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Effects of Anthropogenic Sounds on Fishes

ABSTRACT

There is increasing concern regarding the effect of human-generated (anthropogenic) sounds on marine organisms. While most concern is focused on marine mammals, many of the lower frequency (under 1,000 Hz) sounds are also likely to affect fish. Anthropogenic sounds can range from very intense signals such as noise generated by ships and their sonars to far less intense signals such as background sounds in hatcheries and oceanariums. The sounds may affect behavior and/or physiology, although very little is specifically known about how sounds affect fish. Limited data suggest that short- or long-term exposure to loud sounds may alter behavior, and also result in temporary or permanent loss of hearing. In order to better understand this issue, a series of studies are needed that systematically explore both behavioral and physiological effects of different types of sounds on a select group of species at different stages of their development.

Arthur N. Popper

Popper is a professor with the Department of Biology and with the Neuroscience and Cognitive Science Program at the University of Maryland, College Park. He can be reached at apopper@umd.edu.

The past several years have seen a significant increase in questions and interest related to the effects of anthropogenic (human-made) sounds on marine mammals (e.g., NRC 1994, 2000, 2003; Richardson et al. 1995). This has arisen because of increased public awareness of the level of anthropogenic sound being generated in the marine environment and also by public concern for the safety and health of marine mammals (e.g., NRDC 1999). This interest has not only led to attempts to understand the sources and levels of anthropogenic sounds, but also to attempts to assess the potential effects of such sounds on marine mammals. These concerns have also led to litigation in attempts to control some of the anthropogenic sources.

Though the majority of concerns, research efforts, and even litigation have been focused on marine mammals, the sounds that affect marine mammals also have the potential to affect the safety and well-being of other marine organisms including fish, turtles, aquatic birds, and perhaps even invertebrates (e.g., NRC 1994, 2000, 2003). Fishes are of particular concern since many species use sounds to find prey, to avoid predators, and for social interactions. Moreover, the sensory receptors used by fishes to detect sounds are very similar to those of marine (and terrestrial) mammals, and, as a consequence, sounds that damage or in other ways affect marine mammals could have similar consequences for fishes.

Notes on terminology

Before discussing anthropogenic sound, it is important to define a few terms. Sound levels in this article, and in the literature, are always referenced relative to some arbitrary value. In water, this value is relative to 1 microPascal (μPa). Use of this reference value allows investigators to compare levels recorded in different places and at different times (see www.earthisland.org/immp/eii_sonar_chart.pdf). In contrast to the reference value in water, the reference value in air is 20 μPa. This value was selected using the convention that it is the level of the human hearing threshold at 1,000 Hertz (hz, cycles per second).

Different reference values (20μPa vs. 1 μPa) are used in air and water due to differences in density of the two media. Thus, one cannot directly say that a sound of a certain level in air is the same as that in water. As a general comparison, acousticians will add 61 decibels (dB) to an airborne sound level to get an equivalent sound pressure in water for a stimulus of the same magnitude. To give some sense of how loud various sounds are, 105 dB re 1 μPa (in water) is about the same loudness as a classroom (in air) of 44 dB re 20 μPa, while 151 dB re 1 μPa is equivalent to a New York City subway, and 186 dB re 1 μPa, the sound of some large tankers underway, is about the sound level at which a human listener will feel pain from the loudness of the sound.

What are the sources of anthropogenic sounds?

