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Directional hearing and sound source localization by fishes

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Directional hearing may enable fishes to seek out prey, avoid predators, find mates, and detect important spatial cues. Early sound localization experiments gave negative results, and it was thought unlikely that fishes utilized the same direction-finding mechanisms as terrestrial vertebrates. However, fishes swim towards underwater sound sources, and some can discriminate between sounds from different directions and distances. The otolith organs of the inner ear detect the particle motion components of sound, acting as vector detectors through the presence of sensory hair cells with differing orientation. However, many questions remain on inner ear functioning. There are problems in understanding the actual mechanisms involved in determining sound direction and distance. Moreover, very little is still known about the ability of fishes to locate sound sources in three-dimensional space. Do fishes swim directly towards a source, or instead “sample” sound levels while moving towards the source? To what extent do fishes utilize other senses and especially vision in locating the source? Further behavioral studies of free-swimming fishes are required to provide better understanding of how fishes might actually locate sound sources. In addition, more experiments are required on the auditory mechanism that fishes may utilize.

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Pages: 3329–3350

I. INTRODUCTION

One of the primary roles of the vertebrate auditory system is to determine the location of a sound source in relation to the position 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, relative to their own position in the environment, and respond appropriately. While sound source localization has been well studied in terrestrial vertebrates (see papers in Popper and Fay, 2005), there have been far fewer studies in fishes (Fay, 2005; Sisneros and Rogers, 2016), partly due to difficulties in doing such studies in water.

There are several aspects of sound source localization that need to be considered. Can fishes distinguish between sounds coming from different directions and with what precision can they determine the bearing or direction of a particular source relative to themselves? How well can they actually locate sound sources; that is, determine where in space a sound originates? Can fishes determine the distance to the source?

A major impediment to carrying out such studies has been the suggestion by early and very influential investigators that fishes should not be able to localize sound sources due to the nature of the structure of the auditory system in fishes and the high speed of sound in water (e.g., von Frisch, 1938; van Bergeijk, 1964). As a consequence of those papers, and because of the difficulties in developing appropriate underwater sound fields in order to test whether fishes

can locate sounds, there has been very little work done on sound source localization by fishes.

In the late 1960s, and particularly in the 1970s, there came the realization that the mechanisms for sound source localization in fishes are not necessarily the same as in terrestrial animals (e.g., Schuijf, 1976a; Schuijf and Buwalda, 1980; Schuijf, 1981; Schellart and de Munck, 1987). During that period, a series of studies demonstrated that at least some species of bony fishes and sharks are capable of directional hearing and in some cases they might be able to localize sound sources (e.g., Nelson and Gruber, 1963; Nelson and Johnson, 1972; Schuijf and Siemelink, 1974; Schuijf, 1975; Myrberg *et al.*, 1976; Schuijf, 1976b).

A. Purpose of paper

This paper discusses the nature of sound localization by fishes. However, in doing this review, we “discovered” that the terminology for sound localization is not clearly defined, and terms are used differently by various authors. While it is not our goal to define terms for the field (especially considering that the bulk of the localization literature is on mammals), we did find it necessary to ensure that the terms used herein are made clear. Accordingly, in this paper, the term *directional hearing* refers simply to any degree of discrimination of the direction of a source. Whereas *sound source localization* (or sound localization) refers to the precise location of the source in three-dimensional (3D) space.

The intent of this paper is to critically discuss what is known about directional hearing and sound source localization in fishes and how it is similar to, and different from, that in terrestrial vertebrates. We also pose questions for future research that will move understanding of the topic forward.

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As part of this discussion, we provide a broad review of what is known about the mechanics and function of the inner ear of fishes. We point out that, while the mechanics of the ear are very critical to determining how fishes localize sounds, there are still numerous questions on inner ear functioning that need to be answered. The reader interested in additional discussions of fish sound localization can see recent papers by [Fay \(2005\)](#), [Sisneros and Rogers \(2016\)](#), [Edds-Walton \(2016\)](#), and [Rogers and Zeddies \(2008\)](#). Broader discussions of vertebrate sound source localization can be found in a volume by [Popper and Fay \(2005\)](#). A detailed analysis of the structure of the inner ear of fishes and its adaptations can be found in an excellent paper by [Schulz-Mirbach *et al.* \(2018a\)](#).

B. Fish hearing

For readers not familiar with the likely mechanisms of sound localization by fishes, we provide a brief introduction to relevant topics before our discussion of sound localization. Accordingly, [Sec. II](#) discusses the rudiments of underwater acoustics, with a particular focus on detection of particle motion, and [Sec. III](#) describes the peripheral auditory system of fishes. Readers wanting a deeper understanding of underwater acoustics and fish hearing are directed to several recent reviews ([Webb *et al.*, 2008](#); [Hawkins, 2014](#); [Hawkins and Popper, 2014](#); [Ladich, 2014](#); [Ainslie and De Jong, 2016](#); [Ladich and Schulz-Mirbach, 2016](#); [Popper and Hawkins, 2018](#)).

By detecting sounds, fishes gain major sensory advantages since hearing can provide animals with information from a larger space around them than is possible using other senses. Indeed, 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 analyze the world around them and assign the different elements to particular sources ([Bregman, 1994](#); [Fay, 2000](#); [Fay and Popper, 2000](#)).

In addition to analyzing the auditory scene around them, many fish species produce sounds that are used for intraspecific communication, territorial defense, courtship, agonistic behavior, alarm raising, and many other behaviors (e.g., [Fish, 1954](#); [Moulton, 1963](#); [Tavolga, 1971](#); [Hawkins and Myrberg, 1983](#); [Amorim, 2006](#); [Fine and Parmentier, 2015](#)). Perhaps most importantly, some fishes may be able to determine the direction and even the distance of any sound source, facilitating an appropriate response, whether that is attraction or avoidance. The ability to locate sound sources may be especially crucial where light levels are low and long-distance vision is impaired. Essentially, sound source localization by fishes may enable them to seek out prey and to avoid predators, to find mates, and to detect cues important for navigation and orientation, often under conditions where other senses do not operate effectively.

II. UNDERWATER SOUND

In order to understand sound source localization by fishes it is imperative to have some understanding of the basic principles of underwater sound. While sound in air and

water follow the same “rules,” the greater density of water than air results in the speed of sound in water being of the order of 4.8 times faster than in air, and, of course, the resultant wavelength for a particular frequency is 4.8 times greater in water (e.g., [Rogers and Cox, 1988](#); [Ainslie and De Jong, 2016](#); [Popper and Hawkins, 2018](#)).

Sounds are generated by the movement or vibration of any immersed object, and result from the inherent elasticity of the surrounding medium: water ([Pierce, 1981](#); [Urlick, 1983](#); [Kinsler *et al.*, 1999](#)). As the source moves, kinetic energy is imparted to the water and in turn is passed on, traveling as a propagated longitudinal elastic wave. The wave can be detected as a transient change in pressure above and below the ambient or hydrostatic pressure, termed the sound pressure ([ISO, 2017](#)). The pressure changes are accompanied by a back and forth motion of the component particles of the medium, termed the particle motion. The motion takes place along the axis of transmission of the sound wave and can be expressed as the particle displacement, the particle velocity, or the particle acceleration.

Sound pressure at any particular point in the medium has no directional component; it is a scalar quantity that can be described simply in terms of its magnitude and its temporal and frequency characteristics. Particle motion is an oscillation back and forth in a particular direction; it is a vector quantity that can only be fully described by specifying both the magnitude and direction of the motion. The to-and-fro displacements of the very small body of water (that gives rise to the concept of the particle in particle motion) are of the order of nanometers (1 nm is 10^{-9} m, or one billionth of a meter).

In a free sound field, where there are no close physical obstructions that affect passage of the sound (e.g., the surface, bottom, or discontinuities in the water), and where the advancing wave front is an almost plane surface, the particle velocity (v , the first time derivative of the particle displacement) and the sound pressure (p) are directly proportional to one another (i.e., $v = p/c$, where c is the propagation velocity (m s^{-1}), and ρ is the density of the medium (kg m^{-3}). The quotient (ρ/c) is the acoustic impedance, and is a measure of the acoustic properties of the medium. The particle velocity is measured in meters per second and the sound pressure in Pascals ($1 \text{ Pa} = 1 \text{ N m}^{-2} = 1 \mu\text{bar} = 10 \text{ dyn cm}^{-2}$), but because a great range of amplitudes of both quantities are encountered in nature, it has become conventional to express sound levels in terms of a logarithmic measure—the decibel (dB)—relative to a reference quantity. In water, the reference quantity for sound pressure is one microPascal ($1 \mu\text{Pa}$), and for particle velocity, it has been suggested that it should be one nanometer per second ([ISO, 2017](#)).

Sounds diminish in amplitude as they propagate away from a source. Distant from the source, in a free acoustic field, both sound pressure and particle velocity decline with the inverse of the distance (i.e., by a factor of 2, or 6 dB, for a doubling of distance), and both parameters are in phase with one another. Close to a source, however, where the radiating wave fronts are no longer plane but spherical, this simple relationship does not apply. Instead, the particle velocity is much higher for a given sound pressure. This

region near the source is called the near field, while the region beyond the near field is called the far field. Within the near field, particle velocity from a monopole source (generally an omnidirectional source which is smaller in dimensions than the wavelength) declines with the inverse square of the distance (Harris and van Bergeijk, 1962), and the phase of the particle velocity lags that of the sound pressure (by 90° close to the source). The extent of the near field depends on the wavelength (λ) of the sound (the speed of the wave divided by its frequency, for a sine wave). The near field extends a greater distance for sounds of longer wavelength. The limit of the near field is defined as the distance of $\lambda/2\pi$ from the source. The near field also depends on the nature of the source and whether it is monopole, dipole, or multipole. Whereas monopole radiation is omnidirectional (equal in all directions), dipole radiation produces a bilobed, figure of eight pattern, and multipole radiation is multi-lobed (Harris, 1964).

Close to acoustic boundaries such as the seabed and the sea surface, and in shallow waters, and particularly waters such as bays, rivers, lakes, and streams that are shallower than a wavelength, which are inhabited by many fishes and invertebrates, sound transmission is rather different than in an unbounded medium and the relationship between sound pressure and particle motion is more complex (Popper and Hawkins, 2018), so that it is often necessary to measure particle motion directly. Propagation of sound in shallow-water environments can be especially complex and difficult to predict or model (Rogers and Cox, 1988; Ainslie and De Jong, 2016). The sound pressures associated with low-frequency sounds generated in the water propagate less well through shallow water. However, particle motion levels may be higher close to the water surface as a result of pressure release into the less dense air above the water. Particle motion is also generated by waves travelling along the interface between the water and the substrate (Hazelwood and Macey, 2016), although the level declines rapidly above the substrate. Some low-frequency sounds may propagate over considerable distances by way of the substrate/water interface, although the levels of substrate-borne sound in aquatic environments are not well documented.

III. SOUND DETECTION MECHANISMS OF FISHES

A. The ears of fishes

The ears of fishes are located in the cranial cavity at the level of the medulla (Fig. 1) The ears consist of three semi-circular canals and associated sensory regions (cristae) and three otolith organs, the saccule, utricle, and lagena (Retzius, 1881) (Fig. 2). In addition, some teleost fishes, and all elasmobranchs, have another receptor called the macula neglecta (Tester *et al.*, 1972; Corwin, 1977). In elasmobranchs (sharks, skates, and rays), the macula neglecta may be very large and it is thought to be involved in sound detection (Corwin, 1981b,a, 1989; Casper and Mann, 2007b).

The semi-circular canals are involved in detection of the angular acceleration associated with body rotation (Lowenstein and Sand, 1940; Platt, 1983). The saccule, and likely the other otolith organs, are involved in hearing, the

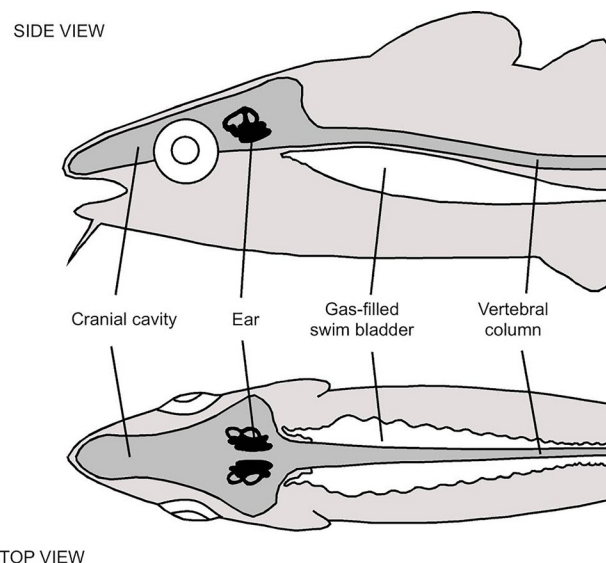


FIG. 1. (Color online) The body of an Atlantic cod (*Gadus morhua*) showing the location of the ear in the cranial cavity and its relationship to the gas-filled swim bladder (anterior is to the left). The Atlantic cod, as a number of other species, has anterior projections of the swim bladder that brings the rostral end of the structure close to the ear. Other species do not have such projections. Figure Copyright 2018 A. D. Hawkins, all rights reserved.

detection of linear motion, and the determination of body position relative to gravity (von Frisch, 1938; Dijkgraaf and Verheijen, 1950; Popper, 1983). Thus, the otolith organs detect linear accelerations, resulting for example from body tilts and swimming, and gravitational forces, as well as sounds (see Hawkins, 1993; Schulz-Mirbach *et al.*, 2018a).

The otolith organs each contain a mass of calcium carbonate crystals which are about three times denser than the rest of the animal's body. In elasmobranchs and non-teleost bony fishes (as well as all terrestrial vertebrates, including humans), these crystals, called otoconia, are embedded in a gelatinous mass (e.g., Carlstrom, 1963). In teleost fishes, however, there is a single, dense, calcareous mass, the otolith, that

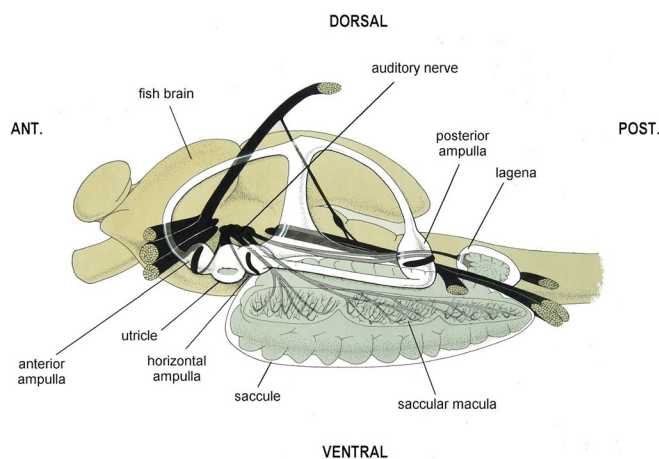


FIG. 2. (Color online) Lateral view of the left ear of an Atlantic cod and its relationship to the brain. Anterior to the left and dorsal to the top. Each of the otolith organs has a single dense calcareous otolith that has a species-specific shape (Popper *et al.*, 2005). [Note that while the saccular macula is visible in this image, this is only for illustrative purposes since it is actually on the medial (brain) side of the end organ.] Dark lines are other cranial nerves. Figure Copyright 2018 Anthony D. Hawkins, all rights reserved.

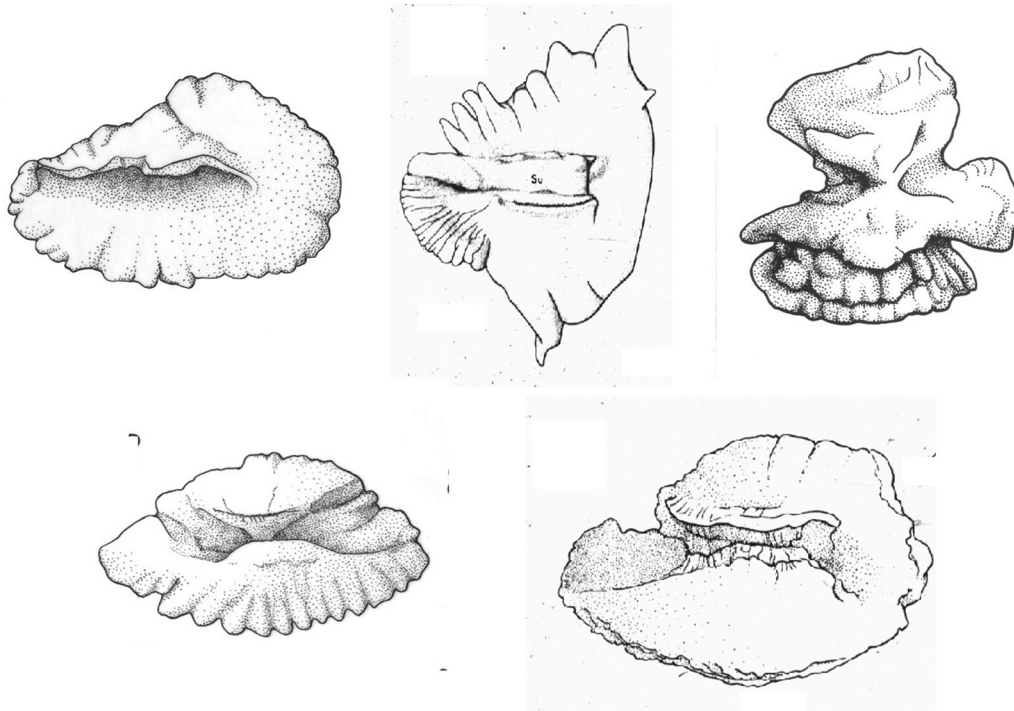


FIG. 3. Medial side of saccular otoliths from various species of bony fishes to show the wide interspecific variation in shapes and extensive “sculpting.” The horizontal elongate regions about half-way from the top in each otolith is the indentation (sulcus acousticus) where the sensory epithelium sits, with the ciliary bundles directed in to the sulcus. Anterior is to the left and dorsal to the top.

expands in size with the age of the animal by the laying down of “rings,” so that otoliths can be used to determine the age of individual fish (Gauldie, 1996; Popper *et al.*, 2005).

