Biotremology: Tapping into the World of Substrate-Borne Waves

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Introduction

The gargantuan sandworms in Frank Herbert's novel *Dune* and the worm-like creatures in the horror film *Tremors* may be fictional, but aspects of their sensory biology are close to real life (see the picture of *Dune* at bit.ly/3PQdixl; the *Tremors* movie clip at bit.ly/3t4Xn4t). These monsters of our imaginations utilize a sensory mode that humans rarely think about unless we live near a seismic fault line. In fact, when considering the environmental information around us, the sensory modes that spring to mind first are likely hearing, vision, and smell.

However, the humans in *Dune* were aware of another mode. Using "thumpers" to hit the ground rhythmically, the characters were able to attract sandworms. These creatures were sensitive to substrate-borne vibrations. In real life, we rarely notice that the substrates in our world are vibrating. Yet the use of vibrations in surfaces is hypothesized to be one of the oldest animal communication forms (Endler, 2014). Like the soundscape around us (Pijanowski et al., 2011), the vibrational landscape is termed the "vibroscape," a term that is applicable to both aquatic (Roberts and Elliott, 2017) and terrestrial (Šturm et al., 2021) systems. And it is only with the recent advance of sensor technologies and computer processing that scientists have started to familiarize themselves with this world (Hill and Wessel, 2016). This article explores biological vibrations selectively in two systems (our own backyard and the seashore) and discusses ways that humans are contributing to the vibrational landscape.

Biotremo- ...What?

Let us start at the beginning. The study of the biological use of vibrational waves, known as "biotremology," is a relatively new discipline that was first outlined in 2016 (Hill and Wessel, 2016). Several different wave types can travel through solids and substrates. Most biotremology studies involve surface waves, either Rayleigh or Bending waves, that travel in the boundaries between two media. The term "substrate-borne vibration" refers to these surface waves that travel in any substrate on which an animal resides such as hard or soft sediment, the water surface, or a plant. Sound waves may also travel in substrates, but biotremology differs from "bioacoustics" in that it refers to animals that use specialized vibrational receptors rather than pressure sensitive "ears" (Hill and Wessel, 2016).

In the animal kingdom, vibrations are used extensively for communication, including for parental care, foraging, detection of environmental cues, recognition, and predator-prey interactions (reviewed in Hill, 2008). Over 30 species of mammals actively produce vibrations, from kangaroo rats (e.g., *Dipodomys* spp.) drumming their hindfeet to elephant (e.g., *Loxodonta africana*) calls propagating into the ground. In the invertebrates, hundreds of thousands of species produce vibrations, including fruit flies (*Drosophila melanogaster*) and stinkbugs (e.g., *Nezara viridula*) tremulating (trembling; see video of fruit flies at youtu.be/519_XzM970s; stinkbugs at youtu.be/Q39C5I9L7mI), pill bugs (*Armadillo officinalis*) stridulating (rubbing body parts together), and crustaceans (Ocypodidae) drumming.

Animals detect incidental vibrations too, for locating prey and avoiding predators. For example, scorpions (*Paruroctonus mesaensis*) use vibrations to detect their arthropod prey (Brownell and Farley, 1979). Tree frog embryos (*Agalychnis callidryas*) hatch early after sensing vibrations from approaching predatory snakes (Warkentin, 2005). Ground-dwelling animals also detect abiotic vibratory cues such as thunder, which may be sensed in the substrate up to 1 km or more from the source (O'Connell-Rodwell et al., 2001), and even from tsunamis (1-100 Hz) as demonstrated in elephants (e.g., *Loxodonta africana*).

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Indeed, vibration detection may be advantageous when other sensory modes (e.g., sound) are masked, such as by strong winds. However, because wind, temperature, and background noise affect acoustics transmission, substrate type and substrate composition also affect vibration transmission.

