The Enigma of Sound Source Localization by Fishes

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Sound Localization — An Overview

Sound source localization, or directional hearing, is a fundamentally important aspect of hearing and a driving force in the evolution of vertebrate hearing (e.g., Pumphrey, 1950). Without the ability to localize sound, animals could not determine the direction of a predator, locate food sources, or interpret communication signals from a potential mate. Indeed, sound localization plays a major role in human hearing — for example, a parent identifying the location of a crying child who is out of sight, a pedestrian discerning the direction of an oncoming vehicle, or a ship captain navigating marine hazards by the sound of a foghorn!

All terrestrial vertebrates can localize sound. The cues used generally involve comparing the sounds received at the two ears and a set of "calculations" by the brain based on any differences; these calculations pinpoint the sound source, often within a few degrees or less. Factors such as signal frequency, head size, and other anatomical and environmental variables can influence the specific acoustic cues used.

While localization is well-studied in terrestrial vertebrates, the question arose early in the 20th century as to whether aquatic vertebrates can localize sound sources. The challenge lies in the unique properties of sound propagation in water. Sound travels about 4.8 times faster in water than in air, resulting in significantly longer wavelengths. Consequently, the interaural travel-time differences available for localization in aquatic environments are much smaller than those in air (e.g., Van Bergeijk, 1966). This raises intriguing questions about the mechanisms aquatic animals employ to overcome these constraints and to localize sound effectively.

Can Aquatic Vertebrates Localize Sound?

The question, then, is whether aquatic vertebrates can determine the direction of a sound source. Indeed, the importance of determining the direction of a sound from a potential mate, predator, or prey is perhaps even more critical in water than in air, as sound is a far more effective medium for conveying information in aquatic environments than any other signal. For example, unlike visual signals, which are often limited by darkness, murky water, and short transmission ranges, acoustic signals travel much farther and remain reliable under various environmental conditions. Thus, the ability to localize sounds from potential mates, predators, or prey becomes indispensable for survival and reproduction in such environments. Given that vertebrate hearing originated in the earliest fish ancestors (e.g., Fay and Popper, 2000) it is logical to concluded that sound localization is an ancient and important feature of the auditory system and served as a foundational adaptation for survival and communication in the aquatic world.

Marine Mammals

Before considering sound localization by fishes, it is worth asking whether marine mammals or reptiles (e.g., turtles and sea snakes) have evolved mechanisms for localizing sound in water. Despite the importance of this question, few studies have explored sound localization by marine mammals, and, to our knowledge, none have investigated turtles or other aquatic reptiles in this context. However, research on bottlenose dolphins (*Tursiops truncates*) demonstrated that they can localize sound in water with a precision comparable to that of the best terrestrial mammals localizing sounds in air (as reviewed in Moore and Popper, 2019).

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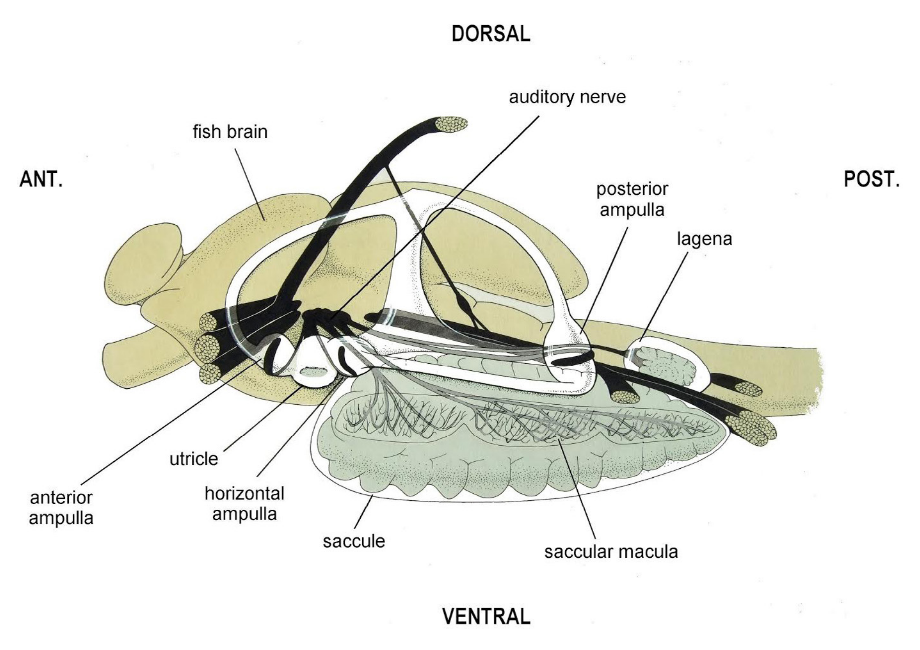


