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Research Methodologies to Study Behavioral and Physiological Effects on Fishes and Aquatic Invertebrates from Particle Motion and Substrate-borne Vibration Exposure

U.S. Department of the Interior
Bureau of Ocean Energy Management
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Research Methodologies to Study Behavioral and Physiological Effects on Fishes and Aquatic Invertebrates from Particle Motion and Substrate-Borne Vibration Exposure: Study and Workshop

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List of Abbreviations and Acronyms

Short form	Long form
AEP	auditory evoked potentials
BOEM	Bureau of Ocean Energy Management
BWRI	Blue World Research Institute
CMA	Center for Marine Acoustics
DAS	distributed acoustic sensing
dB	decibel
DOI	Department of the Interior
LFA	Low Frequency Active
MEC	marine energy converter
NYSERDA	New York State Energy Research and Development Authority
OCS	Outer Continental Shelf
Pa	pascal
PNNL	Pacific Northwest National Laboratory
RMS	root-mean-square
SPL	sound pressure level
µPa	microPascal

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Summary

There are growing needs to understand biological effects on fishes and aquatic invertebrates resulting from exposure to underwater particle motion and substrate-borne vibration associated with offshore energy activities. These activities include, but may not be limited to, offshore renewable energy development regulated by the Bureau of Ocean Energy Management (BOEM). However, studies to investigate such effects face multiple challenges due to the complexity of the acoustic field, which involves water-borne particle motion and substrate-borne vibration. Without appropriate experimental designs and studies, it would be difficult or even impossible to understand the biological and physiological effects on fishes and aquatic invertebrates.

Over the past several years, the scientific community has become increasingly aware that most fishes and aquatic invertebrates sense acoustic energy in the form of particle motion and substrate-borne vibration, and that significant data gaps exist concerning potential biological effects on animals of these disturbances from offshore energy development (e.g., Hawkins et al., 2021; Popper and Hawkins, 2018). However, studies to address these interdisciplinary issues often face challenges regarding the appropriate experimental setting, measurement collection, and data interpretation. In a laboratory environment, careful consideration must be given regarding boundary conditions, sediment types and thickness, and measurements of animals' behavioral, audiometric, and physiological response (Hawkins et al., 2021, p. 2; Roberts et al., 2016b).

To address these issues, BOEM convened a virtual *Workshop on Research Methodologies to Study Biological Effects from Particle Motion and Substrate-Borne Vibration* on 19–20 October 2023. The Workshop brought together researchers and experts in the areas of (1) fish and aquatic invertebrate sensory biology and biotremology (the study of biological use of vibrations), and (2) physical and engineering acoustics. The goal was to provide recommendations on general experimental design, sound and substrate-borne vibration apparatuses, and testing procedures that are appropriate to address specific research questions. These questions include whether fishes and aquatic invertebrates can be grouped under different functional hearing groups based on their auditory mechanisms or hearing sensitivity and whether exposure to anthropogenic particle motion or substrate-borne vibration would cause changes in vital rates or hormone levels in fishes and aquatic invertebrates. In addition, representatives from major funding agencies and regulators also participated the Workshop to gain knowledge of this field.

The workshop included five keynote talks and breakout group discussions. The keynote talks focused on reviews of research designs and fundamental physical acoustic concepts related to study behavioral and physiological effects from underwater particle motion and substrate-borne vibration on fishes and aquatic invertebrates. These keynote talks were the following:

- Arthur N. Popper: “Sound Pressure, Particle Motion, Substrate Vibration – A History of Rethinking Fish (and Invertebrate) Hearing”
- James Martin: “A Review of Vibroacoustic Wave Generation Devices that Are Suitable to Fishes and Invertebrates Acoustic Studies in Laboratory Settings”
- Joseph A. Sisneros: “A Review of Proper Experimental Design and Lessons Learned from Fish Vibroacoustic Research Under Laboratory Settings”
- James H. Miller: “A Review of Physical Characteristics of Particle Motion, Substrate-Borne Vibration, and Interface Waves that Are Biologically Relevant”
- Louise Roberts: “A Review of Proper Experimental Design and Lessons Learned from Invertebrates Vibroacoustic Research Under Laboratory Settings”

Breakout group sessions served as platforms for experts to discuss and respond to a set of questions directed at identifying appropriate research methodologies to study behavioral and physiological effects from underwater particle motion and substrate-borne vibration exposure on fishes and aquatic invertebrates.

A very important outcome of the breakout groups was the idea that one must first determine the research questions and then select the most appropriate experimental approach to answer those questions. Thus, the research question(s) must drive how they are answered.

A second critical outcome of the discussions was how research questions—and research approaches—are likely to differ depending on the species of interest, as well as on the age and size of the animals studied. Thus, an experimental approach that may be appropriate for larval fishes may not be suitable for adults, and an experimental approach that works for a sessile species may not be suitable for a mobile species.

The participants also recognized that the outcome of the current workshop was building upon several earlier workshops conducted by BOEM and other agencies. Based on these prior workshops and associated studies, this report identifies 20 major research questions. These research questions are grouped into four major series: auditory mechanism; hearing effects; behavioral effects; and physiological effects.

To link specific research questions with appropriate experimental designs, the report identifies four basic experimental settings: (1) laboratory tank; (2) in-ground pond/tank or above-ground tank; (3) large water body, such as a pond, river, lake, or ocean/bay with animals confined in cages (open-water, confined); and (4) large water body with free-ranging animals (open-water, free-ranging).

Finally, the report provides initial views of pros and cons of these four different experimental settings to study fishes and aquatic invertebrates and the behavioral and physiological effects from particle motion and substrate-borne vibration exposure. The report then suggests research questions that can and cannot be addressed under each of the experimental settings (Tables 1 and 2 in the main document).

Introduction

Background

As a Federal agency charged with the responsibility of managing the development of U.S. Outer Continental Shelf (OCS) energy and mineral resources in an environmentally responsible way, BOEM must ensure that environmental protection is a foremost and indispensable consideration in its decision-making. Development of OCS energy and mineral resources—such as oil and gas exploration and production, offshore renewable energy facility construction and operation, and marine critical mineral prospecting and extraction—often generate underwater sounds and vibrations that may adversely affect aquatic life (Hawkins et al., 2015; Miller et al., 2016; Mooney et al., 2020; Popper et al., 2024; Popper and Hawkins, 2013, 2016). The urgent need to reduce reliance on fossil fuels to combat climate change has been driving unprecedented development of offshore renewable energy in the U.S. and worldwide. Industrial activities leading to the construction and operations of various offshore renewable energy structures also raised new issues concerning the effects of anthropogenic noises on aquatic life from these activities, and research priorities to understand such effects (Popper et al., 2022b, 2023).

While BOEM has historically supported research into the impacts of industry-generated underwater noise on marine animals (review in Guan et al., 2022; Normandeau, 2013), most of the pre-2010 research focused on marine mammals (e.g., Madsen et al., 2006; Richardson et al., 1995; Southall et al., 2007). However, over the past decade, interest in understanding the impact of underwater anthropogenic sound on fishes and aquatic invertebrates[1] has grown (e.g., Casper et al., 2013; Halvorsen et al., 2012; Hawkins and Popper, 2014; Morley et al., 2014; Popper and Hawkins, 2013, 2016; Solé et al., 2023), although efforts and funding on these taxa are still far less than continuing efforts focused on marine mammals.

To further understand the potential effects of anthropogenic sounds on fishes and aquatic invertebrates, BOEM convened a workshop on the *Effects of Noise on Fish, Fisheries, and Invertebrates in the U.S. Atlantic and Arctic from Energy Industry Sound-Generating Activities* in March 2012. The results of the that workshop was reported in Hawkins et al. (2015) and Normandeau (2013).

It is fundamentally important to understand that, unlike marine mammals (which only detect sound pressure), fishes and aquatic invertebrates sense acoustic energy in the form of particle motion and substrate-borne vibration (Hawkins et al., 2021; Mooney et al., 2010; Nedelec et al., 2016; Popper and Hawkins, 2018). The exceptions are some fish species that also detect sound pressure using hearing specializations such as the air (swim) bladder that converts sound pressure to particle motion, which may then be detectable by the ear (Popper and Hawkins, 2018).

Because of the important role of particle motion and substrate-borne vibrations for sound detection by fishes and invertebrates, one needs to take a very different perspective in formulating specific research questions and approaches for these animals as compared to approaches taken to study marine mammals (Hawkins et al., 2015; Hawkins and Popper, 2017; Popper and Hawkins, 2021). However, studies to address research questions appropriate for fishes and invertebrates often face challenges regarding the appropriate experimental design, data collection, analysis, and interpretation (e.g., Gray et al., 2016; Sisneros et al., 2016). Indeed, the acoustic field in a laboratory tank rarely approximates accurately the natural environment (Popper and Hawkins, 2021; Roberts et al., 2016b; Rogers et al., 2016). Thus, an animal's response to a laboratory acoustic field may be very different from their response in a natural

[1] In the technical paper where the term "invertebrate" is used, it is referring to "aquatic invertebrate."

environment, since the physical interactions between the animal and the tank will affect the nature of the exposure.

Many studies on the potential impacts of anthropogenic sound on fishes have focused on physical injuries and auditory effects (Casper et al., 2013; Dahl et al., 2020; Halvorsen et al., 2012; Jenkins et al., 2022; Popper et al., 2005, 2013, 2016; Smith et al., 2022; Soloway and Dahl, 2014). These acute (i.e., severe, and sudden in onset) effects are usually caused by intense, impulsive sounds (e.g., from underwater detonation, seismic airguns, and impact pile driving) in relatively close range to the animal.

In addition to noise sources that cause acute effects, animals could be exposed to sounds at sufficient distance from the source, resulting in chronic effects. Such sounds are generally from low-level, long-duration acoustic sources, such as operations on an offshore renewable structure and increased vessel traffic. Biological effects on fishes and invertebrates from such long-lasting chronic exposure to particle motion and substrate-borne vibration have not been adequately addressed, especially on wild species (Nedelec et al., 2014; Wysocki et al., 2007).

Furthermore, chronic noise often extends considerable distances from its source and has the potential to affect large numbers of animals. Therefore, research into addressing the effects of chronic noise exposure is important (Popper et al., 2022b, 2023). In particular, offshore renewable energy developments are spatially large, and their activities can last for decades. The long-term effects on fishes and invertebrates in these areas have not been studied, but animals exposed to sounds in renewable development areas may encounter behavioral disturbances, displacement, and changes in reproductive states, hormonal levels, growth, and development (e.g., Hawkins and Popper, 2017; Popper et al., 2022b, 2023).

To address questions related to potential effects of exposure to chronic noise, BOEM's Center for Marine Acoustics (CMA) funded the *Workshop on Research Methodologies to Study Biological Effects from Particle Motion and Substrate-borne Vibration* (Workshop) on 19–20 October 2023. The workshop brought together researchers and experts in the areas of (1) fish and invertebrate sensory biology, bioacoustics, and biotremology (the study of biological use of vibrations) (Roberts and Rice, 2023; Roberts and Wickings, 2022), and (2) underwater, physical, and engineering acoustics. The attendees used a review of existing literature and breakout group discussion to develop recommendations on general experimental design, water-borne particle motion and substrate-borne vibration apparatuses, and testing procedures that are appropriate to address specific research questions.

Purpose of the Workshop

Researchers have been investigating mechanosensory organs and sound and substrate-borne vibration wave detection of fishes and aquatic invertebrates for over 100 years (e.g., Dijkgraaf, 1952; Enger, 1973; Fay, 1984; Hawkins and Horner, 1981). However, many of the older—but very well done and insightful—studies may be poorly known to contemporary researchers (review in Moulton, 1963; Sand et al., 2023). Furthermore, historically, very limited funding has been devoted to addressing anthropogenic acoustic effects on fishes and aquatic invertebrates as compared to the resources allotted to study these effects on marine mammals. Therefore, innovation in laboratory and field research methodologies to investigate particle motion and substrate-borne vibration effects on fishes and aquatic invertebrates is very limited.

The purpose of this workshop was for BOEM, other Federal agencies, scientists, and potential co-funders of future research to acquire knowledge and information on general experimental designs, protocols, and procedures that are appropriate to address specific questions concerning biological effects from anthropogenic particle motion and substrate-borne vibration. As a result of the discussions, all participants also learned more about what is known and not known about the biological effects of particle motion and substrate-borne vibration, allowing the participants to consider questions and approaches based on the most recent (albeit limited) data.

The Workshop

The workshop was an eight-hour virtual meeting spanning two days (four hours each day). It was organized and facilitated by Blue World Research Institute (BWRI) and CONCUR, Inc., with funding provided by the BOEM Center for Marine Acoustics (CMA).

Workshop Overview

Forty participants attended the workshop. Most of the invited participants were subject matter experts in fish and invertebrate bioacoustics, biotremology, sensory biology, underwater acoustics, and physical and engineering acoustics. Workshop participants also included representatives from several Federal funding agencies, such as the U.S. Navy, U.S. Army Corps of Engineers, and the Department of Energy. Approximately half of the subject matter experts had a background in biological sciences and the other half in physics, engineering, or earth sciences. A list of the participants and their affiliations is provided in Appendix A. The workshop included keynote presentations and breakout group discussions. The keynote presentations are discussed in Section 2.3.

Annotated Agenda

Day 1 – October 19, 2023, 11:00 – 15:00 EST

- 11:00 – 11:10 Welcome
    - Welcome and convene the workshop – Jill Lewandowski, BOEM CMA
    - Introduce the workshop objectives – Shane Guan, BOEM Environmental Studies Program
    - Briefly explain simple ground rules for the Workshop – Scott McCreary (CONCUR, Inc.)
- 11:10 – Introduce the two upcoming speakers – Shane Guan
- 11:10 – 11:30 Arthur N. Popper – Sound pressure, particle motion, substrate vibration – A history of rethinking fish (and invertebrate) hearing
- 11:30 – 11:50 James Martin – A review of vibroacoustic wave generation devices that are suitable to fishes and invertebrate acoustic studies in laboratory settings

11:50 – 12:55 Break

- 11: 55 – 12:40 Break-out session A: Small-tank experiments
    - Group 1 – Physical variables
    - Group 2 – Physical variables
    - Group 3 – Biological variables
    - Group 4 – Biological variables

12:40 – 12:50 Break – Time for breakout group rapporteurs and moderators to gather thoughts

- 12:50 – 13:10 Concise report outs from each break-out group
- 13:10 – Introduce the upcoming speaker – Shane Guan
- 13:10 – 13:30 Joseph A. Sisneros – A review of proper experimental design and lessons learned from fish vibroacoustic research under laboratory settings

13:30 – 13:35 Break

- 13:35 – 14:20 Break-out session B: Medium outdoor tank experiments

- Group 1 – Physical variables
- Group 2 – Physical variables
- Group 3 – Biological variables
- Group 4 – Biological variables

14:20 – 14:30 Break – Time for breakout group rapporteurs and moderators to gather thoughts

- 14:30 – 14:50 Concise report outs from each break-out group
- 14:50 – 14:55 Summarizing discussion to reflect on the key findings of Day 1
- 14:55 – 15:00 Final comments or observations about Day 1 – Shane Guan, other presenters, or workshop conveners

15:00 – Day 1 Ends

Day 2 – Oct 20 11:00 – 15:00 EST

- 11:00 – 11:05 Welcome and define terms – Shane Guan
- 11: 03 – 11:05 Overview of the day's activities – Scott McCreary
- 11:05 – 11:15 Breakout groups 3 and 4 report out from Session B Medium Outdoor Tanks
- 11:15 – 11:15 Introduce the two upcoming speakers – Shane Guan
- 11:15 – 11:35 James H. Miller – A review of physical characteristics of particle motion, substrate-borne vibration, and interface waves that are biologically relevant
- 11:35 – 11:55 Louise Roberts – A review of proper experimental design and lessons learned from invertebrate vibroacoustic research under laboratory settings

11:55 – 12:00 Break

- 12:00 – 12:45 Break-out session A: Mesocosm experiments
    - Group 1 – Physical variables
    - Group 2 – Physical variables
    - Group 3 – Biological variables
    - Group 4 – Biological variables

12:45 – 12:55 Break – Time for breakout group rapporteurs and moderators to gather thoughts

- 12:55 – 13:15 Concise report outs from each break-out group
- 13:15 – 13:45 Discussion about emerging themes
    - Review and capture the key observations from the Day 1 and Day 2 breakout sessions
    - Look for cross-cutting themes and important insights that emerge from the discussions
- 13:45 – 14:15 Discussion about the strengths and weaknesses of the different experimental setups

14:15 – 14:20 Break

- 14:20 – 14:30 Thought-sharing session about a bonus topic
    - Are there physical principles or specific tools/metrics that can be used to separate substrate-borne vibration vs. water-borne particle motion?
- 14:30 – 14:35 Final comments or observations on the workshop – Shane Guan, other presenters or workshop conveners
- 14:35 – 14:40 Share the next steps with the workshop participants – Shane Guan

14:40 Workshop Ends

Keynote Presentations

The Workshop five presentations by subject matter experts. The summary of the presentations is provided below as extended abstracts. The slides from the presentations are in Appendix B at the end of this report.

Keynote Presentation 1

Dr. Arthur N. Popper, Professor Emeritus, Biology, University of Maryland, College Park, Maryland

Sound Pressure, Particle Motion, Substrate Vibration – A History Of Rethinking Fish (and Invertebrate) Hearing

Abstract

The interest in research on particle motion and fishes can be traced back at least to work by Dieter Poggendorf (Poggendorf, 1952), but we still do not know much about fish detection of this component of an underwater sound field. However, understanding the role of particle motion in hearing is integral to understanding sound detection by fishes and invertebrates. This is because all fishes detect particle motion, and it is likely that all sound-detecting invertebrates only use particle motion (e.g., Nedelec et al., 2016; Popper and Hawkins, 2018).

The earliest work on fish detection of particle motion by Poggendorf (1952) found that a species of catfish will detect and respond to this sound component. Sven Dijkgraaf (Dijkgraaf, 1960) subsequently supported the idea that particle motion is most important for fishes, and he proposed that it is likely used to determine sound source direction (sound source localization). Then, in 1963, William N. Tavolga and Jerome Wodinsky provided behavioral data showing that some fish species could detect particle motion as well as sound pressure (Tavolga and Wodinsky, 1963).

A critical idea first came from H. de Vries in 1950 and was reinforced in 1967 by Willem van Bergeijk: both argued that the ear of fishes responds to particle motion and not sound pressure (van Bergeijk, 1967; de Vries, 1950). Van Bergeijk further argued that sound pressure is detected only if the animal has a swim bladder that converts pressure to particle motion and is close enough to the ear for this particle motion to be detected. Moreover, both de Vries and van Bergeijk argued that particle motion causes differential

motion between the fish body (and sensory epithelium of the ear) and the otolith that overlies the epithelium. With this differential motion, cilia on the sensory cells (which contract the otolith) are bent, and this stimulates the sensory cells.

A major hurdle to understanding particle motion detection is the difficulty of setting up a particle motion stimulus in a tank (Rogers et al., 2016; Slabbekoorn, 2016). This is because sound reflects off the tank's surfaces, as well as the air/water interface, and creates a complex and hard-to-define particle motion field. Thus, for studies done in most fish tanks, it is not possible to accurately determine the sensitivity of animals to particle motion since the signal cannot be easily calibrated. Moreover, when one measures particle motion in a tank, just putting a fish in the tank changes the sound field from the one measured. This makes it even harder to determine the signal to which a fish was responding since the relevant incident signal is neither the signal measured with the fish absent nor the one measured with the fish present.

Related to issues of particle motion is the much newer idea that many aquatic invertebrates and some fishes are likely to detect substrate vibrations, including those that result from human activities, such as pile driving, since they put energy into the substrate. We know almost nothing about how animals respond to and use substrate-borne vibration, and this is an area of great importance for study along with studies of how animals detect and respond to particle motion.

What is needed to make progress?

1. Understand particle motion detection by fishes and invertebrates. Understand behavior and behavioral responses including sound levels that elicit responses.
2. Develop facilities where investigators can accurately control, measure, and calibrate particle motion.
3. Understand hearing sensitivity in terms of particle motion as well as pressure.
4. Focus on important species related to pile driving, wind farms, etc. Identify five to seven fish species and several invertebrate species that can represent the diversity of animals.
5. Develop easy to use and small devices to measure particle motion.
6. Develop basic designs for tanks and facilities that would enable precise control of the acoustic signal in terms of sound pressure and particle motion.
7. Use similar approaches for the investigation of substrate-borne vibration.
8. Much more focus on these issues for invertebrates.

Take-home messages include the following:

- Increase funding (fishes and invertebrates are more important for human well-being than marine mammals).
- Decide upon the most important questions to get data and focus on these. Need to have comparable data across labs and investigators. Need collaboration across labs.
- Select relevant species of concern by agencies and locales.
- Think about issues from the perspective of the animal, not the perspective of the sound-producing or mitigating device: if the animals are not affected, we would not have to be concerned about mitigation (Popper et al., 2020).

Keynote Presentation 2

Mr. James Martin, Principal Research Engineer, Georgia Institute of Technology, Atlanta, Georgia

A Review of Vibroacoustic Wave Generation Devices that Are Suitable for Fish and Invertebrate Acoustic Studies in Laboratory Settings

Abstract

Work with biological effects of underwater sound began at Georgia Tech in 1993 around concern over Low Frequency Active (LFA) Naval sonar systems' effects on marine mammals and human divers. This work on the LFA program spanned roughly a decade and involved testing in a variety of tanks and the development of a device known as the *Ratabrator* (Delecki, 2002). This traveling-wave tube permitted laboratory-scale acoustic exposure of small mammals (rats and mice) to specific acoustic signals at levels sufficient to produce physiological damage. The Ratabraor provided a known incident signal to an animal with the correct free-field radiation impedance load (i.e., radiation mass). It was designed to produce three canonical incident signals: a plane wave, a pure-pressure signal, and a pure-velocity signal. Although the free-field case generally is considered the most relevant, this is rarely the actual incident signal to which an animal would be exposed in situ because of nearby boundaries and multi-path propagation.

For later studies of pile-driving effects on fish at a laboratory scale, a *Fishabrator* was designed and constructed (Casper et al., 2013; Halvorsen et al., 2012; Martin and Rogers, 2008). This was essentially a Ratabrator in which the subject was free swimming rather than restrained, and the vertical incident angle could be controlled by tilting the device rather than the angle of restraint. More recent work in this area has involved collaborative efforts on in situ testing on fish to assess behavioral changes from seismic exploration signals. Here the problem is one of characterizing rather than controlling the exposure.

The source requirements of the *Ratabrator* and *Fishabrator* exposure chambers followed similar principles to the design of other tank experiments. Sources that produced a force rather than a displacement in response to the driving signal were required because the compliant subject was near the source, where its presence would affect the radiation load on the source. Similarly, a compliant non-resonant source was required to achieve the correct radiation load on the subject. Neither of these requirements would have existed if the subject were in the far field of the source, which is not feasible at a laboratory scale. Sources capable of producing substantial acoustic displacements were also required because the frequencies of interest in all these studies were low (<1,000 Hz). This requirement would have been more problematic if the subject had been in the far field of the source because of geometric spreading. These three requirements led to the selection of electrodynamic (moving coil) sources (Bobber, 1988) for all the sound-exposure systems that were designed. Additionally, a desire to produce an exposure field with a specific incident impedance led to a requirement for a least two sources to be used in each exposure system. The traveling-wave tube experiments differed from the other studies in that they did not require immersion transducers. Only the moving surfaces of the sources in these devices were wet.

In all cases where a sound-exposure system is being designed, the problem of source selection cannot be decoupled from the problem of tank (or body of water) selection. In this context, "small" tanks can be both too small or too large (Martin et al., 2005). The former problem occurs either in behavioral studies, where the tank constrains the natural behavior of the subject, or in any study where it alters the acoustic radiation load on the subject. This makes the subject's response inconsistent with the measured incident signal. The latter problem occurs when there are modes of the tank in the frequency range of interest. In this case, the problem is both one where the tank alters the radiation load on the subject and another where the subject alters the modal structure of the tank. This makes it impossible to meaningfully characterize the incident signal that produces any observed response.

For these reasons, it probably will be desirable to use electrodynamic transducers for most future animal sound-exposure studies. At least two will be required when measurements are made in small bodies of water rather than in situ (where the use of the actual sources of interest is also an option). For behavioral studies, it may be necessary to select electrodynamic sources with permanent field magnets, as these would not require constant cooling, which can add significantly to the background noise confounding the exposure-free baseline.

The cost and availability of appropriate immersion sources appear to be an ongoing issue. Inexpensive electrodynamic immersion sources such as swimming pool speakers tend to have in-band resonances, low inconsistent source levels, and be relatively easy to damage. Standard transducers such as the USRD J-11, -13, and -15 are no longer commercially produced for sale and must be rented at a current cost of about $9,200 per year, with somewhat limited availability. Thus, it would be helpful if equipment were shared between research groups. If there were sufficient demand to warrant it, something functionally similar, or superior, to these sources (in the context of this application) could be constructed around commercially available electrodynamic shakers. This would essentially be a *Ratabrator/Fishabrator* turned inside out.

Keynote Presentation 3

Dr. Joseph A. Sisneros, Professor of Psychology, University of Washington, Seattle, Washington

A Review of Proper Experimental Design and Lessons Learned from Fish Vibroacoustic Research Under Laboratory Settings

Abstract

In this presentation, I review some of the appropriate experimental designs and lessons learned from previous fish vibroacoustic research performed in laboratory settings. The experimental designs presented are based on the research that has been conducted by the Sisneros lab over the past 20 years to investigate fish bioacoustics and hearing.

The first question one might ask when designing fish hearing experiments is, “What is the appropriate stimulus?” To answer this question, one must first understand what is sound.

Sound is a mechanical disturbance that propagates as a longitudinal wave in air and water, and it can be described in terms of both sound pressure and particle motion. Sound pressure is defined as the fluctuation of the force per unit area (pressure) above and below the ambient level, whereas particle motion is defined as the movement of fluid particles caused by the fluctuating forces of pressure.

Now that we know what sound is, we revisit our original question of “What is the appropriate stimulus” or more specifically ask “What acoustic cue (i.e., pressure or particle motion, or both) is the fish ear designed to detect?”

The fish inner ear consists of three semicircular canals (anterior, posterior, and horizontal) and three otolithic end organs (saccule, lagena, and utricle). Fishes have two modes of hearing: an inertial mode and a pressure mode. The inertial mode of hearing involves the use of the otolithic end organs to directly detect acoustic particle motion, while the pressure mode involves the use of the otolithic end organs to indirectly detect sound pressure via the particle motion created by sound-induced pressure fluctuations of the swim bladder or other gas-filled organ.