Given the extent of vibration use, why is this research area so far behind that of airborne communication? The explanation is twofold. First, humans do not sense vibrations as well as they are detected by other species. Our pressure-detecting ears bias us toward the soundscape. Thus, although airborne sounds have been meticulously documented, the realm of substrate-borne stimuli was overlooked for decades as a possibility for communication (Hill, 2008). Furthermore, substrate heterogeneity was thought to prevent this sort of communication.

Second, until sensor technologies and computation improved, the ability to detect vibrations was simply not available to scientists. Now, however, we can record vibrations by utilizing laser vibrometers, accelerometers, geophones, and piezoelectric sensors. Thus, we are aware of the vibrational world.

Vibrations Above and Below the Lawn

The realm of vibrations can be explored beneath the home lawn (**Figure 1**). Here, beneficial earthworms tunnel through the ground, improving the soil structure and recycling nutrients by feeding on organic matter.

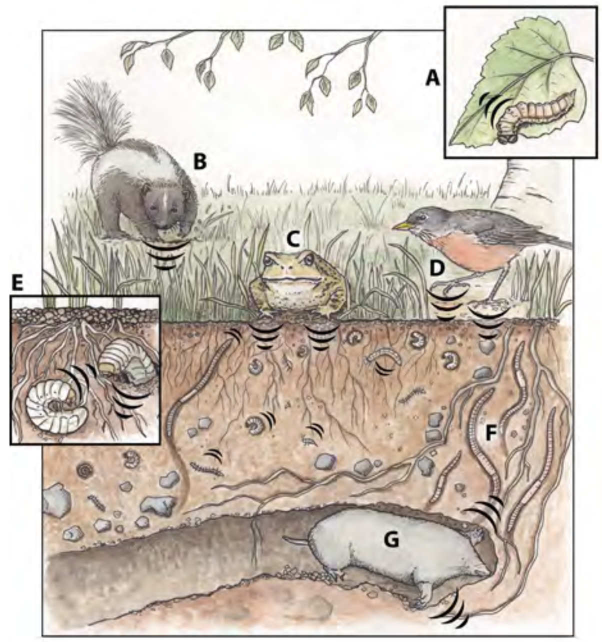


Figure 1. *Cross section of a North American lawn, with vibrational users and producers. Caterpillars produce leaf vibrations (**A**). Skunks are known for "stomping" behavior and for localizing grub prey with great accuracy (**B**). Toads "tremble" the toes (**C**) and birds "paddle" (**D**) during foraging bouts. Beetle larvae have been recorded stridulating (**E**). Earthworms (**F**) flee from the vibrations of their mole predators (**G**). Paintings by Ann Sanderson, © 2022, Ann Sanderson, all rights reserved; see www.annsciart.com.*

Bait collectors use various methods to remove earthworms from the soil (see youtu.be/3ILoGcSxCAY) (Raboin, 2021). These methods include repetitious scraping of a metallic object against a stake (worm "grunting"), the twanging and moving of a garden fork ("charming"), repeated foot stamping, and electric motors applied to the ground (Catania, 2008). In fact, the annual Worm Gruntin' Festival in Sopchoppy, Florida, is in its 20th year!

What do these techniques have in common? Darwin (1882) stated that "earthworms are indifferent to shouts, nor did they [notice] the deepest and loudest tones of a bassoon," indicating a lack of sound reception. However, after placing pots of worms on the keys of a piano, Darwin observed a sensitivity to vibrations. In fact, earthworms have multiciliate sensory cells along the body surface and can detect tactile stimulation across the whole body, making vibration reception highly likely (Laverack, 1960). Vibrational measurements of human-produced "grunts" indicate that they are broadband low frequency (<500 Hz) (Mitra et al., 2009). The bait collectors then are taking advantage of the earthworms' vibrosensitivity.

In tests involving mimics of rainfall (<500 Hz) and of the eastern American mole (*Scalopus aquaticus*) digging (<1,000 Hz), Catania (2008) found that earthworms (*Diplocardia mississippiensis*) were responding to the vibrations of their predator. Fossorial mammals produce these incidental vibrations (e.g., from digging) but also actively produce vibrational signals during territorial defense and competition (Mason and Narins, 2011). Worm grunters have unknowingly been mimicking mole vibrations.