Figure 1. *The left ear of an Atlantic cod showing its position relative to the brain. There are three semicircular canals and three ampullae, for determination of positioning and responses to gravity. The otolith organs (utricle, saccule, and lagena) are all involved in positional responses as well as hearing. The otolith organs contain a sensory macula (or epithelium) with large numbers of sensory hair cells that have their apical ends in contact with the sense calcareous otolith. See text for more details. Figure reproduced, with permission, from Hawkins and Popper, 2018. Copyright 2018 by Anthony D. Hawkins.*

Fishes

While it is intellectually logical that fishes should be capable of sound localization, whether they can actually localize remains enigmatic. And, if fishes can localize, how well do they do it, what are the mechanism(s) used, and how do they overcome the challenges posed by the rapid speed of sound in water? These questions, along with many others, highlight the complexity of this issue.

Addressing these uncertainties is particularly challenging for several reasons. First, conducting sound localization experiments in laboratory tanks presents significant technical challenges, as tank acoustics often differ markedly from acoustics in a natural environments. Second, the immense diversity of the more than 36,000 fish species (see fishbase.org) suggests that there is likely considerable diversity in how (and how well) different species localize sounds. This diversity underscores the need for a broad and nuanced approach to studying sound localization in fishes, accounting for anatomical, behavioral, and ecological differences.

A Primer on Fish Ears and Hearing

Before discussing sound localization by fishes, it is important to have some idea of how they hear. The earliest vertebrate ancestors of fishes had ears, though how these ancestors used them is unknown. The ear further evolved in fishes, and the adaptations seen in terrestrial vertebrates as they transitioned to land were basically only modifications for listening in air rather than water, alongside refinements that improved sensitivity and expanded the range of detectable frequencies. As pointed out by Popper and Fay (1997), all the basic and most important functions of the ear and hearing in modern terrestrial vertebrates are also found in fishes!

A typical fish ear is shown in **Figure 1**. Without going into detail (but see Popper et al., 2003), the fish ear consists of three semicircular canals and three otolithic end organs — the saccule, lagena, and utricle. The canals detect angular acceleration, while the otolith organs respond to positional changes in response to gravity as well as sound, particularly in terms of linear acceleration. Both the semicircular canals and otolithic end organs rely on sensory hair cells for signal detection. These cells are basically the same as those found in the ears of other vertebrates.

Each sensory cell (**Figure 2A**) has a projecting ciliary bundle that, when bent, results in the cell sending a signal to the brain. Bending of the ciliary bundle towards the longest cilium, the kinocilium, produces a larger neuronal signal, whereas bending in other directions causes a graded decrease in signal strength (**Figure 2, center**). In other words, a single sensory cell can signal direction (**Figure 2B**)!

The hair cell response is a function of the interaction of the ciliary bundles with the dense overlying otoliths. Unlike the fish's body, which is roughly the same density as water and moves passively with sound waves, the otoliths are far denser. This density difference causes the otoliths to move at a different amplitude and phase relative to the rest of the ear. As a result, the cilia bend, triggering the hair cell to stimulate the innervating nerve and send sound information to the brain — the fish hears just like humans hear!

