biol. Bull.* 217 (3), 269–282. doi: 10.1086/BBLv217n3p269

Randall, C. J., and Szmant, A. M. (2009b). Elevated temperature reduces survivorship and settlement of the larvae of the Caribbean scleractinian coral, *Favia fragum* (Esper). *Coral Reefs* 28 (4), 917–925. doi: 10.1007/s00338-009-0482-z

Ricardo, G. F., Jones, R. J., Nordborg, M., and Negri, A. P. (2017). Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces. *Sci. Total Environ.* 609, 1367–1378. doi: 10.1016/j.scitotenv.2017.07.153

Richmond, R. H., Tisthammer, K. H., and Spies, N. P. (2018). The effects of anthropogenic stressors on reproduction and recruitment of corals and reef organisms. *Front. Mar. Sci.* 5, 226. doi: 10.3389/fmars.2018.00226

Ritson-Williams, R., Arnold, S., Fogarty, N., Steneck, R. S., Vermeij, M., and Paul, V. J. (2009). New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithson Contrib. Mar. Sci.* 38, 437–457. doi: 10.5479/si.01960768.38.437

Ritson-Williams, R., Arnold, S. N., and Paul, V. J. (2016). Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. *Mar. Ecol. Prog. Ser.* 548, 127–138. doi: 10.3354/meps11688

Ritson-Williams, R., Arnold, S. N., Paul, V. J., and Steneck, R. S. (2014). Larval settlement preferences of *Acropora palmata* and *Montastraea faveolata* in response to diverse red algae. *Coral Reefs* 33, 1119–1124. doi: 10.1007/s00338-013-1113-2

Ritson-Williams, R., Paul, V. J., Arnold, S. N., and Steneck, R. S. (2010). Larval settlement preferences and post-settlement survival of the threatened Caribbean corals *Acropora palmata* and *A. cervicornis*. *Coral Reefs* 29, 71–79. doi: 10.1007/s00338-009-0555-z

Roberts, C. M. (1997). Connectivity and management of caribbean coral reefs. *Science* 278 (5342), 1454–1457. doi: 10.1126/SCIENCE.278.5342.1454

Rodriguez, S. R., Ojeda, F. P., and Inestrosa, N. C. (1993). Settlement of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 97, 135–148. doi: 10.3354/meps097193

Rogers, P. H., and Cox, M. (1988). Underwater sound as a biological stimulus. *Sensory Biol. Aquat. Anim.*, 131–149. doi: 10.1007/978-1-4612-3714-3_5

Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J., and Hardin, J. (1984). Scleractinian coral recruitment patterns at salt river submarine canyon, st. Croix, U.S. virgin islands. *Coral Reefs* 3 (2), 69–76. doi: 10.1007/BF00263756

Rothberg, A. J., Allen, M. S., Di Maio, D., Dirckx, J. J. J., Ewins, D. J., Halkon, B. J., et al. (2017). An international review of laser Doppler vibrometry: Making light work of vibration measurements. *Optics Lasers Eng.* 99, 120–126. doi: 10.1016/j.optlaseng.2016.10.023

Sakai, Y., Kato, K., Koyama, H., Kuba, A., Takahashi, H., Fujimori, T., et al. (2020). A step-down photophobic response in coral larvae: implications for the light-dependent distribution of the common reef coral, *Acropora tenuis*. *Sci. Rep.* 10 (1), 1–11. doi: 10.1038/s41598-020-74649-x

Salmon, M., and Horch, K. (1973). Vibration reception by the fiddler crab, *Uca minax*. *Comp. Biochem. Physiol. A Physiol.* 44 (2), 485–493. doi: 10.1016/0300-9629(73)90506-9

Schmitz, B. (2002). Sound production in Crustacea with special reference to the alpheidae. In *The Crustacean Nervous System*. 269–282. Springer Berlin Heidelberg.