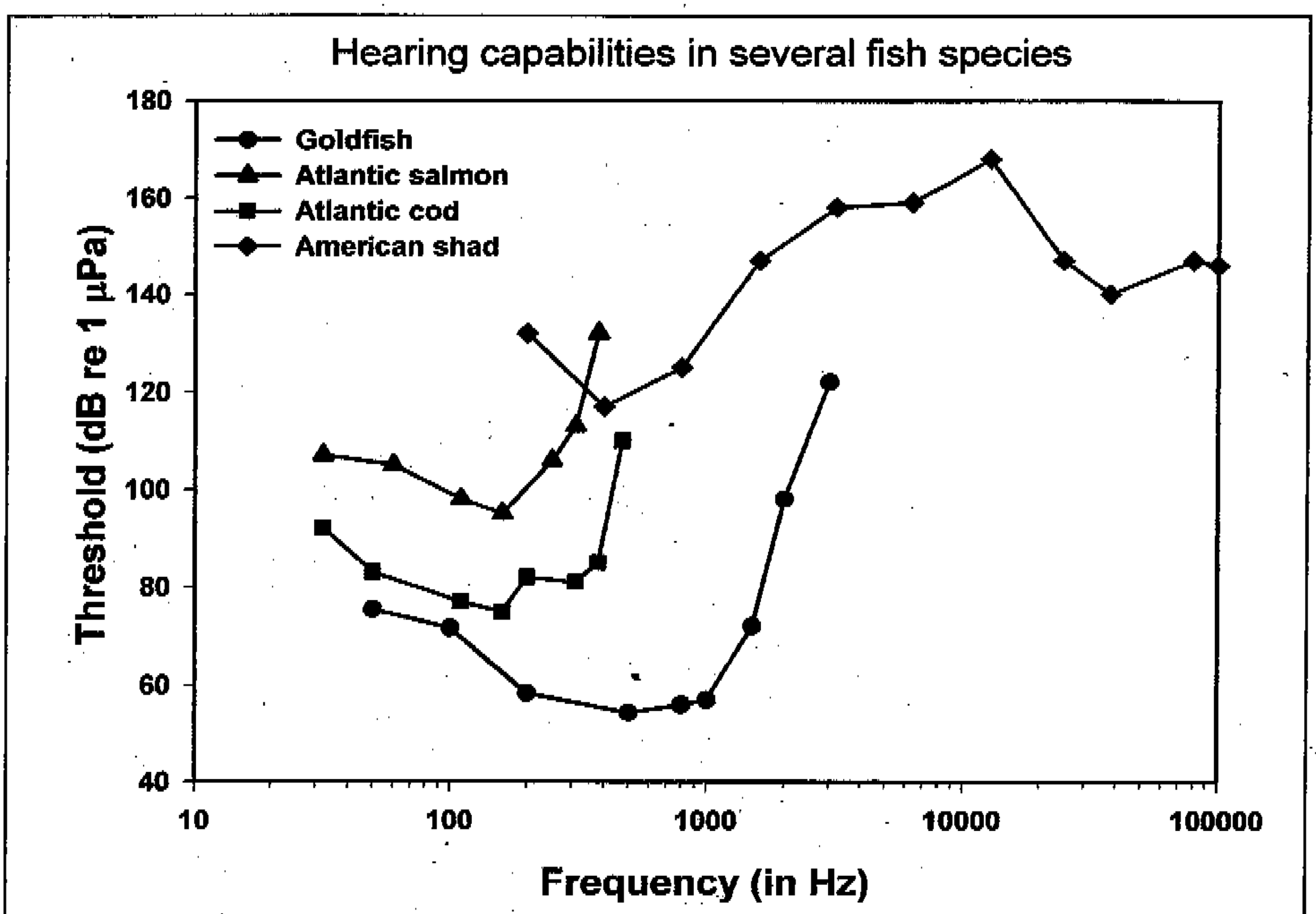
Humans generate a great deal of sound in the aquatic (and terrestrial) environment. Some of the most frequently cited sources relevant to marine mammals (and all aquatic organisms) are shipping, seismic exploration, and sonar, but there are many other sources (e.g., Richardson et al. 1995; NRC 2003). Shipping is probably the most extensive source of noise in the oceans, especially along major shipping channels (e.g., from Alaska to California for supertankers carrying oil) (e.g., Wales and Heitmeyer 2002). While there is broad variation in the sound levels produced by shipping, the frequency range of the sounds is generally below several hundred hertz. In certain locations, and for extended periods of times, air guns used for seismic exploration can also be extremely loud (e.g., McCauley.

