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JASA REVIEW-ARTICLE

Approaches to understanding effects from particle motion and substrate-borne vibration on fishes and invertebrates

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ABSTRACT:
There is a growing awareness of the potential impacts of underwater anthropogenic sound on fishes and aquatic invertebrates. However, the current literature provides limited guidance for developing regulations to protect species that are most likely to be affected by such signals. Accordingly, this paper recommends research approaches to best address and understand the effects of anthropogenic particle motion and substrate-borne vibration on fishes and aquatic invertebrates that are of economic and/or ecosystem importance. Three broad perspectives encompass several key research questions. (1) Careful selection of species for study, (2) identification of specific, high-impact research questions that can be addressed and funded within the next several years to inform regulations, and (3) strategic experimental approaches (e.g., laboratory vs field) to maximize useful data. In addition, we identify four general experimental settings that could be used to address these questions.
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I. INTRODUCTION

In recent decades, international awareness of the potential impacts of anthropogenic (human-made) underwater sounds on marine mammals has grown significantly among researchers, regulatory agencies, and the public (e.g., Southall *et al.*, 2019). This has led to a broad array of research efforts focusing on understanding the characteristics of various anthropogenic sound sources (e.g., military sonar, seismic air gun, shipping, in-water pile driving), sound propagation, and, most importantly, the potential effects on the hearing and behavior of marine mammals (Guan *et al.*, 2021).

More recently, however, interest in potential impacts of anthropogenic sound has extended to fishes and aquatic invertebrates (reviewed in Popper and Hawkins, 2012, 2016; Davies *et al.*, 2024). Yet, despite the vast numbers of these species and their critical roles in marine ecosystems and as human food sources, research on the potential impact of anthropogenic sound on these animals remains relatively limited compared to what is known for marine mammals (Williams *et al.*, 2015). This difference results in part from the far greater research funding for this topic that has been (and is) available to studies of marine mammals. Thus, far more is known about how to develop sound policies and regulatory guidelines to mitigate noise-related impacts on marine mammals (e.g., Guan and Brookens, 2021) than on other marine taxa (Hawkins *et al.*, 2015).

To appreciate the point about research and funding differences, it is important to recognize that marine mammals make up fewer than 0.001% (about 150 species) of all aquatic animals (both fishes and aquatic invertebrates). Marine mammals also have relatively little direct impact on human livelihoods (though we recognize the extraordinary importance of marine mammals to the marine ecosystem).

In contrast, there are over 36,100 known fish species (e.g., Fishbase, www.fishbase.org) and an even greater number of aquatic invertebrates (Appeltans *et al.*, 2012; Collier *et al.*, 2016). Both fishes and aquatic invertebrates show immense diversity in every aspect of their biology, behavior, and ecology (reviewed by Popper *et al.*, 2023; Solé *et al.*, 2023). Furthermore, fishes and aquatic invertebrates make up the primary source of protein for over 17% of the global human population (e.g., Boyd *et al.*, 2022) and play essential roles in maintaining marine ecosystem health (e.g., Wang *et al.*, 2021). These animals perform critical roles in the marine ecosystem by providing food sources to higher trophic level species, while also serving as detritivores and scavengers that recycle nutrients. Moreover, fishes and aquatic invertebrates occupy habitats inaccessible to air-breathing species and contribute greatly to ecosystem stability and biodiversity. Therefore,

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anything that impacts the well-being of these animals has very substantial real and potential impacts on humans and the marine ecosystem.

Because of the importance of fishes and aquatic invertebrates to the marine ecosystem and to humans, the need to invest in research on potential impacts of underwater anthropogenic sound on these animals has been noted, and a critical set of research questions have been posed (e.g., Hawkins *et al.*, 2015; Popper *et al.*, 2022; Popper *et al.*, 2023). Yet very little funding in the United States or elsewhere has been invested to address these research questions, leaving critical knowledge gaps unaddressed.

Moreover, most of the (albeit limited) work done to date has been uncoordinated. With the vast number of potential species to study, there has been little accumulation of data on those species of particular importance to humans (e.g., commercial fisheries) and ecosystems. What has been collected is insufficient for providing the body of data needed to design conservation and mitigation approaches to protect these animals. Consequently, there are substantial gaps regarding our understanding of the potential impacts of anthropogenic sound on fishes and invertebrates. These gaps include (but are not necessarily limited to) a lack of adequate knowledge on hearing mechanisms and behavioral and physiological responses to sound, and particularly to potential effects resulting from anthropogenic sound.

The "bottom line" is that the breadth of issues raised is formidable, as is, in particular, the need to do work on select species, to provide resources, and to find the investigators to do the work. Moreover, the breadth of these issues greatly complicates developing experimental designs and methodologies that are scientifically robust and that appropriately address various research questions. Indeed, even deciding on the appropriate species for study—to give the greatest amount of data most relevant to the ecosystems and human—is an open question!

A. Origin and purpose of this paper

This paper is an outgrowth the U.S. Bureau of Ocean Energy Management (BOEM) *Workshop on Research Methodologies to Study Biological Effects from Particle Motion* and *Substrate-borne Vibration* (BOEM Workshop) which was held virtually in October 2023 (Guan *et al.*, 2024). The BOEM Workshop reviewed and discussed previously published studies on fishes and aquatic invertebrates and summarized various research methodologies (Guan *et al.*, 2024). The outcomes of the BOEM Workshop led to the development of the three guiding principles illustrated in Fig. 1 for prioritizing future research.

This paper builds upon the BOEM Workshop report (Guan *et al.*, 2024) and provides several specific recommendations we deem to be the most important research questions, experimental protocols, and study designs needed to better understand the potential impacts of anthropogenic sound on fishes and aquatic invertebrates. Our recommendations focus on the most immediate questions that need answering from a conservation and regulatory perspective. The paper also suggests priorities for research under the assumption of likely limited future funding support.

At the same time, it is *not* our intent to prescribe specific future research, but more to share guidance arising from the BOEM Workshop to stimulate additional thinking and ideas by others, and at international levels. We expect that readers will have additional ideas on how to do the needed research most effectively and efficiently. Thus, our goal is to stimulate discussion that ultimately develops consensus and collaboration needed to quickly and effectively protect the fishes and invertebrates potentially impacted by anthropogenic sounds in aquatic environments.

