The importance of particle motion to fishes and invertebrates

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This paper considers the importance of particle motion to fishes and invertebrates and the steps that need to be taken to improve knowledge of its effects. It is aimed at scientists investigating the impacts of sounds on fishes and invertebrates but it is also relevant to regulators, those preparing environmental impact assessments, and to industries creating underwater sounds. The overall aim of this paper is to ensure that proper attention is paid to particle motion as a stimulus when evaluating the effects of sound upon aquatic life. Directions are suggested for future research and planning that, if implemented, will provide a better scientific basis for dealing with the impact of underwater sounds on marine ecosystems and for regulating those human activities that generate such sounds. The paper includes background material on underwater acoustics, focusing on particle motion; the importance of particle motion to fishes and invertebrates; and sound propagation through both water and the substrate. Consideration is then given to the data gaps that must be filled in order to better understand the interactions between particle motion and aquatic animals. Finally, suggestions are provided on how to increase the understanding of particle motion and its relevance to aquatic animals. © 2018 Acoustical Society of America. https://doi.org/10.1121/1.5021594

I. INTRODUCTION

A. Overview

Underwater sounds[1] generated by human activities (e.g., Fig. 1) have the potential to affect aquatic animals adversely. While much of the concern regarding man-made sound by regulators and others has focused upon effects on marine mammals, effects upon the vastly greater biomass of fishes and invertebrates, which provide food for the mammals (as well as for humans!), are also critically important and of growing interest (e.g., Popper and Hastings, 2009; Halvorsen *et al.*, 2012c; Hawkins and Popper, 2014; Morley *et al.*, 2014; Popper *et al.*, 2014; Hawkins *et al.*, 2015). A very important issue, however, is that assessments of the potential impact of sound on fishes and invertebrates have often overlooked key factors, including the sensitivity of many of these animals to the particle motion that accompanies the transmission of the sound, rather than the sound pressure. The intent of this paper is to bring the issue of particle motion to the forefront, raise the most important issues, and then suggest approaches to ensure that the importance of particle motion is better understood and fully taken into account in developing guidelines for evaluating the potential effects of sound on fishes and invertebrates.

Many of the acoustic impact assessments carried out on fishes and invertebrates in the past cannot be considered satisfactory because they only considered sound pressure (Hawkins *et al.*, 2015; Hawkins and Popper, 2016; Nedelec *et al.*, 2016). Explanations from regulators as to why such assessments have ignored particle motion include the lack of particle motion measurement standards, lack of easily used

and reasonably priced instrumentation to measure particle motion, and lack of sound exposure criteria for particle motion (e.g., see Popper *et al.*, 2014). However, neither the industries creating underwater sound, nor the regulators responsible for reducing the adverse effects upon aquatic animals, have taken actions to remedy these deficiencies, despite the growing understanding that particle motion is critical to understanding the importance of sound to fishes and invertebrates.

It is therefore important to develop protocols for monitoring particle motion, and to determine those levels of particle motion that have potentially adverse effects in terms of increased mortality, injury to tissues, effects on hearing abilities, and/or changes in behavior and physiology. Currently, sound exposure criteria for fishes and invertebrates have been derived from often poorly designed and controlled studies that have not taken account of the sensitivity of these animals to particle motion (discussed in detail in Popper and Hastings, 2009; Popper *et al.*, 2014; Hawkins *et al.*, 2015). Thus, there is an urgent need to define sound exposure criteria for fishes and invertebrates in terms of particle motion as well as sound pressure, as it will be particle motion that they respond to in most instances.

B. The purpose of this paper

This paper considers the importance of particle motion to fishes and invertebrates and the steps needed to improve knowledge of its potential effects (and, ultimately, its mitigation). It is primarily aimed at scientists investigating the impacts of sounds on fishes and invertebrates, but it is also very relevant to regulators, to those preparing environmental impact assessments (EIAs), and to those industries creating underwater sounds. It is also important that the significance
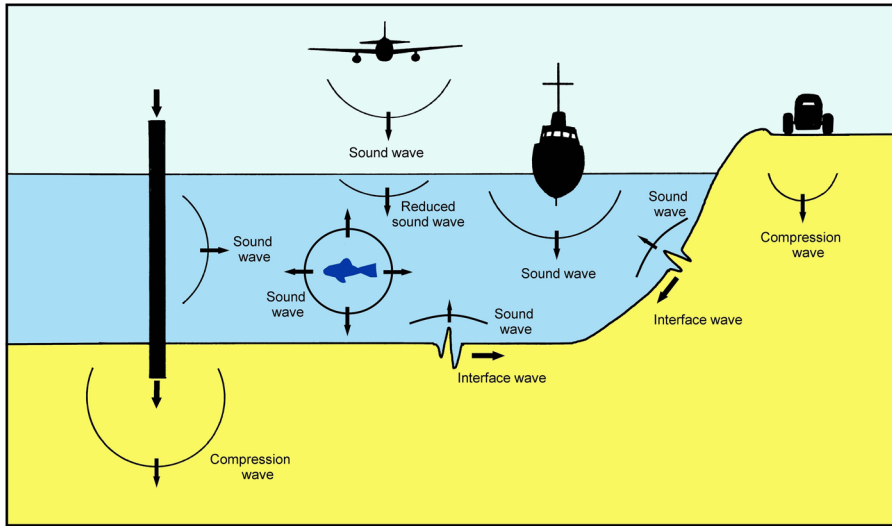
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of particle motion is explained to non-specialists with an interest in environmental impacts.

Thus, the overall aim of this paper is to ensure that proper attention is paid to particle motion as a stimulus when evaluating the effects of sound upon aquatic life (also see Nedelec et al., 2016). Directions are suggested for future research and planning that, if implemented, will provide a far better scientific basis for evaluating and mitigating the impact of underwater sounds on marine ecosystems, and for regulating those human activities that generate such sounds.

In this review we not only look at recent literature, but also examine older literature that addresses many of the current issues in fish bioacoustics. It seems that much of the older literature on fish hearing is not well known to newer investigators. However, there is a wealth of very important material in that literature, and it has much to teach, and also often includes many stimulating ideas and finding. We encourage students and others to examine this literature in some detail.

The paper is divided into several parts. The following three sections provide a background on underwater acoustics that focuses on particle motion. These sections include the importance of particle motion to fishes and invertebrates, sound propagation, and the concept of waves that travel through and on the substrate.

The subsequent four sections focus on issues of information needed—the data gaps—that must be filled in order to ultimately understand the interactions between particle motion and marine animals. In each issues section, recommendations are made as to the most important gaps in knowledge and the studies that are required to start to fill these gaps.

The concluding section provides suggestions on how to increase the understanding of particle motion and its relevance to aquatic animals. Critically, and considering that funding is not easy to get, an approach is proposed whereby efforts are focused on promoting better knowledge of particle motion, rather than supporting research projects that do not really help to focus understanding of the potential effects of underwater sounds on fishes and invertebrates.

Finally, it is important to point out that much of what is discussed in this paper focuses on fishes rather than invertebrates—even though invertebrates are of equal concern with regard to potential effects of sound (and especially particle motion). The difference in treatment is not because of our prejudice as fish biologists, but because of the lack of information about all aspects of invertebrate bioacoustics (as compared to fishes and terrestrial invertebrates), including sound detection, acoustic behavior, and effects of man-made sounds. While some progress has been made in these areas in recent years (e.g., Morley et al., 2014; Edmonds et al., 2016; Solan et al., 2016; Roberts and Elliott, 2017), there are still insufficient data to provide the kinds of guidelines available for fishes (albeit, even those are limited, as discussed below) and marine mammals (Southall et al., 2007; Hawkins and Popper, 2014; Hawkins et al., 2015).

II. WHAT IS PARTICLE MOTION?

A. Underwater sound

Sound is generated by the movement or vibration of objects immersed in water, or any other compressible medium, and results from the inherent elasticity of the medium.[2] As the source moves, kinetic energy (KE) is imparted to the medium and in turn is passed on, traveling as a propagated elastic wave within which particles of the medium are moved back and forth. The term "particle" denotes the smallest element of the medium that represents the medium's mean density. It is important to note that the particles of the medium do not travel with the propagating sound wave, but instead move back and forth over the same location. At the same time, particles transmit their oscillatory motion to their neighbors. The particles oscillate along the line of transmission, and are accompanied by waves of compression (increase in pressure) and rarefaction (reduction in pressure)—referred to as the sound pressure. Particle motion can be specified in terms of the particle displacement, particle velocity, or particle acceleration (ISO/DIS, 2017).

B. Sound pressure and particle motion

The total energy contained in a sound wave consists of the sum of its potential energy (PE) and its KE. The PE

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arises from the compression and expansion of the fluid and hence is related to the sound pressure, whereas the KE arises from the particle motion. In the absence of acoustic boundaries (under free-field conditions, such as in the ocean at some distance from the surface and seabed), the sound pressure radiated from a simple acoustic source falls off as $1/r$, where r is the distance from the source (Harris and van Bergeijk, 1962; Ainslie and de Jong, 2016). Far from the source (in the so-called acoustic "far field"), the energies associated with acoustic pressure and acoustic particle velocity are equal (KE = PE), whereas close to the source (in the acoustic "near field"), the particle velocity component of the field contains more energy (KE > PE). The rate of decline of the particle velocity in the near field depends on the nature of the sound source, and its movement pattern [e.g., whether it is a monopole, dipole, or quadrupole; Harris and van Bergeijk (1962)]. The distance of the transition point is also related to the frequency of the signal, with the distance greater for lower frequencies (van Bergeijk, 1964).

