

# A Review of Hearing by Sturgeon and Lamprey

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## 1. Introduction

Fish bioacoustics is the study of hearing and sound communication by fishes. The discipline includes investigations of: (a) structure, function, and physiology of hearing; (b) sound produced by fish and mechanisms of sound production; and (c) behavior that involves use of sound (e.g., reproductive, territoriality). The body of literature on fish bioacoustics is reasonably extensive (see Zelick et al. 1999; Popper et al. 2003; Ladich and Popper 2004, for reviews). However, in examining the literature in some detail it becomes apparent that all but a few studies on bioacoustics are directed at the advanced bony fishes (teleosts), with a few additional studies on hearing by cartilaginous fishes (sharks and rays). Virtually nothing is known about hearing in the most primitive fishes, the agnatha – indeed, it is not even known if any agnathan is able to hear. And, almost nothing is known about hearing by any non-teleost actinopterygian fish (e.g., lungfish, sturgeons, reedfish, bowfin, and paddlefish), although there are some data that suggests sound production by some of these species.

There is, however, more data on the ears of agnathans and on non-teleost bony fishes, and these data may be useful in developing some preliminary hypotheses on hearing in these species. However, since ears subserve two functions – hearing and positional sense (relationship to gravity – see Platt 1983; Popper et al. 2003), any speculations about hearing derived from ear structure must be treated with the greatest caution since an ear structure may be related to the positional rather than auditory sense.

This review is directed at hearing in two groups of fishes, lamprey and sturgeon. Before discussing what is known about these fishes, this review will first give a brief overview of fish hearing, then discuss the ears of the species of interest, and finally consider whether these species hear and, if they do, the likely sounds they detect. The review will also consider hearing in other species of fish in the Columbia River basin including American shad and salmonids. However, the structure and function of the auditory system in these fishes will not be extensively considered here since there is a good body of literature on both American shad and salmonids. These will be mentioned in the course of the review.

## 2. Hearing Capabilities, Detection, and Sound Production

Fishes have two sensory systems that serve to detect motion. Together they are often referred to as the “octavolateralis system” to refer to their two components – the ear which is innervated by the eighth cranial nerve and the lateral line which is innervated by the lateral line nerves (Popper et al. 1992) (Fig. 1).<sup>1</sup> The lateral line fish fishes used to detect nearby water motion (e.g., Coombs and Montgomery 1999) while the ear is involved in detection of sound as well as the detection of angular acceleration and changes in the fish’s position relative to gravity (Platt 1983; Popper et al. 2003).

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<sup>1</sup> The combined systems have also been referred to as the “acousticolateralis system.” However, the preferred terminology is “octavolateralis” (Popper et al., 1992).

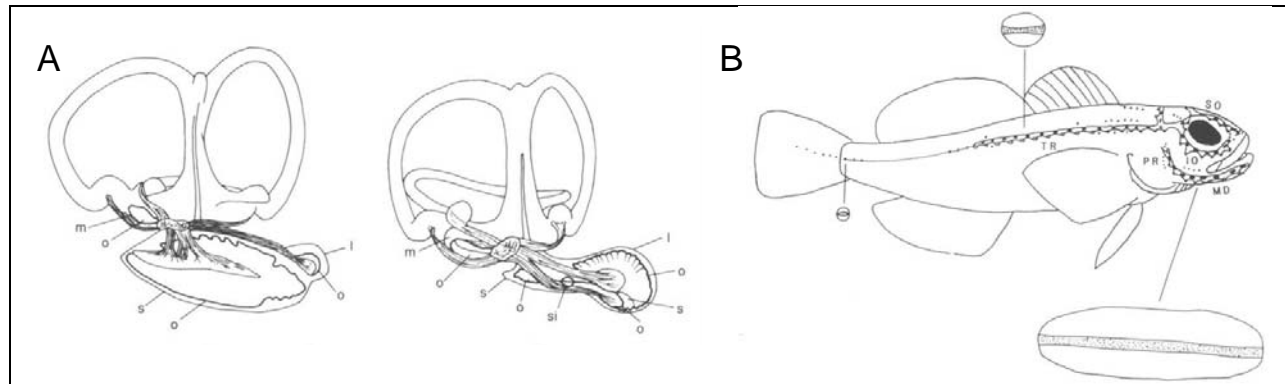


Figure 1: The octavolateralis system of fishes includes the inner ear (A) and the lateral line system (B). (A) Drawing of the medial view of the inner ear of a pikeperch (*Lucioperca sandra*) on the left and an ide (*Leuciscus idus*) on the right. l Lagena; m utricule; o otolith of each otolithic end organ; s saccule; si transverse canal that connects the two ears in otophysan fishes. (B) Drawing of the canal and surface neuromasts on the body of the mottled sculpin (*Cottus bairdii*). The enlarged drawings show the dorsal surface of neuromasts found on the mandible, trunk, and a superficial neuromast, and stippling represents hair cells. MD mandibular canal; SO supraorbital canal; IO infraorbital canal; PR preopercular canal; TR trunk canal. (Drawings in A From Popper and Fay 1973 modified from Retzius 1881; B from Coombs. et al., 1989).

#### a. Sensory cells of the ear

The basic functional unit in the octavolateralis system is the sensory hair cell, a highly specialized epithelial cell (Fig. 2) that is stimulated by mechanical energy (e.g., sound, motion). Mechanical energy causes a number of ionic changes in the cell membrane and the subsequent release of neurotransmitter which excites neurons that synapse on the cell. These neurons carry information about the mechanical stimulation of the sensory cell to the brain for further processing. The sensory cell found in the octavolateralis system is almost the same in all vertebrates from lamprey to humans (Coffin et al. 2004). The ear and the lateral line, send their signals to the brain in separate neuronal pathways. There is evidence, however, that at some level of the brain there is interaction between these two systems and the information is used to provide the fish with a complete picture of its acoustic environment (Coombs and Montgomery, 1999).

#### b. The Lateral Line

While the lateral line is not the focus of this review, it is worth considering briefly since both lamprey and sturgeon have this system, and it may be providing these animals with important information about their environments. Thus, disruption of lateral line function could have an impact on these, and other fish, species.

The lateral line is divided into two parts, the canal system (Fig. 1) and the free neuromasts. Each neuromast contains a group of sensory hair cells that are positioned so that they can detect and respond to water motion around the fish. The canal neuromasts are spaced evenly along the bottom of canals that are located on the head and extending along the body (in most, but not all, species) (see Fig. 1B). The free neuromasts are distributed over the surface of the body. The specific arrangement of the lateral line canals and the free neuromasts vary with

different species and may be related to the precise role the lateral line plays in the life of a particular species (Coombs et al. 1992). The overall pattern of the lateral line canals suggests that the receptors are laid out to provide a long baseline that enables the fish to extract information about the direction of the signal source relative to the animal. The latest data suggest that the free neuromasts detect water movement (e.g., currents), whereas the receptors of the lateral line canals detect hydrodynamic signals. By comparing the responses of different hair cells along such a baseline fish should be able to use the receptors to locate the source of vibrations (Coombs and Montgomery 1999). Moreover, the lateral line appears to be most responsive to relative movement between the fish and surrounding water (its free neuromasts are sensitive to particle velocity; its canal neuromasts are sensitive to particle acceleration).