The paper is organized into several sections. Section II provides a broad and high-level overview of current knowledge on hearing by fishes and aquatic invertebrates. Section III lists several key research questions that address sound detection, behavior, and physiology of fishes and aquatic invertebrates exposed to anthropogenic sound, and particularly to anthropogenic particle motion and substrate-borne vibration. Section IV provides a brief and general overview and evaluation of published experimental settings used to study underwater sound effects on fishes and aquatic invertebrates. Section V links the key research questions raised in Sec. III to the experimental settings reviewed in Sec. IV and describes how these research questions could be addressed with specific experimental designs. Finally, Sec. VI draws conclusions on the current information gaps and provides recommendations for future research to fill these gaps.

Significantly, this paper is *not* intended to be a comprehensive literature review. Instead, we have generally limited ourselves to one or two citations per point in the text as examples of ideas. Many citations are literature reviews that include comprehensive discussions of relevant literature. Thus, our focus is on highlighting key concepts and research priorities rather than exhaustively cataloging existing studies.

B. What is the appropriate research?

Understanding the potential impact of anthropogenic sound on fishes and aquatic invertebrates requires careful consideration of three guiding principles, as indicated in Fig. 1. These principles are: (1) limiting the number of species studied to just a few, focusing on those species that are most likely to be impacted by anthropogenic sound and that are of greatest importance to critical ecosystems and/or to humans as food (see, e.g., Cruz-Trinidad *et al.*, 2014; Popper, 2023), and of greatest regulatory concern (e.g., endangered species, such as sturgeons), (2) clearly defining the research questions to provide the most critical (and immediate) information, allowing regulators and others to start protecting animals and ecosystems, and (3) choosing the most effective methods to get the needed answers and overcome challenges, such as obtaining behavioral responses to anthropogenic sound in environments that acoustically resemble field sites (given that acoustic environments in tanks do not approximate the sound field in the open ocean).

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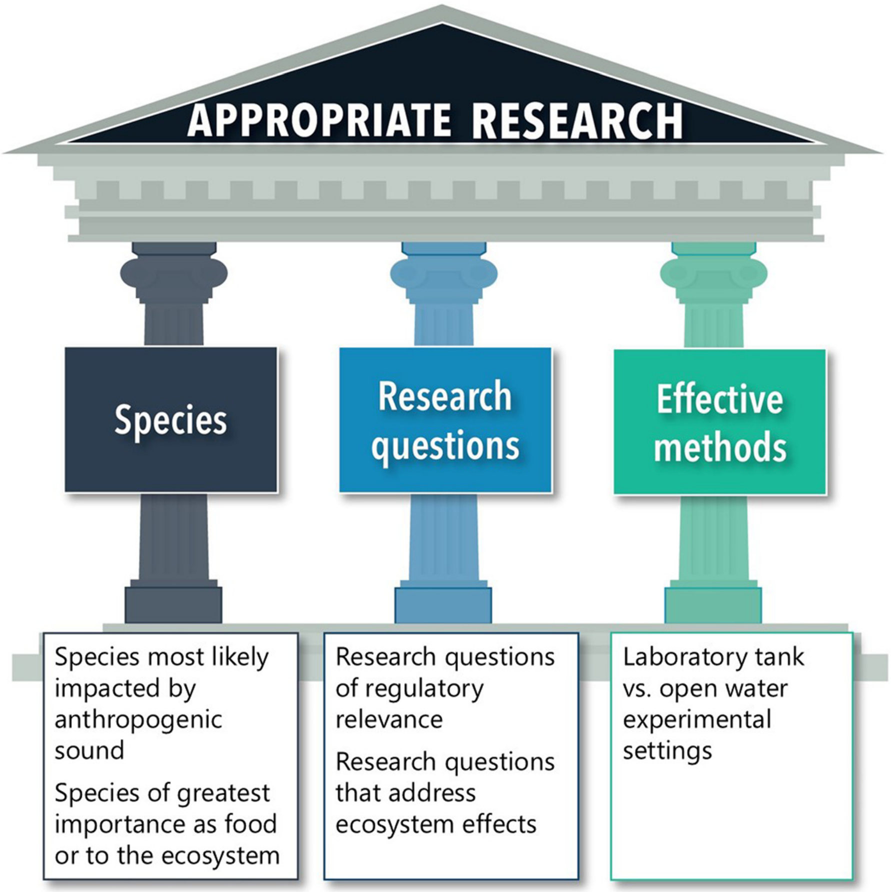

FIG. 1. Three guiding principles to be considered for appropriate research concerning particle motion and substrate-borne vibration on fishes and aquatic invertebrates. Copyright 2025, Russell Yerkes.

II. CURRENT KNOWLEDGE OF HEARING BY FISHES AND AQUATIC INVERTEBRATES

A. Hearing and sound detection

Hearing by marine and terrestrial mammals, as well as most other terrestrial vertebrates, involves perception of sound pressure. Although ears in fishes are structurally and functionally like those in other vertebrates, including mammals, the auditory part of a fish ear responds to the particle motion component of sound rather than pressure (though some fishes can also indirectly detect sound pressure as well) (see Popper and Hawkins, 2018; Sand *et al.*, 2023). Similarly, aquatic invertebrates that hear appear to only detect particle motion, though data are very limited. However, unlike vertebrates, which have a similar receptor system across all species, there are marked differences in virtually all aspects of the receptors in aquatic invertebrates, suggesting multiple origin of these organs, and, potentially, differences in the mechanism for particle motion detection (e.g., Radford and Stanley, 2023; Solé *et al.*, 2023). Moreover, both fishes and invertebrates living on, in, or near the substrate are likely capable of responding to substrate-borne vibration (Roberts and Elliott, 2017; Hawkins *et al.*, 2021).

B. Acoustic pressure, particle motion, and substrate-borne vibration

A significant issue in understanding potential impacts of anthropogenic stimuli on fishes and invertebrates (and, in fact, for all species in understanding their sensory detection more broadly in these groups) is the limited data on their sensitivity to particle motion or substrate-borne vibration (e.g., Nedelec *et al.*, 2016; Hawkins *et al.*, 2021).

There have been several significant issues in determining sensitivity to particle motion and substrate-borne vibration. One issue is that both signals are very hard to measure in a tank (e.g., Gray *et al.*, 2016; Rogers *et al.*, 2016). Moreover, as in shallow water, the particle motion field cannot be predicted by measuring sound pressure due to the complex interactions of the sounds at the interfaces of water surfaces and with the substrate (Rogers *et al.*, 2016; Jones *et al.*, 2025).

Another issue is, that with very few exceptions, the lack of measured behavioral hearing sensitivity (i.e., thresholds) for particle motion (e.g., Fig. 2). The best example of behavioral thresholds was determined for animals far from surface and bottom where sounds could be calibrated in terms of particle motion as well as sound pressure, as shown in Fig. 2 (reviewed in Hawkins and Chapman, 2020). The only behavioral thresholds for particle motion in wild fishes was measured by Hawkins *et al.* (2014), though the study included only a limited number of species, and the thresholds could only be estimated.