It was probably the Acoustic Thermography of Ocean Climate (ATOC) study in the early 1990s (Baggeroer and Munk 1992) that most directly brought anthropogenic sound to the public interest. The goal of that study was to examine changes in global temperatures, by projecting a sound over great distances in the ocean and, from information about time of arrival of the sound at the receiver, determine an average ocean temperature. At the same time, public concern arose as to the potential effects of these sounds on marine mammals and whether the sounds could potentially affect their behavior and/or health. In particular, concerns focused on the relatively high intensity of these sounds and the intent to produce sounds over periods of many years to determine changes in ocean temperature over time.

More recently, there has been considerable concern about use of very high intensity low-frequency sonars by the U.S. and other navies (SURTASS LFA 2001; NRC 2003), and their potential effect on the health and well-being of marine mammals. Other kinds of sound sources such as mid-frequency sonars, seismic air guns, and pile driving have also raised concern about effects on marine mammals and fishes.

In most cases, the sounds produced by humans are relatively low in frequency, with the bulk of the energy below 1,000 Hz. Thus, these sounds are within the hearing range of fishes (Figure 1) and so have the potential to affect fish as well as marine mammals. While the problem for fish would be lessened if the sounds were limited to deep water, an increase in sound often occurs near the shoreline as a result of boat operations (U.S. Maritime Administration 1999). Indeed, with increased inshore shipping, the level of ship-generated sounds in the habitat of many fishes and other aquatic

Figure 1. Hearing thresholds (the lowest sound detectable) of four representative species of fish determined using behavioral methods. Goldfish is considered to be a hearing specialist, while Atlantic cod and Atlantic salmon are not. Note that the American shad, which may also be considered a hearing specialist based on its very broad hearing bandwidth, probably has the widest hearing range of any fish, if not vertebrate species, and has evolved mechanisms to detect the ultrasonic echolocation signals of dolphins. In interpreting these curves (also referred to as audiograms), lower values indicate better hearing. (Data for Atlantic salmon, Atlantic cod, and goldfish in Fay 1988; American shad from Mann et al. 2001.)



organisms will increase even further. Moreover, there is now also concern that higher frequency sonars, as well as echo sounders used by fishing vessels, could affect some fishes because a number of species of clupeid fishes (American shad, menhaden, alewives) can detect sounds at frequencies to over 200 kHz (Mann et al. 2001).

Although the concern regarding the effect of anthropogenic sounds is most often directed at wild animals, the issue is of similar importance with respect to captive animals. Because humans do not hear well under water (Brandt and Hollien 1967) and since the impedance differences between a body of water and air is such that sounds in one environment do not easily get transmitted across the air-water interface (e.g., Akamatsu et al. 2002) (e.g., almost 99.9% of sound generated under water is reflected back from the air-water interface), we are often unaware that human-made environments such as aquaculture facilities, fish hatcheries, and large oceanarium tanks are often relative noisy environments.

A striking parallel is the interest and concern of the federal government on the health of workers in environments where there is long-term exposure to noise (e.g., factories). Importantly, noise does not have to be particularly loud to affect human health. Instead, the effects of exposure appear to be cumulative (NIH 1990), and so a longer exposure to a low intensity noise can be just as damaging as short-term exposure to a very loud noise.

How do fish use sound?

Hearing evolved very early in the history of vertebrates, and fish can perform the same basic auditory tasks, such as discrimination between sounds, determining the direction of a sound, and detecting biologically relevant sounds in the presence of noise, as do terrestrial vertebrates (including mammals) (e.g., Fay and Popper 2000; Popper et al. 2003). Indeed, it has been shown that all species of fish (both bony and cartilaginous) that have been tested are able to hear. Fishes of a number of species including the otophysans (e.g., goldfish, catfish) have specializations that have evolved to enhance hearing capabilities (Figure 1) (reviewed in Popper and Fay 1999; Popper et al. 2003). These fishes, often referred to as "hearing specialists," can detect sounds to over 3,000 Hz, with best hearing sensitivity from about 300 to 1,000 Hz. In addition, some fishes in the family Alosinae, including American shad (*Alosa sapidissima*) and blueback herring (*A. aestivalis*), can detect ultrasonic sounds to over 200 kHz (Mann et al. 2001). Thus, higher frequency sonars, echosounding devices, pingers, and other sources could affect these species.