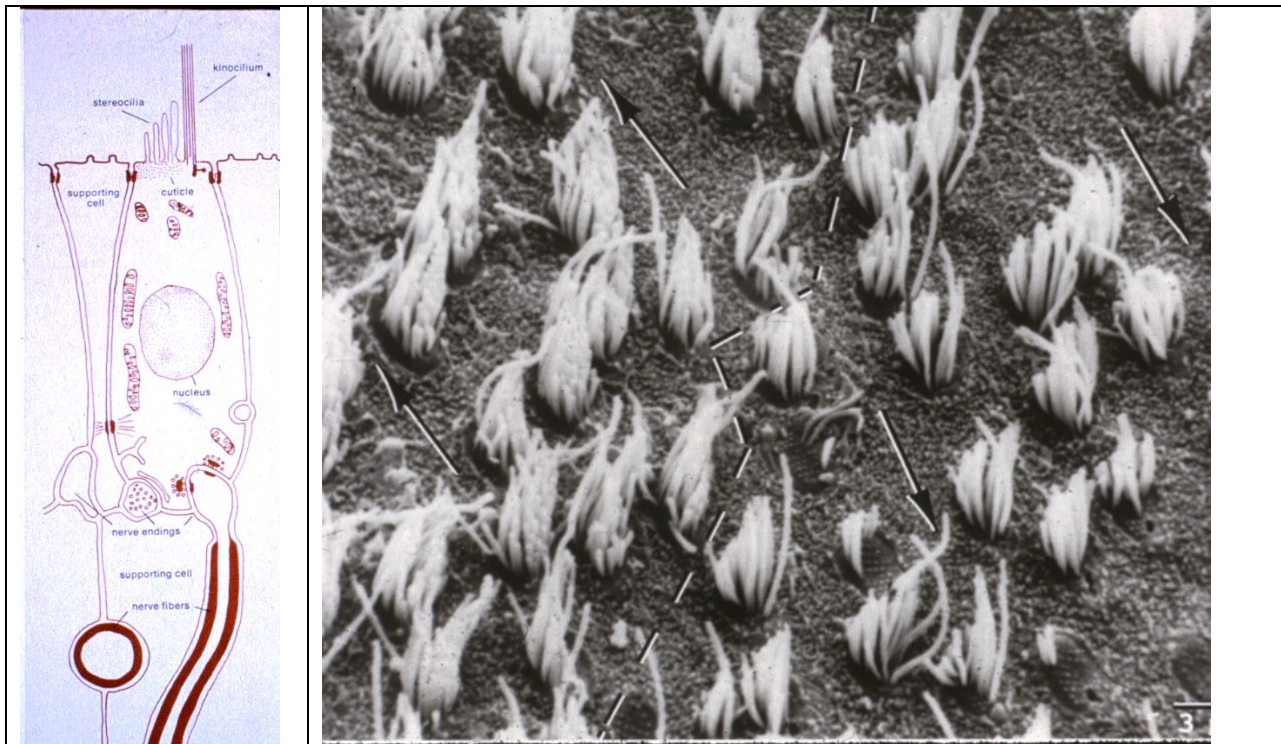
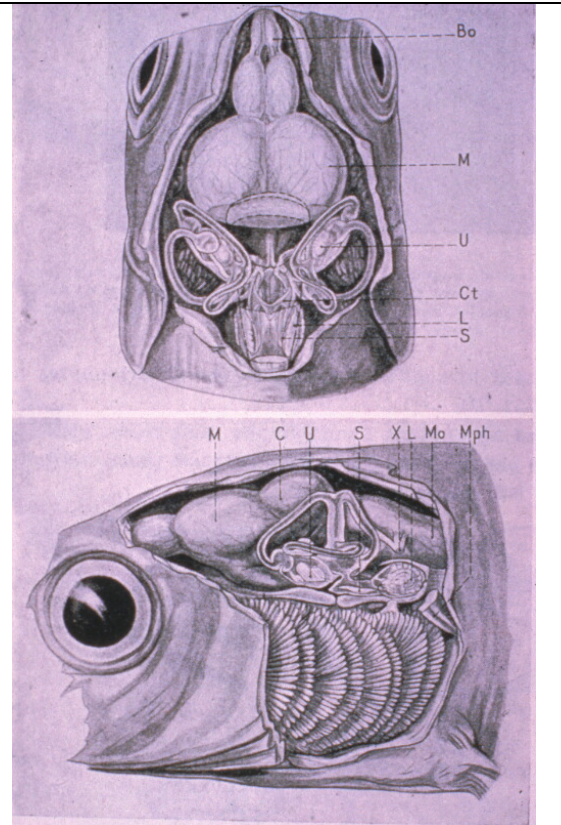


Figure 2: The sensory hair cells of the inner ear. (Left) Schematic drawing of a sensory hair cell. The cell is innervated by both afferent neurons (carrying information to the brain) and efferent neurons (which carry information from the brain to the cell). The apical end of the cell has a cuticular plate and a set of actin-rich cilia that project above the cell into the lumen of the lateral line or inner ear. This projection is a series of cilia which include a single kinocilium and multiple stereocilia. Bending of the ciliary bundle during mechanical stimulation results in opening of small channels and the influx of chemicals that ultimately lead to the release of neurotransmitter and stimulation of the afferent neurons (drawing from Popper and Coombs 1983). (Right) Scanning electron micrograph showing a number of ciliary bundles projecting into the lumen of the saccule (one of the otolithic end organs of the inner ear of fishes) from sensory hair cells such as the one shown on the left. Note that the kinocilium (the longest of the cilia) is on the lower right side of the bundle in the cells to the right of the dashed line (note direction of arrow) while the kinocilium is to the upper left on the left side of the dashed line (SEM from Popper 1983).

The ear and the lateral line overlap in the frequency range to which they respond. The lateral line appears to be most responsive to signals ranging from below one Hz to between 150 and 200 Hz (e.g., Coombs et al. 1992), while the ear responds to frequencies from about 20 Hz to

several thousand Hz in some species (Popper and Fay 1993; Popper et al. 2003). The specific frequency response characteristics of the ear and lateral line varies between different species and is probably related, at least in part, to the life styles of the particular species. There is very little known about the specific characteristics of the lateral line in different species. Perhaps the best studied lateral line system is found in the mottled sculpin (*Cottus bairdi*) where it is known to be part of food catching behavior (e.g., Coombs and Conley 1997a, b; Coombs et al. 2001).

Figure 3: Schematic drawing of the location of the ear in the head of a minnow, *Phoxinus laevis* (from Grassé 1958). Top shows a dorsal view of the head with the top of the cranium and the back part of the brain cut away to show the location of the ears below, and on either side of, the brain. In this fish, which is a member of the superorder Otophysi, the two ears come close to one another along the midline of the cranium (see the drawing of the ear of the ide in Figure 1B for another otophysan ear). In other fishes, such as the sturgeon, the ears are somewhat more lateral. The drawing at the bottom shows a lateral view of the left side of the head to show the location of the ear to the side of the brain. (*Bo* – olfactory lobes of the brain; *ct* – transverse canal; *L* - *lagena*; *M*-midbrain; *Mo* & *Mph* – non-ear structures; *S* - saccule; *U*-utricle; *X* - cranial nerve X:



### c. The Inner Ear

The inner ear in fishes is located in the cranial (brain) cavity of the head just behind the eye (Fig. 3). Unlike terrestrial vertebrates, there are no external openings or markings to indicate the location of the ear in the head. The ear in fishes is generally similar in structure and function that of other vertebrates. It consists of three semicircular canals (and associated sensory regions called cristae) that are used for detection of angular movements of the head, and three otolithic organs that respond to both sound and changes in body position (Platt 1983; Schellart and Popper 1992; Popper and Carlson, 1998; Popper et al. 2003; Ladich and Popper 2004).

The sensory regions of the semicircular canals and otolith organs (Fig. 1) contain many sensory hair cells (Fig. 2). In the otolith organs, the ciliary bundles, which project upward from the top surface of the sensory hair cells, contact a dense structure called an otolith (or ear stone). It is the relative motion between the otolith and the sensory cells that results in stimulation of the cells and responses to sound or body motion. The precise size and shape of the ear varies in

different fish species (Popper and Coombs 1982; Schellart and Popper 1992; Popper et al. 2003; Ladich and Popper 2004).

#### d. *Hearing*

Hearing is better understood for bony fishes than for other fish, such as sharks and jawless fishes (class Agnatha) (Popper and Fay 1993; Ladich and Popper 2004). Fish with specializations that enhance their hearing sensitivity have been referred to as hearing “specialists;” whereas, those that do not possess such capabilities are called “nonspecialists” (or “generalists”). Popper and Fay (1993) suggest that in the hearing specialists, one or more of the otolith organs may respond to sound pressure as well as to acoustic particle motion. The response to sound pressure is thought to be mediated by mechanical coupling between the swim bladder (the gas-filled chamber in the abdominal cavity that enables a fish to maintain neutral buoyancy) or other gas bubbles and the inner ear. With this coupling, the motion of the gas-filled structure, as it expands and contracts in a pressure field, is brought to bear on the ear. In nonspecialists, however, the lack of a swim bladder, or its lack of coupling to the ear, probably results in the signal from the swim bladder attenuating before it gets to the ear. As a consequence, these fishes detect little or none of the pressure component of the sound (Popper and Fay 1993).