Otoliths have characteristic species-specific shapes (Fig. 3) that are often used for taxonomic purposes, though the shapes are thought to have functional significance with respect to hearing and, potentially, determination of sound source direction (Popper *et al.*, 2005). A recent paper discusses the functional role and evolution of fish otoliths (Schulz-Mirbach *et al.*, 2018a). It is suggested that otolith shapes may have evolved along with the considerable diversity of, and improvements in, auditory abilities in teleost fishes.

The otoliths lie in close proximity to the sensory epithelium (or macula) of each otolith organ. The maculae contain sensory hair cells (Figs. 4 and 5), each of which is surrounded by supporting cells [Figs. 5(C) and 5(D)]. These sensory cells serve for transduction of the acoustic signal (Lowenstein, 1957; Flock, 1965; Popper, 1983; Popper *et al.*, 2003).

The apical end of each sensory cell has a ciliary bundle which consists of a single, eccentrically placed kinocilium (a true cilium) and multiple stereocilia. There is considerable variation in the length and overall form of the ciliary bundles in different parts of the maculae of fishes, suggesting functional differences between various epithelial regions (Dale,

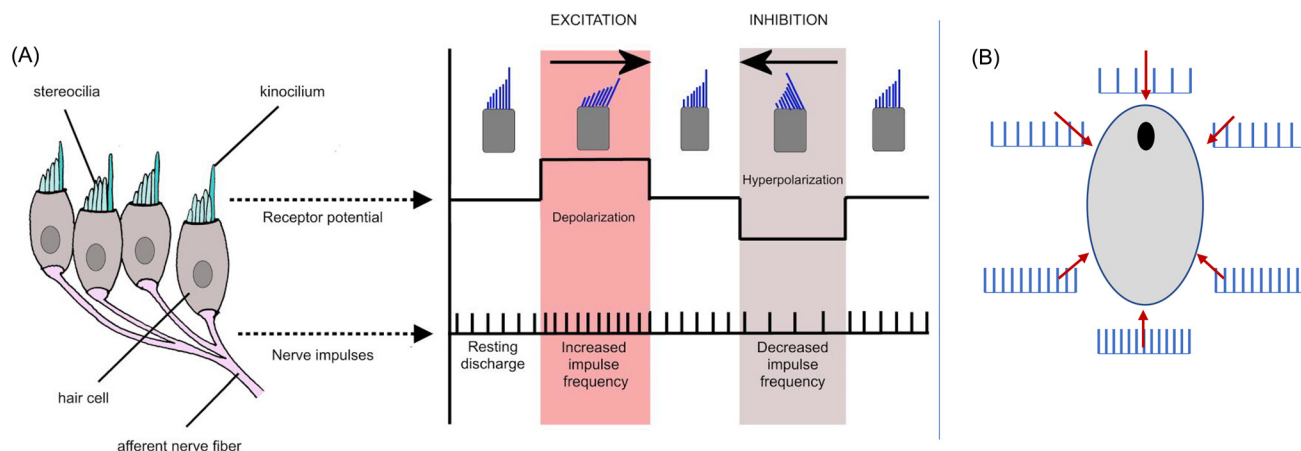


FIG. 4. (Color online) Schematic of sensory hair cells showing the physiological responses to directional stimulation. (A) Bending of the cilia from the stereocilia towards the kinocilium results in excitation of the innervating eighth nerve, which is reflected as an increase in nerve impulses over the normal resting level, while stimulation in the opposite direction results in a decrease in the number of impulses. (B) Looking down on a sensory hair cell (kinocilium is black dot). Stimulation in various directions (red arrows) results in a neural discharge that is somewhat between the maximum excitation (bottom arrow) and inhibition (top arrow). Figure Copyright 2018 Anthony D. Hawkins, all rights reserved.

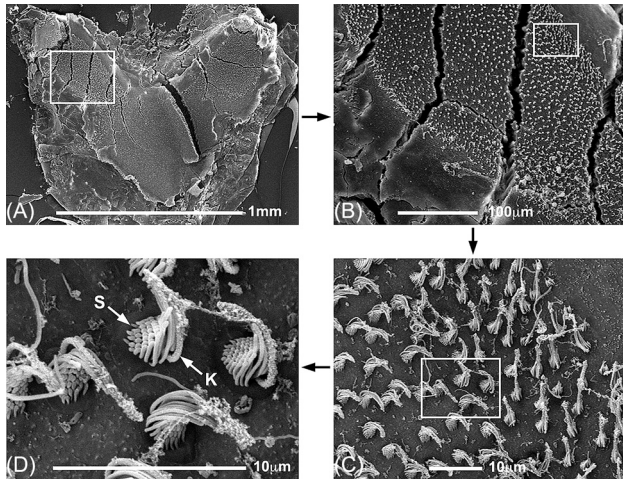


FIG. 5. Scanning electron micrographs (SEM) of the left utricular sensory epithelium of a deep-sea fish, *Melamphaidia acanthomus* (slender big scale). Serial enlargements show details along an orientation dividing line on the macula and hair bundles that orientate to opposite directions. (A) The whole macula (anterior to the left, dorsal to the top). The extent of the macula is the region that has the small white spots, which are, in subsequent images, seen to be the ciliary bundles on the sensory cells. Tissue outside of the macula regions is non-sensory epithelium. Note that the cracks are fixation artifacts. The area in the box is enlarged in (B) which shows the large expanse of ciliary bundles (white dots). The region in the small box in (B) is enlarged in (C) showing ciliary bundles on multiple hair cells. This is further enlarged in (D), which shows the details of the ciliary bundle with the kinocilia (k) and stereocilia (s). Note that the bundles on the left in (D) have their kinocilia on one side of the bundle and the cells on the right are oriented in the opposite direction (see Fig. 3). This represents the dividing line between the larger groups of ciliary bundles in the lower right figure. Figure courtesy of Dr. Xiaohog Deng. Figure Copyright Xiaohog Deng, all rights reserved.

1976; Popper, 1976, 1977; Platt and Popper, 1981; Popper and Platt, 1983; Platt and Popper, 1984). The sensory cells are innervated by the eighth cranial nerve, and many of the sensory cells also receive efferent innervation from the auditory region of the brain (Popper and Saidel, 1990; Walton *et al.*, 2017). Each macula may have anywhere from hundreds to hundreds of thousands of sensory cells, and these are added throughout life as the fish grows (Corwin, 1983, 1985; Lombarte and Popper, 1994).

The sensory epithelium and otolith are separated by a gelatinous otolith membrane (Fig. 6), the detailed structure

varies between fishes and is still not clearly understood (Werner, 1926; Dohlman, 1971; Dunkelberger *et al.*, 1980). The otolith membrane connects the macula to the otolith via fine fibers, maintaining the relative positions of these structures, while allowing some relative motion between the two structures (Popper, 1983; Popper *et al.*, 2003).

B. Sensory hair cell polarization

Bending of the ciliary bundle, as a result of relative motion between the otolith and the sensory epithelium, results in a release of a neurotransmitter that stimulates the innervating nerve fiber (Flock, 1964; Hudspeth and Corey, 1977; Jacobs and Hudspeth, 1990). Moreover, physiological recordings from sensory cells and innervating neurons demonstrate that the morphological polarization is related to a physiological directional polarization (Fig. 4). As such, bending of the ciliary bundle on the axis *towards* the kinocilium results in maximum depolarization of the sensory cell, while bending in the exact opposite direction results in maximum hyperpolarization. Bending of the bundle in other directions results in a graded response from the hair cell, resulting in its being a directionality receptor (Flock and Wersäll, 1962).

C. Hair cell orientation patterns

A critical feature of the sensory epithelia in terms of directional hearing is the precise organization of the sensory cells (Figs. 5 and 7). Of particular importance is that the maculae are divided into “orientation groups” [Figs. 5(D) and 7] in which all of the ciliary bundles have their kinocilium in the same general direction (e.g., Flock, 1964; Dale, 1976; Popper, 1976; Platt, 1977; Popper, 1977). The dividing lines between the different orientation groups is rather sharp. Whereas most teleost fishes have saccular hair cells oriented in four directions (Fig. 7) (Popper and Coombs, 1982; Popper, 1983; Saidel and Popper, 1983b), in otophysan fishes,¹ such as the goldfish (*Carassius auratus*), the saccule has hair cells oriented in two directions.

While innervation of the sensory hair cells has not been studied in great detail, there is evidence that each afferent

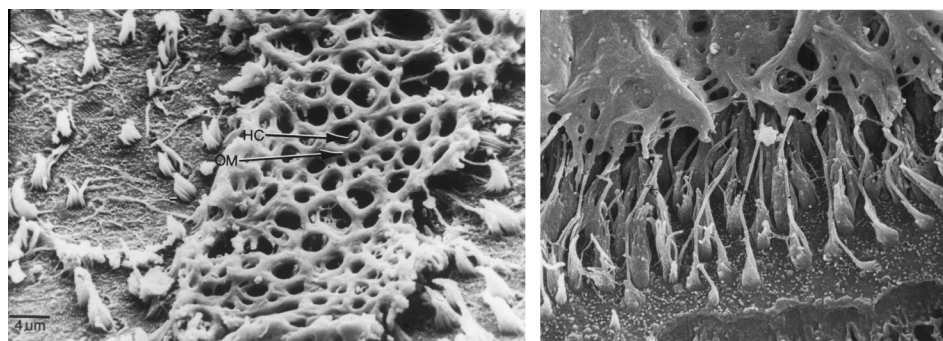
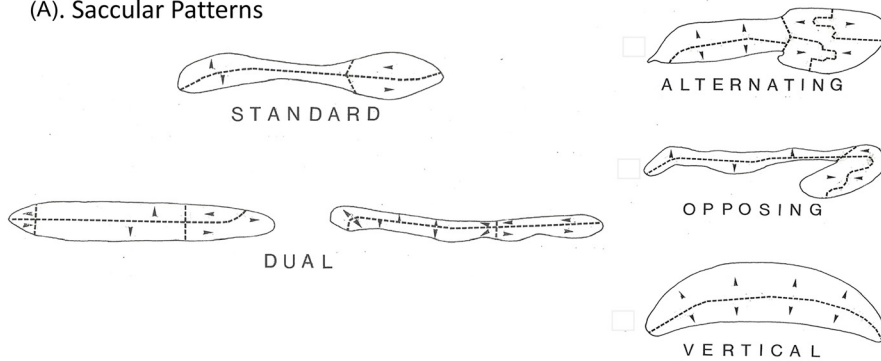


FIG. 6. Saccular sensory epithelium showing the epithelial surface and parts of the otolith membrane. In each case, small pieces of the otolith membrane were fortuitously left in place when the otolith was lifted off during dissection in preparation for scanning electron microscopy. It is important to note that fixation of the tissue results in changes in the chemical structure of the otolith membrane, and this no doubt alters the way the membrane appears. However, these figures do show the general location of the membrane above (left) and around (right) the ciliary bundles. In particular, in the lower figure, note that there are ciliary bundles (HC) surrounded by the otolith membrane (OM), suggesting that the OM extends from the otolith to the epithelium, typing the two structures together.

(A). Saccular Patterns



(B). Lagenar Patterns

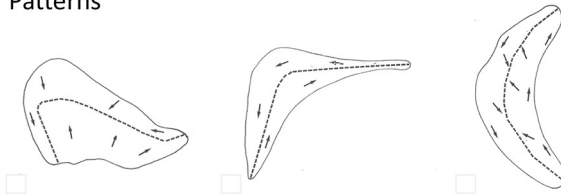


FIG. 7. (Color online) Variations in hair cell orientation patterns on saccular (A) and lagenar (B) maculae of various species. In each case, the dotted line indicates the general dividing point between different hair cell orientation groups. The arrows (or arrowheads) indicate the side of the ciliary bundles on which the kinocilium is found [see Fig. 5(D)]. Note that while these are the most common types of patterns, other patterns may be found in different species.

neuron may innervate 100 or more hair cells (Popper and Hoxter, 1984; Popper and Saidel, 1990).

There is considerable inter-specific variation in hair cell orientation patterns, particularly in the saccule [Fig. 7(A)] (e.g., Popper, 1977; Popper and Coombs, 1982; Buran *et al.*, 2005; Deng *et al.*, 2013; Schulz-Mirbach *et al.*, 2014). In contrast, while there is some interspecific variation in patterns in the utricle and the lagena [Fig. 7(B)], all species tend to have hair cells oriented in two opposing orientations in these organs (Fig. 7, vertical pattern). However, these patterns in the utricle and lagena [Fig. 7(B)] are not simply opposing groups of cells. Instead, and due to epithelial curvature, there is often a gradation in orientations so that hair cells are, in fact, oriented in various directions, with the change in direction rather gradual and parallel with the curvature of the epithelium (as related to the closest edge).

The patterns in the saccule, in contrast, are in many species more complex than in the other otolith organs. In an attempt to understand the variation, Popper and Coombs (1982) proposed that saccules be “classified” into several general orientation patterns [Fig. 7(A)] (see also Popper, 1983; Popper *et al.*, 2003). These patterns are not correlated with particular taxonomic groups of fishes, and any individual pattern may be found in taxonomically very diverse species, suggesting that they evolved multiple times.

It is likely that the most basal saccular pattern is the “bidirectional” or “vertical” pattern, and it is from this that the others likely derived. The bidirectional pattern is found in all non-teleost species including elasmobranchs, and all sarcopterygian (lobe-finned) species including terrestrial vertebrates. The pattern has two opposing hair cell orientation groups, though, as in the other end organs, there may be some shifting in orientation of specific hair cells as the epithelium curves (e.g., Popper, 1978; Popper and Northcutt, 1983; Corwin, 1989).

Interestingly, the vertical pattern is also found in a number of teleosts including the otophysan fishes (goldfish,

catfish) (Platt, 1977; Popper and Platt, 1983) and elephant-nose electric fishes, the Mormyridae (Popper, 1981). Both of these groups have specializations in the auditory system that enhance hearing sensitivity and bandwidth of hearing. Since both groups evolved from teleost groups having saccular hair cells oriented in four directions (Popper and Platt, 1983), it is likely that the bidirectional pattern in these groups evolved for some particular reason associated with specializations for hearing.

Where the hair cells are organized in four directions on the saccule, the two groups on the rostral end of the epithelium are generally oriented on the fish’s rostral-caudal axis, while the cells that are more caudal are organized dorsally and ventrally. The most common pattern has been called “standard” since it is the most frequently encountered pattern across most teleost taxa (Popper and Coombs, 1982). The variants on the pattern are many, but generally fall into groups, all of which have an elaboration of the anterior end of the epithelium where the cells are rostral/caudal (Fig. 7). At the same time, orientation of hair cells on the maculae is probably more complex than just the absolute direction of the ciliary bundles. Instead, the maculae often have various curvatures that give them a 3D shape so that even hair cells in the same orientation group may be oriented in slightly different directions, as demonstrated using 3D reconstruction by Schulz-Mirbach *et al.* (2013) and Schulz-Mirbach *et al.* (2014) in several species.

While there have been no studies examining the functional significance of the various hair cell orientation patterns, macula shape, or the effects of the 3D curvature, there is a clear correlation between having a non-standard pattern and having other specializations that are thought to enhance hearing range and sensitivity. Put another way, fishes that have swim bladders or other gas chambers close to or associated with the ear generally have one of the special orientation patterns.

Perhaps the clearest example of this correlation is found in the Holocentridae (squirrelfishes) where there are several

species that live sympatrically and yet have very different hearing capabilities (Coombs and Popper, 1979). In one of these groups, *Myripristis*, the fish can hear from below 50 Hz to over 3 kHz (a range that is similar to that of the goldfish) and the swim bladder terminates at the ear. The saccular pattern in these species is highly elaborate. In contrast, members of the genus *Adioryx* detect sounds to not much above 1 kHz with poorer sensitivity than in *Myripristis*, and the fish has no specializations of the sacculae, which follows the standard pattern.