While several behavioral response studies on fishes and invertebrates exposed to anthropogenic sounds have been conducted (e.g., Jimenez *et al.*, 2020; Gigot *et al.*, 2023), few consider particle motion. Even so, these studies did not include threshold measures (e.g., Nedelec *et al.*, 2014; Solé *et al.*, 2017).

Moreover, considering only pressure and particle motion in the water column neglects a crucial component of the aquatic sensory environment: substrate-borne vibrations (Hawkins *et al.*, 2021; Roberts and Wickings, 2022). Yet, consideration of vibrational sensing is important to add to future considerations since it is widespread across the animal kingdom, with a prolific number of vibrational communicators and receivers, spanning both invertebrates and vertebrates (Hill and Wessel, 2016). Indeed, there is increasing evidence that many aquatic organisms detect and utilize substrate-borne waves as an alternative sensory channel (reviewed for fishes in Roberts and Rice, 2023 and for invertebrates in Roberts and Elliott, 2017; Hawkins *et al.*, 2021). Moreover, mismatches in data between sound detection abilities and sound production, such as those observed in decapod crustaceans and certain fish species, may be explained by animals using substrate-borne channel, a signal not measured in most studies (Roberts and Rice, 2023; Radford and Stanley, 2023). The substrate may also provide sensory advantages to animals in environments with high ambient sound levels, while at the same time serving as a medium through which anthropogenic sound and/or vibration propagates.

The omission of adequately considering substrate-borne vibration is particularly problematic when studying species that are exclusively benthic or when noise stimuli originate within the substrate itself. However, it is equally relevant for demersal species or when considering indirect sources of vibration. Encouragingly, recent research has begun incorporating substrate-borne measurements in studies involving invertebrates and noise (e.g., Cones *et al.*, 2024; Jézéquel *et al.*, 2022a).

Despite recent progress, vibrational thresholds, measured in a manner comparable to hearing sensitivity tests, remain largely unexplored and are primarily focused on bivalve mollusks and crustaceans (reviewed in Roberts and Elliott, 2017). This limited dataset makes it difficult to biologically interpret vibrational noise sources (Fig. 3). While there are anecdotal reports of vibrational responses in other invertebrate phyla (e.g., Budelmann, 1992), these have not been investigated, leaving many phyla completed untested, despite being strongly associated with substrates.

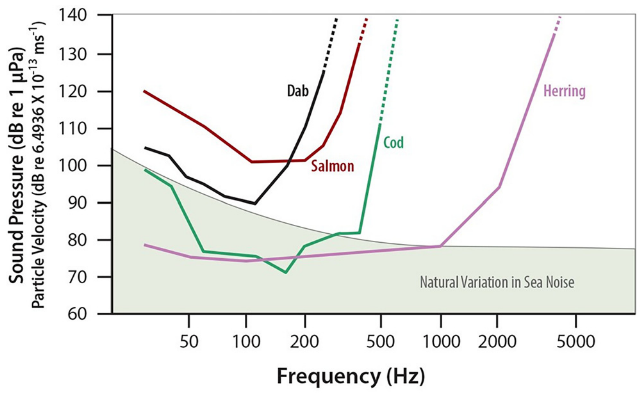

FIG. 2. Sensitivity (thresholds) obtained in free field conditions in a Scottish Loch for four fish species. Data show response to pure tones across frequencies. Atlantic herring (*Clupea harengus*) has most sensitive hearing and a broader hearing bandwidth. Thresholds for Atlantic cod (*Gadus morhua*) and Atlantic herring are likely lower than shown since they were likely masked by natural ambient noise (colored region). If noise levels were higher, as may occur in many natural situations, thresholds would be even higher due to auditory masking. It is also important to note that both Atlantic herring and Atlantic cod detect both sound pressure and particle motion. In contrast, the dab (*Limanda limanda*), a flatfish, and the Atlantic salmon (*Salmo salar*) only detect particle motion. The reference level in this figure for the particle velocity is based on the level existing in a free sound field for the given sound pressure level. Note that, for the particle velocity levels in this figure to match the sound pressure levels in a free sound field, it is necessary to calculate an appropriate particle velocity reference level. Standard reference levels are not used in this figure since the curves will not match one another. Thus, they are not included to keep the figure relatively simple. Copyright 2018, Anthony D. Hawkins.

III. FUNDAMENTAL RESEARCH QUESTIONS

A. The initial question

A major challenge in understanding the impacts of anthropogenic sound on fishes and aquatic invertebrates lies in the very large number of species—each likely have some impact on the ecosystem in which they live. Of these, over 2600 species are of particular importance to humans as a source of food (FAO, 2022). Among the fishes and aquatic invertebrates used for human consumption, 85% are finfish, with the remaining 15% being aquatic invertebrates (FAO, 2022).

At the same time, virtually all the studies on potential impacts of anthropogenic sound have focused on very few species, often selected based on ease of capture, suitability for tank studies, small body size, and other factors that are often for the convenience of the investigation (and investigator). However, for the most part, the species studied have not been those that are most likely to be affected by anthropogenic sound sources in the marine environment or of interest to regulators.

A critical issue is that commercially important finfish species captured for food belong to highly mobile and migratory groups, including small pelagic species, such as sardines and herrings (e.g., Clupeiformes), cod and related species (Gadiformes), and tuna and tuna-like species (e.g., Scombridae) (FAO, 2022). These species are not well-suited for laboratory-based sound exposure studies due to size and/or movement patterns, making traditional tank studies, whether in laboratory tanks or outdoor above-ground tanks or ponds, ineffective for assessing behavioral responses to sound. Instead, more appropriate and ecologically relevant experimental approaches involve open-water settings, either using confined nets (e.g., Sarà *et al.*, 2007; Buscaino *et al.*, 2010; Debusschere *et al.*, 2014) or, ideally, studying unrestrained animals using biotags (McQueen *et al.*, 2023).