In all cases, the actual to-and-fro particle displacements that constitute the sound are extremely small, on the order of nanometers. It is commonplace to characterize a sound by the sound pressure alone, since it can easily be measured with readily available hydrophones, and then to estimate the particle motion, if required, from the sound pressure measurements and a knowledge of the acoustic properties of the medium. This is relatively easy in an acoustic free-field where there are no boundaries to sound propagation. However, close to acoustic boundaries like the seabed and the sea surface, and in the shallow waters that are inhabited by many fishes and invertebrates, the relationship between pressure and particle motion becomes complex (Pierce, 1981) and it is necessary to measure particle motion directly. As will be discussed in Sec. VII A, measurement of particle motion is, for a variety of reasons, rather more difficult than measuring sound pressure. This has led to a dearth of data on particle motion and its importance to, and potential effects upon, animals.

Finally, it should be noted that particle motion, whether it is expressed as particle displacement, velocity, or acceleration, differs from sound pressure in that it is inherently directional, usually taking place along the axis of transmission. The particle displacement, velocity, and acceleration are all vector quantities. A single particle motion detector, if suitably constructed to resolve a signal into its directional components, can detect the axis of propagation. Sound pressure, on the other hand, is a scalar quantity, acting in all directions, therefore requiring several spaced hydrophones to determine the direction of propagation.

C. Why is particle motion important?

1. Detection of sounds by fishes and invertebrates

Sound is important to fishes and to many invertebrates (e.g., Hawkins, 1993; Popper et al., 2001). They may, for example, use sound to communicate with one another, detect prey and predators, navigate from one place to another, and select appropriate habitats (e.g., Tavolga, 1971; Hawkins and Myrberg, 1983; Ladich and Winkler, 2017). The animals essentially glean general information about the environment by detecting and using what is called the "acoustic scene" or soundscape, which, for fishes and invertebrates, would include particle motion (Fay and Popper, 2000; Fay, 2009). In effect, sound detection provides animals with three-dimensional information from a larger space around them than is possible using vision, olfaction (the sense of smell), or electroreception. Many animals, both on land and in the sea, carry out auditory-scene analysis—they break down the overall sound field into separate elements to analyse the world around them and assign the different elements to particular sources (Bregman, 1994; Fay and Popper, 2000).

2. The inner ear as a detector of particle motion

Early modeling suggested that the basic sense organs used to detect sounds (the otolith organs in the ears of fishes, and the various organs used by invertebrates) are actually sensitive to particle motion rather than to sound pressure (Dijkgraaf and Verheijen, 1950; Dijkgraaf, 1952). This is clearly seen in the "design" of the inner ear of fishes, as it closely resembles a mass-loaded inertial accelerometers and other devices, such as geophones, that are used for measurement of particle motion (e.g., Rodgers, 2011; Krysl et al., 2012; Schilt et al., 2012; Schulz-Mirbach and Ladich, 2016). Moreover, the sound detecting structures in various invertebrates, while more diverse than in fishes and less well studied, also are clearly particle motion detectors (e.g., Breithaupt and Tautz, 1990; Packard et al., 1990; Budelmann, 1992; Kaifu et al., 2008, 2011).

The basic structure of the inner ear of fishes is the same as other vertebrates, with three semicircular canals and three otolith organs (Fig. 2). The otolith organs, the accelerometers of teleost fishes, each contain a dense, often highly sculptured calcareous structure (Fig. 2), which sits in close proximity to a sensory epithelium (or macula) that is composed of mechanosensory hair cells (Figs. 3 and 4). Lying between, and loosely connecting the epithelium and otolith, is an otolith membrane (Fig. 3). Non-teleost fishes (and elasmobranchs) and all terrestrial vertebrates have a mass of sense otoconial crystals embedded in a gelatinous membrane that serves the same function as the otolith, but without a species-specific shape (Gauldie, 1996; Popper et al., 2005a).

The body of a fish is very similar in average density and elasticity to water and, as a consequence, the tissues move back and forth with the acoustic particle motion. The otoliths (or otoconial masses) within the ears of fishes function like accelerometers to detect this motion, with the otoliths functioning as a "stationary mass" due to their greater density than the surrounding tissues. Most critically, the sensory hair cells in fishes, as in all vertebrate ears (and the lateral line of fishes) produce electrical signals in response to bending of the ciliary bundles that sit on the apical surfaces of the cells (Fig. 4) (e.g., Flock, 1964b; Hudspeth and Corey, 1977). This bending takes place as a result of the relative motion between the epithelium and the denser overlying otolith, and thus responds to the particle motion within the sound field. It should be noted that the otolith organs of fishes, like those of terrestrial mammals, can also detect linear accelerations (the
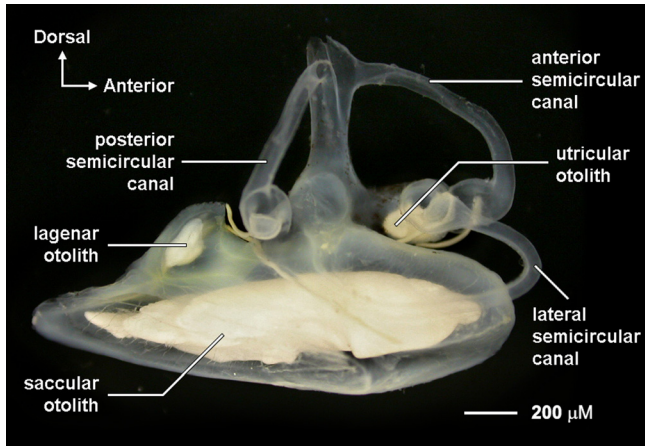
FIG. 2. (Color online) Inner ear of *Antimora rostrata*, a member of the deep-sea cod family Maridae. The otoliths are each located in a sac bearing the same name. The otolith organs are associated with hearing and positional senses (see Platt, 1983). The sensory epithelium of the saccule is not seen here since it is on the medial side of the organ. See Fig. 5 which shows the medial side of the ear of *Amia calva*, showing the sensory epithelium of the saccule and the innervating eighth cranial nerve. The three semicircular canals are part of the vestibular system which is associated with position senses. The "swelling" at the base of each of the semicircular canals is the sensory region for that canal—the crista. For a fuller description of the ear in *Antimora* see Deng *et al.* (2011) (picture copyright 2017 Xiaohong Deng, all rights reserved).

rate of change of velocity as the body moves), and also the orientation of the body with respect to the Earth's gravitational field (Lowenstein and Roberts, 1949; Lowenstein, 1971; Platt, 1983).

The notion that the inner ears of fishes are basically particle motion detectors is supported by a variety of experimental studies. Experiments on Atlantic cod (*Gadus morhua*) and sculpin (*Cottus scorpius*) carried out in midwater in the sea used the near field effect to examine the relevant stimulus (Enger and Andersen, 1967). Close to a sound source, within the near field, large particle motions may accompany relatively small sound pressures (Pumphrey, 1950; Harris and van Bergeijk, 1962). Atlantic cod and sculpin were held at different distances from a sound source and electric potentials (microphonic potentials) were recorded from the sensory hair cells of the inner ear in response to

sounds. In Atlantic cod, the amplitudes of these potentials were proportional to the measured sound pressures, regardless of the distance from the source. In the sculpin, potentials could be recorded only within 1 m of the loudspeaker. Enger and Andersen (1967) were able to estimate the particle motion levels, as the experiments were carried out under free field conditions. They concluded that the Atlantic cod, a fish with a swim bladder, was able to detect sound pressure. The sculpin, a species that does not have a swim bladder, detected only the large particle motion levels found close to the source.

Subsequent experiments in the sea to determine auditory thresholds for Atlantic cod at different source distances (Chapman and Hawkins, 1973) showed that the auditory thresholds were largely independent of the distance of the sound source over the range from 1.7 to 50 m, confirming that cod are sensitive to sound pressure. However, a change-over to particle motion sensitivity was noted at frequencies below 50 Hz when the sound source was moved to within 1 m of the fish. Similar experiments with two species of flatfish that do not have swim bladders (*Pleuronectes platessa* and *Limanda limanda*) (Chapman and Sand, 1974) showed that they were sensitive to particle motion throughout their auditory frequency range.

A similar idea arose from experiments with goldfish (*Carassius auratus*) by Fay and Popper (1974) using a standing wave tube in which the ratio of sound pressure to particle motion could be manipulated. The investigators demonstrated that above several hundred hertz goldfish were using sound pressure for detection. However, if the pressure detecting structure, the swim bladder, was removed, the fish only detected particle motion and they could not hear sounds above several hundred hertz.

