Evaluation of Evidence for Altered Behavior and Auditory Deficits in Fishes Due to Human-Generated Noise Sources

P. L. Edds-Walton
Parmly Hearing Institute
Loyola University Chicago

J. J. Finneran
SSC San Diego

SSC San Diego

Evaluation of Evidence for Altered Behavior and Auditory Deficits in Fishes Due to Human-Generated Noise Sources

P. L. Edds-Walton
Parmly Hearing Institute
Loyola University Chicago

J. J. Finneran
SSC San Diego

SPAWAR
Systems Center
San Diego

SSC San Diego
San Diego, CA 92152-5001

ADMINISTRATIVE INFORMATION

LH

EXECUTIVE SUMMARY

In this study, we have evaluated peer-reviewed publications and contracted reports to provide an overview of what is known about auditory processing by fishes and the behavioral and physiological effects of various noise stimuli as documented by the best and most appropriate studies. We include reviews of work on both cartilaginous (sharks, skates, and rays) and teleost fishes (modern bony fishes) and provide recommendations for research to address remaining issues.

Clear responses to human-generated noise have been documented in several marine species of interest. Sharks may be attracted to low-frequency pulsed sounds, which can change their normal distributions and could increase agonistic interactions between individuals and/or species. However, sharks also learn to ignore sounds that are not associated with food, so that any change in distribution or local density should return to normal levels eventually. There are no studies that show long-term avoidance of an ensonified area, even though a shark may exhibit a startle response at the onset of a sudden loud noise.

Teleost fishes also have specific behavioral responses to some human-generated noise, in particular to seismic surveys and ship noise. The responses range from brief interruptions in normal behavior, such as a startle response or alarm swimming, to changes in distribution that may last days due to departure from an area of continuing noise (avoidance). Physiological responses to noise include increased levels of stress hormones that can affect the overall health of the individual and changes in hearing. Changes in hearing (threshold shifts) that have been measured to date have been temporary. Fishes have the advantage of being able to produce new sensory cells in the ear, thus being capable of repairing damage induced by loud noises.

Unfortunately, the majority of the studies showing temporary threshold shifts have been conducted on hearing-specialist species. The auditory systems of hearing-specialist species respond to the pressure wave of sound due to an accessory air-filled structure that transduces pressure to particle motion, an indirect source of stimulation. Most marine species are not hearing specialists, and their auditory systems are believed to respond best to the direct particle motion of a sound, with little or no sensitivity to the pressure component. Historically, these fish species have been lumped together as "hearing generalists." The experiments using a hearing generalist have not quantified the particle motion at the fish nor controlled for consistent sound fields across experiments. Therefore, the auditory sensitivity of the generalist fish is not evaluated properly and the data on responses to noise are not useful. While it is possible that the auditory system of hearing generalists will exhibit threshold shifts that are qualitatively different from those of hearing specialists, there will undoubtedly be quantitative differences, e.g., the noise levels at which significant shifts occur and, possibly, the time course for recovery.

The time course for recovery from temporary threshold shifts in hearing is critical since monitoring aspects of the auditory scene is important for most, if not all, fish species. Hearing impairment can result in failure to find patchy food (using passive listening for prey or the sounds of feeding conspecifics) or conspecifics (for social interactions, breeding) or failure to detect the approach of a predator. Clearly, even temporary reductions in the ability to hear have the potential for serious outcomes and could ultimately lead to mortality.

CONTENTS

Figures

Tables

1. INTRODUCTION

Concerns about the potential effects of human-generated noise on marine species have been growing as scientific evidence indicates that certain classes of noise produced during naval exercises, geophysical exploration, and underwater construction may cause temporary or permanent auditory damage to some marine vertebrates, including marine mammals, turtles, and fishes (NRC, 1994, 2000; Popper, 2003, Popper et al., 2004a). In cases of sudden onset, very intense noise, such as explosions, noise-induced damage may lead to death. Of equal concern is the potential for concomitant changes in normal behavior that may reduce foraging efficiency, reproductive success, or individual longevity, any of which could result in reduced populations. Negative impacts for any population will in turn negatively affect the species that depend on the affected species for food (i.e., their predators) or initiate a cascade of changes that alter an entire ecosystem if top predators are reduced or eliminated.

Hearing is an important sense for many cartilaginous (primarily sharks) and bony fishes (Myrberg, 2001; Popper et al., 2003). Hearing the sounds produced by prey may be important to maximize the foraging efficiency of predatory fishes. Also, listening for the feeding sounds produced by conspecifics may increase feeding efficiency, even in non-predatory fishes. Since many fishes live in waters with low visibility, fishes that can detect vocalizations of an approaching predator or the low-frequency sound that accompanies lunging or suction feeding (e.g., Karlsen et al., 2004) have a clear advantage over fishes that cannot detect those sounds. Lastly, some species of fishes produce vocalizations that are critical for breeding activities, including identification of conspecifics where multiple species may be spawning (e.g., damselfishes, Myrberg and Spires, 1980), attraction calls of willing mates on nest sites (e.g., toadfishes, Winn, 1964), and the mating sounds produced to coordinate gamete release. Impairing the ability to hear sounds produced during reproductive behaviors can affect entire populations of fishes. Of particular concern are populations of food fishes that are currently being taken in large quantities by fisheries.

Changes in hearing thresholds (the level at which the ear detects a sound at a particular frequency in the absence of background noise) in response to human-generated noise have been documented in a few fish species. However, conducting research into the effects of noises of various types (impulsive, sustained, broadband, narrowband, etc.) requires that the characteristics of the output of the sound source be well understood and quantified, that the sound field be well-defined, and that the received levels at the fish are known (measured or calculated). Not only must the experimental setup be appropriate, but the auditory response of the fish (or the audiogram) must dictate the frequencies and levels used to assess the potential for auditory damage. For example, investigating the potential for auditory damage in response to a very intense 2000-Hz tone is a futile experiment if the fish's auditory system is incapable of responding to that sound frequency. Likewise, appropriate stimuli must be used. For example, some teleost fishes have auditory systems that are sensitive to the pressure component of underwater sound, while other fish species respond well only to the particle motion (kinetic) component. Lastly, if generalizations are to be made based on one series of experiments on a single species of fish, the "representative" species chosen is critical, since specializations of the auditory system are well-documented in a few species (e.g., carp and some herring species), and there are many species for whom no audiogram has been determined.

For this report, we have evaluated peer-reviewed publications and contracted reports to provide an overview of what is known about auditory processing by fishes, the demonstrated effects of various noise stimuli, and what we may conclude about the potential effects of various human-

generated noises on fishes. In addition to studies of the auditory system and hearing, we will provide information about the lateral line system, which is important for orientation, prey detection and localization, and possibly communication (Coombs et al., 1998; Braun et al., 2002).

2. FISH AND FISH EARS

In the context of this report, we will use the term "fishes" as a generalization that includes both cartilaginous and bony fishes. Cartilaginous fishes include the skates, rays, and sharks, all of which have skeletons that are not completely calcified. They are classified as members of the taxonomic class Chondrichthyes. The bony fishes have skeletons that consist of calcified bony elements (although cartilage is also present) and include all members of the taxonomic class Osteichthyes. Within the Osteichthyes are several taxonomic groupings of bony fish. Only the modern fishes, the teleosts, have been the subject of studies evaluating the potential effects of human-generated noise. Therefore, our consideration of bony fishes will be restricted to teleost fishes.

Many people are surprised to learn that fishes can hear and are further surprised to learn that fishes have ears that are very similar to those of mammals. Although there is no external pinna and no obvious entry point for sound to enter the inner ear, fishes have inner ears that contain most of the same components found in the inner ear of humans (Figure 1). The pathway that sound travels is believed to be directly through the body of the fish to the inner ear, since on average, the musculature is about the same density as water. Thus, there is minimal loss as the sound passes into the fish and the inner ear is stimulated directly.
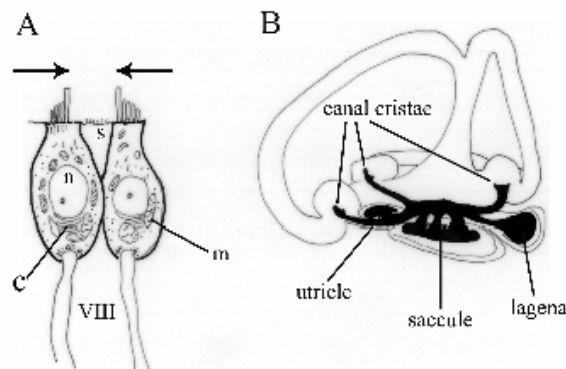
Figure 1. Components of the fish ear. (A) Two hair cells with support cell(s) between them. The surface structures dictate the directional sensitivity of the cells. The arrows indicate the best direction for stimulation of the two cells shown. Some of the cellular organelles involved in metabolic processes are shown: c = cisternae, m = mitochondria, n = nucleus, VIII auditory neurons that carry activity of hair cells to the brain. (B) Generalized ear of a nonspecialist fish. Sensory hair cells are found on the three canal cristae (vestibular) and the otolithic endorgans (utricle, saccule, lagena). Each otolithic endorgan is within a fluid-filled chamber and is associated with a calcareous otolith. The sensory epithelium with the hair cells and the afferents from VIII are shaded black.

The most obvious components of the inner ear are the semicircular canals: three orthogonal, fluid-filled tubes that are responsible for monitoring angular acceleration of the fish's body in all three axes (x,y,z). The sensory hair cells that are concentrated in bulb-like enlargements of the tubes respond to pitch, roll, and yaw. At the base of these canals, there are three endorgans enclosed in fluid-filled sacs. Each of these endorgans has sensory hair cells and support cells on its surface, and each is associated with a calcareous otolith. The otolith maintains contact with the

sensory hair cells via mutual attachment to a gelatinous layer, often called the otolith membrane. The sensory endorgans actually move (in nanometer amounts) in response to stimulation, and shearing of the hair cell surface structures results from the relative lack of movement of the denser, calcareous structures (see below). These endorgans may respond to linear acceleration, gravity, or higher frequency stimuli encoded as auditory for the central nervous system (spinal cord and brain). Although demonstrated physiologically only in cartilaginous fishes, a mixture of functions may be performed by any one of the otolithic endorgans in any fish. In other words, any otolithic endorgan can encode acceleration, but the frequencies at which it responds can vary from very low (vestibular) to higher, auditory frequencies.

To understand auditory processing, it is necessary to understand sensory hair cell structure and function. The hair cell is a modified neuron (nerve cell) that responds to mechanical stimulation. The surface structures vary with species, but in all fishes the hair cell apical (top) surface has an array of stereovillae and a single, taller kinocilium (Figure 1A). The base of the hair cell is embedded in the sensory epithelium. The apical surface is in contact with a gelatinous layer and mechanically coupled to the dense otolith. The relative motion of the apical structures with respect to the denser otolith results in movements that deform the surface structures (Figure 1A). Bending of the kinocilium and stereovillae causes ion channels to open, beginning a cascade of physiological events that ultimately sends a message via the acoustic nerve to the brain. The stimulation of the hair cell may be excitatory (increasing the rate of electrical signals to the brain) or inhibitory (decreasing the rate of or eliminating electrical signals to the brain). For additional details on sensory hair cell function, the reader is referred to Hudspeth and Corey (1977). The information encoded and transmitted to the brain via the eighth cranial nerve includes frequency components (pitch) and relative amplitude (loudness) of the sound (more details below). In addition, there is good evidence that the inner ear of fishes encodes the direction of the sound source (Fay, 1988; Popper et al., 2003). For the purposes of this report, the essential facts are (1) the apical structures on the hair cell are required for encoding stimulation to the ear, and (2) association with an overlying structure (that may or may not have calcareous components) is needed to provide the shearing action that results in movement of the apical structures. The central nervous system uses this information to assess the acoustic environment, which may include sounds produced by waves, bottom elements, conspecifics, prey, and predators.

Sensory hair cells are also found in another sensory system of fishes — the lateral line system. The hair cells are grouped into sensory units called neuromasts that are capped by a gelatinous "cupula" that lacks any calcareous components. The lateral line system can be composed of both superficial neuromasts found on the surface of the body and canal neuromasts that are located in canals in the skin that have periodic openings to the water. Although there is considerable structural diversity in this sensory system among fishes (Coombs et al., 1988), the functions remain similar: monitoring water flow around the fish and detecting mechanical disturbances in the water within a few body lengths of the fish (Denton and Gray, 1988). In addition, although the sensitivity to particle motion can overlap with that of the auditory system, the hair cells of the lateral line system encode frequencies below about 100 Hz (Denton and Gray, 1988). The critical difference in the stimulation of the lateral line versus the ear is that the lateral line responds to external movements of water with respect to the fish's body. The inner ear responds to whole body motion of the fish. The lateral line system is essential for detecting water currents (rheotaxis) and current generating sources such as conspecifics, prey, or predators (Braun et al. 2002).

2.1 AUTITORY PROCESSING IN FISHES

There are four sites in the inner ear of fishes where auditory hair cells may be found: *macula neglecta, utricle, saccule, and lagena*. In cartilaginous fishes, the *macula neglecta* is believed to be the most important endorgan for auditory processing, although there is little experimental evidence in the literature. The macula neglecta is associated with a gelatinous cupula, similar to those of the vestibular canal cristae, and the frequency response is believed to be relatively low (Corwin, 1981, 1989). The size of this endorgan varies among shark species and its role in hearing may vary. Although generally small, the macula neglecta could be an auditory endorgan in skates and rays as well [discussed in Corwin (1989)]. The macula neglecta is also found in some teleost fishes, but in general, the endorgan is very small, and the function is unknown in those species.

Each of the other three potential auditory endorgans of the inner ear (*utricle*, *saccule*, and *lagena*, Figure 1A) has an epithelium with hair cells arranged in various orientations and a calcareous otolith with a gelatinous layer that functionally links the hair cells to the otolith. The orientations of the hair cells are important because of their inherent directionality (see Figure 1A).

The directionality of a particular epithelium is dictated by the array of orientations of the hair cells on its surface and by the orientation of the epithelium in the head of the fish. In most fishes, the utricle is like a flattened, shallow bowl, and it is oriented so that it lies in the horizontal plane of the fish. The saccule and the lagena are generally oriented in the vertical plane, though some twisting and/or curvature of the epithelium is present in some species, resulting in responsiveness beyond the vertical plane.

In general, the utricle of fishes is very similar to the same structure in other vertebrates and likely plays a major role in encoding linear acceleration in the horizontal plane. However, as in most aspects of biology, there are exceptions. Lowenstein and Roberts (1951) found that although most of the utricle of a skate (*Raja clavata)* responds to tilt (a change in orientation of the body in any axis), a small portion responds to vibration. In some teleosts (the herrings) the utricle has distinct subdivisions and at least one clearly functions in auditory processing (Denton et al., 1979).

In elasmobranchs (sharks, skates and rays), the lagena and a portion of the saccule may be sensitive to tilt, as shown by Lowenstein and Roberts (1951). However, they estimated that two-thirds of the saccule responds to sound vibrations. An auditory function for the saccule was demonstrated by Corwin (1981) in the lemon shark, *Negaprion brevirostris* (see Section 2.2).

Among bony fishes, the saccule and the lagena vary in relative size and shape and function. For most teleost fishes examined physiologically to date, the saccule is the major auditory endorgan. The lagena may respond to vibration for auditory processing (e.g., goldfish, Fay, 1984; and a freshwater goby, Lu et al., 2003) and/or respond to tilt for vestibular processing (e.g., toadfish, Locke et al., 1999). The saccule may play a dual role as well (auditory and vestibular), particularly in teleost fishes for whom the utricle encodes auditory stimuli, though there are no studies that have demonstrated a dual function in a bony fish. There is evidence in one fish species, the freshwater, sleeper goby (*Dormitator latifrons*) that there is an auditory function for all three otolithic organs, including the utricle (Lu et al., 1998, 2003, 2004). Lu et al. have suggested that the lagena and utricle, which are less sensitive to auditory frequencies than the saccule, may extend the dynamic range of the auditory system. This idea is of particular interest in the context of auditory damage to fishes, since less sensitive endorgans may remain functional even if the responsiveness of the more sensitive saccule is impaired by noise. However, we do not know the fate of the auditory input from the alternative hearing endorgans. This is important because their afferent input may not be integrated into all the same circuits involved in normal,

5

sound-related behaviors. Therefore, it is possible that the fish may not use the auditory input from those endorgans in the same way as saccular input.