There are similar issues in selecting aquatic invertebrates for study. Except for bivalve mollusk species (e.g., scallops, mussels, clams, and oysters), many other important taxa are mobile or migratory (e.g., cephalopods,

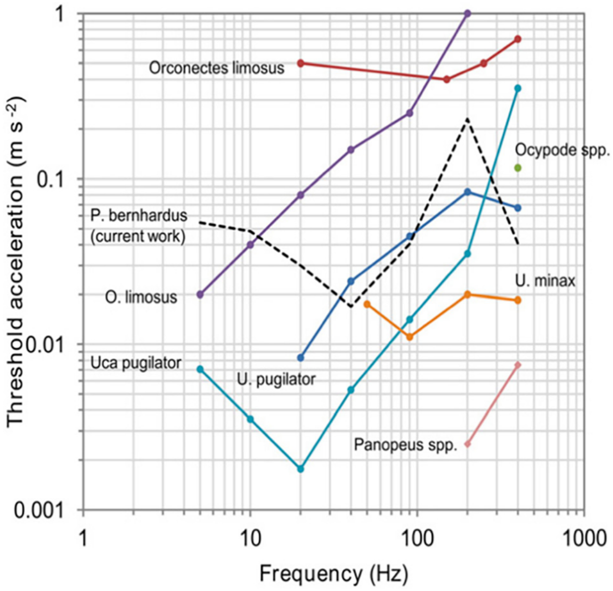

FIG. 3. Behavioral thresholds to vibration (water and substrate-borne) for spiny-cheek crayfish (*Faxonius limosus*, formerly *Orconectes limosus*) (Breithaupt and Tautz, 1988, red; Breithaupt, 2002, purple); Atlantic sand fiddler crab (*Uca pugilator*, Salmon and Atsaides, 1969, dark blue; Aicher and Tautz, 1984, light blue); red-jointed fiddler crab (*U. minax*, Salmon and Horch, 1973, orange); mud crabs (*Panopeus* spp., Hughes *et al.*, 2014, pink); ghost crabs (*Ocypode quadrata* and *O. ceratophthalmus*, Horch, 1971, green); and hermit crab (*Pagurus bernhardus*, Roberts *et al.*, 2016, dotted black). Used with permission from Roberts, Cheesman, Elliott, and Breithaupt, J. Exp. Mar. Biol. Ecol. **474**, 185–194 (2016). Copyright 2016 Elsevier.

crustaceans), which renders somewhat limited applications using laboratory tanks or even outdoor large tanks. Therefore, conducting experiments in open-water environments could be a better way to investigate effects of sound for most economically important aquatic invertebrate species (e.g., Day *et al.*, 2019; Jézéquel *et al.*, 2022b).

Another major issue for the invertebrates is that, far more than for fishes, almost nothing is known about their hearing capabilities, bioacoustics, and the function of their sound detecting systems. For many of these species, initial sound detection studies may be done in a laboratory setting, but a critical issue is that the focus must be on detection of particle motion and substrate-borne vibration and not sound pressure.

An additional critical consideration in selecting species for study, whether fish or invertebrate, is the high degree of biological variability across taxa in virtually every aspect of anatomy, physiology, behavior, and ecology. This variability makes it quite difficult to extrapolate findings from one species to another unless they are closely related and share similar traits in form and function. Thus, we do not know, for example, if recent data on the potential impacts of sound produced during explosions (e.g., Bowman *et al.*, 2024) can be generalized beyond the two species studied.

All these factors lead to the first, and perhaps most important, recommendation for future studies directed at understanding potential impacts particle motion and substrate-borne vibration on fishes and aquatic invertebrates (and, in fact, all anthropogenic sounds–Popper *et al.*, 2023; Popper *et al.*, 2022)–the careful selection of species for study. In selecting species, several principles are worth considering.

1. Considerations for species selection

(1) **Is the species likely to be impacted by a particular anthropogenic source?** Studying a species that is unlikely to encounter a specific sound source may provide little practical value unless the research can clearly demonstrate its broader applicability. For example, zebrafish (*Danio rerio*) are not typically exposed to pile driving or a seismic exploration, making them a poor candidate for such studies. In contrast, Atlantic cod (*Gadus morhua*), a commercially valuable species often found in regions of high anthropogenic activity, would be a far more relevant choice.

(2) **Is the species relevant to regulatory or funding agencies?** Some species, such as zebrafish and goldfish (*Carassius auratus*), have been widely used in laboratory research but are unlikely to be a priority for marine regulatory agencies. In contrast, species like Atlantic cod or American lobster (*Homarus americanus*), which play significant economic and ecological roles, are far more relevant to agencies responsible for environmental management and fisheries regulation.

(3) **Is the species amenable to study?** While some species are biologically and logistically well-suited for research, others may present insurmountable challenges. Zebrafish, for instance, are easy to study but are unlikely to meet the previous two criteria. But bluefin tuna (*Thunnus thynnus*) may be of significant ecological and economic interest, but their large size, high mobility, and husbandry challenges make them difficult to study. Identifying species that balance scientific relevance with practical feasibility will require careful review and discussion.

(4) **Can results from the species be extrapolated to others of interest?** Given the immense biological diversity among fishes and invertebrates, extrapolating data across species must be done with caution. For example, can behavioral data responses of a fast-moving bluefin tuna to a seismic source be meaningfully applied to a sedentary flatfish?

The "bottom line" is that selecting appropriate study species and ensuring consistency among researchers investigating the same issue is critical for optimizing limited funding and producing the most meaningful results in the shortest possible time frame. Moreover, while selecting species with broad applicability is important for maximizing research impact, it is also essential to limit the number of study species to conserve time and funding while generating the most informative data.

Yet, to our knowledge there have only been few attempts to group species to gain maximum data (e.g., Popper *et al.*, 2014) but the approach used, while a useful start and based on a very important analysis, is far too coarse and may not allow the degree of data extrapolation needed at this time. Moving forward, a more refined, collaborative approach to species selection will be essential for advancing our understanding of anthropogenic sound impacts on aquatic life, perhaps in the form of an international workshop.

B. Broad perspectives and key research questions

Over the past decade, several U.S. agencies have convened workshops and meetings for researchers and regulators to discuss and identify research questions addressing potential effects of anthropogenic sounds on fishes and aquatic invertebrates (e.g., Guan *et al.*, 2024; Hawkins *et al.*, 2015; Popper *et al.*, 2023). This section synthesizes the key research questions from these discussions, focusing on particle motion and substrate-borne vibration, their relationship to sound detection, and the effects of behavior and physiology by both fishes and aquatic invertebrates exposed to these stimuli.

Hearing and *hearing effects*: These questions focus on the range of sounds detectable by aquatic animals and implications for anthropogenic sound impacts on hearing capabilities. This area *must include* not only thresholds, but also the very important issues of signal (e.g., frequency and intensity) discrimination, masking, and sound localization. Indeed, these aspects are likely far more significant than hearing threshold determination alone (Popper *et al.*, 2019).