The pressure mode of hearing varies across fish species depending on whether the given species has a swim bladder or other gas-filled structure. Thus, the swim bladder can act as an acoustic organ and permit sound pressure-induced vibrations of the swim bladder (or other gas-filled structures) to be transmitted to the inner ear end organs for hearing. Fishes possess a ‘continuum’ of pressure detection mechanisms that

vary in their pressure sensitivity depending on the proximity of the gas bladder to the inner ear (Popper et al., 2022a; Popper and Fay, 2011). This continuum ranges from fishes that have their swim bladder connected to the inner ear via Weberian ossicles (pressure sensitivity is relatively high; e.g., goldfish and zebrafish), to fishes with the swim bladder close but not connecting to the inner ear (pressure sensitivity is related to how close the swim bladder is to inner ear; e.g., Atlantic cod), to fishes with the swim bladder far from the inner ear (pressure sensitivity is relatively low or no sensitivity; e.g., salmonids), and to fishes with no swim bladder (no pressure sensitivity; e.g., flatfishes and sharks).

In cases where fishes do not have swim bladders (e.g., sharks and flatfishes), the appropriate stimulus to characterize, in terms of hearing, is particle motion or particle velocity or acceleration. These acoustic stimuli can be measured using a triaxial accelerometer. We can produce particle motion stimuli using a shaker table system such as that designed by Professor Richard R. Fay (Fay, 1984; Fay et al., 2023), which produces particle motion in three dimensions. Such a system can be used to characterize the directional sensitivity of fishes or invertebrates to particle motion and can reliably test frequencies lower than those from underwater speakers. The drawback to the shaker table system is that the range of testable frequencies is limited, the size of fish to be tested is limited (must fit in the dish or apparatus), and the data acquisition system is outdated.

A one-dimensional shaker table system also can be used to test hearing in larval fishes. Behavioral assays such as prepulse inhibition, which is a very sensitive behavioral assay to test fish hearing, can be used to characterize fish hearing thresholds, which are much lower than acoustic startle response thresholds (Bhandiwad and Sisneros, 2016). One advantage of this assay is that it does not require conditioning or sacrificing animals. A drawback to this stimulus system and assay is that it only works on very small animals (e.g., larval zebrafish but not adult zebrafish) (Bhandiwad et al., 2013). Also, habituation to startle stimuli used in the prepulse inhibition assay may vary by species.

In cases where fishes are pressure sensitive, we recommend that experimenters measure both the sound pressure and particle motion sensitivities of fishes. Unfortunately, the sound field that is produced in small tanks is very messy due to many factors that include 1) acoustic resonances and reflections of the tank, 2) changes in the relationship between sound pressure and particle motion at and near the tank walls, and water surface, which result in changes in the acoustic impedance at various points in the tank (every tank is different, which makes it difficult to predict or model), and 3) the wavelengths of the frequencies tested are often bigger than the tank and the speed of sound often varies under these conditions (Popper et al., 2019). In sum, the testing of fish hearing in small tanks creates a very unnatural acoustic environment with many inherent problems. However, small tanks can be useful when comparing fishes under different test conditions but in the same experimental tank environment, such as before and after exposure to loud sound (noise exposure), testing the hearing capabilities of fishes under different reproductive or hormone exposure conditions, and comparing the hearing abilities of that differ in stages of development (ontogeny).

The testing of fish hearing in small-tank (artificial) environments does not accurately reflect the hearing capabilities of fishes in the natural environment. Instead of taking the fish into the lab, one solution to this problem is to take the lab to the fish. Current work in the Sisneros lab aims to perform auditory evoked experiments on the hearing capabilities of fishes out in the field in more natural acoustic environments.

Keynote Presentation 4

Dr. James H. Miller, Professor and Chair, and Dr. Gopu Potty, Professor, Department of Oceanography, University of Rhode Island, Narragansett, Rhode Island

A Review of Physical Characteristics of Particle Motion, Substrate-borne Vibration, and Interface Waves that are Biologically Relevant

Abstract

Pile driving for offshore wind farm construction produces high-intensity underwater acoustic disturbances that are known to have adverse effects on marine life (Casper et al., 2013). Over the years, many studies have been carried out to understand pile-driving sound field characteristics and sound propagation to address these environmental concerns and assess the impacts. However, most of these studies to date were focused on acoustic pressure waves in the water column (e.g., Reinhall and Dahl, 2011).

Apart from the high acoustic pressure field being generated in the water column by these devices, these disturbances also include water-borne particle disturbances, compressional and shear waves in the sediment, and interface (Scholte) waves along the seabed. These non-pressure wave phenomena are generally known as particle motion (Miller et al., 2016). Some of these wave disturbances could contain high energy that, in cases of land-based impact pile driving, could cause structure damage to nearby buildings. There is also increasing evidence that fishes and marine invertebrates primarily sense sound as a form of particle motion (Popper et al., 2003; Popper and Hawkins, 2018). Benthic-dwelling species are particularly sensitive to and could potentially be impacted by substrate-borne particle motion (Roberts et al., 2016a).

Notwithstanding such relevance of particle motion detection by fish and invertebrates concerning noise impacts from marine engineering activities, these types of vibroacoustic disturbances have been largely overlooked and rarely monitored (Hawkins et al., 2021). A few studies that investigated particle motion from in-water pile driving or offshore wind farm operations are limited to describing the amplitudes and frequency contents of such disturbances at measurement locations (Potty et al., 2020). Results from recent BOEM-funded studies show that, at ranges of 500 m and 1,500 m, particle acceleration levels measured on the seabed were well above the behavioral sensitivity up to a frequency of approximately 300 Hz for Atlantic salmon, plaice, dab, and Atlantic cod (HDR, 2019, 2020). However, in comparison to acoustic pressure wave propagation, there are very few studies on the propagation or modeling of substrate-borne particle motion that can be used to assess the range of impact (e.g., Miller et al., 2016).

This presentation reviews the fundamentals of interface waves—including definitions of Rayleigh, Scholte, and Stoneley waves—and their relation to compressional waves and shear waves. We showed the results from finite element modeling (Miller et al., 2016) using parameters from the work of (Reinhall and Dahl, 2011). Measurements of particle velocities were shown from the Coastal Virginia Offshore Wind with and without bubble screens. This work showed that bubble screens were not effective for vibrations below about 200 Hz.

A participant asked how the pile driving as a source was modeled. Dr. Miller responded that a force was imposed on the top of the pile. One can put a time-varying spike of force pushing the pile down and use a function with amplitude and decay time. That propagates down the pile and creates a Mach cone. It is linear.

Keynote Talk 5

Dr. Louise Roberts, Lecturer (Assistant Professor), University of Liverpool, Liverpool, United Kingdom

A Review of Proper Experimental Design and Lessons Learned from Invertebrate Vibroacoustic Research Under Laboratory Settings

Abstract

Invertebrates make up 90–92% of all marine species and consist of an exceptionally diverse range of phyla differing greatly in terms of life cycles, habitat use, and body morphology. Three types of mechanoreceptors may be used by invertebrates to detect water-borne particle motion and substrate-borne

stimuli (Budelmann, 1992a, 1992b; Popper et al., 2003; Popper and Hawkins, 2018; Roberts and Elliott, 2017). The statocyst and sensory hair cells are shared by a number of invertebrate groups with varied morphology (Budelmann, 1992b; Solé et al., 2023), whereas the chordotonal organs are found in crustaceans (Budelmann, 1992a). Overall, these receptors detect low-frequency, vibroacoustic stimuli, typically < 1,000 Hz.

Given the prevalence of benthic (bottom-dwelling) and demersal (on or near the bottom) aquatic animals, the consideration of water-borne stimuli alone neglects an important piece of the aquatic sensory environment—that of substrate-borne vibrations (Roberts and Elliott, 2017; Roberts and Wickings, 2022).The use of substrate-borne vibration is prevalent in terrestrial animals, with vibrations used for environmental sensing and communication. The study of vibrational use and communication is known as *biotremology*, a sister discipline to bioacoustics (Hill and Wessel, 2016). Insects, as well as all taxa of vertebrates (especially amphibians and mammals), utilize vibrations. Over 200,000 species of insects use vibrations, with many using vibrations as their sole communication method (Hill, 2008; Hill et al., 2019; Hill and Wessel, 2016). There is growing evidence that substrate-borne waves are being sensed and used by aquatic organisms, particularly those living in, on, and around the seabed (Roberts et al., 2016a; Roberts and Rice, 2023; Roberts and Wickings, 2022).

Currently, underwater bioacousticians work separately from terrestrial biotremologists, yet the two fields technically overlap at the surfaces of aquatic substrates, e.g., sediment, artificial substrate, or plant or animal matter. Therefore, we suggested an alignment between underwater bioacoustics and biotremology, particularly regarding terminology and experimental techniques (Roberts and Wessel, 2023). This alignment involves a reset in thinking to consider substrate-borne vibration in aquatic systems, as well as water-borne particle motion and sound (Roberts and Wessel, 2023). A consideration of substrate-borne stimuli involves a refocus, away from the water column and pelagic animals. Currently substrate-borne stimuli are considered in terms of eliciting water-borne sound. However, the main focus, in the presenters' view, should be stimuli *originating* in the substrate and *directly* eliciting substrate-borne waves—and, of course, animals that are predominantly residing in and on substrate for all or part of their life cycle.

As with the fish literature, the literature base in relation to invertebrates and vibroacoustic stimuli is plagued with difficulties and complexities, thereby making comparisons between studies a challenge (e.g., small unquantified tanks; studies measuring pressure rather than particle motion; limited species coverage). The majority of published studies measure noise in terms of pressure alone and do not consider water-borne particle motion or substrate-borne motion. However, the number of published papers that measure the stimuli relevant to invertebrates is growing, as discussed here.

The basic exposure set-up for invertebrate exposure and sensitivity experiments has similar considerations to fish studies, as outlined by Dr Joseph Sisneros. Water-borne particle motion (velocity or acceleration) can be produced via shaker tables or shakers in either one or all three dimensions, or via underwater speakers. Substrate-borne waves can be produced in a number of ways, depending on the scale of the experimental question to be addressed. These methods range from miniature piezoelectric actuators and tactile speakers to electromagnetic shakers and platforms—techniques used extensively by biotremologists (Aimon et al., 2021; Lewis et al., 2001; Roberts et al., 2015, 2016a). Isolation of the experimental tank from external ground vibrations (and air-borne sound) is necessary in laboratory conditions. An added layer of complexity for invertebrates (and indeed some fish) is the need for appropriate amounts of sediment, or particular substrates, for many benthic species.

Short-term behavioral indices can be used to characterize invertebrate thresholds at a whole animal level, tested in a similar manner as in fish studies. Physiological, behavioral, and physical assays have been utilized in broader vibroacoustic exposure studies. Although conditioning of invertebrates (such as crustaceans) is possible, this procedure has not been explored to any degree in sensitivity experiments.

Sets of audiograms, potentially best described as "vibrograms" in this case, are available for some invertebrate groups but are focused around crustaceans and mollusks, and are limited in the number of species which have been covered (e.g., Roberts and Elliott, 2017). Varying techniques have been used to obtain these sensitivity curves. There are anecdotal observations of vibrational responses of other invertebrate phyla, but these have yet to be explored fully. The ideal scenario is for invertebrate sensitivity tests and exposures to be performed in the natural environment, as for fish. New methods should be mindful of recent developments regarding crustaceans (and cephalopods) feeling pain, and the concept of invertebrate "personality" affecting individual level responses.

Breakout Group Discussion

There were three breakout sessions during the workshop, each focusing on one of three experimental settings: (1) small indoor tank, (2) medium outdoor tank, and (3) mesocosm. During each session, participants were assigned to one of four breakout groups. Groups were assigned and divided to focus on biological variables or physical variables of experimental design. To promote collaboration among different disciplines, each group of approximately 10 persons had a mix of biologists, physicists, and engineers, as well as a moderator and a rapporteur.

During each breakout session, two groups discussed biological variables, and two discussed physical variables. To facilitate a discussion focused on the workshop topics, two sets of questions concerning biological and physical variables were provided to the groups. To allow for adequate discussion on each question during the breakout session, each breakout group was given only three questions from a set of four or five, depending on whether they were discussing physical or biological variables:

Physical Variables

1. What are the best or most appropriate acoustic apparatus (e.g., HICI-FT, shaker table, underwater speaker, subwoofer, scaled-down piling hammer) to re-create the vibroacoustic field of interest?
2. What are potential concerns (e.g., standing waves, reflection, low-frequency cutoff, contamination from external vibration) in each of the experimental settings?
3. How can the recreated vibroacoustic field be accurately measured and validated?
4. Can the vibroacoustic issues presented in the above question can be mitigated, and how?

Biological Variables

1. What type of behavioral assays can be used for fishes and invertebrates to determine the effect of underwater sound on their "natural" behaviors?
2. What types of effect (e.g., non-auditory injury, auditory impact, behavioral disturbance, physiological response, masking) studies are best suited under each breakout sessions' experimental setting focus (small tank, medium outdoor tank, mesocosm)?
3. What are the best or most appropriate methods to measure each of the above effects (e.g., AEP or behavioral audiogram for auditory effects, flinch response for certain aquatic inverts behavioral response)?
4. How do we determine detection threshold when AEPs or full behavioral audiograms are not possible, e.g., flinch response in mussels?

5. How much detail of the structure and function of the mechanosensory organs of fishes and aquatic invertebrates must we know to address (or model) biological effects from anthropogenic particle motion and substrate-borne vibration?

At the end of the workshop, the entire group was given a “bonus question” for discussion:

Are there physical principles or specific tools/metrics that can be used to separate substrate-borne vibration from water-borne particle motion?

The breakout discussions produced valuable insights and recommendations to study particle motion and substrate-borne vibration effects on fishes and aquatic invertebrates in each experimental setting. These insights and recommendations are compiled and summarized in Chapter 3 of this report.

Research Methodology to Address Behavioral and Physiological Effects from Anthropogenic Particle Motion and Substrate-Borne Vibration on Fishes and Aquatic Invertebrates

As mentioned in Section 2.4, a very important outcome of the discussion from the break-out groups was the idea that one must first design the research questions and then select the most appropriate experimental approach to answer those questions. Thus, the research question(s) must drive the way they are answered. It was also clear that many of the methods discussed in the breakout groups were broadly applicable and could be used to answer a range of important research questions!

A second critical outcome of the discussions was that research questions and research approaches are likely to change depending on the species of interest, as well as on the age and size of the animals studied. Thus, an experimental approach that works with larval fish may not apply to adults, an experimental approach that works for a sessile species may not be suitable for a mobile species, and an approach that works well for fishes that hear well may not be suitable for species that have poorer hearing.

The participants also recognized that the outcome of the current Workshop built upon several earlier workshops conducted by BOEM and other agencies. Thus, rather than treat the outcome of the current Workshop in vacuo, the participants recognized the importance of learning from and building upon earlier material.

Thus, Section 3.2 starts with a brief, but broad, overview of the research questions developed in earlier workshops to ensure an integration of ideas after discussion (Section 3.1) of basic underwater acoustic concepts.

2.2 An Overview of Underwater Acoustics: Sound Pressure, Particle Motion, and Substrate-Borne Vibration

This section provides an overview of basic underwater acoustic concepts that are relevant to understanding how anthropogenic sound impacts the aquatic environment. It covers not only acoustic pressure waves, something relatively well understood by most marine bioacousticians, but also particle motion (both water-borne and substrate-borne) (Nedelec et al., 2016, 2021; Popper and Hawkins, 2018) and interface waves (e.g., Scholte wave) (Hawkins et al., 2021). The following subsections generally are written without mathematical formalism so they can be easily understood by readers without a physics or engineering background (Hawkins et al., 2021; Nedelec et al., 2016). For an in-depth understanding of physical acoustics and underwater acoustics, readers are referred to several excellent books (e.g., Kinsler et al., 2000; Medwin and Clay, 1997).

2.2.1 Sound as a Mechanical Wave

In a broad sense, *sound* is a mechanical wave traveling through a medium that was created by a physical disturbance by a source. While the term “vibroacoustic” can be used to describe such mechanical waves that comprise sound and vibration, this term has not been widely accepted in the bioacoustics community, particularly for aquatic animals. Therefore, in this paper, we use the terms “sound and substrate-borne vibration.”

A physical disturbance causes nearby particles to oscillate back and forth, thus creating alternating bands of high and low particle densities. In the acoustic far field (where the propagating waves are planar), the region with high particle density also has high acoustic pressure and high positive particle velocity, while the region with low particle density has low acoustic pressure (lower than the ambient pressure) and high negative particle velocity. The high-pressure region is called *compression*, and the low-pressure region is referred to as *rarefaction*. The area between regions of compression and rarefaction has greater positive or negative particle acceleration. While the physical disturbance in the form of a sound or substrate-borne vibration wave is being propagated rapidly outwards from the source into the surrounding medium, the particles oscillate around their locations.

2.2.2 Acoustic Pressure and Particle Motion

The propagation of a sound or substrate-borne vibration wave can be investigated by its acoustic pressure, particle displacement, particle velocity, and particle acceleration. Among all these quantities, the acoustic pressure is *scalar*, meaning that it has amplitude but not direction. In contrast, particle displacement, particle velocity, and particle acceleration are *vector* quantities, meaning that they have amplitude and directions. These vector quantities collectively are called particle motion. To visualize sound pressure and particle motion, see the tutorial video What is Sound[2]?

Acoustic pressure: *Acoustic or sound pressure* is the change of ambient atmospheric pressure (for air-borne sound) or hydrostatic pressure (for underwater sound) due to wave disturbances. The unit of acoustic pressure in the International System of Units (SI) used to describe acoustic pressure is pascal (Pa) or micropascal (µPa).

Since the acoustic pressure changes are rapid oscillation between compression and rarefaction of the particles, the values used to describe the sound pressure levels are peak (p_{pk} or $p_{0\text{-}pk}$), peak-to-peak ($p_{pk\text{-}pk}$), and root-mean-square (rms) (p_{rms}) (see **Figure 1**).

The *peak sound pressure level* is defined as the maximum sound pressure within a waveform. The peak-to-peak pressure level is the difference between the maximum negative and maximum positive. Therefore, an rms sound pressure level is typically computed to describe the “mean” of the sound pressure. The relationship between peak, peak-to-peak, and rms acoustic pressure values of a sinusoidal wave is shown in **Figure 1**.

[2] Discovery of Sound in the Sea, Tutorial: What Is Sound? Available at https://dosits.org/tutorials/science/tutorial-what-is-sound/

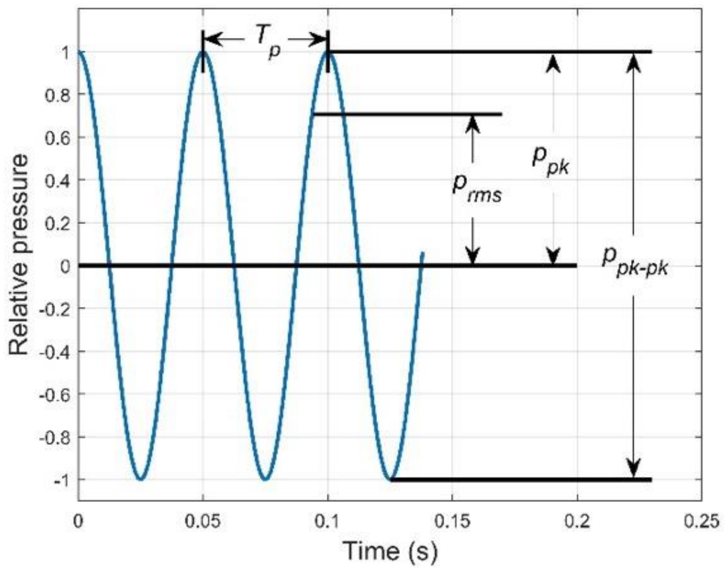

Figure 1. The relationship between peak (P_{pk}), peak-to-peak ($P_{pk\text{-}pk}$), and rms (P_{rms}) acoustic pressure values of a sinusoidal wave
Note: T_p is the period of the sinusoidal wave.

Particle motion: *Particle displacement* is the distance that oscillating particles are displaced from their original position due to mechanical disturbances of the medium. *Particle velocity and particle acceleration* are the velocity and acceleration of the oscillating particles about their origin, respectively. The SI units for particle displacement, particle velocity, and particle acceleration are meter (m), meter per second (m s^{-1}), and meter per second squared (m s^{-2}), respectively.

While particle motion oscillates about their origin, it should be noted that they are not synced. Particle displacement lags particle velocity by 90°, and particle acceleration is 180° out of phase from particle displacement. For example, when particle displacement reaches its maximum positive amplitude, particle acceleration is at its maximum negative value, and particle velocity is zero (**Figure 2**). In the far field away from any boundaries, where the acoustic wave can be approximated as a plane wave, particle velocity (u) can be calculated from acoustic pressure (p_{rms}) using the following equation:

$$u = \frac{p_{rms}}{\rho c} \qquad (1)$$

where ρ is the density of the medium in kg m^{-3}, c is the sound speed in the medium in m s^{-1}, and the product ρc is the characteristic acoustic impedance of the medium in Pa·s m^{-1}.

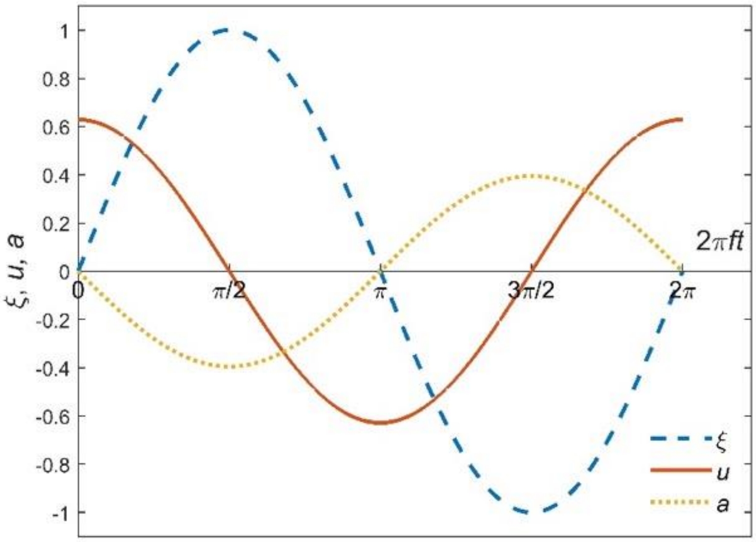

Figure 2. Relationship between particle displacement (*ξ*) (blue line), particle velocity (*u*) (orange), and particle acceleration (*a*) (yellow) of a sinusoidal wave

2.2.3 Sound Levels

The faintest sound pressure a human with excellent hearing can detect at 1kHz has an acoustic intensity of 1 pW m^{-2} (1 picowatt per square meter, or 1×10^{-12} W m^{-2}) (Gelfand, 2016). A F-22A Raptor military jet engine produces acoustic intensities as high as 10 W m^{-2}, which can cause auditory discomfort or injury (Stout et al., 2015). For plane waves, these intensities correspond to air-borne acoustic pressure ranging from 20 μPa to over 64 Pa. To describe sound intensities and pressures with this wide intensity range, it is customary to use a logarithm scale of the ratio of a value to a referenced value. This approach typically compresses the values' range between a single and a couple of hundred digits. These numbers are known as *sound levels*. Sound levels are expressed in decibels (dB) with a notation of the referenced value. For example, the rms sound pressure level (SPL) for a plane wave can be calculated using the following equation:

$$\text{SPL} = 10\log_{10}\left(\frac{p^2/\rho c}{p_{\text{ref}}^2/\rho c}\right) = 20\log_{10}(p/p_{\text{ref}}) \quad (2)$$

where p_{ref} is the referenced SPL, which has values of 20 μPa and 1 μPa for air-borne and underwater sounds, respectively. For example, a blue whale that produces a sound with rms sound pressure of 3 kPa has an SPL of about 190 dB re 1 μPa in water; and the human hearing threshold of 20 μPa at about 1 kHz has an SPL of 0 dB re 20 μPa in air. Note that due to the different reference levels, sound levels in air and water cannot be compared directly.

Likewise, particle motion can also be expressed in various "levels" using dB scales. According to the ISO standards on underwater acoustics (ISO, 2017), the referenced unit for particle displacement level, particle velocity level, and rms particle acceleration level are 1 picometer (pm), 1 nanometer per second (nm s^{-1}), and 1 micrometer per second squared (μm s^{-2}), respectively (see Nedelec et al. (2021) for a detailed discussion).

2.2.4 Sound and Substrate-Borne Vibration Waves in Different Media

Within different media, an *acoustic wave* exhibits different modalities in its propagation. In gas (air) or liquid (water), which are collectively known as fluids, an acoustic wave can only travel parallel to the direction of particle oscillation. Such a wave is called a compressional wave or longitudinal wave. Most mammalian and avian ears only respond to acoustic pressure waves in a fluid (liquid and gas) (Au and Hastings, 2008). While some fish species can also detect acoustic pressure waves, most fishes and all aquatic invertebrates can only detect particle motions in the fluid (Nedelec et al., 2021; Popper et al., 2019; Popper and Hawkins, 2018). Therefore, in a narrow sense, “sound” only refers to acoustic wave that propagates through air or water.

In solids (such as bedrock or animal hard tissues), acoustic waves can travel not only along the direction of particle oscillation but also perpendicular to the direction of the oscillation. Such a wave is called a shear wave or transverse wave. In general, non-compressional waves traveling through a solid substrate are called substrate-borne vibrations. Human activities that generate anthropogenic sound in the water column can also induce acoustic waves in the substrate, either through the direct coupling of the source within the seabed (e.g., in-water pile driving; (Miller et al., 2016) or through the propagation of sound from water into the seabed (e.g., seismic survey; (Hazelwood and Macey, 2016).

Research has shown that many terrestrial invertebrates communicate acoustically through substrate-borne vibration (e.g., Cividini and Montesanto, 2020; Hill et al., 2019; Hill and Wessel, 2016; Pekas et al., 2024; Roberts and Wickings, 2022). In addition, some terrestrial vertebrates also use substrate-borne vibration to communicate and find prey (e.g., Caorsi et al., 2019; Denny et al., 2023; O’Connell-Rodwell et al., 2001; Young, 2003). In comparison, there are very limited studies on fishes’ and aquatic invertebrates’ detection of substrate-borne vibration (e.g., Jézéquel et al., 2022b; Roberts et al., 2015, 2016a; Roberts and Elliott, 2017; Roberts and Laidre, 2019),

Several waves exist at the boundary of two media, rather than in the medium, and are called surface waves (e.g., Aimon et al., 2021; Hawkins et al., 2021; Hazelwood, 2012; Hazelwood and Macey, 2016). For example, the Rayleigh wave at the boundary of a solid substrate and air has an elliptical particle motion, with its major axis perpendicular to the surface and the wave propagation direction. Rayleigh waves, traveling through the ground, are detected by terrestrial animals, such as elephants (O’Connell-Rodwell et al., 2001) and scorpions (Brownell et al., 1979). If the particle motion is oriented with the plane of the surface but perpendicular to the direction of propagation, the wave is called a Love wave. Surface waves can propagate between different types of media. A wave between solid and fluid is called a Scholte wave; a wave between two solids is called a Stoneley wave. A recent BOEM-funded study has shown that Scholte waves generated from impact pile driving during wind farm construction can travel great distances with little attenuation (James H. Miller et al., per. Comm., February 5, 2024). However, how marine animals use Scholte waves for their life function, and how such waves affect these species, has not been studied.