Encoding the direction of a sound source could be one of the functions of any auditory endorgan. The most excitatory direction for a hair cell is easily assessed using scanning electron microscopy to view the apical structures of the epithelium (following specific histological preparations). Studies by Fay and Edds-Walton (1997), Edds-Walton et al. (1999) and Lu and Popper (2001) have shown that the neurons that carry information from the saccule innervate groups of hair cells with similar orientations and provide directional information to the auditory centers in the lower brain (hindbrain). Fay (1984) showed that directionality of the stimulus is encoded by utricular and lagenar fibers as well, in goldfish. Lu et al. (2003, 2004) found directional auditory responses, with higher thresholds, among lagenar and utricular afferents in the sleeper goby. Therefore, there are multiple directional inputs that potentially could be integrated by the fish brain. Although only a few studies have confirmed that directional computations occur along the auditory pathway in the brain (Fay and Edds-Walton, 1999; Edds-Walton and Fay, 2003, 2005; Ma and Fay, 2002), information relevant to sound source location is likely to be included at sensory integration sites in the central nervous system in all fishes.

Thus far, we have discussed how the structure and orientation of a hair cell functions to encode sounds from various directions. Frequency, how high or low the pitch of a sound, is also encoded in the auditory fibers of fishes, as is the relative level or amplitude of the sound. This aspect of the auditory physiology is particularly pertinent for the consideration of the effects of human-generated sound on fishes. If the auditory structures of fishes cannot respond to the frequencies produced, there can be no negative effect on the auditory system. If the auditory system is relatively insensitive to the frequencies produced by a noise source, responses will be absent unless the received level is sufficiently high. Therefore, we will now consider the frequencies that are encoded by the auditory systems of various fishes.

2.2 FREQUENCIES THAT FISHES HEAR

There is no simple generalization that can be made about frequencies detected by fishes as there is considerable variation among the relatively few species investigated to date. When assessing potential effects of human-generated noise on the auditory system of fishes, the range of variation is an important consideration. However, a word of caution is necessary. Interpretation of the validity of a study requires an evaluation of the stimulus system used for determining hearing thresholds (the lowest detectable sound amplitude at a particular frequency), and the nature of the auditory system of the species under investigation.

There are a variety of methods used to obtain an audiogram, a graph of hearing thresholds versus sound frequency. We will not go in to detail about methods here (see Corwin et al., 1982; Fay, 1988; Kenyan et al., 1998 for details), but a general understanding of methodology is required. Older studies used behavioral methods that require training of the fish to behave in a specific manner when a sound is heard (e.g., avoidance, changes in heart rate or respiration). The animal may work for a reward (positive reinforcement, usually food) or to avoid pain (negative reinforcement, such as electrical shock). Sound level and frequency are varied over a series of tests that can take months to perform once the animal is trained (which can also take many months).

More recently, measurements of auditory evoked potentials (AEPs) have gained favor among researchers due to the ease with which a lot of information can be gathered in a short time. AEPs are small voltages generated by the brain in response to sounds. AEPs may be detected using passive electrodes and analyzed to assess if the brain is responding to sounds of particular

frequencies and intensities. A single individual can be tested multiple times over a period of minutes and multiple individuals can be tested over a series of days with no training of the animal. Also, the motivation of the animal is not a variable. However, the audiograms obtained by behavioral methods and AEP may not be directly comparable. In general, among the vertebrates tested, behavioral methods tend to provide lower thresholds than AEP measurements; in other words, AEP measurements tend to *under estimate* the sensitivity (over-estimate threshold) of an animal to sounds of particular frequencies (Katz, 1994). For AEP studies of fish hearing, short-duration "clicks" or tone "pips" have commonly been used as sound stimuli. These stimuli produce short-latency evoked responses, normally called auditory brainstem responses (ABRs). Clicks and tone pip stimuli have relatively broad frequency content, thus ABR audiograms tend to lack the frequency specificity of behavioral methods obtained with pure tones or AEP measurements using longer duration stimuli (e.g., the auditory steady-state response or envelope following response). Short-duration stimuli may also result in higher thresholds due to insufficient time for temporal integration. Despite these limitations of ABR/AEP methods, monitoring *changes* in auditory sensitivity (evaluating relative thresholds) with significant numbers of animals is far more efficient with AEP/ABR methods than behavioral methods (e.g., Yan, 1998) because subjects do not need to be specifically trained for a hearing test.

2.2.1 Teleost Fishes

Most teleost fishes respond best to the kinetic, particle motion component of underwater sound, not to the pressure wave (the stimulus that excites the ears of most terrestrial vertebrates in air). Sound can literally pass through the fish because the soft tissues of the fish have a similar density to that of water. However, many bony fishes have a gas-filled "swim bladder," and this structure may be part of an alternative pathway that responds to the pressure wave. The swim bladder is more compressible than the water or the fish's tissues, allowing its walls to pulsate with the pressure changes of a sound wave. Some fishes have accessory structures that mechanically couple the movements of the swim bladder to the fluids of the inner ear, thereby stimulating the hair cells. Fishes with this accessory (or indirect) sound pathway have been called "hearing specialists." Fishes without the indirect pathway to the ear have been called "nonspecialists" or "hearing generalists."

The otophysines are the group of teleosts for whom the term "hearing specialists" originated. These species are not taxonomically related, but all have modifications of the vertebral spines that provide a mechanical connection between the swim bladder and a fluid-filled cavity (sinus impar) that is in contact with the fluids of the inner ear. The majority of the fishes with this arrangement are freshwater species, such as carp and catfishes.

Another adaptation that functions as an accessory auditory structure occurs in herring and some electric fishes. Those species have a special gas-filled compartment, called an auditory bulla, that lies adjacent to the inner ear. As described for the swim bladder above, the auditory bulla transmits fluctuations in its volume to the fluids of the inner ear (Denton et al., 1979; Denton and Gray, 1993).

The specialist-nonspecialist dichotomy is losing its usefulness as more data are obtained and greater variation in auditory capabilities is revealed, eliminating the ease with which fish can be placed into the specialist versus nonspecialist categories. For example, the movement of the tissues of the swim bladder can be transmitted directly to the fluid-filled chamber housing the inner ear if the two are closely associated (as is the case in cod) or swim bladder movement might be transmitted through the soft tissues that lie between the swim bladder and the inner ear (which could be true for many species of bony fishes). In general, this latter pathway is not believed to be

a significant source of auditory stimulation to the ear due to strong damping of the swim bladder and loss of amplitude in the intervening tissues; however, Jerkø et al. (1989) provided evidence that swim bladder vibrations can be a significant source of stimulation to the ear of European eels (*Anguilla anguilla*). That study suggests that the tissues lying between the swim bladder and the ear are capable of conducting sufficient sound energy to the ear in the absence of a structural link. Conversely, Yan et al. (2000) concluded that the intervening tissues cannot contribute energy to the ear in two teleosts that have no swim bladder connections with the auditory chamber. Yan et al. (2000) used the ABR technique to assess thresholds with swim bladder inflation and deflation, however, the proximity of fish to the water surface may have compromised the validity of the data. Additional studies are needed to assess the role of the swim bladder in hearing in fishes thought to be "nonspecialists." For the purposes of this report, we will use the term "hearing generalist" for a fish species that lacks an accessory pathway for transmitting the pressure component of underwater sound.

The primary effect of pressure sensitivity is to extend the frequency range of hearing to higher frequencies than in fishes that lack the indirect pathway, but it does not improve hearing at lower frequencies (Sand and Enger, 1973; Popper et al., 2003). In fact, Fay and Edds-Walton (1997) have shown that the toadfish (*Opsanus tau*), a species that lacks any direct connection between the inner ear and swim bladder, responds to particle motion as small as 0.1 nm at frequencies to which it is most sensitive (50 – 300 Hz). This value is equivalent to the smallest stimulus level to which the best studied hearing specialist, the goldfish (*Carassius auratus*), responds to a low-frequency particle motion stimulus (Fay, 1984, Popper et al., 2003, p. 17).

To artificially stimulate a fish with particle motion requires that the body of the fish be physically moved as occurs in nature. An underwater speaker produces pressure waves and variable levels of particle motion unless the sound field is designed to maximize particle motion at the location of the fish. Thus, the data obtained do not describe the normal response characteristics of the inner ear in nature. The frequencies to which the fish responds are likely to be similar, but the sensitivity of the fish to each stimulus frequency will not be accurate. For most fishes, cartilaginous and bony, the stimulus parameter that should be measured to accurately assess the responsiveness of the auditory system is the motion (displacement) of particles in the water around the fish during stimulus presentation. The units of measure for particle displacement are usually dB re:1 µm (micrometer).

A plot of the relative sensitivity (minimum level in dB re: 1 µPa for pressure, or re: 1 µm for particle motion) to a range of stimulus frequencies can be used to produce an *audiogram* (Figures 2, 3). Figure 2 compares audiograms for goldfish (from Fay, 1988) that have been plotted with respect to sound pressure sensitivity and with respect to particle motion sensitivity to illustrate the thresholds for a species that is capable of responding to both components of underwater sound.
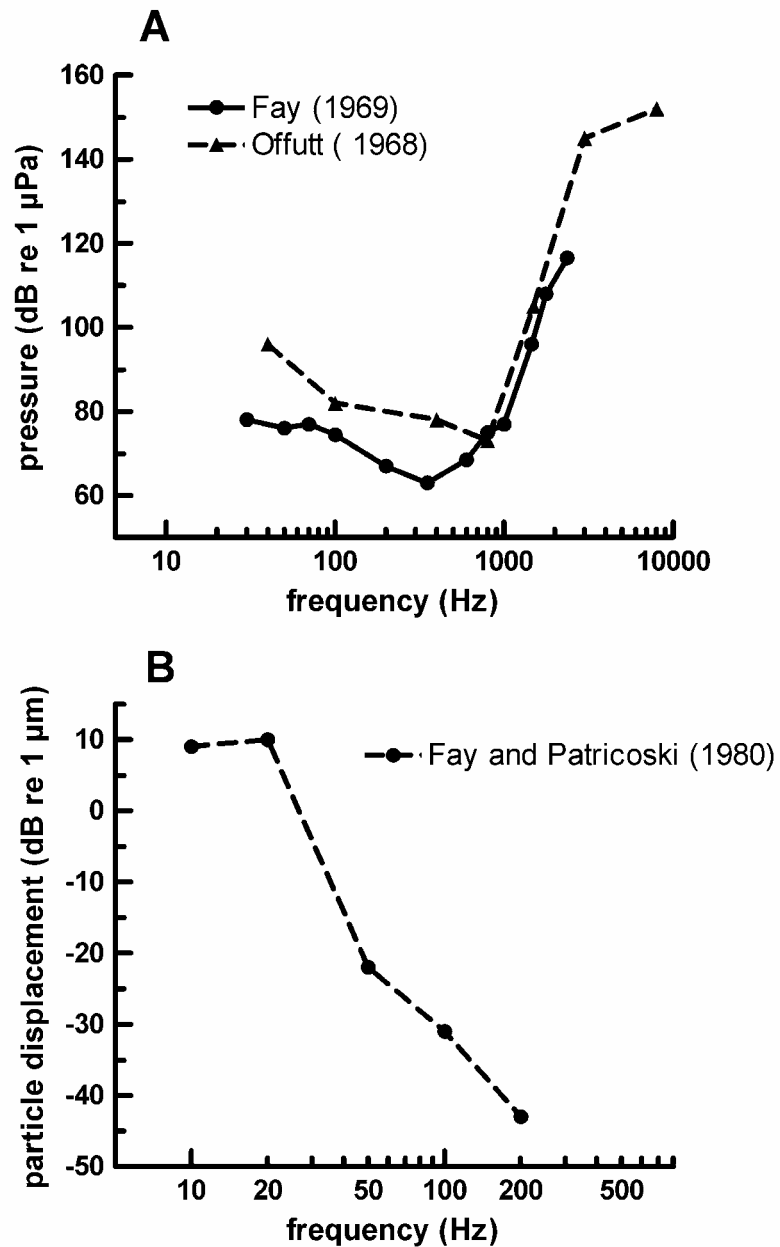
Figure 2. Comparison of audiograms for goldfish (*Carassius auratus*) obtained with different stimuli and methods. (A) Fay (1969) speaker in air (n = 4); Offutt (1968) underwater speaker (n = 31). (B) Fay and Patricoski (1980) vibrated the fish (n = 4). Data taken from Fay (1988).

Figure 3 presents audiograms of several marine species. The presentation is limited because the data obtained for particle motion are very limited. These data were re-plotted from Fay (1988), in which methods and results have been compared in detail. Audiograms for the cod are presented because the cod responds to both the pressure and particle motion components of sound due to the

9

proximity of the swim bladder and the ear (as noted above). The plaice (*Pleuronectes platessa*) is included for comparison as a species lacking a swim bladder. Note that each study was conducted in a different lab under different experimental conditions (see Figure 3 legend and Fay, 1988). In general, thresholds are determined using single tones at different levels, beginning with a level that is very likely to be heard and then decreasing sound level systematically until the test subject does not detect the tone. The duration of a stimulus can affect the listener's ability to detect it (see discussion in Fay and Simmons, 1999); ideally, there should be standardized stimulus sets to facilitate comparisons among species. Such comparable data do not exist at present.

While audiograms are useful, the data vary with experimental stimuli (as illustrated in Figure 2). The stimulus characteristics and the experimental conditions must be evaluated as well as the consistency of the data plotted. In addition, individual variation can be considerable. Audiograms of the greatest value are the result of experimentation on more than two or three animals. The appropriate number of animals depends on the amount of variation observed, greater variation being indicated by a large standard deviation with respect to the mean value calculated for each animal (with multiple presentations of the same stimulus) and/or a large standard error across animals at each frequency. Many published studies either were conducted on a few animals or do not include the standard error of the mean. The experimental data illustrated in Figures 2 and 3 were chosen due to the appropriateness of the methods and the completeness of the data set. In some cases, the paucity of data requires inclusion of studies that are less than ideal.

In an extensive review of the literature on auditory processing in teleost fishes by Popper et al. (2003), the authors note that the majority of species with no special adaptations in the auditory pathway are most sensitive to frequencies below about 300 Hz. Fishes with the alternative sound pathway via a gas-filled structure respond well to frequencies up to around 2000 Hz (2 kHz). However, there is no clear dichotomy in frequency sensitivity. The yellowfin tuna (*Thunnus albacares*), a species without a swim bladder, hears well between 200 and 800 Hz (Iversen, 1967). Behavioral responses to ultrasonic frequencies (above 20 kHz) have been documented in some herring (Mann et al., 1998) and cod (Astrup and Møhl, 1993), although no definitive evidence has been published to date confirming that a component of the inner ear is the receptor responsible for detection. Very high stimulus levels were required to obtain behavioral responses to ultrasound (Mann et al.: over 140 dB re 1 μPa, 50 msec tone, over 170 dB peak-peak for a 50-μsec click with 80-kHz center frequency; Astrup and Møhl: over 185 dB re 1 μPa for a 3-msec pulse) and other pressure receptors may be responsible for ultrasound perception (Astrup and Møhl, 1993; Plachta et al., 2004) have suggested that ultrasound is processed in the cerebellum, separately from the primary ascending auditory pathway in the brain. For our purposes, the important point is that fishes with ultrasound sensitivity, no matter what the mechanism, can respond to frequencies produced by some echolocating marine mammals as well as fishery and naval echo-ranging and sonar equipment.
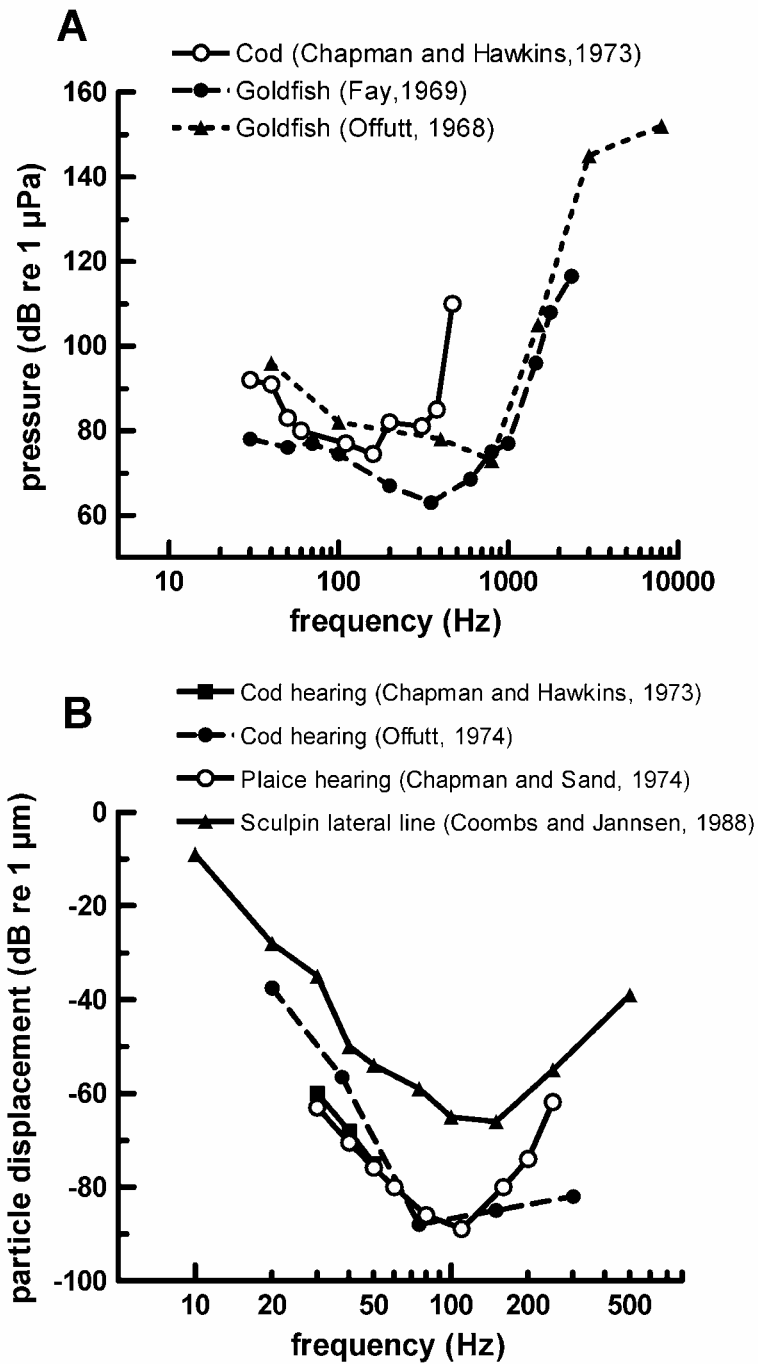
Figure 3. Audiograms for pressure and particle motion sensitivity. (A) Comparison of cod with goldfish (as in figure 2). (B) Particle motion sensitivity for cod ear, plaice ear, and sculpin lateral line. Note that the cod data are represented from two sources: Chapman and Hawkins n = 43; Offutt n = 20, Chapman and Sand n = 3, Coombs and Jansen n = 3. (data from Fay, 1988).

