

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.
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I. INTRODUCTION

A. Overview

Underwater sounds¹ 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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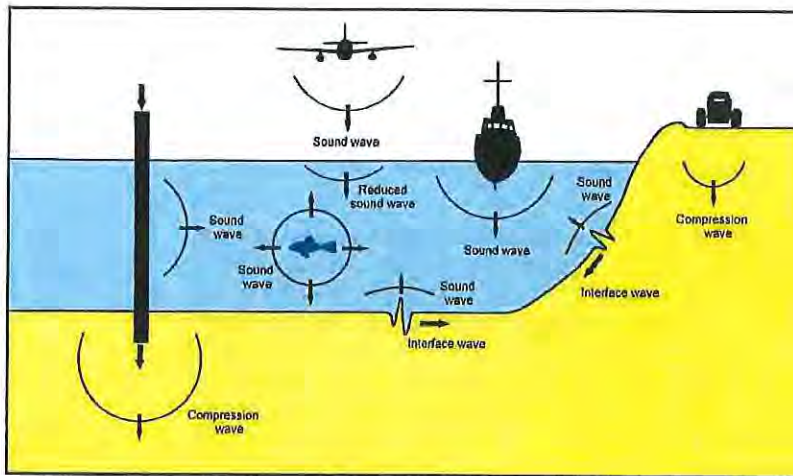


FIG. 1. (Color online) Sounds may be generated in water by natural and human sources located at different positions. The sources may include pile drivers, marine animals, aircraft, ships, and vehicles on adjacent land. The ratio of sound pressure to particle motion may vary greatly depending on the source and its location, the depth, and the distance from the source. Figure copyright 2017 Anthony D. Hawkins, all rights reserved.

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

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., Tavalga, 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

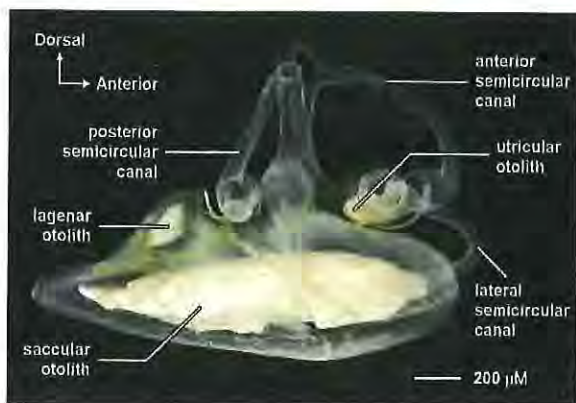


FIG. 2. (Color online) Inner ear of *Antimora rostrata*, a member of the deep-sea cod family Maridae. The otoliths are each located in a sac bearing the same name. The otolith organs are associated with hearing and positional senses (see Platt, 1983). The sensory epithelium of the saccule is not seen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

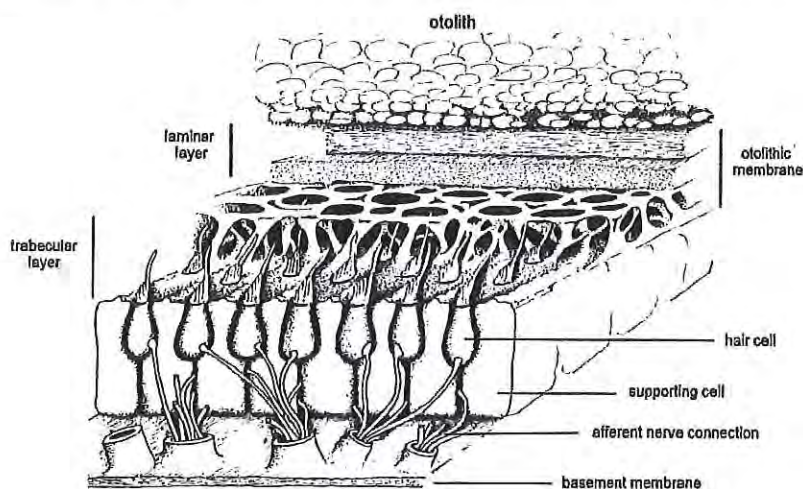


FIG. 3. The sensory epithelium of the Atlantic cod (*Gadus morhua*). The epithelium contains sensory hair cells and supporting cells and is innervated by the eighth cranial nerve. Ciliary bundles on the top of the sensory cells are embedded in the otolith membrane which also connects to the overlying 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.