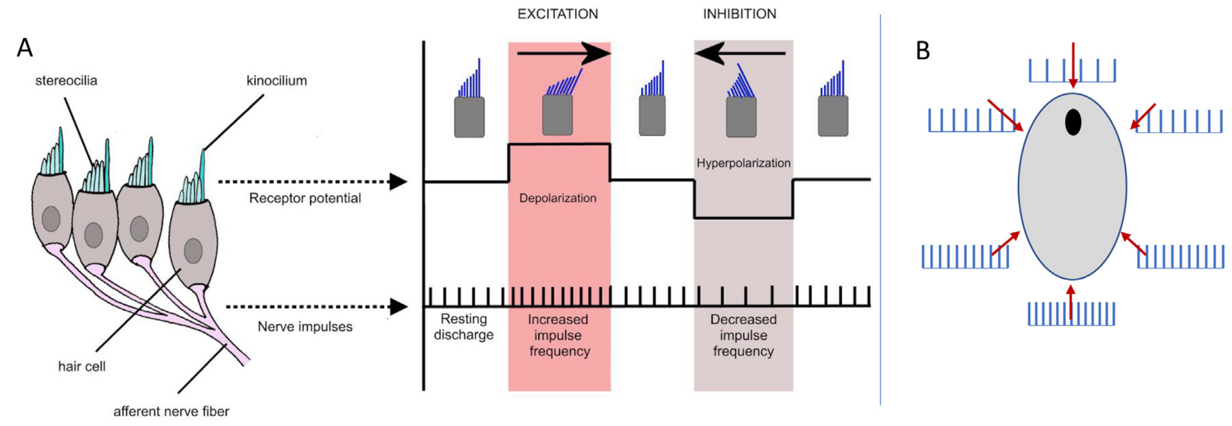
History of Fish Sound Localization Studies

Interest in fish directional hearing and sound source localization spans over 90 years (e.g., von Frisch and Dijkgraaf, 1935), but the number of actual studies is likely fewer than 15, and the results remain equivocal regarding whether, and how, fishes localize sounds. Several factors have contributed to this uncertainty.

First, many early experiments were conducted in tanks or other small enclosures. As we now understand, these environments are inappropriate for studying directional hearing because their complex acoustics of air-bounded tanks fail to provide clear, directional sound signals (e.g., Rogers et al., 2016).

Second, while some early investigators attempted field studies, these presented significant challenges since observing and interpreting the behavior of fishes in natural aquatic environments was difficult. The limitations of these early methods hindered accurate assessments of fish responses to sound direction and localization in their natural environments.

Figure 2. *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 reproduced with permission from Hawkins and Popper, 2018. Copyright 2018 Anthony D. Hawkins.*



Finally, early investigators often approached the question of sound localization in fishes with the assumption that the mechanisms must be like those used by terrestrial vertebrates. This perspective led to a series of misconceptions and unhelpful assumptions, which delayed recognition of the fundamental differences in the principles underlying sound localization in aquatic versus terrestrial environments. Over time, it has become clear that fishes rely on unique mechanisms tailored to the physical properties of underwater sound propagation, which differ significantly from those used by terrestrial vertebrates.

Perhaps the first detailed investigation of directional hearing by fishes was conducted by von Frisch and Dijkgraaf (1935) who examined the behavior of European minnows (*Phoxinus laevis*) in a lake. By rewarding fish with food when they came close to a sound source, the investigators attempted to determine whether the minnows could localize the sound source. They tentatively concluded that fishes could not localize sound unless they were within a few body lengths of the source.

Later, Kleerekoper and Chagnon (1954) conducted experiments in a highly specialized tank and observed that fishes could locate the source of a sound. They concluded that, unlike many terrestrial vertebrates, which often make instantaneous decisions about sound direction, the fishes oriented themselves to an intensity gradient and moved along that gradient to reach the source of the sound.

