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## Hearing and Acoustic Behavior: Basic and Applied Considerations

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### 1. Introduction

Over the past several decades, two different groups of investigators have been involved with fish bioacoustics but with only marginal interaction and cross-fertilization of findings and ideas between them. One group has been trying to understand the basic biology of fish hearing and vestibular system and lateral line function as well as orientation, sound production, acoustic communication, and the acoustic ecology of fishes (see Fay and Edds-Walton, Chapter 3; Bass and Ladich, Chapter 8; Braun and Grande, Chapter 4; Rogers and Zeddies, Chapter 7). The other group, with more applied needs and interests, has sought to use sound and hydrodynamic phenomena for applications in fisheries science (see Mann, Hawkins, and Jech, Chapter 9). Besides the ubiquitous use of various kinds of sonar in fisheries, a topic that is not considered here (but see Mann, Hawkins, and Jech, Chapter 9), a frequent goal of these applications has been to use sound and other hydromechanical stimuli to influence or control fish behavior. Often the objective is to restrict or otherwise alter the local distributions of the fish in a given industry-influenced environment. Although there have been some attempts to bring the ideas and findings of the two separate groups together (e.g., Popper and Carlson 1998), this has not been done extensively.

The purpose of this chapter is to provide a broad overview of the findings and issues of these two research communities and to provide a context for sharing ideas and efforts. The intent is to provide some insights that may facilitate the work of both groups of investigators and to encourage collaboration between them.

The chapter is divided into three parts. The first considers some basic aspects of fish hearing that are most germane to applied issues that are discussed later in the chapter. For a more detailed discussion of the fish auditory system, readers are referred to other chapters in this volume as well as to recent reviews (e.g., Popper and Fay 1999; Popper et al. 2003; Ladich and Popper 2004). Detailed discussions of fish hearing capabilities are presented in Fay and Megela Simmons (1999) and of fish sound localization in Fay (2005). The second part of the chapter considers the efforts that have been made to use sound and other

hydromechanical sensory stimuli, including flows and turbulence, to control local fish distributions, primarily to reduce the harm of human activities for fishes. This material has been reviewed in greater detail by Popper and Carlson (1998). Finally, the chapter addresses the ways in which anthropogenic sounds from human activities ranging from shipping and construction noise to mineral exploration and seismic geology studies, offshore wind farms, and sonar may affect fish.

## 2. Basic Mechanosensory Systems and Capabilities of Fishes

Fishes have evolved a wide array of sensory systems and behavioral responses with which they perceive and respond to their environments (see discussions of the aquatic sensory environment in chapters in Atema et al. 1988 and in Collin and Marshall 2003). The mechanosensory systems of fishes include (1) the hearing of sound pressure oscillations through the inner ears; (2) orientation and body motion sensation (the vestibular system), which is also mediated by the inner ears; and (3) detection of hydromechanical stimulation near the fish that is mediated by the lateral line. The lateral line system consists of an array of neuromasts composed of hair cells and found within pored, bony canals and on the epithelium of the head, trunk, and tail (Coombs et al. 1988; Coombs and Montgomery 1999). It senses local water motions and differential pressures, which are induced by water flows (referred to as “svenning” by Platt et al. 1989 in honor of the extensive and insightful work on lateral line structure and function done by Professor Sven Dijkgraaf [e.g., Dijkgraaf 1963, 1989]).

The evolutionary and functional relationships that relate the auditory, vestibular, and lateral line systems are beyond the scope of this chapter (but see Popper et al. 2003; Ladich and Popper 2004). These sensory capabilities enable a wide variety of life functions including prey and predator location, group cohesion and coordination, mate attraction and courtship, and, perhaps most fundamentally, a general awareness of the environment and things in it (Fay and Popper 2000; Fay 2008).

### *2.1 Origin of Hearing Capabilities in Fish*

Hearing has been studied in a number of fishes and has been reviewed extensively (e.g., Fay 1988; Popper and Fay 1993; Fay and Megela Simmons 1999; Fay and Popper 1999; Popper et al. 2003; Ladich and Popper 2004). One of the fundamental questions to ask with regard to hearing in fish (as in all other vertebrates) is why hearing has evolved. Clearly, hearing is used by many species for interspecific communication (e.g., Myrberg and Spires 1980; Zelick et al. 1999). However, more recent analysis leads to the suggestion that rather than having evolved for acoustic communication per se, hearing evolved to provide fish (and other vertebrates and, perhaps, invertebrates) with a “sense” of their environment that extends a considerable distance from the animal. In effect,

because visual signals are only effective in adequate light and in directions in which the eye is looking and chemical signals do not carry for great distances with any speed or directional characteristics, sound has the potential to provide fish with information about the environment from considerable distances, at high rates of speed, and with significant directional information (Fay and Popper 2000; Fay 2008). In water, turbidity presents an additional problem for light sensing and signaling, and it may be suggested that the selective pressures that resulted in the evolution of hearing were for the detection of distant predators and prey as well as for detection of objects in the environment, the location of coral reefs, and numerous other things (Fay and Popper 2000; Fay 2008).

This overview of the acoustic environment has been called the “auditory scene” (Bregman 1990). The auditory scene provides the animal with a perceptual “world” that extends far beyond other senses, thereby increasing survival chances. Loss of hearing sensitivity, as might occur in a noisy environment (e.g., from human-generated masking sounds), can potentially have a significant effect on the survival of fish and their populations because they would lose the broader perspective of the environment.

In considering the evolution of vertebrate hearing, Fay and Popper (2000) argued that in order for any animal to make use of its “auditory scene,” it must also be able to do “stream segregation,” which is the ability to discriminate between sounds that are and are not of biological relevance (see also Fay 2008). To do stream segregation, all vertebrates must have certain basic auditory functions including the ability to discriminate between frequency and intensity of sounds, determine the direction of a sound source, and detect signals in the presence of other sounds that might otherwise interfere with detection (e.g., “masking” sounds).

## 2.2 *Hearing Capabilities*

Fish demonstrate all of the capabilities needed for use of the auditory scene including the ability to discriminate between signals and determine sound source direction (see reviews by Fay and Megela Simmons 1999; Fay 2005). Measures of hearing sensitivity (see Fig. 2.1) have demonstrated that fish of most species hear over a relatively narrow range of frequencies. Generally, this ranges from 50 Hz or below to 1,000 or 1,500 Hz. Sensitivity at these frequencies is often not very good, and there is considerable variation in hearing sensitivity in different species. As pointed out by Ladich and Popper (2004), there is no known clear correlation between the taxonomic position of species and hearing capabilities, and too little is known about the hearing capabilities in different species to be able to correlate hearing capabilities in different environments or ecological niches. Moreover, there is considerable variation in ear structure and hearing capabilities within some taxonomic groups. For example, Coombs and Popper (1979) showed that two different genera of squirrelfish have very different ear structures and hearing capabilities despite the two species living sympatrically and using similar sounds for communication. As a consequence, without sufficient data, it is

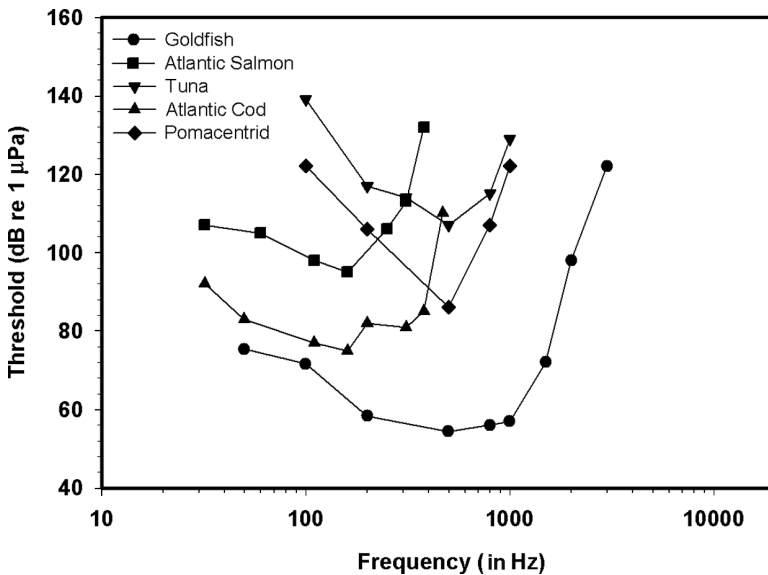


FIGURE 2.1. Auditory thresholds from a select group of teleost fishes. (All data from Fay 1988.)

often not realistic to generalize about hearing capabilities even between closely related taxa.