In contrast, the majority of fishes do not have known hearing specializations and only detect sounds up to 500 to 1,000 Hz, with best hearing from 100 to 400 Hz (Figure 1). Generally, best hearing sensitivity in a specialist is better than in a nonspecialist. However, it should be noted that all fishes are able to detect sounds within the frequency range of the most widely occurring anthropogenic sounds.

It might be argued that the only fishes that would be affected by anthropogenic sounds are species that make and use sound for communication (see Myrberg 1980 and Zelick et al. 1999 for reviews of fish sounds and fish acoustic communication). However, while many species do not make sounds or use sound for intraspecific communication (e.g., goldfish), all species are likely to obtain a good deal of information about their environment from the overall acoustic milieu (e.g., Tavolga 1976; Myrberg 1980; Fay and Popper 2000). Keep in mind that a human can enter a dark room and determine a good deal about the room just from sound that she emits or from the sounds in the room itself. Similarly, it is likely that fishes (and all animals) glean a good deal of information about their environment from sounds that might include waves breaking on the shore, currents moving across the reef, or other diverse sources. This detection of the acoustic environment takes on additional importance when one realizes that if fish had to depend on sight alone to learn what is going on in the world around them, they would have very limited information about potential predators and prey and of their "world," particularly at night or in murky waters. Again, using a human analogy, sound provides us with information from the whole world around us, including the space that is not within our visual field, and a similar use of sound has been demonstrated for at least one fish, the marine catfish (*Arius felis*; Tavolga 1976).

Indeed, it is very likely that the evolution of hearing in vertebrates (and probably in invertebrates) was not for acoustic communication per se but, instead, to broaden the space around the animal from which there was a constant flow of information (see Popper and Fay 1999; Fay and Popper 2000; Popper et al. 2003). It was only later in the course of vertebrate evolution that hearing capabilities in fishes extended to include communication sounds. Additional selective pressures for changes or improvement of hearing probably are related to specific acoustic environments. Perhaps the best example of this is found in a number of fishes that have a broad hearing bandwidth such as the otophysan fishes (e.g., goldfish, catfish), mormyrids (elephant nose fishes), and clupeids (herring, shad) (Popper and Fay 1999; Popper et al. 2003). Many of these fishes are not known to produce sounds or use sounds in reproductive or other behaviors. At the same time, these fishes can detect sounds to over 3,000 Hz as compared to most other fishes (including most sound-producing fishes) which generally can detect sounds to no more than 1,000 Hz (Popper and Fay 1999; Popper et al. 2003). Although the broad hearing bandwidth in these species perplexed investigators for several decades, we now know that only higher frequency sounds propagate beyond a few meters from the source in the shallow waters in which these species presumably evolved (Rogers and Cox 1988). Thus, it is likely that the evolution of high frequency hearing in these fishes most often (though certainly not always) occurred in those populations able to gain more distant information in the shallow water acoustic environment.

Since fishes live in a naturally "noisy" environment (Myrberg 1980) and since they have probably evolved to gain environmental information from this noise, anything that hampers the ability to detect biologically relevant signals will have a potentially deleterious effect on the survival of fish and the health of fish populations.

In what ways might anthropogenic sounds affect fishes?

Anthropogenic sound may have no effect on fish. In other words, fish may not detect such sounds, or, if they detect the sounds, there may be no deleterious effects on either behavior or physiology. However, if one assumes that fish respond like other organisms (including humans) to excessive sound in their environment, there are several different possible outcomes that may vary depending upon the life stage and species of the animal being affected and its specific behavioral and physiological response to the sound.

Behavioral responses to loud noises may include the fish swimming away from the sound source, thereby decreasing the potential effect of the sound, or the animal "freezing" and staying in place, thereby leaving the fish open to considerable damage. In cases where the fish swims away or alters behavior in other ways, the actual effect could be slight or it could be substantial. Just as a human walking down a street might cross the street to avoid the sound of a jackhammer and then return to a normal path, a fish might just move away from the source and then resume normal behavior.