The vast majority of fishes studied to date appear to be non-specialists (Schellart and Popper 1992; Popper et al. 2003), and only a few specialists are known to inhabit the marine environment (although lack of knowledge of specialists in the marine environment may be due more to lack of data on many marine species, rather than on the lack of their being specialists in this environment). Some of the better known marine hearing specialists are found among the Beryciformes (i.e., soldierfish and especially Holocentridae, which includes the squirrelfish) (Coombs and Popper 1979), and Clupeiformes (i.e., herring and shad) (Mann et al. 1997, 2001). Even though there are hearing specialists in each of these taxonomic groups, most of these groups also contain numerous species that are nonspecialists. In the family Holocentridae, for example, there is a genus of hearing specialists, *Myripristis*, and a genus of nonspecialists, *Adioryx* (Coombs and Popper 1979).

Audiograms (measures of hearing sensitivity) have been determined for over 50 fish (mostly fresh water) and four elasmobranch species (Fay 1988; Casper et al. 2003). An audiogram plots auditory thresholds (minimum detectable levels) at different frequencies and depicts the hearing sensitivity of the species. It is difficult to interpret audiograms because it is not known whether sound pressure or particle motion is the adequate stimulus and whether background noise determines threshold. The general pattern that is emerging indicates that the hearing specialists detect sound pressure with greater sensitivity over a wider bandwidth (to 3 kHz or above) than the nonspecialists. Also, the limited behavioral data available suggest that frequency and intensity discrimination performance may not be as acute in nonspecialists (Fay 1988).

Behavioral audiograms for a number of species are presented in Figure 4. Popper and Fay (1993) point out that threshold values are expressed as sound pressure levels because that quantity is easily measured, although this value is strictly correct only for the fishes that respond in proportion to sound pressure. It is uncertain if the thresholds for the plaice and some of the

other non-specialists should be expressed in terms of sound pressure or particle motion amplitude. In comparing best hearing thresholds, hearing specialists are similar to most other vertebrates, when thresholds determined in water and air are expressed in units of acoustic intensity (i.e., Watts/cm<sup>2</sup>) (Popper and Fay 1993).

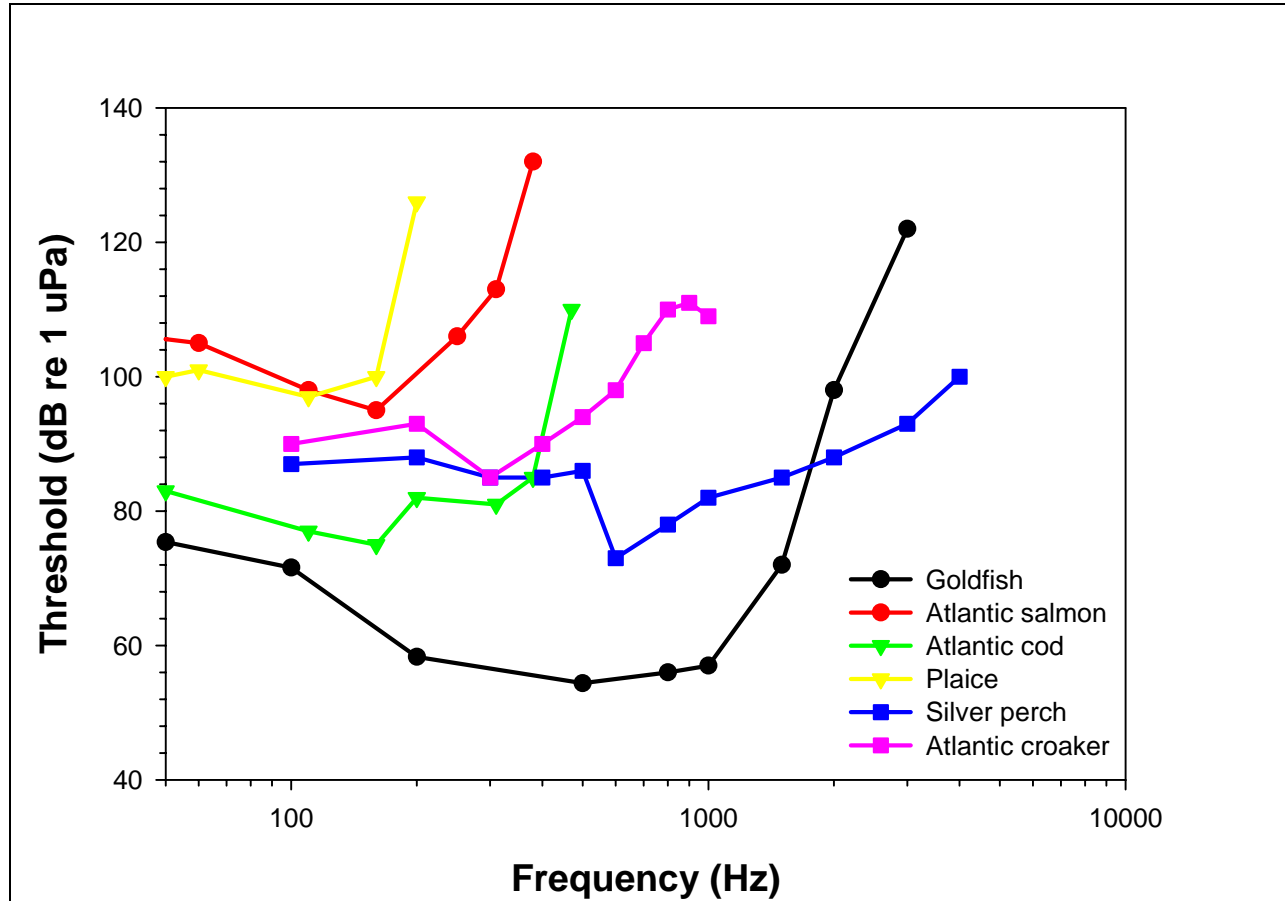


Figure 4: Audiograms of several different fish species. The x-axis shows frequencies tested and the y-axis the lowest sound level detected by the fish at that frequency.<sup>2</sup> Of the species shown here, best hearing in terms of bandwidth is the goldfish, *Carassius auratus*. The bandwidth of hearing is almost as good in the silver perch, but the thresholds (lowest sound level detectable) is poorer in the silver perch than in the goldfish. The poorest hearing is in the plaice, a flatfish, a species that does not have a swim bladder. Both silver perch and goldfish are considered to be hearing “specialists” since they have adaptations that enhance the acoustic coupling between the swim bladder and inner ear. The other species do not have such enhancements and are considered to be hearing “generalists” or “non-specialists.” (Data from Fay, 1988; Ramcharitar and Popper 2004; Ramcharitar et al. 2004)

The specialists whose best hearing is below about 1000 Hz are well adapted to this particular range of frequencies, possibly because of the characteristics of the signals they

<sup>2</sup> It should be noted that “thresholds” are not absolute values and can vary somewhat depending on many factors including motivational state of the animal, and from animal to animal. Indeed, “threshold” is generally defined as the level at which a signal is detected some percent of the time. In many cases, thresholds represent the minimum signal level detected in 50% of the tests. The data presented in figures 4 and 8 generally represent measures for several animals that have been averaged.



produce and use for communication, or the dominant frequencies that are found in the general underwater acoustic environment to which fish listen (Schellart and Popper 1992; Popper et al. 2003). The region of best hearing in the majority of fishes for which there are data available is from 200 Hz up to 800 Hz (reviewed in Fay 1988). Most species, however, are able to detect sounds to well below 200 Hz, and often there is good detection in the low frequency range of sounds. It is likely that as data are accumulated for additional species, investigators will find that more species are able to detect low frequency sounds fairly well.