One issue often discussed about potential impacts of anthropogenic sound on marine mammals is temporary threshold shift (TTS) or permanent threshold shift (PTS). Although TTS has been demonstrated in fishes (reviewed in Smith and Monroe, 2016), it has never been tested in aquatic invertebrates. TTS resulting from exposure to intense sounds is not very likely in fishes because it requires longer, and more intense exposure than the animals are ever likely to encounter. PTS is unlikely since fishes repair or regenerate hair cells damaged by intense sounds.

Masking effects from anthropogenic sound are likely very important to consider. These effects have been demonstrated in a few fish species but has yet to be studied in aquatic invertebrates (e.g., Fay, 1974; Hawkins and Chapman, 1975). Such findings strongly suggest that anthropogenic sounds have the potential to decrease detection of biologically important sounds in fishes and result in impacts on behavior, as suggested in Fig. 2 (also see Simpson *et al.*, 2016).

Some of the key research questions about hearing and hearing effects include the following:

- What are the hearing bandwidth and sensitivity of fishes and aquatic invertebrates to particle motion and to substrate-borne vibration?
- Do different taxa of fishes and aquatic invertebrates vary in their ability to detect particle motion and substrate-borne vibration?
- Can fishes and aquatic invertebrates discriminate signals (e.g., intensity, frequency, pulse rate) and localize sound sources?
- How does the presence of maskers affect particle motion and substrate-borne vibration detection in fishes and aquatic invertebrates?
- Does long-term exposure to particle motion or substrate-borne vibration degrade hearing sensitivity in fishes and aquatic invertebrates?

Behavioral effects: It is critical to understand how animal behavior may be altered by the presence of anthropogenic sounds and vibrations. Potential effects may range from alternations to key behaviors such as foraging, reproduction, and territorial defense, as well as changes in sound production and avoidance of biologically important habitats, such as breeding sites. Additionally, anthropogenic sound could disrupt migratory routes to critical breeding sites. Some behavioral effects may be temporary and subside once the anthropogenic sound ceases or as animal habituate, but others may be long-lasting, potentially impacting fitness and survival. Thus, though it is easier to study potential impacts on individual animals, it is also critical to consider how anthropogenic sound may impact species at the population level (e.g., Slabbekoorn *et al.*, 2010).

Some of the key research questions that fit under this broad perspective on behavioral effects include the following:

- Does exposure to anthropogenic particle motion or substrate-borne vibration alter the behavior of fishes or aquatic invertebrates?
- Does prolonged exposure to particle motion or substrate-borne vibration cause fishes to avoid ensonified areas, potentially disrupting migration routes or access to biologically important habitats?
- Do fishes or aquatic invertebrates habituate to anthropogenic particle motion or substrate-borne vibration over time, allowing them to resume normal activities despite ongoing exposure?
- Can fishes or aquatic invertebrates modify their sound production to compensate for changing noise conditions (e.g., exhibit the Lombard effect), as shown in birds and mammals?

Physiological effects: Harder to study, but of considerable importance, are questions that relate to changes in various physiological state—and potentially health and fitness—because of exposure to anthropogenic sounds. These changes may include heart rate, respiratory rate, and body chemistry, such as alternations in stress hormone levels. It is also important to consider both temporary and prolonged changes and how they impact animals. Moreover, it is important to consider that long-term (e.g., chronic) exposure to anthropogenic sound in a large habitat may have the potential to result in population-level effects (e.g., El-Dairi *et al.*, 2024).

Some of the key research questions that fit under this broad perspective on physiological effects include the following:

- Does long-term exposure to anthropogenic particle motion or substrate-borne vibration affect the development of eggs and larvae, influencing growth, maturation, or reproduction?
- Do anthropogenic particle motion or substrate-borne vibration induce physiological changes? How long does it take for these biomarkers to return to normal levels after the exposure has stopped?
- At what sound levels do these effects occur, and what are the thresholds for physiological impact?

IV. AN OVERVIEW OF EXPERIMENTAL DESIGNS FOR STUDYING SOUND EFFECTS ON FISHES AND AQUATIC INVERTEBRATES

Systematic research efforts to address anthropogenic sound impacts on fishes did not begin until the 2000s (review by Popper and Hawkins, 2019), approximately 20 years behind those for marine mammals (e.g., NRC, 1994, 2000). In addition to the lack of public attention being one of the reasons for the late start, a major challenge has been the technological limitations associated with accurately generating and measuring acoustic pressure, particle motion, and substrate-borne vibration in experimental settings (e.g., Gray *et al.*, 2016; Jézéquel *et al.*, 2022a).

Inexpensive hydrophones for detecting sound pressure have been available for many decades, but devices for measuring three-dimensional particle motion and substrate-borne vibration are far newer and tend to be quite expensive and somewhat difficult to use and involve more sophisticated data processing for analysis. Thus, most earlier studies focused on sound pressure measures, even when the animals of interest primarily, or only, detect particle motion and/or substrate-borne vibration.

Another significant challenge is the variability of experimental acoustic environment, as discussed in Sec. III. The problem has been, and continues to be, that the sound field that animals experience differs greatly depending on the experimental setting, complicating both study design and interpretation. For example, the acoustic properties of a laboratory tank are very different from the natural aquatic environment in which fishes live (e.g., Rogers *et al.*, 2016). This complicates not only experimental design, but also analysis of fish responses to sounds since the signals in tanks are, acoustically, quite different than in the wild, even when the identical stimulus is played through an underwater sound source.

Thus, over the years, various experimental settings were developed and used to investigate underwater anthropogenic sound effects on fishes and invertebrates. These approaches can be generally classified under the four following categories: (1) laboratory tanks, (2) in-ground or above-ground tanks/pools, (3) open-water experiments with animals confined in nets or cages, and (4) open-water experiments with free-ranging animals. Each of these environments differs very substantially not only in construct, but also in the acoustic field that can be reliably generated and used and in the kinds of questions that can be asked concerning the experimental animals.

A. Laboratory tanks

Clearly, the easiest setting for a researcher to use is a laboratory tank. These can be relatively small and provide access to animals in an environment that is easily controlled in terms of temperature, light levels, etc. The major advantage of using laboratory tanks is that one can fully control the environmental parameters (such as water temperature, salinity, pH), making the experiments replicable. The small experimental setting with laboratory tanks can also be cost saving as compared to conducting work in a larger area.

However, only larvae or animals of small size can be studied in laboratory tanks. Also, it is extremely difficult to generate and measure vibroacoustic fields in small tanks, as the boundary condition and low-frequency cutoff also distort sound signals (Akamatsu *et al.*, 2002; Parvulescu, 1964).