In most studies of teleost fish hearing, auditory sensitivity tends to decline sharply below 50 Hz, where it is likely that the lateral line system may also be stimulated under the right stimulus conditions. This potential sensory overlap confounds behavioral studies in which the source of the fish's perception of the stimulus is not known. In addition, few stimulus systems are capable of producing very low frequencies without distortion; therefore, there is little in the literature with respect to relative sensitivity to frequencies below 50 Hz. Detection of infrasound (below 20 Hz) has been revealed in diverse teleost species, including cod, a bottom-feeder (Sand and Karlsen, 1986), the plaice, a flatfish (Karlsen, 1992), Atlantic salmon (Knudsen et al., 1994), European eels (Sand et al., 2000) and roach, a plant-eating minnow (Karlsen et al., 2004). As in the studies of ultrasonic detection (above), each of these studies assessed behavioral responses to infrasound, either avoidance/escape swimming or heart rate changes. Unlike the ultrasound detection studies, there is good evidence that the inner ear is the infrasound receptor (Sand et al., 2001). The best evidence comes from the Karlsen et al. (2004) study of roach (*Rutilus rutilus*). Some of the roach were exposed to cobalt, which reversibly blocks the responsiveness of lateral line receptors (Karlsen and Sand, 1987). No significant changes in responsiveness to infrasound were observed when the lateral line was not functioning, indicating that the inner ear is the site of the receptors responsible for infrasound responses.

2.2.2 Cartilaginous Fishes

There are few studies of hearing in cartilaginous fishes. Corwin (1981) presented an interesting comparison of auditory responses from separate branches of the acoustic nerve that serve the macula neglecta and the saccule of the lemon shark. Using a large electrode (300-μm diameter) to detect activity extracellularly, Corwin (1981) found that the ear responded best to frequencies between 125 and 40 Hz (the lowest frequency measured). Very limited data indicated that the frequency response of the saccule and macula neglecta overlap, but the two endorgans may have different sensitivities to those frequencies. Individual cells were most responsive to frequencies up to 375 Hz, and none responded at all above 500 Hz.

Corwin's physiological data were consistent with the behavioral data collected by Nelson (1967) in that the general shape of the audiogram is similar in both studies. The major difference is the actual threshold values found in each study. Corwin (1981) used a speaker in air, and although a velocity hydrophone was used to estimate the sound field at the location of the shark's head in the seawater within the chamber, the dorsal surface of the shark's head was in air, and it is unclear what stimulus levels were experienced by the shark's ear. Therefore, we will not include the audiogram presented by Corwin. Given that there are great variations in the auditory scene for reef sharks versus deep water, pelagic sharks, for example, different frequency sensitivities should be expected. Sharks do not have swim bladders or gas-filled structures that could respond to the pressure wave of sound (but see below), thus particle motion is the more appropriate unit of measure to assess the levels of auditory stimuli to which the shark ear responds. The audiograms for the lemon shark (*Negaprion brevirostris*) (Banner, 1967) and the horn shark (*Heterodontus francisci*) (Kelly and Nelson, 1975) are compared by Fay (1988). Both studies used underwater sound projectors, but particle displacement was measured and used for plotting the audiograms. The two plots are quite different, possibly due to interference from differing background noise, and their accuracy overall is questionable. Therefore, we will not reproduce them here. Based on work by Corwin (see above) we conclude that sharks probably have their lowest thresholds for frequencies below 500 Hz, but there are no audiograms that can provide behavioral thresholds.

Corwin (1981) suggested that some sharks may be sensitive to the pressure component of sound through a modification of the skull that could transduce pressure to particle motion directed to the

macula neglecta. Subsequently, van den Berg and Schuijf (1983) provided evidence that a catshark (*Chiloscyllium griseum*) could detect pressure and particle motion. Myrberg (2001) provides an excellent discussion of the issues.

A recent study of hearing in a skate warrants consideration because two commonly used methods for obtaining an audiogram were compared, and the authors concluded that the data from the two methods do not differ significantly. Casper et al. (2003) trained little skates (*Raja erinacea*) to associate pulsed sound with a food reward. The sound source was an underwater speaker, and the skate was positioned 1 meter from the speaker. The data obtained in this way were compared with the data obtained from AEP recordings, in which the activity of the brain is monitored during presentation of sound stimuli at different levels. Stimulus levels were measured in both experiments by placing a hydrophone at the position of the skate and, therefore, pressure was measured and not particle motion. As noted above, particle motion is likely to be the stimulus to which the ear of skates responds; the sound pressure measurements do not permit the determination of accurate sound thresholds for this species. In addition, the acoustic environments varied (a tank of unknown composition versus a plastic tub), and the acoustic field was not properly defined. Therefore, the stimuli may not be equivalent. The authors argue, however, that the most important result is the comparison of the data from the two methods. The trends in the data are similar, with increasing thresholds above 200 Hz. Based on their study, we may conclude that the ear of the little skate is a low-frequency receiver, but we must caution that the numeric thresholds obtained may not be accurate.

3. HUMAN-GENERATED NOISE AUDIBLE TO FISHES

For the purposes of this review, we will consider all noise sources with frequencies to which fish respond, even if only at high levels, since the source levels of some human-generated sounds are sufficient to be detected by fishes with relatively high thresholds for the frequencies produced. Cartilaginous fishes are likely to respond to frequencies below 500 Hz, including infrasound (< 20 Hz). There are no data indicating ultrasound sensitivity among sharks, but no one has systematically tested cartilaginous fish for ultrasound sensitivity. Among teleost species, the nonspecialist (or generalist) auditory system will respond to frequencies between about 50 and 500 Hz. The auditory specialists among teleosts have an extended higher frequency response to about 3000 Hz at similar or lower levels than the hearing generalists, and a few specialized teleosts respond to high levels of ultrasound (> 20kHz). Sensitivity to infrasound has been demonstrated in some fishes. Therefore, there is a fairly broad spectrum of sound frequencies that may affect populations of fishes in ocean environments, where many species may be found within the noise shadow of a sound source.

Richardson et al. (1995) provided an excellent summary of human-generated noise sources that could affect marine mammals both in air and underwater. For this evaluation of noise sources of importance to fishes, we will not include aircraft, although low approaches of helicopters can be heard beneath the water surface and could potentially affect the behavior of pelagic species that mate in swarms in shallow waters or feed near the surface. Human-generated noise sources of potential significance to fishes are presented in Table 1. In general, air guns (water guns) used for seismic surveys, dredging, large vessels (including drill ships, research vessels, and pleasure craft), pile driving, and underwater explosions produce frequencies within the audible range of all fishes. The various kinds of fishery and military sonars vary in their detectability by fishes. The sonars above 2 kHz would be detected only by fishes whose auditory systems have relatively high frequency responses (e.g., some herrings). The low-frequency (LFA, Low Frequency Active) sonars and research frequencies for projects such as ATOC (low-frequency acoustic thermometry of ocean temperatures) would be detectable by most, if not all, fishes, if the level of the sound was sufficient at the location of the fish.

3.1 SOURCE LEVEL AND RECEIVED LEVEL

Sound pressure levels are measured at a standard 1 meter from the source to obtain *source levels. Received level* is the more important measurement when considering effects on animals, and it is a difficult theoretical calculation if not measured directly. Underwater sounds with source levels that would cause permanent hair cell loss in a human diver near the source would cause no damage if the diver were sufficiently far away from the source. At some distance, the sound would not be detectable at all by the diver. This is due to loss of amplitude of the sound as energy is lost to the medium through which it travels.

In deep water (that lacks stratification), sound can spread equally in all directions, or spherically from the source. This is called *spherical spreading*. Eventually, the sound energy will reach the surface and the bottom, but the energy in the reflections will be much smaller due to loss along the path to the surface and the bottom.

Table 1. Source levels for human-generated sound sources of potential significance to fishes. Data listed in dB re 1 μPa at 1 meter from the source. Data taken from Richardson et al. (1995) presented in 1/3 octave bands unless otherwise noted. ? = Noise was not quantified, though known to be present.

Source	< 20 Hz	20 – 500 Hz	1 – 3 kHz	> 20 kHz
Ship Noise				
Dredging (two vessels)	?	170 – 178		
Drill ships (two vessels)	?	161 – 177	148 – 1 68	
Large tanker	?	177	169	
Tug and barge (18 km/h)	?	161	157	
Seismic survey air gun (32)	?	210	191	
Greene (1985)		250 – 255		
Pearson et al. (1992)		223		
Echosounders				
Slotte et al. (2004) (38 kHz)				?
Schwartz and Greer (1984) (50 Hz – 2 kHz)		?	?	
Military sonars				
SURATSS LFA[1]		240 (215)		
Mid frequency (AN/SQS-53C)			~235	
Bell 212 helicopter	159	155	142	none noted

[1] Farfield source level is 240 dB re 1 μPa; however, the received level within the nearfield does not exceed 215 dB re 1 μPa (the source level of a single projector in the array).

In shallow water (e.g., coastal or river habitats), the sound energy cannot spread out in all directions equally, thus the sound energy will be constrained by the surface and bottom. This type of spreading is called *cylindrical spreading*. Cylindrical spreading is also characteristic of water that has discontinuities, such as significant temperature or salinity differences that result in the formation of distinct layers with different characteristics (stratification). Sound can essentially be trapped within a layer, as in the deep sound channel, which is well known to the navies of the world. In addition, since hydrostatic pressure (which increases with depth), temperature, and salinity affect the speed of sound, sound will travel differently in different layers of stratified waters, and refraction and reflection of the sound waves can greatly influence the sound levels at various distances and depths from the source.

When calculating received levels at some distance from a sound/noise source, the characteristics of the sound path must be known. Different equations are used to calculate the decrease in acoustic energy due to cylindrical versus spherical spreading; unfortunately, few habitats have characteristics that are easily described by a single equation or combinations of equations. In addition, signal loss varies with frequency. The equations will not be presented here, however, since the concepts are more useful than the calculations for our purposes. The important point is that every sound does not spread the same way in every aquatic environment, and the best

measure of received level is one that is made at the location of the receiver. In laboratory experiments, the location of the actual sensory endorgan is the appropriate location for measurement, since sound fields can vary considerably in tanks (see discussion in Fay, 1988).

3.2 CONTEXT AND RESPONSIVENESS TO NOISE

Wartzog et al. (2004) described some of the reasons why behavioral responses vary among individual marine mammals when exposed to noise at varying levels. A similar consideration is appropriate for fishes. Individual animals, like humans, have slightly different hearing capabilities. Some individuals are more sensitive than others, and a reaction is more likely to occur in more sensitive individuals. In addition, experience can influence the behavioral response. If an animal is habituated to a particular stimulus, the response declines as the animal is repeatedly exposed to a stimulus that does not provide sufficient negative consequences. A fish or school of fishes may flee from an area on first hearing an approaching boat; however, if the boat does not provide an additional negative stimulus, the fish may learn to "ignore" the sound of that boat, and flight is no longer initiated when the boat approaches. Boat noise can have an opposite effect if the noise levels become very high or there is an attempt to catch the fish — those that escape may be "sensitized" to the sound of the boat and will react at lower sound levels or with greater swimming speed when the boat approaches again. There is some evidence that teleost fishes respond differently to an approaching boat (increasing sound levels) than to one that is stationary (constant sound levels), indicating that fish monitor changes in sound levels over time. Fishes also respond differently dependent on their behavior at the time of noise exposure. Fishes that are actively feeding or defending a nest site may not be as likely to show overt behavioral responses in that they are less likely to flee. The reasons for this can be related to the benefits of staying to take advantage of a resource or opportunity that is limited in time and/or space. Under these conditions, fishes may not flee to avoid a noise that could result in auditory threshold shifts, even though under other circumstances the same individual would swim away.

Given that it is difficult, and often impossible, to assess the motivation or internal behavioral state of animals, field studies of species with known life histories and identifiable behaviors are preferable to laboratory studies when assessing normal behavioral responses to human-generated noise. However, laboratory settings provide more control over exposure levels and other factors that might also influence behavior during noise exposure (e.g., the arrival of a predator while testing in the field). With those caveats in mind, we will discuss the data that have been obtained in the field and in laboratory settings to assess the nature and sound levels of human-generated noise that have resulted in either behavioral changes, physical damage to the body or ears, or changes in physiology (e.g., stress responses).

4. BEHAVIORAL RESPONSES TO NOISE

4.1 TELEOST FISHES

Schwarz and Greer (1984) and Pearson et al. (1992) provided useful descriptions of the various behavioral responses observed when fishes are exposed to human-generated noise. We will describe three categories (startle, alarm, avoidance) and provide examples of conditions under which behavioral responses have been documented. Table 2 lists the three behaviors with sound levels and the species for which the evidence is strongest.

4.1.1 Startle

Perhaps the most obvious behavioral response to a noise is a *startle*. Many fishes have a distinct startle reflex that is also called a "C start" due to the shape the fish's body takes during the initial response. Some species, such as black rockfish, may exhibit a shudder or tremor rather than the C posture (Pearson et al., 1992). The startle behavior may occur without further behavioral response, or a startle may be followed by rapid swimming away from the area. Startle responses occur following brief noises with a sudden onset or sustained high-level sounds with a rapid rise time to peak level. Pearson et al. (1992) reported that some rockfish species show a startle response when received levels of air-gun discharges are 200+ dB re 1 µPa, but other species did not have a startle response at the maximum exposure level of 207 dB re 1 µPa. Wardle et al. (2001) described startle responses that accompanied each airgun shot (received level approximately 195 dB re 1 µPa) of a series, but there was no interruption in normal swimming of the fish on an inshore reef unless the bubbles of the air gun were visible to the fish. With the addition of the visual stimulus to the auditory stimulus, fish exhibited directed swimming away from the airgun location (avoidance, see below).

In a study of the response of fishes to mid-frequency sonars (1.6 and 4 kHz), Jorgensen et al. (2005) observed the behavior of four unrelated species (saithe, *Pollachius virens*, wolf fish *Anarhichas minor*, cod *Gadus morhua*, herring *Clupea harengus*) that spawn and develop in coastal waters of Norway. Juvenile herring responded with startle behaviors to both "continuous wave" (CW) and frequency-modulated (FM) sonar signals around 170 dB re 1 µPa, but resumed normal activity after the first few pulses. However, in tests with received levels around 180 – 189 dB re 1 µPa, juvenile herring exhibited startle behaviors followed by abnormal swimming. In addition, strong distress was evident during presentation of a series of 100 FM sonar pulses at around 180 dB re 1 µPa. The other species of juvenile fishes did not exhibit startle responses or any other behavioral evidence that the mid-frequency sonar pulses were detected at any level, as expected for fishes with no known auditory specializations for reception of frequencies above 1 kHz (see Section 2.2). Therefore, startle responses to sudden onset, human-generated sounds are a good indication that the fish detects the sound, and that the fish may be negatively impacted if the sounds continue or the noise levels are increased.