It is not clear as to why higher frequency hearing arose in fishes, and whether it has any real biological value, particularly since sound produced by most fishes (see below) are below 1 kHz. At the same time, extending the frequency range of hearing generally includes improvement in sensitivity at lower frequencies, and so the wider bandwidth may only be a result of improvement in overall sensitivity.

#### e. *Why Do Fish Hear*

The question often arises as to why fish hear, and how they use sound. While the immediate reaction is to think in terms of communication or of hearing potential predators or prey, more recent thinking has posed the suggestion that fish, as all vertebrates, use sound detection to “view” the “auditory scene” (e.g., Bregman 1990; Fay and Popper 2000). Viewing the auditory scene enables animals (and humans!) to learn about the world around them outside of the range of vision or chemical cues or the range of receivers that receive near-by signals such as touch or even the lateral line.<sup>3</sup> In effect, the visual scene is limited by levels of light, clarity of the environment (e.g., water), the visual field of the eyes, and objects in the environment. In many instances, vision provides only a limited view of the world of an organism, and tells nothing about things at a distance or the general nature of the environment.

In contrast, sound has the potential to provide a good deal of general information about the environment that animals use to get a general “sense” of where they are and what is around them. For fishes, this information might include the presence of objects (that change the sound field), proximity of a coral reef, depth of water, and many other things about the environment. Thus, it has been argued that hearing is likely to have evolved to give the earliest vertebrates an extended “view” of their environment beyond the visual field, thus enhancing survival. Perhaps the next step in the evolution (and use) of hearing was for detection of the sounds produced by predators and prey (e.g., swimming sounds), and then came the evolution of communication and use of communication sounds.

#### f. *Sound Production*

Myrberg (1980) pointed out that members of more than 50 fish families produce some kind of sound using special muscles or other structures that have evolved for this role, or by grinding teeth, rasping spines and fin rays, burping, expelling gas, or gulping air. Sounds are

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<sup>3</sup> The auditory scene is very important to humans and enables us to glean information from great distances, or in dark areas. Part of using the auditory scene is a capability, found in fish as well as humans, of “stream segregation” whereby the organism not only knows of the presence of sound sources in the environment, but can also tell the direction of the sound source and can discriminate it from the sounds produced by other sound sources.

often produced by fish when they are alarmed or presented with noxious stimuli (Myrberg 1981; Zelick et al. 1999). Some of these sounds may involve the swim bladder being used as an underwater resonator. Sounds produced by vibrating the swim bladder may be at a higher frequency (400 Hz) than the sounds produced by moving body parts against one another. The swim bladder drumming muscles are often specialized for rapid contractions (Zelick et al. 1999). Sounds are known to be used in reproductive behavior by a number of fish species, and the current data lead to the suggestion that males are the most active producers. Sound activity often accompanies aggressive behavior in fish, often peaking during the reproductive season. Those benthic fish species that are territorial in nature throughout the year often produce sounds regardless of season, particularly during periods of high-level aggression (Myrberg 1981).

### **3. Underwater Acoustics – A brief overview**

Sound in water follows the same physical principles as sound in air except that the higher speed of sound in water (approximately 1,500 m/sec vs. approximately 500 m/sec in air) results in longer wavelengths. This results in some quantitative differences between sound in air and water, but the physics does not change. A more detailed discussion of underwater acoustics can be found in Kalmijn (1988, 1989) and Rogers and Cox (1988).

A sound wave is a pressure disturbance that travels through a medium, such as water. The energy in the sound wave is associated with changes in local pressure and the associated back-and-forth (vibrational) motions of water “particles.” It is very significant for fish hearing that while the particles in a wave field show no net motion over time (e.g., they do not move from their original position), they do have a directional (vectorial) motion at any instant in time. At distances that are relatively close to the sound source, this particle motion or displacement (these terms are used interchangeably, although they are, in fact, only related mathematically along with acceleration) is a major component of a sound field. At greater distances from the source the primary (but not only) component of the field is pressure.

The decrease in particle motion with distance from the source occurs because that the attenuation of motion is considerably more rapid over distance than is the attenuation of pressure. The distance over which particle motion remains a significant component of the sound field is a function of the frequency of the signal. However, the actual rate of attenuation is also a function of the density of the medium through which the sound is traveling. This means that although a source of sound in air and water will both produce particle motion, the distance over which particle motion has any value is far greater in the denser water medium than in air. As a consequence, whereas particle motion is potentially of great significance for fishes, it is not very important for terrestrial vertebrates since the particle motion field has attenuates to almost nothing within a few centimeters of the source.

The literature on fish bioacoustics often refers to the acoustic near field and acoustic far field (e.g., van Bergeijk 1964; Kalmijn 1988, 1989; Rogers and Cox 1988). In general, particle motion in the acoustic near field results not only from the energy accompanying the acoustic pressure wave, but also from the hydrodynamic flow (or net displacement) of the water resulting from the motion of the sound source. Particle motion in the acoustic far field consists only of motion accompanying the pressure component of the signal. It has been suggested that the transition between near and far field can be described as a function of  $\lambda/2\pi$  (where  $\lambda$  = wavelength). This is approximately one-sixth of a wavelength of the sound frequency. However, the precise distance from the source of this transition point depends on the detailed way the sound source moves (van Bergeijk 1964; Kalmijn 1989). For example, if it is

assumed that the velocity of sound in water is 1,500 m/s,<sup>4</sup> the wave length of a 100-Hz signal would be about 15 m (wavelength = velocity/frequency) and the resultant transition between the near field and far field would be about 2.4 m ( $\lambda/2\pi$ ) from the sound source.

It is critical to note that the near and far field components of sound do not suddenly change at the point of  $\lambda/2\pi$ , and this has been an area of some confusion in the literature, as discussed by a number of investigators (e.g., van Bergeijk 1964; Kalmijn 1988; Rogers and Cox 1988). Some fishes may be sensitive enough to particle displacement to detect it well into the far field. In contrast, other species may be so insensitive to particle motion that they do not even detect it in the outer part of the near field. In considering fish hearing, it is thus very important to keep in mind that both pressure and particle displacement are present in both the near- and far fields, but particle motion predominates in the near field and pressure predominates in the far field.

It is also important to consider how well a particular species is able to detect the particle displacement component of a sound with the ear or with the lateral line. If the fish ear is very sensitive to particle displacement, then it may detect the signal over a considerable distance from the source. If the fish ear is not very sensitive to particle displacement, it will not detect the signal even as far as the transition point. Equally important is the idea that the lateral line detects particle displacement gradients along the length of a fish (Denton and Gray 1989). Because the gradient is greatest in the acoustic near field (because the near field attenuates as the inverse square or cube of the distance,  $r$ , from the source – van Bergeijk 1964; Kalmijn 1988), the primary stimulus appropriate for the lateral line will only be found quite close to the source. Thus, if the fish is detecting sounds with the ears, it may be able to detect particle displacement at some distance from the source.

Another critical aspect of underwater acoustics that is relevant to work with sturgeon, lamprey, salmonids and other fishes that live in at least part of their lives in shallower water, such as rivers and streams, is that low frequency sound propagates very poorly in shallow water since the wavelength is larger than the water depth (Rogers and Cox 1988). Low-frequency sounds (both pressure and particle displacement components) attenuate far more rapidly with distance from the source in shallow than in deep water (Rogers and Cox 1988). As water deepens, progressively lower-frequency sounds can be propagated. Over a rocky bottom, for example, the lowest frequency that will be propagated in water 1 m deep is approximately 300 Hz but the lowest propagation frequency is about 30 Hz in water 10 m deep. Substrate also affects attenuation rates; for a given depth, lower frequencies can be propagated over softer bottoms than over hard bottoms. Because low-frequency propagation is affected strongly by depth, fish in shallow habitats probably detect lower-frequency sounds only from sources that are extremely close to them.