2.3 Major Research Questions Regarding Particle Motion and Substrate-Borne Vibration Effects

Several reports and discussions at this Workshop clearly indicated that researching the potential impact of particle motion and substrate-borne vibration on fishes and aquatic invertebrates is critical. Sound pressure also was recognized as a concern. Every species of fish (including sharks and rays) and, most likely, all aquatic invertebrate species detect particle motion and/or substrate-borne vibration, since their sensory receptors are, basically, accelerometers (Hawkins et al., 2021; Mooney et al., 2010; Nedelec et al., 2016; Popper and Hawkins, 2018). Indeed, fishes detect all these signals with their ears, which are homologous to the ears of terrestrial vertebrates (e.g., Popper et al., 2003; Sand et al., 2023). In addition, a limited number of fishes (and likely no invertebrates) are likely to detect sound pressure because of the presence of a swim bladder or other air chamber located near, or connected to, their ears.

Though the workshop focused on determining the appropriate methods to answer research questions, the participants agreed that developing an approach first required understanding the most important research questions. The participants also recognized that research questions concerning specific species or species groups could best be answered using different methods, which require different experimental environments such as laboratory tanks, larger cages in outdoor environments, or the field.

During the discussions, many participants made the critical point that specific experiment design must be linked to specific research questions, and that the research questions should "drive" the methodological approach used. Furthermore, the participants emphasized that without a given research question, it was difficult to evaluate the usefulness of a specific experimental setting. In addition, the participants also emphasized that an analysis of an experimental setting's pros and cons should take into consideration the species being tested, its size, the level of mobility (e.g., mobile vs. sessile), and the developmental stage (e.g., egg, larvae, adult).

Other synthesis studies and reviews, some written by participants in this workshop, also shed light on the types of research questions that may be relevant to BOEM's interests and needs (Bureau of Ocean Energy Management, 2020). One such synthesis by Hawkins et al. (2015) stemmed from a BOEM-sponsored workshop on the *Effects of Noise on Fish, Fisheries, and Invertebrates in the U.S. Atlantic and Arctic from Energy Industry Sound-Generating Activities* in March 2012 (Normandeau, 2013). Hawkins et al. (2015) comprehensively reviewed the information gaps hindering the understanding of noise effects on fishes and aquatic invertebrates The paper pointed out that, at the time, having a clear conclusion about the nature and level of anthropogenic sound impact on these species was almost impossible. Many issues raised at the *Effects of Noise on Fish* workshop are still open questions, and their answers are vital to understanding the effects of anthropogenic sounds on fishes and aquatic invertebrates. Examples of some open questions include the following: What is the appropriate approach to construct specially designed tanks that can play a role in enabling precisely controlled and measured sound stimuli to be presented to fishes and invertebrates? What are the resolutions of methodological difficulties in presenting measurable sounds to fishes and in determining thresholds to different types of sound?

As the potential impact of particle motion and substrate vibration on fishes and invertebrates became increasingly recognized, more researchers recommended incorporating these disturbances into noise impact analyses (e.g., Hawkins et al., 2021; Hawkins and Popper, 2017; Nedelec et al., 2016; Roberts and Breithaupt, 2016; Roberts and Elliott, 2017). Hawkins and Popper (Hawkins and Popper, 2017) pointed out several important issues, including that (1) many of the impact assessments on fishes and invertebrates had focused on sound pressure exposure instead of particle motion and (2) the metrics employed to describe sounds from different sources had been derived from poorly designed and controlled studies.

Rapid development of offshore renewable energy has increased the need to better understand how underwater noise affects fishes and aquatic invertebrates, many of which are commercially important. In 2020, the New York State Energy Research and Development Authority (NYSERDA) convened a workshop on *Sound and Vibration Effects on Fishes and Aquatic Invertebrates for the State of the Science Workshop on Wildlife and Offshore Wind Energy 2020: Cumulative Impacts* (Popper et al., 2021).

Then, in May 2022, the Pacific Northwest National Laboratory (PNNL) convened a workshop on *Measuring and Reporting Acoustic Particle Motion for Marine Energy Environmental Monitoring*. Discussions from both workshops were compiled into two peer-reviewed papers that focused on the potential impacts of wind farm development (Popper et al., 2022b) and alternative marine energy converters (MECs) (Popper et al., 2023), respectively, on fishes and aquatic invertebrates.

Papers from the NYSERDA and PNNL workshops focused heavily on water-borne particle motion and its potential impact on fishes and aquatic invertebrates. Moreover, both built upon the earlier BOEM-sponsored workshop (Normandeau, 2013) that was later published by Hawkins et al (2015).

The report from the 2023 BOEM Workshop focused on similar questions, but with an emphasis on particle motion and substrate-borne vibration. The additional consideration of substrate-borne vibration was that this topic recently has become a topic of concern for both fishes and invertebrates (Hawkins et al., 2021).

Based on the aforementioned prior studies, this current report identifies 20 major research questions about animal behavioral, physiological, and hearing effects, and pairs them with the most appropriate research methodology and experimental settings. These research questions are grouped into four major series: auditory mechanism (A); hearing effects (H); behavioral effects (B); and physiological effects (P).

It is important to note that these four sections are arbitrary and that they overlap substantially. Indeed, these sections are primarily provided only for the sake of organization and convenience, and the questions and issues posed in each of the sections could, in many cases, easily go into other sections. Thus, while the sections are kept for convenience, it is important to recognize that when questions discussed below are raised, answering them may impact more than one of these sections, and they may answer more than one question.

Auditory mechanism (A): Research questions in this category relate to the anatomy, physiology, and function of the auditory system, as well as sound detection capabilities. Given the large number of fishes (over 34,000 species) and aquatic invertebrates (well over 70,000 species that likely detect sound) and their great diversity of mechanisms to detect sound and vibration (e.g., Popper, 2023; Solé et al., 2023), one of the important questions is whether to characterize species into function hearing groups based on their sound detection mode (e.g., water-borne particle motion, substrate-borne vibration, or acoustic pressure), frequency range, etc., as discussed in Popper et al. (2014).

Hearing effects (H): Research questions in this category relate to the effects of anthropogenic signals on hearing capabilities, including masking, frequency discrimination, intensity discrimination, and localization. While acute impacts, such as permanent or temporary shifts of hearing sensitivity from intense sound exposure, are not the focus of this topic, fishes demonstrate masking in the presence of anthropogenic sound (e.g., Fay, 1974; Hawkins and Chapman, 1975; Tavolga, 1967), suggesting that even low-level sound could impair detection of biologically relevant sounds and lead to potential effects on behavior (also see Simpson et al., 2015b). Each of these capabilities is critical for an animal to be able to detect and use sounds (Fay and Popper, 2000)! Little is known about potential effects of anthropogenic signals on invertebrates (Solé et al., 2023).

Behavioral effects (B): Research questions in this category relate to how animals react behaviorally to sound and vibratory disturbances. These responses can range from altering behavior (e.g., stopping foraging), changes in sound production, and/or avoidance of a certain locales. Some of these behavioral effects are temporary and may disappear when the disturbance ceases, or the animals may become habituated to the stimuli. Other responses may be persistent and thus affect the fitness or survival of the population. It is important to focus on the biologically significant effects that affect the species at a population level (e.g., Slabbekoorn et al., 2010)), although impacts on individual animals may also have importance.

Physiological effects (P): Research questions in this category relate to changes in vital rates (e.g., heart rate, breathing rate) and body chemistry (e.g., stress hormone) of animals when exposed to anthropogenic sounds, and how changes could affect the animals' health and fitness. Like behavioral effects, some of the changes may be temporary while others may be prolonged. Chronic exposure to anthropogenic disturbances in a large habitat could lead to population-level effects (e.g., El-Dairi et al., 2024; Slabbekoorn et al., 2010).

Below, we provide the specific research questions under the four major sets of questions:

Initial Question

What limited number of species should be used in all the studies? (Applicable to all other research questions.) (See Section 3.3, below.)

Auditory Mechanism (A):

A1. How do anatomical features influence fishes' and invertebrates' sound detection through water-borne and substrate-borne particle motion?

A2. What is the hearing bandwidth and sensitivity to particle motion and substrate vibration?

A3. Are there interspecific differences among fishes and among aquatic invertebrates in sound (vibration) detection?

Hearing Effects (H):

H1. What level of masking is associated with various anthropogenic sources?

H2: Do anthropogenic sounds alter the ability of fishes to discriminate between signals and localize sounds?

H3: Is sound detection and/or sound and substrate-borne vibration detection affected in aquatic invertebrates by the presence of maskers?

H4. Do fishes and aquatic invertebrates demonstrate signal discrimination and sound source localization?

H5. Can fishes and aquatic invertebrates detect signals in the presence of maskers?

H6: How do hearing functions differ between species?

H7. Does long-term exposure to particle motion or substrate-borne vibration lead to degradation in hearing sensitivity in fishes and aquatic invertebrates?

Behavioral Effects (B):

B1. Will long-duration anthropogenic sources cause fishes to avoid a sound source area and, therefore, alter their migration routes or the location for biologically important functions?

B2. Will the presence of an anthropogenic source alter the behaviors of animals that normally live in a particular region?

B3. Will the presence of an anthropogenic source result in mobile animals moving from their home territories, thereby subjecting them to potential predation and/or a continuing search for new territory resulting in a loss of fitness?

B4. How do animals react at the onset of an anthropogenic source, and will they, over time, habituate to the source and continue their normal activities in the presence of the stimulus? (Though there still may be physiological effects!)

B5. Will animals be able to alter their calls to compensate for changing noise conditions, as shown in birds and mammals (e.g, Fournet et al., 2018; Parks et al., 2011; Thode et al., 2020))?

B6. Are fishes and invertebrates able to differentiate source characteristics and thus exhibit different behavior when exposed to different sources?

Physiological Effects (P):

P1. Does the presence of a continuous anthropogenic source affect the development of eggs and larvae, and are there effects on their development, growth, and maturation?

P2. Do anthropogenic disturbances cause changes in physiological status, such as vital rates and hormone levels, in fishes and aquatic invertebrates?

P3. At what amplitude levels does sound from anthropogenic sources cause physiological effects? Do such levels need to be considered in terms of sound pressure or particle motion?

2.4 Selection of Species for Particle Motion and Substrate-Borne Vibration Studies

Most Workshop participants and earlier reports cited above recognized that the first vital decision for a research project was selecting focal species. Moreover, the Workshop participants agreed that BOEM's future work should focus on relevant species occurring in offshore renewable energy areas, especially ecologically or commercially important specie.

Getting the most information from a study is necessary because of the sheer number of fishes and invertebrates worldwide. There are over 34,000 extant fish species (Helfman et al., 2009), approximately 17,500 species of decapod crustacean species (Davis et al., 2022), and over 43,000 marine mollusk species (Rosenberg, 2014), plus tens of thousands of other ecologically or economically important aquatic macroinvertebrates that likely detect sound. Moreover, there is extraordinary variation in the structure of the animals' detection systems. They also live in far more diverse environments than any groups of terrestrial vertebrates. As a result, it becomes extraordinarily difficult to extrapolate results across taxa and even, for some taxonomic groups, between closely related animals. This diversity necessitates selecting species that provide the most, and most useful, data.

Thus, a fundamental question is which species should be studied in order to consider the potential impacts of particle motion and substrate-borne vibration on aquatic animals. Clearly, there are far too many species to study within a reasonable period (e.g., 5–10 years), even if those chosen are restricted to species of BOEM concern. Thus, limiting the number of studied species is the best hope to achieve any depth of understanding into the interactions and responses of animals to particle motion, substrate-borne vibration, and sound pressure. Put another way, studying more than a few species will result in superficial information unlikely to provide insights that will develop future impact-mitigation measures. Conversely, studying a small number of agency-relevant species will provide data of considerable value to decisions about anthropogenic sound and aquatic life.

The fact is that BOEM (and other agencies) must prioritize certain study species and also require investigators to focus on these species rather than less-relevant animals or lab-amenable animals that lack the important characteristics (e.g., hearing capabilities, behaviors) present in animals relevant to understanding the potential effects of anthropogenic signals. For example, although studying zebrafish (Popper and Sisneros, 2022), goldfish (Fay and Simmons, 1999), and other lab-oriented species may provide great insight into hearing and other auditory functions in some species, the results are irrelevant to understanding sound impacts on tuna, salmonid, and many other species under BOEM stewardship because these laboratory fishes likely hear and respond to anthropogenic sounds very differently.

Selecting relevant species will not be easy—in fact, it is likely to be quite difficult since the species not only need to be of interest to BOEM but also amenable to answering research questions. For example, Atlantic cod may be highly relevant in terms of understanding the potential impacts of wind farms, but they require very large holding facilities. They are difficult to study in small tanks or lab environments. Similarly, some invertebrates require deep sediment for burrowing, which can be a logistical challenge in laboratory conditions.

Earlier Attempt to Prioritize Fish Species

One project—that was supported by BOEM, the National Science Foundation, the Office of Naval Research, and other agencies—developed interim criteria and guidelines to assess the effects of anthropogenic sounds on fishes (Popper et al., 2014). The international group of experts quickly realized that they could not develop criteria for individual species, or even for a few dozen species. Thus, they recommended dividing fishes into three “hearing groups,” as well as eggs and larvae. The fish groups included fishes without a swim bladder that only detect particle motion, fishes with a swim bladder that primarily detect particle motion, and fishes with evolved mechanisms to detect sound pressure as well as particle motion.

A significant outcome of a Popper et al. report was recommendations of criteria for sound levels that could potentially lead to death and severe injury to fishes as well as to recoverable injury and temporary threshold shift (Popper et al., 2014). However, the panel concluded that they could not recommend criteria for sounds that could impact behavior since (a) there were too few properly done behavioral studies upon which to base reliable conclusions, and (b) most fishes detect particle motion and there were virtually no data on responses of fishes to such a signal, so it was impossible to develop criteria based on the limited responses to sound pressure. At the time of the report, there was no real knowledge of substrate-borne vibration.

Aquatic Invertebrate Species

Compared to fishes, far fewer data are available on how invertebrate species’ react to and are potentially impacted by sound or substrate-borne vibration signals (Hawkins et al., 2015; Roberts and Breithaupt, 2016; Roberts and Elliott, 2017). Moreover, there are far more aquatic invertebrate species than fishes (e.g., Rosenberg, 2014), and it is not always clear which invertebrates detect sound or substrate-borne vibration signals. Finally, whereas many fish species may move away from an anthropogenic source (Krebs et al., 2016), many invertebrate species are sessile or move very little, and thus may be more impacted by anthropogenic signals than fishes.

At the same time, many issues relevant to BOEM and other agencies are the same for invertebrates as they are for fishes. However, selecting and developing experiments for invertebrates is likely far harder for invertebrates since so little is known about their mechanisms and abilities to detect sound or substrate-borne vibration signals (Solé et al., 2023). Many more invertebrate species could potentially be impacted compared to fishes. Finally, while criteria to select fish species have been thought out over the past decade (see Section 3.3.1), no such efforts have been made for invertebrates!

Prioritization of Species

Popper et al. (2021) offered NYSERDA a potential approach to prioritize species of interest that BOEM could follow. (Popper et al., 2021). We have modified and updated this approach below:

- Select species that occur within areas of interest to BOEM (e.g., Friedland et al., 2021).
- Select species where a sufficient number of animals can be obtained for research, and it is possible to hold the species in captivity.
- Focus on species with different hearing capabilities and mechanisms, as done in the 2014 study cited above (Hawkins et al., 2020; Popper et al., 2014).
    - Since little is known about hearing in most fishes (and invertebrates), BOEM could select species based on updated and modified criteria from Popper et al. (Popper et al., 2014) as well as from a detailed and extensive evaluation of what is known about invertebrate hearing. This approach involves an early research focus on the hearing capabilities of potential representative animals, but with a focus on hearing thresholds for particle motion along with sound pressure.
- Select species that represent a range of ecological niches (different habitats, diets, etc.).
- Other relevant bases for species selection include (but are not limited to) one or more of the following:
    - Species of recreational and commercial importance.
    - Species of ecosystem importance.
    - Protected and at-risk species.
- Species potentially vulnerable to offshore wind, including:
    - Species that spawn in or near offshore wind development sites or travel through these areas to reach reproductive sites.
    - Species that may be attracted to structures such as wind farms and other energy-producing devices (Degraer et al., 2020).
    - Species that are expected or known to be sensitive to displacement from offshore wind construction or operations.
    - Species that may be vulnerable to substrate-borne vibration at one or more life stages.

2.5 Recommendations on Experimental Settings for Particle Motion and Substrate-Borne Vibration Studies

2.5.1 A Historical Review of Experimental Settings for Bioacoustics Studies on Fish and Aquatic Invertebrates

Despite major information gaps concerning the auditory capabilities, behavioral uses of sound, and effects of anthropogenic sound on marine animals, bioacoustics research on fishes has a much longer history than that of any other aquatic organisms (reviewed in Sand et al. 2023). Many pioneering studies on fish hearing were done on captive species and performed in relatively small tanks (e.g., von Frisch, 1923; von Frisch and Dijkgraaf, 1935; Poggendorf, 1952); (review by Ladich, 2023; Sand et al., 2023)), where the sound field is very complex (e.g., Parvulescu, 1964; Rogers et al., 2016; Slabbekoorn, 2016). It was recognized in the early days of bioacoustics studies that fishes detect particle motion (e.g., van Bergeijk, 1966; Dijkgraaf, 1960; Tavolga and Wodinsky, 1963; de Vries, 1950). However, researchers continue to use small tanks in fish bioacoustics studies despite the inability, even today, to calibrate the particle motion of the sound in such environments. Indeed, the realization of physical acoustics concerns in small-tank settings (e.g., Gray et al., 2016; Jézéquel et al., 2022a; Okumura et al., 2002b) prompted researchers to rethink their experimental setups and, in particular, the size and overall design of the experimental enclosures.

Over the years, researchers have developed various experimental settings for testing hypotheses and answering research questions. The earliest devices were tubes or tube-like structures developed first by Per Enger (Enger, 1966) and colleagues for fishes where the particle motion could be more accurate and more accurately measured. An alternative approach was to test fishes in open and deep water lochs (in Scotland), where the sound field was "normal" (review in Hawkins and Chapman, 2020).

Fay (1984) developed the most recent device for fishes (Fay, 1984) with a shaker table that moved fish, mimicking stimulation from all directions (Fay, 1984; Lu et al., 1996; Lu and Fay, 1995; Meyer et al., 2012). However, shaker tables are only effective for smaller animals, and the signals are artificial in the sense that they do not include sound pressure along with the movement that "mimics" particle motion.

2.5.2 Experimental Settings Considered

During this Workshop, we focused our discussions on which experimental designs may best fit a research question and species, and around three enclosure sizes that we referred to as experimental settings: (1) small indoor tank, (2) medium outdoor tank, and (3) mesocosm (see Section 2.4).

However, in this Technical Report, we further divide the mesocosm into settings with caged vs. free-ranging animals. Therefore, this report considers the following four experimental settings:

(1) Laboratory tank (lab tank; (e.g., Hubert et al., 2022; Jézéquel et al., 2021; Jimenez et al., 2020; Lara and Vasconcelos, 2021; McCormick et al., 2019; Mooney et al., 2020; Neo et al., 2015; Olivier et al., 2022; Roberts et al., 2016a; Smith et al., 2011; Spiga et al., 2017; Voellmy et al., 2014));
(2) In-ground pond/tank or above-ground tank (outdoor tank; (e.g., Davidson et al., 2009; Jones et al., 2023; Song et al., 2021));
(3) Large water bodies such as a pond, river, lake, or ocean/bay with animals confined in cages (open-water, confined; (e.g., Buscaino et al., 2010; Day et al., 2017, p. 201; Hawkins and Chapman, 2020; Hubert et al., 2020; Jézéquel et al., 2022a, 2023c, 2023a, 2023b; Magnhagen et al., 2017; Sarà et al., 2007)); and
(4) Large water body with free-ranging animals (open-water, free-ranging; (e.g., McQueen et al., 2022, 2023; Puig-Pons et al., 2021; Simpson et al., 2005, 2016b, 2016a; Staaterman et al., 2020)).

Although this approach is subjective, we believe that it is a reasonable way to discuss the experimental settings appropriate for addressing specific research questions and species.

2.5.3 Sound and Substrate-Borne Vibration Field in Different Experimental Settings

Lab Tank: Though studying fish and aquatic invertebrates in small laboratory tanks is practical and economical from the perspective of working with the animals, such tanks have inherent issues concerning the complexity of the sound field, both in terms of acoustic pressure and particle motion (Parvulescu, 1964; Rogers et al., 2016). A lab tank's rigid walls and water surface, as well as their small size, create reverberations at frequencies higher than the tank's resonant frequencies and attenuate frequencies lower than the resonant frequency. This distorts the acoustic signals within the tank (Rogers et al., 2016). For example, frequencies between 20 (or lower) and 1,000 Hz, which are relevant to fishes and aquatic invertebrates, have wavelengths between 1.5 and 75 m. These wavelengths are much longer than the dimension of a typical lab tank. Additionally, at the tank's outer boundaries and surface, the acoustic pressure falls to near zero (i.e., pressure release), but particle velocity does not (Kinsler et al., 2000; Parvulescu, 1964; Rogers et al., 2016). Thus, the complexity of a lab-tank sound field makes controlling and measuring acoustic signals extremely difficult (Akamatsu et al., 2002; Okumura et al., 2002; Gray et al., 2016).

These deficiencies could, hypothetically, be reduced by selecting frequencies different from the tank's minimum resonant frequency and placing a hydrophone within the attenuation distance of the sound source (Akamatsu et al., 2002). However, these modifications would limit the applicability of small-tank experiments and prevent behavioral studies where animals must move around the tank. Another mitigating method uses specialized testing chambers that produce a traveling wave simulating the far-acoustic field in a free field (e.g., Martin and Rogers, 2008; Parvulescu, 1964); also see discussion by Martin, Section 2.3.2 and Appendix B.2). However, these chambers are very bulky, have thick walls, and are costly to build, as discussed in Section 2.3.2; (see also Rogers et al., 2016). To overcome the boundary condition, one technique uses a "tank-in-a-tank" design, where the study animals are placed in a small lab tank which is placed into a much larger tank (e.g., Hubert et al., 2022; Olivier et al., 2022). Even with these mitigation efforts, small-tank settings may suffer since a fish's presence in a tank changes the acoustic field (Rogers et al., 2016).

Outdoor Tank (and In-Ground Ponds): Like lab tanks, acoustic fields in outdoor tanks also suffer from boundary conditions and limited spatial dimension. However, their larger size somewhat reduces low-frequency attenuation compared to lab tanks. Also, our "outdoor tank" categorization includes in-ground ponds, which may have more natural boundaries. Artificial large outdoor tanks can be fitted with sand and/or soil bottoms to simulate natural conditions, which reduces bottom-boundary conditions to a certain degree. Therefore, outdoor above-ground tanks and in-ground ponds may be reliable settings for acoustic experiments focusing on small fish and invertebrates that live in shallow waters (Rogers et al., 2016).

Open-Water: Open-water environments, like the natural environment, have only natural surface and bottom-boundary conditions. The large dimension of open-water settings allows sound to propagate distances without distortion, even if the animals are in cages, as long as the cage material does not interfere with the sound field. The sound field in an open-water environment often closely represents the "real world" where animals live. Therefore, open-water experimental settings are often considered the most appropriate setting for acoustics research on fishes and aquatic invertebrates (Banse et al., 2023; Jézéquel et al., 2022b; Slabbekoorn, 2016). However, the presence of extraneous boats, other animals, etc., can introduce unwanted sound into the experimental setting, thus making control and comparison difficult. For example, elevated background noise could cause auditory masking, thus affecting how the study animal would respond to a biologically relevant sound if the masker was not present.

2.5.4 Appropriate Acoustic Sources and Receivers for Different Experimental Settings

Sound and Substrate-Borne Vibration Sources

As discussed in Section 3.1, all sound and substrate-borne vibration waves contain pressure oscillation and particle motion. Therefore, all sound sources that generate sound pressure waves produce particle motion. Sources that are coupled with the seabed also introduce substrate-borne vibration at and below the sea bottom (Section 3.1.4). However, there is a limited selection of acoustic sources that can be controlled to generate the sound and substrate-borne vibration waves necessary for specific research designs. Off-the-shelf source examples include underwater speakers (often designed for use in swimming pools) and J series transducers produced by the U.S. Navy. Besides these commercially available devices, researchers have custom-designed and built sources to meet their specific needs. In laboratory settings (and small-scale field scenarios), electromagnetic shakers (e.g., Brüel & Kjær (Nærum, Danmark)), tactile speakers, and "bass shaker" type transducers (common in-home cinema systems) can be used to produce vibrational signatures, techniques prevalent within the biotremology research community for reproducing bending, Love, and Rayleigh waves.

Open-water environments may use a real source or scaled-down real source to generate sound and substrate-borne vibration waves that closely represent real-world scenarios (e.g., vessel noise] and pile driving].

Sound and Substrate-Borne Vibration Receivers

Unlike hydrophones, which have been widely accessible for decades to measure underwater sound pressure, commercial instrumentation that measures particle motion has only been available for a much shorter time. The need for particle motion research in the context of underwater anthropogenic sound assessment has produced several papers on particle motion sensors (e.g., Martin et al., 2016; Nedelec et al., 2016, 2021). Readers should see these references for detailed information on the particle-motion sensor's functionality and application. Below, we summarize only the available sensors appropriate for the experimental settings defined during the Workshop and in this report. Martin et al. (Martin et al., 2016) classifies sensors suitable for particle motion measurements into three categories: (1) accelerometer, (2) velocity sensor, and (3) hydrophone array. Accelerometers and velocity sensors are called vector sensors since they measure acoustic particle motion directly. In contrast, hydrophone arrays that derive particle motion from the pressure gradient between hydrophone elements.

Although vector sensors are available in compact forms (e.g., laser velocimeter or accelerometer [Rogers et al., 2016]) for use in lab tanks or outdoor tanks/ponds, hydrophone arrays are usually too large for lab tanks and even outdoor tanks/ponds.