In a second study, Fay and Popper (1975) found similar results for another species that hears well, the channel catfish (*Ictalurus punctatus*). However, they also showed that the African mouthbreeder (*Tilapia macrocephala*), a species with no specialized structures to enhance hearing, only detected particle motion even when the swim bladder was present.
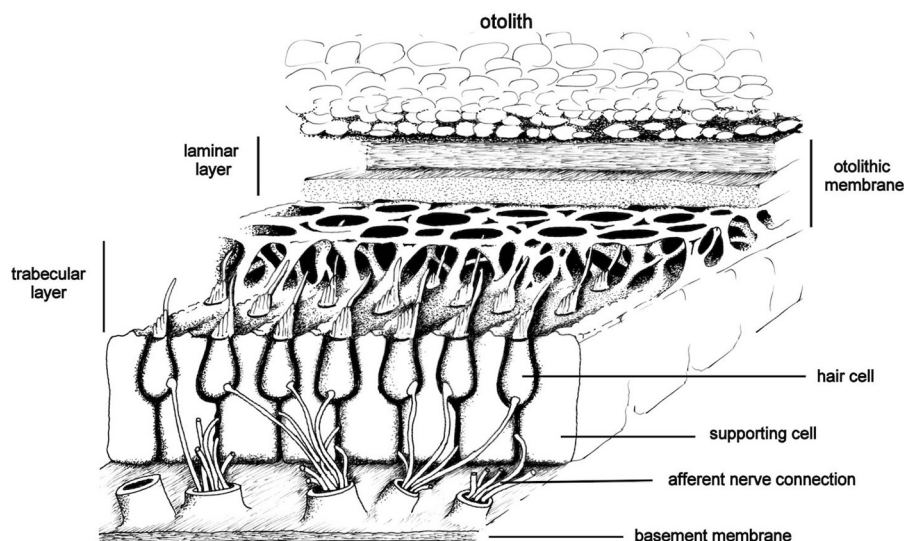
FIG. 3. The sensory epithelium of the Atlantic cod (*Gadus morhua*). The epithelium contains sensory hair cells and supporting cells and is innervated by the eighth cranial nerve. Ciliary bundles on the top of the sensory cells are embedded in the otolith membrane which also connects to the overlying otolith. The exact structure of the otolith membrane is not known, but it generally appears to be gelatinous and allows relative motion between the otolith and epithelium. See Fig. 4 for related images. Figure copyright 2017 Anthony D. Hawkins, all rights reserved.
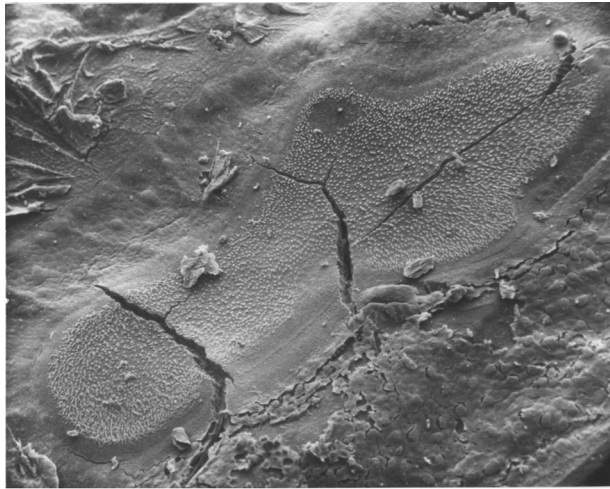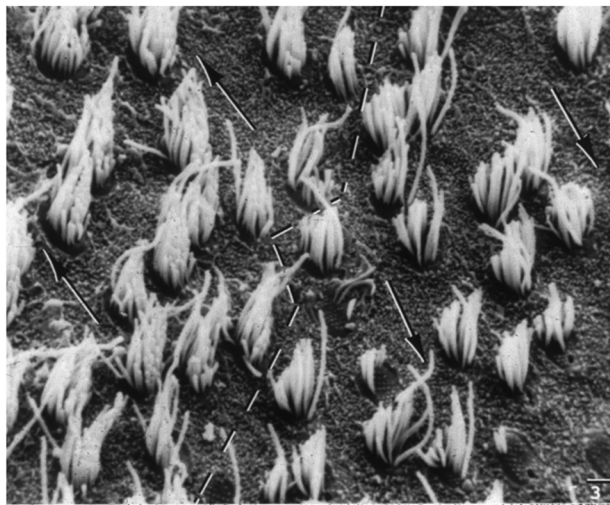
FIG. 4. (a) Sensory epithelium from the saccule, the primary hearing otolith organ, in a gobiid fish. The white dots on the epithelium represent individual hair cell ciliary bundles. (b) Higher magnification scanning electron micrograph of the saccular epithelium of a lizardfish. Each ciliary bundle has one long kinocilium on one side, and a series of graded stereocilia. Bending of the bundle along the axis from the kinocilium through the stereocilia results in maximum hyperpolarization of the sensory cell. Bending in the other directions results in a graded response that depends on the axis of bending with minimal response when bending is perpendicular to the primary axis of hyperpolarization. The cells on the epithelium are divided into orientation groups, with all cells in one region oriented in one direction and in other regions oriented in other directions, as indicated by the arrows. The dashed line shows the sharp division between orientation groups.

Other experiments have been carried out in the sea and in specially-designed acoustic tanks to ascertain which stimuli are most important to fishes (Cahn *et al.*, 1969; Hawkins and MacLennan, 1976; Fay, 1984). Results have confirmed that the otolith organs respond to particle motion.

These studies also showed that detection of frequencies above several hundred hertz, which only occurs in some species, is a function of the presence of a gas-filled chamber, most often the swim bladder, lying in close proximity to the ear (Sand and Hawkins, 1973; Fay, 1975; Popper *et al.*, 2003). Indeed, many teleosts possess a modification of the anterior end of the swim bladder which may influence the functioning of the ear (e.g., Alexander, 1966). Best known are fishes of the order Cypriniformes (the ostariophysan fishes, which includes the aforementioned goldfish and catfish), where the anterior end of the swim bladder is coupled to the ear by a chain of movable bones, the Weberian ossicles (Weber, 1820; Alexander, 1964). Expansion or contraction of the anterior chamber of the swim bladder results in motion of the ossicles (Evans, 1930; Poggendorf, 1952; Alexander, 1964). This motion subsequently causes fluid motion in a small sinus, filled with perilymph, which is then communicated to an endolymph-filled transverse canal connecting with the lumen of both saccules of the inner ear.

A similar enhancement of hearing occurs in fishes that have close contact between the anterior end of the swim bladder and the inner ear, or where there is a gas bubble intimate to the ear (e.g., Coombs and Popper, 1982; McCormick and Popper, 1984; Fletcher and Crawford, 2001; Schulz-Mirbach *et al.*, 2013b). Such conditions are found across a wide range of teleost taxa, and even closely related species may show diversity in swim bladder-inner ear relationships associated with differences in hearing capabilities (Coombs and Popper, 1979).

For example, the system in clupeid fishes (herrings and relatives) such as (*Clupea harengus*) includes a pair of pro-otic bullae, each divided into gas- and liquid-filled parts by a membrane under tension and making up part of the wall of the utricle (O'Connell, 1955; Allen *et al.*, 1976). The gas-filled part of the bulla is connected to the swim bladder by a long gas-filled duct. Motion of the membrane in the bulla generates motion in the perilymph which is transmitted to the sensory epithelium of the utricle (and perhaps the saccule and lagena), displacing the sensory processes of the hair cells relative to the overlying otolith (Higgs *et al.*, 2004). It is thought that this mechanism is involved in detection of sounds to over 4000 Hz in all clupeids (Enger, 1967; Mann *et al.*, 2001), and into the ultrasonic range (to over 100 kHz) in some species (Mann *et al.*, 1998).

In conclusion, it appears that the swim bladder and other gas-filled organs in fishes essentially act as acoustic transformers, converting sound pressure into particle motion. Incident sound pressures cause the compressible body of gas within the organ to pulsate, generating a much higher amplitude of particle motion than would otherwise have existed (Alexander, 1966). The locally high particle motion may be coupled directly to the otolith organs of the inner ear, or may simply propagate through the surrounding tissues to stimulate the otolith organs (Sand and Hawkins, 1973). Thus, in such fishes, in addition to receiving the particle motion directly from the source, parts of the otolith organs also receive indirect stimulation from these gas-filled organs. Detection of the indirect signal enables the fish to hear higher frequency sounds than would be possible from reception of the direct particle motion alone, thereby expanding the frequency range detected and increasing the sensitivity of hearing so that the fish can hear lower intensity sounds.

There is still, however, a lack of knowledge of the pattern of otolith motion relative to the sensory epithelium in response to stimulation by particle motion. Both measurements of otolith movements (Sand and Michelsen, 1978) and

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modeling of the motion of complicated shapes under plane harmonic wave excitation (Krysl et al., 2012) provide evidence that the movements are more complex than a simple back-and-forth oscillation in the direction of the progressive sound wave. Rocking motion appears to take place with some otoliths, and this may provide stimuli that the fish might process to provide additional directional cues. Indeed, one explanation for the evolution of the very complex species-specific shapes of otoliths seen in different species [beautifully illustrated by Retzius (1881) and Deng et al. (2013)] may be that different shapes produce different movement patterns, and different hearing capabilities or mechanisms (e.g., Popper et al., 2005a; Tuset et al., 2016).

Finally, there is much less information available on the ability of aquatic invertebrates to detect sounds. However, they do have a variety of different organs all of which are most likely responsive to particle motion rather than to sound pressure (e.g., Cohen and Dijkgraaf, 1961; Breithaupt and Tautz, 1990; Goodall et al., 1990; Popper et al., 2001). These may include hairs on the body that respond to mechanical stimulation via associated sensory cells, chordotonal organs associated with joints that may respond to low frequency sounds or, in the cases of some crabs, vibrations transmitted through the exoskeleton from the substrate (e.g., Salmon et al., 1977). In addition, crustaceans may have organs called statocysts, which include dense structures (statoliths) associated with cells that, in some ways, resemble the sensory hair cells in vertebrate ears. While still not fully clear, such receptor systems appear to have an equilibrium function and also have the potential to detect particle motion, and may even be directionally sensitive (e.g., Cohen and Dijkgraaf, 1961; Cate and Roye, 1997; Popper et al., 2001).

D. Directional hearing and the importance of particle motion

One of the primary roles of the vertebrate auditory system (and probably that of invertebrates—though this is much less studied) is to determine the position of a sound source in relation to that of the animal (Masterton et al., 1969; Fay and Popper, 2000; Heffner and Heffner, 2016). Animals are able to determine the direction, and in some cases the distance, of sound sources such as predators and prey, in the environment, and respond appropriately. In the earliest studies, it was thought that fishes could not localize sound. Indeed, von Frisch (1938) suggested that a fish with a single sound pressure receptor, the swim bladder, was not able to determine sound direction, as the sound pressure at any single point contains no information about the direction of sound propagation. Later, it was proposed that directional hearing was restricted to the acoustic near field (van Bergeijk, 1964) where the sensitive lateral line system was thought to play a part (Harris and van Bergeijk, 1962).