Other examples of wide variation in saccular hair cell orientation patterns associated with enhanced hearing capabilities are found in some members of the Sciaenidae (croakers and drum fishes) (Ramcharitar *et al.*, 2006) and in diverse groups of deep sea fishes (Buran *et al.*, 2005; Deng *et al.*, 2011, 2013). Moreover, in sciaenids, species with deeper (dorsal/ventral) anterior regions of the saccular maculae appear to have better hearing than species with less deep maculae (Ramcharitar *et al.*, 2001), and similar observations have been made in cichlids (Schulz-Mirbach *et al.*, 2014).

D. Mechanics of the inner ear

1. Particle motion stimulation of the ear

Dijkgraaf (1960) and others proposed that when stimulated by sound, the tissues of the fish, including the inner ear, move with the particle motion generated in the surrounding water since the density of the body tissues is about the same as that of the water. However, due to their much higher density, the otoliths exhibit greater inertia and this results in shearing forces being applied to the cilia of the hair cells (de Vries, 1950; Pumphrey, 1950) relative to the body of the hair cells, which are embedded in the sensory epithelium (Fig. 6). This results in deflection of the ciliary bundles in the direction of the particle motion and, as a consequence, a directional response from the sensory cell that is graded (Fig. 4).

This mechanism for the direct detection of particle motion by the otolith organs is found in all fishes, including elasmobranchs. However, many species of bony fishes (but not elasmobranchs) have gas-filled structures close to the ear, most often the swim bladder, where the gas is more compressible than the surrounding tissues and water. The pressure changes accompanying the passage of a sound cause changes in the volume of the gas-filled structure, which, in turn, may re-radiate the sound as particle motion, and this has been referred to as an indirect stimulus (Fay and Popper, 1974, 1975). The radiated particle motion component of this sound has the potential to stimulate the otoliths, thereby enabling the ear to respond, indirectly, to the pressure component of the sound field. Indeed, Poggendorf (1952) and de Vries (1950) examined the particle displacement levels that might be provided by re-radiation of energy from the swim bladder. They concluded that if an appropriate mechanism existed for coupling the motion of the swim bladder to the ear, such as the Weberian ossicles of the Otophysan fishes, then larger levels of particle motion might stimulate the otolith organs over a wide range of frequencies. Poggendorf (1952), Van Bergeijk (1967), and Alexander

(1966), went further and suggested that in some species, the swim bladder might be capable of stimulating the ear even in the absence of a mechanical linkage. Pulsations of the swim bladder, induced by sound pressure, might be communicated to the ear simply through the intervening body tissues. This has been shown to take place in the Atlantic cod that has anterior projections from the swim bladder that bring its rostral end close to the ear (Fig. 1) (Enger and Andersen, 1967; Chapman and Hawkins, 1973; Sand and Hawkins, 1973). The resonance frequency of the swim bladder in the Atlantic cod is just above the frequency range of hearing, and although the motion of the swim bladder is heavily damped, the gas-filled organ radiates particle displacements at a higher level than those generated in a free sound field, especially at higher frequencies (Sand and Hawkins, 1973). However, although the particle motion radiated from the swim bladder may increase sensitivity to sounds, it should be noted that it comes from one direction only, related to the location of the swim bladder, and may not provide information on the direction of the sound source itself. Moreover, the swim bladder is not involved in hearing in all of those species that possess this organ (Hawkins and Johnstone, 1978; Yan *et al.*, 2000).

2. Inner ear mechanics

One of the biggest, and most important, questions regarding sound localization relates to the actual mechanics of the inner ear in fishes. How do the otolith organs respond to both direct and indirect stimulation? Put another way, in the presence of a sound, do the otoliths move (relative to the epithelium) just “back and forth” in the direction of the particle motion or are the movements more complex, resulting in differential stimulation of various macula regions in response to different sounds? Analyzing otolith motion and the role of otoliths in inner ear function is vital to understanding of how the ear detects and processes auditory and vestibular information (Popper *et al.*, 2005; Schulz-Mirbach *et al.*, 2018a). There are major questions over how otoliths move relative to the sensory epithelium and how properties such as otolith mass and shape, and other anatomical features, influence their motion in response to forces from different directions.

Several observations lead to the suggestion of “complex” motions. One might predict that to have a simple response the shapes of the otoliths would be simple so that there is no “disturbance” in the pattern of motion as the otolith moves within the fluids of the ears. However, otolith shapes are not simple (e.g., Fig. 3), and in many cases the otoliths have highly complex species-specific shapes that include extensive sculpting on the surface (e.g., Lychakov and Rebane, 1992; Popper *et al.*, 2005; Lychakov *et al.*, 2006). This is especially the case with the sacculae. Indeed, from the perspective of evolution, one must assume that the complex shapes have arisen for some functional purpose, and the logical purpose is involvement in inner ear function, including hearing (Popper *et al.*, 2005; Schulz-Mirbach *et al.*, 2018a).

There have been some studies of the nature of otolith motion, though primarily based upon modeling (Lychakov *et al.*, 2006; Kotas *et al.*, 2011; Krysl *et al.*, 2012). Some experimental data, albeit limited, support the idea of complex motion (Sand and Michelsen, 1978; Schulz-Mirbach *et al.*, 2018a; Schulz-Mirbach *et al.*, 2018b). For example, Sand and Michelsen (1978) used laser vibrometry to examine otolith motion in the perch (*Perca fluviatilis*). They observed that vibration of the fish in the horizontal plane along its long axis resulted in vertical movements of both ends of the otoliths at several driving frequencies. An area of minimum vertical movement appeared around the midpoint of the otolith at different frequencies, indicating the existence of a horizontal axis of rotation or rocking. Subsequent finite element modeling of the movements of the saccular otolith in the white sea bass (*Atractoscion nobilis*) by Krysl *et al.* (2012), in response to low-frequency planar progressive acoustic waves, predicted that the otolith oscillated both in the direction of the propagation of the progressive waves and also in the plane of the wave front as a result of angular motion.

Most recently, Schulz-Mirbach *et al.* (2018b) examined the *in situ* motion of the otoliths in two cichlid species, *Steatocranus tinanti* and *Etoplus maculatus*, using x-ray phase-contrast imaging, which allowed for a detailed examination of the motion of the otoliths of all end organs. The investigators found that each of the three otoliths in each ear showed different motion patterns as expected by their different *in situ* orientation and attachment to the respective underlying sensory epithelium. These results therefore strongly support the idea that the motion of complicated shapes such as otoliths under plane harmonic wave excitation may be more complex than the simple back-and-forth oscillation in the direction of the progressive waves that was suggested by Pumphrey (1950) and de Vries (1950).

While the pattern of otolith motion is a major factor in determining the way in which the ear responds to sound, and particularly to sound direction, other factors must be taken into consideration in thinking about hearing in fishes. One such factor is that the movements of otoliths are also constrained within the otic capsule not only by the otolith membrane (see above), but most likely also by the walls of the end organ chamber which may not be any larger than the otolith itself. This morphology will restrict and guide the direction of motion of the otoliths. The density of the otolith, and the viscosity of the fluid or endolymph within each otolith organ may also influence the motion of the otoliths.

Another factor is the 3D configuration of the epithelia and the fact that they curve along their length, as shown in micro-computed tomography (CT) analysis by Schulz-Mirbach and colleagues (Schulz-Mirbach *et al.*, 2011; Schulz-Mirbach *et al.*, 2013). This suggests that even as the otolith moves, the pattern of stimulation of hair cells may differ even along a single orientation group. This finding may provide insight into understanding the basis for the small amount of evidence suggesting that different regions of the saccular macula may be stimulated by different frequencies in both the goldfish (Furukawa and Ishii, 1967; Smith *et al.*, 2011) and Atlantic cod (Enger, 1981), although the extent of this regionalization is not likely to be the same for different species.

Finally, an added “complication” to understanding otolith function may be that they grow over the life of fishes (adding “growth rings” which are used to age fish) and there is some correlation in size and shape of otoliths with the ecological niche of many species (Lombarte and Cruz, 2007; Lombarte *et al.*, 2010). Thus, there may be dynamic changes in the way otoliths respond in a sound field as the animals age and otoliths get larger and potentially have some changes in shape.

It is evident that our knowledge of how exactly all these factors influence the motion of the otoliths is currently incomplete.

E. The hearing abilities of fishes

There is an extensive literature on fish auditory sensitivity (for reviews see Fay, 1988; Ladich and Fay, 2013). However, as pointed out recently (e.g., Hawkins *et al.*, 2015; Nedelec *et al.*, 2016; Popper and Hawkins, 2018), there are many problems with most of the earlier data, most notably because (a) studies were done in tanks where the acoustic environment could not be calibrated (Duncan *et al.*, 2016; Rogers *et al.*, 2016) and so it is not possible to know the actual signal to which a fish was responding and (b) the vast majority of studies were done with signals monitored in terms of sound pressure, even though we now know that most fishes are primarily detectors of particle motion—a parameter that was often not measured (Popper and Hawkins, 2018).

It is clear that all fishes can detect sounds and that the majority primarily detect signals from below 50 Hz to anywhere from 300 to 1000 Hz, depending on the species. Species that detect sound pressure may be able to detect frequencies above about 300 Hz, while species that have specializations that bring a gas chamber close to (or into contact with the inner ear) may hear frequencies up to 3000 Hz or above. There is a great deal of variation in sensitivity to sounds, reflecting the high level of diversity in fishes.

Fishes are able to discriminate between sounds of differing amplitude and frequency (Jacobs and Tavalga, 1967, 1968; Fay, 1970; Fay and Passow, 1982). Fay and Passow (1982) pointed out that the teleost ear may be especially well adapted for distinguishing the temporal structure of sounds (see also Fay, 1994, 1995). Behavioral studies of sound communication have indicated that fish discriminate between calls on the basis of differences in repetition rate and duration, rather than frequency or bandwidth (Fine, 1978; Spanier, 1979; Myrberg, 1981). The goldfish can discriminate between sounds that differ in phase; that is, between sounds that begin with a compression and those that begin with a rarefaction (Piddington, 1972). It was shown that the goldfish can discriminate between a given click and its phase inversion, which humans cannot do. Fishes are also able to improve their detection of sounds in the presence of background noise, showing evidence of complex auditory processing, in some cases involving frequency filtering (Tavalga, 1974; Hawkins and Chapman, 1975; Fay *et al.*, 1978; Fay, 2012). In the natural environment the ability to detect sounds against the ambient noise background is likely to be more important than absolute sensitivity (Chapman, 1976). Masking of a given frequency is confined to a narrow band

of noise frequencies (the critical band), close to the signal frequency.

IV. EVIDENCE FOR DIRECTIONAL HEARING IN FISHES

A. Early experiments

Early experiments on sound source localization in fishes gave negative results. Attempts were made by von Frisch² and his student Dijkgraaf to condition European minnows (*Phoxinus phoxinus*) to locate a sound source in a shallow lake, using food as a reward (von Frisch and Dijkgraaf, 1935). Although the minnows showed a conditioned arousal response to the sound, they were not observed moving towards the feeding station, and it was concluded that they could not locate underwater sound sources. von Frisch (1938) subsequently proposed that Otophysan fishes like the minnow, with what he supposed was a single sound pressure receptor, the swim bladder, were not able to determine sound direction, as the sound pressure at any single point contains no information about the direction of sound propagation.

A similar conclusion was later drawn by van Bergeijk (1967) who went on to argue that fishes, in general, could not localize sounds using their ears. He based his argument on the assumption that fishes must use the mechanism of localization described for terrestrial vertebrates, and especially mammals, where the brain compares the sounds arriving at the two ears and calculates direction (Masterton *et al.*, 1969; Popper and Fay, 2005; Heffner and Heffner, 2016). Such localization is based on differences in time of arrival, signal phase, and/or intensity of the sounds at the two ears, depending on sound frequency and other characteristics. van Bergeijk (1964) argued that such localization is not possible in water since the speed of sound is faster than in air and the wavelengths proportionally larger. He concluded that the cues used for localization in terrestrial mammals would not be available for fishes, especially since, in most species, the ears are very close together. Van Bergeijk also pointed out, as did von Frisch, that since there is only a single sound pressure receptor in fishes (the swim bladder), there is no difference in the sound pressure signals reaching the two ears (see Fig. 1).

van Bergeijk (1964) suggested that directional hearing would be possible only very close to a sound source, with the fish utilizing the lateral line. This view contrasted with that of Dijkgraaf (1963), who had proposed that the lateral line served mainly to detect and locate moving objects at short range on the basis of current-like water disturbances. The lateral line system was not involved in the detection of propagated sound waves. Evidence now strongly supports Dijkgraaf's view of the lateral line as an independent sensory system, detecting local movements of the surrounding water (e.g., Coombs and Conley, 1997; Sand and Bleckmann, 2008).

B. Studies of sound localization by fishes

1. Elasmobranchs

Despite initial doubts, it has now been established that some fishes tested (albeit still only very few species) can swim towards sources of sound, although whether a

mechanism exists for sound source localization is still not clear. Swimming towards a source does not necessarily indicate that the fish knows where the source is in 3D space. Such a response may be termed "phonotaxis," defined as the oriented movement of an animal with respect to a source of sound. Using phonotaxis, a fish may simply be sampling the sound level at different locations and moving towards the highest levels. Or the fish may simply be able to determine the direction of the source relative to its own orientation, but not its precise location.

One of the earliest demonstrations of phonotaxis in fishes came from work of Nelson and Gruber (1963) who demonstrated that the sounds of struggling fish were effective in attracting predatory sharks (see also Nelson and Johnson, 1972; Nelson, 1977). Large sharks, in their natural environment, were attracted to low-frequency (predominantly 20 to 60 Hz) pulsed sounds in the far field, but apparently not to higher frequency (400 to 600 Hz) pulsed sounds, or to low-frequency continuous sounds (e.g., Richard, 1968). Similar results were found by Wisby *et al.* (1964) who used light aircraft to observe that sharks could detect and swim towards a source of sounds from a distance of almost 200 m. Subsequently, using underwater television, Richard (1968) confirmed that demersal predatory teleosts and sharks were attracted by pulsed low-frequency acoustic signals. Similarly, Myrberg *et al.* (1969) observed and recorded the attraction of free-ranging sharks to a sound source. Several species of shark, including the silky shark *Carcharhinus falci-formis* were attracted by irregularly pulsed signals, confirming that these fishes could also swim towards sources of sound in the sea. It has since been confirmed that sharks may identify and track down their prey by means of sound, often over large distances (Myrberg *et al.*, 1976). The effectiveness of such sounds in eliciting approach responses increased with pulse irregularity, increased pulse rate and lower frequencies. It has been suggested that such impulsive sounds simulate the sounds produced by feeding fish and the struggling movements of prey animals.

Whether these sharks were engaged in sound source localization is still not clear. For example, it is not clear whether the sharks swam directly to the sound source as they knew its precise location or direction, or whether they sampled sounds along the way by swimming across the sound field, thereby potentially following a path towards the loudest sound levels. Moreover, as pointed out by Casper and Mann (2009), there may have been mitigating circumstances in those field studies, such as the sharks actually responding when close to the electromagnetic radiation from the sound sources or that, at least in one study (Richard, 1968), the sharks may have been following bony fishes to the source and not actually localizing the sound source themselves.

There is also the issue that since elasmobranchs do not have any compressible discontinuities that would allow for sound pressure detection; they are only detecting particle motion (Casper and Mann, 2007a,b, 2009). Considering that the studies on shark sound localization have suggested that at least some animals are detecting particle motion from sound sources that are over 1000 m from the initial position of the animal, the question arises as to whether sharks are

exquisitely sensitive to particle motion and/or whether they are detecting larger particle motion levels that may be associated with pressure release at the sea surface or from the transmission of interface waves along the substrate.

While experimental data are limited, there are some data suggesting that at least the white-spotted bamboo shark (*Chiloscyllium plagiosum*) is particularly sensitive to particle acceleration from a dipole sound source, which closely resembles the sounds from a struggling or swimming fish, compared to earlier studies that only used monopole sources (Casper and Mann, 2007a). The involvement of the ear in directional hearing was also shown by placing white-spotted bamboo sharks on a shaker table (a flat surface which is moved back and forth in various directions to simulate directional particle motion)—a technique first used by Enger *et al.* (1973) and Fay (1984). Using a shaker table, Casper and Mann (2007b) found that the inner ear of the sharks responded differently to motion in different directions. However, they also found that the responses in the otolith organs of the bamboo shark were less directional than those found in the goldfish by Fay and Olsho (1979), though the reason for the difference may have been that the shaker table did not stimulate the macula neglecta in the bamboo shark; this may be the major organ for sound detection and sound localization in elasmobranchs. Indeed, there is evidence that the pathway of sound to the ears in sharks comes through the endolymphatic fossa, a fluid-filled area on the top of the head that leads directly to the macula neglecta (Tester *et al.*, 1972; Fay *et al.*, 1974; Corwin, 1989; Casper and Mann, 2007b,a).