As with many studies in marine bioacoustics, early field research using particle motion sensors focused on marine mammals due to these sensors' capability of bearing and localization (e.g., Greene et al., 2004; Thode et al., 2012; Wilcock, 2012). To research the effects of noise on fishes and aquatic invertebrates, BOEM has funded studies using ocean-bottom seismometers (OBX) and Geosled sources for particle motion and substrate-borne vibration measurements associated with offshore wind constructions (HDR, 2021; 2022). In the laboratory, single and tri-axial accelerometers (such as by Brüel & Kjær) can be used for substrate-borne measurements, as well as single and tri-axial geophones and laser doppler vibrometry. The results indicate that these instruments, initially developed for seismology research, are excellent tools for fish and aquatic invertebrate bioacoustic studies.

Most recently, researchers are exploring the use of distributed acoustic sensing (DAS) technology to detect and monitor undersea biological sounds (e.g., Bouffaut et al., 2022; Wilcock et al., 2023; Guo et al., 2023; Landrø et al., 2020). DAS infers acoustic disturbance in an area using the phase shift of backscattering from a laser pulse being injected into the fiber optic cable. It is most sensitive to frequencies between 0.001 Hz and below 1 kHz and potentially could be a great tool to track soniferous fishes and aquatic invertebrates in a large area.

2.5.5 Advantages and Disadvantages of Different Experimental Settings

Based on the Workshop discussions and other published information, the participants provided examples of the pros and cons of the Workshop's four experimental settings in Table 1 below. The participants recognized that this table is a starting point to discussion of the use of different experimental settings and anticipate future changes.

Table 1. Initial views of pros and cons of four different experimental settings to study fishes and aquatic invertebrates behavioral and physiological effects from particle motion and substrate-borne vibration

Experimental Setting	Pro	Con
Lab Tank	Easy control of environmental parameters such as temperature, salinity, light pH, substrate type, etc. Once the sound field is established and mapped, it is potentially repeatable Perhaps most suitable for physiological experiments that look at blood and other parameters	Very difficult to create a realistic sound and substrate-borne vibration field (e.g., pile driving) Concerns about boundary conditions, standing waves, external vibrations, etc. that make measuring the sound field very difficult Acoustic parameters are different from those experienced when testing species in the wild Unlikely to obtain information on animals' behavior in the wild since the size of the tank severely limits animal behavior Particle motion is impossible to predict or measure and the presence of animals in the tank, especially fishes with a swim bladder, will very likely change the sound field from that measured without the animal. Particle motion will vary substantially over the whole tank in a non-definable manner Tanks may be too small to accommodate animals larger than a moderate size Most tanks studies have used freshwater species that are easier to care for and not the marine species of most interest to BOEM and other agencies Hard to mimic substrate vibrations in such tanks – if nothing else, the depth of the bottom is likely very limited in such tanks

Experimental Setting	Pro	Con
Outdoor Tank (or In-Ground Pond)	Generally easy control of environmental parameters such as temperature, salinity, light, pH, substrate type, etc. Once the sound field is established and mapped, is repeatable If the body of water is much larger than the fish, the presence of fish will likely not alter the sound field too much (though this has never been tested). Suitable for physiological studies	Difficult to create a realistic sound and substrate-borne vibration field (e.g., pile driving, seismic air gun) May be hard to develop a substrate that would support realistic substrate vibrations Depending on frequency, could be concerns about boundary conditions, standing waves, external vibrations, etc. Depending on species, environmental parameters could be different from those experienced by the test species in the wild Tested animals' behavior may not mimic their behavior in the wild
Open-water: Confined	Possible to create a realistic sound and substrate-borne vibration field Few, if any, concerns about boundary conditions, standing waves, etc. Environmental parameters reflect those experienced by the species studied Some species may be able to exhibit behaviors that are seen in the wild	Impossible to control certain environmental parameters (e.g., temperature, salinity, pH, etc.), thus making some repeatability difficult Environmental factors such as weather, presence of other boats, etc. are generally not controllable and could impact the conduct of studies or even results Due to the changing environment, the sound field may vary from day to day The presence of human observers may alter the behavior of animals Some species may still be confined and may not exhibit the same behaviors as in the wild Requires far more support, such as boats, divers, etc., than lab studies
Open-water: Free-ranging	Realistic sound and substrate-borne vibration field Few concerns about boundary conditions, standing waves, etc. Environmental parameters reflect those experienced by the tested species With proper setting, tested animals' behavior can reflect their response in the wild	Impossible to control certain environmental parameters (e.g., temperature, salinity, pH, etc.), thus making repeatability difficult Environmental factors such as weather, presence of other boats, etc. are generally not controllable and could impact the conduct of studies or even results Due to the changing environment, the sound field may vary from day to day May be difficult to observe animals throughout the study range. The presence of human observers may alter the behavior of animals Requires far more support, such as boats, divers, etc., than lab studies

2.5.6 Types of Questions and Species that Can and Cannot be Addressed in Each Experimental Setting

Due to constraints of acoustic properties, sources, and receivers, not all the Workshop experimental settings can address the research issues listed in Section 3.2, and especially not for all species or life stages. For topics related to auditory mechanisms, where understanding the functional anatomy of an animal's sound-detecting organ is crucial, small laboratory tanks tend to be the most appropriate setting.

Researchers are now considering different approaches to investigate fish and aquatic invertebrate mechanosensory organs and hearing mechanisms, particularly for particle motion and substrate-borne vibration detection. One approach proposed adapts the finite element method (FEM), a technique used to investigate low-frequency hearing of baleen whales by examining the biomechanical and acoustic properties of their skulls (Cranford and Krysl, 2015; Tubelli et al., 2012) to fishes (Marcé-Nogué and Liu, 2024). Related approaches analyze fish ear function with microCT, providing a detailed observation of ear function in whole animals and the ear's responses to sound (Maiditsch et al., 2022; Schulz-Mirbach et al., 2019, 2020)

In contrast, studies on the behavioral and physiological effects of anthropogenic sound exposure often require a setting closely resembling the animals' natural environment. Behavioral responses from a confined mobile animal are unlikely to reflect responses in the wild, especially when such behavior involves movement or migration. However, it is possible to conduct such studies on sessile invertebrate species (e.g., Roberts et al., 2016b)). For physiological effects, physical confinement itself could stress the testing animal, making it difficult to relate changes in vital rates or stress hormones to solely acoustic disturbances. Open-water, free-ranging experimental settings using tracking tags and /or video cameras are most appropriate for studying the behavioral or physiological effects of noise on fishes and aquatic invertebrates. While controlled exposure experiments using acoustic tags have been used over the past two decades to study marine mammal behavioral responses to anthropogenic sound (e.g., Southall et al., 2019)), the technique has not been widely adopted for fish or aquatic invertebrate studies (McQueen et al., 2022, 2023; McQueen and Sivle, 2023). A primary challenge is that these tags are often too large to place on medium-sized fishes. Though smaller tags are available and often have the ability to gather a good deal of data, they generally have very short transmission ranges, short battery lives, and need a high density of receivers in order to have the signals detected.

Finally, the effects of low-intensity noise on animal hearing (e.g., auditory masking) potentially could be studied in most experimental settings, as long as the acoustic field can be accurately mapped and measured (e.g., (Buerkle, 1969; Hawkins and Chapman, 2020, 1975).

Table 2 below provides an initial summary of different experimental settings that can best address certain research questions and species groups (fishes vs. aquatic invertebrates). Future discussion and research likely will modify the material in the table.

Table 2. Suggested research questions that can and cannot be addressed under each of the experimental settings for fishes and aquatic invertebrates

Initial Question: What limited number of species should be used in all of the studie**s**? *(Applicable to all other research questions.)*

Research Question	Lab Tank	Outdoor Tank	Open-water: Confined	Open-water: Free-ranging
A1. How do anatomical features influence fishes' and invertebrates' sound detection through water-borne and substrate-borne particle motion?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe
A2. What is the hearing bandwidth and sensitivity to particle motion and substrate vibration?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe
A3. How do fishes and aquatic invertebrates differ in sound (or vibration) detection?	Fishes: Maybe Inverts: Maybe	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes
H1. What level of masking is associated with various anthropogenic sources?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes
H2. Do anthropogenic sounds alter the ability of fishes to discriminate between signals and localize sounds?	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes

Research Question	Lab Tank	Outdoor Tank	Open-water: Confined	Open-water: Free-ranging
H3. Is sound detection and/or sound and substrate-borne vibration detection affected in aquatic invertebrates in the presence of maskers?	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes
H4. Do fishes and aquatic invertebrates demonstrate signal discrimination and sound source localization?	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes
H5. Can fishes and aquatic invertebrates detect signals in the presence of maskers?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe
H6. How do hearing functions differ between species?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Maybe Inverts: Maybe	Fishes: Maybe Inverts: Maybe
H7. Does long-term exposure to particle motion or substrate-borne vibration lead to degradation in hearing sensitivity in fishes and aquatic invertebrates?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes
B1. Will long-duration anthropogenic sources cause fishes to avoid a sound source area and, therefore, alter their migration routes or the location for biologically important functions?	Fishes: NA Inverts: NA	Fishes: NA Inverts: NA	Fishes: No Inverts: No	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA
B2. Will the presence of an anthropogenic source alter the behaviors of animals that normally live in a particular region?	Fishes: NA Inverts: NA	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Yes Inverts: Yes
B3. Will the presence of an anthropogenic source result in animals moving from their home territories, thereby subjecting them to potential predation and/or a continuing search for new territory resulting in a loss of fitness?	Fishes: NA Inverts: NA	Fishes: NA Inverts: NA	Fishes: No Inverts (mobile): No Inverts (sessile): NA	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA
B4. How do animals react at the onset of an anthropogenic source, and will they, over time, habituate to the source and continue their normal activities in the presence of the stimulus?	Fishes: No Inverts (mobile): No Inverts (sessile): Maybe	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Yes Inverts (mobile): Yes Inverts (sessile): Yes
B5. Will animals be able to alter their calls to compensate for changing noise conditions, as shown in birds and mammals?	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA	Fishes: Yes Inverts (mobile): Yes Inverts (sessile): NA
B6. Are fishes and invertebrates able to differentiate source characteristics and thus exhibit different behavior when exposed to different sources?	Fishes: No Inverts (mobile): No Inverts (sessile): NA	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): NA	Fishes: Yes Inverts (mobile): Yes Inverts (sessile): NA
P1. Does the presence of a continuous anthropogenic source affect the development of eggs and larvae, and are there effects on their development, growth, and maturation?	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Maybe Inverts (mobile): Maybe Inverts (sessile): Yes	Fishes: Yes Inverts (mobile): Yes Inverts (sessile): Yes

Research Question	Lab Tank	Outdoor Tank	Open-water: Confined	Open-water: Free-ranging
P2. Do anthropogenic disturbances cause changes in physiological status, such as vital rates and hormone levels, in fishes and aquatic invertebrates?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes
P3. At what amplitude levels does sound from anthropogenic sources cause physiological effects? Do such levels need to be considered in terms of sound pressure or particle motion?	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes	Fishes: Yes Inverts: Yes

Note: A: auditory mechanism; B: behavioral effects; P: physiological effects; H: hearing effects.

2.5.7 Summary and Conclusions

Despite our growing understanding that anthropogenic, underwater sound could adversely impact fishes and aquatic invertebrates, very little is known about sounds' actual and specific effects. Major obstacles to our knowledge include the lack of information on the general sound detection mechanism of fishes and aquatic invertebrates, as well as their auditory, behavioral, and physiological responses to underwater sounds (including particle motion and substrate-borne vibration).

Another significant issue is that, unlike marine mammals, with only about 135 species and substantial similarities in sound detection mechanisms, there are far more species of fishes and even more aquatic invertebrates. Thus, even if limited to the few hundred species of likely concern to BOEM and other agencies, the results of sound impact studies will be immensely difficult to extrapolate between species. These species' sound detection mechanisms, their physiological and physical responses to intense sounds, and their behavioral response to anthropogenic sounds are immensely diverse.

An additional critical issue is that most fish species and all invertebrates do not respond to acoustic pressure but rather to particle motion and substrate-borne vibration (for benthic species) at frequencies < 1 kHz. Most studies to date have focused (erroneously) on responses to sound pressure, and it is clear that major challenges exist in proper experimental design concerning generating, measuring, and validating sound or substrate-borne vibration fields to which these animals are exposed.

The ultimate problem is that the large number of species and their great diversity in size, life history, and distribution make it impossible to have a "one-size-fits-all" approach to experimental design and procedure. The Workshop participants recognized that experimental settings to address sound effects on fishes and aquatic invertebrates should be based on specific research questions and species/taxa.

Finally, though not discussed at the Workshop, it is increasingly clear in the literature on terrestrial anthropogenic sound that animals are often exposed to multiple anthropogenic stimuli (pressures) at the same time, and these stimuli will have synergistic effects on the responses of the animals. Work on multiple anthropogenic pressures are very limited for fishes, particularly when they include sound (and substrate-vibration), and this area needs consideration (e.g., Thomsen and Popper, 2024)). The fact is that a fish may respond to a sound in one way when it is the only anthropogenic pressure, but the response may be very different (or even not take place) when other anthropogenic pressures (e.g., a visual stimulus) are also present.

In conclusion, in comparison to our understanding of anthropogenic noises' effects on marine mammals, there is a great knowledge gap in our understanding of noises' effects on fishes and aquatic invertebrates. However, given that many fish and invertebrate species provide more than 15% of the human population's protein source, and they have critical marine ecological roles (Boyd et al., 2022; Tidwell and

Allan, 2001), more funding for studies on anthropogenic noise effects on fishes and aquatic invertebrates is critically needed.

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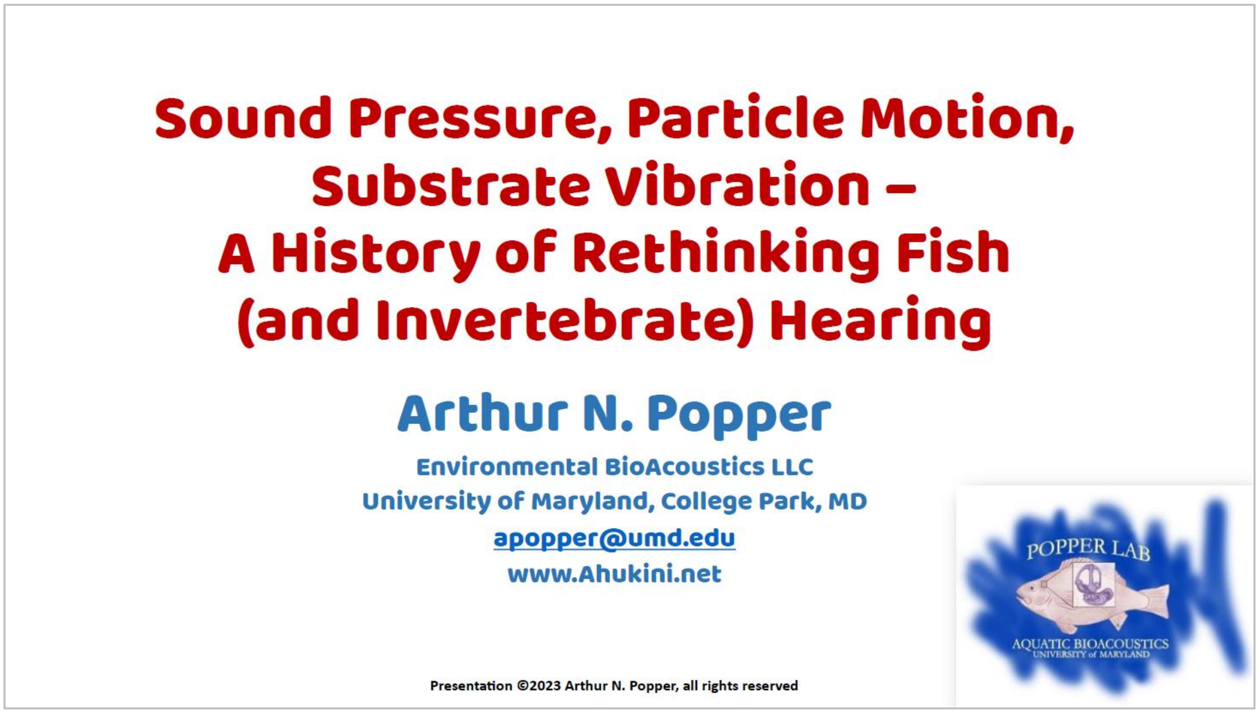
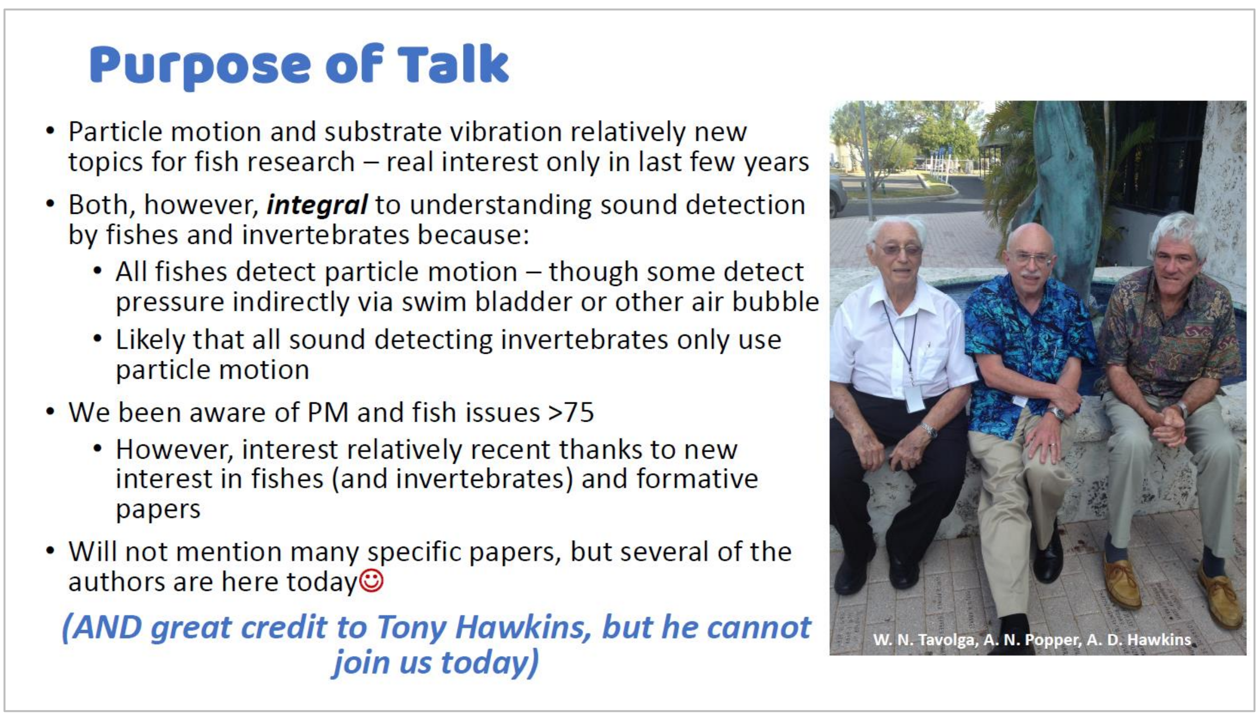
Appendix A: Workshop Participants

Name	Affiliation
Shima Abadi	University of Washington
Megan Ballard	University of Texas Austin, Applied Research Laboratory
Brandon Casper	U.S. Navy
Benjamin Colbert	U.S. Navy, OPNAV N4I
Seth Cones	Woods Hole Oceanographic Institution
Emma Cotter	Pacific Northwest National Laboratory
Sam Denes	Bureau of Ocean Energy Management
Daniel Deng	Pacific Northwest National Laboratory
Shane Guan	Bureau of Ocean Energy Management
Michele Halvorsen	JASCO Applied Sciences
Jade Haug	Bureau of Ocean Energy Management
Joseph Haxel	Pacific Northwest National Laboratory
Hilary Kates Varghese	Bureau of Ocean Energy Management
Katherine Kim	Greeneridge Sciences Inc.
Stan Labak	Bureau of Ocean Energy Management
Hsing-Zen "Mark" Lee	Bureau of Ocean Energy Management
Emily Leedham	University of Aukland, New Zealand
Jill Lewandowski	Bureau of Ocean Energy Management
Brad Lipovsky	University of Washington
David Mann	Loggerhead Instruments
Bruce Martin	JASCO Applied Sciences
James Martin	Georgia Institute of Technology
Morgan Martin	Bureau of Ocean Energy Management
James H. Miller	University of Rhode Island
Aran Mooney	Woods Hole Oceanographic Institution
Sophie Nedelec	University of Exeter, UK
Arthur N. Popper	University of Maryland
Gopu Potty	University of Rhode Island
Craig Radford	University of Aukland, New Zealand
Michael Rasser	Bureau of Ocean Energy Management
Molly Reeve	Bureau of Ocean Energy Management
Louise Roberts	The University of Liverpool, UK
Erica Staaterman	Bureau of Ocean Energy Management
Amy Scholik-Schlomer	National Oceanographic and Atmospheric Administration
Donna Schroeder	Bureau of Ocean Energy Management
Joseph A. Sisneros	University of Washington
Heather Spence	Department of Energy
Kathy Vigness Reposa	INSPIRE Environmental
Christa Woodley	U.S. Army Corps of Engineers
David Zeddies	JASCO Applied Sciences

Appendix B: Keynote Presentation Slides

B-1. Sound Pressure, Particle Motion, Substrate Vibration – A History of Rethinking Fish (and Invertebrate) Hearing (Arthur N. Popper)





Dieter Poggendorf (1952)

"The labyrinthine sensory cell of the ostariophysi are stimulated not only by vibrations in the swim bladder and transmitted to the ...labyrinth, but also by direct stimulation by **water particles** [e.g., particle displacement] vibrating due to the sound field in the water. ...After elimination of the Weberian ossicles (including the swim bladder) these vibrations alone will act on the labyrinth."

Poggendorf, D. (**1952**). "Die absoluten Hörschwellen des Zwergwelses (*Amiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparates der Ostariophysen," Zeitschrift für vergleichende Physiologie **34**, 222-257. 10.1007/bf00298202

Sven Dijkgraaf (1960)

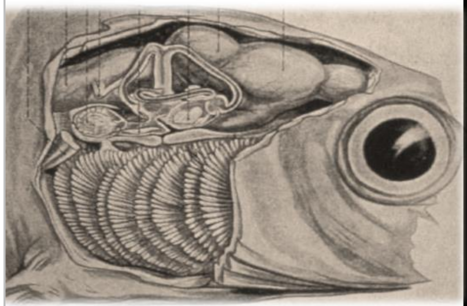
"...The ears of specialist fishes are predominantly pressure receptors (Poggendorf I952). In the normal fishes, on the other hand, the ears presumably act as movement detectors... Since the density of the fish does not differ much from water, the whole animal will vibrate with the surrounding body of water. This may cause the specifically heavier otoliths of sacculus and lagena to stay back at every reversal of movement, thus stimulating the hair cells of the maculae. ... So the stimulation intensity of sound waves when acting on otolith organs might be different according to their direction, and this could possibly offer a basis for sound location."

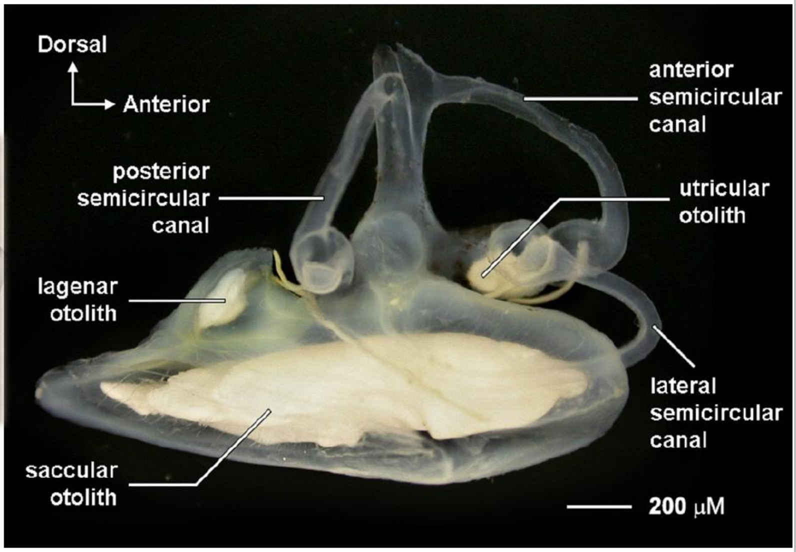
Dijkgraaf, S. (**1960**). "Hearing in bony fishes," Proceedings of the Royal Society B: Biological Sciences **152**, 51-54

A Tad of History!

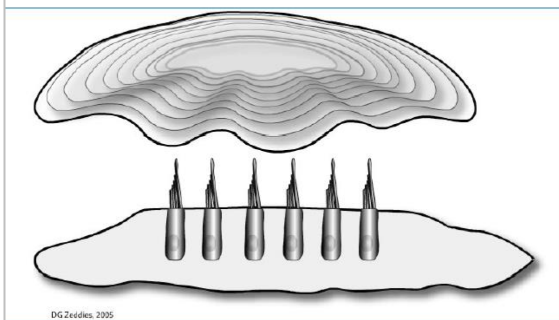
- Tavolga and Wodinsky (1963) did behavioral hearing in nine fish species - Classic paper
  - While they could not measure particle motion, they made it clear that the direct stimulus for the ear was particle motion and not sound pressure (Tavolga, W. N., and Wodinsky, J. (**1963**). "Auditory capacities in fishes: pure tone thresholds in nine species of marine teleosts.," Bulletin of the American Museum of Natural History **126**, 177-240.)
- Willem van Bergeijk (1966) argued that the vertebrate ear (in fishes!) evolved to respond to particle motion
  - He pointed out that "...thanks to the pressure-to-displacement transformer-action of the swim bladder, the inner ear is now sensitive to pressure waves. It *hears."* (p.372) (van Bergeijk, W. (**1966**). "Evolution of the Sense of Hearing in Vertebrates," American Zoologist **6**, 371-377.)

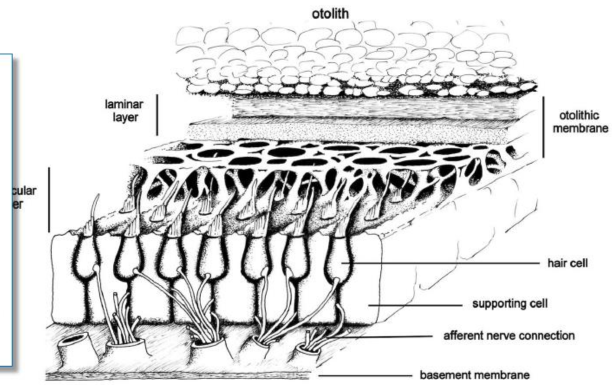
Fish Ears Respond Only to Particle Motion!