Other animals have similar strategies to trigger prey emergence. The wood turtle (*Clemmy insculpta*) performs bouts of "stomping" to lure various segmented worms to the surface (see youtu.be/YAPTHDrAQw8). The turtle rocks from one foot to the other in a rhythmic trampling motion while periodically checking for emerged prey in the leaf litter (Kaufman, 1989). Birds also paddle the ground, discussed in **From the Lawn to the Seashore**. In anurans, a behavior called "toe twitching" has been described where the toes are vibrated, creating a "toe lure" of both visual and vibrational cues (Gridi-Papp and Narins, 2010). The brown marsh frog (*Rana baramica*), for example, vibrates the longest middle toe of each foot to attract prey (Grafe, 2008).

Above the lawn in the tree canopies, vibrational use is also widespread. Here a number of caterpillars, such as those of the moth family Drepanidae, actively produce leaf vibrations (Yack et al., 2001). The masked birch caterpillar (*Drepana arcuata*) builds silk nests on the leaf and defends the nest with signals consisting of "rasps" and "drums." Resident caterpillars are silent when solitary but use the open mandibles to strike the leaf and/or use the abdomen to scrape the surface to produce repetitive signals (see the supplementary videos at bit.ly/3t1GN5k).

Caterpillars do not have sound-sensing organs, so it is thought that the vibrational component is the primary informational source. The signals are elicited when the intruder is only 2-3 cm away, yet the vibrations travel much further and are stronger than required to signal to the intruder alone. This has led researchers to hypothesize that the signal is meant to attract the attention of predatory birds, putting the intruder at risk until the contest has ceased (Yack et al., 2001).

Leaf vibrations can also provide cues to other organisms. The incidental vibrations produced by caterpillars when chewing (for an example, see youtu.be/oEGIL9T73cQ) are detected by the plant itself, triggering a chemical defense response (Appel and Cocroft, 2014).

In the upper soil layers, beetle larvae can be found feeding within the turf thatch (an organic layer of roots, stems, and shoots), whereas other larvae are found deeper in the soil, feeding on decaying wood and tree roots. Stag beetle (*Lucanus cervus*), rose chafer (*Cetonia aurata*), and lesser stag (*Dorcus parallelipipedus*) larvae stridulate during active periods, such as when feeding, producing signals in the region of 0.4-3 kHz (**Figure 2**) (Harvey et al., 2011). Similarly, the common (*Melolontha melolonth*) and forest (*M. hippocastani*) cockchafers also stridulate, with peak frequencies of 1.7 to 3 kHz that vary in duration depending on species (Görres and Chesmore, 2019).

Figure 2. *An adult slug beetle (*Lucanus cervus*). Larvae of the stag beetle are known to stridulate. Photo by Lucos Houska.*

The ecological meaning of these larval signals is unknown, but the use of vibration for communication venues such as reproduction, competition, and predator avoidance has been demonstrated in adult insects (reviewed in Hill, 2008). There is also evidence to suggest that the pupal stage uses vibration. The extra-large larvae of Japanese rhinoceros beetles (*Trypoxylus dichotoma*) beat the prothorax against the pupal wall (see the supplementary videos at bit.ly/3yJOY9y). The vibrations are produced in response to approaching larvae, the first evidence for communication between larvae and pupae (Kojima et al., 2012).

Eavesdropping on Soil Vibrations

Who else might be listening to such sounds and vibrations in the soil? Early evidence suggests that the plant roots themselves are eavesdropping (Thode, 2019). For example, pea shoots (*Pisum sativum*), given a "choice" between growing through two tubes to reach nutrients, have been found to grow toward the vibrations/sounds of water alone, even when physical moisture was absent (Gagliano et al., 2017). Although receptor mechanisms have not yet been identified, it is hypothesized that the roots may be detecting vibrations in a frequency-selective way.