## **4. Bioacoustics of sturgeon and lamprey**

### *i. Lamprey bioacoustics*

Lampreys are considered to be the most “primitive” of extant vertebrates and may represent the most primitive conditions in many aspects of their biology. The ear is unique among extant vertebrates in that it only has two semicircular canals and the otolithic end organ consists of a single continuous epithelial regions with three sections (Fig. 5) (Hoshino 1975; Popper and Hoxter 1987). While there have been some physiological studies of the vestibular response of the lamprey ear (Lowenstein and Osborne 1964; Lowenstein et al. 1968; Lowenstein

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<sup>4</sup> This varies depending on a number of factors including salinity and water temperature.

1970), there have been no studies to determine the responses of the ear to sound or whether lampreys respond to sound behaviorally. While it might be argued that lamprey, as other vertebrates, may use the “auditory scene” to learn about their environment, their behavioral repertoire is generally rather limited, and so it may be possible that sound is not relevant to them at all.

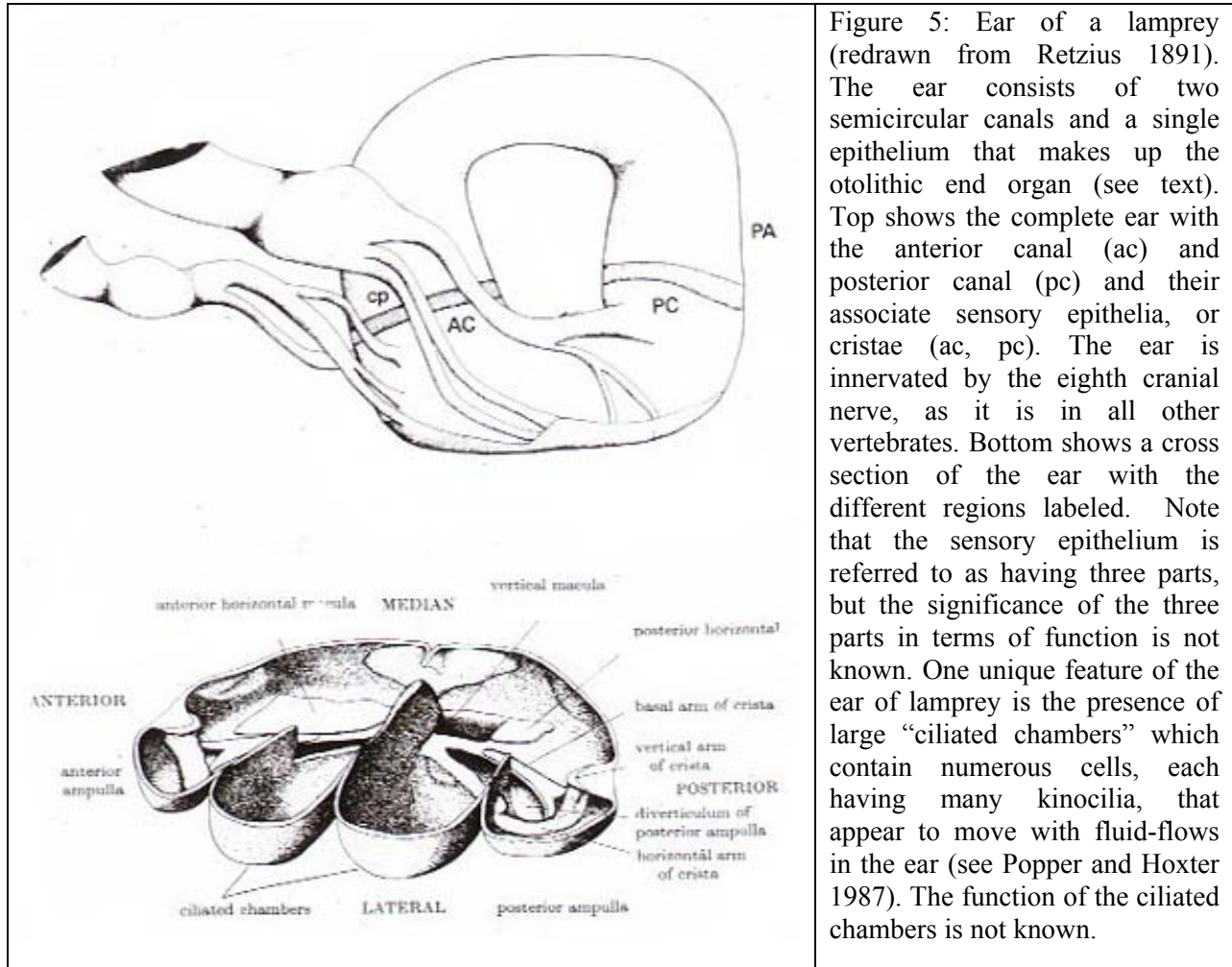


Figure 5: Ear of a lamprey (redrawn from Retzius 1891). The ear consists of two semicircular canals and a single epithelium that makes up the otolithic end organ (see text). Top shows the complete ear with the anterior canal (ac) and posterior canal (pc) and their associate sensory epithelia, or cristae (ac, pc). The ear is innervated by the eighth cranial nerve, as it is in all other vertebrates. Bottom shows a cross section of the ear with the different regions labeled. Note that the sensory epithelium is referred to as having three parts, but the significance of the three parts in terms of function is not known. One unique feature of the ear of lamprey is the presence of large “ciliated chambers” which contain numerous cells, each having many kinocilia, that appear to move with fluid-flows in the ear (see Popper and Hoxter 1987). The function of the ciliated chambers is not known.

*ii. Sturgeon*

The ear of a sturgeon is shown in Figure 6. It is typical of other fishes in having three semicircular canals and their associated cristae and three otolithic organs, the saccule, lagena, and utricle (compare to Figure 1). However, unlike teleost fishes, the saccule and lagena are in a single chamber, although the two epithelia are clearly distinct from one another (Fig. 6). Moreover, unlike teleost fishes which have a single dense calcareous otolith in each end organ, the calcium carbonate material in sturgeon more nearly resembles that of the otoconia that are found in other non-teleost fishes and all other vertebrates (e.g., Carlström 1963). These otoconia are small calcium carbonate crystals embedded in a gelatinous matrix which sits by the sensory epithelium, much as the otolith sits close to the epithelium in teleosts.

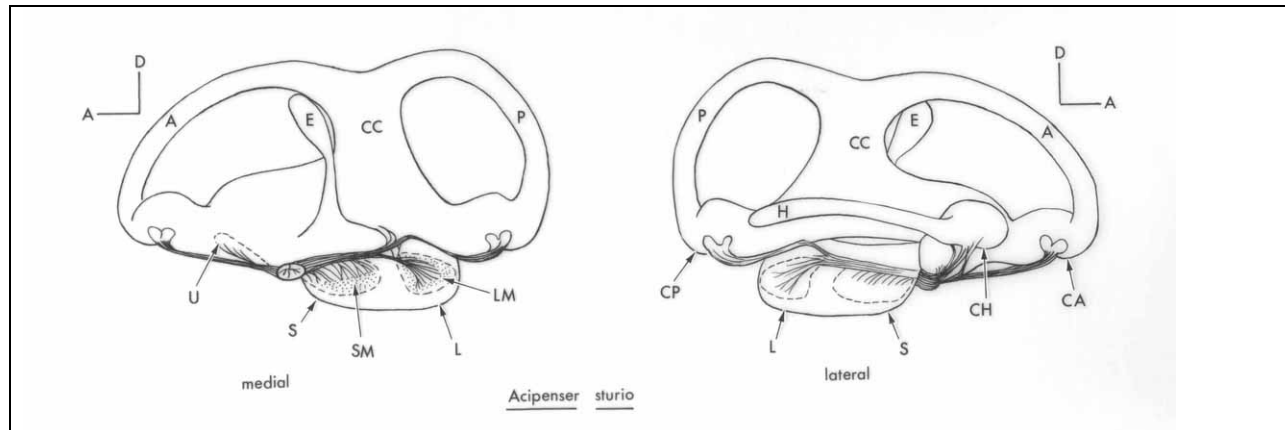


Figure 6. The right ear of a sturgeon, *Acipenser sturio*, redrawn from Retzius 1881. Medial view on the left and lateral view on the right. There are three semicircular canals (Anterior, A; Horizontal, H; Posterior, P) and their associated cristae (CA, CH, CP) and a common canal (CC), along with an endolymphatic duct (E). The utricle (U) is in a distinct pouch whereas the saccule (S) and lagena (L) are in the same pouch. The saccular and lagenar maculae (LM, SM) are not connected to one another, however. (A-anterior; D-dorsal)