Nevertheless, specialized acoustic apparatuses have been developed. For example, Halvorsen *et al.* (2011) used a specialized wave tube to investigate tissue injuries of various fish species exposed to simulated pile driving sound (e.g., Halvorsen *et al.*, 2012a; Halvorsen *et al.*, 2012b). The tube had a moving shaker at each end of the tube, allowing it to generate precisely controlled underwater far-field propagating plane acoustic pressure waves and particle velocity within the tube. Therefore, wave tubes could be used to study tissue injuries from intense impulsive sound exposures of small fishes in a controlled laboratory setting.

Other methods can be adopted to arrange the sound source or retrofit the tank to address certain research questions related to fish or invertebrate hearing. For example, generating controlled sound source and/or particle motion can be achieved by carefully selecting the locations of sound sources and with specially designed tank walls (e.g., Rogers *et al.*, 2016). While a source being placed within a small and thin-walled tank would generate high uniform acoustic pressure but small particle motion, having the sound source placed within a thick-walled cylindrical tank would produce high particle motion (e.g., Hawkins and MacLennan, 1976).

A promising new approach is the "tank-in-a-tank" experimental setup—in which a smaller tank containing the experimental animal is housed within a much larger aquarium tank with the sound source—has recently been used to overcome the limitation of small tank acoustics (e.g., Hubert *et al.*, 2022; Hubert *et al.*, 2023; Veith *et al.*, 2024). This design keeps the testing subject in a desired location that can be well measured and characterized and expands the available experimental space while minimizing boundary effects at the air–water interface, improving the reliability of sound propagation in the test environment.

For investigating particle motion or substrate-borne vibration detection by fishes or aquatic invertebrates, specially designed shaker systems have been used (e.g., Fay, 1984; Roberts *et al.*, 2016; Aimon *et al.*, 2021). When conducting experiments on substrate-borne vibrations, it is critical to consider the composition of the substrate in relation to the natural habitat and husbandry requirements of the animal. While some species can be tested without sediment to simplify the vibrational conditions, re-creating complex seabed environments is challenging. Of note, there are many substrates present under water that are not as complex and within which vibrations can travel. For sessile invertebrate species, results of behavioral and/or physiological responses obtained from experiments using laboratory tanks may be extrapolated for natural conditions (e.g., Roberts *et al.*, 2015), with the same behavioral caveats encountered by acoustic studies.

Although the vibroacoustic condition in laboratory tanks can be better controlled using a shaker system or tank-in-a-tank approach, structural coupling with artificial flooring (e.g., concrete floor), water pumps, etc., can introduce unwanted noise and must be carefully considered and mitigated with anti-vibration and isolation materials.

Ultimately, while laboratory tank studies provide valuable insights, findings obtained under this experimental setting cannot necessarily be extrapolated to predict how fishes and invertebrates respond to anthropogenic sound in the wild.

Despite their limitations, laboratory tanks remain an essential tool for investigating specific aspects of acoustic exposure in controlled conditions, particularly when the complexities of vibroacoustic conditions can be managed. These settings can provide valuable insights, particularly for studies focusing on small species, larvae, and sessile invertebrates. Additionally, in the absence of species sensitivity information, laboratory tanks studies could provide initial insights when a large-scale field study cannot be implemented due to funding constraints.

B. In-ground pond/tank or above-ground tank

This experimental setting includes in-ground pond/tanks, above-ground tanks, and small artificial ponds dug into the ground. These are relatively large bodies of water in comparison with the size of subject animals, but this experimental setting still has boundaries (e.g., Song *et al.*, 2021; Jones *et al.*, 2023; Gutscher *et al.*, 2011). Sound sources are deployed in water and are either bottom-mounted or suspended in the water column. This setting allows for more realistic sound propagation while still maintaining control over environmental parameters (e.g., water temperature, pH, salinity), enabling replicable experiments.

Due to the relatively larger size of the environment and the semi-natural condition in comparison to laboratory tanks, these environments can help mitigate some of the acoustic issues associated with smaller tanks. In particular, boundary effects are reduced because the walls are farther from the animals, minimizing signal reflections and distortions.

Additionally, the larger spatial scale means distances within the tank may exceed the wavelengths of biologically relevant sounds. For example, the wavelength of a 200 Hz sound is approximately 7 m in water, which is larger than most laboratory tanks but often smaller than many outdoor ponds.

This experimental setting also could potentially be suitable for studies of responses to substrate-borne vibrations, even if the bottom is not precisely the same as one would find in the marine environment.

The large size of the environment also makes it possible to investigate behavioral and physiological responses to certain species that are sessile or semi-sessile, or small individual or groups of individual animals that typically congregate within a limited area. However, these settings are not suitable for species with large home ranges, long-distance migratory behaviors, or deep-water habitats.

In-ground ponds and large tanks can provide a valuable middle ground between small laboratory tanks and open-water experiments, but they still have spatial limitations that make them unsuitable for wide-ranging or deep-water species. Nevertheless, they offer a more realistic acoustic setting than laboratory tanks while maintaining a degree of environmental control, making them useful for studies on species with relatively localized movement patterns.

C. Open water with animals confined in nets or cages

Under this experimental setting, studies would be conducted in large natural water bodies, such as a river, lake, or coastal marine environments, with animals confined in cages that may be very large (e.g., Sarà *et al.*, 2007; Jézéquel *et al.*, 2022b). This experimental setting utilizes the natural environment so that realistic vibroacoustic signals and fields can be generated. One significant advantage of this method is the ability to deploy sound sources at varying distances and locations, enabling researchers to examine responses based on sound levels, distances, and other contexts—which cannot be easily manipulated in smaller testing environments—such as by Hawkins and colleagues in lochs in Scotland (reviewed in Hawkins and Chapman, 2020). Furthermore, this setup allows for experiments using real-world sound sources (e.g., Popper *et al.*, 2007), providing insights into how animals respond to vibroacoustic stimuli.

Since the test animals remain in an environment that is very similar to their natural environment, results may be more applicable to real-world conditions compared to those obtained in laboratory tanks or artificial ponds. However, the confinement of animals within nets or cages still presents certain limitations, making this experimental setting unsuitable for mobile species that require larger home ranges or for making behavioral observations. Like the experimental setting using in-ground pond/tank as described above, this method is most suitable for sessile, semi-sessile, or naturally aggregating species (e.g., Roberts and Elliott, 2017).

However, it is possible to test some mobile species in large net enclosures, as seen in Mediterranean studies where tuna is kept in very large netted areas (Sarà *et al.*, 2007).