Mammals such as the striped skunk (*Mephitis mephitis*) and North American raccoon (*Procyon lotor*) may also be tapping into vibratory cues. These species dig and overturn the turf when seeking their below-ground prey (white grubs, Scarabaeidae larvae). Digging is highly localized at grub hotspots. Given the sound production of white grubs discussed previously in **Vibrations Above and Below the Lawn**, vibroacoustic cues may play a role in this foraging activity, an area that our research is currently exploring. Vibrational detection seems particularly likely in skunks, given the stomping behavior performed when threatened (see youtu.be/HLYD5BdNd90) (Crabbe, 1948).

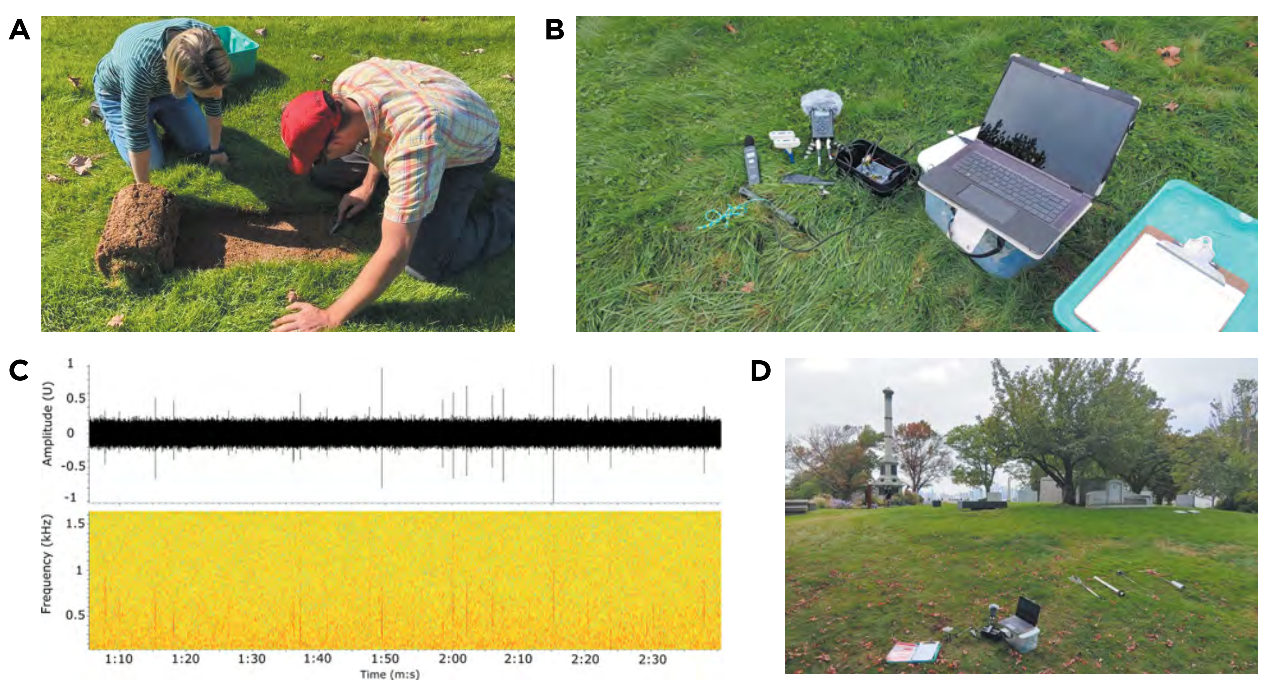
Humans are the other listeners. Distributions of unseen root-feeding pests (white grubs) can be mapped using sounds and vibrations (**Figure 3**) (Zhang et al., 2003). Soil probes, such as microphones or accelerometers pushed into the soil, record the short, pulsed signals below (Brandhorst-Hubbard et al., 2009).