Contrary to Harris and van Bergeijk (1962), Dijkgraaf (1960) pointed out that a particle motion detector, such as the inner ear in fishes, is inherently directional in its response since the stimulation of the hair cells by movement of the otolith would vary with the direction of the incident sound
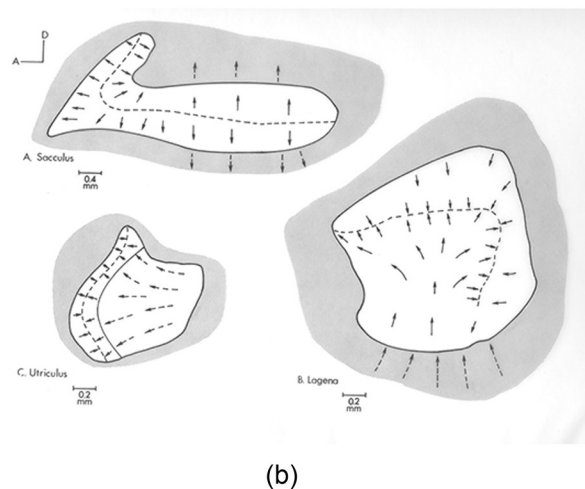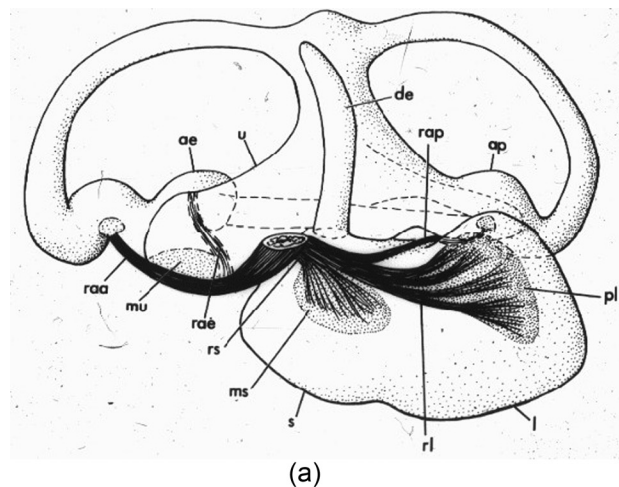

(a)

(b)

FIG. 5. Right ear (a) and sensory hair cell orientation patterns from the three otolith organs (b) in the bowfin, *Amia calva*. (Note, anterior is to the left and dorsal to the top.) The arrows (b) show the direction of orientation of the hair cells in that region (regions separated by dashed lines), with the kinocilium being on the side of the cells indicated by the arrow tips (see Fig. 3). The stippled areas are regions with low hair cell density. Note that the utricle lies parallel to the horizontal axis of the fish while the saccule and lagena maculae lie on the animal's vertical plane. Ear from Retzius (1881). Hair cell orientation from Popper and Northcutt (1983). de – endolymphatic duct; ae, ap – ampullae of semicircular canals; l – lagena; ms – saccular macula; mu – utricular macula; pl – lagena macula; s – saccule; raa, rap, rl, roe, rs – parts of eighth cranial nerve; u – utricle.

wave. This was confirmed by Enger et al. (1973), who showed that the magnitude of the microphonic potentials generated by a localized group of hair cells varied with the angle of stimulation by particle motion.

This idea was strongly supported by the discovery that the ciliary bundles on the sensory hair cells are morphologically polarized (Figs. 4 and 5) (Flock, 1964b; Dale, 1976; Popper, 1976, 1977). As a result, the physiological level of response of each cell depends on the direction of stimulation, with maximum response when the bundle is bent along the axis of the kinocilium toward the stereocilia, whereas minimal response occurs when the bending is perpendicular to that axis (Flock, 1964a). Generally, the hair cells on the otolithic organ epithelia are divided into "orientation groups," where all the cells in one region are oriented in the same direction [Fig. 4(b); Fig. 5(b)]. Thus, all of the cells in a

single group will respond in the same way to a stimulus coming from a particular direction, while cells in different orientation groups will give a lower level response to the signals from the same direction.

Following these observations, it was proposed that by combining and comparing the different levels of response from groups of hair cells of differing orientation as they respond to a signal from a particular direction (Figs. 5 and 6), the central nervous system of the fish is potentially able to extract the relative direction of motion of the overlying otolith and thus determine the direction of the sound (particle motion) relative to the fish (Enger et al., 1973; Popper et al., 1988; Rogers et al., 1988; Popper et al., 2003). Moreover, the ability to determine direction is potentially further refined since the six otolith organs of a fish (three in each ear) lie in different planes (e.g., Schulz-Mirbach et al., 2013a; Schulz-Mirbach and Ladich, 2016), thereby providing additional directional input (Enger et al., 1973; Rogers et al., 1988).

Experimental data on sound localization show that fishes can, indeed, localize sounds and also discriminate sounds from different directions [reviewed in Fay (2005) and Sand and Bleckmann (2008)]. Various behavioral studies have shown that teleost fishes are able to discriminate between spatially separated sources under far-field conditions, both in the horizontal plane (Schuijf et al., 1972; Chapman and Johnstone, 1974; Schuijf and Buwalda, 1975) and vertical plane (Hawkins and Sand, 1977). Indeed, they are also able to distinguish between sources at different distances (Schuijf and Hawkins, 1983), an ability that is less developed in many terrestrial vertebrates (Masterton et al., 1969).

Electrophysiological studies with well-controlled motional stimuli have also demonstrated patterns of directional sensitivity from the various otolith organs of the fish ear (Fig. 6) (e.g., Enger et al., 1973; Sand, 1974; Fay and Olsho, 1979; Hawkins and Horner, 1981; Lu and Popper, 1998; Lu et al., 1998). Thus, it is clear that particle motion is important in enabling fishes to determine the direction from which a sound is coming, and this has recently been confirmed in behavioral studies with the plain midshipman, *Porichthys notatus*, a toadfish (Zeddies et al., 2012). Essentially, by comparing the responses of differently orientated groups of hair cells, the fish should be able to determine the axis of propagation of a sound by a process of vector weighing (Popper et al., 1988; Rogers et al., 1988).

One limitation of this model of directional detection, however, is that detection of the axis of propagation does not, in itself, indicate the bearing of the source. Particle motion alternately takes place toward and away from the source, and the hair cells are inherently bidirectional so that a simple vector weighing yields a 180° ambiguity in the detection of the source. Nevertheless, experiments carried out in the sea have shown that a fish like the Atlantic cod can discriminate between opposing sound sources (180° apart) in both the horizontal and vertical planes (Buwalda et al., 1983). In these experiments, it was shown that the phase relationship between sound pressure and particle motion is crucial for enabling a fish like the Atlantic cod to discriminate between sounds from opposing directions.
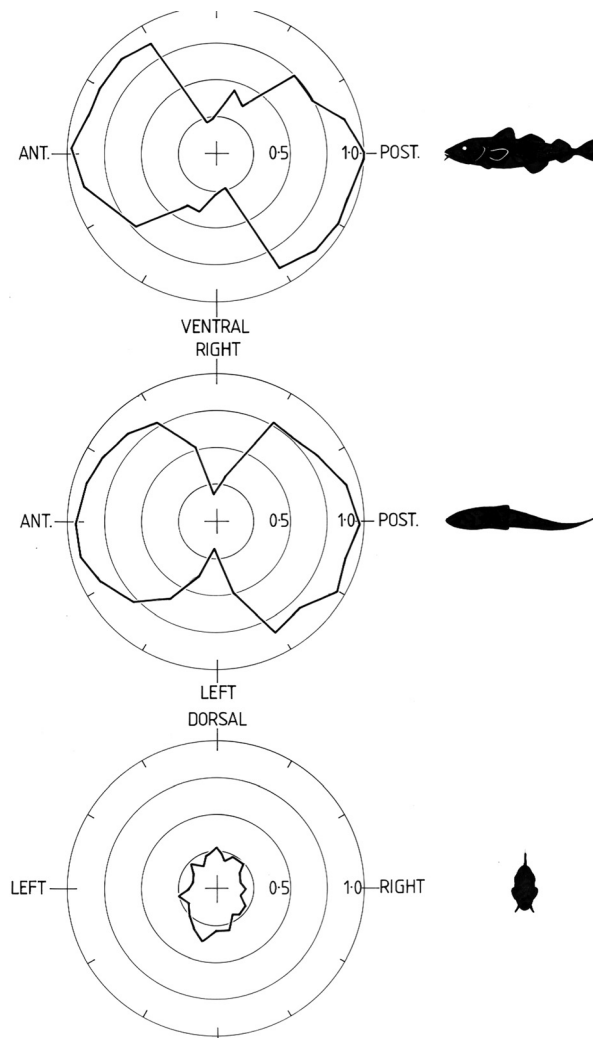

FIG. 6. Changes in the electrophysiological responses from the otolith organ of a fish exposed to particle motion from different directions (dark lines). The polar diagrams represent the level of response from a single afferent nerve fibre within the ear, reflecting the output of a group of physiologically polarized sensory hair cells. The response is highly directional, demonstrating that this group of hair cells is responding to the direction of movement of the otolith relative to the epithelium, and thus to the directional particle motion component of the sound field (Hawkins and Horner, 1981).

Phase comparison between the directly received particle motion and the particle motion re-radiated from the swim bladder appears to provide the basis for eliminating the ambiguity in directional detection. However, is not yet clear how other species, and in particular those lacking a swim bladder, resolve the ambiguity (if they do so).