At the same time, as shown in Fig. 2.1, there are some species, referred to as hearing “specialists” as opposed to the aforementioned hearing “generalists,” that are able to detect sounds to greater than 3,000 Hz. Moreover, even at the lower frequencies that both types of fish can hear, the specialists can detect lower intensity sounds than the generalists so that the specialists hear better in the frequency range that they share with the generalists and also hear over a wider frequency range.

### 2.2.1 Hearing Specialists versus Generalists

The hearing specialists, which include species as diverse as otophysans (goldfish, carp, catfish), mormyrids (elephantfishes), and possibly myctophids (deep-sea lantern fishes), all have specializations peripheral to the ear that mechanically couple the motion of the swim bladder (or other air bubble), which vibrates in response to pressure stimulation, directly to the inner ear. Because a gas bubble expands and contracts in response to pressure signals much more than does water or fish tissue, the air bubble converts pressure to motion and thereby stimulates the auditory end organs of the inner ears. In hearing specialists, this motion is coupled directly to the ear with minimal loss of energy. In contrast, hearing generalists often have a swim bladder, but they do not have a coupling between the gas bubble and the ear. Thus, much less of the pressure-generated motion of the swim bladder gets to the ear than is the case in the specialists. How

much, if any, pressure-generated motion gets to the ear in the generalists is not known, although there is reason to believe that there may be some swim bladder contributions to hearing in at least some generalists.

Specializations to enhance hearing vary widely among different hearing specialist species. The best-known specializations are the Weberian ossicles in the otophysan fishes (e.g., goldfish, catfish, carp, and relatives). This series of bones, derived from parts of vertebrae, directly connects the swim bladder to the fluids of the inner ear, thereby coupling swim bladder motions to the ear. Other specialist species have anterior projections from the swim bladder that terminate near or are directly in contact with the inner ear, thereby bringing pressure-generated motions to the ear without intervening structures. Finally, there are fishes such as mormyrids (elephantfishes) and clupeids (herrings, anchovies, shads, and relatives) in which there is an ancillary bubble of air near or in contact with the ear.

### 2.2.2 Infrasound and Ultrasound

Although hearing specialists generally hear to no more than 3–5 kHz, recent studies show that fish in one clupeid subfamily (the Alosinae or the anadromous herrings and menhadens) can detect sounds well into the ultrasonic range (Kynard and O'Leary 1990; Mann et al. 1997, 2001). As discussed in Section 3.8, there is evidence suggesting that the evolutionary origin of ultrasound detection may have enabled these animals to detect and avoid dolphin predators.

Finally, a number of species are able to detect sounds into the infrasonic range (below the human lower range of about 20 Hz; e.g., Sand and Karlsen 1986; Sand and Karlsen 2000; Sand et al. 2000, 2001; Popper et al. 2003). Although there has not been an extensive analysis of infrasound detection, this has been demonstrated in species as diverse as Atlantic salmon (*Salmo salar*), Atlantic cod (*Gadus morhua*), and European silver eels (*Anguilla anguilla*) (Sand et al. 2000). In all cases, however, infrasound detection seems to primarily take place when the fish is relatively near the sound source.

## 2.3 Structure and Function of the Inner Ear

The inner ear of sharks and bony fishes (Fig. 2.2) consists of three semicircular canals, three otolith organs (sacculae, lagenae, and utricle), and, in some species, a relatively diminutive macula (or papilla) neglecta (see Popper et al. 2003 for a detailed description of fish ears).

The transducing elements of the ear, or the cells that convert mechanical energy into a signal that can stimulate the nervous system, are the sensory hair cells. Each sensory hair cell has a typical cell body as well as an apically located ciliary bundle made up of a single kinocilium and many stereocilia (or stereovilli; see Fig. 2.3). Bending of the ciliary bundle by mechanical energy results in a cascade of intracellular events that leads to the release of a neurotransmitter and the stimulation of the innervating eighth cranial nerve (e.g., Hudspeth 1985, 1997).

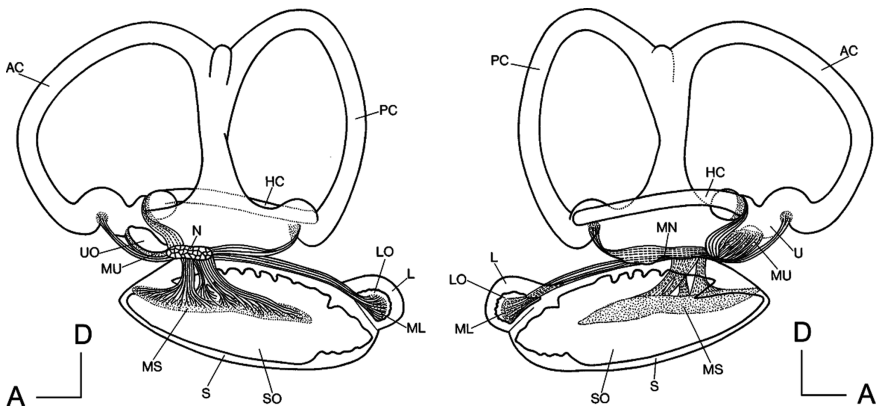


FIGURE 2.2. Inner ear of a perch (from Ladich and Popper 2004). Medial view on the left and lateral view on the right. AC, HC, PC, anterior, horizontal, and posterior semicircular canals; L, lagena; LO, lagena otolith; MN, macula (papilla) neglecta; MU, utricular epithelium; MS, saccular epithelium; N, eighth cranial nerve; S, saccule; SO, saccular otolith; UO, utricular otolith.



FIGURE 2.3. Ciliary bundles from a teleost fish. The apical surface of each sensory cell has a group of cilia, the longest of which is the kinocilium. The longest of the graded stereocilia (or stereovilli) is closest to the kinocilium. Each of the sensory cells is surrounded by support cells that have apical microvilli. Note that all of the ciliary bundles are oriented so that the kinocilium is to the upper right in the figure. That is, they are all oriented in the same direction.

The three semicircular canals are oriented in three mutually perpendicular planes and each has a sensory region or ampulla at its base. Movement of fluids in the canal, resulting from angular acceleration of the head, produces bending of a gelatinous cupula in which are embedded ciliary bundles from sensory hair cells. Cupula motion results in bending of the ciliary bundles that results in neural activity and the detection of angular acceleration (Platt 1983; Popper et al. 2003).