This approach would have great benefits to pest managers. Without manually sampling the soil, grub hotspots cannot be located accurately, and managers therefore turn to blanket pesticide treatments instead. Vibroacoustics provides a novel alternative monitoring strategy. Presently, processing these signals requires a combination of manual listening and automated computer algorithms. There is still much to be learned to enable us to distinguish pest from nonpest and between species. This promising methodology is more common in other substrates such as tree trunks, plants, and crops such as fruit, grain, and timber (Mankin et al., 2011).

From the Lawn to the Seashore

On the seashore (**Figure 4**), crabs use vibrations (Popper et al., 2001). The family Ocypodidae (fiddler and ghost crabs) "rap," "rasp," "drum," and "honk" during complex courtship and territorial displays, producing signals in the range of 0.3 to 3 kHz. Male crabs beat the ground either inside or in front of their sandy burrows, signaling to other males and advertising their attractiveness to females. Other crustaceans, such as marsh and mangrove

Figure 3. *Current practices for locating white grubs in turfgrass involve manually hand sampling, as illustrated in the photograph of Louise Roberts and Kyle Wickings (**A**). Vibroacoustic sampling with soil probes, here shown at Green-Wood Cemetery, Brooklyn, New York (see green-wood.com), offers a promising noninvasive monitoring method for characterizing the distribution and abundance of pests in these areas (**B** and **D**). Exemplar oscillogram (amplitude units are provided in terms of relative Raven software units; **top**) and spectrograms of multiple pulses (**bottom**), hypothesized to be biologically produced, recorded by Louise Roberts and Kyle Wickings (**C**). Photos by Ramom V. Pereira (**A**), used with permission, and Louise Roberts (**B** and **D**).*



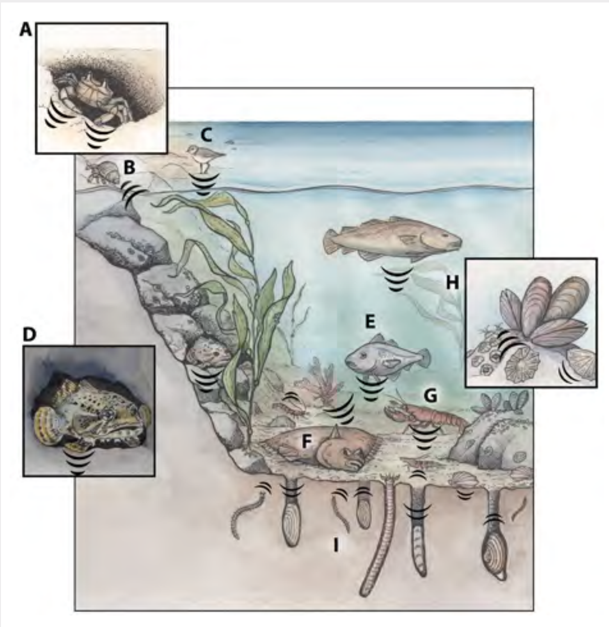


Figure 4. *Cross section of an East Coast aquatic system, with vibrational users and producers. Ghost crabs produce vibrations on the shore (**A**). Hermit crabs are sensitive to vibrations (**B**). Wading birds, such as plovers, paddle on the shore to capture prey (**C**). Oyster toadfish produce loud waterborne calls, hypothesized to translate into the substrate (**D**). Demersal fish such as haddock and cod also produce waterborne sounds close to the sediment (**E**). Benthic fish and invertebrates, such as flatfish (**F**) and brown shrimp (**G**), plus sessile organisms such as barnacles, limpets and mussels (**H**) are responsive to vibrations. Burrowing bivalves have known sensitivities to vibrations (**I**). Paintings by Ann Sanderson, © 2022, Ann Sanderson, all rights reserved; see www.annsciart.com.*

(Sesarmidae and Grapsidae, respectively) crabs produce similar sounds, which may also transmit vibrations into the ground. These signals consist of leg movements such as "stamping," and "tapping." The signals are produced during burrow defense, reproductive contests, and even as postfight victory displays (Goh et al., 209).