(a)



(b)

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 protic 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

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

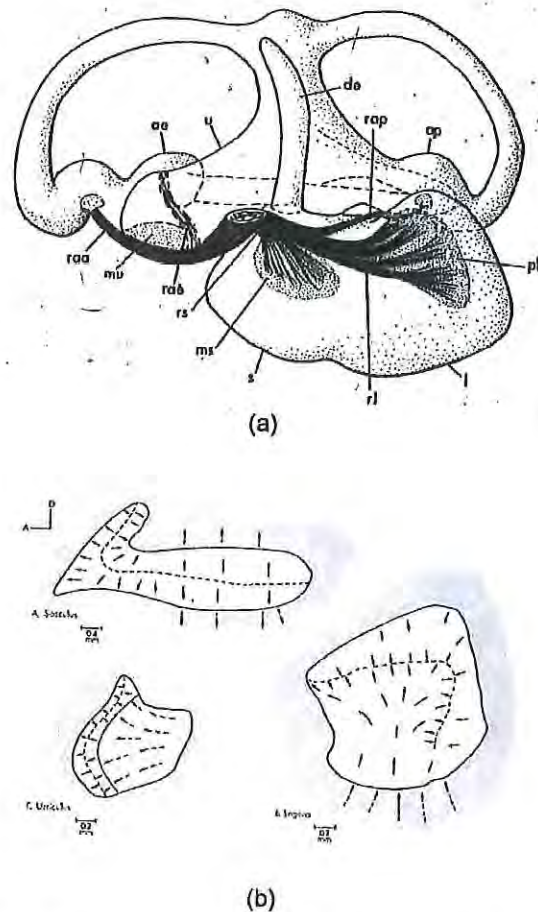


FIG. 5. Right ear (a) and sensory hair cell orientation patterns from the three otolith organs (b) in the bowfin, *Amia calva*. (Note, anterior is to the left and dorsal to the top.) The arrows (b) show the direction of orientation of the hair cells in that region (regions separated by dashed lines), 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.

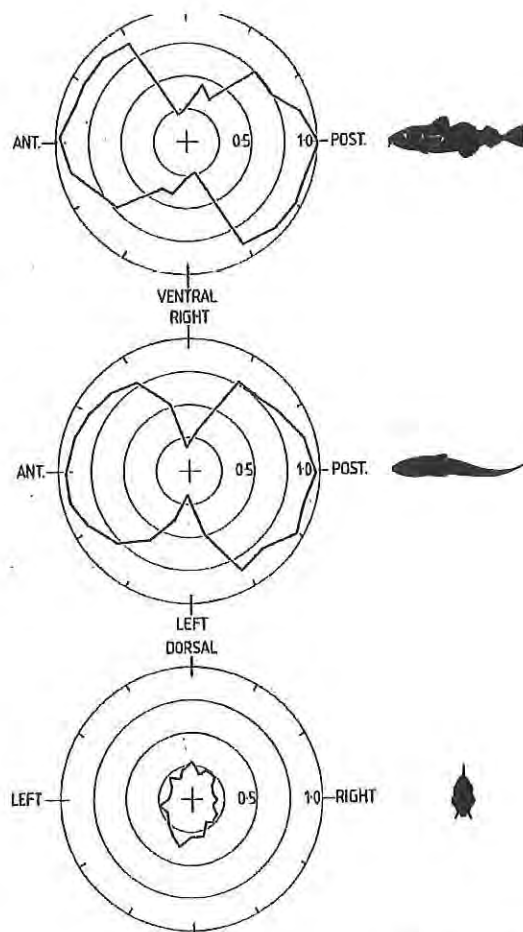


FIG. 6. Changes in the electrophysiological responses from the otolith organ of a fish exposed to particle motion from different directions (dark lines). The polar diagrams represent the level of response from a single afferent nerve fibre within the ear, reflecting the output of a group of physiologically 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, it 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),