2. Bony fishes

A number of studies have demonstrated that teleost fishes are sensitive to sound source direction. Tavalga (1958) showed that male and female gobies (*Bathygobius soporator*) approached a sound projector emitting male courtship calls. It has also been shown that the round goby (*Neogobius melanostomus*) can directionalize, and possibly localize, conspecific calls (Rollo *et al.*, 2007; Rollo and Higgs, 2008). Moulton and Dixon (1967), in a paper that provides an exceptional review of directional hearing up to that year, conditioned goldfish *Carassius auratus* to show a directional tail-flip response towards a sound source in response to a food reward, although whether sound source localization took place is questionable since the investigators did not calibrate the sound field in the tank. Olsen (1969) demonstrated clear directional avoidance responses by Atlantic herring schools in a pen floating in a fjord to the playback of sounds. Later, Olsen (1976) observed the attraction of a school of saithe (*Pollachius virens*) conditioned to come to a pulsed 150 Hz pure tone, at distances of up to 80 m, and also reported directional avoidance responses by free-swimming herring (*Clupea harengus*) to impulsive sounds. Winn (1972) showed that female oyster toadfish (*Opsanus tau*) were attracted to playback of the male's "boatwhistle" call. However, some of these responses from teleosts may simply have demonstrated phonotaxis, based either on detection of the direction, or upon sampling of the

sound level at different locations. Winn subsequently showed that gravid female plainfin midshipman *Porichthys notatus* also exhibited phonotaxis to the playback of advertisement calls and pure tones that resembled these calls (Cohen and Winn, 1967). Popper *et al.* (1973) demonstrated that several species of Hawaiian squirrelfish of the genus *Myripristis* in an acoustically transparent cage floating in a small bay would swim towards a speaker emitting conspecific sounds.

It has been demonstrated through conditioning experiments that some fishes can discriminate between sounds from different directions and distances. A number of these experiments were carried out on captive fish held in cages in midwater in the sea. Schuijff *et al.* (1972) showed that the Ballan wrasse (*Labrus bergylta*) was able to detect a change in the direction of a sound. Chapman (1973) noted that the masking effect of noise on the detection of a pure tone by the Atlantic cod was reduced when the masking noise was transmitted from a separate sound projector spatially separated from the signal projector. Subsequently, Chapman and Johnstone (1974) repeated the experiment with Atlantic cod using four sound projectors, allowing a wider range of separation between signal and masker. For angles greater than 10°, there was a significant decrease in the mean threshold:noise ratio of about 7 dB. Experiments were then carried out where Atlantic cod and haddock were conditioned to respond to a short period of switching of a pulsed tone from one loudspeaker to another at a different angle in the horizontal plane. The fish readily detected the switching of direction when the loudspeakers were separated by 20° or more.

Further experiments under field conditions showed that Atlantic cod were able to discriminate between sound sources in the median vertical plane as well as the horizontal plane (Hawkins and Sand, 1977). Atlantic cod could also discriminate between pure tones emitted alternately from two aligned sound projectors at different distances (Schuijff and Hawkins, 1983). The amplitude of the pulses was varied randomly to ensure that discrimination was not based on amplitude differences. It was suggested that since the phase relationship between sound pressure and particle motion varies with distance from a source, it might therefore provide distance cues to the fish. These experiments demonstrated that the cod is well able to discriminate between separate low frequency sound sources in 3D space. The abilities of the Atlantic cod to discriminate between sound sources at different distances and in different directions appear to exceed those of many terrestrial vertebrates, perhaps because fishes like the Atlantic cod live in a 3D medium rather than being restricted to living on a surface. They may be able to maintain a 3D image of the acoustic scene surrounding them.

In a later series of experiments, the ability of Atlantic cod to discriminate between diametrically opposed loudspeakers in both the horizontal and vertical planes was investigated (Buwalda *et al.*, 1983). The experiments involved a number of loudspeakers suspended from a raft in different positions relative to the fish (Fig. 8). The set up was designed to determine whether the Atlantic cod was able to discriminate sounds from opposing directions, and also whether a

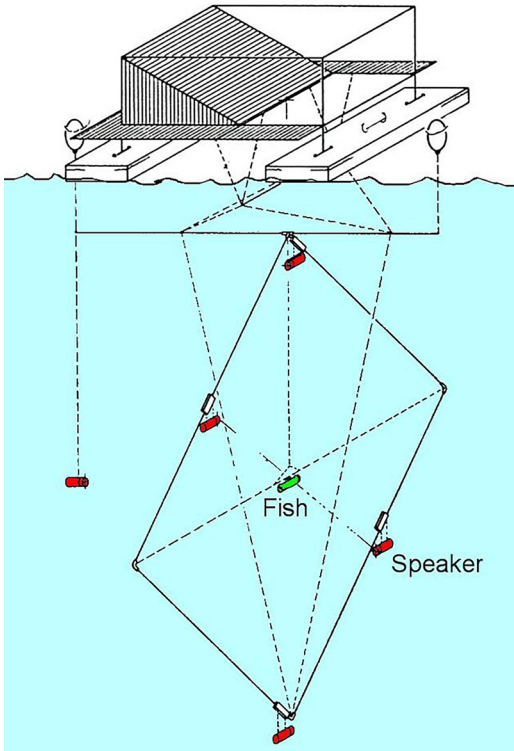


FIG. 8. (Color online) Schematic of setup used by [Buwalda et al. \(1983\)](#) to study directional discrimination between sound sources in a deep Scottish sea loch. The raft at the surface acted as a working platform. The four underwater sound projectors were mounted on a vertically orientated diamond of scaffolding tube hung beneath the raft, each projector being capable of being moved. Within each pair, the two projectors were always arranged symmetrically with respect to the acoustic center. The fish cage and associated hydrophones were slung from a polyvinyl chloride bar. The suspension system was designed to isolate the diamond from movement of the raft on the waves. The ability of Atlantic cod to discriminate between sound waves coming from opposing directions was verified. It was concluded that the detection of sound propagation direction was based on comparison of the phase relationship between particle motion and sound pressure.

phase reversal of sound pressure with respect to particle motion was experienced by the fish as a 180-degree change in direction. Switching a continually pulsed 120 Hz pure tone stimulus from a reference source to an opposing source was detected. However, discrimination between the two sources was not possible when a standing wave was added to the opposing source, locally inverting the phase of sound pressure with respect to the acoustic particle motion. It was concluded that the detection of sound propagation direction was based on the characteristic phase relationship between particle motion and sound pressure.

Although these conditioning studies essentially showed that fishes could effectively discriminate between sounds coming from different directions and even distances, they did not definitely demonstrate sound source localization by fishes, as the fish were not required to actually move towards the source. The experiments simply demonstrated discrimination of sounds from different angles and distances. Some of the directional responses observed from free-living fishes (e.g., [Wisby et al., 1964](#); [Olsen, 1976](#); [McKibben and Bass, 1998](#)), may have involved sound source localization. Nevertheless, [Kalmijn \(1997\)](#) pointed out that to find a source, fish did not necessarily need to know precisely where the source was

actually located. They could find their way to a sound source by swimming in a direction that maintained a constant angle between the fish and the axis of particle motion. The fish did not necessarily have to determine the precise orientation of the local particle motion vector, it just had to behave in a way that maintained a constant angle with the particle motion vector. It would then eventually arrive at the source.

More recently, [Zeddies et al. \(2010\)](#) and [Zeddies et al. \(2012\)](#) performed phonotaxis experiments on the plainfin midshipman (*Porichthys notatus*) to investigate how fish may locate sound sources. The experiments were carried out in a circular concrete tank (4 m diameter, 0.75 m deep) where the particle motion components in different directions could be estimated from measurements of the sound pressure gradient, thereby providing a map of the directional sound fields within the tank. Gravid female midshipman followed straight or slightly curved paths to the monopole sound projector that was producing a signal that emulated the advertisement calls of male fish. The sound projector was visually occluded so that the fish were forced to rely on acoustic cues to locate it. The study by [Zeddies et al. \(2010\)](#) was the first to describe in detail the paths that fish take towards a sound source, showing that the fish swim along the axis of the particle motion vectors in the monopole sound field. Interestingly, no evidence was found that the midshipman fish were confused by the 180° ambiguity of the particle motion (see later discussion of this point). At the same time, what [Zeddies et al.](#) may have seen is the final approach behavior of the females rather than how they behave when they first hear the sound in the wild. The fish were examined relatively close to the source.

In a subsequent study on the same species, [Zeddies et al. \(2012\)](#), a dipole sound projector was utilized rather than a monopole. Whereas monopole radiation is omnidirectional (equal in all directions), dipole radiation produces a bi-lobed, figure of eight pattern. When released along the dipole vibratory axis, the responding female fish took essentially straight paths to the source. However, when released approximately 90 degrees to the source's vibratory axis, the responding females took highly curved paths to the source that were approximately in line with the local particle motion axes. Essentially, the fish swam towards the source along pathways parallel to the axes of particle motion at this location in the field. It was concluded that the local particle motion is an important cue that guides sound source localization behavior in the midshipman fish. Gravid females can use acoustic cues to localize dipole sound sources. The fish did not necessarily "know" where the source was, but by adopting a 0-degree orientation angle relative to the local particle motion vector they were able to reach the source.

A number of studies have investigated the possible use of sound as a sensory cue for navigation by fishes, including the larvae of reef fishes, which are said to locate suitable habitats using sound (e.g., [Leis et al., 2003](#); [Tolimieri et al., 2004](#); [Simpson et al., 2005](#)). These investigators suggest that sounds emanating from reefs provide useable cues for settlement-stage larvae searching for settlement sites, although the mechanism for such homing responses is not known.

3. Conclusions on whether fishes can localize sound sources

It is now clear that fishes, as other vertebrates, can discriminate between sound sources in different directions and in some cases at different distances. This conclusion is based on a wide range of behavioral studies on diverse species. However, the extent of behavioral data is still very limited, and there are far more questions to be asked before we have a good understanding of whether sound source localization is possible in both bony fishes and elasmobranchs. It is still not clear whether fishes can locate the actual position of a sound source in 3D space.

To date, the majority of studies have focused on animals that are restrained and where physiological or conditioning studies are used to measure responses. While these are critical studies and provide a great deal of insight into potential mechanisms of hearing, including directional responses, it will only be behavioral studies with free-swimming animals that will provide a detailed understanding of how fishes might actually go about locating a sound source.

Accordingly, the most important studies to date are those on the midshipman, indicating that females are able to follow the direction of the sounds emitted by males. However, while the studies provide some insight into how one species may find the sound source, there are a number of issues that must be kept in mind. For example, it is clear that the conditions for this experiment were not ideal, as the fish started out at a point close to the sound source (80 to 100 cm) and particle motion levels were especially high in comparison to conditions in a free sound field, where one would expect that the initial detection of the male sound would be at some distance from the sound source and also rather distant from reflecting boundaries. In addition, it is possible that the sound was also travelling through the concrete substrate. In reality, even in the case of toadfish, it is likely that the female often detects the males at some substantial distance from the source as she is looking for a mate, but nothing is yet known about the path that is used in the field to move to the vicinity of the males, or from how far she will hear and seek a male. For example, do the females take a straight path to the source, as seen in the studies by Zeddies and his colleagues, where the females start close to the source, or do they “sample” the sound field and go in approximate directions, frequently changing direction as they test the sound levels? Indeed, some of the very same questions raised about directional hearing in sharks (Sec. IV B 1) may be applied to toadfishes since there is evidence that these species, like sharks, only use particle motion for sound detection (Yan *et al.*, 2000).

Another issue is that the only behavioral data are for one species in a (albeit large) tank with a cement bottom. How will other species locate sounds, and how do they localize at different distances from the source as well as at different water depths? Indeed, it is highly likely that the females of many species find their mates by listening to calls, and so the questions raised for toadfish are of equal importance to species as diverse as sciaenids (Luczkovich *et al.*, 2008) and gadoids (Casaretto *et al.*, 2014; Casaretto *et al.*, 2015).

V. EXAMINING THE MECHANISMS OF DIRECTIONAL HEARING

A. Examining binaural mechanisms

As discussed earlier, it had initially been thought highly unlikely that fish utilize the same direction-finding mechanisms as terrestrial vertebrates in air. However, surgical elimination experiments on the Atlantic cod have shown that both the ears are essential for directional detection at a distance from the source, as in terrestrial vertebrates (Schuijf, 1975). In that study, Schuijf unilaterally severed the saccular and lagenar nerves in an Atlantic cod and found that this deprived the fish of its acoustic localization ability, but not its acoustic detection ability. Schuijf and Buwalda (1975) also tested the ability of Atlantic cod to discriminate between sound waves coming from the direction of the fish's head or tail. The positive results obtained indicated that binaural differences were not always required for the determination of the direction of the sound source, as the sounds presented were binaurally symmetrical. In a later paper, Schuijf *et al.* (1977) demonstrated the ability of the ide (*Leuciscus idus*, an Otophysan fish) to discriminate between sound waves coming from the direction of the head or tail, providing a control by interchanging the two sources.

B. Physiological studies

As discussed in Sec. III and elsewhere, the otolith organs themselves detect particle motion (Dijkgraaf, 1960; Hawkins and MacLennan, 1976; Lu *et al.*, 2004, 2010; Popper and Hawkins, 2018). Indeed, in his classic paper, Dijkgraaf (1960) also made the critical point that a particle motion detector is inherently directional in its response.

1. Directional response to particle motion

It is clear that, depending on the suspension of the otolith and the orientation of the hair cells in the macula, the stimulation of the morphologically and physiologically polarized sensory hair cells by relative movement of the otolith will vary with the direction of the incident sound wave. This idea was supported experimentally, first by Enger *et al.* (1973), who monitored microphonic potentials from the sacculus of the haddock as the fish was subjected to oscillatory motion from different directions. Microphonics are the electrical potentials generated by the hair cells as they are stimulated by motion of the otoliths. The levels of the saccular microphonics varied as the fish was shaken at different angles of azimuth on a vibrating table where the direction of vibration could be controlled. Maximum amplitude from the sacculus was obtained when the fish was vibrated along its long axis. Using a more sophisticated controlled vibrating table, Sand (1974) showed that the two bilateral sacculi in the perch *Perca fluviatilis* had different axes of maximum sensitivity in the horizontal plane. The angle between the optimal vibration for the two sacculi was 45° and was independent of the stimulus frequency and the locus of the recording. Following from this, Fay and Olsho (1979) recorded the discharge patterns of lagenar and saccular afferent neurons in the eighth cranial nerve of the goldfish in

response to vibration in three orthogonal directions. The neurons from both otolith organs showed similar patterns of directional sensitivity which corresponded quite well with the orientation patterns of the hair cells. These results were further supported using the same methodology in other species (Lu *et al.*, 1998; Lu and Popper, 2001; Meyer *et al.*, 2011).

The morphology of the ears of bony fishes shows that there are hair cells oriented in numerous directions. This idea derives from several morphological characteristics. First, the two ears of most bony fishes are oriented in different directions (e.g., see Fig. 1), thereby providing animals with end organs oriented in many different ways. Thus, even though the saccules (for example) of the aforementioned perch have the same patterns, the cells on the two saccules would be 45 degrees apart. Second, hair cells oriented in different directions on single maculae, as well as curvature within maculae, means that even hair cells within the same orientation group actually have their axes of best response in different directions (see Fig. 9), providing fishes with receptors oriented in many different directions.

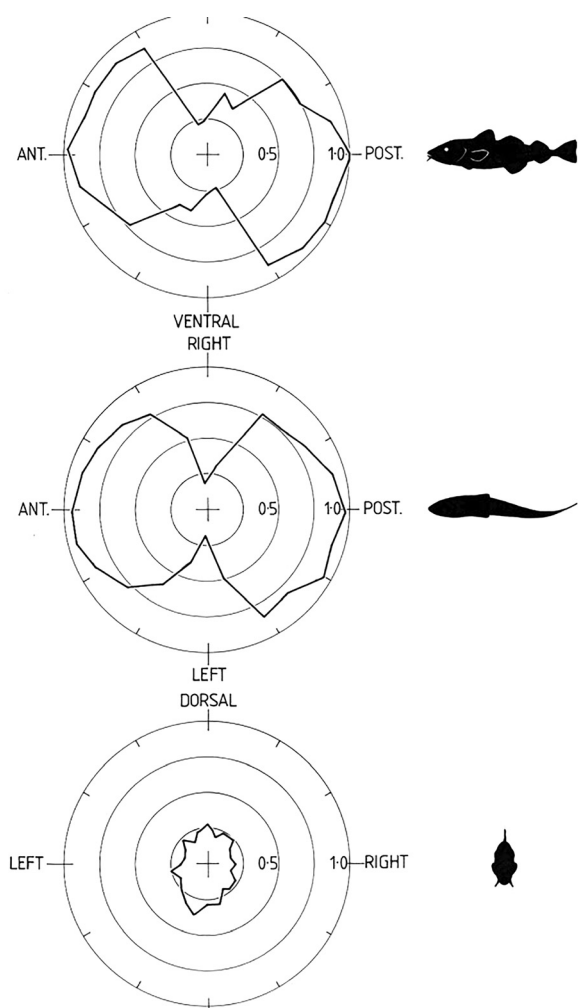


FIG. 9. The directional response in different planes of the signals generated within a single neuron from the saccule of the Atlantic cod at a frequency of 63 Hz by Hawkins and Horner (1981). The fish was placed on a table capable of being vibrated in all three planes. The response of the neuron was monitored for each angle as the number of electrical spikes per cycle of the stimulus.