Terrestrial hermit crabs (*Coenobita* spp.) that reside on the tropical seashore also produce vibrations. These crabs carry an empty snail shell, a transportable home, to protect their delicate bodies. On occasion, shell fights break out, with attackers attempting to wrench other crabs from their homes. In this context, a repetitive "chirping" sound can be heard, which sounds a little like a frog (0.4- to 11.2-kHz peak) (**Figure 5**) (Roberts, 2021) See **Multimedia File 1** at acousticstoday.org/robertsmedia that shows a shell contest, with audible "chirps" throughout.

The vibration varies according to the architecture of the shell itself. In this way, by swapping their shells regularly, the hermit crabs may also be varying the information they are "communicating" to other crabs. During earlier stages of these shell contests, defending crabs "shake" in their shell when touched by attacking crabs. Tests have shown that the amplitude of the shaking vibration defines the response of the attacker. Greater amplitude vibrations were more likely to deter attacks, with crabs spending less time assessing shells and being less likely to flip the shell over to examine it (Roberts and Laidre, 2019). The responses of *Coenobita compressus* to shell shaking can be seen in videos at bit.ly/3N0mPA3.

Vibrational prey capture, discussed in **Vibrations Above and Below the Lawn**, is also observed on the seashore, here exhibited in birds of the intertidal area. The ringed plover (*Charadrius hiaticula*) stands on one leg vibrating the toes rapidly against the surface of the sediment (see youtu.be/jq9_k75foS8). This behavior triggers prey surfacing (lugworms, polychaetes, nematodes, and small crustacea), initiated to increase foraging success (Pienkowski, 1983). In laboratory experiments with a mechanical bird foot (!), researchers found that vibration triggers movement of similar prey species, making prey more visible (Osborne, 1982). Paddling, trembling, and leg shaking are particularly prevalent in plovers and other wading birds as well as gulls (family Laridae; see youtu.be/9yr4ZZUH-YQ).

Aquatic Biotremology

Aquatic biotremology, a research area in its infancy compared with terrestrial studies, encompasses every substrate type below the waves, from soft sediments, hard substrata, artificial structures to algal fronds, and perhaps even sessile animals themselves. Studies should include animals living on the surface of the seabed, such as flatfishes, those burrowing down in the sediment, such as mollusks, or even animals that lay eggs on surfaces, such as squid.

Although biotremologists do not yet know much about vibration production in this system, vibration sensitivity is widespread in aquatic organisms. Mollusks, worms (annelids, nematodes, and polychaetes), coelenterates