While their work was not pursued further and was conducted in a large tank rather than a natural setting, the idea that fishes localize sound using intensity gradients is significant. As we will explore further, this mechanism may represent the original localization strategy in both bony fishes and sharks, suggesting an ancient evolutionary adaptation for directional hearing and sound source localization in aquatic environments.

Steering in the Wrong Direction

Van Bergeijk (1966) published a highly influential paper arguing that fishes could not determine sound direction. He based his argument on the higher speed of sound in water, combined with the relatively small distance between the two ears in most fishes (even in larger species), resulting in minimal differences in intensity, time of arrival, and phase between the two ears. These binaural differences, crucial for sound localization in terrestrial vertebrates, were assumed to be negligible or nonexistent for fishes.

Another critical issue raised by van Bergeijk was the assumption that fishes rely on sound pressure for localization. The problem, he argued, was that fishes only have a single pressure detector, the air-filled swim bladder in the abdominal cavity, which sends the same signal to both ears. This setup, he argued, would effectively eliminate the possibility of binaural comparison for determining sound direction.

Van Bergeijk believed fishes and terrestrial vertebrates rely on similar mechanisms for sound localization, but we now see this assumption as fundamentally flawed. Indeed, it is likely that fishes have mechanisms that are uniquely adapted to the physical properties of sound in water and the anatomical constraints of their auditory systems.

Revisiting Directional Hearing

In many ways, van Bergeijk's conclusions stalled progress in the study of directional hearing in fishes for nearly a decade by suggesting that fishes lacked the necessary mechanisms to localize. It was not until researchers began thinking "outside the box" that this field of study was revitalized.

Pioneering studies to restart localization research was performed by Arie Schuif and his colleagues in the Netherlands (reviewed in Schuijf and Buwalda, 1980). The group conducted innovative field studies that exposed fishes to highly controllable and measurable acoustic fields, thereby providing important insights into the mechanisms of sound localization by fishes.

In one set of studies, Schuijf's group used behavioral experiments to demonstrate that some species of fish studied are capable of directional hearing for low frequency sounds (e.g., below 100 Hz) by testing whether restrained animals could detect changes in the direction of a sound source on the horizontal plane. These experiments revealed that Atlantic cod (*Gadus morhua*) could discriminate identical sounds originating from different horizontal directions, provided the sources were separated by more than 22 degrees (compare to less than 2 degrees in many terrestrial animals and dolphins). While these findings confirmed that fishes can discern the direction of a sound source, their precision is notably lower than that of most terrestrial animals.

Moreover, since fishes live in a three-dimensional world, it would be important to be able to also discriminate sound directions in the vertical plane. Building on Schuijf's work, Hawkins and Sand (1977) showed that Atlantic cod could discriminate sound in the median vertical plane. Similarly, Buwalda et al. (1983) demonstrated that some species could distinguish between diametrically opposed sound sources in both the transverse and the median horizontal planes. In all cases, however, the precision of discrimination was relatively limited, typically no better than 10 to 20 degrees.

It is worth noting, however, that all these experiments exclusively utilized simple and consistent sound stimuli, such as pure tones. In natural environments, fishes are more likely to encounter complex sounds, such as those produced by conspecifics, predators, or environmental factors. Consequently, further research is necessary to determine how well fishes localize ecologically relevant sounds in the natural environment.

Notably, none of the studies in the 1970s provided clear evidence that fishes, despite their ability to discriminate between sounds from different directions, could use this information to localize a source without first "sampling" signals as they move towards or away from the signals. In other words, perhaps trained animals can discriminate direction, but can they use that information to go to a food source or move away from a predator? This gap left open the question of whether directional hearing by fishes was merely a perceptual ability or it played a direct role, without sampling, in guiding ecologically relevant actions.