Enger *et al.* (1973) and Sand (1974) were concerned that the presence of a swim bladder in fishes might obscure the directional responses of the hair cells to the detection of directly received particle motion stimuli; the high levels of particle motion radiated from the swim bladder might exceed those levels received directly from the sound source. However, scanning electron microscopic studies of hair cell orientation in the perch by Enger (1976), in a salmonid, the lake whitefish (*Coregonus clupeaformis*) by Popper (1976), and in the Atlantic cod by Dale (1976), found that the anterior saccular hair cells in taxonomically diverse fish species are oriented rostro-caudally, whereas the more caudal cells had a dorso-ventral sensitivity axis (Fig. 5) (see also Popper, 1977, 1981). Sand (1974) suggested that the particle motion radiated from the swim bladder would only stimulate those hair cells oriented towards the particle motion radiating from the swim bladder, leaving the other hair cells, with their different orientation, to respond to the particle motion generated directly by the sound source.

Later, Buwalda and van der Steen (1979) showed that the level of the saccular microphonics of Atlantic cod, held in a free sound field, depended on the direction of the sound. A cosine dependence of microphonic levels upon sound direction was found, compatible with a vector detector function for the left and right saccules, the main axes of sensitivity of the two sacculi differing by 73°. Similar results were found for goldfish (Fay and Olsho, 1979; Fay, 1984) and sleeper goby, *Dormitator latifrons* (Lu *et al.*, 1998), and lake sturgeon, *Acipenser fulvescens* (Meyer *et al.*, 2011) using shaker tables.

2. Segregation of directional information in the eighth cranial nerve

Studies using auditory microphonics showed that different parts of the ear show different directional responses based upon the orientation patterns of the sensory hair cells. Further, studies monitoring the responses of the afferent nerve fibers suggested that the differing directional information from these regions is maintained as separate streams within the eighth cranial nerve and then into the brain.

The first such study, by Furukawa and Ishii (1967), suggested that different single neurons from the saccule respond either to hair cells oriented upwards or downwards (see Fig. 5—vertical orientation), although they did find a subset of neurons that innervated across the line between hair cell groups. The later experiments by Fay and Olsho (1979) on the goldfish confirmed that the neurons from the otolith organs showed similar patterns of directional sensitivity to the hair cells that they innervated. Hawkins and Horner (1981) working with Atlantic cod showed directional responses at the level of the primary afferent neurons. Vibration at different angles in the horizontal and vertical planes resulted in changes in the response of each individual neuron (Fig. 9). The spike activity of the auditory units was highly synchronized with the waveform of the stimulus. This synchronization is termed phase-locking and occurs when the action potentials of the auditory neurons coincide with a particular phase of the sound being received.

Later, morphological and physiological studies in several species confirmed that individual neurons only innervate sensory hair cells oriented in one direction (Saidel and Popper, 1983a,b; Popper and Saidel, 1990; Lu and Popper, 2001). More recent studies, primarily with the oyster toadfish, clearly show segregation of information from different regions of the ear and from the different end organs themselves in the eighth nerve (Fay and Edds-Walton, 1997b; Edds-Walton *et al.*, 1999), strongly supporting the idea that there is likely separation of information from the hair cells of different macular orientation groups within the brain.

Hawkins and Horner (1981) showed that the majority of saccular units in the Atlantic cod were sensitive along the long axis of the fish (0 or 180 degrees) or at a small angle of offset from this axis, with their minima at right angles. Approximately the same axis was obtained at different frequencies. Utricular units were also strongly directional in their response, again yielding a bi-lobed polar diagram in the horizontal plane, often at right angles to the long axis of the fish. However, not all utricular units showed the same axis of orientation. There was considerable variation compared with the relatively narrow angle of orientation of the saccular units, which is not unexpected considering the wide range of hair cell orientations found in the utricle (e.g., Lu *et al.*, 2004). Interestingly, the mean direction of the relatively narrow range of best angles for the saccule did not coincide with the orientation of the hair cells in the saccular macula in the Atlantic cod. A majority of hair cells in the middle part of the macula are orientated largely in the vertical plane, although some hair cells at the extreme anterior and posterior ends are orientated along the horizontal line of the macula.

The directional responses of the otolith organs have now been examined for a number of additional species (e.g., Fay and Edds-Walton, 1997a; Lu and Popper, 1998; Edds-Walton *et al.*, 1999; Fay and Edds-Walton, 2000; Lu and Popper, 2001; Lu *et al.*, 2004; Meyer *et al.*, 2011). For example, Fay (1984) re-investigated the directionality of the afferent fibers from the saccule, utricle, and lagena in the goldfish and found that they were all highly directional. Subsequently, Fay and Edds-Walton (1997a) examined the directional response properties in the oyster toadfish *Opsanus tau*, a species using “boat whistle” calls to locate conspecifics, using a vibrating table. The most sensitive saccular afferents responded with a phase-locked response to displacements as small as 0.1 nm. Eighty percent of the afferents had 3D properties that would be expected if they innervated a population of hair cells with the same directional orientation within the macula. In general, the directionalities of saccular afferents corresponded qualitatively with the orientation of the sensory epithelium and with regional patterns of hair cell orientation. Fay and Edds-Walton (2000) suggested that directional hearing in the horizontal plane probably depended on the processing of interaural differences in overall response magnitude. These response differences arise from the gross differences in the orientation of the two saccules. In the vertical plane, elevation might be computed from differences in the response of afferents from different parts of the saccule. At the same time, there is evidence in toadfish (Maruska and Mensinger,

2015) and sleeper goby (Lu *et al.*, 2004) that the utricle responds differently to sound coming from different directions, suggesting that it is likely to contribute to sound localization in at least some species.

There is a problem in determining the relationship between the direction of motion of the actual otoliths, and the orientation of the hair cells within the macula. The movements of the otoliths themselves may be rather complex. It is not clear how otolith mass and shape, and the relationship between the sensory epithelium and overlying otolith, influence the motion of the otoliths (Schulz-Mirbach *et al.*, 2018b). It is also not entirely clear how their motion translates into directional information that can be computed based on the hair cell orientation patterns. In effect, it is not clear how the movements of the otoliths interact with the directional orientation of the sensory cells on the maculae.

C. Central auditory system

Central processing, which entails integration of information from different sources including the two ears, is the basis of sound source localization in terrestrial vertebrates where each ear provides information that, by itself, has no directional properties (e.g., Colburn and Kulkarni, 2005; Trahiotis *et al.*, 2005). It is clear in fishes that there is already considerable differentiation of responses from various directions both in the otolith organs and the auditory nerves of fishes. Fishes are getting directional information from different parts of each ear, which is not the case for terrestrial animals. An additional question is whether this information alone is sufficient for sound localization or whether additional processing of signals takes place in the central nervous system (CNS).

Though studies have focused on only a few species, it is now apparent that there is directional representation of sound both in the brainstem and as high as the torus semicircularis of the midbrain (reviewed by Fay, 2005; Edds-Walton, 2016; Walton *et al.*, 2017). The most thorough analysis to date is for the oyster toadfish, where Edds-Walton and Fay have done an extensive analysis of the responses from the ear to the midbrain (for an excellent review of these studies, see Edds-Walton, 2016).

Anatomical studies show that each of the octaval nuclei, located in the hindbrain, receive input from each of the otolithic end organs in a number of diverse species (Horner *et al.*, 1980; McCormick, 1999; Tomchik and Lu, 2005; Edds-Walton and Fay, 2008, 2009). Moreover, at least in goldfish, there is evidence that single cells in the descending octaval nucleus of the goldfish receive input from more than one otolithic end organ (McCormick and Wallace, 2012). Further adding to the connectivity is evidence that along with the convergence of connections between the different end organs of one ear, that there are commissural connections between regions of the left and right descending octaval nucleus (e.g., Nieuwenhuys and Pouwels, 1983). Such results strongly support an idea that there are likely binaural interactions in the brainstem of fishes (reviewed in Walton *et al.*, 2017).

It has also been shown, based on physiological studies, that the majority of neurons in the brainstem octaval nuclei of the oyster toadfish show directional preference when the animal is stimulated in a shaker table, and there is evidence that these units are bringing together response from hair cells oriented in different directions, at least from one ear (Edds-Walton *et al.*, 1999). These observations lead to the suggestion that the brain may use such information to refine directional responses to give more accurate directional information than is possible with a single end organ. In the oyster toadfish, approximately 60% of the cells of the dorsal descending nucleus have sharpened directional responses (in azimuth and/or elevation) as compared to other cells coming into the nucleus from the saccules, which have more of a cosine function (Edds-Walton and Fay, 2008). The mechanism of this sharpening is not clear, but may result from binaural computation and/or inhibitory responses (Fay, 2005)

Edds-Walton and Fay (2008) went further into the CNS and found that there is additional directional sharpening of cells in the midbrain areas (nucleus centralis of the torus semicircularis) that are on the auditory pathway (Edds-Walton and Fay, 2003, 2005b,a). This sharpening was found in about 85% of the cells studied, particularly when the cells were associated with determining azimuthal direction. Findings of directional responses in the torus have also been found in other species including a salmonid (Wubbels and Schellart, 1997).

Taken together, these results strongly support a hypothesis that information from multiple end organ receptor regions are integrated in the CNS to give the fish refined directional information about a sound source (Popper *et al.*, 1988; Rogers and Cox, 1988; Fay, 2005; Walton *et al.*, 2017). At the same time, numerous questions remain as to how this processing of information is actually used, as well as whether the mechanisms are the same in different species.

D. Theoretical aspects

It is now generally accepted that fishes locate sound sources by detecting the axes of particle motion using their otolith organs (reviewed by Schuijf, 1975; Popper and Hawkins, 2018) although the actual mechanisms used in localization are likely based on integration of information from hair cells oriented in many directions rather than just a simple analysis of which orientation groups are stimulated by a sound from a particular direction. By comparing the outputs of differently orientated groups of hair cells the fish may be able to determine the axis of propagation of the sound from that source. Given that the fish has two ears, each containing three otolith organs that are potentially sensitive to sound, each with its own distinctive pattern of hair-cell orientation, then a system is available which is potentially capable of determining the axis of propagation in 3D space.

There are several problems with this model of directional detection, however. First, detection of the axis of propagation does not in itself indicate the location of the source. Particle motion alternately takes place towards and away from the source, and the hair cells are inherently

bidirectional so that a simple vector weighing of the kind proposed yields a 180 degree ambiguity in the detection of the source. Kotas *et al.* (2011) elaborated on this ambiguity, which remains for plane acoustic waves even when the line of bearing of the source can be determined by the directionally sensitive otolith organs.

As discussed in Sec. IV B 2, experiments conducted in mid-water in the sea have demonstrated that the Atlantic cod can discriminate between opposing sound sources (180 degrees apart) in both the horizontal and vertical planes (Buwalda *et al.*, 1983). Models of directional hearing in fish with mechanisms to resolve the 180-degree ambiguity include the “phase model” proposed by Schuijf and colleagues (Schuijf, 1975, 1976a; Schuijf and Buwalda, 1975) that involves comparison of the phase of the pressure and particle motion components of sound to resolve the ambiguity. Interestingly, some terrestrial animals, including humans, are unable to discriminate between opposing sound sources in the median vertical plane, where the stimuli reaching the two ears are identical.

Other models have been suggested for fishes that involve simultaneous detection of both particle motion and sound pressure to resolve the 180° ambiguity. An “orbital” model by Schellart and de Munck (1987) suggested that sound pressure and particle motion together cause the otolith orbits to rotate either clockwise or counterclockwise depending on whether the source is to the left or right. A computational model by Rogers *et al.* (1988) also required both pressure and particle motion sensitivity. However, as Sisneros and Rogers (2016) point out, many fish species seem to lack the ability to detect sound pressure. They also suggest that another difficulty with the phase model is that it requires the use of sinusoidal signals, while broadband signals such the clicks transmitted by cod and haddock are far more common than sinusoidal signals in nature and cannot be used with the phase model. Against that, however, it has been shown by Piddington (1972) that fish can discriminate between a given click and its phase inversion.

It is particularly difficult to determine how far the models developed for fish like the Atlantic cod, which can detect sound pressure using the swim bladder, can be applied to other species of fish, especially those lacking a swim bladder. However, a study on the grey bamboo shark *Chiloscyllium griseum* (Van den Berg and Schuijf, 1983) has suggested that this species is sensitive to both particle motion and sound pressure, though the actual pressure to displacement transformer is unknown, as sharks lack a swim bladder (see Sec. III D). Schuijf (1981) postulated an alternative to sound pressure detection as a phase reference from the vertical particle motions reflected from the substrate and the water surface.

Rogers and Zeddies (2008) examined alternative mechanisms by which fishes with and without sound pressure detection could determine the direction to a sound source and resolve the 180° ambiguity. They drew attention to the differences between monopole, dipole, or quadrupole sensors of sound. The response of a monopole sensor is simply proportional to the incident sound pressure. The response is independent of the direction of incidence of the sound. The

response of a dipole sensor to an arbitrary incident field is proportional to the pressure gradient and the particle motion. A dipole sensor is characterized by a vector response. In general, it yields a cosine response pattern. They agreed with [Schuijf \(1975\)](#) and others that dipoles could be used to determine the direction of a sound source if they also incorporated data from a monopole channel to resolve the 180° ambiguity.

In fish without a monopole detector, [Rogers and Zeddies \(2008\)](#) suggested that hair cells that were not directly under an overlying otolith (which they call “uncovered” hair cells), as has been observed in the sacculle of a number of fish species (e.g., [Popper, 1980](#); [Deng et al., 2013](#)) could serve as quadrupole detectors. A quadrupole and a dipole sensor could resolve the 180° ambiguity in much the same way as a monopole and a dipole. Uncovered hair cells could thus provide a mechanism for fish without a gas-filled chamber to resolve the ambiguity. Interestingly, this model by [Rogers and Zeddies \(2008\)](#) is one of the few that addresses how the 180° ambiguity might be resolved for fish without a gas bubble, although it may only be applicable in the far field.

More recently, [Sisneros and Rogers \(2016\)](#) suggested that the direction of energy flow (i.e., the acoustic intensity) can be determined by fishes to provide information on the direction of the sound source. They say that this is true in the free-field for monopole and for dipole sources, and it is even true for most non-free-field propagation conditions. They conclude that time averaged intensity provides a physics-based approach to source localization with wide applicability with regard to source type, acoustic environment, and time waveform. However, they do not explain how the fish auditory system deals with this time-averaged intensity approach. Thus, it is clear that the details of the auditory mechanisms used by different fishes to discriminate direction need further examination. It is not yet clear whether all the otolith organs of the ear are implicated, nor is it clear whether certain parts of the ear are isolated from stimulation via the swim bladder, enabling directional responses to the particle motion to be retained and conveyed to the central nervous system.

As [Sisneros and Rogers \(2016\)](#) have pointed out, the 180° ambiguity problem has dominated most of the theoretical and empirical work on directional hearing in fishes since the 1970s and all new experiments on sound source localization in fish must confront this problem. It would appear that terrestrial animals, including humans, have some problems discriminating between sounds coming from opposing directions. Recently, [Hazelwood and Macey \(2016\)](#) have pointed out the 180° ambiguity that may exist for plane acoustic waves may be resolved for the particle motion generated by interface waves, travelling along the interface between the water and the substrate. The water motion driven by such waves, often termed “ground roll,” has components orthogonal to the propagation direction. If these components can be detected, the elliptical particle motion within seismic wavelets may provide a mechanism whereby benthic creatures could resolve the direction from which the ground roll is traveling. [Hazelwood and Macey \(2016\)](#) suggested that this is feasible for animals with three axis inertial sensors, even

when they are small in comparison to a wavelength. In many aquatic environments, including rivers, shallow lakes, and coastal waters, ground roll from various natural sources may be especially important to the fishes inhabiting these waters. In a more recent paper [Hazelwood et al. \(2018\)](#) have carried out further modeling work on the propagation of seismic vibration wavelets. These special wavelets are associated with high peak levels of the associated water particle velocity as they ripple outwards from the source.