The otolithic end organs each have an epithelium composed of sensory and nonsensory cells (Fig. 2.3). The sensory cells number in the thousands to hundreds of thousands depending on the species and the size of the fish (Lombarte and Popper 1994). The sensory epithelium lies close to a dense calcareous otolith and is separated from the otolith by a thin otolithic membrane that mechanically couples them together (Popper et al. 2003, 2005a).

Hair cell stimulation results from the relative motion between the sensory epithelium and the otolith. In effect, the epithelium and otolith move at different amplitudes and phases because of their different densities.

Fish otolithic end organs are likely to have two functions. One is to determine head position relative to gravity as in terrestrial vertebrates (see Platt 1983 for a review). The saccule, lagena, and, very likely, the utricle are also involved in sound detection (e.g., Popper et al. 2003). The precise role of each end organ is not known, and the relative contributions of each to sound detection may vary in different species. For example, in the otophysan fishes, the connection between the swim bladder and saccule may result in that end organ being the primary detector of sound pressure (Rogers and Zeddies, Chapter 7), whereas in clupeiform fishes, the utricle may be the major sound detection end organ, at least for higher frequency sounds (e.g., Mann et al. 2001; Higgs et al. 2004; Plachta et al. 2004).

### 2.3.1 Sensory Cell Organization on the Otolithic End Organs

A significant feature of the otolithic end organs is that the sensory cells are organized into “orientation groups” based on the position of the eccentrically placed kinocilium (Fig. 2.3). All ciliary bundles in each region on the epithelium are oriented with the kinocilium in the same direction. The morphological polarization is accompanied by a physiological polarization whereby bending of the bundle results in hair cell responses that are graded and proportional to the vector component in the axis of best physiological sensitivity (Hudspeth 1985; Lu and Popper 2001). Thus, each sensory cell is potentially capable of measuring the direction of the particle motion of a sound source.

On discovery of this orientation pattern (e.g., Dale 1976; Popper 1976), it was suggested that this grouping of like-oriented hair cells may provide fishes with an ability to determine the direction of the particle motion of a sound source and thus provide information about sound source direction (Popper et al. 2003; Fay 2005; Rogers and Zeddies, Chapter 7).

Recent physiological data support this hypothesis (e.g., Lu et al. 1996; Fay and Edds-Walton 1997; Edds-Walton 1998; Lu and Popper 2001). The assumption is

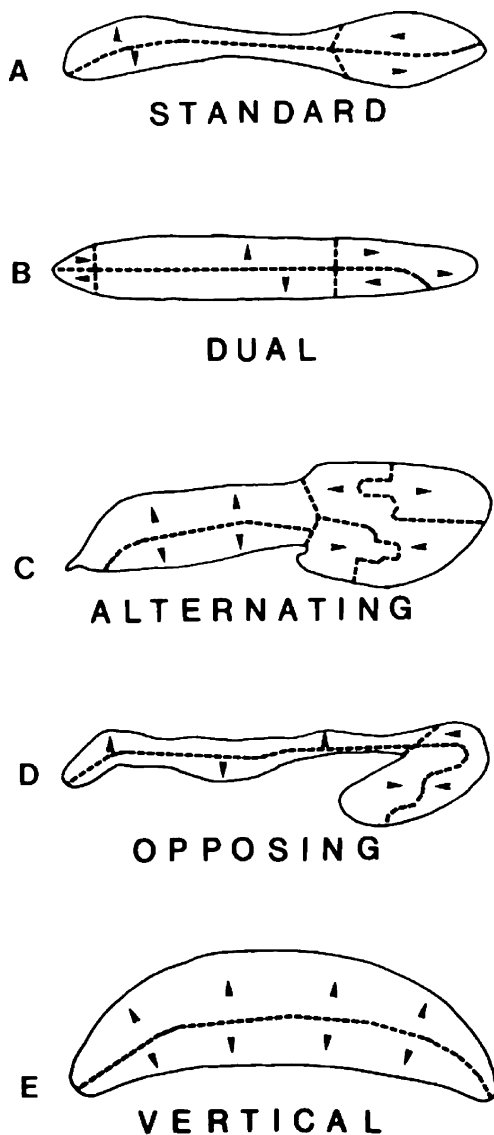


FIGURE 2.4. Saccular hair cell orientation patterns from different fishes. Anterior is to the right and dorsal to the left. The dotted lines are the areas of what is generally an abrupt transition in orientation between directions. The arrowheads indicate the direction of the kinocilia on the hair cells in each region of the epithelium (e.g., the tip of the arrow would be to the upper right in Fig. 2.3). The "Standard" pattern is typically found in fishes that are hearing generalists; the other patterns are most often found in hearing specialists. There is no taxonomic relationship for these patterns. The same basic pattern can be found in taxonomically diverse fishes. For example, the vertical pattern, which includes no rostrally and caudally oriented cells, is found in all otophysans



that each neuron from the saccule (the only end organ studied to date) innervates only hair cells oriented in a particular direction (Lu and Popper 2001) and that this information is carried to the central nervous system (CNS) where the directional response properties of neurons from sensory cells with different orientations are compared (Edds-Walton 1998) and the direction “calculated” (Popper et al. 1988; Rogers et al. 1988).

### 2.3.2 Comparative Ears

There is striking diversity in the inner ear structures of different fish species (Fig. 2.4) (e.g., Popper et al. 2003; Ladich and Popper 2004), yet the functional significance of the diversity is not known and there is only the most limited understanding of any correlations between ear structure and function (Schellart and Popper 1992; Ladich and Popper 2004).

There is, however, an apparent correlation between the general orientation of the sensory hair cells on the saccular epithelium and whether fishes are hearing generalists or specialists (Fig. 2.4). The hearing specialists show more “complex” saccular hair cell orientation patterns than generalists, which often have only the “standard” saccular pattern (Fig. 2.4) (Popper and Coombs 1982; Popper et al. 2003). The diversity in saccular hair cell orientation pattern in hearing specialists appears to be correlated, at least to some degree, with the acoustic coupling between the swim bladder and the saccule. And, most significantly, the diversity in saccular hair cell orientation patterns associated with hearing specializations shows functional convergence across taxonomically diverse species.

The other aspects of inner ear structure that show substantial diversity but with unknown function are the size and shape of the otoliths and, particularly, of the saccular otolith (Popper et al. 2005a). Popper et al. (2005a) pointed out that very little is known about the specific function of the otoliths other than they provide a body with a different density than the rest of the fish for stimulation of the sensory cells (see also Rogers and Zeddies, Chapter 7). However, it has been suggested that the very diverse shapes of the otoliths may be related to hearing and/or vestibular function of the ear (e.g., Popper et al. 2003). Moreover, there are differences in the percentage of area of the sensory epithelium of the saccule that is covered by the otolith. Whereas in most species studied, the otolith covers the whole epithelium and may even extend beyond it, there are species such as some myctophids and other deep-sea fishes in which the otolith may only



FIGURE 2.4. (Continued) (goldfish, catfish, and relatives) and in the elephantfishes (mormyrids). The alternating pattern is found in fishes as diverse as many eels and deep-sea gadids. (From Popper and Coombs 1982.)

cover half the epithelium. In these fishes, the only connection to the rest of the epithelium is through the otolith membrane, which lies between the otolith and epithelium and extends out to the uncovered areas (Popper 1980; Popper et al. 2005a).