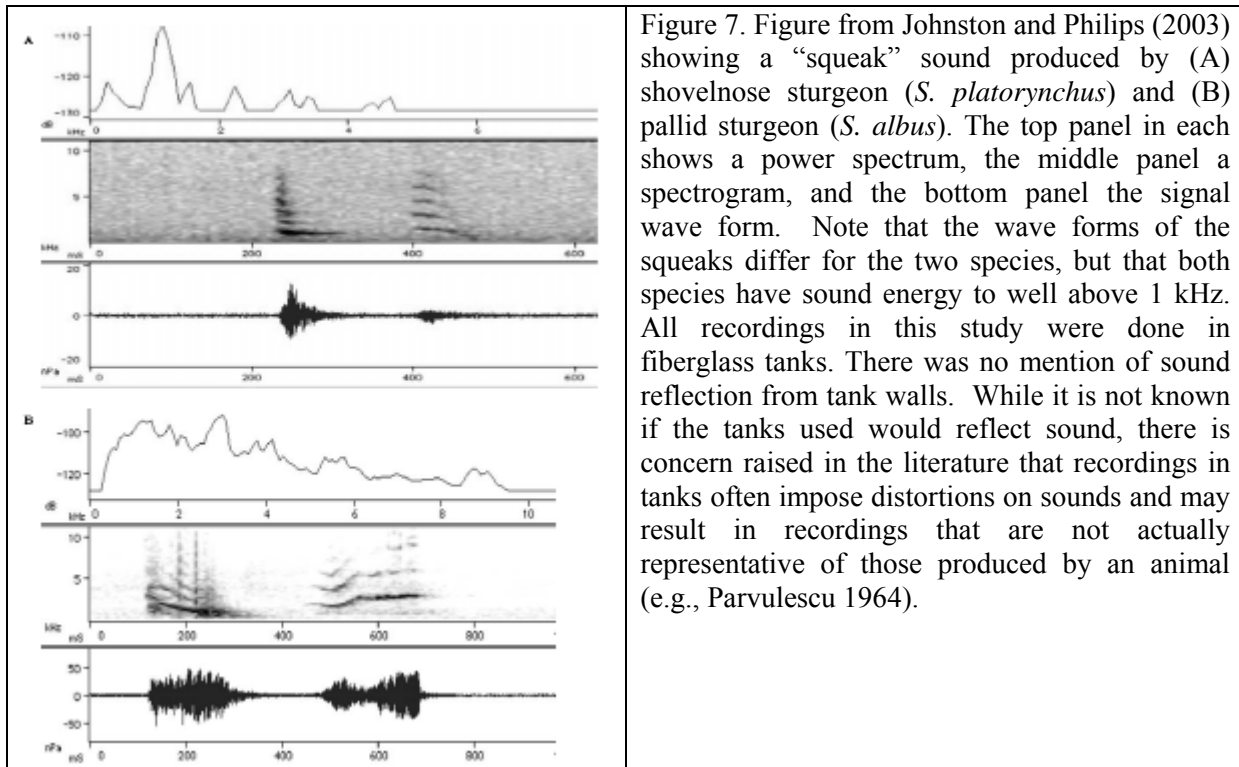
There are few data on hearing in sturgeon, and none in the published literature. Initial studies by Meyer and Popper (unpublished) measuring responses of the ear using physiological methods suggest that a species of *Acipenser* may be able to detect sounds from below 100 Hz to perhaps 1,000 Hz or a bit more. However, thresholds were not determined. The results do suggest, however, that sturgeon should be able to localize sound (determine the direction from which it comes) but again, data are very limited.

While the data on sturgeon sound production is equally limited, a recent paper by Johnston and Phillips (2003) reports that both the *Scaphirhynchus albus* (pallid sturgeon) and *S. platyrhynchus* (shovelnose sturgeon) produce sounds during the breeding season and the same paper reports on unpublished Russian work suggesting that several species of *Acipenser* also make sounds. The mechanism of sound production has not been determined for *Scaphirhynchus*.

Johnston and Phillips (2003) reported that both species of *Scaphirhynchus* had four different types of sounds, each of which different in sound spectrum (see example in Fig. 7). The energy in the signals varied by sound type and species, but in some cases included energy to over 1 kHz. The amplitudes of sounds were not presented nor was there a specific behavioral context reported other than that the sounds took place during the breeding season. Interestingly, the sounds of *S. platyrhynchus* were slightly higher in frequency content than for *S. albus*, with the highest frequencies being around 2 kHz. While based only on the most preliminary hearing data (Meyer and Popper, unpublished), it is of potential interest that much of the energy in the sounds of both sturgeons may be above the range of best hearing (or any hearing) of these species.

While it is of considerable interest and importance that sturgeon produce sounds, and potentially use them in behaviors (though this has not been documented), it would be important to replicate this work under better acoustic conditions. The concern is that the sound recordings were done in tanks, and it is well known that reflections from tank walls and the water surface can significantly distort the sounds recorded (Parvulescu 1964). Moreover, since the fish were

not always in the same part of the tank when sounds were produced, some of the differences in sounds may actually result from differences in tank acoustics rather than differences in the sounds produced by the fish itself.



## 5. Hearing by other species in the Columbia River

Hearing data are available for a number of Columbia River species, or on species closely related to those in the river. These data are shown in Figure 8. While data are not available on hearing by *Ptychoceilus grandis* (pikeminnow), it is an otophysan fish and is likely that its hearing capabilities are similar to that of the goldfish, an otophysan fish for which there are substantial data (Fig. 8). Behavioral and physiological studies of hearing by *Alosa sapidissima* (American shad) demonstrate that this species, as other members of the genus *Alosa*, is able to detect sounds to over 180 kHz (Fig. 8) (Mann et al. 2001). *Alosa* may have the widest hearing range of any organism ever studied, and certainly the widest hearing range of any vertebrate.<sup>5</sup>

The only published data for hearing by any salmonid is for the Atlantic salmon (*Salmo salar*), as shown in Figure 8. While there are no as yet published data for any Pacific salmon of the genus *Oncorhynchus*, soon to be published data<sup>6</sup> for several different species including *O. mykiss* (rainbow trout = steelhead) and *O. tshawytscha* (chinook salmon) suggest that their

<sup>5</sup> Hearing of ultrasound by American shad is thought to be for the detection of echolocating dolphin predators (Mann et al. 1997; Plachta and Popper 2003).

<sup>6</sup> These are studies in the lab of the author of this report. Data for both rainbow trout and Chinook salmon will be included in forthcoming papers that report on the effects of human-generated sounds on fish hearing.

sensitivity may be a bit better than that for *Salmo* and that they may have a somewhat wider hearing bandwidth and be able to detect sounds to over 800 Hz.