4.1.2 Alarm

Lower levels of noise may result in behaviors associated with *alarm* in the absence of a startle response. When schooling fish are alarmed, there is a general increase in activity, and some species may form tighter schools or circle an enclosure repeatedly. Pearson et al. (1992) found that alarm responses occurred at different levels for different species of rockfish, but, in general, alarm was observed following exposure to noise from a single air gun at received levels around 180 dB re 1 µPa. Alarm behavior was observed at much lower levels, below 112 dB re 1 µPa,

in a study of Pacific herring (*Clupea harengus*) behavior by Schwarz and Greer (1984). Synthesized sounds were used to test responsiveness, and all sounds with "essentially instantaneous rise times" routinely caused alarm. In other words, sudden, very loud sounds, with no ramped increase from low to high level, always resulted in an alarm response. Jorgensen et al. (2005) also recorded an increase in swimming activity of juvenile herring that they considered a weak response to mid-frequency sonar pulses (1 – 3 kHz) under 160 dB re 1 µPa received level. The juvenile herring resumed normal swimming after the initial alarm response.

Table 2. Documented behavioral responses to human-generated noise.

Response	Stimulus[1]	Species	Reference
Startle	3 air-gun array RL = 190 dB +	epibenthic gadoids (reef fish)	Wardle (2001)
	single air gun RL = 200-205 dB (mean peak pressure)	*Sebastes* spp.	Pearson et al. (1992)
Alarm	single air gun RL = 180 dB (mean peak pressure)	*Sebastes* spp.	Pearson et al. (1992)
Avoidance (vertical or horizontal)	single air gun RL = 178 dB	whiting	Chapman and Hawkins (1969)
	vessel noise [2] RL < 112 dB	herring	Schwarz and Greer (1984)
	40 air gun (5×8 array) RL = 200-210 dB	blue whiting, demersal spp.	Dalen and Knutsen (1986)
	airgun array SL = 253±3 dB	cod, haddock[3]	Engås et al. (1996)
	20 air-gun arrays (2 alternating)	herring, blue whiting, others	Slotte et al. (2004)

[1] all are dB re 1 µPa, RL received level, SL source level

[2] fish habituated quickly after ship noise ceased

[3] larger fish affected most; small fish did not show signficant avoidance

Territorial reef fishes may respond differently than schooling pelagic fishes. In the reef fish study by Wardle et al. (2001), alarm responses were not reported, but one fish stopped swimming in its usual pattern when a boat arrived. On reefs, in particular, mobile predators may be attracted to individual fish exhibiting alarm behaviors. In this case, alarm behavior may be similar to that seen in some mammals. When alarmed, some mammals cease movement or "freeze" (e.g., rabbits, deer), and this response may be more advantageous for individual fishes when any movement could reveal their presence to a visual predator. Behavioral differences must be considered when assessing the levels of noise to which a fish species responds. The key

observation indicating alarm may be a sudden change in behavior. Sometimes *alarm* is best measured physiologically, for example, by monitoring heart rate or levels of stress hormones in the blood (see Section 6).

4.1.3 Avoidance

Avoidance may be exhibited as horizontal movement (increasing horizontal distance between the fish and the noise source) and/or vertical movement (an increase or decrease in depth). Movement toward the surface can reduce the received sound pressure level if there is little wave activity and the Lloyd mirror effect results in a quiet zone directly beneath the surface. Avoidance may be beneficial to fishes if proximity to the noise causes damage to the auditory system or results in a physiological stress response (see below); however, the relocation of the fish may increase their exposure to predators or may decrease their ability to feed on concentrations of prey.

Avoidance of fishing vessels by targeted fish species has been noted by both fishers and scientists conducting fishery surveys (Mitson and Knudsen, 2003). The source of noise to which the fish are responding may be either the low-frequency noise of the ship itself or the higher frequencies of the echo sounders used to locate the fish schools prior to setting the nets. In some cases, the repetition rate of the high-frequency source might be detected. Responsiveness to the relatively high frequencies of echo-sounders and sonars may be species-dependent due to different auditory sensitivities. For example, Astrup and Møhl (1998) found that cod respond to ultrasound pulses (peak around 35 kHz), with a threshold of 194 dB re 1 µPa in a laboratory study. In contrast, Schwarz and Greer (1984) found that Pacific herring (*Clupea* spp.) did not respond to recordings of sonar and echo-sounders in their field study; however, the received levels were quite low, and the quality of the recordings may not have adequately represented the sonar spectrum. In another experiment, they found that the noise of an approaching large ship caused avoidance for 75% of the herring schools they observed. The fish resumed normal activity within minutes as the noise level from the departing ship decreased. Unfortunately, no attempt was made to correlate the received levels of noise with changes in behavior. Although habituation (cessation of a response in the presence of the stimulus) to small-boat noise was observed in that study, habituation to large-ship noise was dependent on the noise level. Habituation appeared to be less likely at higher noise levels. It is important to recognize that there are alternative interpretations to habituation in this case. It is possible that the fish learn to ignore the noise (true habituation); but it is also possible that the auditory system may have suffered threshold shifts from sustained noise, resulting in decreased detection sensitivity (not habituation).

In the study of juvenile herring responses to mid-frequency sonar by Jorgensen et al. (2005), the authors suggested that under free-swimming conditions, the fish may have moved away from the sound source, based on an increase in swimming activity as sonar levels at the fish increased above 160 dB re 1 µPa. In those experiments, the fish were restrained in an acoustically transparent bag and, therefore, could not exhibit avoidance behavior.

Fishers have complained that the noise from seismic surveys affects their ability to catch fish on traditional fishing grounds, which has stimulated research to address this issue. Pearson et al. (1992) note that due to surface and off-axis effects, fish exposed to air-gun arrays during track-line runs are exposed to ramped sounds as the boat approaches, maximum intensity and minimum rise time when the fish are on the axis of the beam, and then downward ramped (damped) sounds again as the ship passes the fish. Their study showed that fish that are likely to avoid a geo-physical survey vessel are likely to do so when the received levels are about 180 dB re 1 µPa,

as the ship approaches. Those fish that do not avoid the approaching ship may exhibit alarm swimming and/or flee when they are on the beam axis at received levels of about 200 dB re 1 µPa.

Vertical avoidance can result in fish staying at depths below the vertical limit of fishing nets; horizontal avoidance results in a significant proportion of fish moving away from an area in which they were previously abundant. Vertical avoidance was observed when a free-swimming school of whiting was exposed to a single air gun (Chapman and Hawkins, 1969) at levels around 180 dB re 1 µPa. Slotte et al. (2004) documented a significant increase in the depth of two targeted pelagic species (herring and blue whiting) and a mass of mesopelagic fishes when exposed to continuous seismic shooting.

Pearson et al. (1992) used a floating enclosure system in their field study to actually observe individual responses in groups of rockfish to seismic survey noise. A sound boat varied the location of the air-gun stimuli with respect to the enclosed fish, which permitted an estimate of threshold levels for the behavioral responses. Behavioral observations were conducted during a control period that preceded each exposure, during the 10--minute exposure, and post-exposure. Five *Sebastes* species were captured for the experiments. Only one species was involved in most of the five experiments (olive rockfish, *Sebastes serranoides*); however an interesting species difference is worth noting. Two of the species (black rockfish, *S. melanops*; blue rockfish, *S. mystinus*) schooled more strongly in response to air-gun sounds, but vermilion rockfish (*S. miniatus*) and olive rockfish had more individual responses. A comparison of the pre-exposure behavior and avoidance responses to higher levels of air-gun noise indicates that initially, rockfish may simply move to a *different* depth — species that school at shallower depths tend to descend, and species that school more deeply tend to ascend. Although movements of the fish in this study were restricted by the enclosure, the observations argue against generalizations about behavioral responses across even closely related species in the same body of water. The potential for altered behavior in threatened species is best assessed via actual field observations.

In the study by Pearson et al. (1992), the rockfish returned to their normal behavior within minutes of cessation of the seismic noise stimulus used for their behavioral assessments; however, their field data indicated that continuous air-gun noise could reduce catchability of free-ranging rockfish, which moved out of the range of the hooks-and-lines used by fishers (Skalski et al., 1992).

A longer study revealed persistent changes in the horizontal distribution of two important food fish following 5 days of continuous seismic shooting during surveys (shot every 10 s, 125 m between 10-nmi transects). In their field study, Engås et al. (1996) measured the abundance of cod and haddock for 7 days before, 5 days during, and 5 days after the seismic survey. Acoustic measurements (echo sounder), trawling, and longline fishing were used to assess abundance and catch rates in an area 40×40 nmi to measure changes in density and distribution around the survey area. Although both trawling and longline fishing result in the removal of fishes, the authors estimated that fishing effort removed only 3% of the population. The best data come from the acoustic assessments and trawling due to inconsistencies in soak-time and effort by the longline fishers. The decline in the trawling catch attributed to movement of the fish away from the seismic shooting area was 69% for cod and 68% for haddock. Sampling areas adjacent to the shooting area were also affected, with more modest, but significant reductions in catch. The acoustic abundance comparisons provide further compelling evidence of the magnitude of the effect: for cod, 33,000 tons pre-shooting, 16,500 tons during, 9700 tons post-shooting; for haddock, 6000 tons pre-shooting, 3200 tons during, 3100 tons post-shooting. The acoustic abundance data indicate that the fish had moved to sites over 18 nmi from the shooting area. There was no evidence of fish mortality as a result of the seismic shooting. An additional

interesting finding was that there was a size effect among cod: after shooting, cod over 60 cm in length were less common in the catch than smaller cod. The authors suggested two possibilities. The larger cod can swim faster and are able to leave the area more quickly than smaller cod, *or* the auditory system of larger cod is more sensitive, and they must travel farther to reach an acceptable received level of the noise. Neither hypothesis has been tested. Perhaps of greatest importance is their observation that the decline in fish density in the shooting area persisted for at least 5 days, at which point the study was ended.

Slotte et al. (2004) also used acoustic surveys to track the movements of two pelagic species (herring and blue whiting), as well as mesopelagic assemblages of fishes. Preliminary acoustic surveys confirmed the schooling behavior of the fish species and diurnal vertical migrations of the herring and blue whiting (deeper during the day), while the mesopelagic fishes migrated upward during the day. However, during seismic shooting, both the pelagic species and the mesopelagic species were found an average of 10 – 50 m deeper in the water column, independent of time of day. Although their data were inconsistent, possibly due to reactions to the survey vessels, the fish also exhibited some horizontal avoidance, consistent with the 20-nmi reaction distance found in other species exposed to seismic survey noise. In addition, the authors note that the herring and blue whiting were in a migratory phase, which may have affected their readiness to swim out of the area.

Taken together, the studies by Pearson et al (1992), Engås et al. (1996), and Slotte (2004) indicate that to determine appropriate mitigation measures for populations or species of concern, field observations are needed to determine the extent and duration of the natural response to human-generated noise. While a 5-day shift in fish density/catchability may seem small and inconsequential, fishers do not view such changes as small, given the time limits placed on fishing for some species of commercial importance. From a strictly biological point of view, fishes are found in particular locations for ecological or physiological reasons, and forcing a departure from those areas can reduce the overall fitness of a population. Mitigation may be as simple as timing seismic surveys to avoid interfering with peaks of reproductive swarming, seasonal feeding, and the brief fishing season for species of economic importance. Jorgensen et al. (2005) and Kvadsheim and Sevaldsen (2005) suggested seasonal limitations on mid-frequency sonar exercises to mitigate the potential for negative effects on juvenile herring maturing in coastal waters along Norway. Their detailed knowledge of the life history of the herring allowed them to provide guidelines for the use of sonars in specific locations of concern. Such guidelines should be possible for other well-known species of commercial importance.

Avoidance behavior appears to be less likely in territorial fishes (like those on coral reefs or defending nest sites) for whom departure from an area would carry a heavy biological price. Fishes that are actively feeding on patchy prey or that are part of a spawning aggregation are also less likely to abandon their location in the presence of noise levels that would cause avoidance under other circumstances. Obviously, diminished auditory capabilities are more likely to occur in species that do not avoid an intense noise source, but the effect on the population will be directly related to the role that sound plays in the normal behavior of the species involved.

4.2 SHARKS

Patterned pulses of sound can act as attractants to sharks. Several field studies have shown that sharks in both coastal and pelagic habitats are attracted to sites where broadband, low-frequency pulses (25 – 200 Hz) are being broadcast (Myrberg et al., 1972; Nelson and Johnson, 1972, and see their Table 1; Myrberg et al., 1976). In addition, the pulsed sounds are most attractive when pulse presentation is intermittent and not continuous. These low-frequency pulses are similar to

the sounds produced by struggling prey or actively feeding fish. In the study by Nelson and Johnson (1972), pulses were played from a U.S. Navy J9 transducer at 156 dB re 1 μPa at 1 m (= 138-dB spectrum level at 50 Hz). Some behavioral observations were included in the report that are of interest. One of the five species of sharks seen most commonly (gray reef) exhibited agonistic behavior following a rapid approach, which the authors interpreted as highly motivated food-searching behavior; other species milled about the transducer. Sharks often continued to arrive at the transducer site for approximately 2 minutes after the broadcasting had ended, indicating that the sharks could continue their approach in the absence of the sound stimulus. Some of the sharks exhibited a startle response if they were within a meter of the speaker when pulsing began following a pause in pulse-train presentation. However, the authors also noted that those sharks did not exhibit any avoidance behavior after the initial startle reaction. Finally, the Nelson and Johnson study described habituation to the pulsed sounds that seemed to be the result of the sharks approaching, searching for an edible source, and eventually learning that no prey were associated with the sounds.

These and other studies listed in Table 1 of Myrberg (2001) indicate that any high-level, low-frequency pulses could attract sharks from hundreds of meters away. The resulting redistribution of sharks could alter normal behavioral patterns as well as cause an increase in aggressive interactions between/among sharks that normally would not interact. While there is evidence that habituation would occur if the pulsed sound were on for days, there is also the possibility that the hunting ability of the sharks in the area could be impaired if the normal sounds of struggling or feeding prey are masked by low-frequency pulsed signals. Myrberg et al. (1972) also suggested that the rotors of low-flying/hovering helicopters could produce pulsed sounds below the water surface at levels sufficient to attract epipelagic sharks. Therefore, low-flying tourist helicopters could also affect the distribution of sharks.

5. PHYSIOLOGICAL EFFECTS OF NOISE

5.1 SWIM BLADDER DAMAGE AND RELATED EFFECTS

The gas bladder is a gas-filled structure found in many, though not all, bony fishes (also called the swim bladder or air bladder). There are several potential roles for the gas bladder, depending on species. Most often it is a buoyancy device that permits the fish to maintain its position at different depths. In addition, the gas bladder may be an accessory respiratory structure or part of a sound-producing system involving specialized muscles. The greatest physical effects from human-generated noise have been documented in fishes with swim bladders exposed to underwater explosions and water guns, which have been used for seismic surveys. An intense impulse of any kind causes a sudden, massive change in local pressure as the pressure wave passes. Depending on the proximity of the fish, the effects may be sub-lethal (though debilitating) or lethal. According to analyses by Dalen and Knutsen (1986), water-gun pulses produce more serious injuries to fishes than air guns because water gun pulses have an initial negative pressure wave; the initial phase for an air-gun pulse is compression. Although compression can cause lethal injury, compression followed by expansion does not destroy tissue as readily as initial expansion. As the expansion phase passes through the body of the fish, the swim bladder and blood vessels suddenly expand. Rapid gas bladder expansion can cause extrusion of the components of the digestive system (stomach or intestine); in more severe cases the gas bladder ruptures, and massive hemorrhaging occurs throughout the body and in the eyes (Yelverton et al., 1975; Govoni et al., 2003). In a very useful report, Baxter et al. (1982) reviewed other studies using commercially important fishes and graphed probability of fish kill with respect to fish size, depth, explosive size, and distance. None of these studies examined the ears of the fishes, but it is likely that structural damage was present there as well. This is particularly likely for species with a gas-filled structure or the gas bladder itself lying adjacent to the ear.

Fishes without gas bladders (e.g., the flatfishes) are less likely to be injured by explosive noise. Goertner et al. (1994) used the hogchoker, a common flatfish in the Chesapeake Bay, to quantify the distances at which a fish without a gas bladder would suffer minimal to maximal blast effects. The blasts were produced by 10-pound pentolite charges, and the fish were placed at the same depth, but different distances from the explosion. Hogchokers less than a meter away from the explosion were almost certain to experience severe injuries or death. At around 2 meters from the explosion, there were no deaths or fishes with severe hemorrhaging, but about 50% of the fishes did not swim normally, probably due to injury to components of the vestibular system. There was no examination of the structures of the ear in this study, so we have no data on structural correlates to the behavioral changes observed. At greater distances from the blast, hogchokers were not affected.