## *2.4 The Vestibular System*

The vestibular senses mediate body orientation, balance, and accelerations (e.g., Platt 1983; Popper et al. 2003) and thus play a major role in fish behavior. Although a detailed discussion of the vestibular system is beyond the scope of this chapter, it is important to note that the sensory receptors of the inner ear that mediate the vestibular senses involve the same kind of sensory hair cells found in the otolithic end organs and the lateral line. Moreover, the receptor organs involved in the vestibular senses in fishes not only include those of the semicircular canals but also of the three otolithic end organs. Indeed, nothing is known about how the nervous system of fish separates vestibular from auditory signals from the otolithic end organs. It is possible that there are different populations of sensory cells on the end organs that mediate the different senses or the difference may be in the frequency of the stimulation, with very low frequency signals being sent to the vestibular part of the brain while higher frequency signals are sent other places.

## **3. Applied Aspects of Fish Bioacoustics**

There are a number of different issues to be considered when discussing applied fish bioacoustics. The first is the use of fish-produced sounds and hydrodynamic disturbances to assay fish distribution, abundance, and behavior. This is discussed in detail in Chapter 9 by Mann, Hawkins, and Jech and involves the use of a transducer to detect and record fish-produced sounds or hydrodynamic phenomena. This “listening-to-fish” aspect of acoustic biology is sometimes called “passive” acoustics to distinguish it from the “active” acoustics fields of fisheries acoustics (sonar, which is used to sample fish abundance and distribution; also discussed in Chapter 9) and from acoustic tagging and telemetry (which permit remote tracking of individual fish). Because these “active” acoustics categories do not involve the hearing, lateral line, or vestibular systems of the fish, they are outside the present discussion. Instead, the discussion of “active” bioacoustics in this chapter focuses on the use of anthropogenic sounds and water motions to affect fish behavior, usually to influence local distribution.

### *3.1 Use of Flows and Turbulence to Control Fish Distribution*

A potentially important applied use of sound involves using sound or water motion to manipulate local fish distributions. This manipulation might be for

a variety of uses including aggregating fish for harvest in aquaculture environments, capture of wild fish, bycatch reduction in commercial fishing operations, fish protection at industrial sites, and the exclusion of unwanted or invasive fishes from some waterways. This approach involves the development and deployment of sound, flow, or turbulence-producing systems to attract fish (perhaps toward a fishway or other fish bypass system) or repel them (e.g., away from a turbine or cooling-water intake). The production of sound stimuli can be fairly straightforward for reasonably high-frequency sound but is far more challenging for lower frequencies. The generation of sound and hydrodynamic flows is unavoidable in the operation of industrial water management facilities. Understanding the effects of natural or human-caused flow patterns and sound in attracting or repelling fish as well as the use of designed stimuli to direct fish movements is what is of interest here.

### *3.2 Control Local Fish Distributions*

Wherever humans divert large volumes of water for industrial, municipal, or other uses, there are potential costs to fish populations. The most obvious costs are in entrainment or impingement of fish, including eggs and larvae. Entrainment refers to drawing fish into a water withdrawal route such as a cooling-water intake. In contrast, impingement refers to fish striking or being trapped by flow against screens or other engineered structures. Entrainment and impingement are important sources of environmental impact at many industrial water facilities. The need to improve facility design and operations to reduce fish losses by impingement and entrainment has long been recognized (Schuler and Larson 1975; Hocutt 1980), and methods to resolve these problems have often involved the use of sound to control the movement of fish away from areas where they could be impinged or entrained.

Any structure in an aquatic environment may attract fish by providing cover, shade, aggregated prey, artificial light, or other stimuli (Love et al. 2000; Dempster and Kingsford 2003). Engineered structures inevitably produce mechanosensory and other stimuli that potentially are detectable by fish. Some industrial sites, such as large hydropower dams, can be very noisy across wide frequency ranges, including those detectable by most species of fish, and also involve powerful and complex hydrodynamic flows that can move fish directly into areas of danger (e.g., turbines).

The effects of ambient noise, in terms of either sound pressure or hydrodynamic flow, on the hearing, vestibular, and lateral line systems are little studied. It is likely that a large industrial project, like a lock-and-dam project or a cooling-water intake, is rich in many kinds of acoustic signals that may stimulate, interfere with, overwhelm, or even damage a fish's orientation, navigation, and locomotion systems. Mitigation of some applications may simply involve fish exclusion from an avoidable hazard such as a water intake. Where fish passage is required, such as populations migrating through the world's increasingly dammed river systems, and the best available passage route is a small proportion of the

total project water passage, as in the case with a hydropower dam, it is important to provide opportunities for migrants to discover, enter, and take the more benign passage routes (Rainey 1997).

Besides making systemwide changes in watersheds (Freeman et al. 2001) and violating the interconnected nature of river systems (Dynesius and Nilsson 1994; Pringle et al. 2000), engineered structures such as locks and dams can interfere with fish migrations (Dadswell et al. 1987; McAllister et al. 2000; Dixon 2003) that may be requisite for the fish's life cycles (Dadswell et al. 1987; Dixon 2003; Limburg and Waldman 2003). Sometimes even small overflow dams can impede or stop fish migration (Beasley and Hightower 2000; Zigler et al. 2004). Conversely, some engineered changes in waterways have opened new migration routes to invasive fishes (Fuller et al. 1999; Chick and Pegg 2001) that can cause unpredictable perturbations of aquatic ecosystems. In many cases, on highly regulated rivers such as the Columbia-Snake River System in the US Pacific Northwest, juvenile fish may encounter many dams in their migration to the sea and cumulative stresses may be important (Budy et al. 2002).

Construction projects in or near water bodies that involve blasting or pile or pipe driving as well as offshore seismic exploration (e.g., Engås et al. 1996; Slotte et al. 2004) may stress, injure, or kill fish. The impacts of anthropogenic sound on fish and fisheries are discussed in Section 4. Here the point is that sometimes, where local fish distribution presents particular challenges, it would be desirable to exclude fish from the vicinity of job sites, facilities, or dangerous passage routes. In these cases, bioacoustics may sometimes be useful for fish exclusion or protection. Being able to either attract or repel fish, especially if it were reasonably inexpensive and reliable, would have a number of uses to benefit both industry and fish conservation at industrial and other water management sites. However, although this use of sound still appears to hold potential, there has been almost no data in the peer-reviewed literature that point to any successes in achieving these goals other than for the use of ultrasonic sound (see Section 3.8). Indeed, data in the peer-reviewed and gray literature are often highly equivocal, and reported "successes" in using sound to control fish are very limited and in prescribed environments and may not work under other, even slightly different, conditions. Moreover, even when there may be successes, data are often limited to very few species and limited age classes within those species. As a consequence, applicability to animals of different ages, maturity, etc. is not known.

### *3.3 Mechanosensory Stimuli for Fish Control*

It is reasonable to consider using sound or water motions to control fish distributions in engineered environments. Fish of all the species tested so far can detect both sound pressure and hydrodynamic stimuli. The interest in having stimulus systems for control of free-ranging fish goes back several decades (reviewed in Popper and Carlson 1998). Early views were rather simplistic "command and control" models that lacked appreciation for the complexity, mutability,

and unpredictability of the aquatic environment and the fish response to it. The response of a fish or any animal to stimuli depends on many physiological, temporal, and environmental factors (Schilt and Norris 1997). Some of these may be evident or, at least, measurable (sound, current, light, turbidity, temperature), but others (fish motivation and condition, hunger, predation threat) may be less accessible. The response may be specific not only to fish species but also to life stage, time of day and year, presence of predators, and countless other known and unknown variables. Perhaps because stimuli are presented against different backgrounds in different places, stimulus efficacy may be site specific. Habituation to a stimulus is important, especially with resident populations but also with migrants, which may be near a given site for hours or days.