Alternatively, the responses to the sound could affect behavior more extensively and result in the fish leaving a feeding ground (e.g., Engås et al. 1996) or an area in which it would normally reproduce or in some other way affect long-term behavior and subsequent survival and reproduction. Of course, the changes may be insignificant, but there may also be a more permanent long-term effect if feeding or reproduction is impeded. Moreover, if fishes such as Alosinae herring that are being sampled or tracked by ultrasonic sound pulses change their behavior and distribution in response to the sound, the data collected will be biased.

Another behavioral effect might occur if the increased ambient noise prevented fish from hearing biologically relevant sounds. This interference, called masking, is a consequence of noises being in the same frequency range as communication or other biologically relevant sounds. As a result of the presence of the masker, a fish may not be able to hear biologically important sounds (e.g., Myrberg 1980), just as a human has trouble hearing a fellow speaker in a noisy restaurant or when near a jackhammer or a loud rock band. For example, sharks, which are not known to be sound producers, are attracted to the sounds of struggling fish (or humans!) which serve as their prey (e.g., Myrberg et al. 1976). If there is excess noise in the environment, it would lessen the chances that the shark would hear the prey, thereby decreasing its ability to find food.

Of recent concern are the increased environmental sounds in the vicinity of coral reefs. Larval reef fish of many species spend part of their lives offshore and away from reefs and then settle on a reef where they will live for the remainder of their lives (e.g., Leis and McCormick 2002). Recent evidence suggests that at least some larval fish use the reef sounds to find the reefs and that the fish will go to regions of higher level sounds (e.g., Tolimieri et al. 2002). Thus, intense offshore sounds may confuse larval fish. Alternatively, such sound may mask reef sounds, again preventing larval fish from finding the reef.

Physiological and physical effects are also potentially similar to those found in other vertebrates. Humans and other organisms having long-term exposure to sound may show changes in stress levels (imagine a human adult having to sit near a loud rock band for an evening) or may experience temporary loss of hearing that may last from minutes to days (e.g., Hattingh and Petty 1992). While it is hard to predict the consequences of changes in stress levels on fish (or any organism), a temporary loss of hearing (whether it be full or partial) could mean that a fish loses some ability to detect predators or prey, communicate acoustically, and/or determine the structure of the acoustic environment. Clearly such effects would alter the survival of a fish.

Longer-term effects are also possible. It is known that exposure to very intense sounds, even for short periods of time, will cause permanent loss to the sensory cells of the ears of humans and other terrestrial animals, and loss of such cells means deafness (Lehnhardt 1986). Since the sensory cells of fishes are virtually the same as found in terrestrial vertebrates (see Popper et al. 2003), it is likely that exposure to loud sounds might permanently deafen fish and, again, decrease the survival chances. (Of course, there is evidence that fishes, unlike mammals, are able to regenerate sensory hair cells in the ear [Figure 2], at least after exposure to certain ototoxic drugs [Lombarte et al. 1993]. However, there is yet no evidence as to whether fishes will regenerate sensory hair cells after noise damage.)

What is the evidence for the effect of anthropogenic sounds on fishes?

There have been only a few studies on the effect of anthropogenic sounds on fishes. The data are limited partially because this has not been an issue of interest until recently and partly because the experiments are often hard to do. Since sounds needed to do the appropriate experiment are very loud, they are not easily done in a lab where people or other animals might be bothered.