Jorgensen et al. (2005) found that juvenile herring may sustain mortal injuries from intense mid-frequency sonar pulses. The frequencies used in that study (1 – 3 kHz) overlap with the resonant frequency of the gas bladders of the juvenile fishes and, therefore, the impact of the intense noise was magnified by resonance. Estimation of the mortality rate was confounded by deaths among the control fishes not exposed to sonar pulses, but the experimental mortalities are worth noting given that no other experiments resulted in deaths and twice the number of experimental fish died compared to the controls. About 20% of the fishes died immediately after exposure to 20 sonar pulses at 189 dB dB re 1 μPa [202 dB re 1 μPa^2s, CW at 1.5 kHz] and 30% died within 10 days after exposure to 180 dB re 1 μPa [193 dB re 1 μPa^2s, 1.5-kHz CW and 191 dB re 1 μPa^2s, 3.4-kHz CW]. Worth noting is that frequency-modulated sonar signals of the

same frequency range and intensities did not cause mortality. In a follow-up study modeling risk volume for schools of herring during sonar exercises (hull-mounted and towed arrays with frequencies up to 8 kHz), Kvadsheim and Sevaldsen (2005) recommended restricted use of CW sonar to minimize negative impacts on juvenile fishes with gas bladders and concurred with the finding that FM sonars in the same frequency range pose no significant danger to fish stocks.

Sharks lack gas bladders and, therefore, are unlikely to suffer the same levels of physical/ physiological trauma seen in fishes with gas bladders. However, the hemorrhaging seen in the livers of bony fishes exposed to explosives may have deleterious effects on the buoyancy function provided by the livers of some sharks.

5.2 EFFECTS ON AUDITORY SYSTEMS OF TELEOST FISHES

5.2.1 Definitions — Threshold Shifts and Auditory Damage

A *threshold shift* has occurred when the previously measured minimum level of sound at a particular frequency (the threshold) must be exceeded to evoke a response. There are two kinds of threshold shifts: temporary threshold shift (TTS) or permanent threshold shift (PTS). A TTS may last a few minutes or hours, perhaps days or weeks, after which there is complete recovery of the previous responsiveness. TTS is the result when the auditory system has been insulted, but not permanently damaged. PTS has been documented in vertebrates from both chronic exposures to high noise levels and when severe damage is incurred from a single highly traumatic incident. The auditory system never recovers from a PTS.

For humans, temporary threshold shifts are commonly experienced after loud concerts, exposure to construction noise, or listening to music via headphones. The mechanisms of TTS have been described in other vertebrates and can include metabolic stress in the sensory hair cell, uncoupling of the hair cell tip links (proteins that connect the stereovillae and are involved in excitation of each hair cell) as described in chicks (Husbands et al., 1999) or uncoupling of or damage to the tectorial membrane that overlies mammalian hair cells (Clark, 1991). Temporary threshold shifts have been documented in fishes (see Section 7), but the mechanisms have not been revealed. Given that hair cells in fishes are structurally like those of mammals and are coupled to an overlying otolith, otoconia, or cupula, uncoupling or disruption of the tip links could occur, similar to the uncoupling of the tectorial membrane and hair cells in the mammalian cochlea. No studies have investigated this possibility as yet; however, eliminating damage during processing is a huge challenge to overcome if one is to examine changes in the relationship between the hair cells and the otolith. Metabolic stress also is a potential result of auditory over-stimulation in fishes since the hair cells of all vertebrates have similar metabolic mechanisms.

Permanent threshold shifts can be incurred by the human operators of pneumatic drills, pilots, and other workers that experience high noise levels in the workplace on a daily basis if they do not wear devices to protect the inner ear. In addition, brief, very loud pulses of sound, such as an explosion, can cause massive changes in hearing, even deafness. In mammals, permanent threshold shifts may be due to damage to the middle ear (tympanic membrane or auditory ossicles), to the hair cells of the inner ear, or the nerve fibers that innervate the ear (Bohne and Harding, 2000). Massive vibrations can cause shearing of the bundles to the extent that they are broken off (Levine et al., 1998). Severe damage to the hair cell results in cell death, and the loss of many hair cells can lead to death of adjacent cells and the nerves innervating that area of the cochlea (Bohne and Harding, 2000). In the adult mammalian cochlea, dead hair cells are not replaced by production of new hair cells, resulting in permanent loss of auditory receptors in the area damaged.

Damage to the ciliary bundles of hair cells has been documented in a teleost fish (Hastings et al., 1996) . However, in fishes, production of new hair cells is possible following hair cell loss (e.g., Lombarte et al., 1993), and given sufficient recovery time, threshold shifts may disappear (see Section 5.2.2). It is important to note that the regeneration of hair cells in fish was documented following use of an ototoxic (destroys hair cells) drug and the damage incurred by loud sound may differ in ways that would limit or eliminate recovery (e.g., disruption/destruction of the otolithic membrane). Recent studies on bullfrog saccules in culture indicate that there are sublethal levels of damage (e.g., loss of the ciliary bundle) that can be repaired by the hair cell itself (Baird et al., 2000; Gale et al., 2002). But as in the studies with fishes, the damage was incurred using an ototoxic drug and not high levels of sound.

In general, the most comprehensive studies on the effects of particular levels of noise on fishes have been conducted on hearing "specialists" with accessory auditory structures linking a gas-filled chamber to the ear. Those fishes are more sensitive to a broader bandwidth of sound, in particular, higher frequencies. Few studies have measured the sound field and reported the levels of particle motion at the location of the experimental fish. Thus, there are limited data on the sound levels that cause threshold shifts in the majority of marine fishes that are hearing generalists.

Two approaches have been used to assess the effects of noise on the auditory system. For the first, the fish is exposed to noise and then tested for changes in auditory responsiveness (i.e., changes in hearing sensitivity or threshold shifts). The most popular methodology for this kind of study is to use AEP (ABR) measurements to estimate hearing thresholds for each fish at frequencies of interest, expose those fish to noise, then estimate post-exposure thresholds to determine if there have been threshold shifts. A variation on this method is to use a set of control fish to establish baseline thresholds, expose another group of experimental fish to noise to measure their hearing thresholds after exposure, then compare the hearing thresholds from the exposure group to the baseline thresholds of the control group. The number of control and experimental animals must be greater for this approach in order to dilute the effects of individual variation.

The second approach to assess the effects of noise on the auditory system is to expose fishes to noise and then examine the sensory tissues of their ears to determine the condition of the individual sensory hair cells. The ciliary surface bundles of hair cells can be sheared off when noise levels are sufficiently high, or the hair cell may suffer severe physiological damage leading to death of the cell. When hair cells die, debris or holes in the surface of the sensory tissue can be seen using high-powered (electron) microscopy.

To date, there has been only one study that has combined the two approaches described here (summarized in DoN, 2005). Each of the pertinent studies will be discussed below.

5.2.2 Evidence of Threshold Shifts

The earliest study of threshold shifts in a teleost fish was conducted on the goldfish by Popper and Clarke (1976). The speaker delivering the noise stimulus was mounted in air, above the tank, and the measured noise levels were obtained with a pressure hydrophone at various points around the tank. The authors reported that SPL (sound pressure level) did not vary more than ± 2 dB; thus the exposure level was close to 150 dB re 1 µPa. The exposure duration was 8 hours. This study showed that temporary threshold shifts can occur in a teleost fish. Also of interest were the data indicating that in goldfish, as in mammals, TTS was not limited to only the test frequency. Specifically, in the Popper and Clarke study, the TTS induced by an intense 800-Hz tone also was evident at lower frequencies as well (500 Hz, but not at 1000 Hz).

Scholik and Yan (2001a,b) studied TTS induced by band-limited white noise (equal power at all frequencies within a specified band) in a fathead minnow (*Pimephales promelas*), which is a relative of the goldfish and also a "hearing specialist" with a physical connection between the gas bladder and the ear. The first step in these series of experiments was to estimate hearing thresholds using the ABR technique. Then small groups of fish were placed in a plastic tub with 5.5 cm of water. The broadband noise (300 Hz – 4 kHz) was reportedly projected at 142 dB re 1 µPa by a speaker suspended in air above the plastic tub. ABR thresholds were obtained immediately following noise exposure to document the occurrence of TTS, and additional ABR thresholds were obtained over subsequent days to document the time course for recovery to pre-exposure sensitivities. The methods used for this study are not ideal as the received level is difficult to assess since the sound field probably was not uniform in the plastic tub. In addition, Hastings and Popper (2005, see footnote 11) caution that the authors should have provided spectral density levels ($µPa^2$/Hz) for an accurate representation of the level for band-limited white noise. Based on their calculations, the source levels may have been 174 dB re 1 µPa. However, some of the results are of interest even without actual received levels. One group of fish was exposed to the white noise for 24 hours and tested immediately at the end of the exposure period. The white noise caused the maximum TTS (10 – 20 dB) in the range of frequencies to which the fathead minnow was most sensitive in the pre-exposure audiogram (800 – 2000 Hz). Shorter exposure periods were used to assess the time course of TTS at those frequencies, and the authors found that after only 1 hour of noise exposure, significant TTS was evident. By 2 hours, the magnitude of the average TTS was equivalent to that measured after 24 hours of exposure. This was the first evidence for an asymptotic threshold shift in a teleost fish, a phenomenon that had been described for mammals (Yost, 1994). Of additional interest was the recovery time from TTS in those experiments. After 24 hours for recovery, the mean thresholds at 800 and 1000 Hz were at baseline values for fish exposed to either 2 hours of white noise or 24 hours of white noise. The authors also noted that the return to baseline threshold was substantially slower at the higher frequencies tested (1500 and 2000 Hz) after 24 hours of exposure than after only 2 hours of exposure. These data are suggestive of different underlying physiological responses that warrant further experimentation and clarification.

Scholik and Yan (2002a) used the same experimental paradigm on a hearing generalist (bluegill sunfish, *Lepomis macrochirus*). The authors report that the ABR data indicated a significantly lower sensitivity to all the test frequencies than they had found in the fathead minnow (above). Unfortunately, the particle motion in the test apparatus was not measured, and the audiogram was determined only with regard to sound pressure level. In addition, since the pre-exposure data were obtained in one container and the white noise exposure was in another container with multiple animals, there is no valid way to compare the signal levels. Given the way this experiment was conducted, we cannot conclude that the ear of the bluegill sunfish would not exhibit threshold shifts under other noise exposure conditions.

In another series of experiments, Scholik and Yan (2002b) evaluated threshold shifts following exposure to a common human-generated noise: an outboard motor. The noise from an idling 55-hp engine was recorded at 50 cm from the source and then played through the in-air speaker, again over a plastic tub with a small amount of water in it. They used only the fathead minnow for these experiments. The boat noise had a peak frequency at 1.3 kHz, and the maximum sound pressure level was 142 dB re 1 µPa at the speaker to make the noise level comparable to the previous white noise experiments. The exposure duration was 2 hours. Threshold shifts were observed at the test frequencies around 1.3 kHz, with a maximum threshold shift of 13.5 dB (mean of five fish at 1.5 kHz). Based on the similarity of the threshold shift in this study and the previously described study using white noise on the same species, it is likely that recovery from

the boat-induced threshold shifts would be complete in less than a week following a 2-hour exposure. However, recovery assumes no further exposure to similar or higher levels of noise. In the natural environment, fishes are likely to be exposed to boat noise repeatedly on popular fishing grounds. To date, no study has examined the effects of repeated exposures to these relatively low-level, relatively long-duration noises. Such studies are warranted since episodic noise at levels that cause TTS when presented singly can cause PTS in mammals when presented episodically for months (e.g., Lonsbury-Martin et al., 1987). As noted above, the white noise study (Scholik and Yan, 2001a) indicated differing recovery times for 2-hour versus 24-hour exposure, which suggest there may be cumulative effects on the structures of the ear.

   White noise was also used to assess threshold shifts in goldfish and a freshwater catfish (*Pimelodus pictus*) after 12 hours or 24 hours of noise exposure (Amoser and Ladich, 2003). As in all studies conducted in plastic buckets, the exposure levels are not certain as the flexible sides would affect the sound field in unpredictable ways, and the fish were freely swimming during sound exposure. The authors state that the exposure level was 158 dB re 1 µPa. Auditory responses were recorded using the ABR technique prior to exposure and at various times following exposure to track recovery. Both of these fish species are hearing specialists, however, the ABR indicated a greater sensitivity to frequencies above 2 kHz in *Pimelodus*. The ABR measurements were repeated on days 3 and day 7 after exposure. The goldfish had fully recovered normal hearing by day 3, consistent with other studies, but recovery took longer for the catfish (more than 1 week for frequencies above 1 kHz). The authors propose that greater shifts in threshold require longer recovery times, possibly due to microanatomical injuries and hair cell death. New hair cells can be produced within several days (Lombarte et al. 1993), but no one has yet determined whether those hair cells are innervated and functional. It is important to note that the threshold shifts in both species were temporary, even though the time course for recovery differed.

   In another study, the effects of long-term exposure (up to 28 days) to white noise were compared in goldfish (as a representative hearing specialist) and a hearing generalist (tilapia, *Oreochromis niloticus*) by Smith et al. (2004a,b). The white noise was presented at 130 – 170 dB re 1 µPa for the long-term noise experiments. Hearing thresholds were measured using the ABR method. As noted previously, sound pressure level is an appropriate measure of a noise stimulus for fish with a pressure transduction mechanism associated with the ear, but does not adequately describe the actual noise levels for the hearing generalist that lacks a pressure transducer. Thus, the tilapia data will not be discussed. In the goldfish, measurable threshold shifts were apparent after 24 hours of exposure to white noise (130 dB re 1 µPa or larger); the threshold shift 7 days after exposure to 170 dB re 1 µPa was not significantly different from the shift after 21 days. These data show that threshold shifts reach an asymptote or maximum, after which continuing noise does not result in additional damage [as shown by Scholik and Yan (2001a) for another auditory specialist]. The asymptotic threshold shift (ATS) has been well documented in mammals (Yost, 1994), and the occurrence in fishes suggests similar mechanisms may be at work. The data also indicate that in fish, threshold shifts were due to reversible processes or repairable damage: the goldfish showed improved thresholds within 24 hours and recovered normal hearing at most frequencies within 14 days following 21 days of noise exposure at the highest level (Smith et al., 2004a). Given that production of new hair cells is possible in the ears of adult fishes (but not in the adult mammalian cochlea), it is unclear whether the return to normal thresholds was due to metabolic recovery, recovery of damaged surface structures on the hair cells, or replacement of dead hair cells. The improvements seen within 24 hours suggest that at least some of the improvement was due to recovery rather than replacement.

Popper et al. (2005) completed a study of the potential for threshold shifts in three species of fish exposed to repeated firing from an airgun array in the McKenzie River Delta. One of the species is a hearing specialist (lake chub, *Couesius plumbeus*) and the other two species have no known auditory specializations (northern pike, *Esox lucius*; broad whitefish, *Coregonus nasus*). Fish were held in an enclosure in shallow water and exposed to 5 shots or 20 shots. ABR thresholds were obtained for a group of control animals not exposed to air-gun noise, and ABR thresholds were obtained for experimental animals immediately following noise exposure and for some groups, 18 – 20 hours following exposure. A caveat is needed with regard to the stimuli used for threshold determinations in these experiments. Popper et al. (2005) provided a measure of the particle velocity (dB re 1 nm/s) in the test tank at the head of the fish for comparison with the pressure levels (100 dB re 1 μPa) for the frequencies used for threshold determinations (100, 200, 400, 800, 1600 Hz). The variations indicate that the sound field was variable across the frequencies tested, making threshold measurements at different frequencies difficult to compare for the two species that lack a pressure-sensitive ear (pike and whitefish). For example, the largest particle velocity occurred at 100 Hz (72 dB re 1 nm/s), with lower particle velocity at 200 Hz (58 dB re 1 nm/s) than at 400 Hz (67 dB re 1 nm/s). Since the stimulus levels at each test frequency were controlled with regard to pressure (dB re 1 μPa), the threshold comparisons are more appropriate for the fish with a pressure sensitive auditory system, the lake chub. In addition, sample sizes were small (as few as two fish, with a maximum of seven) and some of the results were understandably inconsistent. The strongest conclusion reached by the authors is that, on average, the ABR thresholds were within normal range less than 24 hours after exposure to air-gun noise even for fishes with the greatest threshold shifts (20 – 30 dB). Although no data were presented with regard to the condition of the tissue of the inner ear, the authors did note that there was no evidence of disorientation that might indicate damage to vestibular hair cells, and the recovery of normal hearing indicates there was no permanent damage to the auditory hair cells.

The tissues of the inner ear were examined after noise exposure in another study by the Popper lab (Hastings and Popper, 2005, Department of Navy (DoN), 2005, and Popper et al., in press) in which two species of fishes were exposed to high levels of LFA sonar. No physical trauma was discovered in the ears of fish for whom threshold shifts were likely. The design of the experiment is important and will be described in detail. Fishery-raised rainbow trout (*Oncorhynchus mykiss*) or channel catfish (*Ictalurus punctatus*) were distributed into groups called "baseline" (ABR thresholds only, no experimental manipulation), "controls" (handled like experimental fish but no sonar, ABR thresholds followed handling), and "experimental" fish (LFA sonar exposure followed by ABR threshold assessment). Thus, the same fish were not used to measure pre- and post-exposure thresholds. The control and experimental fish were placed in a large acoustically transparent box that was lowered into the water to a depth of 10.8 meters. The control fish remained in the water for an equivalent time as the experimental fish, but were not exposed to LFA sonar. In the presence of the experimental fish, a U.S. Navy Surveillance Towed Array Sensor System (SURTASS) LFA sound projector, located about 15 meters below the fish box, produced three LFA sonar series, each consisting of three FM sweeps, three tones, and three higher frequency FM sweeps (DoN, 2005), with a range of about 155 – 325 Hz, at a maximum received level of 193 dB re 1 μPa (rms).