There are a number of approaches to improve fishing efficiency and reducing bycatch. These are sensory-based aspects of methods for both small scale (artisanal) and industrial fisheries that use fish response to stimuli (Parrish 1999), and mechanosensory responses may sometimes be involved in modern fish capture (Wardle 1993). However, acoustic aspects of fishing gear, such as sounds made by fish trawls, have not been extensively studied. Orbach (1977) briefly discusses the use of small explosive charges and even the practice of banging on the side of a tuna seiner to prevent the escape of fish before the purse seine can be closed. Finneran et al. (2000) have suggested that wild yellowfin tuna (*Thunnus albacares*) might be attracted for harvest at sea with the sounds produced by the dolphin schools with which they travel, although it is not clear that the sounds produced by the dolphins are in the frequency range detectable by tuna (Iversen 1967, 1969). Clearly, increased understanding of fish sensory response might be used to make fish capture methods more efficient. Still, Parrish (1999) argued that using behavioral and sensory research to increase catches requires caution and may not be sustainable. Indeed, there is evidence that the sounds of fishing boats and trawls may actually result in fish moving away, thereby decreasing catches (reviewed in Mitson 1995; Mitson and Knudsen 2003). Thus, knowledge of fish hearing could conceivably be used to increase gear specificity so as to increase catches or to reduce bycatch of nontarget fish (Broadhurst et al. 1999).

### 3.4 Fish Handling in Aquaculture

Relatively little has been done in the aquaculture to use sound to control fish behavior, although there was early interest in using sound to aggregate fish (Hashimoto and Maniwa 1967; Chapman 1976). Willis et al. (2002) experimented with training triploid grass carp (*Ctenopharygodon idella*) to aggregate at a sound source so that they can be retrieved from water bodies where they have been put for weed control. Parrish's (1999) warnings regarding the use of behavioral science for fisheries applications should also apply to fish farming.

At the same time, aquaculture facilities can be relatively noisy environments as a result of the use of pumps and other devices. Little is known about whether such sounds have any impact on fish, although one study (Wysocki et al. 2007) suggests that the sounds imposed by pumps and other aquaculture equipment

are below the levels that have any effect on the growth and hearing of rainbow trout. Still, these sounds may occur, the effects could range from increasing stress levels to damage to hearing, and the results may range from no effect to decreased growth and/or survival (e.g., Wysocki et al. 2006).

### *3.5 Control of Invasive Fishes*

The use of sound to control invasive fishes is largely unexplored, although there may be an increasing need as more invasive species enter new environments. As more invasive fishes are introduced across wider new ranges, they will increasingly interfere with and jeopardize native species, communities, and ecosystems. Recently, fisheries managers in North America have been faced with a growing number of invasive and sometimes very prolific fish species (Fuller et al. 1999), which can cause severe ecological problems including extinction of native species (Lassuy 1995). An especially vexing problem involves several species of very large and prolific Asian carp that were introduced into aquaculture facilities and have escaped and spread through the major river systems of the middle of North America (Chick and Pegg 2001) and that now threaten to invade the Great Lakes. Acoustic and hydrodynamic barriers offer potential tools to control these (Taylor et al. 2005) and other unwanted species, but they remain largely untested and the work that has been done is sometimes of questionable quality and often remains outside the peer-reviewed literature. Unlike fish protection wherein any reduction in stress, delay, or mortality is beneficial, the barrier that protects a waterway from a robust, prolific, and harmful invader must be very nearly perfect because even one gravid female getting through can, as a worse case, lead to a successful invasion and establishment of a population beyond the barrier.

### *3.6 Fish Exclusion at Polluted or Construction Sites*

The use of sound to potentially provide exclusion of fish from polluted sites or construction remains largely unrealized. In the case of pollution emergencies such as chemical spills, it might be impractical to mobilize a behavioral control system, even if one were available, in time to actually protect fish. But at construction sites, where drilling, blasting, pile driving, or other activities may be predicted to be problematic, an effective acoustic deterrent might provide at least a partial solution.

### *3.7 Fish Protection and Passage at Hydropower Dams and Other Industrial Sites*

There is a history of successful and unsuccessful attempts at improving fish protection and passage at industrial facilities throughout the world (Haymes and Patrick 1986; Fletcher 1990; Jungwirth et al. 1998; Coutant 2001; Pavlov et al.

2002). In many cases, these efforts capitalize on the natural responses of fish to signals in the environment (e.g., natural sounds).

Efforts toward developing acoustic-based tools to enhance fish passage and protection go back at least to the early 1950s in the United States (Burner and Moore 1953). Using fish mechanosensory (ear- and lateral line-mediated) behavioral responses to direct fish movement is especially appealing for several reasons (reviewed in Schilt and Nestler 1997; Popper and Carlson 1998). However, attempts to reduce fish entrainment and impingement at industrial water intakes or to otherwise redistribute fish over long time periods using sound stimuli have largely proved unsuccessful (reviewed in Popper and Carlson 1998). Positive results have been reported at one site (e.g., Hanson Environmental, Inc. 1996; tests were conducted at a slough in California), but similar treatments do not work at other times and places (Ploskey et al. 2000; tests were done at a large main-stem dam on the Lower Columbia River). Unfortunately, failures are less likely to be published than are successes. On the other hand, sometimes a study that finds no effect for a specific sound treatment may come to a very general conclusion. For example, Goetz et al. (2001) found no effect in an attempt to use a 200- to 300-Hz signal to change juvenile salmon distributions in a large navigation lock and concluded that “low-frequency sound is not an effective means of guiding salmon smolts.” Of course, there might be many sound characteristics including amplitude, duration, rise time, and repetition rate, which might influence efficacy, and it may be unwise to infer that all “low-frequency sound” is ineffective from one series of experiments. Unfortunately, in many studies involving sound and fish behavior, the stimulus and noise fields are poorly described if they are described at all.

Effective reductions of fish entrainment at power-generating sites have been reported for pneumatic guns (Haymes and Patrick 1986), electronic sound sources (Hanson Environmental, Inc. 1996), and a mechanical “hammer.” Even in cases in which a sound source is found to be efficacious at a given site, some sound-production systems, especially low-frequency impulse generators such as air and water “guns” and electric “sparkers” used in seismic exploration, may still have important dependability and (human) safety issues.

Beyond the use of sound, there has been considerable work with the use of hydrodynamic flows and turbulence to protect fish in hydropower applications, with the assumption that fish detect such signals with the lateral line. Industrial water impoundment and withdrawal systems often involve spectacularly large, powerful, and turbulent water flows, some of which can be directed through fishway (also called fish ladders) or fish lift (fish elevator) routes as “attraction flow” to draw upstream migrants to their downstream entrances (Barry and Kynard 1986). The positive rheotaxis (upstream swimming) of adult anadromous fishes such as salmonids and alosine herrings as well as the upstream-migrating juveniles of the catadromous eels has enabled the development of fairly successful fishway architectures for many of those fishes. The development of upstream passage routes has been relatively successful, although substantial challenges remain at some sites and with some species including



upstream-migrating American shad (*Alosa sapidissima*) in the Canadian and US eastern seaboard and Pacific lamprey (*Lampetra tridentata*) in western Canada and the US Pacific Northwest (Moser et al. 2002).