VI. INFORMATION GAPS AND FUTURE RESEARCH PRIORITIES

It has been shown that some fishes can discriminate between sounds from different directions and distances. This not only comes from experiments that tested their ability but also from a pragmatic view of the “purpose” of hearing and the realization that fishes, like other vertebrates, use hearing to glean information about the “auditory scene” around them ([Bregman, 1994](#); [Fay, 2008](#); [Popper and Fay, 2011](#); [Fay and Popper, 2012](#)). While it is possible that some animals are only using sound to be aware of the nature of their environment, it is far more likely that fishes, as other vertebrates, extract a good deal of information about the source from the sounds, and, most importantly, the direction of the source relative to the animal. Without such an ability, a fish might hear the sound of a predator, try to escape, but swim right to the source. Conversely, the fish might hear the sound of a coral reef on which it might want to settle, but not know the direction in which to swim to find the reef. Indeed, [Masterton et al. \(1969\)](#) have argued that the ability to localize sound sources was the major factor in driving the evolution of mammalian (and likely vertebrate) hearing.

That said, and despite the range of experiments conducted on directional responses by fishes, we still know very little about their ability to actually locate sound sources in 3D space, or the actual mechanisms involved in determining direction and distance. In addition, considering the diversity of hearing capabilities of various species, as well as the variation in ear structure and environments in which different species live, it is reasonable to suggest that sound localization capabilities and mechanisms may vary considerably between species.

There are several major gaps in our knowledge. Foremost perhaps, is a much better understanding of the behavioral responses to sound direction. Do fishes swim directly to a source, or do they “sample” sound levels and move towards a sound by successive approximation of direction? What is the minimum discrimination ability (known as minimum audible angle, or MAA) for fishes—can they discriminate between two sound sources that are only a few degrees apart or, as suggested by the current data on just a few species, or is the MAA much larger—on the order of 15 degrees or more. By way of comparison, the MAA for a bottlenose dolphin is less than 1 degree ([Renaud and Popper, 1975](#)). And, since fishes live in a 3D world, how well do they localize in all three dimensions. It was shown by [Hawkins and Sand \(1977\)](#) that Atlantic cod can discriminate between sources in the median vertical plane, and by [Schuijf](#)

and Hawkins (1983) that they can also discriminate between sound sources at different distances, but there has been no additional work on other fish species. These capabilities have only been shown in one species, and there is dire need to replicate the results and examine similar capabilities in other species, and especially species that show diversity in behavior and auditory anatomy and physiology.

The second major set of questions relates to physiological mechanisms of localization. This starts with questions about the role of the ear and whether the very complex hair cell orientation patterns, macula shapes, ear curvatures, otolith shapes, and other aspects of morphology have evolved to enable fishes to localize sounds. The hair cell orientation patterns alone suggest that the different groups of cells respond best to sounds from different directions. However, it is not entirely clear how the otoliths move in response to sounds from different directions, or how they move in response to linear acceleration of the fish or to changes in fish orientation relative to the Earth's gravitational field. There is a real need to examine the motion patterns of the otoliths in order to understand more fully how the hair cells are stimulated by sounds from different directions, especially when one considers that the hair cell orientation patterns in the maculae appear to have evolved for detection of direction.

As discussed earlier, it is hypothesized that the broad range of directions of cells in different parts of each end organ, combined with input from different end organs, could provide a good picture of sound direction, even in species, such as elasmobranchs, that do not have a sound pressure detector. At the same time, even if the ear itself provides a very good indication of direction, there remains the 180° ambiguity that needs to be resolved. While data suggest that fish can do this by using information from the ear and swim bladder, this has been demonstrated in only a few species and, in each case, the fish was restrained and the stimuli were pure tones as opposed to far more complex biologically relevant sounds (Rogers *et al.*, 1988; Sisneros and Rogers, 2016).

A third set of questions relate to the processing of directional information in the CNS. Mammals and other terrestrial vertebrates generally localize sounds by comparing information from the two ears, and this comparison is done at some level(s) of the CNS where information from the two ears are brought together (e.g., Carr, 2004; Ashida and Carr, 2011; Walton *et al.*, 2017). There are also data on the central auditory pathways in a few fish species, and there seems to be reasonable consistency in anatomy between species, for the most part (McCormick, 1999; Walton *et al.*, 2017). There is also evidence, albeit very limited, that there are interactions between the different end organs of individual ears, and perhaps binaurally, in the CNS. However, data are still very limited, primarily for one species (the oyster toadfish—a species that primarily detects particle motion), and do not provide the levels of cellular interactions between hair cells from different regions to allow for a working hypothesis for how sound direction is processed in the CNS. Indeed, what is needed are data comparable to those available in mammalian systems (Carr, 2004; Ashida and Carr, 2011) and in the teleost electroreception system (Bell and Maler, 2005) in

order to provide a better understanding of localization (and its evolution).

What this comes down to is that there remains a plethora of questions about how well fishes can localize sound sources; and if they can, how they may achieve this. In addition, the questions are further “complicated” by the extraordinary diversity of fishes, the diverse environments in which they live, and how they detect and use sound. There is no reason to think that the 33 000+ species of fishes all localize sound in the same way, and so any addressing of localization must, ultimately, be comparative.

One reason for the lack of data is the difficulty in doing localization studies. One of us (A.N.P) started his doctoral dissertation studying sound source localization and decided not to continue that topic since he quickly realized that the complexities of acoustics in tanks made it virtually impossible to develop a sound field that provided clear directional cues that were similar to those any fish would have evolved to use. The other of us (A.D.H) was far more successful in doing directional hearing studies, but he had to deal with the extraordinary complexities of doing experiments in the field where a pristine sound field could be generated. The point being that anyone pursuing sound source localization in fishes today needs to be very aware of the stimulus, and be particularly cognizant of issue related to detection of sound pressure and particle motion (Popper and Hawkins, 2018). At the same time, we are convinced that sound localization is the single most fascinating question in fish bioacoustics and we hope that future investigators will get as excited about exploring sound localization as we have for over 100 combined career years.

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¹The Otophysans also includes a diverse range of mostly freshwater fishes such as goldfish and catfish, all of which have a set of bones, the Weberian ossicles, connecting the swim bladder to the inner ear. With a few exceptions, all otophysans can hear frequencies to over 3 kHz.

²Who later went on to win the Nobel Prize in Medicine and Physiology for his work on the dance language of bees.

- Ainslie, M., and De Jong, C. (2016). "Sources of underwater sound and their characterization," in *The Effects of Noise on Aquatic Life II*, edited by A. N. Popper and A. Hawkins (Springer Science+Business Media, New York), pp. 27–35.
- Alexander, R. (1966). "Physical aspects of swimbladder function," *Biol. Rev. Cambridge Philos. Soc.* **41**, 141–176.
- Amorim, M. C. P. (2006). "Diversity of sound production in fish," in *Communication in Fishes*, edited by F. Ladich, S. P. Collin, P. Moller, and B. G. Kapoor (Springer, Vienna), pp. 71–104.
- Ashida, G., and Carr, C. E. (2011). "Sound localization: Jeffress and beyond," *Curr. Opin. Neurobiol.* **21**, 745–751.
- Bell, C. C., and Maler, L. (2005). "Central neuroanatomy of electrosensory systems in fish," in *Electroreception*, edited by T. H. Bullock, C. D. Hopkins, A. N. Popper, and R. R. Fay (Springer New York), pp. 68–111.
- Bregman, A. S. (1994). *Auditory Scene Analysis: The Perceptual Organization of Sound* (MIT Press, Cambridge, MA).
- Buran, B. N., Deng, X., and Popper, A. N. (2005). "Structural variation in the inner ears of four deep-sea elopomorph fishes," *J. Morphol.* **265**, 215–225.
- Buwalda, R., Schuijf, A., and Hawkins, A. (1983). "Discrimination by the cod of sounds from opposing directions," *J. Comp. Physiol.* **150**, 175–184.
- Buwalda, R. J. A., and van der Steen, J. (1979). "The sensitivity of the cod sacculus to directional and non-directional sound stimuli," *Comp. Biochem. Physiol. Part A: Physiol.* **64**, 467–471.
- Carlstrom, D. (1963). "A crystallographic study of vertebrate otoliths," *Biol. Bull.* **125**, 441–463.
- Carr, C. E. (2004). "Timing is everything: Organization of timing circuits in auditory and electrical sensory systems," *J. Comp. Neurol.* **472**, 131–133.
- Casaretto, L., Picciulin, M., and Hawkins, A. D. (2015). "Seasonal patterns and individual differences in the calls of male haddock *Melanogrammus aeglefinus*," *J. Fish Biol.* **87**, 579–603.
- Casaretto, L., Picciulin, M., Olsen, K., and Hawkins, A. D. (2014). "Locating spawning haddock (*Melanogrammus aeglefinus*, Linnaeus, 1758) at sea by means of sound," *Fish. Res.* **154**, 127–134.
- Casper, B. M., and Mann, D. A. (2007a). "Dipole hearing measurements in elasmobranch fishes," *J. Exp. Biol.* **210**, 75–81.
- Casper, B. M., and Mann, D. A. (2007b). "The directional hearing abilities of two species of bamboo sharks," *J. Exp. Biol.* **210**, 505–511.
- Casper, B. M., and Mann, D. A. (2009). "Field hearing measurements of the Atlantic sharpnose shark *Rhizoprionodon terraenovae*," *J. Fish. Biol.* **75**, 2768–2776.
- Chapman, C. J. (1973). "Field studies of hearing in teleost fish," *Helgoländer wissenschaftliche Meeresuntersuchungen* **24**, 371–390.
- Chapman, C. J. (1976). "The hearing capacities of fish," in *Sound Reception in Fish*, edited by A. Schuijf and A. D. Hawkins (Elsevier, Amsterdam), pp. 19–25.
- Chapman, C. J., and Hawkins, A. (1973). "A field study of hearing in the cod, *Gadus morhua* L.," *J. Comp. Physiol.* **85**, 147–167.
- Chapman, C. J., and Johnstone, A. (1974). "Some auditory discrimination experiments on marine fish," *J. Exp. Biol.* **61**, 521–528.
- Cohen, M. J., and Winn, H. E. (1967). "Electrophysiological observations on hearing and sound production in the fish, *Porichthys notatus*," *J. Exp. Zool.* **165**, 355–369.
- Colburn, H. S., and Kulkarni, A. (2005). "Models of sound localization," in *Sound Source Localization*, edited by A. N. Popper and R. R. Fay (Springer, New York), pp. 272–316.
- Coombs, S., and Conley, R. A. (1997). "Dipole source localization by the mottled sculpin. II. The role of lateral line excitation patterns," *J. Comp. Physiol. A* **180**, 401–415.
- Coombs, S., and Popper, A. N. (1979). "Hearing differences among Hawaiian squirrelfish (family Holocentridae) related to differences in the peripheral auditory system," *J. Comp. Physiol. A* **132**, 203–207.
- Corwin, J. T. (1977). "Morphology of the macula neglecta in sharks of the genus *Carcharhinus*," *J. Morphol.* **152**, 341–362.
- Corwin, J. T. (1981a). "Audition in elasmobranchs," in *Hearing and Sound Communication in Fishes*, edited by W. N. Tavolga, A. N. Popper, and R. R. Fay (Springer, New York), pp. 81–105.
- Corwin, J. T. (1981b). "Peripheral auditory physiology in the lemon shark: Evidence of parallel otolithic and non-otolithic sound detection," *J. Comp. Physiol.* **142**, 379–390.
- Corwin, J. T. (1983). "Postembryonic growth of the macula neglecta auditory detector in the ray, *Raja clavata*: Continual increases in hair cell number, neural convergence, and physiological sensitivity," *J. Comp. Neurol.* **217**, 345–356.
- Corwin, J. T. (1985). "Auditory neurons expand their terminal arbors throughout life and orient toward the site of postembryonic hair cell production in the macula neglecta in elasmobranchs," *J. Comp. Neurol.* **239**, 445–452.
- Corwin, J. T. (1989). "Functional anatomy of the auditory system in sharks and rays," *J. Exp. Biol.* **252**, 62–74.
- Dale, T. (1976). "The labyrinthine mechanoreceptor organs of the cod *Gadus morhua* L. (Teleostei: Gadidae)," *Norweg. J. Zool.* **24**, 85–128.
- Deng, X., Wagner, H. J., and Popper, A. N. (2011). "The inner ear and its coupling to the swim bladder in the deep-sea fish *Antimora rostrata* (Teleostei: Moridae)," *Deep Sea Res.* **58**, 27–37.
- Deng, X., Wagner, H. J., and Popper, A. N. (2013). "Interspecific variations of inner ear structure in the deep-sea fish family Melamphaidae," *Anat. Rec.* **296**, 1064–1082.
- de Vries, H. (1950). "The mechanics of the labyrinth otoliths," *Acta Otolaryngol.* **38**, 262–273.
- Dijkgraaf, S. (1960). "Hearing in bony fishes," *Proc. R. Soc. B. Biol. Sci.* **152**, 51–54.
- Dijkgraaf, S. (1963). "The functioning and significance of the lateral-line organs," *Biol. Rev. Cambridge Philos. Soc.* **38**, 51–105.
- Dijkgraaf, S., and Verheijen, F. J. (1950). "Investigations on the sense of hearing in fish," *Acta Physiol. Pharmacol. Neerl.* **1**, 503–505.
- Dohlman, G. (1971). "The attachment of the cupulae, otolith and tectorial membranes to the sensory cell areas," *Acta Otolaryngol.* **71**, 89–105.
- Duncan, A. J., Lucke, K., Erbe, C., and McCauley, R. D. (2016). "Issues associated with sound exposure experiments in tanks," *Proc. Mtgs. Acoust.* **27**, 070008.
- Dunkelberger, D. G., Dean, J. M., and Watabe, N. (1980). "The ultrastructure of the otolithic membrane and otolith in the juvenile mummichog, *Fundulus heteroclitus*," *J. Morphol.* **163**, 367–377.
- Edds-Walton, P. L. (2016). "What the toadfish ear tells the toadfish brain about sound," in *Fish Hearing and Bioacoustics: An Anthology in Honor of Arthur N. Popper and Richard R. Fay*, edited by J. A. Sisneros (Springer International Publishing, Cham), pp. 197–226.
- Edds-Walton, P. L., and Fay, R. R. (2003). "Directional selectivity and frequency tuning of midbrain cells in the oyster toadfish, *Opsanus tau*," *J. Comp. Physiol. A* **189**, 527–543.
- Edds-Walton, P. L., and Fay, R. R. (2005a). "Projections to bimodal sites in the torus semicircularis of the toadfish, *Opsanus tau*," *Brain, Behav. Evol.* **66**, 73–87.
- Edds-Walton, P. L., and Fay, R. R. (2005b). "Sharpening of directional responses along the auditory pathway of the oyster toadfish, *Opsanus tau*," *J. Comp. Physiol. A* **191**, 1079–1086.
- Edds-Walton, P. L., and Fay, R. R. (2008). "Directional and frequency response characteristics in the descending octaval nucleus of the toadfish (*Opsanus tau*)," *J. Comp. Physiol. A* **194**, 1013–1029.
- Edds-Walton, P. L., and Fay, R. R. (2009). "Physiological evidence for bin-audial directional computations in the brainstem of the oyster toadfish, *Opsanus tau* (L.)," *J. Exp. Biol.* **212**, 1483–1493.
- Edds-Walton, P. L., Fay, R. R., and Highstein, S. M. (1999). "Dendritic arbors and central projections of physiologically characterized auditory fibers from the sacculle of the toadfish, *Opsanus tau*," *J. Comp. Neurol.* **411**, 212–238.
- Enger, P. (1976). "On the orientation of hair cells in the labyrinth of perch (*Perca fluviatilis*)," in *Sound Reception in Fish*, edited by A. Schuijf and A. D. Hawkins (Elsevier, Amsterdam), pp. 49–62.
- Enger, P. (1981). "Frequency discrimination in teleosts—Central or peripheral?," in *Hearing and Sound Communication in Fishes*, edited by W. A. Tavolga, A. N. Popper, and R. R. Fay (Springer, New York), pp. 243–255.
- Enger, P., and Andersen, R. (1967). "An electrophysiological field study of hearing in fish," *Comp. Biochem. Physiol.* **22**, 517–525.
- Enger, P., Hawkins, A., Sand, O., and Chapman, C. (1973). "Directional sensitivity of saccular microphonic potentials in the haddock," *J. Exp. Biol.* **59**, 425–433.
- Fay, R. R. (1970). "Auditory frequency generalization in the goldfish (*Carassius auratus*)," *J. Exp. Anal. Behav.* **14**, 353–360.
- Fay, R. R. (1984). "The goldfish ear codes the axis of acoustic particle motion in three dimensions," *Science* **225**, 951–954.
- Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook* (Hill-Fay Associates, Winnetka, IL).
- Fay, R. R. (1994). "Perception of temporal acoustic patterns by the goldfish (*Carassius auratus*)," *Hear. Res.* **76**, 158–172.
- Fay, R. R. (1995). "Perception of spectrally and temporally complex sounds by the goldfish (*Carassius auratus*)," *Hear. Res.* **89**, 146–154.