Although the behavioral observations suggest short-term changes, the ABR data indicate temporary threshold shifts of considerable magnitude for both species. Rainbow trout moved to the bottom of the box at onset of the sonar, which is a common avoidance response (see Section 4.1.3). Their behavior returned to what is called "milling" around inside the box after the LFA sonar was turned off. Channel catfish exhibited two behaviors. First, they reacted to the onset of the sound at each presentation with a sudden change in body posture (potentially a startle or alarm

response, see Sections 4.1.1, 4.1.2) and then lined up facing the source until the source was turned off. This latter response is especially intriguing since the fish were orienting with respect to the source. We can only guess at the functional significance of this behavior, but it is possible that input to the ears is minimized in that orientation in this species, and this possibility should be investigated further. When the source was turned off, the fish returned to behavior that was "statistically no different" from pre-exposure milling.

The ABR threshold data were collected at only three frequencies for rainbow trout, a hearing generalist (100, 200, 400 Hz) and four frequencies for the channel catfish, a hearing specialist (200, 600, 800, 1000 Hz). Popper et al. (2005) reported that both species exhibited threshold shifts immediately after exposure, although the magnitude of the shifts varied. Threshold shift was around 20 dB in the rainbow trout (reported at 400 Hz) with considerable variation across individuals. The maximum threshold shift in the catfish was around 10 dB at 200 Hz (400 Hz was not tested), but catfish also had higher thresholds at the highest frequency tested, well above the frequency high of 325 Hz in the LFA sonar.

Given that the LFA sonar frequencies ranged from 155 – 325 Hz, the threshold shift data may seem unexpected for both species. Two issues are pertinent here. First, all of the threshold data are reported in terms of pressure (dB re 1 µPa), so the data for rainbow trout (with no known auditory sensitivity to sound pressure) can only be viewed as an indication of a threshold shift, not evidence for a specific magnitude at a specific frequency. Second, with regard to potential differences in the extent and time course for TTS, there may be different mechanisms responsible for threshold shifts in generalist fishes and specialist fishes. Recordings from primary auditory fibers (from the ear to the brain) in both generalist and specialist fish species indicate that auditory cells usually respond to many frequencies, with bandwidths in the range of 10s to 100s of Hertz. For example, cells that respond to 150 Hz might also respond well to 100 or 200 Hz, or both. Another subset of cells might respond well to sounds 300 – 400 Hz. In the presence of LFA sonar, all of these cells could be affected. Therefore, threshold shifts may be manifest as a frequency response beyond that of the stimulus due to altered responses in cells with broad frequency responses. However, based on the presence of a threshold shift across all frequencies (up to 1000 Hz) in channel catfish in the LFA study conducted by Popper (DoN, 2005), there might be a change in responsiveness at the level of the peripheral auditory *system* rather than the hair cells or the endorgan. A candidate mechanism is a change in the gas bladder volume in response to the high pressure levels of the noise stimulus. This is worthy of investigation since a change in gas bladder volume is essentially a reflex response, and the rate of recovery to pre-exposure thresholds would be fairly rapid and equivalent across the frequencies that depend on that accessory, pressure pathway. Detailed documentation of the time course of recovery is needed, e.g., testing immediately following exposure, and then 6, 12, 18, and 24 hours following exposure in auditory specialist species, as the TTS may have an even shorter duration than reported for those species. The time course for recovery from TTS in nonspecialists appears to be longer (perhaps more than 48 hours; DoN 2005), but again, more data are needed.

Johansen et al. (2005) noted that negative effects were more likely when fish were exposed to tones (or CW sounds) than to FM sonar signals. The LFA sonar signal used in the SURTASS LFA study by Popper (DoN 2005) that caused threshold shifts in both species tested consisted of a combination of frequency sweeps and tones, with the tones at 200 – 230 Hz. Given that TTS was observed with that mixture of components, future experiments should be directed at comparing the potential for threshold shifts with the mixed LFA sonar signal currently in use with an LFA signal that consists only of FM sweeps.

5.2.3 Evidence of Auditory Damage

Very few studies have examined the structures of the ear in detail following exposure to high levels of sound. As described above, the Popper lab showed that threshold shifts can occur with no physical evidence of damage to the structures in the ear (DoN, 2005). The earliest study to provide evidence for auditory damage was conducted by Enger on cod and reported in a book chapter (Enger, 1981) with few details about the methods. Enger noted that the codfish was placed in an aluminum tube and exposed to high-pressure stimuli, but small particle displacement. As described earlier, cod have an extension of the gas bladder that lies near the inner ear, providing the fish with the necessary transducer of pressure to particle motion. Enger showed that the surface structures of hair cells on the saccule can be destroyed by high sound pressure levels in the range of frequencies to which the cod was most sensitive (50 – 350 Hz at approximately 180 dB re 1 µPa). The duration of the noise exposure was varied (1 – 5 hours), but no correlation between amount of damage and exposure time was included.

Hastings et al. (1996) used a freshwater fish (oscar, *Astronotus oscellatus*) without auditory accessories (i.e., a hearing generalist) to investigate auditory damage following exposure to pulsed (20% duty cycle) and continuous tonal noise at relatively high levels (maximum 180 dB re 1 µPa). Although the experimental enclosure was designed to permit a traveling wave stimulus with consistent particle motion at the location of the fish in the chamber, sound particle velocities were likely several times larger than those that would have accompanied progressive plane waves with the same sound pressure level. Two frequencies were used (60, 300 Hz). The fish were permitted to survive for either 1 day or 4 days after 1 hour of exposure, and then the ears and portions of the lateral line were examined for hair cell damage. Preparation of the tissues is a critical phase in the analysis of hair cell structure. Damage to the hair cells due to handling the tissue can be difficult to distinguish from damage due to excessive levels of sound exposure. Unfortunately, the inconsistency of the data in this study does not allow us to completely eliminate the possibility that the damage seen was due to handling the tissue rather than the effects of excessive noise exposure. A very small swath of hair cell damage was seen in four of five fishes stimulated by 300 Hz at the highest level (approximately 60 dB over threshold at that frequency), though not in a consistent location. Only one of those fish had damage in the same endorgan on both sides, and none of the fish had damage in the saccule, despite the fact that a behavioral audiogram (Yan and Popper, 1992) indicated that the oscar is most sensitive to frequencies around 200 Hz, and the saccule is likely to be the primary auditory endorgan in this species. Hastings et al. (1996) also suggested that more damage may have been apparent if the fish had been held longer; however, Enger fixed the cod tissue for histological examination immediately after noise exposure and saw the levels of damage that Hastings et al. (1996) had expected to see. Thus, there is no obvious cause-and-effect explanation for the data obtained from the oscar.

Significant hair cell damage was seen in another study. McCauley et al. (2003a,b) examined the saccules of pink snapper (*Pagrus auratus*) following exposure to repeated air-gun noise. The vessel with the air-gun array moved past the fish (6 pulses/minute), approaching from hundreds of meters away to within 5 – 15 m of the fish, in an attempt to simulate expected exposure levels during a standard survey. The fish were free-swimming, but their movement was restricted by an enclosure. Received levels were between 150 – 180 dB re 1 µPa during the approaches, with greatest energy between 20 – 200 Hz. A single saccule was examined from each of the fishes in three groups: controls with no noise exposure, three fish exposed to the survey noise and sacrificed 18 days post exposure, and five fish sacrificed 58 days post exposure. The sample sizes are small for these experiments, but the data provide good preliminary evidence that exposure to impulsive noise, such as air-gun shots, can cause significant hair cell loss that is not visible until more than 2 weeks after exposure. The saccules from the fish sacrificed 18 days after exposure

did not have significant hair cell loss, but fish sacrificed 58 days after exposure had lost as much as 15% of the hair cells in one region of the saccule. Measurements of hearing thresholds were not part of the experimental design for this field study and, at present, there is no way to know whether the fish experienced hearing loss. In mammals, hair cell losses less than 30% do not affect thresholds in the low-frequency region of the cochlea (e.g., 500 Hz; Bohne and Harding, 2000), but the cochlea is organized very differently from the fish saccule, particularly with regard to gain control, and comparisons with fishes may not be valid. Thus, there is a clear need for measurements of hair cell loss versus threshold shift in fishes following exposure to sources of human-generated noise.

Although the time course for recovery from hair cell damage induced by ototoxic drugs is known in some fishes (e.g., Lombarte et al., 1993), the time course for noise-induced damage is not well documented. As suggested by Hastings et al. (1996) with regard to the lack of consistent damage in a hearing generalist fish 4 days after noise exposure, it is possible that metabolic or physiological stress causes damage that is evident only after sufficient time has passed for visible damage to result. Alternatively, over-stimulation of the auditory system may result in metabolic changes that are easily repaired. Studies in hearing specialists have documented recovery from threshold shifts within 1 – 3 days of exposure to damaging noise (Scholik and Yan, 2001a, 2002a; Amoser and Ladich, 2003; Smith et al., 2004). We need careful documentation of the time course of threshold shifts, the appearance of physical damage, and recovery times for both auditory sensitivity and structural integrity of the sensory tissues in the ears of hearing generalists and specialists among the fishes.

5.3 EFFECTS ON LATERAL LINE SYSTEM OF TELEOST FISHES

Few studies have examined the effects of human-generated noise on the overall responsiveness or the individual hair cells of the lateral line system. A single study (Hastings et al., 1996) did not find damage when a generalist fish was exposed to 60-Hz tones at a maximum of 180 dB re 1 μPa. As noted previously, the lateral line does not respond to the pressure component of sound that was quantified in this study, so the exposure level is not meaningful, but the lack of damage is included here for completeness. Denton and Gray (1993) estimated that particle velocities of 150 mm/sec could result in damage to the individual components (neuromasts) of the lateral line system, but no data exist to support or refute this hypothesis.

In general, the lateral line is sensitive to particle displacement near the fish's body. Although the relative sensitivity may vary among species, the system is not believed to function well beyond a few body lengths of the fish. Therefore, concern for damage to the lateral line system would be restricted to fish that are less than a meter from an intense low-frequency source. There is one caveat: in some taxonomically distant species, e.g., some herrings (order Clupeiformes), a butterfly fish (Perciformes), and an estuarine minnow (Cypriniformes), stimulation of the gas-filled auditory bullae or swim bladder can indirectly stimulate the lateral line (discussed in Popper et al. 2003). Therefore, high-level pressure stimuli may have a greater effect than expected on the lateral line system in these species and potentially in others in which a connection exists but has not been described. However, there are no studies that have examined the effects of loud sources on the lateral line system of fishes with this connection. Jorgensen et al. (2005) attempted to examine the neuromasts of juvenile herring exposed to high levels of mid-frequency sonars, but difficulties with tissue preparation resulted in damage to both control and experimental larval neuromasts. Thus, none of the damage seen can be attributed to noise with any confidence.

5.4 EFFECTS ON AUDITORY SYSTEMS OF CARTILAGINOUS FISH

At the time of this writing, there are no published studies or reports that provide evidence of damage to the auditory system of sharks from human-generated noise. Although startle responses have been observed at the onset of a high-level, human-generated sound (see Myrberg, 2001), no study has examined the inner ear of sharks exposed to potentially harmful levels of noise. Although sharks do not have gas-filled structures, there is evidence that some species may have a specialized or derived auditory pathway (see Section 2.2.2). Thus, the species investigated should be chosen carefully to represent the diversity of auditory systems in the group. In addition, exposure to loud impulsive sounds may have unexpected impacts on sharks given that one of the structures often damaged in bony fishes is the liver, and many shark species rely on oil held in the greatly enlarged liver (squalene) for buoyancy.

6. NON-AUDITORY PHYSIOLOGICAL EFFECTS: GROWTH AND STRESS

There are few studies of the effects of noise on growth and development. This is obviously a difficult concern to address as it requires repeated observation and measurement without loss of individuals from disease or predation. An early study by Banner and Hyatt (1973) at an aquaculture facility is frequently cited, but the stimuli were not similar to any human-generated noise of concern. In their study, Banner and Hyatt exposed eggs and larval fishes of two killifish species (*Cyprinodon variegatus* and *Fundulus similes*) to noise produced by two bubbling air stones. Turbulence was eliminated as a factor by placing the air stones far from the basket holding the eggs or fish. The noise was measured with respect to ambient noise measurements in the ocean (with heavy ship traffic, from Wenz, 1962) and shallow water ambient noise (see Banner and Hyatt, 1973, Figure 2). Both the control tank and the experimental tank had noise levels above ambient ocean/shallow water below 200 Hz, but the noisy tank had higher levels (approximately 5 – 15 dB) at those frequencies than the control tank. Egg mortality was not significantly different in the noisy tank for either species. Larval *Fundulus* did not show any difference in survival rate for control versus noisy tanks, but *Cyprinodon* larvae had higher mortality in the noisy tank. The data are not impressive due to small numbers of individuals in each experiment, but the authors found statistically significant differences in growth (length and weight) for the larvae of both species. Individuals raised in the noisier environment were shorter and weighed significantly less. This study reveals that more work needs to be done on growth in larval fishes that may encounter high levels of human-generated environmental noise. Stress can alter hormonal levels important for growth and, therefore, can potentially affect growth rates.

Stress causes physiological responses in fishes that are similar to those documented in other vertebrates (see Moberg and Mench, 2000). Until recently, stress in fishes had been evaluated primarily in response to handling (Mazeaud et al., 1977, Waring et al., 1996) or conditions in aquaculture facilities (Barton et al., 1988). The major concern has been to minimize stress responses that can impact survival, growth, and reproduction (e.g., Schreck et al., 2001). Few studies considered environmental noise as a potentially serious source of stress (but see Bart et al., 2001).

A recent study by Smith et al. (2004a) on goldfish indicates noise levels that cause an observable alarm response can also initiate a physiological stress response. The physiological stress response is initiated automatically by the nervous system. Hormones released from the brain are distributed throughout the body to coordinate a response ("fight or flight") via the circulatory system (in the plasma). A cascade of events results in the release of cortisol and then sugars (glucose) from storage sites into the blood stream to provide energy to the components of the body involved in the response (e.g., muscles). Smith et al. (2004a) took blood samples from goldfish after exposure to white noise (0.1 – 10 kHz) with received levels of 160 – 170 dB re 1 μPa for varying periods of time. Although the fish were stressed by the procedures to obtain blood samples, there were trends in the data that appear to be evidence for a limited stress response to the noise. A startle response and alarm swimming were observed at onset of the white noise, and cortisol levels in the plasma had tripled after 10 minutes of noise exposure. However, plasma samples taken following 60 minutes of exposure revealed normal plasma cortisol levels. These data indicate that the fish had recovered from the initial alarm, even though the noise had continued for an hour. Plasma glucose levels were also measured. There was no statistically significant change in mean glucose levels at 10 minutes or 60 minutes of noise exposure; however, there was a trend of increasing plasma glucose. The most important finding was the lack

of a long-term effect. No significant elevation of cortisol or glucose levels was apparent, even after 21 days of noise exposure.

Physiological stress responses are a potential concern in areas where human-generated noise could interfere with normal behavior of local populations of fish (i.e., not migratory species passing through an area). However, continuous low-level noise or noises that do not initiate a startle or alarm response are unlikely to cause a long term physiological stress response. Smith et al. (2004a) note that exposing fish to discontinuous, repeated noise (more similar to human-generated noises of concern) might yield different physiological results. This is clearly worthy of further study, particularly in species of economic importance.

Jorgensen et al. (2005) examined the growth rates of saithe (*Pollachius virens*), wolf fish (*Anarhichas minor*), and cod (*Gadus morhua*) after exposure to CW sonar pulses at 1.5, 4, and 6.5 kHz (wolf fish not included in the latter group). The number of pulses were varied as well: 4, 20, or 100 (no wolf fish in the latter group). There were no significant differences in length or weight of the experimentally exposed fish compared to the controls of the same species up to a month later, even for fish exposed to levels greater than 180 dB re 1 μPa. Given that the three fish species chosen probably do not hear the frequencies used in this study, the data merely indicate no non-auditory effects were seen following exposure to the sonar pulses. Mortality of juvenile herring also included in this study was discussed in Section 5.1.