Although many challenges remain in the upstream passage at specific sites and with particular species, the understanding of downstream orientation and enhancement of passage and survival at hydropower dams present more difficult and more recently addressed problems. There is a special interest in the use of mechanosensory information in the orientation and behavior of downstream-migrating juvenile anadromous salmonids (Knudsen et al. 1992) and catadromous eels (Richkus and Dixon 2003), which are affected by dam passage.

In general, the study and development of the downstream passage at hydropower dams have a more recent evolution and present more difficult challenges than does the upstream passage of adults. Typically, adult migrants are large, powerfully swimming fish with strong motivation to go upstream. Juvenile downstream migrants are young, small, and much less well understood. There is a good deal of computational fluid dynamics modeling, which describes and predicts water motions, done at many engineered sites such as the forebays of large hydropower dams. These may be helpful, at least, in knowing where fish might be unable to resist entrainment, but for understanding fish navigation through such systems, the spatial scale of such modeling studies is typically very large compared to the scale at which fish are likely to perceive the world with the lateral line systems wherein the fish's size absolutely limits the system array size (Coombs et al. 1988). Even if there were appropriately scaled models or measurements of the hydrodynamic environment through which fish pass, we do not know, to any great extent, what sensory stimuli guide downstream-migrating juvenile fish.

### 3.8 Use of Ultrasound to Control Fish Behavior

Although there generally has been little success in using sound to control fish behavior, one of the areas in which there has been considerable success has been the use of ultrasonic sound to keep herring in the subfamily Alosinae (Family Clupeidae) from entering cooling-water intakes and large power plants. Ultrasonic sensitivity in an alosine herring (American shad, *Alosa sapidissima*) was discovered by Boyd Kynard when, in 1982, he was using ultrasonic (about 160-kHz) sonar to sample down-running (spent) adult American shad in a canal associated with Holyoke Dam on the Connecticut River, MA. Subsequent work at the site indicated that the sound field was effective at temporarily concentrating down-running adults but that the fish would finally pass through or perhaps under the sonar beam. Up-running (prespawning) shad were more successfully concentrated by the sound (Kynard and O'Leary 1990).

#### 3.8.1 Ultrasound Detection

Although these studies showed ultrasonic detection in Alosinae, it was not until Mann et al. (1997) did behavioral tests on hearing in the American shad that



the ultrasonic hearing capability was quantified. In this and a subsequent study (Mann et al. 2001), it was demonstrated that several *Alosa* species can detect ultrasound up to almost 200 kHz, whereas members of the subfamily Clupeinae (the sea herrings and allies including sprats, sardines, pilchards, and relatives) are able to detect sounds only to about 4 or 5 kHz (also Enger 1967; Mann et al. 2005).

Not only can the alosine herrings hear ultrasound, they also show avoidance reactions to pulsed ultrasounds (Plachta and Popper 2003). The sensitivity to such high-frequency clicks may be adapted as a predation-avoidance response to the echolocation clicks of some marine mammals (Nestler et al. 1992; Mann et al. 1998; Astrup 1999; Plachta and Popper 2003).

A major question is how alosine herrings detect and directionalize ultrasonic sounds. Although evidence is still indirect, it appears that the utricle is involved (e.g., Higgs et al. 2004; Plachta et al. 2004). The utricles in all clupeids that have been examined are morphologically different from those found in any other vertebrate studied to date. In clupeids, the utricular sensory epithelium is divided into three distinct parts (Popper and Platt 1979), whereas other vertebrates have only a single epithelium. Most significantly, the center epithelial region in clupeids is suspended over fluid associated with an air bubble (Higgs et al. 2004) that may resonate at greater than 100 kHz (Hastings and Popper, unpublished data). Ultrasonic hearing is not found in young *Alosa* until the utricle is fully developed (Higgs et al. 2004).

### 3.8.2 Use of Ultrasound for Control of Fish Behavior

In 1989, net pen experiments were carried out on the upper Savannah River, GA (Nestler et al. 1992) in which captive adult blueback herring (*A. aestivalis*) were found to have significant avoidance responses over fairly short (to 15 min) time durations. The investigators found a reduction in fish abundance in the presence of the ultrasound compared to when it was off. Subsequent to this finding, ultrasound has been placed in operation to control the movement of several *Alosa* species (e.g., Dunning et al. 1992; Ross et al. 1993, 1996; Nestler et al. 1995; Ploskey et al. 1995). Gregory and Clabburn (2003) reported that the 200-kHz side-looking sonar with which they sample upstream-migrating Atlantic salmon (*Salmo salar*) must be turned off at intervals because it has the unforeseen consequence of stopping the concurrent upstream migration of the alosine twaite shad (*Alosa fallax*).

## 4. Anthropogenic Sound and Fish

An issue of growing interest deals with the effects of anthropogenic sound on fish (Popper et al. 2003; Popper et al. 2004; Hastings and Popper 2005). Those sounds might result from systems designed for sound production, such as offshore minerals exploration or sonar devices, or from systems for which sound

is just a by-product, such as shipping or sea-based wind farms. Human-generated hydrodynamic flows that might cause stress to or otherwise harm fish include turbine, fish bypass, and spillway passage routes at hydropower dams. The possible harmful effects of anthropogenic sound on marine mammal populations have received considerable attention recently (e.g., National Research Council 2000; Popper et al. 2003; Hastings and Popper 2005; Popper et al. 2005b, 2007), but the effects on fish and other nonmammals are also of growing interest. However, to date, there are few peer-reviewed experimental studies to assess the effects of anthropogenic sounds on fishes.

In the following sections, anthropogenic sound is discussed in terms of the different types of potential effects on fish. It must be kept in mind, however, that the data are for very few species, and considering the diversity of fishes, one must be very cautious with any attempts to extrapolate to other species (Hastings et al. 1996; McCauley et al. 2003; Popper et al. 2005b, 2007).

#### *4.1 Nonauditory Injury*

Most of the concern about the effects of sound on fishes is associated with the sensory detectors because they are likely to be overstimulated by intense sounds. There has been some concern that these same sounds could produce nonauditory injuries that could range from cellular disruption to gross damage of the swim bladder and circulatory system. How such damage might occur has yet to be demonstrated, and in the few cases where there has been good pathology of exposed tissues, there has been no apparent damage (e.g., Hastings and Popper 2005; Popper et al. 2005b, 2007). Indeed, most of the data suggesting such injuries comes from studies that examined the effects of explosives on fish (e.g., Yelverton et al. 1975; see review in Hastings and Popper 2005).

At the same time, studies of the effects of sound on terrestrial mammals have resulted in some damage to the lungs and other organs as a result of sound exposure (e.g., Fletcher and Busnel 1978; Yang et al. 1996). Some gray literature reports suggest that high sound pressure levels may cause tearing or rupturing of the swim bladder of some (but not all) fish species (e.g., Gaspin 1975; Yelverton et al. 1975), and there is evidence that fish very close to the impulsive sounds from pile driving may suffer death or damage (e.g., Caltrans 2004).

#### *4.2 Permanent Hearing Loss and Inner Ear Damage*

A number of studies have examined the effects of high-intensity sound on the sensory hair cells of the ear. Loss of these cells results in permanent hearing loss in terrestrial animals (e.g., Fletcher and Busnel 1978; Saunders et al. 1991), and it may be hypothesized that comparable damage to sensory hair cells could also result in hearing loss. However, there has yet to be any study that has examined

fish hearing before and after exposure to sounds that are also known to damage to sensory cells (but see Smith et al. 2006).