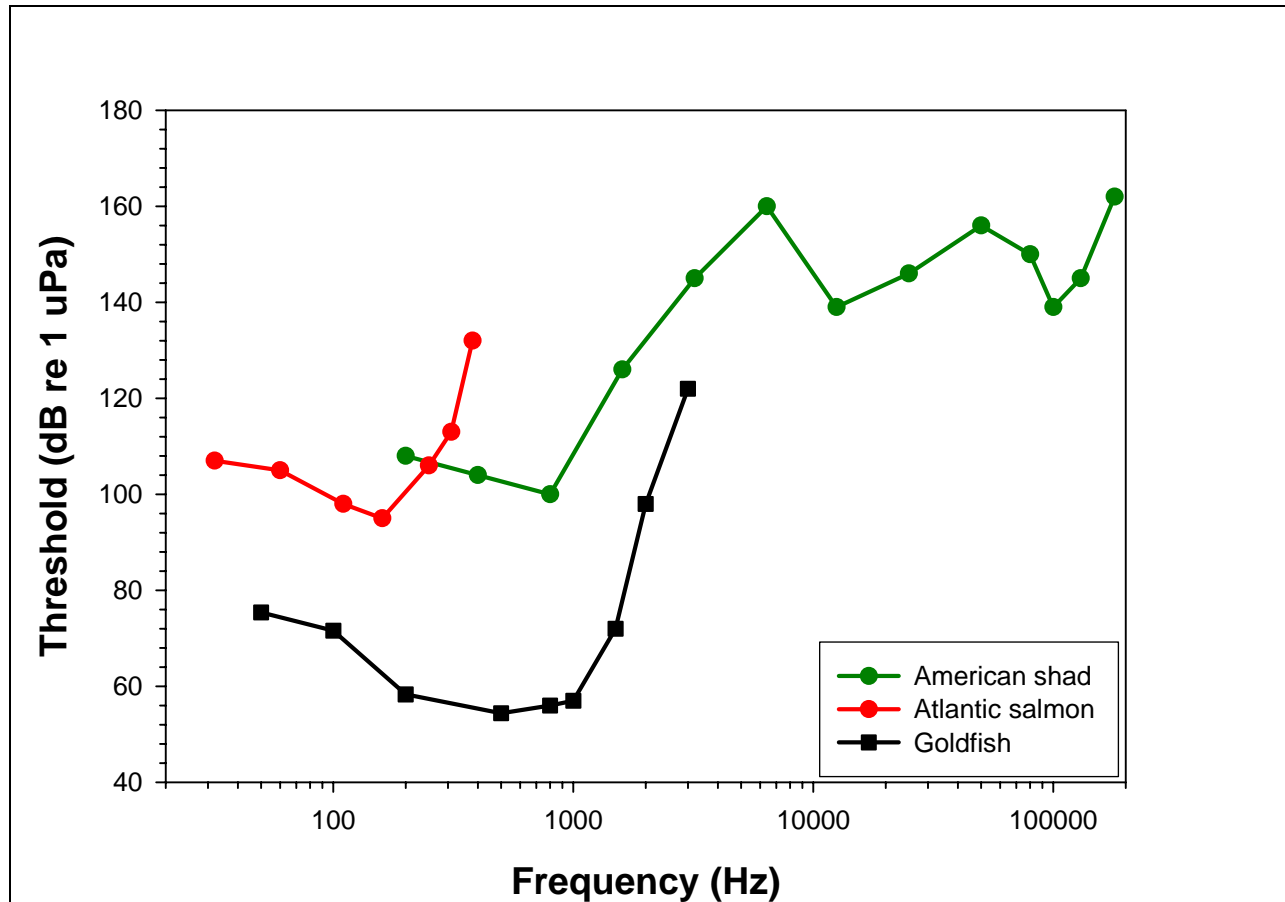


Figure 8: Hearing data for American shad and two other species that are likely to be representative of species in the Columbia river. The hearing capabilities of goldfish are possibly similar to those of the pikeminnow since both species are members of the superorder Otophysi. All of these fishes are known to have excellent hearing due to their having a set of bones, the Weberian ossicles, to acoustically couple the swim bladder to the inner ear. This appears to enhance sensitivity and frequency range of hearing. The data for Atlantic salmon are representative of that for Pacific salmonids, although Pacific species may have a wider hearing bandwidth than does the Atlantic species. (Data from Fay, 1988; Mann et al., 1997)

## 6. Effects of seal-deterrent noise on hearing

### a. Background on effects of human-generated sound on fishes

There is growing concern that human-generated sounds may have an impact on fishes and marine mammals (see reviews in Popper 2003; Popper et al. 2004; Wartzog et al. 2004). If sounds are sufficiently loud to be detected by fish (and within their hearing range), it is possible that effects may range from a minimal change in behavior (e.g., a “startle response” at the onset of sound) to killing of fish. The possible effects also include significant changes in behavior (e.g., animals leaving the location of the sound and thus leaving a breeding or feeding site,

changes in migration routes), temporary hearing loss, masking of biologically relevant sounds so that fish cannot hear predators or prey, permanent hearing loss, and/or damage to non-auditory tissues (also see the review in Hastings and Popper 2005).

Actual data on effects of human-generated sounds are limited, not only in the scope of sounds tested but also in the number of species studied in response to these sounds. Several studies have shown that relatively extended exposure to intense sounds may result in damage to the sensory hair cells of the ear (Enger 1981; Hastings et al. 1996; McCauley et al 2003), while other sounds may result in temporary loss of hearing that recovers over time (e.g., Popper and Clarke 1976; Scholik and Yan 2001, 2002; Smith et al. 2004a, b; Popper et al. 2005; Wysocki and Ladich 2005).

Data on effects of human-generated sound on Columbia River fish are not available. However, a study of the effects of exposure to a seismic air gun at a mean peak sound level of 207 db re 1 $\mu$ Pa (at the fish; Sound Exposure Level of 177 dB re 1  $\mu$ Pa<sup>2</sup>·s) showed no hearing loss in another salmonid, the broad whitefish (*Coregonus nasus*) (Popper et al. 2005). Exposure of rainbow trout (*Oncorhynchus mykiss*) to a continuous tone at a received level of 193 dB re 1  $\mu$ Pa (RMS) only showed a hearing loss at 400 Hz, and there is evidence of recovery post exposure (Popper et al. unpublished).

#### *b. A model to predict hearing loss in fishes*

While the most effective way to determine if a specific sound has any potential to impact a fish is to measure hearing and other behaviors in response to such a signal, this is often difficult and requires special expertise. It will, therefore, be important to ultimately have a “model” upon which to predict the potential for hearing loss. To date, the best such model come out of a number of studies that examined effects of different sound levels on fishes. This model attempts to predict the amount of temporary hearing loss, or temporary threshold shift (TTS) that results from sound exposure.<sup>7</sup>

These studies have led to the hypothesis that the effects of high intensity sound on the hearing capabilities of teleost fishes is related to the level of the stimulus sound above the hearing threshold of the fish (Hastings et al., 1996; Smith et al., 2004a, b).<sup>8</sup> In effect, it has been suggested that noise-induced changes in hearing (temporary threshold shifts) in fish are linearly related to the difference between the sound pressure of the noise and the baseline hearing threshold of the fish. In other words, for a given sound to result in hearing loss, the sound must be a certain intensity above the threshold of the fish for that sound. For example, and based on this model, if a fish has a threshold of 110 dB re 1  $\mu$ Pa at 400 Hz, the sound may have to be xyz<sup>9</sup>

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<sup>7</sup> Temporary threshold shift (TTS) often occurs in humans and other animals after exposure to loud sounds. The result of such exposure is a temporary decrease in hearing sensitivity that recovers over minutes, hours, or days. The rate of recovery depends on many factors that range from the intensity of the exposure sound to the duration of exposure to the health of the ear of the listener, etc. Attendees at loud concerts often experience TTS. Beyond TTS is Permanent Threshold Shift (PTS) in which hearing loss results from actual damage to the sensory receptor cells as a result of extensive over stimulation. These cells die, and hearing is lost permanently.

<sup>8</sup> The relationship of this idea to non-teleost fishes such as sturgeon and lamprey is an open question.

<sup>9</sup> The use of a real number here is inappropriate for several reasons. First, the number is likely to be different for each species, or at least for each group of species. Second, this number is not known for any of the species of



dB above threshold (or  $110+xyz$  dB re 1  $\mu$ Pa) for there to be any threshold shift. If a fish hears well, and the threshold is 70 dB, then a  $70+xyz$  dB re 1  $\mu$ Pa sound may result in threshold shift.

This model has been called the linear threshold shift, or LINTS, hypothesis (Smith et al. 2004b). While the original work on the LINTS hypothesis was based on exposure of fish to continuous noise (Smith et al. 2004a, b), there is evidence that it also applies to impulsive sounds, such as those produced by seismic air guns (Popper et al. 2005).

Most importantly, the LINTS hypothesis predicts a linear relationship between the level of a noise above the threshold of a fish and the amount of TTS. At the same time, it must be kept in mind that the LINTS hypothesis is *only* related to temporary hearing loss and does not predict permanent hearing loss (presumably due to higher intensity or longer-duration sounds) or whether there will be changes in behavior even without hearing loss of any type.