7. CONCLUSIONS

Fishes are a very diverse group of vertebrates. As noted in several studies, there are species-specific differences in how and when an individual or a school of fish responds to human-generated noise. In addition, fishes may respond differently to approaching noise sources than to noise sources with sudden, high-level onsets. Sudden intense sound, such as explosions, can result in immediate death or severe injury with eventual death for animals within a critical range. Beyond the critical range, the received levels are low enough that the animals may exhibit other behavioral responses, such as startle, alarm swimming, or avoidance. Although the behavioral responses may appear to be non-life-threatening, they may attract the attention of predators or end feeding or reproductive activities. Eventually, even brief behavioral responses could have a negative cumulative effect on a population.

Laboratory evidence indicates that temporary threshold shifts occur in fishes, but the majority of species for which TTS has been demonstrated are hearing specialists. As described in Section 2, hearing specialists have an accessory pathway that transduces the pressure component of a sound wave into particle motion (through vibration of a gas-filled structure that causes particle motion in the fluids surrounding the sensory hair cells). Although TTS has been indicated in generalist fish (e.g., DoN, 2005), no study has been done in which particle motion was varied systematically and thresholds monitored for a hearing generalist species. There are good reasons to encourage this work, given that the majority of marine fish species are hearing generalists (for which particle motion is the best stimulus for the ear), and it is this group that is most likely to be exposed to increasing levels of human-generated noise. In addition, evidence that TTS occurs without visible damage to the auditory system of specialist or generalist fishes (DoN, 2005) indicates that examination of the auditory system alone cannot be used to infer the absence of TTS.

Permanent threshold shifts (and resulting deafness) have not been demonstrated in any fish. However, there is evidence that hair cell destruction caused by acoustic trauma can be severe and long term (McCauley et al., 2003a,b). McCauley et al. (2003a,b) did not obtain audiograms or test the fish for threshold shifts, and we cannot conclude that there was a significant deficit in hearing given that, in a mammal, hair cell loss is not always accompanied by measurable auditory deficits (Bohne and Harding, 2000). Studies correlating the magnitude or duration of threshold shifts with anatomical changes in the ear are necessary before we can predict the time course of auditory deficits in any fish based on anatomical data alone. These studies should include cartilaginous fishes, such as pelagic and benthic sharks, skates, and rays, since their auditory systems have potentially important variations in structures and morphology.

Several studies have shown that teleost fish exhibit asymptotic threshold shifts, in which threshold shifts increase with increasing exposure duration up to a maximum duration (likely to be species specific), after which the loss of sensitivity at a particular frequency no longer changes significantly with increasing exposure duration. However, there is evidence that although the threshold shift does not increase, the damage incurred may be increasing. The damage incurred by the peripheral auditory system may be progressive, with different categories of injury present for different combinations of frequency, sound level, and duration of the stimulus (Saunders et al., 1991). Recovery from longer exposures or greater sound levels may require much longer recovery times in fish, as suggested by Scholik and Yan (2001a). This phenomenon has been noted in mammals (Saunders et al., 1991). Therefore, it is important not only to document threshold shifts with various levels of experimental stimulation, but tracking recovery from TTS is also extremely important if we are to understand how to minimize damage to the auditory systems of fishes while

maximizing the likelihood of recovery under conditions where exposure to human-generated noise is considered unavoidable. The results of repeated exposure to the same noise must also be considered since fishes may not be able to regenerate lost hair cells under conditions of continuing or repeated exposure to the same damaging stimulus. In effect, multiple temporary threshold shifts may result in "functionally permanent" hearing deficits if insufficient recovery time is permitted between exposures.

In addition, some studies have indicated that two or more of the otolithic organs in the ear (saccule, lagena, utricle) may be involved in hearing, but each may vary in the frequencies and/or intensities of sounds to which it responds. Therefore, one endorgan may be more greatly affected than others by loud noises of particular frequency compositions. For this reason, all potential auditory endorgans should be examined when investigating auditory deficits. Lastly, we should not assume that limited hearing deficits will not cause important changes since convergence of the various sources of auditory input may be required for sound localization or the coordination of complex behavioral responses to sounds.

The physiological transition from temporary threshold shifts to permanent threshold shifts in fish might have a different time course than in mammals, although the initial mechanisms (destruction of ciliary bundles or the crippling of metabolic machinery) may be similar. Unlike mammals, fish can regenerate lost hair cells; however, as noted above, we do not know at what point damage to the hair cells or the supporting structures of the inner ear is so extensive that fish cannot regenerate hair cells and would have permanent loss of sensitivity to certain frequencies or total loss of hearing. Damage to the blood supply within the ear is likely to result when other soft tissues of the body are damaged by intense noise. Under those conditions, regeneration may be impossible; however, under the conditions of serious injury as seen following explosions (Baxter et al., 1982), immediate death is more likely to be the result of damage to soft tissues other than the inner ear.

8. RECOMMENDATIONS

Stimuli used for experimental studies thus far are either broadband impulse sounds with rapid rise times, white noise, tonal bursts, or sustained tones. Nearly all noise studies were conducted with hearing specialist species, and the stimulus parameter that was varied quantitatively was the sound pressure level. Given that sensitivity to sound pressure is highly variable among fishes and may be completely absent in some fishes (in particular cartilaginous fishes), sound pressure is not the best variable to use to assess the effects of noise on fishes in general.

If we consider the existing data for hearing specialists that can detect sound pressure, there is some evidence that the sound pressure *difference* between threshold and the noise level is the critical parameter to consider when predicting the potential for threshold shifts in those species. More data are needed from species with different audiograms, i.e., different best frequencies, to confirm that the received level above threshold is the most relevant parameter to measure.

When hearing generalist species were included in noise studies, the particle motion was not quantified nor produced at equivalent levels with respect to the thresholds of the species under experimentation. Thus, the published conclusions that the hearing generalist shows no threshold shift at the same levels that induce TTS in hearing specialists are not valid, since the stimulus levels are *not* the same given the different sensory modes of the auditory systems.

When describing particle motion of a sound wave, one can measure the particle displacement (in nanometers or microns), the velocity (nm/sec) or acceleration (nm/sec/sec or velocity changes over time). Hastings et al. (1996) provide the important observation that acoustic particle acceleration is more important to consider than pressure for many, perhaps most, fish. Acoustic particle acceleration increases proportionally with frequency for a harmonic plane wave of sound. Hastings et al. (1996) provide the following example. Given two frequency stimuli presented at the *same* sound pressure level, the acoustic particle acceleration at 300 Hz is five times greater than the particle acceleration at 60 Hz. Therefore, one of the greatest needs in future studies attempting to evaluate effects (or lack thereof) from human-generated noise on fishes is an appropriate quantification of the sound stimulus parameter to which the fish is most sensitive.

Research recommendations follow:

1. Additional studies of the behavioral and physiological effects of human-generated noise are needed on species that are of commercial importance. Although all species of fish are important at the ecosystem level, more is known about the behavior and life histories of fishes of economic importance. It is also likely that funding would be more easily obtained for studies of those species. Epibenthic species (e.g., cod, hake), pelagic fishes without gas bladders (e.g., tuna) and auditory specialists, such as herring, would be appropriate species for study.

2. All studies of the effects of human-generated noise must include the absolute exposure level (received level and time of exposure) and the received level in dB above threshold. This requires an audiogram for the experimental species as well as careful measurements of the sound field at the location of the fish. Hastings et al. (1996) suggested that 90 – 140 dB above threshold may be sufficient to cause damage (depending on exposure duration). This is easily tested if the appropriate experimental conditions are maintained.

3. Researchers need a calibrated system that is easily obtained and user-friendly to accurately measure particle motion in a sound field (as well as the sound pressure levels) if the fish are free-moving, or at the fish if the fish is restrained.

4. Long-term studies of fish exposure to actual human-generated sound are needed. Repeated exposures over weeks and months may reveal different levels of auditory damage and different time courses for repair than laboratory studies have shown thus far. Fish should be followed for at least a week after exposure ends, and preferably longer, since the physiological processes that result in the death of hair cells and/or the growth of replacement hair cells can extend over that time period. It is important to use realistic exposure levels, exposure durations, and repetitions to assess how quickly fish might recover in nature if escape from the noise is not possible or is unlikely due to territorial behavior or restrictive habitat requirements, for example. The ideal experiments would identify individuals (e.g., using tags) and utilize the same individuals as their own controls. This is clearly not possible for studies examining the anatomical correlates for physiological changes. However, since one study has shown that threshold shifts can occur without any physical evidence of damage to the ear, tracking changes in auditory thresholds appears to be the most efficient method of making initial assessments. In addition, recovery from threshold shifts should be tracked in greater detail in auditory specialists, ideally using repeated measures on the same individuals since there is evidence that recovery can occur within a day. Recovery could be even faster if the broadband threshold shifts seen in specialist fishes result from changes in gas bladder volume.

5. Large sample sizes are needed to provide biologically relevant and statistically significant data on individual variation in auditory thresholds pre-exposure and post-exposure. At present, there are no good data on the natural variation in audiograms of individuals in a population. It is likely that for fish, as in other animals, some individuals will be more susceptible to noise damage than others, requiring a population approach to really understand the ramifications of introducing noise into the critical habitat of a commercially important species.

6. One of the difficulties in evaluating the potential seriousness of threshold shifts is that auditory fibers respond broadly (across tens to hundreds of Hz) in addition to having a range of sensitivities. Narrower tuning (narrower frequency responses) appears to be the result of higher order processing (e.g., midbrain, Lu and Fay 1993; Edds-Walton and Fay 2003). Threshold shifts measured at the brainstem level may reflect temporary elimination of an entire population of sensory neurons, which could more broadly affect auditory processes (e.g., perception) that require the convergence of those inputs. In other words, threshold shifts do not merely indicate that fishes may not hear as well prior to exposure to noise, but they may not be able to assess specific features of their acoustic environment due to the altered auditory inputs (as suggested by Wysocki and Ladich, 2005). Given that threshold shifts can be produced predictably in auditory specialist fishes, studies are needed to assess the potential for concomitant changes in auditory processing such as sound discrimination.

9. LITERATURE CITED

Amoser, S and F. Ladich. 2003. Diversity in noise-induced temporary hearing loss in otophysine fishes. J. Acoust. Soc. Am. 113:2170-2179.

Astrup, J and B. Møhl. 1993. Detection of intense ultrasound by the cod *Gadus morhua*. J. Exp. Biol. 182:71-80.

Astrup, J and B. Møhl. 1998, Discrimination between high and low repetition rates of ultrasonic pulses by the cod. J. Fish. Biol. 52:205-208.

Baird, RA, MD Burton, DS Fashena, and RA Naeger. 2000. Hair cell recovery in mitotically blocked cultures of the bullfrog saccule. Proc. Natl. Acad. Sci., USA. 97(22):11722-11729.

Banner, A. 1967. Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey). In: PH Cahn (ed.) Lateral Line Detectors, Indiana University Press, Bloomington, Indiana, pp. 265-273.

Banner, A and M Hyatt. 1973. Effects of noise on eggs and larvae of two estuarine fishes. Tans. Am. Fish. Soc. 1:134-136.

Bart, AN, J Clark, J Young, and Y Zohar. 2001. Underwater ambient noise measurements in aquaculture systems: a survey. Aquacult. Eng. 25:99-110.

Barton, BA, CB Schreck, and LG Fowler. 1988. Fasting and diet content affect stress-induced changes in plasma glucose and cortisol in juvenile Chinook salmon. Prog. Fish. Cult. 50:16-22.

Baxter, L II, EE Hays, GR Hampson, and RH Backus. 1982. Mortality of fish subjected to explosive shock as applied to oil well severance on Georges Bank. Woods Hole Oceanographic Institution Technical Report, WHOI-82-54.

Bohne, BA and GW Harding. 2000. Degeneration in the cochlea after noise damage: primary versus secondary events. Am. J. Otol. 21(4):505-509.

Braun, CB, S Coombs, and RR Fay. 2002. What is the nature of multisensory interaction between octavolateralis sub-systems? Brain, Behav. Evol. 59(4):162-176.

Casper, BM, PS Lobel, and HY Yan. 2003. The hearing sensitivity of the little skate, *Raja erinacea*: A comparison of two methods. Environ. Biol. Fishes. 68:371-379.

Chapman CJ and AD Hawkins. 1969. The importance of sound in fish behavior in relation to capture by trawls. FAO Fish. Rep. 62(3):717-729. [ref. in Pearson et al. 1992]

Clark, WW. 1991. Recent studies of temporary threshold shift (TTS) and permanent threshold shift (PTS) in animals. J. Acoust. Soc. Am. 90(1):155-163 [review].

Coombs, S, J Janssen, and JF Webb. 1998. Diversity of lateral line systems: Evolutionary and functional considerations. In: Sensory biology of aquatic animals, Atema, J, RR Fay, AN Popper, and WN Tavolga, eds. Springer-Verlag, New York, pp.553-593.

Corwin, JT 1981. Peripheral auditory physiology in the lemon shark: evidence of parallel otolithic and non-otolithic sound detection. J. Comp. Physiol. 142:379-390.

Corwin, JT. 1989. Functional anatomy of the auditory system in sharks and rays. J. Exper. Biol. (Zool. Suppl.)2:62-74.

Corwin, JR, TH Bullock, and J Schweitzer. 1982. The auditory brainstem response in five vertebrate classes. Electroencephalogr. Clin. Neruophysiol. 54:629-641.

Dalen, J and GM Knutsen. 1986. Scaring effects in fish and harmful effects on eggs, larvae and fry by offshore seismic exploration. In: Progress in Underwater Acoustics. Merklinger, HM (ed.) Plenum Press, New York ,pp. 93-102.

Denton, EJ and JAB Gray. 1988. Mechanical factors in the excitation of the lateral lines of fishes. In: Sensory Biology of Aquatic Animals, J Atema, RR Fay, AN Popper, and WN Tavolga, eds., (Springer, New York), pp. 595-617.

Denton EJ and JAB Gray. 1993. Stimulation of the acoustico-lateralis system of clupeid fish by external sources and their own movements. Phil. Trans. R. Soc. Lond (B). 341:113-127.

Denton, EJ, JAB Gray, and JHS Blaxter. 1979. The mechanics of the clupeid acousticolateralis system: frequency responses. J. Mar. Biol. Assoc. UK. 59:27-47.

Department of the Navy (DoN). 2005. Draft Supplemental Environmental Impact Statement Surveillance Towed Array Sensor System, Low Frequency Active (SURTASS LFA) Sonar, pp. 4-10 – 4-15.

Edds-Walton PL and RR Fay. 2003. Directional selectivity and frequency tuning of midbrain cells in the oyster toadfish, *Opsanus tau.* J. Comp. Physio. A 189: 527-543.

Edds-Walton, PL and RR Fay. 2005. Sharpening of directional responses along the auditory pathway of the oyster toadfish, *Opsanus tau*. J. Comp. Physiol. A (in press).

Edds-Walton PL, RR Fay, and SM Highstein. 1999. Dendritic arbors and central projections of auditory fibers from the saccule of the toadfish (*Opsanus tau).* J Comp Neurol 411: 212-238.

Engås, A, S Løkkeborg, E Ona, and AV Soldal. 1996. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 53:2238-2249.

Enger, PS. 1981. Frequency discrimination in teleosts—central or peripheral? In: Hearing and Sound Communication in Fishes, W.N. Tavolga et al., eds. Springer-Verlag, New York, pp. 243-255.

Fay, RR. 1984. The goldfish ear codes the axis of acoustic particle motion in three dimensions. Science. 225:951-954.

Fay, RR. 1988. Hearing in vertebrates: A psychophysics databook. Hill-Fay Assoc., Winnetka, IL.

Fay, RR and PL Edds-Walton. 1997. Directional response properties of saccular afferents of the toadfish, *Opsanus tau*. Hear Res. 111:1-21.

Fay RR and PL Edds-Walton. 1999. Sharpening of directional auditory responses in the descending octaval nucleus of the toadfish (*Opsanus tau*). Biol. Bull.197: 240-241.

Fay, RR and AM Simmons. 1999. The sense of hearing in fishes and amphibians. In: RR Fay and AN Popper (ed.) Comparative Hearing: Fish and Amphibians, Springer-Verlag, New York, pp. 269-318

Gale, JE, JR Meyers, A Periasamy, and T Corwin. 2002. Survival of bundleless hair cells and subsequent bundle replacement in the bullfrog's saccule. J. Neurobiol. 50(2):81-92.

Goertner, JF, ML Wiley, GA Young, and WW McDonald. 1994. Effects of underwater explosions on fish without swimbladders. Naval Surface Warfare Center. (NSWC TR 88-114)

Govoni, JJ, LR Settle, and MA West. 2003. Trauma to juvenile pinfish and spot inflicted by submarine detonations. J. Aquat. Anim. Health. 15(2):111-119.

Green, CR. 1985. A pilot study of possible effects of marine seismic air-gun array operation on rockfish plumes. (unpub. report cited in Engås et al. 1996; original not seen)

Hastings, MC, AN Popper, JJ Finneran, and PJ Lanford. 1996. Effects of low-frequency underwater sound on hair cells of the inner ear and lateral line of the teleost fish *Astronotus ocellatus*. J. Acoust. Soc. Am. 99(3):1759-1766.