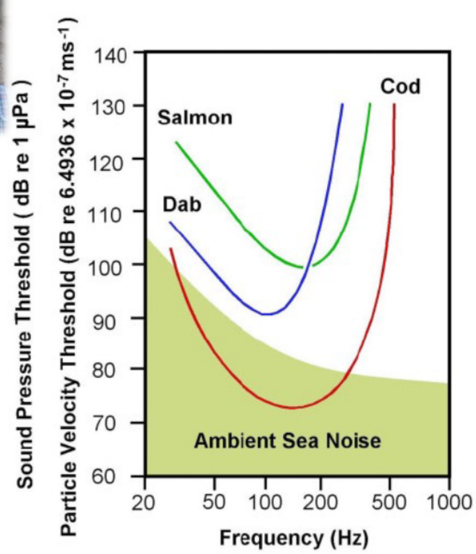
Sensory Epithelium and How Stimulated





First Studies Showing Particle Motion Involvement in Hearing

- Tony Hawkins & Colin Chapman
- Cod detects sound pressure
- Dab (flatfish) and salmon only respond to particle motion
- Hawkins did most of the very few studies that looked at particle motion
- Did in Loch Torriden (mid-1970s)



Most Past Studies Focused on Sound Pressure

- Even as late as 2015 (and sometimes now!), many workers did not acknowledge particle motion or had no sense of its importance!
- Problems in asking questions in terms of PM
  - Hard to measure – devices very large, expensive, etc.
  - Tank acoustics very complex
    - PM in tanks very complex (Parvulescu 1964, 1967)
    - PM very hard to measure accurately in tanks
  - Moreover,
    - fish in tank totally changes any measures may have made
    - PM is 3D and must measure in all directions
- Thus, while "hearing" described in terms of sound pressure, what do the data really mean if the fish is detecting particle motion?
- *In fact, still know VERY little about fishes and detection and use of particle motion; have few data on PM thresholds!*

Substrate Vibration

- Interest in substate vibration even more recent
- First time many of us heard about it was in 2008 in Nyborg – topic raised by Dick Hazelwood
- Of great importance to animals in, on, and just above substrate
- Other than some invertebrate work (Lucille Roberts!) know very little
- BUT clear that we need to know more and that it likely to have great impact on fishes and invertebrates

What is Needed to Make Progress? - 1

- Particle motion "hearing" by fishes (and invertebrates):
  - Focus on particle motion as the stimulus, and present data in terms of particle motion
  - Understand behavior and behavioral responses of fishes in terms of PM, including sound levels that elicit responses from fish
- Experiments in facilities where can accurately determine PM – which means not in fish tanks!
- Acoustics
  - Need to understand hearing sensitivity in terms of PM as well as pressure
  - Need to understand when and where PM can be estimated in terms of sound pressure – trouble is, many environments in which fishes live are too shallow to do this!

What is Needed to Make Progress? - 2

- Studies on species of importance to major issues such as pile driving, seismic air guns, wind farms, etc.
  - AND not on zebrafish, goldfish, or other "lab species"
  - Trouble is, species of importance are often very hard to work with since cannot easily be done in a "small" enclosure or in a lab
  - Need to drop from 34,000 fish species to very few that give good representation of diversity in animals
- Need small and easy to use devices to measure PM so regulators and others can use them and apply the data to real-world situations
- Need some basic designs for tanks and facilities that would enable precise control of the acoustic signal in terms of pressure and PM

- Need similar approaches for investigation of substrate vibration
- Much more focus on all these issues for invertebrates

Caveats

- Substrate vibrations may not only be detected by an ear – possibly other receptor systems related to touch, lateral line, etc.
  - How do we account for these systems in thinking about substrate vibration?
  - Even if the ear does not respond to substrate vibration, we may be impacting animals if they detect with their touch or somatosensory systems!
- Lateral line also detects particle motion signals and perhaps take that into account
- Thus, in considering these stimuli, it is not only the ear to think about!

Take Home

- Need to:
  - Get funding for fish and invertebrate research at levels now only devoted to marine mammals
  - *(When is the last time you ate a marine mammal vs. when you last ate a salmon or lobster or cod or Maryland blue crab?)*
  - Develop a common methodological approaches for important questions about particle motion detection by fishes and invertebrates to get comparable data from different labs
  - Ask similar questions across investigators so data can be validly compared to answer most important questions
  - Selected species that broaden our overall understanding of the issues of concern – which means no goldfish, no zebrafish, no perch, etc.
  - Collaborate across labs and individuals so we work together to most effectively and efficiently get the data needed

Finally:

When asking questions about any anthropogenic sounds and potential impacts on animals, we must always think about issues from the perspective of the animal, and not the prospective of the sound producing or mitigation devices!!!!

Popper, A. N., Hawkins, A. D., and Thomsen, F. (**2020**). "Taking the animals' perspective regarding underwater anthropogenic sound," Trends in Ecology and Evolution **35**, 787-794. https://doi.org/10.1016/j.tree.2020.05.002

A Few Citations

- Hawkins, A. D., Hazelwood, R. A., Popper, A. N., and Macey, P. C. (**2021**). "Substrate vibrations and their potential effects upon fishes Nedelec, S. L., et al. (**2016**). "Particle motion: The missing link in underwater acoustic ecology," Methods in Ecology and Evolution **7**, 836-842.
- Popper, A. N., and Hawkins, A. D. (**2018**). "The importance of particle motion to fishes and invertebrates," The Journal of the Acoustical Society of America **143**, 470-486.
- Popper, A. N., Hawkins, A. D., and Thomsen, F. (**2020**). "Taking the animals' perspective regarding underwater anthropogenic sound," Trends in Ecology and Evolution **35**, 787-794.
- Popper, A. N., et al.(**2022**). "Offshore wind energy development: Research priorities for sound and vibration effects on fishes and aquatic invertebrates," The Journal of the Acoustical Society of America **151**, 205-215.
- Roberts, L., and Howard, D. R. (**2022**). "Substrate-borne vibrational noise in the anthropocene: From land to sea," in *Biotremology: Physiology, Ecology, and Evolution*, edited by P. S. M. Hill et al. (Springer International Publishing, Cham), pp. 123-155.

B-2. A Review of Vibroacoustic Wave Generation Devices that Are Suitable for Fish and Invertebrate Acoustic Studies in Laboratory Settings (James Martin)

Vibroacoustic Wave Generation Devices

A review of vibroacoustic wave generation devices that are suitable to fishes and invertebrates acoustic studies in laboratory settings

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Georgia Institute of Technology
Woodruff School of Mechanical Engineering
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* Often mistaken for a technician
Sometimes mistaken for a physicist
Never mistaken for a biologist

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Vibroacoustic Wave Generation Devices

My History with biological effects of underwater sound

~**1993:** Concerns over Low Frequency Active (LFA) Naval SONARs
Effects on marine mammals and human divers (physical injuries)
Testing on rodents, pigs, and humans in small(ish) tanks
Construction of the Ratabrator

~**2006:** Concerns over pile driving (physical injury)
Effects on fish, testing with fish
Construction of the Fishabrator AKA HICI-FT ("hissyfit")

~**2017:** Concerns over seismic exploration signals
Effects on commercially important fish
In situ testing on fish

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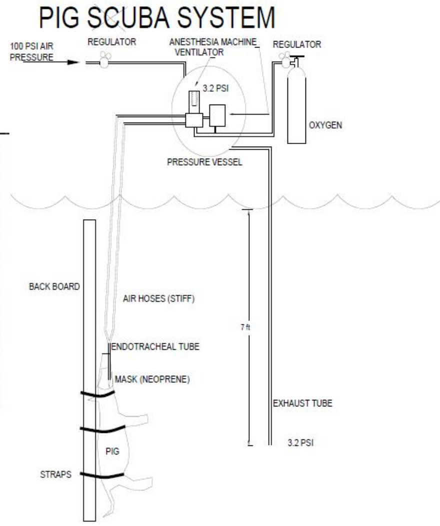
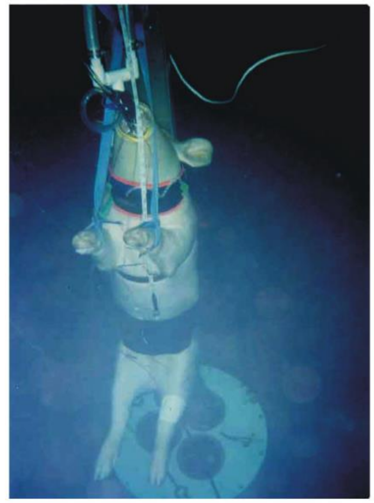
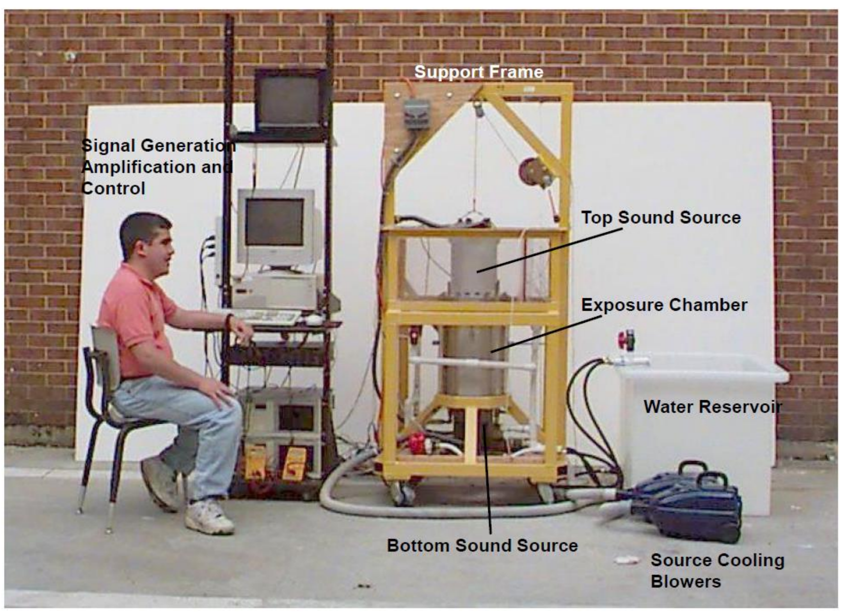
Vibroacoustic Wave Generation Devices

LFS-1 Project (1994-5) Lung Resonance Measurements on Diving Pigs

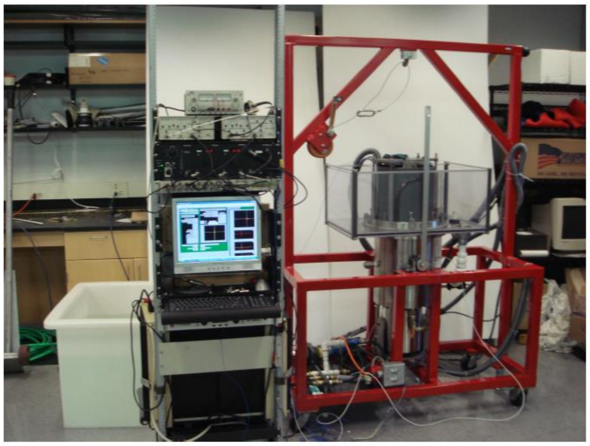


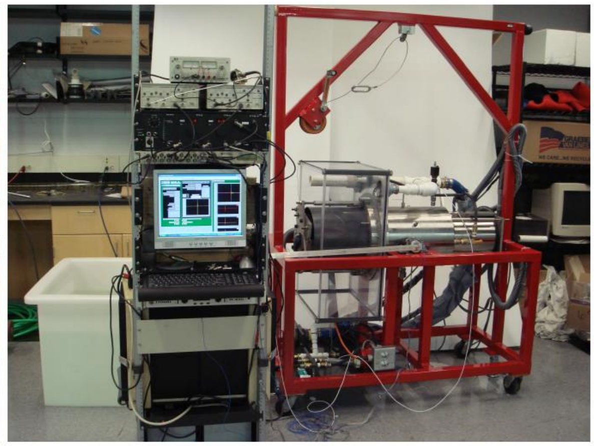


Vibroacoustic Wave Generation Devices



Vibroacoustic Wave Generation Devices





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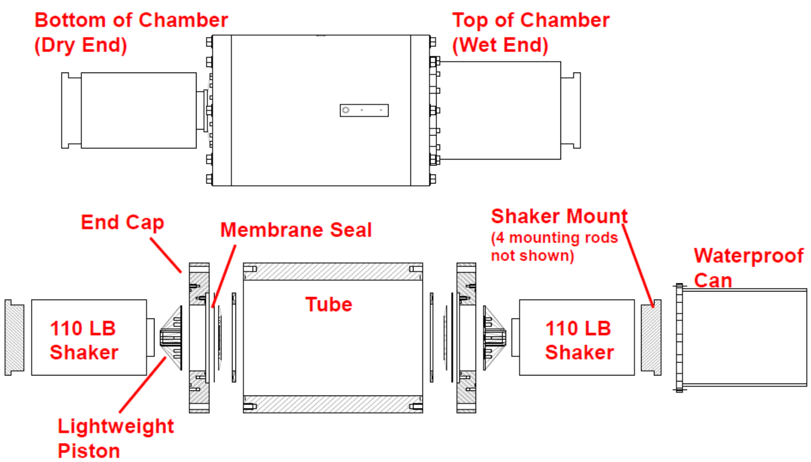
Vibroacoustic Wave Generation Devices

Details of Animal Exposure Chamber



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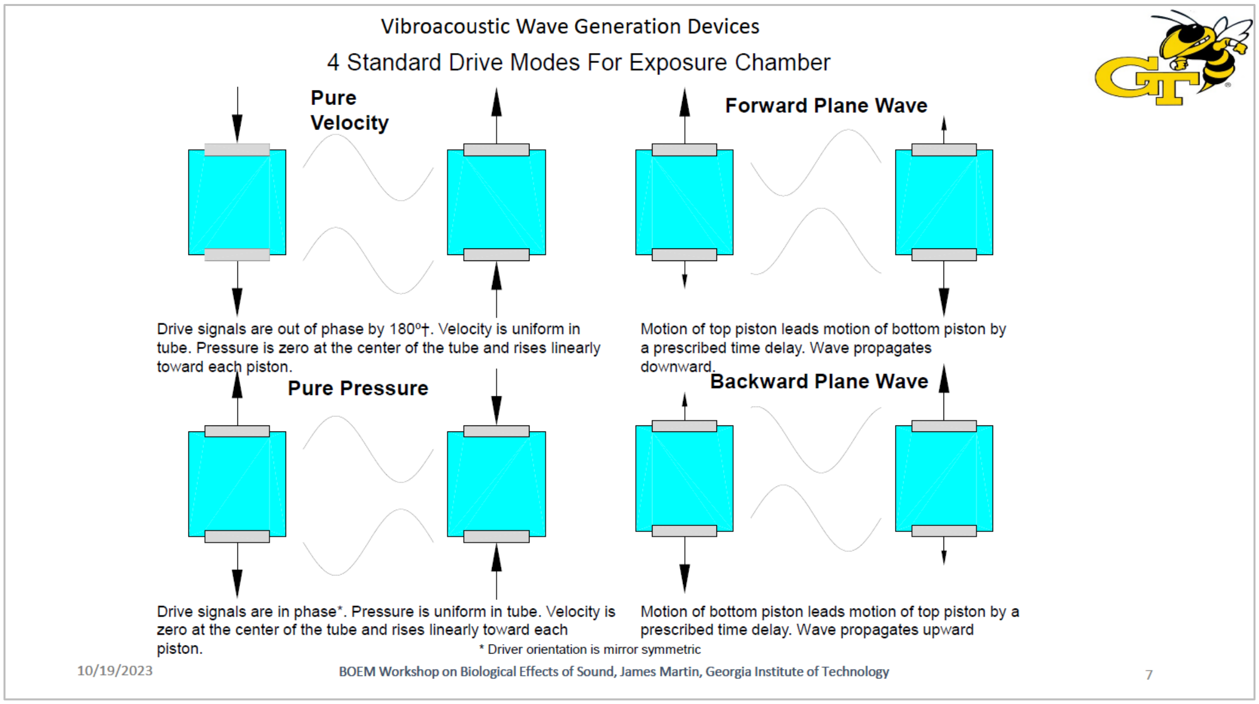
Vibroacoustic Wave Generation Devices
4 Standard Drive Modes For Exposure Chamber
Pure Velocity
Forward Plane Wave
Drive signals are out of phase by 180°†. Velocity is uniform in tube. Pressure is zero at the center of the tube and rises linearly toward each piston.
Motion of top piston leads motion of bottom piston by a prescribed time delay. Wave propagates downward.
Pure Pressure
Backward Plane Wave
Drive signals are in phase*. Pressure is uniform in tube. Velocity is zero at the center of the tube and rises linearly toward each piston.
Motion of bottom piston leads motion of top piston by a prescribed time delay. Wave propagates upward
* Driver orientation is mirror symmetric
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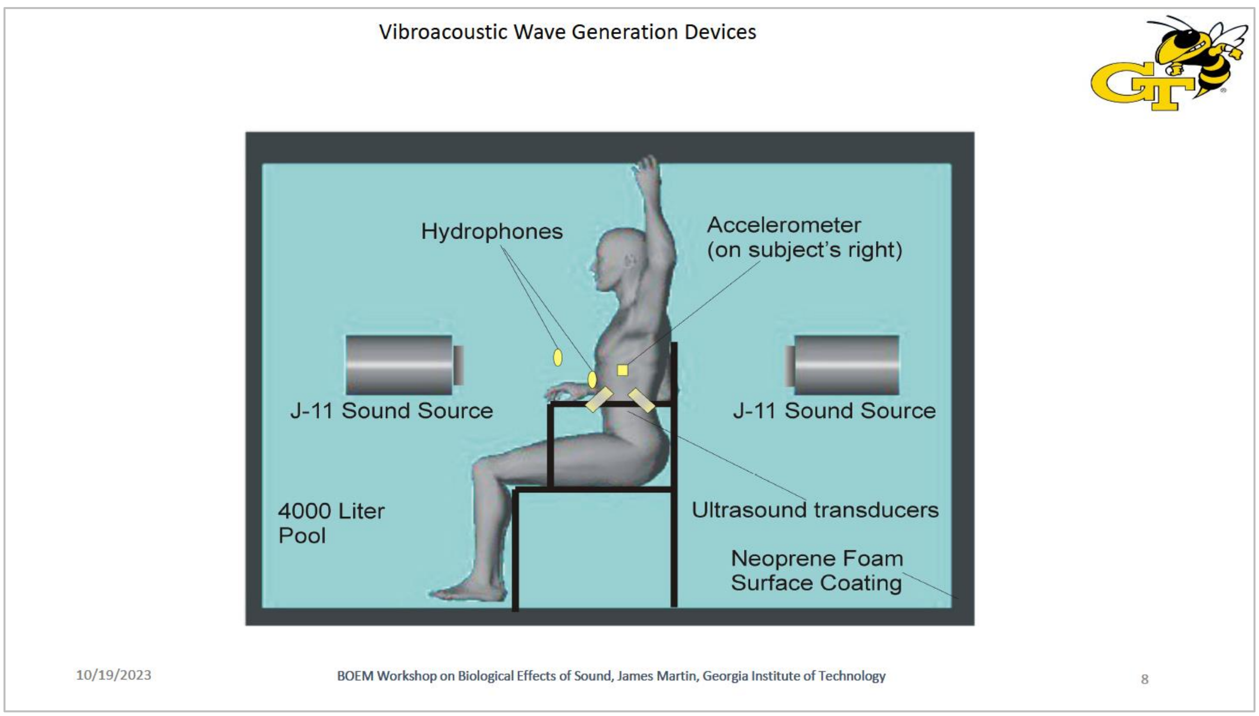
Vibroacoustic Wave Generation Devices
Hydrophones
Accelerometer
(on subject's right)
J-11 Sound Source
J-11 Sound Source
4000 Liter
Pool
Ultrasound transducers
Neoprene Foam
Surface Coating
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Vibroacoustic Wave Generation Devices

Sound Exposure System Requirements:

- Sufficient dynamic range:
  - Signal must be large enough to produce desired effect
  - Signal must dominate “ambient” noise
- Sufficient frequency range
- Appropriate incident impedance:
  - Plane wave?
  - Pure pressure or velocity?
  - Incident direction?
- Measurable incident signal:
  - This is harder than it sounds
- Appropriate time-domain signal:
  - Linearity?
- Nonintrusive WRT animal’s response:
  - Behavioral response
  - Physical response

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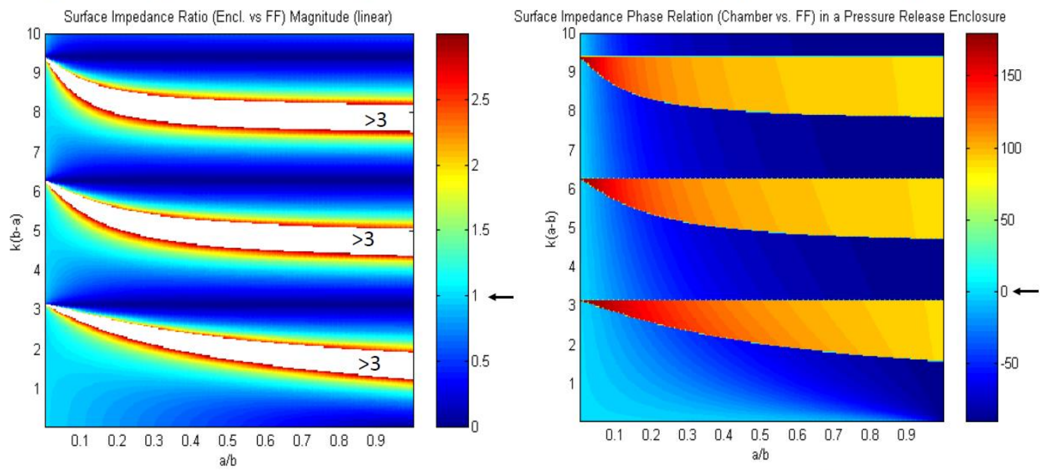
Vibroacoustic Wave Generation Devices

The exposure system is made up of both the sound source(s) and the body of water.



Sometimes, small tanks are too small. Sometimes, small tanks are too big.

(JASA 117(4) pp 2291-2300, 2005)

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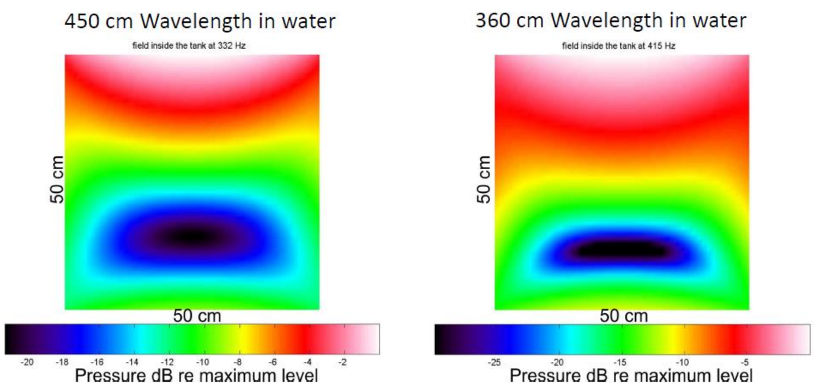
Vibroacoustic Wave Generation Devices

Acoustically small tanks do not guarantee field uniformity

source location

source location



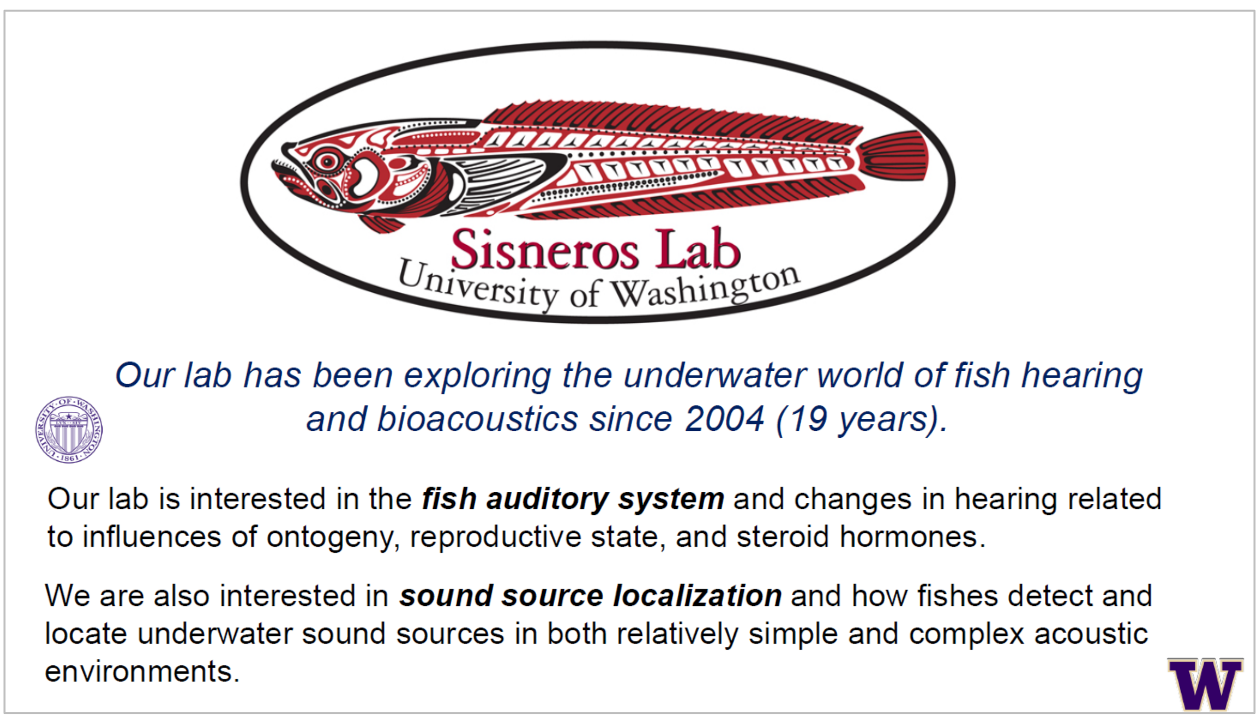
Vibroacoustic Wave Generation Devices

Conclusion: We will probably want to use electrodynamic transducers (at least 2) with permanent field magnets

- Controllable signals
- Linearity
- Large volume displacements (i.e. high source levels at low-frequency)
- Compliant suspensions

Some examples: USRD type J-9, J-11, J-13, J-15, pool speakers, shakers

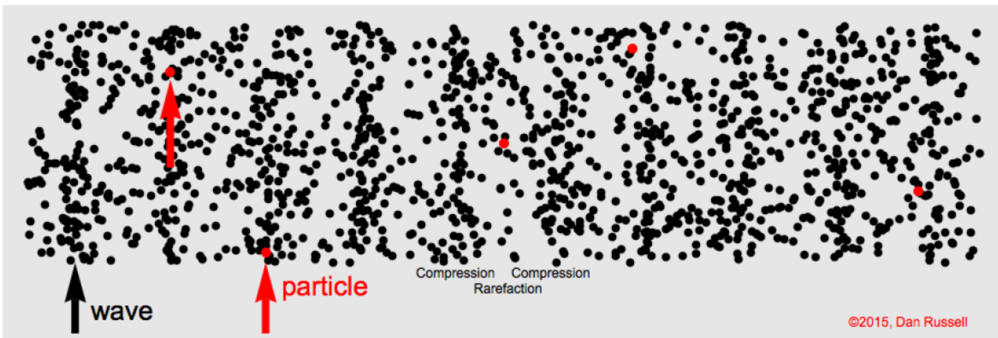
B-3. A Review of Proper Experimental Design and Lessons Learned from Fish Vibroacoustic Research Under Laboratory Settings (Joseph A. Sisneros)



When Designing the Proper Fish Vibroacoustic Expt Under Laboratory Settings,

One of first questions to ask is: ***what is the appropriate stimulus??***

***Sound** is a mechanical disturbance that propagates as a longitudinal wave in air and water.*

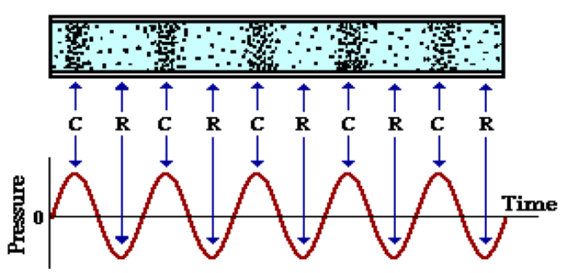


Description of Sound

Sound can be described in terms of both ***pressure*** & ***particle motion***

Pressure = *fluctuation of the force per unit area* (pressure) above and below the ambient level.