Thus, the Atlantic cod, and probably many other species of fish, are able to locate sound sources in three dimensions and have a real acoustical sense of space. This ability not only enables fishes to locate particular sources of sound but may also assist them in discriminating sounds from a particular source against the general non-directional noise background.

At the same time, there is evidence that sound localization is possible without the presence of a gas bubble. For example, field observations of freely ranging sharks (which lack a swim bladder) showed that they are capable of orientating toward sound sources, often from great distances (Nelson and Gruber, 1963; Myrberg et al., 1969),

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presumably using a very sensitive system for the detection of particle motion (Casper and Mann, 2007a,b). However, it is not clear whether the sharks make "instantaneous" decisions as to the direction of a sound source, as presumably is possible in teleosts using the mechanisms discussed above, or whether the sharks detect the general direction of the particle motion and then "sample" the level of the signal over time and swim in the direction of the most intense signal.

E. Detection of substrate signals

There is growing evidence that invertebrates and fishes may be capable of detecting sounds traveling through and on the substrate. For example, Roberts *et al.* (2016a, 2016b) considered the responsiveness of benthic invertebrates to sediment sound transmission (which they termed vibration) based on laboratory and semi-field trials with two marine species: the mussel (*Mytilus edulis*) and hermit crab (*Pagurus bernhardus*). The results indicated that such animals are sensitive to, and respond directly to, anthropogenic stimuli propagating within and immediately above the sediment. However, it is not only the responses of benthic animals that may be affected. There are intimate links between the benthic infauna and the sediment, with some species playing a major role in structuring the sediments (Gray and Elliott, 2009). There may be indirect effects on the benthos in terms of habitat destruction and sediment re-sorting, as a result of sound transmission through and on the substrate. It has also been suggested that substrate transmitted sound may be used by the deep-sea scavenger shrimp *Pandalus borealis* to detect large falling prey items (Klages *et al.*, 2002), and the rumbling sounds produced by the mantis shrimp *Hemisquilla californiensis* may be detected via the sediment (Patek and Caldwell, 2006).

There have been no studies of the detection of substrate signals by fishes. However, since fishes are sensitive to particle motion, it is evident that species living on or in the substrate will detect sounds transmitted through and on the substrate. Gobies, blennies, and many flatfishes live on and even within the seabed, while other species are often found swimming close to it. Such fishes are likely to detect particle motion associated with substrate transmission of sound, which is discussed in Sec. III.

III. CHARACTERIZING UNDERWATER SOUNDS

A. Characterizing the stimulus

A critical issue to appreciate is that the relevance of any assessment of the impact of underwater sound depends greatly on if and how an animal responds to a sound. If there are no potential effects upon animals then there is no reason to be concerned about a sound source, or any need to mitigate. In contrast, where effects upon biological organisms have been demonstrated and are of concern, it is important to adequately measure and describe the stimuli that the animals receive and to which they respond, as well as to potentially consider mitigation to lessen the impacts of the sounds.

Thus, the metrics that are used to describe the sound and the characteristics of the source must relate to the potential effects upon biological receptors. Sounds of differing characteristics (e.g., impulsive vs continuous; short vs long term) have different effects. Those characteristics that are especially damaging to fishes and invertebrates need to be defined so that impacts might be reduced. For example, when considering the potential effects upon behavior, or masking by continuous sound (as from shipping), the critical aspect might be the root-mean-square (rms) sound pressure or particle motion. If there is concern about the effects of impulsive pile driving on physiology or anatomy, then the appropriate metrics might be the peak amplitude of the impulsive sound or the total energy within the pulse, as described by the sound exposure level (SEL) (Popper and Hastings, 2009). Where impulsive sounds are repeated, then the cumulative SEL over a defined time period may be important. The critical point, however, is that careful consideration must be given to the appropriate metrics for each kind of source, and it will ultimately be important to develop agreed standards, so that there is common ground for the description and regulation of each source.

B. Definition of terms

The International Organization for Standardization (ISO) defines many terms and expressions used in the field of underwater acoustics (including natural, biological, and anthropogenic, i.e., man-made, sound) in ISO 18405:2017 "Underwater Acoustics—Terminology" (ISO/DIS, 2017). The term sound can refer to any type of mechanical wave motion, in a solid or fluid medium, that propagates via the action of elastic stresses and that involves local compression and expansion of the medium. Sound pressure is the difference between the instantaneous total pressure and the static pressure that would exist in the absence of sound, expressed in units of pascals (Pa). Particle motion can be characterized by one of a number of quantities: Sound particle displacement refers to the instantaneous displacement of a material element of the medium (the particle) from what would be its position in the absence of a sound wave. It is expressed in units of meters (m). Sound particle velocity is the contribution to instantaneous velocity of a material element caused by the action of sound waves, expressed in units of meters per second (m/s). Sound particle acceleration is the contribution to instantaneous acceleration of a material element caused by the action of sound wave, expressed in units of meters per second squared (m/s^2). The sound intensity is the product of the sound pressure and the sound particle velocity, and is expressed in units of watts per meter squared (W/m^2). The term particle is defined by ISO as the smallest element of the medium that represents the medium's mean density.

Another term that is often mentioned is "vibration." Vibration is generally defined as a mechanical phenomenon that involves the oscillation of a structure (e.g., a loud speaker or a pile as it is being driven into the substrate). Vibrations will often produce sound and, in fact, sounds produced by tuning forks or musical instruments are a result of vibration of some structure (e.g., the strings of a piano). In terms of underwater acoustics, the term vibration is

sometimes used to refer to particle motion accompanying waterborne or substrate-borne sounds. In this paper, we reserve the term to describing the oscillation of structures, bearing in mind, however, that vibration of the substrate or any structures in the water may produce sounds that are potentially detectable by fishes and invertebrates via the particle motion. In the context of this paper, we only use vibration in terms of the motion of a source, and not of its acoustical output.

Another way of thinking about the distinction between sound pressure and particle motion might be by considering the difference between "shaking" and "squeezing" to express an animal being moved back and forth (e.g., through exposure to particle motion or by attaching the animal to a vibrating source), or being exposed to fluctuations around the hydrostatic pressure (e.g., through exposure to sound pressure). Using these terms, first proposed by Carlson (2017), the fish moving back and forth during exposure to particle motion (shaking) causes direct stimulation of the inner ear (Fay and Popper, 1974), whereas fluctuations in the surrounding pressure (squeezing) is the prime source of stimulation of gas-filled organs (such as the swim bladder) and the basis for sound pressure reception (Sand and Hawkins, 1973).

C. The nature of underwater sound fields

It is important to take account of both sound pressure and particle motion in looking at effects of water borne sounds upon fishes and aquatic invertebrates. The relationship between sound pressure and particle motion may vary greatly, depending on the location of both the source and the animals. Within the aquatic environment animals may receive sounds from a variety of sources (Fig. 1). Sounds may enter water from the air, although with strong attenuation of the particle motion. Sounds may be generated at the surface of the water, and within the water itself (Bradbury and Vehrencamp, 1998). In addition, sound may be generated within the substrate, especially by human activities such as pile driving, dredging, and the passage of vehicular traffic along adjacent highways and bridges.

Propagation of sound in shallow-water environments can be especially complex and difficult to predict or model. There are a number of aspects of shallow-water propagation to consider (Rogers and Cox, 1988; Jensen et al., 1994; Ainslie et al., 2014). There may be a direct transmission path through the water from the source to the receiver. There is also reflection from the water surface, from the substrate, from discontinuities in the water, and any immersed objects. There is also refraction (a change in direction at an interface), diffraction (where the sound wave encounters an obstacle or passes through an aperture), and sound absorption effects arising from differences in the properties of the water itself, which often contains sound-absorbing air bubbles. In any body of water, distinct and highly reflective boundaries are present (the water surface and the substrate), and there are changes within the medium itself that can substantially affect the propagation of sound. The coherency of the original signal is also degraded by reverberation within the environment; that is, by the aggregation and merging of reflected sounds from different surfaces and objects.

The propagation of low-frequency sounds with long wavelengths may be constrained in shallow water (Rogers and Cox, 1988; Jensen et al., 1994). The sound pressures associated with low-frequency sounds generated in the water propagate less well through shallow water. For example, if the water depth is 12 m, then sound pressures at frequencies below about 60 Hz (having a wavelength of greater than 25 m) do not propagate well (Rogers and Cox, 1988; Ainslie, 2010; Nedelec et al., 2016), although the precise cutoff frequency is dependent on the speed of propagation through the substrate and its density. It is important to note, however, that this constraint does not necessarily apply to particle motion. Close to the water surface, sound pressure may be converted into particle motion as a result of the lower density and greater elasticity of the air above the water. Moreover, sounds may also travel within the substrate or accompany waves that are traveling along the interface between the water and the substrate. Some low-frequency sounds may propagate over considerable distances by way of the substrate/water interface.

D. Ambient levels of particle motion

Ambient noise levels, including sounds from natural and man-made sources, can affect the ability of animals to detect biologically relevant sounds (including biologically important parts of the acoustic scene). Interference with the detection of one sound (generally called the signal) by another sound is called masking, and the sound that does the masking is generally called the masker (see Fay and Megela Simmons, 1999). It is especially critical to examine how much ambient levels are altered by the presence of man-made sounds and the degree to which natural signals are masked by such sounds (often termed "noise"). It has been established that in the sea, the Atlantic cod is not limited by its absolute sensitivity, but by its inability to detect sounds against the background of ambient noise—even under relatively quiet sea conditions (Chapman and Hawkins, 1973; Hawkins and Chapman, 1975). Any increase in the level of ambient noise, either naturally as a result of a storm, or imposed artificially by replaying broadband white noise, results in an increase in the auditory threshold (a decline in sensitivity).