Hastings, MC and AN Popper. 2005. Effects of sound on fish. Contract Report, California Department of Transportation No. 43A0139, Task Order 1. [www.dot.ca.gov/hq/env/bio/files/Effects of Sound on Fish 23Aug05.pdf]

Hudspeth, AJ and DP Corey. 1977. Sensitivity, polarity, and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli. Proc. of the Natl. Acad. Sci. USA, 74:2407-2411.

Husbands, JM, SA Steinberg, R Kurian, and JC Saunders. 1999. Tip-link integrity on chick tall hair cell stereocilia following intense sound exposure. Hear. Res. 1999:135-145.

Iversen, RTB. 1967. Response of the yellowfin tuna (*Thunnus albacares*) to underwater sound. In: Marine Bioacoustics, vol. 2. WN Tavolga, ed. Pergamon Press, Oxford.

Jerkø, H, I Turunen-Rise, PS Enger and O Sand. 1989. Hearing in the eel (*Anguilla*). J. Comp. Physiol. 165A:455-459.

Jorgensen, R, KK Olsen, I-B Falk-Petersen, and P. Kanapthippilai. 2005. Investigations of potential effects of low frequency sonar signals on survival, development and behaviour of fish larvae and juveniles. Norwegian College of Fishery Science, University of Tromso, N-9037, Norway.

Karlsen, HE. 1992. Infrasound sensitivity in the plaice (*Pleuronectes platessa*). J. Exp. Biol. 171:173-187.

Karlsen, HE and O Sand. 1987. Selective and reversible blocking of the lateral line in freshwater fish. J. Exp. Biol. 133:249-262.

Karlsen, HE, RW Piddington, PS Enger, and O Sand. 2004. Infrasound initiates directional fast-start escape responses in juvenile roach. J. Exp. Biol., 207:4185-4193.

Katz, J. 1994. Handbook of clinical audiology. Williams and Williams, Baltimore, MD.

Kelly, JC and D. Nelson. 1975. Hearing thresholds of the horn shark, *Heterodontus francisci.* J. Acoust. Soc. Am. 58:905-909.

Kenyon, TN, F Ladich and HY Yan. 1998. A comparative study of hearing ability in fishes: the auditory brainstem response approach. J. Comp. Physiol. A 182:307-318.

Knudsen, FR, PS Enger, and O Sand. 1994. Avoidance responses to low frequency sound in downstream migrating Atlantic salmon smolt, *Salmo salar*. J. Fish Biol. 45(2):227-233.

Kvadsheim, PH and EM Sevaldsen. 2005. The Potential impact of 1 – 8 kHz active sonar on stocks of juvenile fish during sonar exercises. Forsvarets Forskningsinstitutt, PO Box 25, NO-2027, Kjeller, Norway. (FFI/Rapport-2005/01027)

Levine, S, P Hofstetter, XY Zheng, and D Henderson. 1998. Duration and peak level as co-factors in hearing loss from exposure to impact noise. Scan. Audiol. 27:27-36.

Locke R, J Vautrin, and S Highstein. 1999. Miniature EPSPs and sensory encoding in the primary afferents of the vestibular lagena of the toadfish, *Opsanus tau*. Ann NY Acad. Sci. 871:35-50.

Lombarte, A, HY Yan, AN Popper, JS Chang, and C Platt. 1993. Damage and regeneration of hair cell ciliary bundles in a fish ear following treatment with gentamycin. Hear. Res. 64:166-174.

Lonsbury-Martin, BL, GK Martin, and BA Bohne. 1987. Repeated TTS exposures in monkeys: Alterations in hearing, cochlear structure, and single unit thresholds. J. Acoust. Soc. Am 81:1507-1518.

Lowenstein, O and TDM Roberts. 1951. The localization and analysis of the responses to vibration from the isolated elasmobranch labyrinth. A contribution to the problem of the evolution of hearing in vertebrates. J. Physiol. 114:471-489.

Lu, Z and RR Fay. 1993. Acoustic response properties of single units in the torus semicircularis of the goldfish, *Carassius auratus*. J. Comp Physiol. A 173:33-48.

Lu, Z and AN Popper. 2001. Neural response directionality correlates of hair cell orientation in a teleost fish. J. Comp. Physiol. A. 187:453-465.

Lu, Z, J Song, and AN Popper. 1998. Encoding of acoustic directional information by saccular afferents of the sleeper goby, *Dormitator latifrons*. J. Comp. Physiol. A 182:805-815.

Lu, Z, Z Xu, and WJ Buchser. 2003. Acoustic response properties of lagenar nerve fibers in the sleeper goby, *Dormitator latifrons*. J. Comp. Physiol. A 189(12):889-905.

Lu, Z, Z Xu, and WJ Buchser. 2004. Acoustic response properties of utricular nerve fibers in the sleeper goby, *Dormitator latifrons*. J. Comp. Physiol. A 190(11):923-938.

Ma W-LD and RR Fay. 2002. Neural representations of the axis of acoustic particle motion in nucleus centralis of the torus semicircularis of the goldfish, *Carassius auratus.* J. Comp. Physiol. A 188:310-313.

Mann, DA, Z. Lu, MC Hastings, and AN Popper. 1998. Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). J. Acoust. Soc. Am. 104(1): 562-568.

Mazeaud MM, F Mazeaud, and EH Donaldson. 1977. Stress resulting from handling in fish: primary and secondary effects. Trans. Am. Fish. Soc. 106:201-212.

McCauley, RD, J Fewtrell, and AN Popper. 2003a. Effects of impulsive air-gun signals on fish and squid. WESPAC8, 8th Western Pacific Acoustics Conference: Acoustics on the Move, Melbourne (Australia), 7-9 April 2003. World Meeting Number 000 6825)

McCauley, RD, J Fewtrell and AN Popper. 2003b. High intensity anthropogenic sound damages fish ears. J. Acoust. Soc. Am. 113(1):638-642.

Mitson, RB and HP Knudsen. 2003. Causes and effects of underwater noise on fish abundance estimation. Aquatic Living Res. 16(3):255-263.

Moberg, GP and JA Mench. 2000. The biology of animal stress – Basic principles and implications for animal welfare. CABI Publ. New York, NY.

Myrberg, AA, Jr. 2001. The acoustical biology of elasmobranchs. Environ. Biol. Fishes, 60(1-3): 31-46.

Myrberg, AA and JY Spires. 1980. Hearing in damselfishes: An analysis of signal detection among closely related species. J. Comp. Physiol. 140:135-144.

Myrberg, AA, Jr., CR Gordon, and AP Klimley. 1976. Attraction of free ranging sharks by low frequency sound, with comments on its biological significance. In: Sound reception in fish. A Schuijf and AD Hawkins, eds. Elsevier, Amsterdam. (pp. 205-228)

Myrberg, AA, Jr., SJ Ha, S Walewski, and JC Banbury. 1972. Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull. Mar. Sci. 22:926-949.

Nelson, DR. 1967. Hearing thresholds, frequency discrimination and acoustic orientation in the lemon shark, *Negaprion brevirostris* (Poey). Bull. Mar. Sci. 17:741-768.

Nelson, DR and RH Johnson. 1972. Acoustic attraction of Pacific reef sharks: Effect of pulse intermittency and variability. Comp. Biochem. Physiol. A, 42:85-95.

NRC. 1994. Low-frequency sound and marine mammals. Current knowledge and research needs. (Committee on Low-Frequency Sound and Marine Mammals, Ocean Studies Board) National Academy Press, Washington, DC.

NRC. 2000. Marine mammals and low-frequency sound. Progress since 1994. (Committee to Review results of ATOC's Marine Mammal Research Program, Ocean Studies Board) National Academy Press, Washington, DC.

Pearson, WH, JR Skalaski, and CI Malme. 1987. Effects of sounds from a geophysical device on fishing success. OCS Study MMS-87-0020. Prepared by Battelle Memorial Institute under Contract No. 14-12-0001-30273 to the Department of the Interior, Minerals Management Service, Pacific Outer Continental Shelf Region, Los Angeles, CA.

Pearson, WH, JR Skalaski, and CI Malme. 1992. Effects of sounds from a geophysical survey device on behavior of captive rockfish (*Sebastes spp*.). Can. J. Fish. Aquatic Sci. 49:1343-135

Plachta, DTT, J Song, MB Halvorsen, and AN Popper. 2004. Neuronal encoding of ultrasonic sound by a fish. J. Neurophysiol. 91:2590-2597.

Popper, AN. 2003. Effects of anthropogenic sounds on fishes. Fisheries. 28(10):24-31.

Popper, AN and NL Clarke. 1976. The auditory system of the goldfish (*Carassius auratus*): effects of intense acoustic stimulation. Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol. 53:11-18.

Popper, AN, RR Fay, C Platt, and O Sand. 2003. Sound detection mechanisms and capabilities of teleost fishes. In: Sensory processing in aquatic environments. SP Colin and NJ Marshall, eds., Springer-Verlag, New York, pp. 3-38.

Popper, AN, J Fewtrell, ME Smith, and RD McCauley. 2004. Anthropogenic sound: Effects on the behavior and physiology of fishes. Mar. Tech. Soc. J., 37(4):35-40.

Popper, AN, DTT Platchta, DA Mann, and D Higgs. 2004. Response of clupeid fish to ultrasound: a review. ICES J Mar. Science. 61:1057-1061.

Popper, AN, ME Smith, PA Cott, BW Hanna, AO MacGillivray, ME Austin, and DA Mann. (in press). Effects of exposure to seismic airgun use on hearing of three fish species. J. Acoust. Soc. Amer. (2005).

Richardson, WJ, CR Greene, Jr., CI Malme, and DH Thomson. 1995. Marine mammals and noise. Academic Press, New York, NY.

Sand, O, and HE Karlsen. 1986. Detection of infrasound by the Atlantic cod, J. Exper. Biol. 125:197-204.

Sand, O and PS Enger. 1973. Acoustic properties of the cod swim bladder. J. Exper. Biol. 58:797-820.

Sand, O, PS Enger, HE Karlsen, F. Knudsen, and T Kvernstuen. 2000. Avoidance responses to infrasound in downstream migrating European silver eels, *Anguilla anguilla*. Environ. Biol. Fishes. 57(3):327-336.

Sand, O, PS Enger, HE Karlsen, and FR Knudsen. 2001. Detection of infrasound in fish and behavioral response to intense infrasound in juvenile salmonids and European silver eels: a minireview. Am. Fish. Soc. Symp. 26:183-193.

Saunders, JC, YE Cohen, and YM Szymko. 1991. The structural and functional consequences of acoustic injury in the cochlea and peripheral auditory system: A five year update. J. Acoust. Soc. Am. 90:136-146.

Scholik, AR and HY Yan. 2001a. Effects of underwater noise on auditory sensitivity of a cyprinid fish. Hear. Res. 152:1-2:17-24.

Scholik, AR and HY Yan. 2001b. The effects of underwater noise on auditory sensitivity of fish. Proc. I.O.A. 23(4):27-36.

Scholik, AR and HY Yan. 2002a. The effects of noise on the auditory sensitivity of the bluegill sunfish, *Lepomis macrochirus*. Comp. Biochem. Physiol. A, 133(1):43-52.

Scholik, AR and HY Yan. 2002b. Effects of boat engine noise on the auditory sensitivity of the fathead minnow, *Pimephales promelas*. Environ. Biol. Fishes, 63(2):203-209.

Schreck, C, BW Contreras-Sanchez, and MS Fitzpatrick. 2001. Effects of stress on fish reproduction, gamete quality, and progeny. Aquaculture. 197:3-24.

Schwarz, AL and GL Greer. 1984. Responses of Pacific herring, *Clupea harengus pallasi*, to some underwater sounds. Can. J. Fish. Aquat. Sci. 41:1183-1192.

Skalski, JR, WH Pearson, and CI Malme. 1992. Effects of sounds from a geophysical survey device on catch-per-unit-effort in a hook-and-line fishery for rockfish (Sebastes spp). Can. J. Fish. Aquat. Sci. 49:1357-1365.

Slotte, A, K Hansen, J Dalen, and E Ona. 2004. Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. Fish. Res. 67: 143-150.

Smith, ME, AS Kane, and AN Popper. 2004a. Noise-induced stress response and hearing loss in goldfish (*Carassius auratus*). J. Exp. Biol. 207:427-435.

Smith, ME, AS Kane, and AN Popper. 2004b. Acoustical stress and hearing sensitivity in fishes: does the linear threshold shift hypothesis hold water? J. Exp. Biol. 207:3591-3602.

van den Berg, AV and A Schuijf. 1983. Discrimination of sounds based on the phase difference between particle motion and acoustic pressure in the shark *Chiloscyllium griseum.* Proc. R. Soc. Lond. B 218: 127–134.

Wardle, CS, TJ Carter, GG Urquhart, ADF Johnstone, AM Ziolkowski, G. Hampson, and D. Mackie. 2001. Effects of seismic air guns on marine fish. Cont. Shelf Res. 21(8-10):1005-1027.

Waring, CP, RM Stagg, and MG Poxton. 1996. Physiological responses to handling in the trout. J. Fish Biol. 48:161-173.

Wartzog, D, AN Popper, J Gordon, and J Merrill. 2004. Factors affecting the responses of marine mammals to acoustic disturbance. Mar. Tech. Soc. J. 37(4):6-15.

Wenz, GM. 1962. Acoustic ambient noise in the ocean: spectra and sources. J. Acoust. Soc. Amer. 34(12):1936-1956.

Winn, HE. 1964. The biological significance of fish sounds. In: Marine Bioacoustics, Tavolga, WN (ed.), Pergamon Press, NY, pp. 213-231.

Wysocki, LE and F Ladich. 2005. Effects of noise exposure on click detection and the temporal resolution ability of the goldfish auditory system. Hear. Res. 201:27-36.

Yan, HY. 1998. Auditory role of the suprabranchial chamber in gourami fish. J. Comp. Physiol. A 183:325-333.

Yan, HY and AN Popper. 1992. Auditory sensitivity of the cichlid fish *Astronotus ocellatus* (Cuvier). J. Comp. Physiol. A. 171:105-109.

Yan, HY, ML Fine, NS Horn, and WE Colon. 2000. Variability in the role of the gas bladder in fish audition. J. Comp Physiol. A. 186:435-445.

Yelverton, JT, DR Richmond, W Hicks, Sanders, and E R Fletcher. 1975. The relationship between fish size and their response to underwater blast. Topical Report DNA 3677T. Defense Nuclear Agency, Department of Defense, Washington, DC.

Yost, WA. 1994. Fundamentals of hearing (3rd edition). Academic Press, New York, NY.

REPORT DOCUMENTATION PAGE

1. REPORT DATE (DD-MM-YYYY)	2. REPORT TYPE	3. DATES COVERED (From - To)
04–2006	Technical	

4. TITLE AND SUBTITLE

Evaluation of Evidence for Altered Behavior and Auditory Deficits in Fishes Due to Human-Generated Noise Sources

5a. CONTRACT NUMBER

5b. GRANT NUMBER

5c. PROGRAM ELEMENT NUMBER

6. AUTHORS

P. L. Edds-Walton
Parmly Hearing Institute
Loyola University Chicago

J. J. Finneran
SSC San Diego

5d. PROJECT NUMBER

5e. TASK NUMBER

5f. WORK UNIT NUMBER

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

Loyola University Chicago
Chicago, Il 60626

SSC San Diego
San Diego, CA 92152–5001

8. PERFORMING ORGANIZATION REPORT NUMBER

TR 1939

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

Office of Naval Research
800 North Quincy Street
Arlington, VA 22217-5660

Naval Sea Systems Command
1333 Isaac Hull Avenue S. E.
Washington Navy Yard, DC 20376

10. SPONSOR/MONITOR'S ACRONYM(S)

ONR/NAVSEA

11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT

Approved for public release; distribution is unlimited.

13. SUPPLEMENTARY NOTES

This is the work of the United States Government and therefore is not copyrighted. This work may be copied and disseminated without restriction. Many SSC San Diego public release documents are available in electronic format at http://www.spawar.navy.mil/sti/publications/pubs/index.html

14. ABSTRACT

In this study, the authors have evaluated peer-reviewed publications and contracted reports to provide an overview of what is known about auditory processing by fishes and the behavioral and physiological effects of various noise stimuli as documented by the best and most appropriate studies. Included are reviews of work on both cartilaginous (sharks, skates, and rays) and teleost fishes (modern bony fishes). Recommendations for research to address remaining issues are provided.

15. SUBJECT TERMS

Mission Area: Navigation and Applied Sciences
auditory processing in fishes
behavioral responses to noise

human-generated noise audible to fishes
physiological effects of noise

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT	b. ABSTRACT	c. THIS PAGE			J. J. Finneran
U	U	U	UU	55	19B. TELEPHONE NUMBER (Include area code) (619) 767–4098

INITIAL DISTRIBUTION