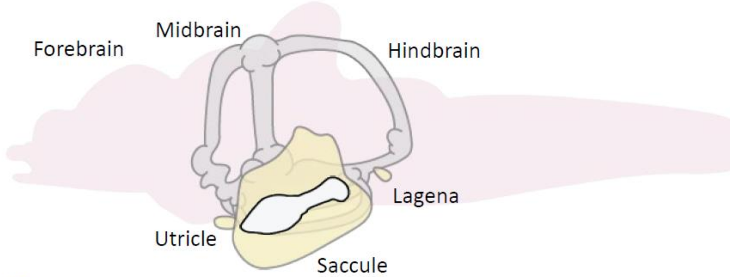
Particle motion = *the movement of fluid particles* caused by the fluctuating forces of pressure.



What acoustic cue(s) is the fish ear is designed to detect???

What is the appropriate stimulus for a given set of expts?

How Do Fish Hear?



Hawaiian sergeant fish
(Abudefduf abdominalis)
Maruska & Tricas 2009

The Fish Inner Ear

consists of:

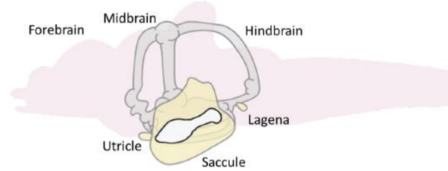
- **three semicircular canals** (ant., pos. & hor.)
- **utricle** ∗ (otolithic end organ)

} *major vestibular parts of the ear*

- **saccule** (otolithic end organ)
- **lagena** (otolithic end organ)

} *major auditory parts of the ear*

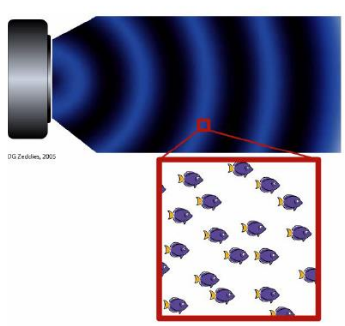
How Do Fish Hear?

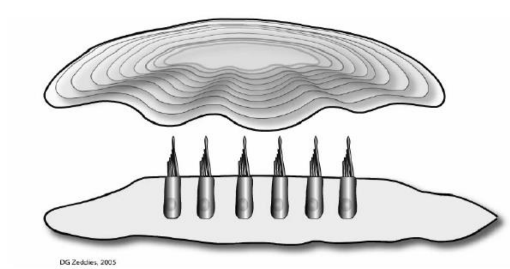


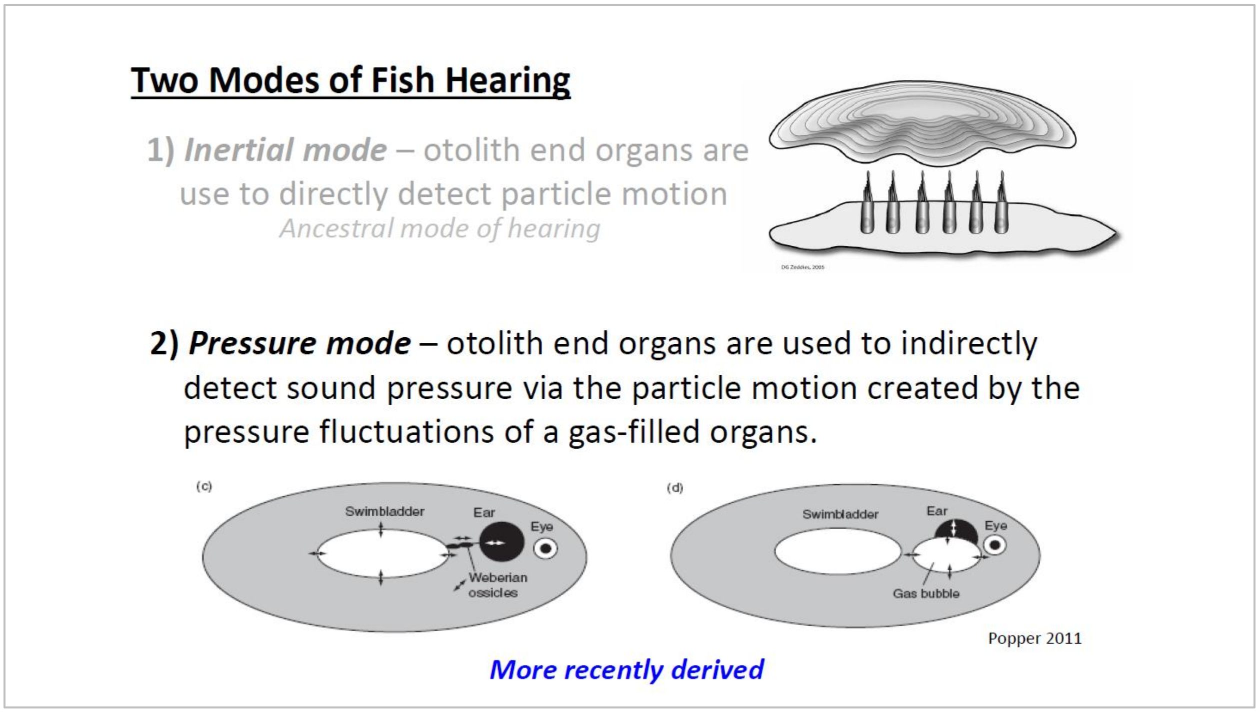
Two Modes of Fish Hearing

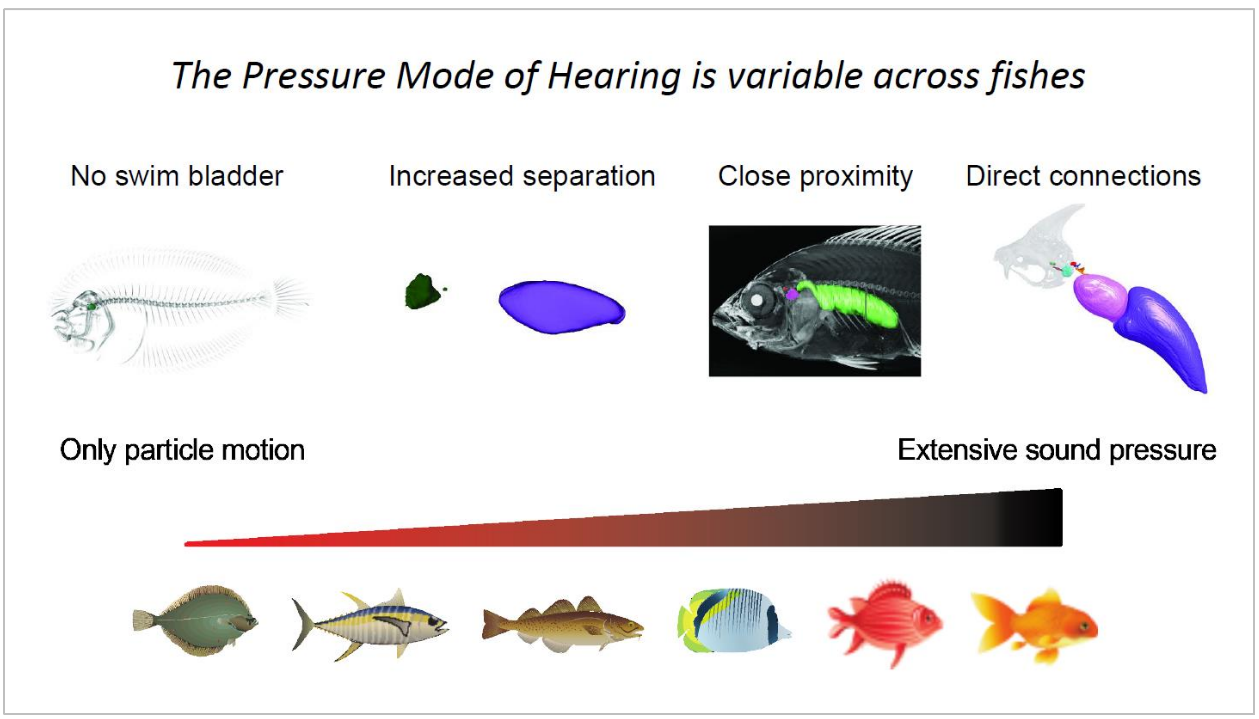
1) ***Inertial mode*** – otolith end organs are use to directly detect particle motion

Ancestral mode of hearing





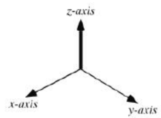

Two Modes of Fish Hearing
1) Inertial mode – otolith end organs are use to directly detect particle motion
Ancestral mode of hearing
2) Pressure mode – otolith end organs are used to indirectly detect sound pressure via the particle motion created by the pressure fluctuations of a gas-filled organs.
(c)
Swimbladder
Ear
Eye
Weberian ossicles
(d)
Swimbladder
Ear
Eye
Gas bubble
Popper 2011
More recently derived

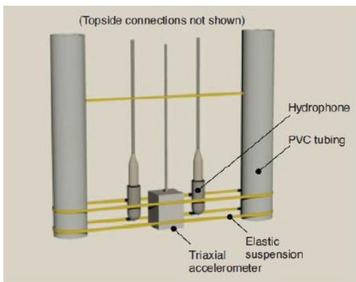

The Pressure Mode of Hearing is variable across fishes
No swim bladder
Increased separation
Close proximity
Direct connections
Only particle motion
Extensive sound pressure

In cases, where fishes do not have swim bladders (e.g., sharks, flatfish, etc), the ***appropriate stimulus to characterize in terms of hearing is***:
particle motion / particle velocity / acceleration

Stimulus Measurement:

Generally, measured in 3 axes because particle motion is a vector quantity





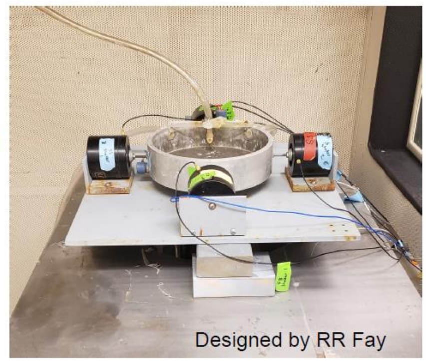
triaxial accelerometer Zeddies et al. (2012)

Stimulus Production:

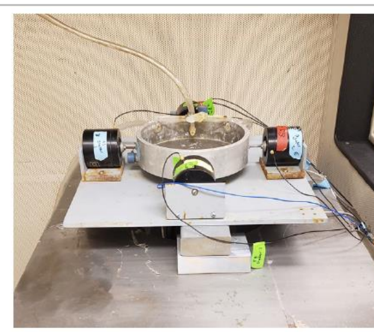
Shaker Table System

-produces particle motion in 3 dimensions

- originally designed by Richard Fay



3D- Shaker Table System



Pros:

- can be used to characterize directional sensitivity to particle motion (primarily **auditory** physiology)
- can test frequencies lower ($\leq$ 65Hz) than that of underwater speakers
- used in combination with a sound attenuation booth and air table can yield good auditory threshold measures

Cons:

- can be used to test frequency sensitivity ***but testable frequencies are limited***
- size of fish to be tested is limited (has to be able to fit in dish)
- data acquisition system is date (need to be updated)

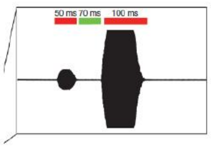
1D-Shaker Table System

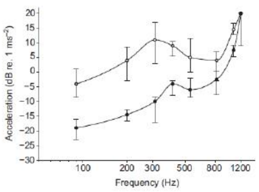
- used to test “hearing” in larval zebrafish with particle motion stimulus

Larval zebrafish without Weberian apparatus (not pressure sensitive!)

Adult zebrafish with SB & Weberian apparatus (pressure sensitive!)

can utilize the **acoustic startle response**

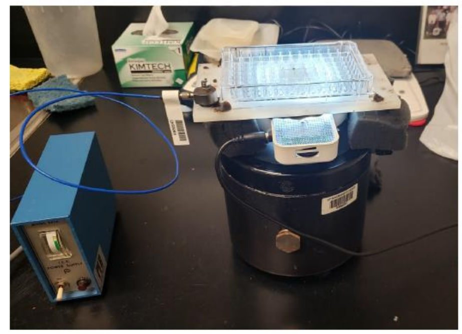




Prepulse inhibition paradigm to test “hearing”

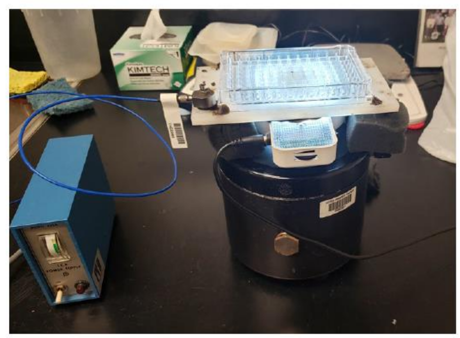
PPI thresholds are more sensitive than startle thresholds

Bhandiwad et al. (2013)



1D-Shaker Table System

- for use in testing “hearing” thresholds in larval fish with a particle motion stimulus



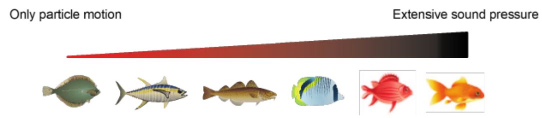
Pros:

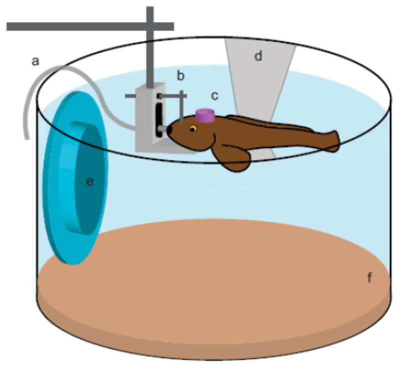
- very sensitive behavioral measure to test hearing that utilized innate startle response
- does not require conditioning or training
- does not require “sacrificing” animals after the expt

Cons:

- only works on larval zebrafish
- need to have access to many individuals
- habituation to startle my vary by species (especially in adult zebrafish)

In cases, where ***fish are pressure sensitive*** researchers have used speaker or sound projections in small tanks (**not ideal**)

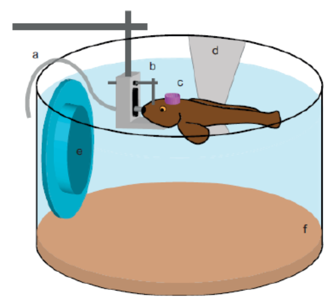




Hearing studies that examine pressure sensitive fish
- both *sound pressure & particle motion* sensitivities should be measured.

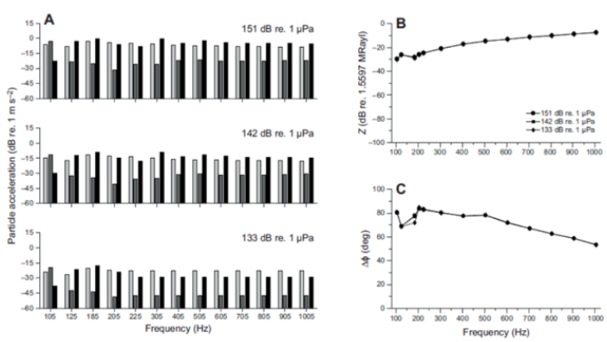
What are the **pros** vs **cons**??

Many Cons:



The sound field is very messy in small tanks due to many factors:

- acoustic resonances and reflections in the tank
- *relationship between sound pressure & particle motion changes close to tank walls and water surface which results in changes in acoustic impedance at various points in the tank*
  (every tank is different which makes it difficult to predict or model)

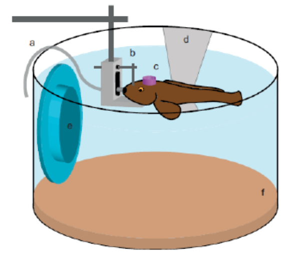


Rogers and Sisneros (2020)

As suggested by Popper et al. (2019) that the acoustic impedance (ratio of p/v for a given stimulus freq) should be measured at various positions in the tank & compared to that of seawater in a free-field environment.

May allow for more meaningful comparisons of different experimental tank acoustic environments in other physiology & behavior expts.

Many Cons:



The sound field is very messy in the tank due to many factors:

- acoustic resonances and reflections in the tank

- *relationship between sound pressure & particle motion changes close to tank walls and water surface which results in changes in acoustic impedance at various points in the tank*
(every tank is different which makes it difficult to predict or model)

- wavelengths of freqs tested are often bigger than the tank and speed of sound often varies under these conditions (***In sum, creates a very unnatural acoustic environment***)

Pros:

Can be useful when comparing fish under different test conditions:

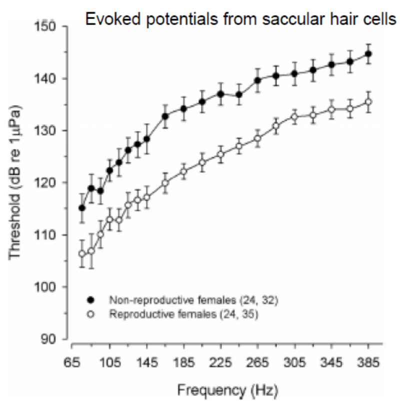
- before and after exposure to louds sound (noise exposure)
- fish under different reproductive or hormone exposure conditions
- fish that differ in stages of development (ontogeny)

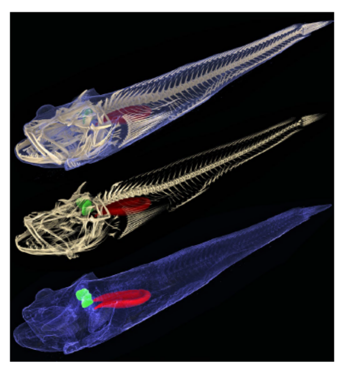
Pros:

Can be useful when comparing fish under different test conditions:

- before and after exposure to louds sound (noise exposure)
- fish under different reproductive states or hormone exposure conditions
- fish that differ in stages of development (ontogeny)

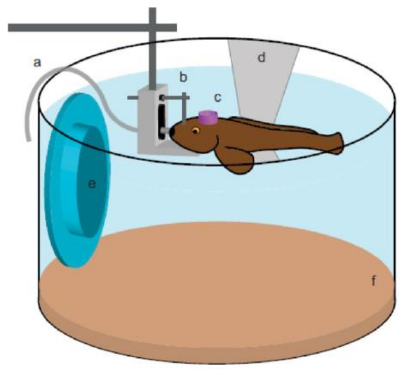
Plainfin midshipman
(*Porichthys notatus*)





Question: ***In small tank (artificial) environments, are we getting a true measure of the fish's auditory (or hearing) sensitivity compare to that in the natural environment?***

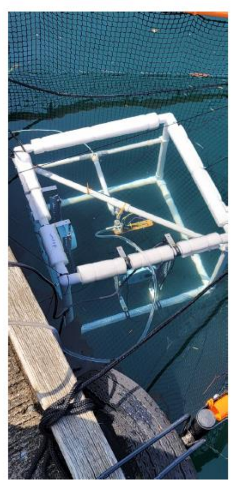
NO!

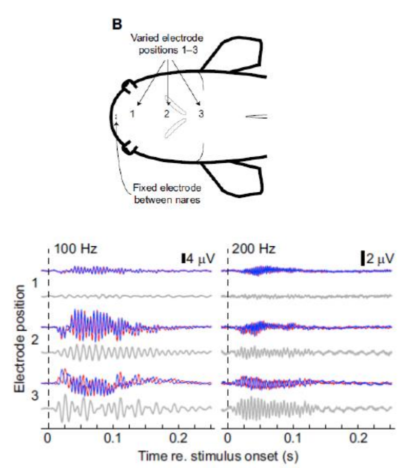


Instead of taking the fish into the lab, we are taking the lab to the fish!

Performing AEP expts out in the field in more natural acoustic environments

Friday Harbor Labs, WA





Thank You! **BOEM organizers**

Sisneros Lab
University of Washington

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Jim Martin
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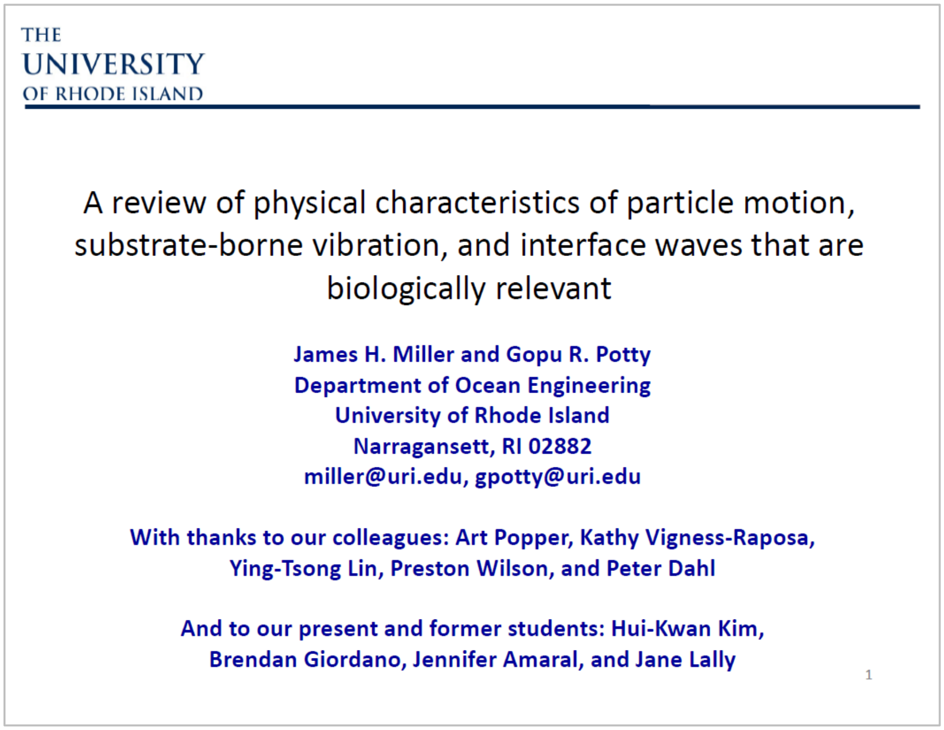
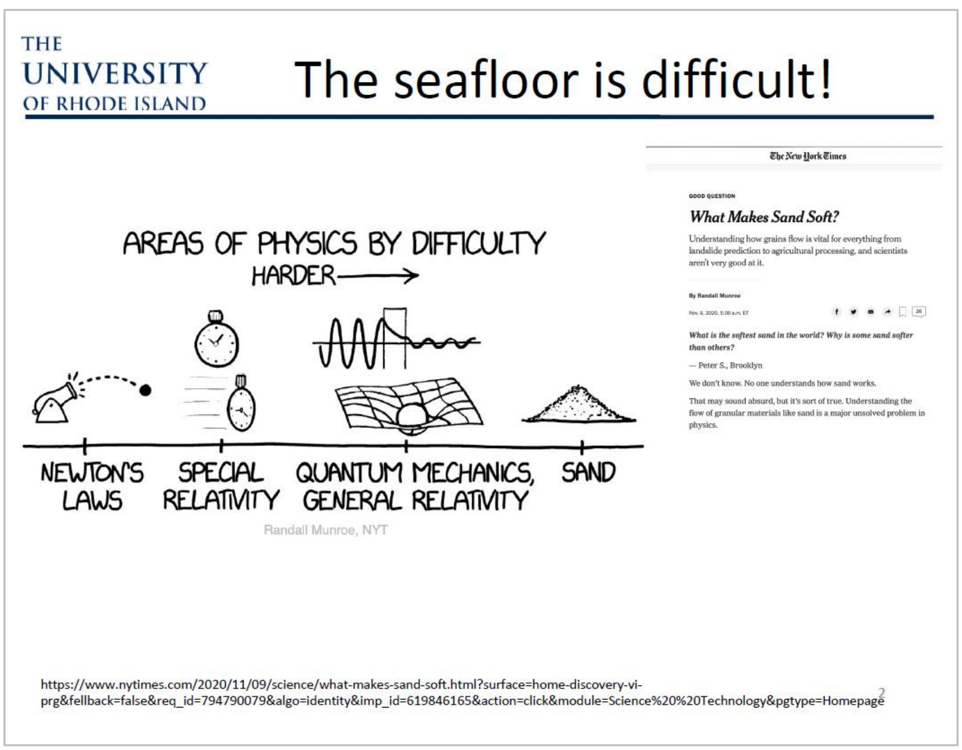
Art Popper

Funding Sources:
NSF
Virginia Merrill Bloedel Hearing Research Center
UW Royalty Research Fund
W UNIVERSITY *of* WASHINGTON