However, virtually all of the data on ambient sound in both open oceans and shallow-water environments focuses on sound pressure (e.g., Cato, 1976; Dahl et al., 2007; Martin and Popper, 2016). As a consequence, there is very little information available on the background levels of particle motion in the sea and other aquatic environments. There is a need to investigate natural ambient particle motion levels and to determine the directional characteristics of natural sounds from different sources. It is not yet clear which are the main sources generating background levels of particle motion and which cues within the background noise might assist with orientation and navigation by aquatic animals. It has been suggested (Potter and Chitre, 1999) that ambient sound can be used to produce images of submerged objects

using the mean intensity of the backscattered energy, a technique coined "acoustic daylight" because of its direct analogy to vision. It is possible that man-made sounds might interfere with the use of such cues.

E. Particle motion and substrate signals

1. Importance of the substrate

As discussed earlier, animals living close to the substrate are subject to particle motion stimuli from a number of acoustic or acoustically-induced waves (e.g., Roberts *et al.*, 2016a; Roberts and Elliott, 2017). These include the particle motion associated with an impinging sound wave in the water column (the incident, reflected, and transmitted portions), acoustic waves traveling through the substrate, and also waves traveling along the interface or boundary between the substrate and the water. The levels of substrate-borne sound, both natural and man-made, in the marine environment are not well documented (Lee *et al.*, 2017; Roberts and Elliott, 2017), but it is clear that human activities may add considerably to substrate transmission through activities including dredging, pile-driving, drilling into the seabed, and the conduct of seismic surveys for oil and gas (where sounds generated in water by air gun arrays are directed at creating sound within the substrate).

2. Substrate and interface transmission

In addition to sound being transmitted through the substrate itself (often at a higher speed than sound transmission through the water), waves may also be transmitted along the interface between the substrate and the water. Such interface waves are often dispersive (with different frequencies traveling at different speeds) and are characterized by slow propagation speeds but large particle motion amplitudes. The large amplitude particle motion levels associated with these interface waves may propagate over considerable distances, but transmission is mainly at frequencies less than about 30 Hz. Such low frequencies, called infrasound, are detectable by some fishes (e.g., Sand and Karlsen, 2000) and perhaps by some invertebrates. If infrasound is produced, it may be detected by animals that are sensitive to particle motion, especially those living close to the substrate. Substrate transmission may result in sounds being transmitted as particle motion at frequencies below the acoustic cutoff frequency that characterizes underwater sound channels in shallow water. Within the interface waves, both the solid and fluid particle motion follow a closed elliptical path in a vertical plane parallel to the direction of propagation, unlike the linear ("to & fro") water particle velocities associated with plane pressure waves (Hazelwood and Macey, 2016b). The term "ground roll" is sometimes applied to these waves (Hazelwood and Macey, 2016a).

The energy from substrate and interface waves can be reradiated into the water, combining with the energy that has been transmitted directly through the water. However, both the particle motion and sound pressure may decline steeply with distance above the substrate, the rate of decay depending upon the nature of the substrate and the nature of the interface wave.

The low frequency particle motion accompanying the transmission of interface waves is potentially of major significance to aquatic animals living close to, or within, the substrate. Such animals are well coupled to the substrate or to the water close to the substrate and are primarily sensitive to particle motion (e.g., Edmonds *et al.*, 2016). For animals living close to the seabed, or river beds, the ambient sound levels to which they are exposed may be dominated by interface waves and their associated particle motion. Such waves may provide key information about the environment and may provide directional cues that may assist the ability of these animals to orient and navigate. It is also possible that some of these animals may generate such waves themselves, to communicate with one another.

IV. INITIAL CONCLUSIONS

As demonstrated in this first part of the paper, particle motion is of substantial importance for the lives of fishes and aquatic invertebrates, although there have been fewer experimental studies on the latter organisms. However, it is also evident that the focus of most studies to date, and the focus of regulatory activities, has been on sound pressure—the component of sound that is only detected by a limited number of species. We have also introduced the idea that not only is sound in water of importance to fishes and invertebrates, but it is likely that signals in, and emanating from the substrate, are of importance to these species, although very little is known about their actual significance.

We have also suggested the importance of considering particle motion in the regulatory environment. At the same time, unless we know about how animals detect and use particle motion and the importance of particle motion in behavior, it is impossible to develop guidelines for understanding the potential effects of man-made sounds on animals. Moreover, guidelines for particle motion are critical to the future evaluation and regulation of sounds. Indeed, guidelines based on sound pressure may be irrelevant for most fishes and invertebrates, especially in shallow water (below a few wavelengths in depth) since effects on fishes and invertebrates may actually be associated with particle motion. It is of great significance that particle motion levels in these environments cannot always be predicted from sound pressure measurements.

A number of issues still need to be explored if we are to better understand particle motion, its potential impact on fishes and invertebrates, and how it should be dealt with in a regulatory environment. These issues, and recommendations for how to deal with them, are discussed in the Secs. V, VI, VII, and VIII.

V. ISSUE 1: THE USE OF PARTICLE MOTION BY FISHES AND INVERTEBRATES

A. Sensitivity of fishes and invertebrates to particle motion

There have been very few measurements made of the sensitivity of different fishes and invertebrates to particle motion (e.g., hearing thresholds at different frequencies,

including infrasound) for many of the reasons discussed earlier in this paper. At the same time, acquiring greater knowledge of the hearing abilities and behavior of fishes and invertebrates with respect to particle motion is not just of academic interest. Hearing threshold curves, or audiograms, based on presumed sensitivities to sound pressure are already being used in environmental statements and guidelines to assess whether these animals are potentially affected by man-made sounds (e.g., Popper *et al.*, 2014). However, it is not clear that the sound pressure thresholds reflect actual hearing capabilities since the animals studied may have been responding to unmeasured particle motion signals that have no simple relationship to the sound pressure levels applied. Thus, it is important to adopt a more science-based approach to impact assessment, and to obtain more reliable measurements of hearing abilities based on sensitivity to particle motion.

The hearing data for fishes [summarized in Fay (1988) and Ladich and Fay (2013)] show a substantial reduction in hearing sensitivities to low frequencies (often below 100 Hz). However, it is likely that this reduction is more a function of investigators using sound sources (underwater loudspeakers) that cannot produce low frequency energy than loss of hearing by fishes at low frequencies. Indeed, several studies have shown that at least the few species that have been tested are able to detect sounds within the infrasonic range, extending below 10–20 Hz (e.g., Sand *et al.*, 2000; Sand and Karlsen, 2000), in addition to detecting linear acceleration. This may be the same for other species. And, it is also well-known that fishes can detect bulk water motion using the lateral line (e.g., Sand and Bleckmann, 2008). Thus, there is a particular need to determine sensitivity thresholds to very low frequency sounds, including infrasound, as sounds at these frequencies may propagate very well as interface waves.

It is also important to examine the sensitivity of different animals to sound source direction. Can they discriminate between sounds emanating from different directions, and can they locate the source of a sound without ambiguity? To what extent can they reduce the impact of masking by noise? In particular, nothing is known about the directional capabilities of aquatic invertebrate species, and investigations are needed on their capabilities and the potential mechanisms they employ.

Perhaps most critically, very little is known about behavioral responses to sound by fishes or invertebrates in their natural habitat. And, even when there are data, behavioral responses to sound are always discussed in terms of sound pressure, whereas the fishes are in many cases responding to particle motion. There are almost no observations obtained on the actual behavioral responses of fishes and invertebrates exposed to natural or man-made sounds under controlled or field conditions, where both sound pressure and particle motion levels have been determined.

B. Recommendations

It is critical to better understand the role of sound in the lives of fishes and invertebrates so that the potential impact of man-made sounds can be better assessed. All such studies must be done under appropriate acoustic conditions, and the species selected for study should reflect different sound detection mechanisms found in both fishes and invertebrates rather than done on "species of convenience" to individual investigators (for examples of selection of such species see Popper *et al.*, 2014). The initial studies need to focus on the following:

- measuring hearing sensitivity of fishes and invertebrates to agreed standards, with a focus on particle motion and including directional detection, masking, signal discrimination, and other basic aspects of hearing;
- determination of behavioral responses, in the wild, of fishes and invertebrates to both particle motion and sound pressure signals; and
- determining the responses of these animals to sounds that come from the substrate.

VI. ISSUE 2: EFFECTS OF HIGH PARTICLE MOTION LEVELS ON FISHES AND INVERTEBRATES

A. Possible adverse effects of exposure to particle motion

There has been considerable concern that man-made sound has the potential to adversely affect the behavior of fishes and invertebrates (Popper and Hawkins, 2012, 2016), and that high levels of such sounds could harm animals physically (e.g., through tissue damage) and/or physiologically (e.g., increased stress levels) (Kight and Swaddle, 2011; Halvorsen *et al.*, 2012c). However, in all cases, to date, the focus has been on the determination of effects in terms of sound pressure although there it is very possible that the particle motion component of the sound field is the major cause of any effects.

Moreover, to date, in the guidelines and regulations designed to protect fishes (there are no guidelines for invertebrates) the effects are described solely in terms of sound pressure (either effects of pressure peak, rms, or total sound energy—SEL). Indeed, virtually all experiments have only measured, and provided guidance, in terms of sound pressure (e.g., Halvorsen *et al.*, 2011; Bolle *et al.*, 2012; Casper *et al.*, 2012; Halvorsen *et al.*, 2012a, 2012b; Casper *et al.*, 2013; Bolle *et al.*, 2016). Yet, since the high intensity sources that produce large sound pressure levels may also produce high levels of particle motion, it is very possible that many of the effects seen to date (e.g., Halvorsen *et al.*, 2011, 2012b) are a result of exposure to particle motion, or the combination of shaking and squeezing from the two sound components at the same time. It is impossible, however, without proper measurements, to determine the particle motion levels accompanying a very high intensity source, particularly at close distances to the source, the region within which damage is likely to take place. Moreover, without experiments that isolate sound pressure and particle motion as sources (something possible in properly designed, and highly complex and expensive, acoustic tubes—see Sec. VII B), it will not be possible to really understand potential effects on animals.