*c. Seal-deterrent and potential effects on fish*

It is of concern as to whether the seal deterrents being used at Bonneville will have any impact on the fish that are migrating past the dam. Whether there is an effect is clearly related to the hearing capabilities of the fish in question, and on the frequency components of the deterrent and whether they are within the hearing range of fish and of sufficient loudness to be detectable.

The data on the spectrum of the signal from typical deterrent devices suggests that virtually all of the sound energy emitted is from 10 kHz and above. As can be seen from Figures 4 and 8, this energy is well above the hearing range of salmonids and other Columbia River species other than the American shad (Fig. 8). Moreover, it is above the hearing range of all other species studied to date (e.g., Fay 1988; Ladich and Popper 2004) other than members of the Alosinae (Mann et al. 2001), as is the American shad.

Furthermore, while data are not available for hearing on either lamprey or sturgeon, it is highly likely that neither group of fishes detects sound to even close to 10 kHz. This suggestion is based on studies of over 100 species of fish where there are specializations that enhance hearing and widen the bandwidth so that fishes detect sounds to upwards of several thousand Hz (see Popper and Coombs 1982; Fay 1988; Popper et al. 2003; Ladich and Popper 2004). In virtually every species studied, there is some specialization, and most notably in the connection between the inner ear and some air bubble, that serves to widen the hearing bandwidth. And, in most of these species, the anatomy of the inner ear shows one or more morphological specializations that are never found hearing generalists (see page 7).

Although we have no data on hearing in lamprey (indeed, or even if they do hear, see page 11), their ear is relatively simple and there is nothing within the structure of the ear or associated structures to suggest any specializations that would make them into anything but a hearing generalist, with maximum hearing to no more than several hundred Hz. Similarly, while

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concern in the Columbia River. Third, any presentation of a real number here could have the effect of being taken as a real value and be used by various individuals to suggest that certain sounds will or will not affect a fish. Finally, it is possible that the actual values will change depending on the nature of the sound, such as whether it is continuous or impulse, etc.

there are only few data on sturgeon (see page 12), the evidence from preliminary studies of hearing and of the ear suggest no structures that would lead to hearing specialization.

The only species potentially impacted by the deterrent devices are American shad. As shown in Figure 8, this species (and other members of the Alosine) are able to detect sounds to over 180 kHz (Mann et al. 2001). Since the range of hearing in the American shad is considerably wider than that for any marine mammal, including sea lions and seals (see Fay 1988), any deterrent device used for marine mammals would be, if of sufficient intensity, audible by American shad.

What is not clear is whether the sounds would cause any change in the behavior of the American shad. The only relevant data are from behavioral studies of American shad in tanks showing that they exhibited little reaction to click-like sounds with maximum energy at about 175 dB re 1  $\mu$ Pa, a directional response away from the sound when it was about 185 dB re 1  $\mu$ Pa, and a highly energetic and “chaotic” response to sounds at about 190 dB re 1  $\mu$ Pa (Plachta and Popper 2003). Plachta and Popper (2003) proposed that the American shad were showing fright responses to sounds that mimicked echolocation sounds of predatory dolphins.

The Plachta and Popper study was done in tanks with captive animals and used frequencies that are well above the hearing range of most seals and sea lions. They did not, however, use sounds that are more reasonable deterrents for seals and sea lions (10-30 kHz) and so it is not known if American shad would react to seal deterrent devices. Moreover, the reactions of the American shad in the Plachta and Popper study were to relatively high intensities, but they might encounter such intensities if they came very close to the deterrent devices.

In effect, while it is not likely that most Columbia River fish would ever hear the deterrent devices if they are above several thousand Hz, it is possible that the devices could be detected by, and alter the behavior of, American shad.

#### *d. Non-auditory effects*

Up to now, the discussion has focused on sounds that the fish might hear. Such sounds could potentially alter hearing. Alternatively, detection of the sounds might alter the behavior of the fish. However, there are other possibilities that a high intensity sound, even if not heard by the fish, could have non-auditory effects, such as damage to the swim bladder or other air bubbles in fishes with such structures, or damage to other tissues.

Predicting such effects are very difficult especially since any related data are exceedingly limited. In particular, all data showing non-auditory effects have been in response to explosives at pressure levels that well exceed any levels from a deterrent device (e.g., Gaspin 1975; Yelverton et al. 1975).<sup>10</sup> (At the same time, it is important to note that devices that produce sounds at levels loud enough to do non-auditory damage to fish would most likely do non-auditory damage to marine mammals as well). In the one study using sound at 193 dB re 1  $\mu$ Pa

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<sup>10</sup> Most studies showing effects of explosives on fishes are in the gray literature.

(received RMS) that involved a complete necropsy and thorough histopathology by a trained pathologist, non-auditory effects were not found (Popper et al. unpublished).

## **7. Future studies on species of interest**

The major gap in being able to predict effects of deterrent devices on fishes is lack of data on detection of the deterrent sounds by the fish of concern. While there are data soon to be published on salmonids, data are needed on hearing in sturgeon and lamprey. If, as hypothesized above, neither species detects sounds in the range of the deterrents, it would be reasonable to assume that such sounds have no auditory or behavioral effects on these species. If they can detect sounds, then it would be of considerable value to do more extensive studies to evaluate the level of effect, such as possible hearing loss and general behavioral responses, of the species to the deterrent sounds.

Initial evaluation of hearing in both species may be accomplished using the auditory evoked potentials (Auditory Brainstem Response or ABR) (see Smith et al. 2004a, b; Popper et al. 2005). This technique provides information on detection of sound by restrained animals and enables a fairly rapid determination of hearing bandwidth and lowest detectable sound.

If it is found that fish can detect a signal using ABR, additional studies might be required (as below for American shad) to determine the nature of any behavioral response. As it has been shown that American shad react differently to different levels of echolocating sounds (see page 18), it is possible that sturgeon and lamprey would also have differences in behavioral responses as sound change.

American shad are able to detect the deterrent sounds if they are of sufficient amplitude (page 18). Thus, more extensive studies are needed on this species to determine if the sound levels encountered have any long-term effect on hearing. Moreover, since we know that American shad show behavioral responses to ultrasonic pulsed sounds, it would be of importance to examine the nature of responses to the deterrent signals. It is possible that the deterrents are not in a frequency range of biological importance to American shad and they may not have a behavioral response to signals until they get to somewhat higher frequencies, similar to those produced by echolocating dolphins. At the same time, since dolphin echolocation signals can range anywhere from somewhat above 10 kHz to over 100 kHz (Au 2000), American shad may actually show behavioral responses to the sounds of the deterrents.

### *Summary of research projects*

1. Determine whether lamprey are able to detect sound and, if so, the frequency range and thresholds for these animals.
2. Measure hearing bandwidth and thresholds for Columbia River sturgeon. (While not likely that sturgeon detect the seal-deterrent, if they do, then analyze changes in behavior to the sound.)

3. Determine behavioral responses of American shad to the seal-deterrent devices to ascertain whether the fish respond behaviorally to the sound and, if so, the nature of the responses. Do at different sound levels since fish behavior may change with signal level.
4. Expose fish of concern to the highest intensity seal-deterrent system and examine non-auditory effects such as on internal organ systems and tissues.

Additional studies that have a broader implication for understanding sturgeon hearing and that might be applicable to work in bodies of water around the U.S.

1. Determine hearing capabilities of several additional sturgeon species that are found in other parts of the U.S.
2. Examine behavioral responses of sturgeon to sounds within their hearing range in order to determine if sound can be used to affect their behavior (keep from plant intakes, etc.)

## 8. Conclusions

Limited, and indirect, data suggest that deterrent systems is not likely to be detected by any fish in the Columbia River other than American shad. This is based on data on hearing sensitivity of a number of Columbia River species or on closely related species.

Issues are different for sturgeon and lamprey. Although very limited morphological data may be used to hypothesize that neither species will be able to detect the sounds of deterrents, it is of considerable importance that data are obtained on hearing in both species.

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