Shanks, A. L. (2009). Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216, 373–385. doi: 10.1086/bblv216n3p373

Siboni, N., Abrego, D., Puill-Stephan, E., King, W. L., Bourne, D. G., Raina, J. B., et al. (2020). Crustose coralline algae that promote coral larval settlement harbor distinct surface bacterial communities. *Coral Reefs* 39, 1703–1713. doi: 10.1007/S00338-020-01997-5

Siboni, N., Abrego, D., Seneca, F., Motti, C. A., Andreakis, N., Tebben, J., et al. (2012). Using bacterial extract along with differential gene expression in *Acropora millepora* larvae to decouple the processes of attachment and metamorphosis. *PloS One* 7, e37774. doi: 10.1371/journal.pone.0037774

Simpson, S. D., Meekan, M. G., Jeffs, A., Montgomery, J. C., and McCauley, R. D. (2008). Settlement-stage coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef noise. *Anim. Behav.* 75, 1831–1838. doi: 10.1016/j.anbehav.2007.11.004

Simpson, S. D., Meekan, M. G., McCauley, R. D., and Jeffs, A. (2004). Attraction of settlement-stage coral reef fishes to reef noise. *Mar. Ecol. Prog. Ser.* 276, 263–268. doi: 10.3354/meps276263

Simpson, S. D., Meekan, M., Montgomery, J., McCauley, R., and Jeffs, A. (2005). Homeward sound. *Sci.* (1979) 308, 221. doi: 10.1126/science.1107406

Simpson, S. D., Radford, A. N., Tickle, E. J., Meekan, M. G., and Jeffs, A. G. (2011). Adaptive avoidance of reef noise. *PloS One* 6, e16625. doi: 10.1371/journal.pone.0016625

Sneed, J. M., Riston-Williams, R., and Paul., V. J. (2015). Crustose coralline algal species host distinct bacterial assemblages on their surfaces. *ISME J.* 9, 2527–2536. doi: 10.1038/ismej.2015.67

Sneed, J. M., Sharp, K. H., Ritchie, K. B., and Paul, V. J. (2014). The chemical cue tetrabromopyrrole from a biofilm bacterium induces settlement of multiple Caribbean corals. *Proc. R. Soc. B: Biol. Sci.* 281, 20133086. doi: 10.1098/rspb.2013.3086

Solé, M., Lenoir, M., Fontuño, J. M., Durfort, M., van der Schaar, M., and André, M. (2016). Evidence of cnidarians sensitivity to sound after exposure to low frequency noise underwater sources. *Sci. Rep.* 6, 37979. doi: 10.1038/srep37979

Spalding, M. D., and Brown, B. E. (2015). Warm-water coral reefs and climate change. *Sci.* (1979) 350, 769–771. doi: 10.1126/science.aad0349

Stake, J. L., and Sammarco, P. W. (2003). Effects of pressure on swimming behavior in planula larvae of the coral *Porites astreoides* (Cnidaria, scleractinia). *J. Exp. Mar. Biol. Ecol.* 288, 223–238. doi: 10.1016/S0022-0981(03)00018-2

Stanley, J. A., Radford, C. A., and Jeffs, A. G. (2010). Induction of settlement in crab megalopae by ambient underwater reef sound. *Behav. Ecol.* 21, 113–120. doi: 10.1093/beheco/arp159

Stanley, J. A., Radford, C. A., and Jeffs, A. G. (2012a). Effects of underwater noise on larval settlement. *Adv. Exp. Med. Biol.* 730, 371–374. doi: 10.1007/978-1-4419-7311-5_84

Stanley, J. A., Radford, C. A., and Jeffs, A. G. (2012b). Location, location, location: Finding a suitable home among the noise. *Proc. R. Soc. B: Biol. Sci.* 279, 1050–1056. doi: 10.1098/rspb.2012.0697

Stocks, J. R. (2012). Response of marine invertebrate larvae to natural and anthropogenic sound: A pilot study. *Open Mar. Biol. J.* 6. doi: 10.2174/1874450801206010057

Strader, M. E., Davies, S. W., and Matz, M. V. (2015). Differential responses of coral larvae to the color of ambient light guide them to suitable settlement microhabitat. *R Soc. Open Sci.* 2, 150358. doi: 10.1098/rsos.150358

Sutton, G. P., Clarke, D., Morley, E. L., and Robert, D. (2016). Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields. *Proc. Natl. Acad. Sci. U.S.A.* 113, 7261–7265. doi: 10.1073/pnas.1601624113