It was also unclear how fishes were able to discriminate sounds from different directions, and particularly whether they could differentiate sounds coming from the front versus the back, as the acoustic signals reaching the two ears are essentially identical in both cases. A critical clue arose from work of Piddington (1972), who demonstrated that goldfish (*Carassius auratus*) could discriminate between rarefaction and compression phases in a sound field. This led Schuijf and colleagues to propose that fishes might determine direction by comparing the phase of the particle motion, directly detected by the ear, with the phase of sound pressure, detected by the swim bladder and re-radiated to the ear as particle motion.

This hypothesis was confirmed by Buwalda et al. (1983), who showed that Atlantic cod could resolve the front/back ambiguity (also known as the "180-degree ambiguity" problem) by utilizing both particle motion and sound pressure cues. Furthermore, Schuijf and Hawkins (1983), conducting a study in open water, showed that restrained Atlantic cod could also discriminate sounds originating from different distances. They argued this ability was possible because the phase difference between particle motion and sound pressure changes with distance of the sound source from the fish. These findings significantly advanced our understanding of the mechanisms underlying directional hearing by fishes, highlighting the integration of multiple acoustic cues to resolve spatial ambiguities.

Open Issues Regarding Fish Sound Localization

While these studies demonstrated that, restrained, at least some fish species can discriminate the location and even the direction of a sound source, there were (and still are) several major problems with the hypothesis that remain unresolved. First, the work was conducted on a very limited number of species, all of which had auditory systems capable of detecting and integrating both sound pressure and particle motion. However, this sample group does not represent most fish species, including many of commercial importance (e.g., tuna, haddock, flatfish, sturgeon), which are sensitive only to particle motion. These fishes either cannot detect sound pressure or lack swim bladders close enough to the ear to convert sound pressure into particle motion. Consequently, these species would not be able to use the phase difference hypothesis proposed in the studies.

Second, while the experiments were methodologically rigorous and elegant, they focused on the assumption that fishes can instantly determine sound source direction, much like many terrestrial animals (including humans). Put another way, if a human closes their eyes and is presented with a sound, they not only can point in the direction of the source, but they can also move in the direction of that source without hearing the sound again, though estimating distance might require further auditory cues. Whether fishes are capable of instantaneous directional localization remains unclear. Indeed, current evidence, as we discuss below, suggests that fishes need to continuously sample acoustic information to localize a sound source, which contrasts with the rapid, single-instance localization seen in terrestrial vertebrates.

Third, the work done in the 1970s used simple acoustic signals that do not resemble the complex, natural sounds fishes typically encounter in their environments. It remains uncertain whether fishes can perform the same types of discriminations shown in these studies when exposed to the real-world sounds they are likely to encounter, such as the calls of other fishes, environmental ambient sounds, or the complex acoustic signals produced by predators and prey.

These limitations highlight the need for broader studies encompassing a wider range of species, experimental designs that mimic natural conditions, and an emphasis on understanding how fishes process ecologically relevant sounds in real-world scenarios.

The Role of the Ear

Beyond the argument that fishes can determine sound direction lies the question of how this localization is achieved, particularly given the anatomical and physical constraints of their auditory systems discussed earlier. Despite these challenges, insights into the potential role of the ear in directional hearing emerged as early as 1950.

Both Pumphrey (1950) and de Vries (1950) proposed that the otolith end organs of the inner ear detect particle motion, a vector quantity with both magnitude and direction, rather than sound pressure, which is the major stimulus source for terrestrial vertebrates and marine mammals. This idea suggested that fishes might use the directional sensitivity of particle motion to localize sound. Building on this assumption, Dijkgraaf (1960) hypothesized that the otolithic end organs of fish ears are inherently directional in their response to sound stimuli (see **Figure 2**). However, at that time, there was little empirical evidence to confirm the directional properties of the ear, leaving these proposals unresolved. Yet, these early studies laid the groundwork for further exploration into the mechanisms of directional hearing in fishes, which would continue to evolve with advancements in experimental techniques.