B-4. A Review of Physical Characteristics of Particle Motion, Substrate-Borne Vibration, and Interface Waves that Are Biologically Relevant (James H. Miller)





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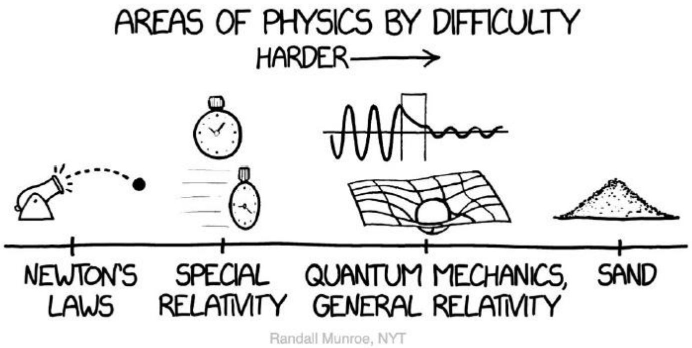
The seafloor is difficult!



real ocean bottom (off the chart hard)

Graphic modified by Preston Wilson, UT-ARL.

https://www.nytimes.com/2020/11/09/science/what-makes-sand-soft.html?surface=home-discovery-vi-prg&fellback=false&req_id=794790079&algo=identity&imp_id=619846165&action=click&module=Science%20%20Technology&pgtype=Homepage

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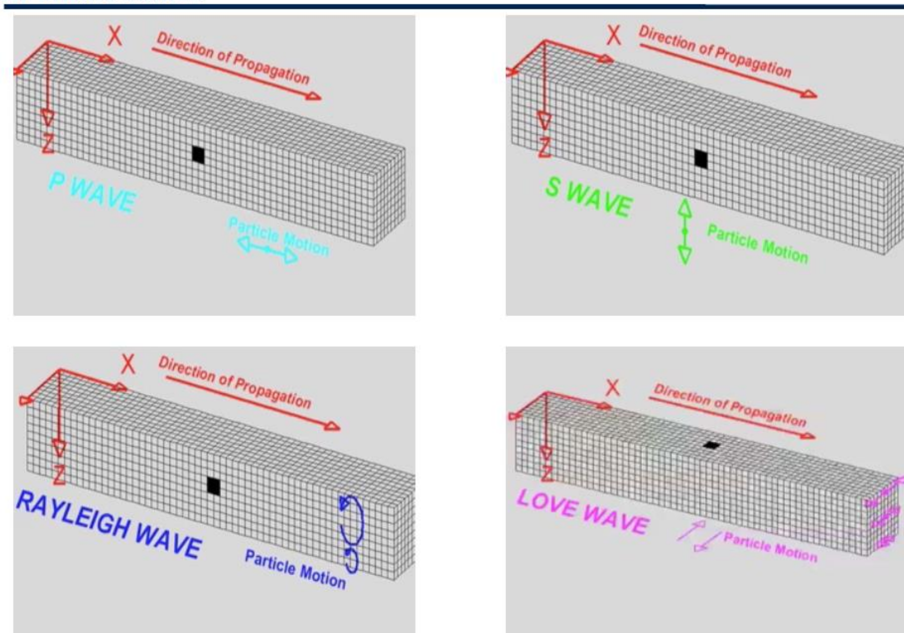
Different Waves in Elastic Media



4

Animations by Larry Braile, Purdue University. https://www.iris.edu/hq/inclass/animation/seismic_wave_motions4_waves_animated

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Solid medium with an interface

- When the solid (elastic) media have boundaries, interface waves can propagate.
  - Solid-vacuum (i.e., air) -> Rayleigh waves
  - Solid-fluid -> Scholte waves
  - Solid-solid -> Stoneley waves
- These waves are sometimes call P-SV waves and are often the most damaging waves from earthquakes.

https://www.cbsnews.com/news/japan-earthquake-how-big-was-it/

5

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Damage from Love Waves

A solid (elastic) medium with a free surface (e.g., air) can also propagate Love waves, also called SH waves.

https://www.intechopen.com/books/surface-waves-new-trends-and-developments/properties-and-applications-of-love-surface-waves-in-seismology-and-biosensors

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Scholte Waves: Solid-Fluid

Scholte waves travel along the surface between a fluid and an elastic solid.

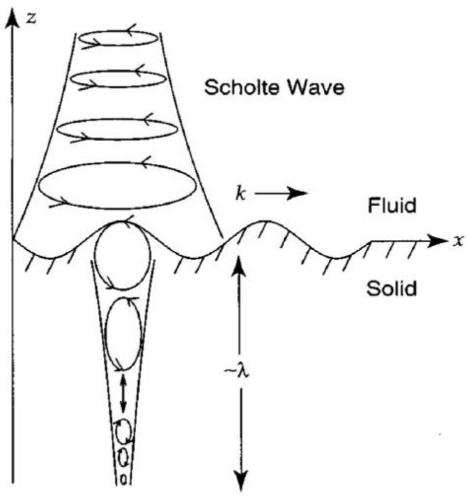

FIG. 5. Schematic representation of particle trajectories in a Scholte wave.

J. Acoust. Soc. Am., Vol. 106, No. 4, Pt. 1, October 1999 Meegan *et al.*: Nonlinear Stoneley and Scholte waves

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Stoneley Waves: Solid-Solid

Stoneley waves travel along the surface between two elastic solids.

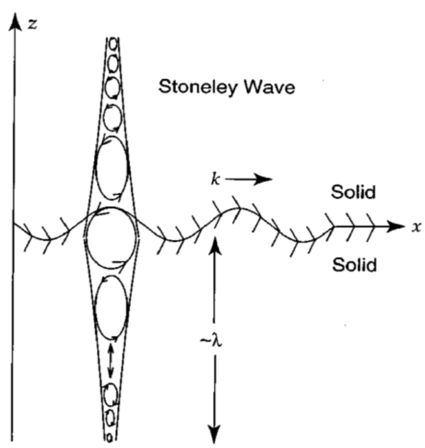

FIG. 3. Schematic representation of particle trajectories in a Stoneley wave.

J. Acoust. Soc. Am., Vol. 106, No. 4, Pt. 1, October 1999 Meegan *et al.*: Nonlinear Stoneley and Scholte waves

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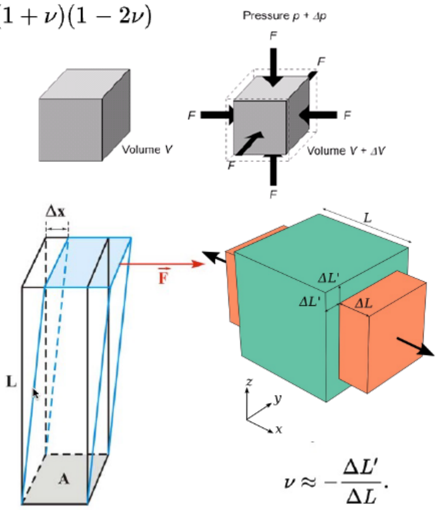
Moduli

$$\lambda = \frac{E\nu}{(1+\nu)(1-2\nu)}$$

- A few elastic constants (moduli) are usually used to describe isotropic solids:
  - Young's Modulus, E
  - Poisson's ratio, ν
  - Lambda param., λ
  - Bulk Modulus, K
  - Rigidity Modulus, G
    - same as Lame's
    - aka Shear Modulus



$$\nu \approx -\frac{\Delta L'}{\Delta L}.$$

http://www.spaceflight.esa.int/impress/text/education/Mechanical%20Properties/MoreModuli.html
http://faraday.physics.utoronto.ca/PHY182S/WilberforceRefShear.pdf

$$G = \frac{\text{shear stress}}{\text{shear strain}} = \frac{F/A}{\Delta x / L} = \frac{F\,L}{A\,\Delta x}$$ (units are Pascals)

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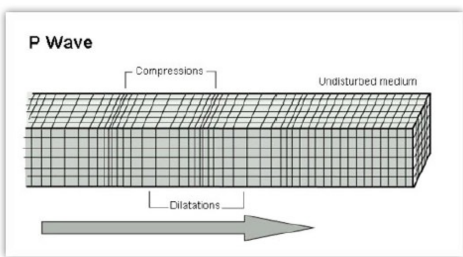
Equations of Motion: P-wave

$$\lambda = \frac{E\nu}{(1+\nu)(1-2\nu)}$$

- P-waves or pressure waves have a wave equation

$$\rho\frac{\partial^2\Delta}{\partial t^2} = (\lambda + 2\mu)\nabla^2\Delta$$

We get the wave equation for dilatation or compression or pressure, or p-wave with speed $\sqrt{\frac{\lambda+2\mu}{\rho}}$



fractional expansion or contraction

where $\Delta = \varepsilon_{xx} + \varepsilon_{yy} + \varepsilon_{zz}$

https://www.esgsolutions.com/english/view.asp?x=857

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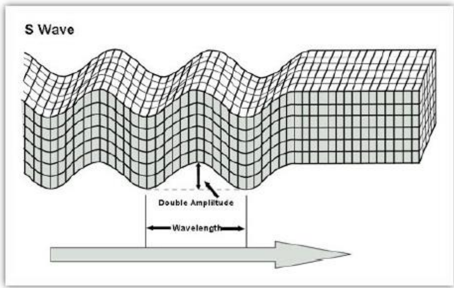
Equations of Motion: S-wave

- S-waves or shear waves also have a wave equaition but with a slower speed.

$$\rho \frac{\partial^2 u}{\partial t^2} = \mu \nabla^2 u$$

$$\rho \frac{\partial^2 v}{\partial t^2} = \mu \nabla^2 v$$

$$\rho \frac{\partial^2 w}{\partial t^2} = \mu \nabla^2 w$$



and the speed of shear waves is $\sqrt{\frac{\mu}{\rho}}$

https://www.esgsolutions.com/english/view.asp?x=857

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Relative speeds

		Seafloor – silty sand typical values
Compressional or P-wave speed is always greater than shear wave speed in the same material.	$c_p = \sqrt{\frac{\lambda+2\mu}{\rho}}$	1650 m/s
	$c_s = \sqrt{\frac{\mu}{\rho}}$	220 m/s
Love wave speed is shear wave speed.	$c_{\text{love}} = c_s$	220 m/s
Rayleigh waves travel at about 90% of shear wave speed.	$c_{\text{rayleigh}} \approx 0.9 c_s$	200 m/s

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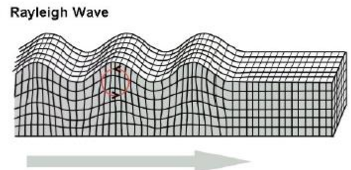
Rayleigh Waves

- Rayleigh waves are surface or interface waves as we mentioned.
- The existence of Rayleigh waves was predicted in 1885 by Lord Rayleigh, John William Strutt.



The 3rd Lord Rayleigh established a laboratory in the west wing, which remains to this day. Indeed he used apparatus from this laboratory to isolate argon in the cellar of Terling Place, Essex in 1894, for which he was awarded the Nobel Prize in Physics in 1904. Photo by Robert Palmer.

http://en.wikipedia.org/wiki/Lord_Rayleigh

Lord Rayleigh (John William Strutt), “On waves propagated along the plane surface of an elastic solid.” Proc. London Math. Soc. 17 (1887) 4–11.

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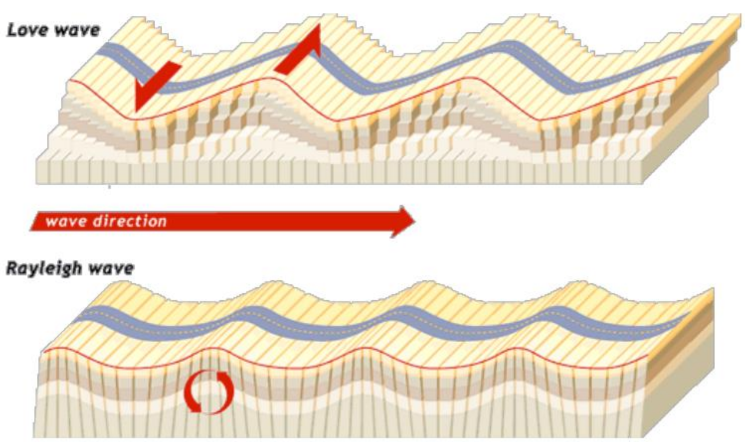
Love and Rayleigh Waves



http://www.csulb.edu/~rodrigue/geog140/lectures/tectoniczones.html

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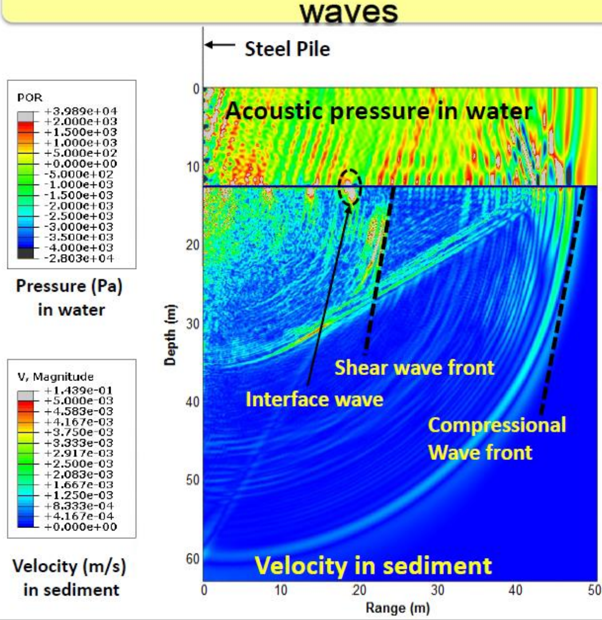
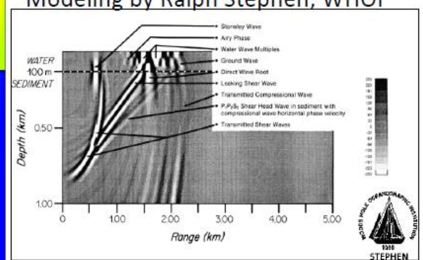
Finite Element Modeling of Impact Pile Driving

Compressional, shear and interface waves

$c_p > c_s > c_{rayleigh}$



Comparison to Finite Difference Modeling by Ralph Stephen, WHOI



Miller, JH, Potty, GR, Kim, H-K. 2016. Pile-driving pressure and particle velocity at the seabed: Quantifying effects on crustaceans and groundfish. In AN Popper and AD Hawkins (Eds.), The Effects of Noise on Aquatic Life II, Springer, New York, pp. 719-728.

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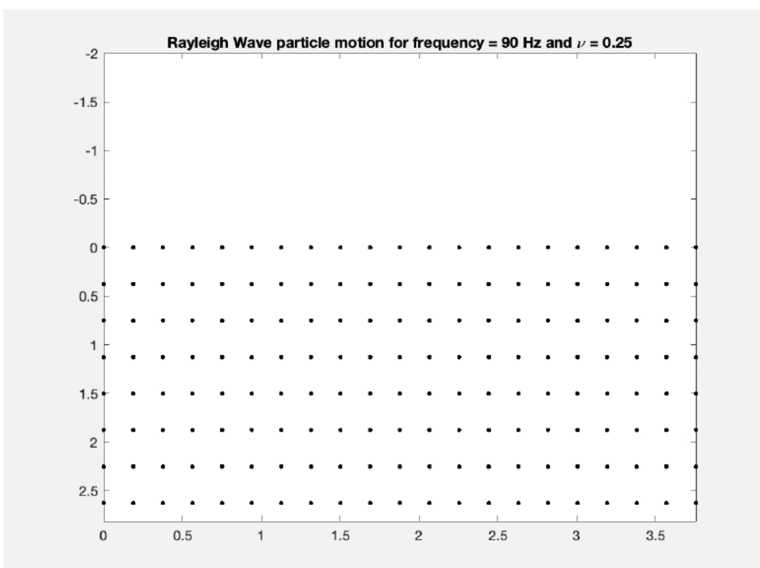
Particle Motion Video

f = 90 Hz
c_s = 200 m/s

Equations of motion from Kolsky's "Stress Waves in Solids", Dover, 1963,



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Interface waves in sediments

These interface waves can be envisioned by watching some jello shake.

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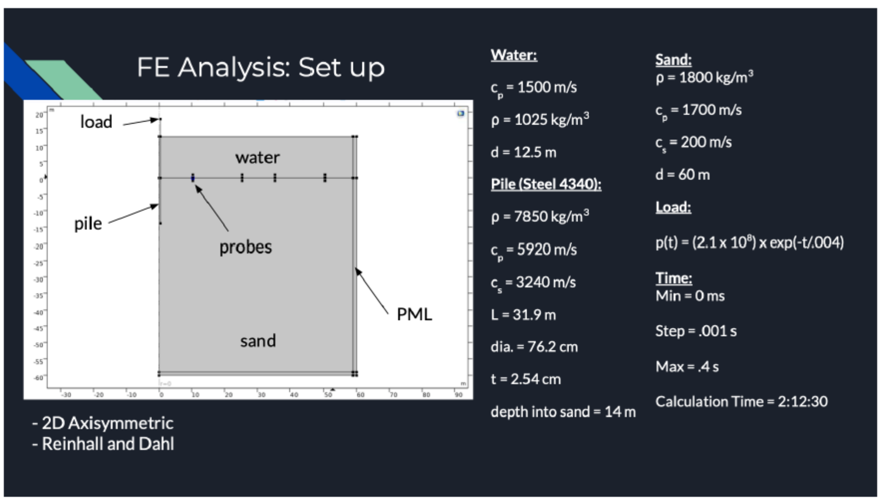
Latest FE Modeling



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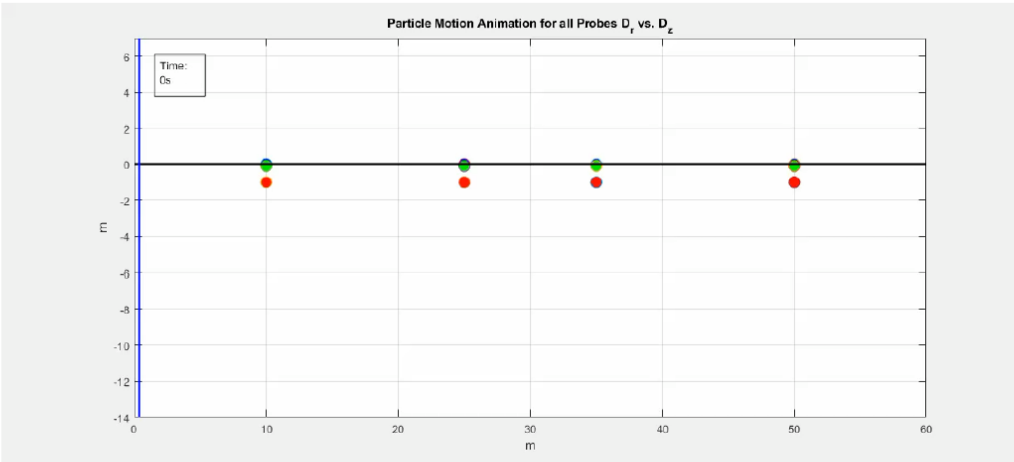
Video



Particle motions exaggerated by about a factor of 10000 for ease of observation.
From graduate student Brendan Giordano's thesis research.

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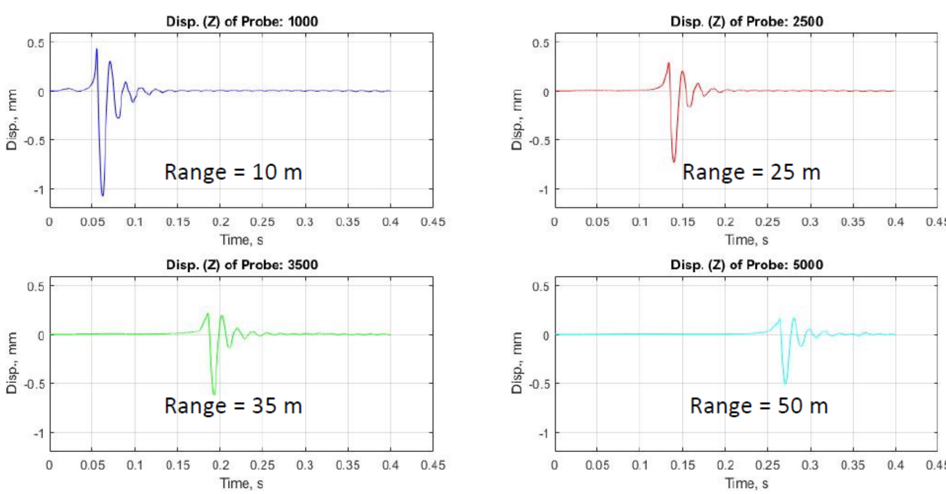
Displacements at seafloor



From graduate student Brendan Giordano's thesis research.

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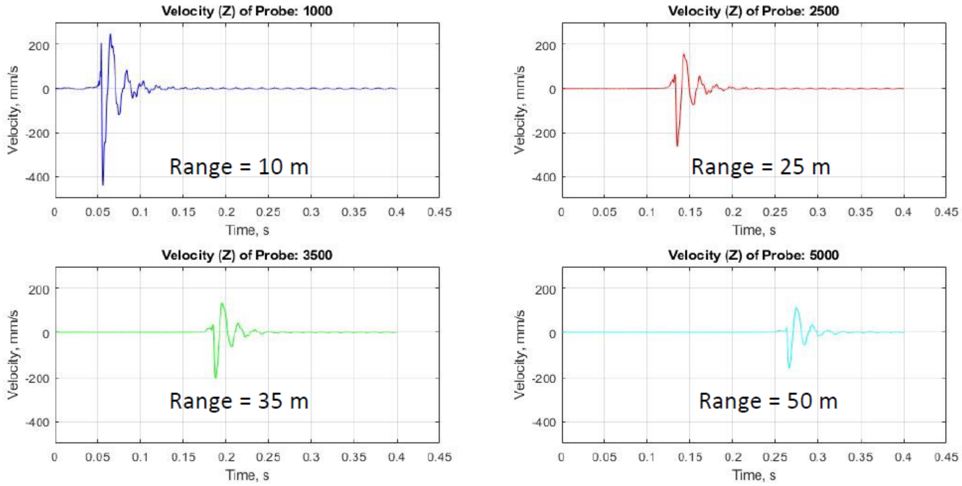
Particle velocities at seafloor



From graduate student Brendan Giordano's thesis research.

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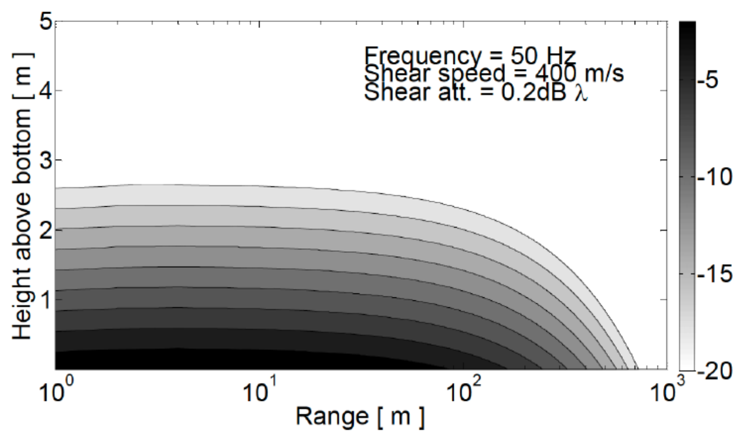
Farther ranges



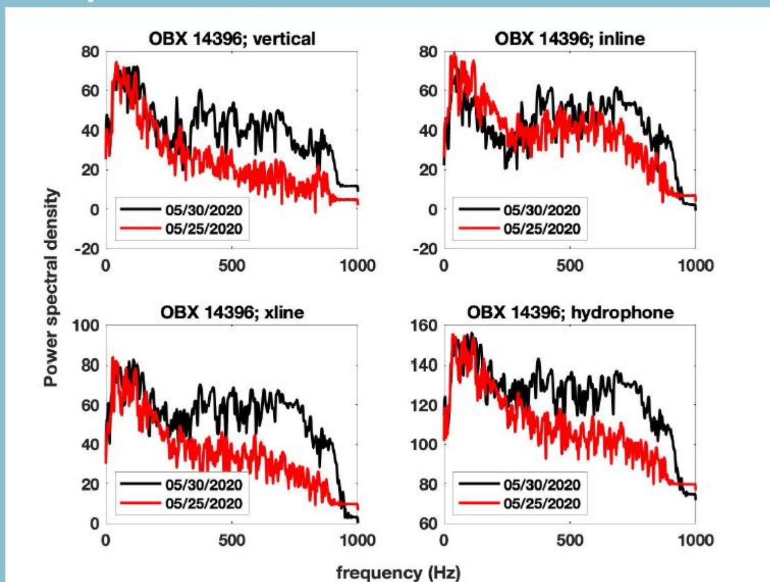
Normalized amplitude of a 50 Hz interface wave as a function of range and combined height above bottom.

Jens M. Hovem, "Particle motions caused by seismic interface waves," 37th Scandinavian Symposium on Physical Acoustics, Geilo 2nd - 5th February 2014.

22

Y.T. Lin, Arthur Newhall, James H. Miller, Gopu Potty, Jennifer Amaral, Adam Frankel, Tim Mason, Kristen Ampela, and Anwar Khan, "CVOW Project RODEO Program Construction Phase Underwater Acoustic Monitoring – Preliminary Results," August 4, 2020

OBX - Comparison with and without bubble curtain



1500 m range from CVOW monopiles

The RODEO Program

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Biological Implications

- The particle motion from interface waves generated by human activities have the potential to affect fish and invertebrates close to the seafloor.
- Popper and Hawkins (2018) make the case for experiments to determine the extent of the effects of particle motion including.

- determining those levels of particle motion that cause injury or detrimental changes in physiology in fishes and invertebrates, including those levels that may affect their ability to detect sounds;
- developing a better understanding masking by sounds on fish and invertebrate hearing; and
- examining the behavioral responses of animals to high levels of particle motion. Included in this is a need to understand the impact on hearing and behavior of changes in ambient particle motion levels resulting from increased man-made sounds.

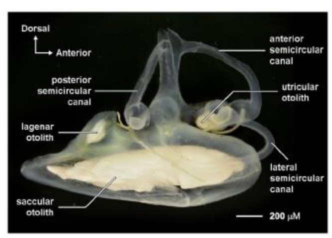

FIG. 2. (Color online) Inner ear of *Antimora rostrata*, a member of the deep-sea cod family Maridae. The otoliths are each located in a sac bearing the same name. The otolith organs are associated with hearing and positional senses (see Platt, 1983). The sensory epithelium of the saccule is not seen here since it is on

Arthur N. Popper, Anthony D. Hawkins; The importance of particle motion to fishes and invertebrates. J. Acoust. Soc. Am. 1 January 2018; 143 (1): 470 488. https://doi.org/10.1121/1.5021594

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Next steps

- Extend the range of the model to 10’s of km using Parabolic Equation model developed by YT Lin of Scripps
- Compare to our measurements at CVOW and other wind farms under construction.
- Predict propagation of interface waves and potential biological effects as a function of range out to 10’s of km.