- Fay, R. R. (2000). "Spectral contrasts underlying auditory stream segregation in goldfish (*Carassius auratus*)," *J. Assoc. Res. Otolaryngol.* **1**, 120–128.
- Fay, R. R. (2005). "Sound source localization by fishes," in *Sound Source Localization*, edited by A. N. Popper and R. R. Fay (Springer-Verlag, New York), pp. 36–66.
- Fay, R. R. (2008). "Sound source perception and stream segregation in non-human vertebrate animals," in *Auditory Perception of Sound Sources*, edited by W. Yost, A. Popper, and R. Fay (Springer-Verlag, New York), pp. 307–323.
- Fay, R. R. (2012). "Listening in noise," in *The Effects of Noise on Aquatic Life*, edited by A. N. Popper and A. D. Hawkins (Springer, New York), pp. 129–134.
- Fay, R. R., Ahroon, W. A., and Orawski, A. A. (1978). "Auditory masking patterns in the goldfish (*Carassius auratus*): Psychophysical tuning curves," *J. Exp. Biol.* **74**, 83–100.
- Fay, R. R., and Edds-Walton, P. L. (1997a). "Directional response properties of saccular afferents of the toadfish, *Opsanus tau*," *Hear. Res.* **111**, 1–21.
- Fay, R. R., and Edds-Walton, P. L. (1997b). "Diversity in frequency response properties of saccular afferents of the toadfish, *Opsanus tau*," *Hear. Res.* **113**, 235–246.
- Fay, R. R., and Edds-Walton, P. L. (2000). "Directional encoding by fish auditory systems," *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **355**, 1281–1284.
- Fay, R. R., Kendall, J. I., Popper, A. N., and Tester, A. L. (1974). "Vibration detection by the macula neglecta of sharks," *Comp. Biochem. Physiol. A* **47**, 1235–1240.
- Fay, R. R., and Olsho, L. W. (1979). "Discharge patterns of lagenar and saccular neurones of the goldfish eighth nerve: Displacement sensitivity and directional characteristics," *Comp. Biochem. Physiol. A* **62**, 377–386.
- Fay, R. R., and Passow, B. (1982). "Temporal discrimination in the goldfish," *J. Acoust. Soc. Am.* **72**, 753–760.
- Fay, R. R., and Popper, A. N. (1974). "Acoustic stimulation of the ear of the goldfish (*Carassius auratus*)," *J. Exp. Biol.* **61**, 243–260.
- Fay, R. R., and Popper, A. N. (1975). "Modes of stimulation of the teleost ear," *J. Exp. Biol.* **62**, 379–387.
- Fay, R. R., and Popper, A. N. (2000). "Evolution of hearing in vertebrates: The inner ears and processing," *Hear. Res.* **149**, 1–10.
- Fay, R. R., and Popper, A. N. (2012). "Fish hearing: New perspectives from two 'senior' bioacousticians," *Brain Behav. Evol.* **79**, 215–217.
- Fine, M. L. (1978). "Seasonal and geographical variation of the mating call of the oyster toadfish *Opsanus tau* L.," *Oecologia* **36**, 45–57.
- Fine, M. L., and Parmentier, E. (2015). "Mechanisms of fish sound production," in *Sound Communication in Fishes*, edited by F. Ladich (Springer Vienna, Vienna), pp. 77–126.
- Fish, M. P. (1954). "The character and significance of sound production among fishes of the western North Atlantic," *Bull. Bingham Oceanogr. Collect.* **14**, 1–109.
- Flock, A. (1964). "Structure of the macula utriculi with special reference to directional interplay of sensory responses as revealed by morphological polarization," *The J. Cell Biol.* **22**, 413–431.
- Flock, A. (1965). "Transducing mechanisms in the lateral line canal organ receptors," *Cold Spring Harb. Symp. Quant. Biol.* **30**, 133–145.
- Flock, A., and Wersäll, J. (1962). "A study of the orientation of the sensory hairs of the receptor cells in the lateral line organ of fish, with special reference to the function of the receptors," *J. Cell Biol.* **15**, 19–27.
- Furukawa, T., and Ishii, Y. (1967). "Neurophysiological studies on hearing in goldfish," *J. Neurophysiol.* **30**, 1377–1403.
- Gauldie, R. W. (1996). "Fusion of otoconia: A stage in the development of the otolith in the evolution of fishes," *Acta Zool.* **77**, 1–23.
- Harris, G. G. (1964). "Considerations on the physics of sound production by fishes," in *Marine Bio-Acoustics*, edited by W. A. Tavolga (Pergamon, New York), pp. 233–247.
- Harris, G. G., and van Bergeijk, W. A. (1962). "Evidence that the lateral-line organ responds to near-field displacements of sound sources in water," *J. Acoust. Soc. Am.* **34**, 1831–1841.
- Hawkins, A. D. (1993). "Underwater sound and fish behaviour," in *Behaviour of Teleost Fishes*, edited by T. J. Pitcher (Chapman and Hall, London), pp. 114–153.
- Hawkins, A. D. (2014). "Examining fish in the sea: A European perspective on fish hearing experiments," in *Perspectives on Auditory Research*, edited by A. N. Popper and R. R. Fay (Springer, New York), pp. 247–267.
- Hawkins, A. D., and Chapman, C. J. (1975). "Masked auditory thresholds in the cod, *Gadus morhua* L.," *J. Comp. Physiol.* **103**, 209–226.
- Hawkins, A. D., and Horner, K. (1981). "Directional characteristics of primary auditory neurons from the cod ear," in *Hearing and Sound Communication in Fishes*, edited by W. N. Tavolga, A. N. Popper, and R. R. Fay (Springer, New York), pp. 311–328.
- Hawkins, A. D., and Johnstone, A. D. F. (1978). "The hearing of the Atlantic salmon, *Salmo salar*," *J. Fish. Biol.* **13**, 655–673.
- Hawkins, A. D., and MacLennan, D. N. (1976). "An acoustic tank for hearing studies on fish," in *Sound Reception in Fish*, edited by A. Schuijff and A. D. Hawkins (Elsevier, Amsterdam), pp. 149–170.
- Hawkins, A. D., and Myrberg, A. A., Jr. (1983). "Hearing and sound communication underwater," in *Bioacoustics, A Comparative Approach*, edited by B. Lewis (Academic Press, New York), pp. 347–405.
- Hawkins, A. D., Pembroke, A., and Popper, A. (2015). "Information gaps in understanding the effects of noise on fishes and invertebrates," *Rev. Fish. Biol. Fish.* **25**, 39–64.
- Hawkins, A. D., and Popper, A. (2014). "Assessing the impacts of underwater sounds on fishes and other forms of marine life," *Acoust. Today* **10**, 30–41.
- Hazelwood, R., Macey, P., Robinson, S., and Wang, L. (2018). "Optimal transmission of interface vibration wavelets—A simulation of seabed seismic Responses," *J. Mar. Sci. Eng.* **6**, 61.
- Hawkins, A. D., and Sand, O. (1977). "Directional hearing in the median vertical plane by the cod," *J. Comp. Physiol.* **122**, 1–8.
- Hazelwood, R. A., and Macey, P. C. (2016). "Intrinsic directional information of ground roll waves," in *The Effects of Noise on Aquatic Life II*, edited by A. N. Popper and A. D. Hawkins (Springer, New York), pp. 447–453.
- Heffner, H. E., and Heffner, R. S. (2016). "The evolution of mammalian sound localization," *Acoust. Today* **34**, 20–27.
- Horner, K., Sand, O., and Enger, P. S. (1980). "Binaural interaction in the cod," *J. Exp. Biol.* **85**, 323–332.
- Hudspeth, A., and Corey, D. (1977). "Sensitivity, polarity, and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli," *Proc. Natl. Acad. Sci. U.S.A.* **74**, 2407–2411.
- ISO (2017). ISO 18405, *Underwater Acoustics—Terminology* (ISO, Geneva, Switzerland).
- Jacobs, R., and Hudspeth, A. (1990). "Ultrastructural correlates of mechano-electrical transduction in hair cells of the bullfrog's internal ear," in *Cold Spring Harbor Symposia on Quantitative Biology* (Cold Spring Harbor Laboratory Press, New York), pp. 547–561.
- Jacobs, D. W., and Tavolga, W. N. (1967). "Acoustic intensity limens in the goldfish," *Anim. Behav.* **15**, 324–335.
- Jacobs, D. W., and Tavolga, W. N. (1968). "Acoustic frequency discrimination in the goldfish," *Anim. Behav.* **16**, 67–71.
- Kalmijn, A. J. (1997). "Electric and near-field acoustic detection, a comparative study," *Acta Physiol. Scand. Suppl.* **638**, 25–38.
- Kinsler, L. E., Frey, A. R., Coppens, A. B., and Sanders, J. V. (1999). *Fundamentals of Acoustics*, 4th ed. (Wiley, New York).
- Kotas, C. W., Rogers, P. H., and Yoda, M. (2011). "Acoustically induced streaming flows near a model cod otolith and their potential implications for fish hearing," *J. Acoust. Soc. Am.* **130**, 1049–1059.
- Krysl, P., Hawkins, A. D., Schilt, C., and Cranford, T. W. (2012). "Angular oscillation of solid scatterers in response to progressive planar acoustic waves: Do fish otoliths rock?," *PLoS One* **7**, e42591.
- Ladich, F. (2014). "Diversity in hearing in fishes: Ecoacoustical, communicative, and developmental constraints," in *Insights from Comparative Hearing Research*, edited by C. Köppl, G. A. Manley, A. N. Popper, and R. R. Fay (Springer, New York), pp. 289–321.
- Ladich, F., and Fay, R. R. (2013). "Auditory evoked potential audiometry in fish," *Rev. Fish Biol. Fish.* **23**, 317–364.
- Ladich, F., and Schulz-Mirbach, T. (2016). "Diversity in fish auditory systems: One of the riddles of sensory biology," *Front. Ecol. Evol.* **4**, 28.
- Leis, J. M., Carson-Ewart, B. M., Hay, A. C., and Cato, D. H. (2003). "Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some times," *J. Fish. Biol.* **63**, 724–737.
- Lombarte, A., and Cruz, A. (2007). "Otolith size trends in marine fish communities from different depth strata," *J. Fish Biol.* **71**, 53–76.
- Lombarte, A., Palmer, M., Matallanas, J., Gómez-Zurita, J., and Morales-Nin, B. (2010). "Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae," *Environ. Biol. Fish.* **89**, 607–618.
- Lombarte, A., and Popper, A. N. (1994). "Quantitative analyses of postembryonic hair cell addition in the otolithic endorgans of the inner ear of the

- European hake, *Merluccius merluccius* (Gadiformes, Teleostei)," *J. Comp. Neurol.* **345**, 419–428.
- Lowenstein, O. (1957). "The acoustico-lateralis system," in *The Physiology of Fishes*, edited by M. E. Brown (Elsevier, New York), pp. 155–186.
- Lowenstein, O., and Sand, A. (1940). "The individual and integrated activity of the semicircular canals of the elasmobranch labyrinth," *J. Physiol.* **99**, 89–101.
- Lu, Z., and Popper, A. N. (1998). "Morphological polarizations of sensory hair cells in the three otolithic organs of a teleost fish: Fluorescent imaging of ciliary bundles," *Hear. Res.* **126**, 47–57.
- Lu, Z., and Popper, A. N. (2001). "Neural response directionality correlates of hair cell orientation in a teleost fish," *J. Comp. Physiol. A* **187**, 453–465.
- Lu, Z., Song, J., and Popper, A. N. (1998). "Encoding of acoustic directional information by saccular afferents of the sleeper goby, *Dormitator latifrons*," *J. Comp. Physiol. A* **182**, 805–815.
- Lu, Z., Xu, Z., and Buchser, W. J. (2004). "Coding of acoustic particle motion by utricular fibers in the sleeper goby, *Dormitator latifrons*," *J. Comp. Physiol. A* **190**, 923–938.
- Lu, Z., Xu, Z., and Buchser, W. J. (2010). "Frequency coding of particle motion by saccular afferents of a teleost fish," *J. Exp. Biol.* **213**, 1591–1601.
- Luczakovich, J. J., Pullinger, R. C., Johnson, S. E., and Sprague, M. W. (2008). "Identifying Sciaenid critical spawning habitats by the use of passive acoustics," *Trans. Am. Fish. Soc.* **137**, 576–605.
- Lychakov, D., and Rebane, Y. T. (1992). "Effect of otolith shape on directional sound perception in fishes," *J. Evol. Biol. Physiol.* **28**, 707–714.
- Lychakov, D. V., Rebane, Y. T., Lombarte, A., Fuiman, L. A., and Takabayashi, A. (2006). "Fish otolith asymmetry: Morphometry and modeling," *Hear. Res.* **219**, 1–11.
- Maruska, K. P., and Mensinger, A. F. (2015). "Directional sound sensitivity in utricular afferents in the toadfish *Opsanus tau*," *J. Exp. Biol.* **218**, 1759–1766.
- Masterston, B., Heffner, H., and Ravizza, R. (1969). "The evolution of human hearing," *J. Acoust. Soc. Am.* **45**, 966–985.
- McCormick, C. A. (1999). "Anatomy of the central auditory pathways of fish and amphibians," in *Comparative Hearing: Fish and Amphibians*, edited by R. R. Fay and A. N. Popper (Springer, New York), pp. 155–217.
- McCormick, C. A., and Wallace, A. C. (2012). "Otolith end organ projections to auditory neurons in the descending octaval nucleus of the goldfish, *Carassius auratus*: A confocal analysis," *Brain Behav. Evol.* **80**, 41–63.
- McKibben, J. R., and Bass, A. H. (1998). "Behavioral assessment of acoustic parameters relevant to signal recognition and preference in a vocal fish," *J. Acoust. Soc. Am.* **104**, 3520–3533.
- Meyer, M., Popper, A. N., and Fay, R. R. (2011). "Coding of sound direction in the auditory periphery of the lake sturgeon, *Acipenser fulvescens*," *J. Neurophysiol.* **107**, 658–665.
- Moulton, J. M. (1963). "Acoustic behaviour of fishes," in *Acoustic Behaviour of Animals*, edited by R. G. Busnel (Elsevier, Amsterdam), pp. 655–693.
- Moulton, J. M., and Dixon, R. H. (1967). "Directional hearing in fishes," in *Marine Bio-Acoustics II*, edited by W. A. Tavolga (Pergamon, New York), pp. 187–228.
- Myrberg, A. A., Jr. (1981). "Sound communication and interception in fishes," in *Hearing and Sound Communication in Fishes*, edited by W. N. Tavolga, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 395–426.
- Myrberg, A. A., Jr., Banner, A., and Richard, J. (1969). "Shark attraction using a video-acoustic system," *Mar. Biol.* **2**, 264–276.
- Myrberg, A. A., Jr., Gordon, C. R., and Klimley, A. P. (1976). "Attraction of free ranging sharks by low frequency sound, with comments on its biological significance," in *Sound Reception in Fish*, edited by A. Schuijff and A. D. Hawkins (Elsevier, Amsterdam), pp. 205–228.
- Nedelec, S. L., Campbell, J., Radford, A. N., Simpson, S. D., and Merchant, N. D. (2016). "Particle motion: The missing link in underwater acoustic ecology," *Meth. Ecol. Evol.* **7**, 836–842.
- Nelson, D. R. (1977). "On the field study of shark behavior," *Am. Zool.* **17**, 501–507.
- Nelson, D. R., and Gruber, S. H. (1963). "Sharks: Attraction by low-frequency sounds," *Science* **142**, 975–977.
- Nelson, D. R., and Johnson, R. H. (1972). "Acoustic attraction of Pacific reef sharks: Effect of pulse intermittency and variability," *Comp. Biochem. Physiol. A* **42**, 85–95.
- Nieuwenhuys, R., and Pouwels, E. (1983). "The brain stem of actinopterygian fishes," in *Fish Neurobiology*, edited by R. G. Northcutt and R. E. Davis (University of Michigan Press, Ann Arbor, MI), pp. 25–87.
- Olsen, K. (1969). *Directional Responses in Herring to Sound and Noise Stimuli* (International Council for the Exploration of the Sea, Copenhagen, Denmark).
- Olsen, K. J. (1976). "Evidence for localization of sound by fish in schools," in *Sound Reception in Fish*, edited by A. Schuijff and A. D. Hawkins (Elsevier, Amsterdam), pp. 257–270.
- Piddington, R. (1972). "Auditory discrimination between compressions and rarefactions by goldfish," *J. Exp. Biol.* **56**, 403–419.
- Pierce, A. D. (1981). *Acoustics: An Introduction to its Physical Principles and Applications* (McGraw-Hill, New York).
- Platt, C. (1977). "Hair cell distribution and orientation in goldfish otolith organs," *J. Comp. Neurol.* **172**, 283–287.
- Platt, C. (1983). "The peripheral vestibular system of fishes," in *Fish Neurobiology*, edited by R. G. Northcutt and R. I. Davis (University of Michigan Press, Ann Arbor, MI), pp. 89–123.
- Platt, C., and Popper, A. N. (1981). "Fine structure and function of the ear," in *Hearing and Sound Communication in Fishes*, edited by W. N. Tavolga, A. N. Popper, and R. R. Fay (Springer, New York), pp. 3–38.
- Platt, C., and Popper, A. N. (1984). "Variation in lengths of ciliary bundles on hair cells along the macula of the sacculus in two species of teleost fishes," *Scan. Electron. Microsc.* **1984**, 1915–1924.
- Poggendorf, D. (1952). "Die absoluten Hörschwellen des Zwergwelses (*Amiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparates der Ostariophysen" ("The absolute threshold of hearing in the bullhead (*Amiurus nebulosus*) and contributions to the physics of the Weberian apparatus of the Ostariophysen"), *Z. Vgl. Physiol.* **34**, 222–250.
- Popper, A. N. (1976). "Ultrastructure of the auditory regions in the inner ear of the lake whitefish," *Science* **192**, 1020–1023.
- Popper, A. N. (1977). "A scanning electron microscopic study of the sacculus and lagena in the ears of fifteen species of teleost fishes," *J. Morphol.* **153**, 397–417.
- Popper, A. N. (1978). "Scanning electron microscopic study of the otolithic organs in the bichir (*Polypterus bichir*) and shovel-nose sturgeon (*Scaphirhynchus platyrhynchus*)," *J. Comp. Neurol.* **181**, 117–128.
- Popper, A. N. (1980). "Scanning electron microscopic study of the sacculus and lagena in several deep-sea fishes," *Am. J. Anat.* **157**, 115–136.
- Popper, A. N. (1981). "Comparative scanning electron microscopic investigations of the sensory epithelia in the teleost sacculus and lagena," *J. Comp. Neurol.* **200**, 357–374.
- Popper, A. N. (1983). "Organization of the inner ear and auditory processing," in *Fish Neurobiology*, edited by R. G. Northcutt and R. I. Davis (University of Michigan Press, Ann Arbor, MI), pp. 125–178.
- Popper, A. N., and Coombs, S. (1982). "The morphology and evolution of the ear in actinopterygian fishes," *Am. Zool.* **22**, 311–328.
- Popper, A. N., and Fay, R. R. (2005). *Sound Source Localization* (Springer, New York).
- Popper, A. N., and Fay, R. R. (2011). "Rethinking sound detection by fishes," *Hear. Res.* **273**, 25–36.
- Popper, A. N., Fay, R. R., Platt, C., and Sand, O. (2003). "Sound detection mechanisms and capabilities of teleost fishes," in *Sensory Processing in Aquatic Environments*, edited by S. P. Collin and N. J. Marshall (Springer-Verlag, New York), pp. 3–38.
- Popper, A. N., and Hawkins, A. D. (2018). "The importance of particle motion to fishes and invertebrates," *J. Acoust. Soc. Am.* **143**, 470–486.
- Popper, A. N., and Hoxter, B. (1984). "Growth of a fish ear: 1. Quantitative analysis of hair cell and ganglion cell proliferation," *Hear. Res.* **15**, 133–142.
- Popper, A. N., and Northcutt, R. G. (1983). "Structure and innervation of the inner ear of the bowfin, *Amia calva*," *J. Comp. Neurol.* **213**, 279–286.
- Popper, A. N., and Platt, C. (1983). "Sensory surface of the sacculus and lagena in the ears of ostariophysan fishes," *J. Morphol.* **176**, 121–129.
- Popper, A. N., Ramcharitar, J., and Campana, S. E. (2005). "Why otoliths? Insights from inner ear physiology and fisheries biology," *Mar. Freshw. Res.* **56**, 497–504.
- Popper, A. N., Rogers, P. H., Saidel, W. M., and Cox, M. (1988). "Role of the fish ear in sound processing," in *Sensory Biology of Aquatic Animals*, edited by J. Atema, R. R. Fay, A. N. Popper, and W. A. Tavolga (Springer, New York), pp. 687–710.
- Popper, A. N., and Saidel, W. M. (1990). "Variations in receptor cell innervation in the sacculus of a teleost fish ear," *Hear. Res.* **46**, 211–227.