Ear Anatomy and Directional Hearing

As often happens in science, multiple research labs will independently, and simultaneously, ask similar questions and achieve similar findings. This situation happened in 1976 when the first author of this paper (Popper, 1976), simultaneously with Per Enger (1976) in Norway and Tor Dale (1976) in Denmark, published papers that used scanning electron microscopy to examine the detailed structure of the ears in different fish species. All authors found that the sensory hair cells in the otolith organs had hair cells arranged in rather distinct groups, with each group oriented in different directions (**Figure 1**). Given the way the hair cells are stimulated through their interaction with the otoliths, this arrangement has significant implications. When the otolith moves relative to the sensory epithelium in response to sound, it stimulates some hair cells more than others, depending on the direction of motion. Popper (1976) proposed that the brain could then "calculate" the direction of motion of the sound by tracking the differential levels of stimulation across these distinct groups of sensory hair cells.

Of course, a single ear provides only limited directional information, as each otolith organ has four groups of hair cells oriented on a single plane. But things clear up when we realize that the three otolith organs within one ear are oriented in different planes. Rogers et al. (1988) proposed that the brain refines sound direction detection by integrating input from all three organs using vectorial weighting. Combining this with input from the other ear, where hair cells are oriented on opposing planes, allows fishes to accurately "calculate" sound direction based solely on ear-derived input. This sophisticated mechanism highlights the remarkable adaptations of fishes to their acoustic environment!

The Problem Continues! And a Solution

The challenges, of course, remain the same as those raised by Schuijf and colleagues. First, even with input from six otolith organs oriented in different planes, there is still an inherent ambiguity between signals originating from opposite directions. In other words, a sound coming from directly in the front of a fish will produce an identical ear response to a sound coming from 180 degrees behind it. Second, there remains the question as to whether fishes can make instantaneous decisions on sound direction, like mammals, or whether they need to continuously update directional information as they swim to (or away from) a sound source.

For fish species capable of detecting sound pressure, the 180-degree ambiguity might be resolved by integrating sound pressure cues with particle motion cues to distinguish between opposing directions, as proposed by Schuijf and colleagues. However, this hypothesis leaves an open question for species that lack the ability to detect sound pressure (e.g., elasmobranch fishes [sharks, skates, and rays], flatfishes, tunas, and many other species of economic and ecosystem importance). How do these fishes resolve this directional ambiguity?

In fact, the potential solution to this "problem" is to again think outside the box and consider that fishes might localize through successive approximations rather than instantaneous directional determination, as is common in mammals, and as suggested by Kleerekoper and Roggenkamp (1954). This explanation would mean that fishes may detect a sound and, using vectorial weighting from their otolith organs, form a general sense of direction. This estimate does not need to be precise; it might even be off by 20 or 30 degrees or more, as suggested by the Dutch group. The fish then moves based on this initial approximation and continues sampling the signal.

As the fish moves a few body lengths, it evaluates changes in the sound's intensity. If the sound becomes louder, the fish is likely moving toward the source (e.g., food or a mate). Conversely, if the sound diminishes, the fish adjusts its movement to head in the opposite direction, potentially away from a predator. By continuously sampling the sound and refining its direction based on intensity and vectoral input, the fish effectively navigates toward or away from the sound source. This iterative process may represent a fundamental strategy for sound localization in fishes, particularly those lacking the ability to use sound pressure cues.

Behavioral Evidence for Sampling

Sharks Sample Sound

Perhaps one of the earliest pieces of evidence suggesting that fishes sample sound as they move toward a source came from observations in the 1960s and 1970s on the behavior of wild sharks (reviewed by Myrberg, 2001). Using small aircraft to spot sharks at sea, Myrberg's research group tracked the sharks' movements in response to playback of sounds mimicking struggling fish, a potential food source, broadcast from distances of a kilometer or more.