Engås and colleagues (Engås et al. 1996; Engås and Løkkeborg 2002) examined the effect of seismic air guns on catch rate off the coast of Norway (also see Wardle et al. 2001). Air guns are air-powered devices used for underwater oil exploration as well as for general oceanographic geologic studies. They produce intense low-frequency sounds that are fired repetitively for hours or days in the same general area, and the sound is directed downwards. Sound levels can be up to 255 dB re 1 μPa in the frequency range of 20 to 150 Hz (Engås and Løkkeborg 2002). The echoes from the sounds reflect the nature of the sub.bottom geology. Engås et al. (1996) first determined catch rate in a normal fishing area. An air gun was then brought into the area for a period of time. Results showed a significant decline in catch rate that lasted for several days after termination of air gun use, and then the rate returned to normal. The conclusions were that the air gun caused the decline in catch rate and suggested that the fish may have left the fishing grounds for a period of time in response to the sound. It is not known if the sound just scared fish away or if the fish in the area were damaged (or killed) and others moved into the area to replace those lost. Similar results were found in a rockfish fishery where a single air gun at 186-191 dB re 1 μPa caused a decline of 52% in catch rate (Skalski et al. 1992).

There is also some evidence that low-frequency noise produced by fishing vessels and their associated gear may cause fish to avoid the vessels (e.g., Suzuki et al. 1980). While all of the data on the effect of sounds on fishing need replication, they do suggest that sounds may affect fish behavior and thereby, fisheries. Of course, we also do not know the way in which the sounds affect the fish—do they scare the fish from the fishing site? Do they kill the fish? Clearly, movement of fish from a feeding area, or killing them, could have an adverse effect on the higher members of a food chain, and therefore have long-term consequences despite not killing or maiming the predatory fish themselves.

In addition to behavioral changes, there is evidence of physiological changes that may be temporary or permanent. Several studies have shown that presentation of loud sounds for a few minutes to a few hours will result in a temporary loss of hearing in several different species including goldfish (*Carassius auratus*), tilapia (*Oreochromis nilotica*), and sunfish (*Lepomis macrochirus*) (e.g., Popper and Clarke 1976; Scholik and Yan 2002; Smith, Kane, and Popper, unpublished data). In each case, hearing was measured before and after exposure to loud sounds. Hearing sensitivity was substantially reduced when measured just after the end of the presentation of the loud sounds but improved over time. In studies in our laboratory, we found that it took two weeks for hearing to return to normal in goldfish after seven days of stimulation. In contrast, Scholik and Yan (2001) did not always find recovery 14 days after the termination of 24 hours of noise exposure in the fathead minnow (*Pimephales promelas*).

The actual amount of hearing loss appears to be related to the level of the sound above the hearing threshold, or sensitivity, (Figure 1) of a fish (Smith, Kane, and Popper, unpublished data). Thus, a 170 dB sound will cause hearing loss in goldfish when the sound is about 80 dB above the lowest sound level that the fish can normally detect (threshold), but it would take a 210 dB sound to cause an equivalent loss in tilapia since the threshold of this fish is well above that of goldfish. Very loud sounds may have long-term implications for fish that hear well, although the sounds may have less effect on fishes that normally do not hear very well (see also Scholik and Yan 2002).

Do loud sounds affect the hearing organs of fishes (Figure 2)? Only a few studies have attempted to answer this question. Enger (1981) found that pure tone sounds above 180 dB re 1 μPa