- Popper, A. N., Salmon, M., and Parvulescu, A. (1973). "Sound localization by the Hawaiian squirrelfishes, *Myripristis berndti* and *M. argyromus*," *Anim. Behav.* **21**, 86–97.
- Pumphrey, R. J. (1950). "Hearing," *Symposia Soc. Exp. Biol.* **4**, 3–18.
- Ramcharitar, J., Gannon, D. P., and Popper, A. N. (2006). "Bioacoustics of the family Scaenidae (croakers and drumfishes)," *Trans. Am. Fish. Soc.* **135**, 1409–1431.
- Ramcharitar, J., Higgs, D. M., and Popper, A. N. (2001). "Scaenid inner ears: A study in diversity," *Brain Behav. Evol.* **58**, 152–162.
- Renaud, D. L., and Popper, A. N. (1975). "Sound localization by the bottlenose porpoise *Tursiops truncatus*," *J. Exp. Biol.* **63**, 569–585.
- Retzius, G. (1881). "Das Gehörorgan der Fische und Amphibien" ("The hearing organs of fishes and amphibians"), in *Das Gehörorgan der Wirbelthiere*, Vol. 1 (Wallin, Stockholm, Sweden).
- Richard, J. D. (1968). "Fish attraction with pulsed low-frequency sound," *J. Fish. Res. Bd. Canada* **25**, 1441–1452.
- Rogers, P. H., and Cox, M. (1988). "Underwater sound as a biological stimulus," in *Sensory Biology of Aquatic Animals*, edited by J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga (Springer-Verlag, New York), pp. 131–149.
- Rogers, P. H., Hawkins, A. D., Popper, A. N., Fay, R. R., and Gray, M. D. (2016). "Parvulescu revisited: Small tank acoustics for bioacousticians," in *The Effects of Noise on Aquatic Life II*, edited by A. N. Popper and A. D. Hawkins (Springer Science+Business Media, New York), pp. 933–941.
- Rogers, P. H., Popper, A. N., Hastings, M. C., and Saidel, W. M. (1988). "Processing of acoustic signals in the auditory system of bony fish," *J. Acoust. Soc. Am.* **83**, 338–349.
- Rogers, P. H., and Zeddies, D. G. (2008). "Multiple mechanisms for directional hearing in fish," in *Fish Bioacoustics*, edited by J. F. Webb, R. R. Fay, and A. N. Popper (Springer Science+Business Media, LLC, New York), pp. 233–252.
- Rollo, A., Andraso, G., Jansen, J., and Higgs, D. (2007). "Attraction and localization of round goby (*Neogobius melanostomus*) to conspecific calls," *Behaviour* **144**, 1–21.
- Rollo, A., and Higgs, D. (2008). "Differential acoustic response specificity and directionality in the round goby, *Neogobius melanostomus*," *Anim. Behav.* **75**, 1903–1912.
- Saidel, W. M., and Popper, A. N. (1983a). "Spatial organization in the sacculus and lagena of a teleost: Hair cell pattern and innervation," *J. Morphol.* **177**, 301–317.
- Saidel, W. M., and Popper, A. N. (1983b). "The sacculus may be the transducer for directional hearing of nonostariophysine teleosts," *Exp. Brain Res.* **50**, 149–152.
- Sand, O. (1974). "Directional sensitivity of microphonic potentials from the perch ear," *J. Exp. Biol.* **60**, 881–899.
- Sand, O., and Bleckmann, H. (2008). "Orientation to auditory and lateral line stimuli," in *Fish Bioacoustics*, edited by J. F. Webb, R. R. Fay, and A. N. Popper (Springer Science+Business Media, LLC, New York), pp. 183–222.
- Sand, O., and Hawkins, A. D. (1973). "Acoustic properties of the cod swim bladder," *J. Exp. Biol.* **58**, 797–820.
- Sand, O., and Michelsen, A. (1978). "Vibration measurements of the perch saccular otolith," *J. Comp. Physiol. A* **123**, 85–89.
- Schellart, N. A., and de Munck, J. C. (1987). "A model for directional and distance hearing in swimbladder-bearing fish based on the displacement orbits of the hair cells," *J. Acoust. Soc. Am.* **82**, 822–829.
- Schuijf, A. (1975). "Directional hearing of cod (*Gadus morhua*) under approximate free field conditions," *J. Comp. Physiol.* **98**, 307–332.
- Schuijf, A. (1976a). "The phase model of directional hearing in fish," in *Sound Reception in Fish*, edited by A. Schuijf and A. D. Hawkins (Elsevier, Amsterdam), pp. 63–86.
- Schuijf, A. (1976b). "Timing analysis and directional hearing in fish," in *Sound Reception in Fish*, edited by A. Schuijf and A. D. Hawkins (Elsevier, Amsterdam), pp. 87–112.
- Schuijf, A. (1981). "Models of acoustic localization," in *Hearing and Sound Communication in Fishes*, edited by W. N. Tavolga, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 267–310.
- Schuijf, A., Baretta, J., and Wildshut, J. (1972). "A field discrimination on the discrimination of sound direction in *Labrus Berggylta* (Pisces: Perciformes)," *Neth. J. Zool.* **22**, 81–105.
- Schuijf, A., and Buwalda, R. (1975). "On the mechanism of directional hearing in cod (*Gadus morhua* L.)," *J. Comp. Neurol.* **98**, 333–343.
- Schuijf, A., and Buwalda, R. J. (1980). "Underwater localization—A major problem in fish acoustics," in *Comparative Studies of Hearing in Vertebrates*, edited by A. N. Popper and R. R. Fay (Springer, New York), pp. 43–77.
- Schuijf, A., and Hawkins, A. (1983). "Acoustic distance discrimination by the cod," *Nature* **302**, 143–144.
- Schuijf, A., and Siemelink, M. (1974). "The ability of cod (*Gadus morhua*) to orient towards a sound source," *Experientia* **30**, 773–775.
- Schuijf, A., Visser, C., Willers, A., and Buwalda, R. (1977). "Acoustic localization in an ostariophysian fish," *Experientia* **33**, 1062–1063.
- Schulz-Mirbach, T., Hess, M., and Metscher, B. D. (2013). "Sensory epithelia of the fish inner ear in 3D: Studied with high-resolution contrast enhanced micro CT," *Front. Zool.* **10**, 63.
- Schulz-Mirbach, T., Hess, M., and Plath, M. (2011). "Inner ear morphology in the Atlantic molly *Poecilia mexicana*—First detailed microanatomical study of the inner ear of a cyprinodontiform species," *PLoS One* **6**, e27734.
- Schulz-Mirbach, T., Ladich, F., Plath, M., and Heß, M. (2018a). "Enigmatic ear stones: What we know about the functional role and evolution of fish otoliths," *Biol. Rev. Cambridge Philos. Soc.* doi: 10.1111/brv.12463.
- Schulz-Mirbach, T., Ladich, F., Plath, M., Metscher, B., and Heß, M. (2014). "Are accessory hearing structures linked to inner ear morphology? Insights from 3D orientation patterns of ciliary bundles in three cichlid species," *Front. Zool.* **11**, 25.
- Schulz-Mirbach, T., Olbinado, M., Rack, A., Mittone, A., Bravin, A., Melzer, R. R., Ladich, F., and Heß, M. (2018b). "In-situ visualization of sound-induced otolith motion using hard X-ray phase contrast imaging," *Sci. Rep.* **8**, 3121.
- Simpson, S. D., Meekan, M., Montgomery, J., McCauley, R., and Jeffs, A. (2005). "Homeward sound," *Science* **308**, 221–221.
- Sisneros, J. A., and Rogers, P. H. (2016). "Directional hearing and sound source localization in fishes," in *Fish Hearing and Bioacoustics: An Anthology in Honor of Arthur N. Popper and Richard R. Fay*, edited by J. A. Sisneros (Springer International Publishing, Cham), pp. 121–155.
- Smith, M. E., Schuck, J. B., Gilley, R. R., and Rogers, B. D. (2011). "Structural and functional effects of acoustic exposure in goldfish: Evidence for tonotopy in the teleost sacculus," *BMC Neuro.* **12**, 19.
- Spanier, E. (1979). "Aspects of species recognition by sound in four species of damselfishes, genus *Eupomacentrus* (Pisces: Pomacentridae)," *Z. Tierpsychol.* **51**, 301–316.
- Tavolga, W. N. (1958). "The significance of underwater sounds produced by males of the gobiid fish, *Bathygobius soporator*," *Physiol. Zool.* **31**, 259–271.
- Tavolga, W. N. (1971). "Sound production and detection," in *Fish Physiology*, edited by W. S. Hoar and D. J. Randall (Academic Press, New York), pp. 135–205.
- Tavolga, W. N. (1974). "Signal/noise ratio and the critical band in fishes," *J. Acoust. Soc. Am.* **55**, 1323–1333.
- Tester, A. L., Kendall, J. I., and Milisen, W. B. (1972). "Morphology of the ear of the shark genus *Carcharhinus*, with particular reference to the macula neglecta," *Pac. Sci.* **26**, 264–274.
- Tolimieri, N., Haine, O., Jeffs, A., McCauley, R., and Montgomery, J. (2004). "Directional orientation of pomacentrid larvae to ambient reef sound," *Coral Reefs* **23**, 184–191.
- Tomchik, S. M., and Lu, Z. (2005). "Octavolateral projections and organization in the medulla of a teleost fish, the sleeper goby (*Dormitator latifrons*)," *J. Comp. Neurol.* **481**, 96–117.
- Trahiotis, C., Bernstein, L. R., Stern, R. M., and Buell, T. N. (2005). "Interaural Correlation as the basis of a working model of binaural processing: An introduction," in *Sound Source Localization*, edited by A. N. Popper and R. R. Fay (Springer, New York), pp. 238–271.
- Urick, R. J. (1983). *Principles of Underwater Sound* (McGraw-Hill, New York).
- van Bergeijk, W. A. (1964). "Directional and nondirectional hearing in fish," in *Marine Bio-Acoustics*, edited by W. A. Tavolga (Pergamon, New York), pp. 281–299.
- van Bergeijk, W. A. (1967). "The evolution of vertebrate hearing," in *Contributions to Sensory Physiology*, edited by W. D. Neff (Academic Press, New York), pp. 1–49.
- Van den Berg, A., and Schuijf, A. (1983). "Discrimination of sounds based on the phase difference between particle motion and acoustic pressure in

- the shark *Chiloscyllium griseum*,” *Proc. R. Soc. Lond. B. Biol. Sci.* **218**, 127–134.
- von Frisch, K. (1938). “The sense of hearing in fish,” *Nature* **141**, 8–11.
- von Frisch, K., and Dijkgraaf, S. (1935). “Can fish perceive sound direction,” *Z. vergl. Physiol.* **22**, 641–655.
- Walton, P. L., Christensen-Dalsgaard, J., and Carr, C. E. (2017). “Evolution of sound source localization circuits in the nonmammalian vertebrate brainstem,” *Brain Behav. Evol.* **90**, 131–153.
- Webb, J. F., Fay, R. R., and Popper, A. N. (2008). *Fish Bioacoustics* (Springer Science+Business Media, LLC, New York).
- Werner, C. F. (1926). “Die Cupula im Labyrinth der Fische” (“The cupula in the labyrinth of fishes”), *Z. Zellforschung Mikroskopische Anat.* **4**, 459–474.
- Winn, H. E. (1972). “Acoustic discrimination by the toadfish with comments on signal systems,” in *Behavior of Marine Animals*, edited by H. E. Winn and B. L. Olla (Plenum Press, New York), pp. 361–385.
- Wisby, W. J., Richard, J. D., Nelson, D. R., and Gruber, S. H. (1964). “Sound perception in elasmobranchs,” in *Marine Bioacoustics*, edited by W. A. Tavolga (Pergamon Press, New York), pp. 255–268.
- Wubbels, R. J., and Schellart, N. A. (1997). “Neuronal encoding of sound direction in the auditory midbrain of the rainbow trout,” *J. Neurophysiol.* **77**, 3060–3074.
- Yan, H. Y., Fine, M. L., Horn, N. S., and Colon, W. E. (2000). “Variability in the role of the gasbladder in fish audition,” *J. Comp. Physiol. A* **186**, 435–445.
- Zeddies, D. G., Fay, R. R., Alderks, P. W., Shaub, K. S., and Sisneros, J. A. (2010). “Sound source localization by the plainfin midshipman fish, *Porichthys notatus*,” *J. Acoust. Soc. Am.* **127**, 3104–3113.
- Zeddies, D. G., Fay, R. R., Gray, M. D., Alderks, P. W., Acob, A., and Sisneros, J. A. (2012). “Local acoustic particle motion guides sound-source localization behavior in the plainfin midshipman fish, *Porichthys notatus*,” *J. Exp. Biol.* **215**, 152–160.