Suzuki, G., Okada, W., Yasutake, Y., Yamamoto, H., Tanita, I., Yamashita, H., et al. (2020). Enhancing coral larval supply and seedling production using a special bundle collection system "coral larval cradle" for large-scale coral restoration. *Restor. Ecol.* 28, 1172–1182. doi: 10.1111/REC.13178

Suzuki, Y., Takabayashi, T., Kawaguchi, T., and Matsunaga, K. (1998). Isolation of an allelopathic substance from the crustose coralline algae, *Lithophyllum* spp., and its effect on the brown alga, *Laminaria religiosa miyabe* (Phaeophyta). *J. Exp. Mar. Biol. Ecol.* 225, 69–77. doi: 10.1016/S0022-0981(97)00208-6

Szmant, A. M., and Meadows, M. G. (2006). "Developmental changes in coral larval buoyancy and vertical swimming behavior: Implications for dispersal and connectivity," in *Proceedings of the 10th International Coral Reef Symposium*, Vol. 1, 431–437.

Tebben, J., Motti, C. A., Siboni, N., Tapiolas, D. M., Negri, A. P., Schupp, P. J., et al. (2015). Chemical mediation of coral larval settlement by crustose coralline algae. *Sci. Rep.* 5, 10803. doi: 10.1038/srep10803

Tebben, J., Tapiolas, D. M., Motti, C. A., Abrego, D., Negri, A. P., Blackall, L. L., et al. (2011). Induction of larval metamorphosis of the coral *Acropora millepora* by tetrabromopyrrole isolated from a *Pseudoalteromonas* bacterium. *PloS One* 6, e19082. doi: 10.1371/journal.pone.0019082

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1–45. doi: 10.1111/j.1469-185X.1950.tb00585.x

Tolimieri, N., Haine, O., Montgomery, J. C., and Jeffs, A. (2002). Ambient sound as a navigational cue for larval reef fish. *Bioacoustics* 12, 283–284. doi: 10.1080/09524622.2002.9753700

Tolimieri, N., Jeffs, A., and Montgomery, J. C. (2000). Ambient sound as a cue for navigation by the pelagic larvae of reel fishes. *Mar. Ecol. Prog. Ser.* 207, 219–224. doi: 10.3354/meps207219

Tran, C., and Hadfield, M. G. (2011). Larvae of *Pocillopora damicornis* (Anthozoa) settle and metamorphose in response to surface-biofilm bacteria. *Mar. Ecol. Prog. Ser.* 433, 85–96. doi: 10.3354/meps09192

Tran, C., and Hadfield, M. G. (2013). Localization of sensory mechanisms utilized by coral planulae to detect settlement cues. *Invertebrate Biol.* 132, 113–121. doi: 10.1111/ivb.12025

Tranter, P. R. G., Nicholson, D. N., and Kinchington, D. (1982). A description of spawning and post-gastrula development of the cool temperate coral, *Caryophyllia smithi*. *J. Mar. Biol. Assoc. United Kingdom* 62, 343–359. doi: 10.1017/s0025315400044106

Tuttle, L. J., and Donahue, M. J. (2022). Effects of sediment exposure on corals: a systematic review of experimental studies. *Environ. Evid.* 11, 2. doi: 10.1186/s13750-022-00256-0

Urick, R. J. (1983). *Principles of underwater sound, 3rd Edition*. Peninsula Publising Los Atlos, California, 22, pp.23–24.

Vandermeulen, J. H. (1975). Studies on reef corals. III. fine structural changes of calicoblast cells in *Pocillopora damicornis* during settling and calcification. *Mar. Biol.* 31, 283–288. doi: 10.1007/BF00390649

Vardi, T., Hoot, W. C., Levy, J., Shaver, E., Winters, R. S., Banaszak, A. T., et al. (2021). Six priorities to advance the science and practice of coral reef restoration worldwide. *Restoration Ecology* 29 (8), e13498.