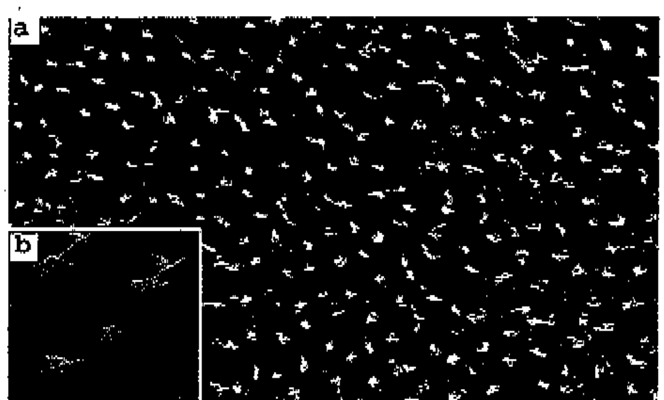


Figure 2. Scanning electron micrograph of a normal sensory epithelium from the saccule (one of the otolithic end organs of the ear involved in hearing) of the pink snapper (*Pagrus auratus*). (a) shows a normal expanse of epithelium while (b) shows a higher magnification of just a few ciliary bundles. These ciliary bundles sit on top of the sensory hair cells of the epithelia of each inner ear end organ. Bending of these bundles, as a result of relative motion between the epithelium and the otolith which lies above the epithelium, occurs during sound stimulation. Bending produces changes in channels in the walls of these cilia and causes the release of neurotransmitter which stimulates the nerve innervating the sensory cells, and sends a signal of "sound" to the brain. Scale bar in (a) is 20 μm while in (b) it is 2 μm. (From McCauley et al. 2003, with permission.)

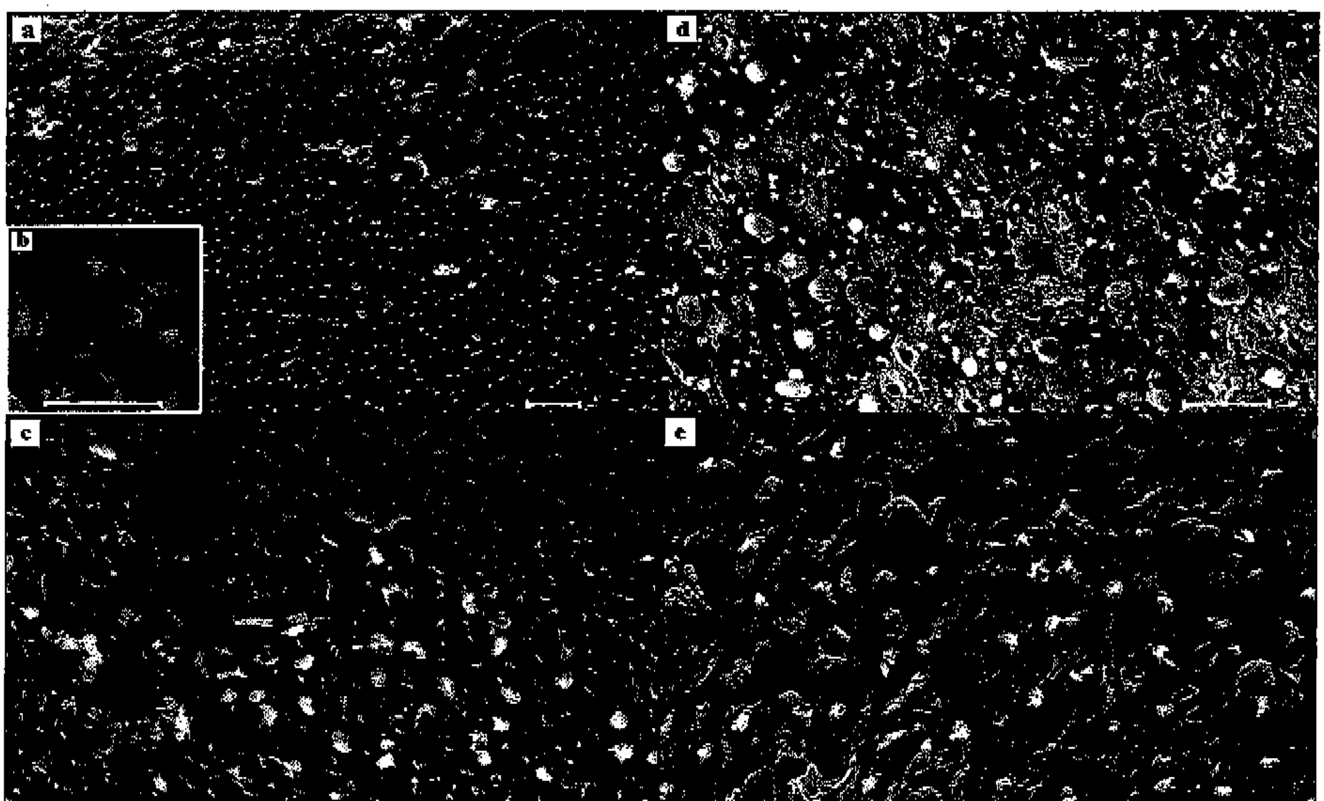
presented for several hours will damage the ears of Atlantic cod (*Gadus morhua*), and Hastings et al. (1996) obtained similar results in the oscar (*Astronotus ocellatus*). In both cases, scanning electron microscopy (SEM) was used to examine the sensory epithelium of the ear, and the results showed loss of ciliary bundles which are found on the apical ends of the on the sensory hair cells (Figure 2). Loss of the ciliary bundles results in loss of function of these mechanosensory cells.