Despite its advantages, conducting experiments in open water presents many challenges including environmental variability. Such factors—including temperature, salinity, currents, and ambient sound levels—generally cannot be controlled, making it challenging to ensure consistency across trials and treatments. In addition, these experimental settings are typically more expensive and difficult to work in as compared to laboratory-based studies or experiments in smaller outdoor ponds/tanks, due to the challenges of setting up and maintaining net enclosures and calibrating/deploying sound sources.

Open-water cage experiments provide a more ecologically valid approach to studying the effects of sound on aquatic animals, but they require careful consideration of species selection, logistical constraints, and environmental variability. This method is most beneficial when studying localized species or when simulating real-world acoustic exposure, but it may not be suitable for highly mobile species or precise physiological measurements, due to the lack of environmental control.

D. Open water with free-range animals

Under this experimental setting, studies are conducted in large natural water bodies, allowing test animals to move freely without physical restraints. This approach is like the open-water cage experiments, except that animals are not confined within a designated area. Researchers can track behavioral responses and movement through direct visual observation (Simpson *et al.*, 2016; Roberts and Laidre, 2019) or electronic tags implanted in test animals (Iafrate *et al.*, 2016; McQueen *et al.*, 2023). However, current tracking methods are effective only within restricted areas, except where sophisticated telemetry networks have been established, such as the system used by Iafrate *et al.* (2016) off the coast of Florida. Additionally, biologging tags can be used to measure internal state changes (e.g., heart rate, body temperature, and electronic brain activity) to identify physiological responses to anthropogenic sounds in open-water settings (Watanabe and Papastamatiou, 2023).

A key advantage of this approach is that behavioral responses, particularly movement patterns, are not influenced by physical confinement. Results obtained from this setting can accurately reflect natural responses to anthropogenic sound, making this method highly suitable for investigating the behavioral and physiological effects of underwater anthropogenic sound in a real-world context.

Therefore, the open-water free-ranging approach provides the most ecologically valid method for studying the effects of anthropogenic sound on fishes and aquatic invertebrates. However, challenging logistics, high costs, and difficulty in controlling environmental variables make this setting less feasible for highly controlled experimental designs. Despite these limitations, it remains a powerful tool for assessing large-scale movement patterns, habitat use, and behavioral and physiological responses to sound exposure in natural conditions.

V. RECOMMENDATIONS FOR DESIGNING EXPERIMENTAL SETTINGS TO INVESTIGATE UNDERWATER PARTICLE MOTION AND SUBSTRATE-BORNE VIBRATION EFFECTS ON FISHES AND INVERTEBRATES

Section III categorized three broad research question areas related to the effects of underwater particle motion and substrate-borne vibration: (1) hearing and hearing effect,; (2) behavioral effects, and (3) physiological effects. The following discussion attempts to address the most suitable experimental settings for each of these effect types. A summary of these discussions is provided in Table I.

Hearing and *hearing effects*: Research questions in this category focus on sound detection and effects of sound on the auditory organs of animals. Assuming that realistic sound pressure or particle motion signals could be generated in small (laboratory) tanks or outdoor tanks/ponds using engineering solutions, it is likely for a study in these settings to obtain data on hearing capabilities (e.g., thresholds, masking, discrimination, localization) of fishes and aquatic invertebrates exposed to controlled stimuli (Popper *et al.*, 2019). However, controlled stimuli used under these experimental settings are likely to be playbacks of acoustic signals that are either broadband or tonal. It is impossible to include realistic anthropogenic sounds, such as *in situ* pile driving sounds, as part of the acoustic stimuli. Therefore, whether playbacks of recorded sounds or computer-generated sounds can be used to obtain data on sound detection capabilities that are comparable to sound exposure in the wild must be carefully evaluated.

Although hearing effects in terms of TTS or PTS are unlikely to be major concerns for fishes and aquatic invertebrates (see Sec. III), auditory masking from anthropogenic sound is one of the hearing effects worth investigating for fishes and aquatic invertebrates. Like the study of sound detection and estimation of hearing threshold, it is possible to conduct research on auditory masking in laboratory tanks and outdoor tanks/ponds by exposing the animals to controlled masking sounds. However, it is unclear whether the results obtained from detection of playback or synthetic sounds with artificial maskers reflects the effects under real situations.

Therefore, we conclude that study of hearing and hearing effects is best conducted in an open-water environment where animals are confined *in situ* under controlled conditions. This approach, combined with behavioral conditioning (e.g., Hawkins and Chapman, 1975, 2020), allows for more ecologically relevant measurements of auditory function.

Behavioral effects: Behavioral effects are modification of the behavioral states that fishes or aquatic invertebrates may exhibit when exposed to anthropogenic particle motion or substrate-borne vibration. The modification of behavioral states includes, but not limited to, ceasing certain

TABLE I. A summary of experimental settings that are appropriate to address broader research questions of anthropogenic particle motion and substrate-borne vibration impacts on mobile fishes and mobile and sessile aquatic invertebrates. 1, not appropriate; 2, appropriate with consideration; 3, most appropriate).

Broad research questions	Experimental settings			
	Laboratory tank	Outdoor tank/pond	Open-water–confined animals	Open-water– free-ranging animals
Hearing and hearing effects	Mobile: 2 Sessile: 2	Mobile: 2 Sessile: 2	Mobile: 3 Sessile: 3	Mobile: 1 Sessile: 1
Behavioral effects	Mobile: 1 Sessile: 2	Mobile: 2 Sessile: 3	Mobile: 2 Sessile: 3	Mobile: 3 Sessile: 3
Physiological effects	Mobile: 1 Sessile: 2	Mobile: 2 Sessile: 3	Mobile: 2 Sessile: 3	Mobile: 3 Sessile: 3

biologically important activities, such as feeding or mating behavior (e.g., ceasing spawning related chorus), avoiding biologically important habitats, or changing migration routes.

Behavioral effects that relate to the change of movement and migration are best studied in open-water experimental settings with free-ranging animals. One may argue that certain behavioral changes that do not require the movement of an animal, such as cessation of feeding or mating behavior, could be studied in a laboratory tank or outdoor tank. However, the potential for abnormal behaviors when keeping a mobile species in a captive enclosure could lead to abnormal behavior (see review by Smith *et al.*, 2024) may impact the results from such experimental settings. Nevertheless, it is feasible to design a behavioral response study on species of low mobility or fully sessile aquatic species, if abundant care is taken in designing conditions, which closely mimics its natural habitat (Branscomb and Rittschof, 1984; Choi *et al.*, 2013).