Several studies have examined the effects of high-intensity sounds on fish ears. In the first such study, Enger (1981) showed that exposing Atlantic cod (*Gadus morhua*) to high-intensity pure tones resulted in damage to sensory hair cells (as determined with scanning electron microscopy). Subsequently, Hastings et al. (1996) showed that exposure of a generalist freshwater fish (the oscar, *Astronotus ocellatus*) to an hour-long continuous 300-Hz sound with a received level of 180 dB produced some damage to the sensory hair cells of the lagena and utricle. However, Hastings et al. did not find any damage resulting from a similar exposure to other frequencies or to noncontinuous sounds or shorter stimulation times. Significantly, damage to the 300-Hz signal only showed up several days after exposure, a result that was similar to that found in another species by McCauley et al. (2003).

McCauley et al. (2003) examined the effects on caged pink snapper (*Pagrus auratus*) of exposure to a seismic air gun with a source level at 1 m of 222.6 dB re 1  $\mu$ Pa (peak to peak) or 203.6 dB re 1  $\mu$ Pa (RMS). They found considerable damage to the ciliary bundles of the sensory hair cells of the saccular sensory epithelium (the other end organs were not examined). The extent of damage increased with an increase in the time the animals were kept postexposure. The animals maintained the longest, to 58 days postexposure, had the greatest damage to the ciliary bundles.

In contrast to these findings, recent investigations found no permanent damage to the ears of fish of three species that were exposed to a sound from a seismic device and then examined immediately after or 24 hours after exposure, although several species showed temporary hearing loss (Popper et al. 2005b). Moreover, exposure to a low-frequency (200- to 500-Hz) sonar at 193 dB re 1  $\mu$ Pa (RMS) did not result in damage to the ears of rainbow trout (*Onchorhynchus mykiss*) or channel catfish (*Ictalurus* species) even up to 96 hours postexposure (Popper et al. 2007).

The tentative conclusion one may reach from these studies is that there are differences in the effects of high-intensity sounds on fish of different species. However, further conclusions are premature at this point because there are so many variables in the different studies. Most importantly, the sounds used were all quite different from one another, and not enough is known about how sounds with different onsets or other characteristics might impact sensory receptors (see Hastings and Popper 2005). The aquatic environment in which experiments are conducted, whether in a laboratory tank or “in the field” where water depth can change sound propagation characteristics (see Rogers and Cox 1988), especially of low-frequency sound, can have important effects that can reduce a study’s application to other environments. Moreover, one issue to be considered in any analysis of the effects of sound on the ears of fishes is that fish, unlike mammals, have the potential to regenerate sensory hair cells (Lombarte et al. 1993). If regeneration occurs after damage and the fish survives, regeneration may result in restored hearing and so there may be no long-term effects.

### 4.3 Temporary Loss of Hearing

Although not much is known about permanent hearing loss in fish, there is a growing body of literature showing that exposure to sounds that are well above normal ambient noise may result in a temporary change in hearing sensitivity from which the fish will recover over time. This loss of hearing, temporary threshold shift (TTS), is well known in mammals and often occurs in humans as a result of exposure to loud noises such as those encountered in a noisy workplace or at a loud concert.

The first study of hearing loss on fish was conducted on goldfish when Popper and Clarke (1976) showed that exposure to 8 continuous hours of sound at 149 dB re 1  $\mu$ Pa (RMS, received level) resulted in more than a 10-dB threshold shift.

Smith et al. (2004a,b) examined the effects of higher background noise on the hearing capabilities of the goldfish, a hearing specialist, and tilapia (*Oreochromis niloticus*), a hearing generalist, to determine how fish hearing might be affected as a result of exposure to somewhat elevated background noise as might be encountered in a hatchery, aquarium, or aquaculture facility or as might occur if the background noise levels rise as a result of human activity in an area. They found that goldfish showed a 5-dB TTS after only 10 minutes of exposure to band-limited noise (0.1 to 10 kHz, approximately 170 dB re 1  $\mu$ Pa [RMS] overall spectral sound pressure level). After 3 weeks of exposure to the same stimulus, goldfish had a 28-dB TTS, and the fish took more than 2 weeks to return to normal hearing. In contrast, tilapia showed no hearing loss to any of these sounds.

Similar results were obtained for goldfish exposed to white noise at 158 dB re 1  $\mu$ Pa for 24 hours by Wysocki and Ladich (2005), with recovery to normal hearing taking up to 2 weeks. Wysocki and Ladich (2005) also performed studies to determine whether the temporal resolving power of goldfish was affected by noise exposure. They found a decrease in temporal resolution capabilities that continued up to 3 days. This kind of hearing loss could be critical because fish of many species appear to use temporal patterns of sounds to discriminate between sounds (e.g., sounds of different species) (Myrberg and Spires 1980). Thus, the effects of noise exposure in fish may be not only on the level of the lowest sound detectable (threshold) but also on the way that fish resolve signals from one another.

Different results between hearing specialists and generalists were also found by Scholik and Yan (2001), who studied another hearing specialist, the fathead minnow (*Pimephales promelas*). They found a substantial hearing loss that continued for more than 14 days after termination of a 24-hour exposure to white noise (0.3–2.0 kHz) with an overall spectral sound pressure level of 142 dB re 1  $\mu$ Pa (RMS). In contrast, Scholik and Yan (2002) found no TTS in the bluegill sunfish (*Lepomis macrochirus*), a hearing generalist.

The studies discussed so far showed a TTS in response to increases in background levels of sound that are comparable to what a human might encounter in a noisy workplace, walking down a city street, or in a noisy classroom. Other

studies have examined the effects of considerably higher intensity sounds on fish hearing such as those produced by high-intensity low-frequency sonars, pile driving, or seismic exploration using air guns (or nearby movement of large ships). Several such studies have also tested the effects of such high-intensity sound not only on hearing but also on other nonauditory structures (e.g., swim bladder, heart, brain, liver). In each case, the study was designed to provide an exposure that is far greater than any that a fish is likely to actually encounter and to have all appropriate controls to ensure that the results were from the noise and not from handling or other factors.

In one study, Popper et al. (2005b) examined the effects of exposure to a seismic air gun array on the hearing capabilities of three species of fish found in the Mackenzie River Delta near Inuvik, Northwest Territories, Canada. The species included one hearing specialist, the lake chub (*Couesius plumbeus*), and two species that are not known to have specializations that would enhance hearing, the northern pike (*Esox lucius*) and the broad whitefish (*Coregonus nasus*). The fish were caged and exposed to 5 or 20 shots from a 730-in.<sup>3</sup> (12,000-ml) air gun array that produced levels with an average mean peak SPL of 207 dB re 1  $\mu$ Pa (the mean 90 % RMS sound level was 197 dB re 1  $\mu$ Pa). Popper et al. (2005b) found a temporary hearing loss in both lake chub and adult northern pike to both 5 and 20 air gun shots. There was no hearing loss in the broad whitefish, a relative of salmon. Hearing loss was on the order of 20-25 dB at some frequencies for both the northern pike and lake chub, and recovery to normal hearing took place within 24 hours and fish hearing returned to normal. This study reinforces the view that there are potentially substantial differences in the effects of sound on the hearing thresholds of different species.