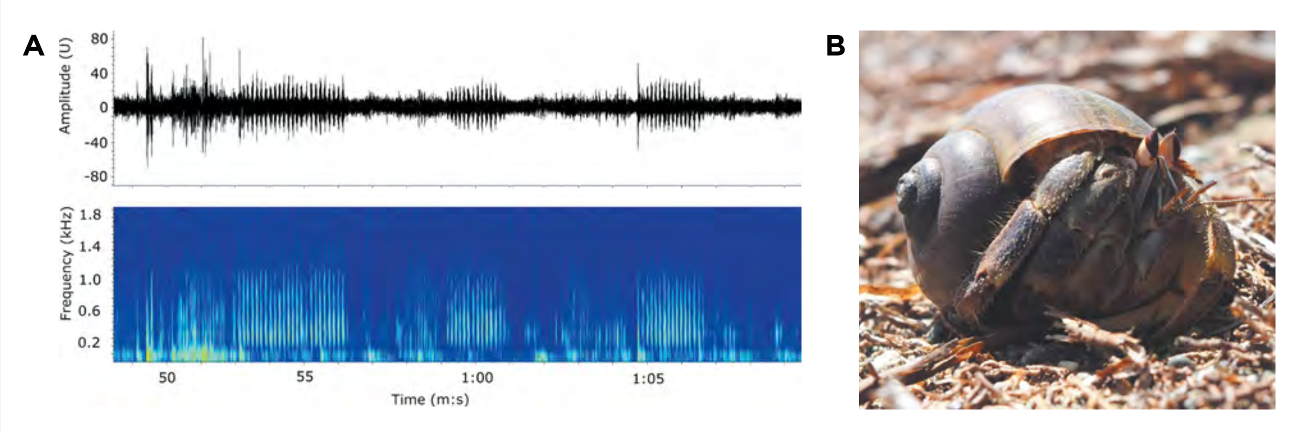


Figure 5. ***A:*** *multiple chirps of* Coenobita compressus*, measured in the sediment adjacent to the crabs using a laser Doppler vibrometer, shown as oscillogram (amplitude units are provided in terms of relative Raven software units;* ***top****) and spectrogram (****bottom****).* ***B:*** C. compressus *in laboratory conditions. Recordings by Louise Roberts. Photo by Elliott Steele, used with permission.*

(anemones, polyps, and comb jellies), arthropods (crustaceans) (reviewed in Budelmann, 1992), and even some sediment-dwelling chordates (e.g., flatfishes) can detect vibrations (Berghahn et al., 1995). Much like a human hearing test, where a sound is played and a response is given by the listener, the vibrational sensitivity of animals can be assessed by monitoring repetitive behavioral responses. Blue mussels (*Mytilus edulis*) fully or partially close their shells after exposure to sediment vibrations, allowing their frequency responsiveness to be quantified (Roberts et al., 2015). Similarly, the response of the hermit crab (*Pagurus bernhardus*) to vibration is predictable enough that monitoring movement changes can inform us of their sensitivities (Roberts et al., 2016).

We have animals sensing vibrations below the waves, but who is producing the vibrations? Certainly, animals moving in, on, and around surfaces will be producing incidental vibrations, but others may be actively signaling, too.

Although speculative at present, aquatic biotremologists may hypothesize that fishes that sit on the seabed could create vibrations when producing waterborne sound. The three-spined toadfish (*Batrachomoeus trispinosus*) produces "hoot" and grunting sounds during mating to attract females to their dens (Rice and Bass, 2009). Similarly, members of the sediment-dwelling Sciaenidae (croakers and drums; see sounds at bit.ly/3GuUi35) are active sound producers (Ramcharitar et al., 2006). Given that these fishes are sitting on or near the bottom when signaling, it seems highly likely that there is a substrate-borne component to these signals.

Mantis shrimps (*Hemisquilla californiensis*) "rumble" and "rattle" from within their burrows in response to approaching objects (see youtu.be/F2yLsXL74XE). These low-frequency signals also likely propagate through the substrate (Patek and Caldwell, 2006). When vibrational sensors become more standard in aquatic research, it seems probable that vibrational production will be found to be widespread.

How might understanding such vibrations be useful? Much in the same way that bioacousticians can monitor sounds to measure species diversity and abundances, biotremologists can monitor vibrations for the same purpose. This would be particularly useful given that many bottom-dwelling organisms are cryptic in much the same way as soil dwellers. Understanding natural aquatic vibroscapes is also likely crucial to our understanding of the potential impacts of human-made vibrations, as discussed in **Humans Are Shaking the Earth**.

Humans Are Shaking the Earth

The term "noise" is typically used for unwanted sounds that we, as humans, can perceive. Some noises such as lawn mower engines in suburbia or the rumble of traffic from the city center may spring immediately into mind (see Slabbekoorn, 2018). In the water, this noise would include the sound of boat engines for a swimmer or the sound of bubbles when diving down to the ocean depths. Noises propagating in these media (air and water) have gained biologists' research attention largely because our ears are able to detect these sounds.

However, noise also exists in the context discussed here, as surface vibrations (Raboin, 2021). In this medium, human contributions overlap in frequency and amplitude with the natural vibroscape. Here, the term "vibrational noise" is used, defined as being any anthropogenically produced vibration. For clarity, we use "acoustic noise" to refer to the air- or waterborne equivalent.