It is evident that many different parameters may influence whether high level sounds have an adverse impact upon fish and invertebrates. The characteristics of the sounds themselves are likely to be very important: whether they are continuous or intermittent, their amplitude, rise time, duration, and repetition rate. The circumstances under which sounds are presented are also critical in determining behavioral responses: whether the animals have previously experienced such sounds, and whether they resemble natural sounds of interest to them. In many sound playback experiments, the stimulus and background noise fields are very poorly described, if they are described at all (e.g., Popper and Schilt, 2008). In particular, particle motion levels are rarely specified.

An ANSI-accredited report providing guidelines for fishes (Popper *et al.*, 2014) sets out the sound pressure levels for different sound sources that are likely to result in each of the above effects. However, little is known about the potential effects of particle motion. In particular, there have been no studies of the injuries caused to fishes and invertebrates from exposure to high-levels of particle motion (exposure to shaking).

B. Recommendations

In order to develop guidelines for effects of any man-made sound on fishes and invertebrates, it is necessary to include particle motion as a major focus of such studies. Among the studies most needed are as follows:

- 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.

VII. ISSUE 3: MEASUREMENT OF UNDERWATER SOUNDS

There are two major issues with regard to measurement of underwater sound. One is the measurement of particle motion and the second is measuring sound (including particle motion) in tanks, where many studies on effects of man-made sound have been done in the past. In contrast, measuring sound pressure, especially in open bodies of water (e.g., deep oceans), is well understood and the instrumentation, pressure hydrophones, are widely available, easy to use, and can be obtained in configurations that best suit a particular experimental question.

A. Measurement of particle motion

One of the problems in properly describing the overall sound field for fishes and invertebrates (both sound pressure and particle motion) is that in contrast to hydrophones for sound pressure measurements, there are far fewer devices (and fewer scientists skilled in their use) for detection and analysis of particle motion (Banner, 1973; Gray *et al.*, 2016a; Martin *et al.*, 2016). Indeed, detection of particle motion requires different types of sensors than those utilized for pressure hydrophones. Such sensors must specify the particle motion in terms of the particle displacement, or its time derivatives (particle velocity or particle acceleration) in three dimensions.

Particle motion sensors are not as readily available, and they often have to be made for a specific purpose, sometimes actually using as their basis devices called geophones which were designed originally to detect motion of the ground (in either air or water). Particle motion hydrophones can be assembled from three moving coil geophones (arranged orthogonally) contained within a neutrally buoyant container, giving sensitivity to particle velocity (Banner, 1973). However, geophones sensing particle velocity are often only useful up to a few tens of hertz. Alternatively, particle motion hydrophones can be assembled from three seismic accelerometers, giving sensitivity to particle acceleration. The advantage of accelerometers over velocity sensors is that the accelerometers generally have a wider frequency range and are usually more appropriate for acoustic measurements.

An alternative approach to determining particle motion is to measure the sound pressure gradient in the water and derive the particle motion from that. An estimate of the sound pressure gradient can be made using two hydrophones separated by a known spacing to measure the two different sound pressures $p1$ and $p2$.

It should be noted, however, that there are several practical considerations to be satisfied when implementing this approach. The differential pressure $p1$ minus $p2$ is typically created using a differencing amplifier to subtract one measurement of pressure from another; the result will generally be much smaller than each of the individual sound pressures. If there is an error in the measurement of either pressure, it may easily dominate the result. Thus, it is critically important that the hydrophones are well matched in both the magnitude and phase of their sensitivity (e.g., see Zeddies *et al.*, 2010; Zeddies *et al.*, 2012).

Calculations of particle motion based on sound pressure measurements and plane wave assumptions can lead to substantially erroneous conclusions (Gray *et al.*, 2016b). Measurements of particle motion levels made close to the substrate have confirmed that they may be larger than expected. Indeed, Banner (1968) found that the levels of ambient particle velocity measured in very shallow water were considerably higher than the levels that would accompany the same sound pressure levels under free-field conditions, particularly at low frequencies. More recently, Ceraulo *et al.* (2016) showed that the particle velocities generated by a pile driver in a shallow water environment were again higher, particularly for the vertical (z) axis, with a magnitude of 1 to 10 times (average 3.5) that of the predicted velocity for a plane wave at the same sound pressure. It is important, however, in making such measurements to distinguish

between the vibration of the substrate itself, and the particle motion that is subsequently generated in the water above the substrate.

In addition to just the general problems of measuring particle motion *per se*, there is also the issue that it is a vector quantity. As a consequence, it is necessary to monitor its direction as well as level. Measurement of the pressure gradient using a single pair of hydrophones, as described above, will only provide the particle velocity along the axis joining the two hydrophones. At least four sound pressure hydrophones are necessary to measure the amplitude and direction of particle velocity in three dimensions (e.g., MacGillivray *et al*., 2004; Popper *et al*., 2005b). Similarly, when using velocity sensors or accelerometers it is necessary to mount three orthogonally orientated sensors together to monitor the three spatial components of the particle motion. These measurements may be assessed separately, or summed to produce a combined vector, depending on what is required. The recent development of vector sensors, that combine a sound pressure hydrophone with three orthogonal particle motion sensors, may be most useful for future use (Jing *et al*., 2014; Martin *et al*., 2016). However, they can be rather expensive to purchase.

Measuring sound pressure or particle motion can be especially difficult at locations with high current speeds or highly turbulent flows since the flows will result in the sensor moving, and this has the potential to overwhelm the system so that it is not able to detect the far lower levels of the signals of interest. The sensor package may be more stable if it is mounted on the substrate, but it may have to be placed in mid water to avoid being affected by seabed vibration, either by using a mount fixed to the substrate, designed to decouple the sensors from substrate vibration, or by suspending it from a positively buoyant device (e.g., a subsurface float). In the latter case the package may be especially vulnerable to local water movements that generate vertical or horizontal motion of the package itself. The large, very low frequency spurious signals generated through linear acceleration of the sensors may be filtered out using a high pass filter. However, since some fishes and invertebrates are sensitive to very low frequencies (described as infrasound) such filtering may not be appropriate.

The problems arising from water movements are especially pronounced for particle motion sensors. They may be protected to some degree by placing them within a streamlined acoustically transparent housing. It will always be important, however, to distinguish between the particle motion signals generated by bulk water movements, those generated by sounds propagated through the water, and those generated within the substrate or at the interface between the substrate and the water.

B. Measurement in tanks and enclosed bodies of water

Much work on bioacoustics of fishes and invertebrates has been, and continues to be, done in laboratory tanks—some with glass walls and some with walls made of other materials of various thicknesses. Attempts have been made to improve the sound field in these tanks using a wide range of absorptive materials from "horse hair" to sand to air-filled bubbles such as those used to ship packages. The actual fact is, however, that these (or other) devices have only marginal value in modifying the acoustics of the tanks (e.g., Rogers *et al*., 2016)! They may reduce the reflection of high frequency sounds, but will have very little effect at the low frequencies to which fish are sensitive, where the sound wavelength often exceeds the dimensions of the tank.

In small tanks in the laboratory, close proximity to the source and the presence of reflecting boundaries (e.g., walls, water surface, bottom), leads to a complex relationship between particle motion and sound pressure. Moreover, the direction of the particle motion may be affected by the presence of hard and soft surfaces. Over 50 years ago, Parvulescu (1964, 1967) outlined the difficulties encountered when carrying out underwater acoustic experiments in small tanks of water having dimensions that are inevitably much smaller than the wavelength of the sound being used. The small size of the tanks, the large-impedance and sound-speed differences between the water and surrounding air, and the elasticity of the tank walls and support structure, combine to make the acoustic field within the tank very complicated and difficult to model, or even characterize through measurements (Duncan *et al*., 2016; Rogers *et al*., 2016).

Within an aquarium tank, the walls of the tank are usually so thin and flexible that they act as pressure release boundaries (Parvulescu, 1964, 1967). That is, the tank behaves like a "brick" of water surrounded by air. When the acoustic source is in the water, the sound pressure must fall to zero at the walls, bottom, and surface, greatly increasing the levels of particle motion. All six surfaces (four walls, air/water interface, bottom) are nearly perfect sound reflectors. Close to the water surface the ratio of KE to PE can be enormous.

The situation is similar in larger tanks as well. Gray *et al*. (2016b) presented measurements of sound pressure and particle motion fields in quite "large" aquarium tanks. They concluded that even large tanks are not appropriate surrogates for open-water environments or are they any better suited to addressing a particular hearing test objective than standard small aquarium tanks. Sound interactions with the tank boundaries may make simple or otherwise desired in-water acoustic conditions difficult to achieve. Resonant tank walls may dominate in-water acoustic field characteristics.

As a consequence of the relatively unpredictable and unmeasurable acoustics of tanks, data from earlier studies that deal with hearing sensitivity, bandwidth of hearing, behavioral responses to sound, and other issues must be interpreted with considerable caution. Early data were inevitably reported in terms of sound pressure, but we now know that many fishes and invertebrates are primarily detectors of particle motion. However, we cannot simply convert sound pressure measures in a tank to particle motion, even if they were measured properly for a tank environment—something that was not often the case. [In contrast, it is possible to do such a conversion if the work is done in the free field without acoustic boundaries (Hawkins, 2014).] In some circumstances, the presence of the fishes themselves may alter the

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sound field because of the presence of the gas-filled swim bladder. Measurements made in the absence of the fishes cannot be utilized in such circumstances.