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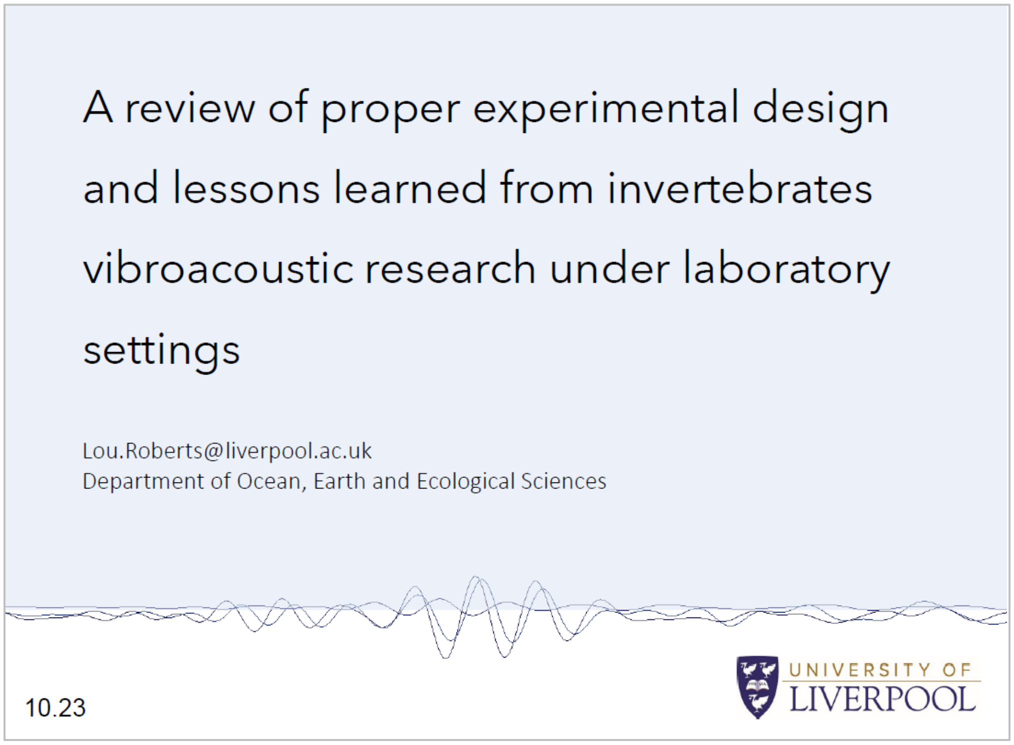
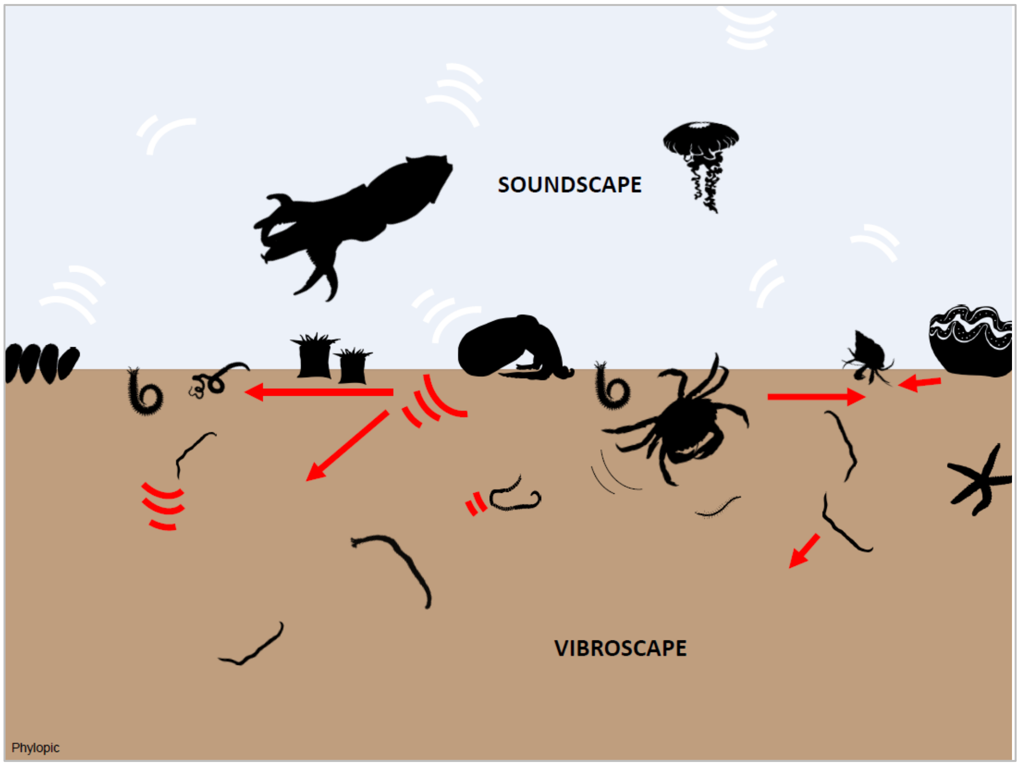
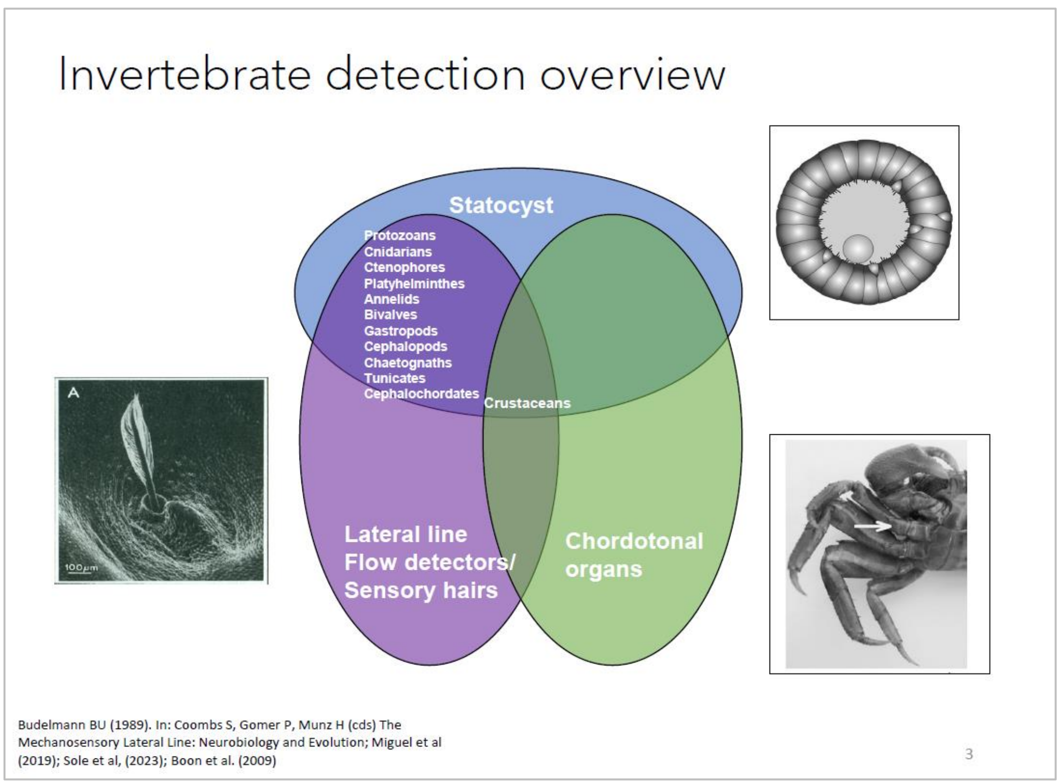
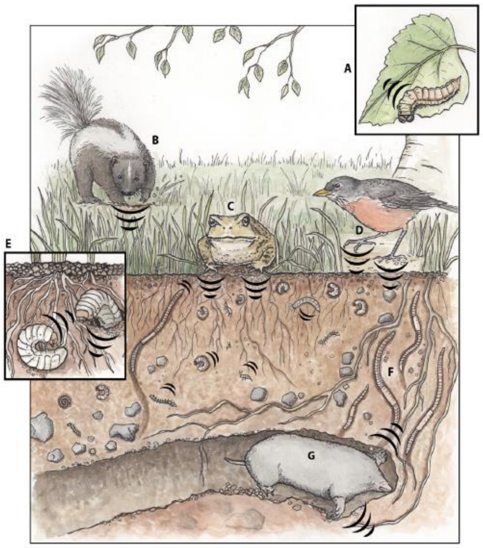
B-5. A Review of Proper Experimental Design and Lessons Learned from Invertebrate Vibroacoustic Research Under Laboratory Settings (Louise Roberts)




SOUNDSCAPE
VIBROSCAPE
Phylopic


Invertebrate detection overview
Statocyst
Protozoans
Cnidarians
Ctenophores
Platyhelminthes
Annelids
Bivalves
Gastropods
Cephalopods
Chaetognaths
Tunicates
Cephalochordates
Crustaceans
Lateral line
Flow detectors/
Sensory hairs
Chordotonal
organs
A
100 µm
Budelmann BU (1989). In: Coombs S, Gomer P, Munz H (cds) The Mechanosensory Lateral Line: Neurobiology and Evolution; Miguel et al (2019); Sole et al, (2023); Boon et al. (2009)
3

Substrate-borne vibrations



Biotremology ⟷ Bioacoustics

The **most ancient** and widespread communication form

All terrestrial taxa of vertebrates, especially amphibians and mammals.

200,000< insect species use vibration. Plus many other invertebrates

Endler (2014); Hill, (2008)
Painting by Ann Sanderson, in Roberts and Wickings *Acoustics Today* (*2022*) doi.org/10.1121/AT.2022.18.3.49

4

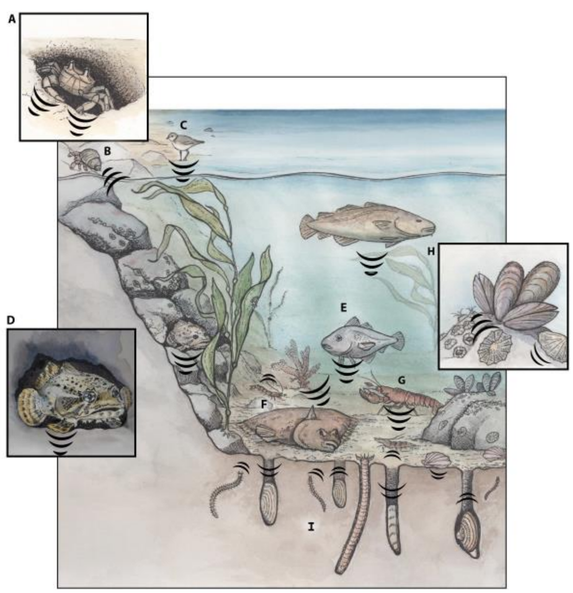
A re-set of thinking

Step away from **water** and consider the substrate perspective

e.g. noise stimuli **originating** in the substrate

e.g. animals which are **predominantly or solely** bottom-dwelling

Consider terminology



Roberts and Wessel (2023) doi.org/10.1007/978-3-031-10417-6_136-1.
Painting by Ann Sanderson, in Roberts and Wickings *Acoustics Today* (*2022*) doi.org/10.1121/AT.2022.18.3.49

Literature assessment difficulties

- Artificial vs Field conditions
- Great variability in experimental tank set-ups
- Variability in exposure characteristics
- Considering the ‘relevant’ stimuli
- Limited species coverage

… difficult to draw conclusions or make comparisons

Popper and Hawkins (2018); Popper et al. (2014); Popper et al. (2020); and see ref list.

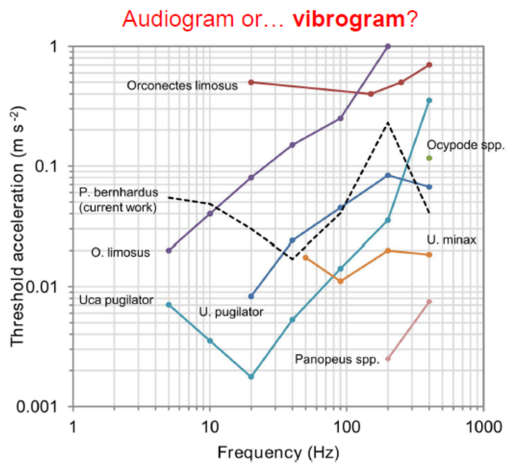
6

Literature overview

	Water p.m. or sub-borne measurement	Pressure measurement only
LABORATORY	c.a. 17 papers (of those, 3 sediment vibration)	
FIELD	c.a. 19 papers (11 sediment vibration)	c.a. 5 papers

Table 1. Summary of collated noise/sensitivity studies regarding invertebrates and water-borne particle, substrate-borne vibration and pressure (search Oct 2023).

Sensitivity



Summarised sensory thresholds to vibration (water and substrate-borne) for crustaceans

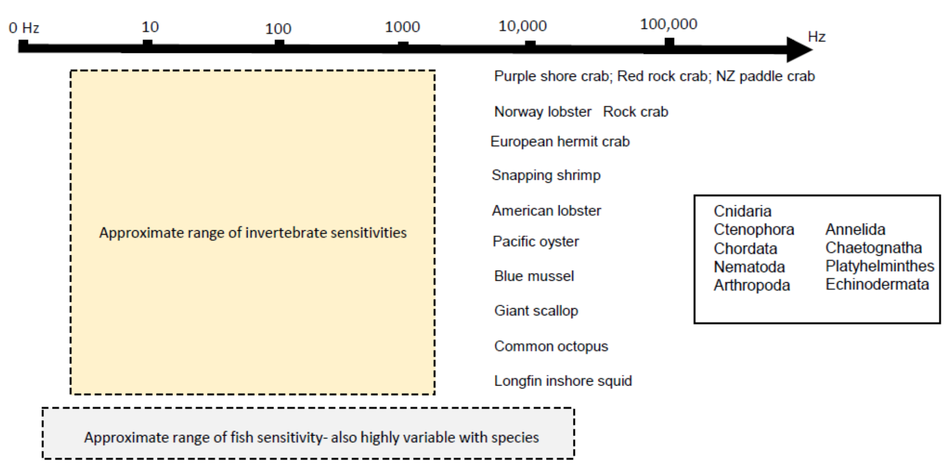
Water vs Substrate

Behavioural vs Physiological

Varied methods of testing and different exposure stimuli

Roberts et al., (2016) doi.org/10.1016/j.jembe.2015.09.014

Known frequency ranges



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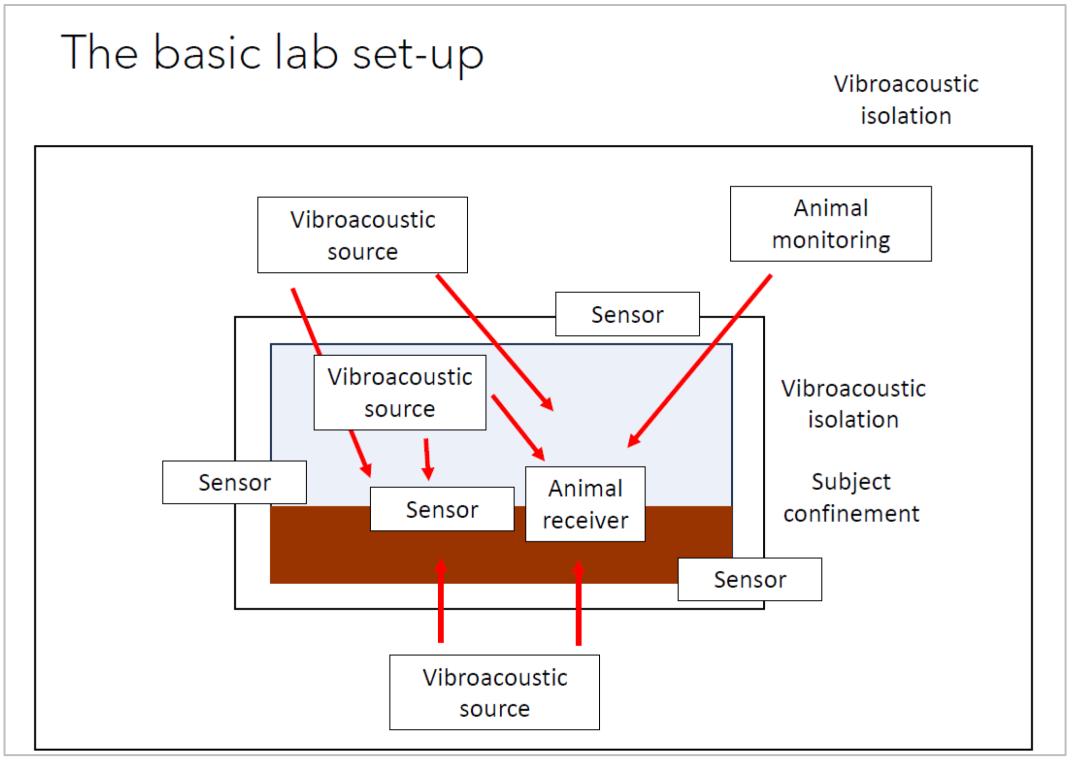
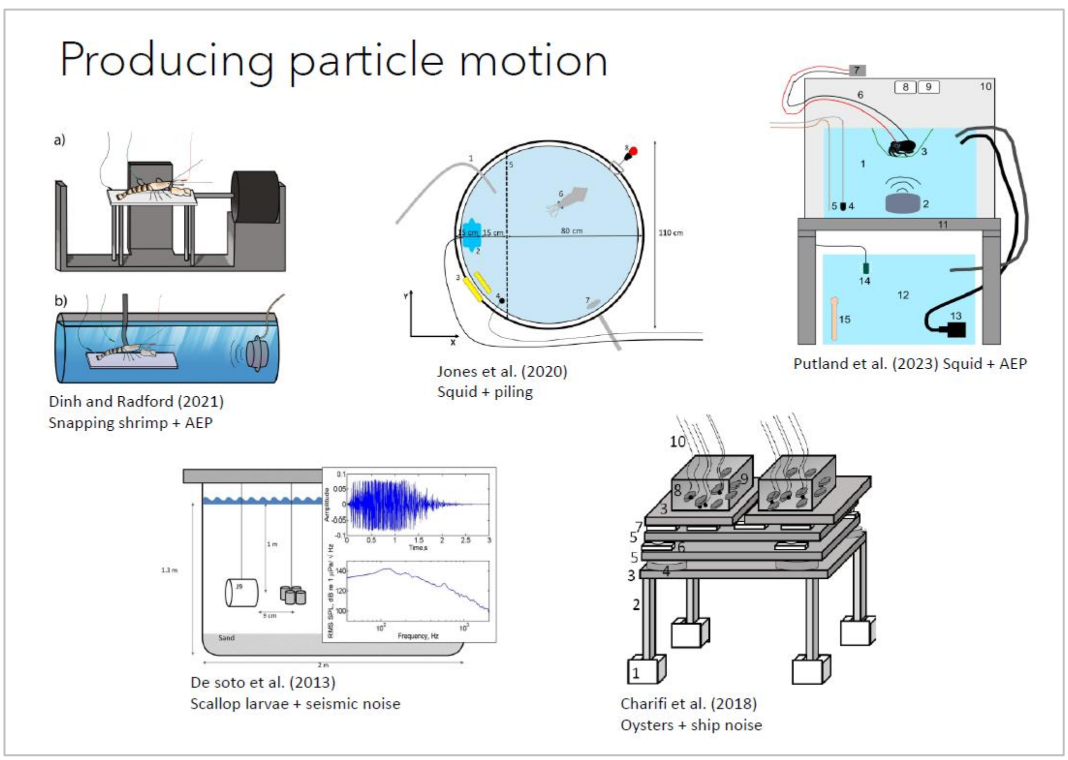
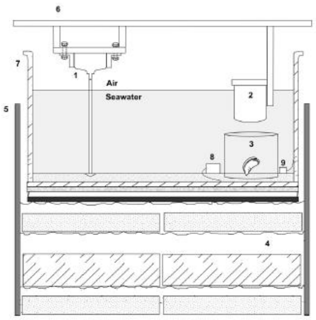
Roberts (2015); Roberts et al. (2016); Roberts et al. (2015); Charifi et al 2017; Dinh and Radford (2021); Jezequel et al. (2021); Jezequel et al. (2023); Radford et al. (2022); Sole et al. (2023)

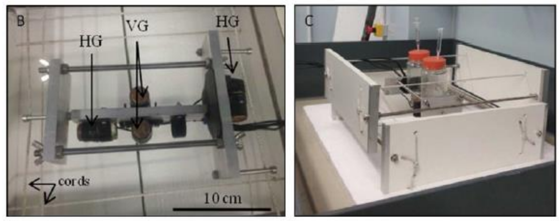

The basic lab set-up
Vibroacoustic isolation
Vibroacoustic source
Animal monitoring
Sensor
Vibroacoustic source
Vibroacoustic isolation
Subject confinement
Sensor
Sensor
Animal receiver
Sensor
Vibroacoustic source


Producing particle motion
a)
b)
Dinh and Radford (2021)
Snapping shrimp + AEP
Jones et al. (2020)
Squid + piling
Putland et al. (2023) Squid + AEP
De soto et al. (2013)
Scallop larvae + seismic noise
Charifi et al. (2018)
Oysters + ship noise

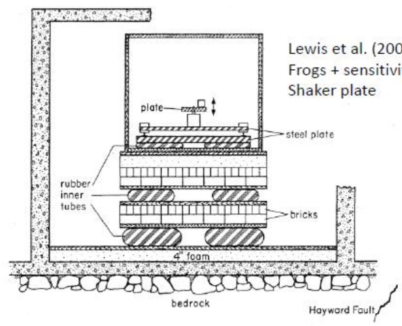
Producing substrate-borne



Roberts et al. (2015, 2016)
Invertebrates + behavioural thresholds
Stinger rod.



Aimon et al. (2021)
Crabs + physiological/behavioural responses
whole tank "shake"

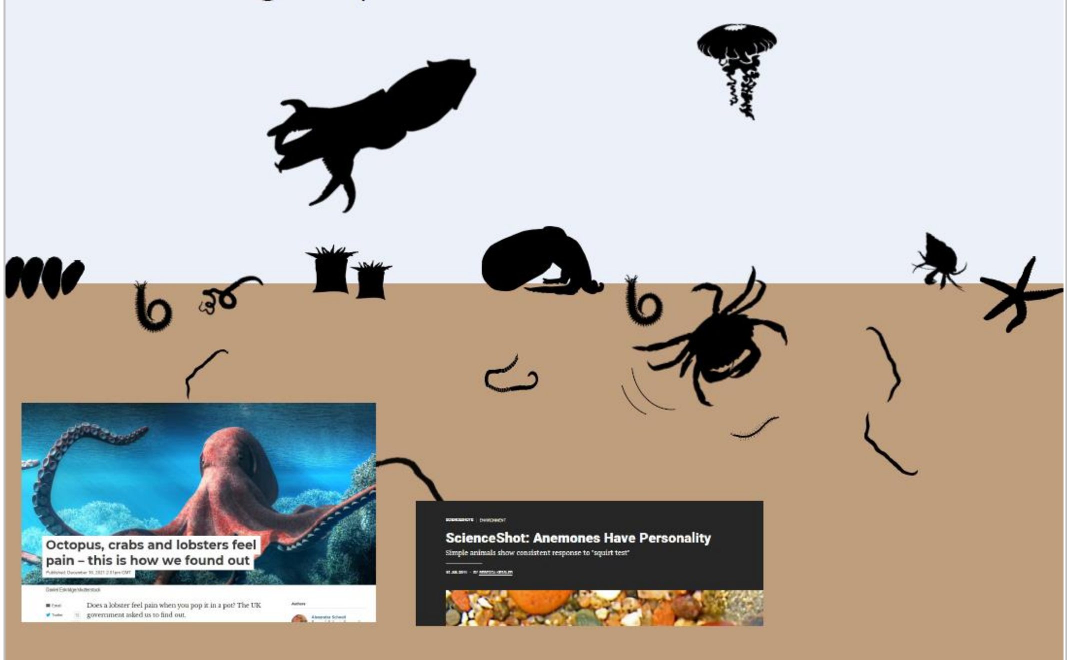


Lewis et al. (2001)
Frogs + sensitivity
Shaker plate

- Physical impact e.g. mini-piling
- Electromagnetic shakers
- Tactile speakers
- Linear resonant actuators
- Piezoelectric actuators/disks

} a question of scale

Measuring responses



Phylopic

Behavioural assays

GROUP	Feeding	Anti-predator	Resource/environ use	Communication
ARTHROPOD: CRUSTACEAN	Feeding rate and orientation towards food	Righting behaviour; avoidance; flee/freeze/startle; burial; shelter	Location and orientation to resources; energy budget; locomotion; colour variation	Temporal patterns; vibroacoustic characteristics
MOLLUSC: CEPHALOPOD	Prey capture rates/pursuit	Alarm response	Colour variation	Colour variation
MOLLUSC: BIVALVE + GASTROPOD	Clearance rate; siphonal and valve movements	'Flinch'; valve movements; digging; siphonal retraction	Digging; siphonal/valve movements	
ANNELID + ECHINODERM	Sediment bioturbation	Burial/digging	Sediment bioturbation	
CNIDARIA	Tentacle retraction/flinch	Retraction/flinch		

Porifera; Ctenophora; Platyhelminthes; Nermertea; Priapula; Sipuncula; Bryozoa; Brachipoda; Chaetognatha; Hemichordata; Chordata ?

Phylopic

Physiological and physical assays

GROUP	Stress response	Oxygen	Sensory tissue/organ damage	Body tissue damage	Development + Growth
ARTHROPOD: CRUSTACEAN	Stress biomarkers e.g. glucose, total protein, heat-shock proteins, haemocytes	Consumption	Statocyst whole damage; Sensory hair cell damage/removal; Antenna damage + lesions		Growth rate; settlement;
MOLLUSC: CEPHALOPOD		Consumption	Statocyst whole damage Statocyst hair cell damage/missing		Growth rate;
MOLLUSC: BIVALVE + GASTROPOD	THC protein; glucose; enzyme activity e.g. esterase	Consumption		DNA damage	Shell size; growth; settlement; developmental abnormalities
ANNELID + ECHINODERM	Enzymes in immune response measured e.g. Esterase	Consumption			
CNIDARIA		Consumption	Lesions		

Phylopic

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