Vazzana, M., Celi, M., Maricchiolo, G., Genovese, L., Corrias, V., Quinci, E. M., et al. (2016). Are mussels able to distinguish underwater sounds? assessment of the reactions of *Mytilus galloprovincialis* after exposure to lab-generated acoustic signals. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 201, 75–82. doi: 10.1016/j.cbpa.2016.06.029

Vermeij, M. J. A., Marhaver, K. L., Huijbers, C. M., Nagelkerken, I., and Simpson, S. D. (2010). Coral larvae move toward reef sounds. *PloS One* 5, e10660. doi: 10.1371/journal.pone.0010660

Vermeij, M. J. A., and Sandin, S. A. (2008). Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology* 89, 1997–2002. doi: 10.1890/07-1296.1

Veron, J. E. N. (2000). *Corals of the world. 1st ed.* Ed. M. Stafford-Smith Townsville (Mc, Queensland: Australian Institute of Marine Science and CRR Ald Pty Ltd). 138–139.

Veron, J. E. N. (2011). "Corals: Biology, skeletal deposition, and reef-building," in *Encyclopedia of modern coral reefs: Structure, form and process*. 275–281. doi: 10.1007/978-90-481-2639-2_9

Veron, J., Stafford-Smith, M., DeVantier, L., and Turak, E. (2015). Overview of distribution patterns of zooxanthellate scleractinia. *Front. Mar. Sci.* 2, 81. doi: 10.3389/fmars.2014.00081

Wale, M. A. (2017). The effects of anthropogenic noise playbacks on marine invertebrates (Edinburgh Napier University).

Wallace, C. (1985). Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. *Mar. Ecol. Prog. Ser.* 21, 289. doi: 10.3354/meps021289

Wallace, C. C., and Bull, G. D. (1981). "Patterns of juvenile coral recruitment on a reef front during a spring-summer spawning period," in *Proceedings of the 4th International Coral Reef Symposium, Manila.* 2, pp. 345–350.

Webster, N. S., Smith, L. D., Heyward, A. J., Watts, J. E., Webb, R. I., Blackall, L. L., et al. (2004). Metamorphisis of a Scleractinian Coral in Response to Microbial Biofilms. *Appl. Environ. Microbiol.* 70 (2), 1213–1221.

Wellington, G. M., and Fitt, W. K. (2003). Influence of UV radiation on the survival of larvae from broadcast-spawning reef corals. *Mar. Biol.* 143, 1075–1082. doi: 10.1007/s00227-003-1150-4

Whalan, S., Webster, N. S., and Negri, A. P. (2012). Crustose coralline algae and a cnidarian neuropeptide trigger larval settlement in two coral reef sponges. *PloS One* 7 (7), e30386. doi: 10.1371/journal.pone.0030386

Wilkens, S. L., Stanley, J. A., and Jeffs, A. G. (2012). Induction of settlement in mussel (*Perna canaliculus*) larvae by vessel noise. *Biofouling* 28 (3), 301–310. doi: 10.1080/08927014.2011.651717

Williams, B., Lamont, T. A. C., Chapuis, L., Harding, H. R., May, E. B., Prasetya, M. E., et al. (2022). Enhancing automated analysis of marine soundscapes using ecoacoustic indices and machine learning. *Ecol. Indic.* 140, 108986. doi: 10.1016/J.ECOLIND.2022.108986

Winkler, N. S., Pandolfi, J. M., and Sampayo, E. M. (2015). Symbiodinium identity alters the temperature-dependent settlement behaviour of *Acropora millepora* coral larvae before the onset of symbiosis. *Proc. R. Soc. B: Biol. Sci.* 282, 20142260. doi: 10.1098/rspb.2014.2260

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., and Graham, N. A. J. (2019). Coral reef ecosystem services in the anthropocene. *Funct. Ecol.* 33 (9), 1700–1710. doi: 10.1111/1365-2435.13331

Woods Hole Oceanographic Institution (WHOI). (2023). Reef Solutions. Available at: https://reefsolutions.whoi.edu/. (Accessed on 21 February 2023).

Zhadan, P. M. (2005). Directional sensitivity of the Japanese scallop *Mizuhopecten yessoensis* and swift scallop *Chlamys swifti* to water-borne vibrations. *Russ J. Mar. Biol.* 31 (6), 357–362. doi: 10.1007/s11179-005-0040-7