Since having a well-defined sound field is critical for many aquatic bioacoustic studies, it is important to create an appropriate stimulus. As a consequence, it becomes clear that acoustic experiments on fishes and invertebrates should be undertaken in an acoustic environment as close as possible to that of the animal's natural environment. For mid-water fishes and zooplankton, sounds should be presented and measured in a free sound field, whereas shallow water and bottom-dwelling fishes and invertebrates should be exposed to sounds in shallow water with an appropriate substrate and without any other reflecting bodies present other than those that might be found under natural conditions. It is important to ensure that the signals received by the animals have the appropriate mixture of sound pressure and particle motion (including both vertical and horizontal components of the motion).

If work in the field is not possible, then it is desirable to use specially designed sound exposure chambers in which it is possible to control the relative magnitudes of particle motion and sound pressure. Such tanks have been used for hydrophone calibration (Beatty, 1966), in fish hearing studies (Hawkins and MacLennan, 1976), in underwater sound exposure studies (Martin and Rogers, 2008; Halvorsen *et al.*, 2012c), and to examine the response of invertebrates to particle motion (Klages *et al.*, 2002). Such tanks are generally made from a thick-walled steel tube with sound projectors at each end. By varying the phase of the signals fed to the sound projectors it is possible to vary the ratio of sound pressure to particle motion at the center of the tube. In some instances, the response of fishes and invertebrates to particle motion has been investigated by attaching them to vibrating surfaces (Enger *et al.*, 1973; Roberts *et al.*, 2016a), or by shaking the container housing the animal.

C. Calibration of particle motion detectors

It is important that any sensors used to detect particle motion are properly calibrated (Banner, 1973). This may be achieved by placing the sensors in specially designed calibration tanks or attaching them to a vibrating object where the magnitude of the particle motion or vibration can be determined. Alternatively, they can be placed in a free sound field, distant from reflectors, where the particle motion can be estimated, or where it can be calculated from measurements of the sound pressure gradient.

D. Recommendations

There have been comparatively few actual measurements of particle motion levels, despite their importance in bioacoustic studies (but see Banner, 1968; Kugler *et al.*, 2007; Sigray and Andersson, 2011, 2012), largely because the techniques for monitoring particle motion are not widely understood, and because particle motion sensors are not readily available. It is especially important to

- develop standards for particle motion sensors as well as sound pressure sensors;
- develop protocols for making particle motion measurements; and
- establish calibration facilities for such devices in the field and in the laboratory.

In addition, and while not a complete list, some specific issues that need to be addressed include

- determination of the best sensors to deploy;
- development of methods to mount and suspend sensors so they are not affected by water currents and turbulence;
- determination of appropriate metrics to use for particle motion; and
- development of particle motion sensors to use in tanks.

VIII. ISSUE 4: MODELING OF PARTICLE MOTION SOUND FIELDS

A. Usefulness of current models for particle motion

Having defined those particle motion levels that potentially have effects on fishes and invertebrates, whether they be behavioral and/or physiological, it is necessary to estimate the extent of those geographic areas over which those effects might take place. There is often a requirement from regulators to define "zones of influence" around a source at which the sound levels are above threshold values that indicate the levels at which animals may be adversely affected. To assist in the assessment of the overall potential effects of a source of man-made sound, the propagation of sound arising from that source needs to be modeled and the potential effects on species of interest then evaluated, perhaps by defining such zones. Alternatively, it may be possible to estimate how close to a protected species or habitat a particular noise-making activity can take place without having an adverse impact.

Regulations often involve the setting of single number "thresholds" so that violations can be avoided. Setting such a threshold is intended to provide a clear guideline for those noise makers whose activities are being regulated. It must be understood, however, that using a single number in a guideline for effects of sound, or a single value for a "zone of influence," is not always biologically realistic. This is because the actual responses by an animal, either behaviorally or physiologically, to a sound are certainly affected by a wide range of variables that might include its age, the season of the year, time of day, whether the animal is in some particular motivational state (e.g., feeding, mating), etc. For example, an animal might show a behavioral response to a sound and swim away from it during migration, but if the animal is feeding or mating it may not "pay attention" unless the sound is much more intense.

Moreover, a particular problem in assessing effects on fishes and invertebrates is that propagation modeling is often carried out in terms of sound pressure rather than particle motion. Modeling of sound propagation, particularly in relatively shallow waters (inshore, on reefs, in rivers) must take account of the frequency range of the sound, its temporal

structure, water depths (bathymetry), the properties of the adjacent media including the nature of seabed sediments, and water temperature and salinity profiles, and it must incorporate both sound pressure and particle motion when considering fishes and invertebrates. A few such models exist but are generally proprietary to specific companies, and in many instances, have not been utilized, and their assumptions and/or limitations have not been well characterized.

Another issue is that modeling the propagation of particle motion in shallow water, or close to the surface or bottom in deeper water, is also rather complex (Banner, 1968; MacGillivray *et al.*, 2011; Pangerc and Theobald, 2015). Under shallow water conditions, the repeated reflections and scattering of sound at the seafloor interface and the surface interface may result in strong spatial variations in the amplitude of particle motion and its direction. In addition, and depending on the properties of seabed sediments, sound may be transmitted through the seabed and along the seabed interface, to emerge later into the water column. In preparing impact assessments for fishes and invertebrates, including those living close to, on, or within the substrate, the presence of substrate transmission and interface waves, and the high levels of particle motion that may be generated, are often ignored in modeling the propagation of sound from manmade sources.

B. Recommendations

In order to ensure that the predictions of propagation models are correct, it is necessary to validate them by making field measurements of the sound pressure and particle motion levels at different locations. In practice, sound modeling for EIAs is often carried out using simplistic models, with limited environmental data, and without field measurements to ground-truth the model predictions (Farcas *et al.*, 2016). In some cases, proprietary models are employed, without the assumptions and computational methods being disclosed. As a consequence, there is a need to examine existing sound transmission models to ensure that they take account of particle motion and interface effects as well as to consider whether new models are required and how to develop such models if necessary.

IX. CONCLUSIONS AND FINAL RECOMMENDATIONS

EIAs intended to examine the potential effects of sound on fishes and invertebrates often overlook key factors, and especially the sensitivity of many of these animals to the particle motion component of sound rather than sound pressure. There are several reasons why these assessments fail to deal with particle motion adequately. These include the difficulty in measuring and modeling particle motion, the lack of experimental data on the responses of fishes and invertebrates to potentially damaging levels of particle motion, and the absence of guidelines—based on particle motion—that indicate the levels of particle motion that are likely to have adverse effects upon animals.

The first step that needs to be taken is to overcome the difficulties in measuring and modeling particle motion in different aquatic environments. There is a need to examine the main obstacles standing in the way of quantifying particle motion, and then to remove them. Standard protocols are required to ensure that particle motion measurements are carried out appropriately using properly calibrated sensors. Progress might be made in achieving this by bringing together an international team of experts to prepare protocols and then to educate scientists in understanding and monitoring particle motion. That would enable biologists, with the assistance of engineers/acousticians, to carry out experiments, under appropriate acoustic conditions, to examine the effects of exposure of fishes and invertebrates to particle motion.

Such experiments are needed for a variety of purposes, as outlined in the earlier parts of this paper. Some of the more important of these experiments include the following:

- Investigating the sound detection abilities of fishes and invertebrates and achieving a better understanding of the mechanics and physiology of particle motion detectors in these animals and to establish their sensitivity to particle motion. Such experiments should include exposure to infrasonic frequencies, and should also address the issue of directional sensitivity, especially of invertebrates, to underwater sounds.
- Examining the effects of high particle motion levels, in terms of mortality, injury and hearing loss, masking and changes in physiology and behavior. If particle motion results in injury, determining the mechanism of such effects.
- Measuring the particle motion levels generated by human sources, in order to assess their effects upon the particle motion cues used by fishes and invertebrates.

In addition to obtaining data related to particle motion, there is also a substantial need for regulators and others to understand and appreciate that particle motion must be taken into consideration when planning and regulating activities likely to generate sound within the aquatic environment, especially where fishes and invertebrates are present. We recognize that this may be difficult to achieve. Although the scientific case is clear, regulators and planners are not necessarily influenced by the science itself. What drives them is pressure from politicians, industry, environmental bodies, and the general public. Currently, regulators are providing very little funding for research into particle motion. It may take greater public awareness of this issue to generate interest by the regulators. That might be achieved by publicizing the results of experiments showing major impacts upon fish and invertebrate populations.

The precise approach to achieving these recommendations is not clear. However, a starting point is an agreement among the parties most involved to have a focused effort that leads to a clear set of results, as per the recommendations in this paper. This approach is in contrast to normal scientific efforts where individual scientists pursue research questions that interest them, but which may not necessarily fit into a more global understanding of the issues and solutions.

In effect, the approach should start with an international steering committee that defines the questions and the approaches that will give answers to the most critical questions about particle motion soundscapes, propagation, modeling, behavioral responses to particle motion, effects of intense particle motion, etc. Such a committee will require adequate funding to support investigators who will do peer-reviewed studies that directly address these questions. It is recognized that funding is the big issue, and how that is to be achieved is something to be considered as a priority.

As data are obtained, the results would be promulgated through use of various communication media, but, most importantly, through a series of workshops where funded investigators and others expert in the field would get together to share findings, ideas, and approaches. The specific methodology of these workshops would be determined by the aforementioned steering committee.

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[1]The term noise is often used to describe unwanted sound. Noise is also used to describe background levels of sound in the sea, including sound from natural sources. In this paper the term "sound," rather than noise, is used to refer to identifiable man-made sources, or distant man-made sources that cannot be located.

[2]An animation that helps understand particle motion as compared to sound pressure can be viewed at https://dosits.org/science/sound/what-is-sound/.

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