Rather than swimming directly towards the sound in a straight line, the sharks exhibited a zigzagging movement pattern. They repeatedly adjusted their course, moving back and forth along a general path to the sound source. This behavior suggests that the sharks were continuously sampling the sound's intensity and characteristics as they swam, refining their directional sense and adjusting their trajectory to home in on the source. This iterative approach to sound localization likely reflects a broader strategy used by fishes to navigate the acoustic landscape, particularly in dynamic and three-dimensional aquatic environments.

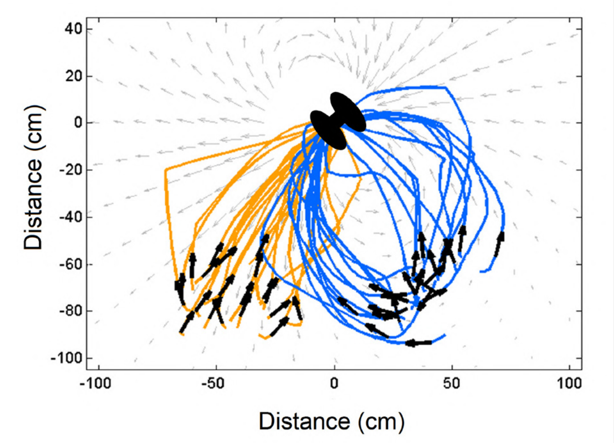
Fishes Sample Sound as They Swim

Perhaps the most compelling and clearest evidence that fishes can locate sound sources in three-dimensional space comes from studies of phonotaxis behavior in the plainfin midshipman (*Porichthys notatus*). In the late 1990s, it was shown that reproductive females exhibit robust movement to a sound source in response to the playback of simulated male advertisement calls (McKibben and Bass, 1998). This behavior, an unconditioned response, is not as easily observed in other fish species, making plainfin midshipman particularly valuable for studying sound localization.

Subsequently, in the early 2010s, another research group conducted a series of experiments with plainfin midshipman to explore their strategies and cues to locate sound sources in both simple (monopole) sound fields and more complex (dipole) sound fields (Sisneros and Rogers, 2016). Results revealed that fishes rely on local particle motion vector cues generated by the sound source to guide their sound source localization behavior.

Zeddies et al. (2012) used a dipole sound projector rather than a monopole sound source. While a monopole emits sound omnidirectionally (equally in all directions), a dipole produces a bi-lobed, figure-eight radiation pattern. In these experiments, midshipman displayed distinct navigation behaviors depending on their release position relative to the source's vibratory axis (**Figure 3**). When released along the dipole's vibratory axis, the fish followed nearly straight paths directly to the sound source. However, when released approximately 90 degrees from the vibratory axis, their paths became highly curved, aligning closely with the local particle motion axes. This suggests that the fish oriented toward the source by swimming along pathways parallel to the particle motion vectors at their initial location.

Figure 3. *Response pathways of plainfin midshipman (*Porichthys notatus*) localizing a dipole sound source.* ***Orange*** *traces show fish released with in-line particle motion vector cues;* ***blue*** *traces show fish released with orthogonal cues.* ***Gray arrows*** *indicated the particle velocity vectors, and* ***black arrows*** *show initial fish directions. Reproduced with permission from Zeddies et al., 2012.*



One unresolved aspect of midshipman phonotaxis studies, however, is the precise strategy or strategies these fish use to locate sound sources based on their sensitivity to local particle motion vectors cues. In the experiments, midshipman consistently exhibited positive phonotaxis, moving toward the sound source along smooth, continuous paths. The midshipman movement was characterized by an average zero-degree orientation relative to the particle motion axis, suggesting they aligned directly with the directional vector and swam toward the source.