Physiological effects: Physiological effects are changes in vital states (e.g., heart rate, respiratory rate, metabolism rate, etc.) and body chemistry (e.g., stress hormone). Like experimental designs for behavioral effect studies, it is best to use an open-water setting with free-ranging animals for mobile species. For example, an animal may choose to move away from the sound source, and the type and/or level of physiological stress it may experience in its natural environment would be impossible to observe under a confined situation. Moreover, wild fishes or mobile invertebrates may exhibit certain physiological responses by being kept in an enclosure (see review by Smith *et al.*, 2024). However, it is also possible that physiological effects from anthropogenic particle motion or substrate-borne vibration could be studied on low mobility or sessile invertebrates in a confined enclosure if the environment being test closely resembles their natural habitat.

VI. CONCLUSIONS

There has been great increase in awareness of underwater anthropogenic sound impacts on fishes and aquatic invertebrates in the past decade; research efforts and funding to address issues related to anthropogenic sound are still lacking in comparison to comparable studies of marine mammals. Moreover, most of the studies addressing hearing and sound effects use species that are not ecologically or economically important, and do not provide data applicable to those species of value to the ecosystem or as food for humans (e.g., goldfish, zebrafish). Given the high biological diversity of fishes and aquatic invertebrates in comparison to marine mammals, results from existing studies may not be applicable or relevant to the species that are of highest interest for regulatory agencies. Therefore, selecting species for study is a fundamental issue and species selection must be a priority to ensure that research findings are relevant to regulatory agencies and conservation efforts.

Among various questions that need to be answered regarding the underwater sound effects, we identified three broad areas for consideration: (1) hearing and hearing effects, (2) behavioral effects, and (3) physiological effects. The design of experiments to address these topics should carefully consider both technical feasibility and biological relevance. This includes the accurate generation, calibration, and measurement of underwater vibroacoustic fields, as well as accommodating species-specific biological factors, such as movement patterns, daily ranges, and natural behaviors.

Among the four of the experimental settings analyzed, we consider open-water settings to be the most appropriate for addressing key research questions across all three perspectives. Open-water settings not only are the best solution for introducing real-world sound source for testing, they also provide a natural environment that would not be available in laboratory tanks or outdoor tanks/ponds, thereby eliminating certain unknown factors that may influence results.

At the same time, we very much appreciate that doing experiments of the type we recommend is also difficult and very expensive. Considering the limited amount of funding available (see Sec. VI A), it would be worthwhile to develop a designated research site (or a few sites) with programmatic rolling permit approvals where experiments could be conducted in "semi-wild" conditions: environments that simulate open-water conditions (at least to some degree) while being carefully calibrated and acoustically well-characterized. Such sites could enhance the reliability of research findings and facilitate better extrapolation to real-world conditions.

Finally, it also would be efficient and useful to develop tank environments that could be used widely but which are designed to provide the best possible acoustic environment, are easy to use, and provide data that could be extrapolated between different laboratories.

A. What work should be done?

As highlighted throughout this paper, one of the real issues in understanding the potential impacts of anthropogenic sound on fishes and aquatic invertebrates is the disproportionate focus on marine mammals in research funding. Despite the critical ecological and economic importance of fishes and aquatic invertebrates, these groups have received minimal funding and research attention compared to marine mammals.

Unfortunately, this imbalance is unlikely to change soon, meaning that limited financial resources will continue to constrain the scope of studies needed for fishes and invertebrates to address key knowledge gaps. Moreover, the current nature of research funding is to have different investigators doing studies on a wide range of animal groups and asking a wide range of questions. This approach yields a very limited amount of usable data that is "spread thin" and does not provide the answers needed to make truly informed decisions as to potential impacts of anthropogenic sound on fishes and aquatic invertebrates.

Therefore, our final suggestion is to establish an international mechanism to pool research priorities, and, if feasible, funding. (Though we do recognize the challenges of developing and coordinating funding by a single international group.) By coordinating resources and expertise, the scientific community could: (1) identify the highest priority species and research questions, ensuring that studies focus on species of ecological, economic, and regulatory significance, (2) strategically fund projects that yield the most impactful and applicable data, rather than spreading resources thinly across numerous, less-focused studies, and (3) facilitate co-funding from multiple sources, maximizing financial efficiency and allowing for more ambitious, large-scale investigations.

Our point is that over the next 5–10 years, we desperately need data on impacts of anthropogenic sound on species that are focal to many ecosystems and that humans consume. We need to inspire the funding entities to develop creative and collaborative strategies to maximize use of available resources. By working across institutions, countries, and funding agencies, the scientific community can ensure that limited funds are directed toward answering the most pressing questions about the impact of anthropogenic sound on fishes and aquatic invertebrates.

B. Anthropogenic sound in a broader context

One issue regarding anthropogenic signals is that studies on aquatic animals tend to focus on a single type of signal, whether it be sound (as addressed in this paper), light, chemicals, etc. (Thomsen and Popper, 2024). Most studies on fishes have focused on sound in isolation, even though these animals are often simultaneously exposed to anthropogenic light, chemicals, and other environmental changes.

Each of these anthropogenic signals alone may result in some kind of response, but the responses may be very different when animals are exposed to several different signals at the same time. For example, a fish or crab exposed to the sound of a boat motor may exhibit one type of behavioral response, while the visual presence of the boat (or its shadow) may trigger a different response. When both stimuli are presented together, the combined response may be entirely distinct from the response to either stimulus alone. Considerable effects are being made in many terrestrial animal studies to think about a broader range of anthropogenic signals that may "interact" in how they ultimately impact animals and elicit responses (Buxton *et al.*, 2020; Hammond *et al.*, 2020; Thomsen and Popper, 2024).

This paper (and many others) focuses on anthropogenic sounds in the marine environment (e.g., Popper and Hawkins 2012, 2016; Popper *et al.*, 2024). However, we suggest that investigators in the future need to think in terms of complexes of anthropogenic signals when trying to understand the impact of any one anthropogenic signal (Thomsen and Popper, 2024). Although controlled experiments often isolate a single variable, researchers must remain aware that in natural environments, animals are exposed to multiple, overlapping anthropogenic stimuli. Understanding how these combined signals affect behavior, physiology, and survival is essential for accurately assessing the true impact of human activity on aquatic life. By integrating multi-sensory research approaches, future studies can provide more ecologically relevant insights and help inform effective conversation and management strategies.

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AUTHOR DECLARATIONS
Conflict of Interest

The authors have no conflicts to disclose. All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations.

DATA AVAILABILITY

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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