Many of the sources associated with acoustic noise are in direct contact with a solid (e.g., the ground but also other surfaces such as plant stems or tree trunks) and thus create vibrational noise (Roberts and Howard, 2022). In both terrestrial and aquatic systems, human activities relating to farming, fishing, construction, energy development/production, mineral exploitation, and transportation all have parts directly in contact with the earth. Foundational structures of wind turbines, for example, directly contact the ground in both on- and offshore systems, making vibration a concern in addition to sound (Popper et al., 2022). Even those activities not in contact with the ground may produce sounds that indirectly translate into the substrate, such as seismic surveys (Hawkins et al., 2021).

As with acoustic noise, vibrational noise may be impulsive or continuous or broadband or tonal. Sources may be mobile or stationary or single point or multiple sourced. Noise may radiate through the substrate, air, water, or perhaps all three. Yet the vibroscape is by no means quiet naturally. Other vibrational contributions include plants and animals (incidental or active) and abiotic sources such as air, sediment, and water movement. Additional vibrational noise may mask cues and signals, distract, and elicit changes at behavioral, physiological, and physical levels in much the same way as acoustic noise (Popper and Hawkins, 2019).

Despite the prevalence of vibrational noise, research relating to potential impacts is sparse, with less than 25 species tested across all environments (reviewed in Roberts and Howard, 2022). The available aquatic data relate mostly to bivalve mollusks and crustacea. Here, behavioral changes have been observed, which include "flinching," burial, and siphonal retraction in bivalves such as cockles (*Cerastoderma edule*) and scallops (*Pecten fumatus*). In crustaceans, locomotory bursts, impaired feeding, changes in environmental information use, and modified antipredator responses have been observed.

Increased mortality, compromised homeostasis (scallops), and physical damage (rock lobsters; *Jasus edwardsii*) have been demonstrated after exposure to vibroacoustic sources. On land, vibrational noise elicts stress in mice and in farm animals such as cattle, pigs, and chickens. For insects, noise has been shown to distract from producing signals and detecting cues, impact activity budgets, and affect reproduction (parental care, offspring numbers, pair formation).

Below the ground, a recent study found that earthworm abundance decreased with increasing wind farm turbine vibrations but that the vibrational noise did not impact small invertebrates (Velilla et al., 2021).

Taken together, these studies suggested that vibrational noise may impact animal fitness in similar ways to acoustic noise. (Kight and Swaddle, 2011). However, the small number of studies in this area to date mean that it is difficult to draw firm conclusions so far, and there is much to be learned.

The Future for Applied Biotremology

Based on the ubiquity of animal use of vibrational stimuli and that many anthropogenic sources produce such signals, there is clearly an urgent need for experiments evaluating the potential impacts of vibrational noise. How might this be done? The task can be approached with methodologies already found in bioacoustics. Animals may be exposed to actual or replicated anthropogenic sources in carefully controlled exposure or playback studies. However, unlike airborne and waterborne studies, vibrational studies have an additional layer of complexity relating to how vibrations pass through different substrates (Hill, 2008). Acting as a selective frequency filter, the substrate impacts the playback signal, and thus a prefiltration of playback signals is required. Nevertheless, biotremologists use a range of techniques to elicit vibrations in substrates. Piezo actuators may shake plant stems, electromagnetic shakers may tremble a table, thumpers (as in *Dune*) may hit the ground, and ruggedized tactile speakers can shake the ground. If all else fails, hammering a stake into the ground can be sufficient!

But how to study biological vibrations in a world dominated by anthropogenic sources? In the laboratory, air tables, dampeners, gaskets, and suspension reduce external vibrations but typically must be coupled with sound reduction to avoid indirect transmission. It seems then that the rite of passage of a biotremologist is to work in a bunker of one sort or another, in an out-of-the-way campus location, or in a forgotten basement corner.

Regardless of the study location, any research that improves our understanding of vibrational noise is likely to be as critical as the acoustic equivalent, given the prevalence of vibrations used in the animal kingdom for communication. Just a teaser of biotremology has been provided here. The reader might explore this area further in the overview book by Hill (2008).

Acknowledgments

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