The second study using high-intensity sound examined the effects of exposure to high-intensity, low-frequency sonar on fish (Popper et al. 2007). In this study, rainbow trout (a hearing generalist) and channel catfish (a hearing specialist) were exposed to 324 seconds of low-frequency sonarlike sounds at 193 dB re 1  $\mu$ Pa (received level) as emitted by a sonar transducer. Interestingly, as in the Popper et al. (2005b) seismic study, there were no fish mortalities and no evidence of damage to any body tissues even 5 days postexposure. Fish of both species showed a small hearing loss. This loss recovered within 48 hours in the catfish, and preliminary evidence indicates recovery after 96 hours in rainbow trout. At the same time, there was no hearing loss in several other hearing generalists after the same exposure regimen (Halvorsen et al. 2006).

#### 4.4 Effects of Different Noise Levels on Hearing Loss

Hastings et al. (1996), after reviewing their own studies and other work to that date, proposed the hypothesis that sounds 90–140 dB above a fish's hearing threshold may have the potential to injure the inner ear of a fish. This suggestion was supported in the findings of Enger (1981) who showed injury to Atlantic cod only when the stimulus was 100–110 dB above threshold. Hastings et al. (1996) derived the values of 90–140 dB above threshold by examining the sound levels

that caused minimal injury in their test fish, the oscar, and then hypothesizing that extensive injury would require more energy.

This idea received support from the work of Smith et al. (2004a,b) and Scholik and Yan (2001, 2002). Smith et al. (2004b) further hypothesized that noise-induced threshold shifts in fish are linearly related to the difference in sound pressure difference (SPD) between that of the noise and the baseline hearing threshold of the fish, the *linear* threshold shift (LINTS) hypothesis. The actual SPD required to cause TTS in a fish is very likely related to the frequency because the normal hearing levels in fishes vary by frequency. Other variables are likely to be the duration of sound exposure, whether the sound is continuous (as in Smith et al. 2004a,b), or whether they are impulsive.

Although preliminary, there is evidence that the LINTS hypothesis may also hold for impulsive as well as continuous signals. This was suggested based on an analysis of the Popper et al. (2005b) air gun results that showed the same relationship for these sounds as found by Smith et al. (2004b) for continuous noise. And although the Smith et al. (2004b) results supported the LINTS hypothesis only for hearing specialists, the much higher sound levels used by Popper et al. (2005b), which must involve a greater SPD, showed a similar effect in hearing generalists.

#### 4.5 Behavioral Effects of Anthropogenic Sound

Another critical issue with regard to anthropogenic sound is whether it may have some impact(s) on fish behavior other than loss of hearing or damage to tissues other than in the auditory system. In other words, will such sounds affect communication capabilities (e.g., mask communication sounds), cause fish to leave prime feeding grounds, hiding places, or territories, or have other effects that could reduce individual fish survival and reproduction and thereby, potentially, jeopardize population or species survival?

As for hearing loss, there are only a few studies to date that address this issue. Using caged fish, Klimley and Beavers (1998) found no response to a 75-Hz phase-modulated signal (37.5-Hz bandwidth; 145–153 dB re 1  $\mu$ Pa received level) to three species of rockfish (*Sebastes flavidus*, *S. ariculatus*, and *S. mystinus*), which presumably are, but have not been demonstrated to be, hearing generalists.

There is some, although equivocal, evidence that the low-frequency sounds produced by fishing vessels and their associated gear result in fish avoiding the vessels (see Mitson 1995; Mitson and Knudsen 2003). There is also some evidence for a decrease in catch rate after seismic air gun activity (Pearson et al. 1992; Skalski et al. 1992; Engås et al. 1996; Engås and Løkkeborg 2002; Slotte et al. 2004). An issue of major importance is that, in most cases, the behavior of uncaged fish could not be observed, and so it is not known whether changes in catch rate result from damage to fish, their movement from a fishing area, or other factors. However, Slotte et al. used sonar to observe behavior and found

that fishes in the vicinity of the air guns appeared to go to greater depths after air gun exposure compared to their vertical position before the firing of the air gun.

In the only study with extensive observation of behavior of uncaged fish during exposure to high noise levels, Wardle et al. (2001), using a video system mounted on a reef, showed no overt reactions or damage to fish resulting from emissions from a seismic air gun (peak level of 210 dB re 1  $\mu$ Pa at 16 m from the source and 195 dB re 1  $\mu$ Pa at 109 m from the source).

Although these studies examined specific effects of high-intensity sounds on fish behavior, there is also the possibility that sounds will have a more subtle effect that results in their not being able to detect biologically relevant sounds including communication sounds, sounds of prey, or sounds of predators (Myrberg 1981; Popper et al. 2004). The decrement in the ability to detect signals because of the presence of other sounds is called masking. Masking can take place whenever the received level of signal exceeds ambient noise levels or the hearing threshold of the animal (e.g., Fay and Megela Simmons 1999).

The studies on auditory masking in fish have been limited in the number of species studied, and none of these studies has directly tested whether there are behavioral changes that result from masking. The results show that species that have been studied are generally affected by masking signals in much the same way as are terrestrial animals for which such data are available (Fay 1988; Fay and Megela Simmons 1999). If the masking signal is of a significantly different frequency from the frequencies of importance to the fish, then much less (or no) masking may occur, although there is also some evidence that in at least some species, any noise signal will mask other signals and that the degree of masking may be frequency independent.

## 5. Opportunities and Challenges

In 1993, Popper and Fay suggested research questions that were pertinent from their perspective. Those questions (learning, response behaviors, sensitivity and bandwidth, the effects of noise on detection and response, fish capacities for frequency, sound level, temporal, and source localization perception) still bear investigation. We can also add several that would especially help develop potentially useful stimuli for fish management in an industrial context.

One of the most important and least studied issues is the nature and mechanism of habituation with respect to stimuli used in attempts to affect fish behavior. With any sensory-mediated response, habituation (Peeke and Petrinovich 1984) can be an important issue. In most fish passage and protection applications, fish may be present in a fairly small area (a hydropower dam's powerhouse or spillway forebay or a cooling-water intake) for hours or even days and a stimulus that habituates quickly will not be very effective for very long.

In what cases and to what extent are sensory capacities and responses similar across fishes and when are they not? All of the alosine herrings so far investigated have been sensitive to ultrasound but are the others around the world as well? It



would be attractive to think so, but Bullock and Heiligenberg (1986) cautioned that, especially when a new sensory capacity is being explored (in that case electrosensing), it is important to remember that responses may be quite variable between closely related species. It is also instructive that a behavioral response (rheotaxis) has been found to be opposite in two conspecific but ecologically distinct populations of juvenile Atlantic salmon (*Salmo salar*; Nemeth et al. 2003).

Just as acoustic noise can obscure a stimulus signal, so can light level, time of day, current, temperature, the presence of other species including predators, crowding, and untold other factors affect behavioral responses (Schilt and Norris 1997). That is why laboratory, net pen, and field experiments are all important. Laboratory studies, sometimes starting with neurological work, can point the way toward better and more refined field studies. Net pen studies can allow for free-swimming but not free-ranging fish responses, habituation studies, and manipulation of signal and noise regimens. Field studies at an actual application site can discover unforeseen strengths or, more likely, weaknesses in an approach and test “real-world” responses of animals that cannot be foreseen in laboratory studies.

*Acknowledgments.* We are grateful to Dr. Jacqueline Webb for reviewing an earlier copy of this manuscript and Helen A. Popper for reviewing and editing the manuscript.

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Fish Bioacoustics

Webb, J.F.; Fay, R.R.; Popper, A.N. (Eds.)

2008, XIV, 322 p. 85 illus., Hardcover

ISBN: 978-0-387-73028-8