Interestingly, in the Zeddies et al. (2012) study, five individual fish released near the 90-degree position exhibited a different behavior, swimming directly to the source and seemingly disregarding the dominant particle motion vector cue (see Figure 8C in Zeddies et al., 2012). This deviation suggests these fish may have relied on alternative cues, such as the direction of energy flow or the acoustic intensity gradient, to determine the source's location.

Sisneros and Rogers (2016) proposed a time-averaged intensity-based mechanism for sound source localization in fishes. This hypothesis posits that acoustic intensity provides directional information that fishes can use for sound localization, offering a potential explanation for the observed behavior in these experiments.

Thus, an intriguing question remains: could midshipman phonotaxis, in part, be explained by the fish's orientation to spatial change in sound intensity, effectively "climbing up" the intensity gradient? The experimental tank indeed featured a sound intensity gradient, approximately 0.3 dB per cm (see Figure 5 in Zeddies et al. 2012). However, the discrimination limen for intensity in midshipman has yet to be determined, leaving open the possibility that their behavior might reflect a combination of tropotaxis and gradient-following mechanisms.

There Are Many Remaining Questions!

Based on recent data about the structure/function of the ear and its potential for engagement in sound localization and the work with plainfin midshipman showing an intensity mechanism for localization, it becomes clear that at least some fishes can determine the direction of a sound and adjust their movement accordingly. However, with over 36,000 species of fishes exhibiting immense diversity in behavior, physiology, and auditory structures, it remains unclear whether the mechanisms observed thus far are widespread among fishes or if other, as-yet unexplored, species employ different strategies for directional hearing. Furthermore, it is also possible that many fishes have limited or poor localization abilities.

Recently, the mechanism for directional hearing, originally proposed by Schuijf and Buwalda (1975), has been confirmed by Veith et al. (2024), but only for freshwater otophysan species with highly specialized hearing adaptations that connect the swim bladder to the inner ear (e.g., goldfish, catfish, carps, and relatives). The mechanism has not, however, been tested in species without the otophysan auditory adaptations.

Indeed, and in contrast, the studies described on plainfin midshipman, a representative of the broader group of species lacking these specific specialized adaptations, reveal that they possess hearing capabilities enabling them to detect sound pressure cues, though not in the same way as otophysans, and resolve the 180-degree ambiguity problem. Furthermore, midshipman and other fish species may rely on a combination of alternative mechanisms and strategies for sound localization, including vector weighting and the use of acoustic intensity cues.

Ultimately, we still have much to learn about how, and how well, fishes localize sound. Given their critical role as a human food source and as integral components of ecosystems, it behooves us to invest significantly more effort into understanding fish sound localization and hearing. This imperative is particularly urgent in the light of the increasing prevalence of underwater anthropogenic sound, which has the potential to disrupt the hearing and behavior of marine animals (e.g., Popper and Hawkins, 2019).

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Arthur N. Popper is emeritus professor of Biology at the University of Maryland (College Park) and emeritus editor of *Acoustics Today*. His research interests focused on hearing by fishes, and this interest has more recently evolved into a focus on applied issues on effects of human-made sound on aquatic animals. Dr. Popper retired as editor of the Springer Handbook of Auditory Research, a series of over 77 books. He is a fellow of several societies, including the American Association for the Advancement of Science and the Acoustical Society of America (ASA), and a recipient of the ASA's Gold Medal.

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Joseph A. Sisneros is Professor and Chair of the Department of Psychology at the University of Washington (Seattle). His research focuses on neuroethology and sensory neurobiology, exploring how fishes, particularly the plainfin midshipman, use auditory cues for communication and sound localization. Dr. Sisneros earned his PhD from the Florida Institute of Technology (Melbourne) and completed his postdoctoral training at Cornell University (Ithaca, New York). A fellow of the Acoustical Society of America, he also serves as an associate editor for *The Journal of the Acoustical Society of America* and is senior editor of the Springer Handbook of Auditory Research.