The most recent study assessing the effects of sounds on fishes investigated the effect of a seismic air gun on the ears of caged fish. In this study, McCauley et al. (2003) exposed fish to a stimulus paradigm that is similar to what a fish in the wild might encounter during an air gun survey. The only (and important) difference was that the fish were caged and so could not escape the air gun during several hours of intermittent exposure. The results showed little or no damage 18 hours after stimulation, but after 24 hours, extensive damage was evident. Sensory cells were actually missing from the epithelium and there was considerable evidence of dying cells (Figure 3). Interestingly, damage was present even as long as 58 days after exposure to the air gun, and there was little or no evidence for repair of the ear, although repair has been shown in the oscar after exposure to drugs that kill sensory hair cells in the ear (Lombarte et al. 1993).

The results from these studies clearly show that intense sounds are able to damage the sensory hair cells of the ears of fishes. (Because the same kind of sensory hair cells are found in the lateral line, it is conceivable that this end organ is also affected, but no studies have addressed this issue.) Even if the sounds do not kill the fish directly, permanent (or even temporary) loss of hearing will clearly affect the chances of survival of exposed fish.

However, it is necessary to be cautious in interpreting the experiments done to date for several reasons. For example, the fish used in all of the studies were kept near the sound source and could not get away. In the normal environment, fish have the potential to escape loud sounds, and if they can get away fast enough, the effect of the sound may be

Figure 3. Scanning electron micrographs of the ear of the pink snapper (*Pagrus auratus*) after exposure to an air gun (see McCauley et al. 2003). (a to c) Scanning electron micrographs of saccular sensory epithelia from fish 18 hours after exposure to the air gun. The photographs show numerous holes and "blebbing" where normal sensory cells should be found. The holes represent sensory cells that have died and have been lost from the epithelium, while the "blebs" are presumed to be dying sensory cells. (a) shows the edge of an epithelium, while (b) shows an enlargement of one of the holes to show the space in which a sensory hair cell should have been, and (c) shows a more central epithelial region. (d and e) Electron micrographs from saccular epithelia of fish that were examined 58 days after exposure. This tissue shows far more extensive damage than the tissue from animals sacrificed 18 hours after exposure. These results show the massive damage imposed by a short exposure to a seismic air gun (in caged fish). They also support an argument that tissue examined right after exposure to an anthropogenic sound may not show much damage but that the damage will continue to grow over time. Scale bars: a, 20 µm; b, 2 µm; c, d, e, 20 µm. (From McCauley et al. 2003, with permission.)



mitigated. Of course, the normal "fright" response of many fishes is to freeze in place, and many other fishes do not move very fast, and so the effect on these animals could be considerable.

Another "caveat" to the results to date is that only a few species have been studied, and most have little or no commercial importance. It is not clear how reasonable it is to extrapolate from the species studied to other species. At the same time, it is important to note that the auditory systems of the species studied so far are similar enough to those of commercially important species to suggest that we can extrapolate, with caution.

Finally, the sounds used in most studies, other than the air gun investigation, were generally pure tones and thus different from most anthropogenic sounds since they generally contain energy over a broader range of frequencies. Thus, more extensive studies are needed on sounds similar to those produced by shipping, sonar, or other sources. Such studies need to include sounds of the appropriate intensity, duration, and duty cycle as common anthropogenic sounds.

The behavioral and physiological results suggest that loud sounds can affect fish and clearly point to the need for much more data. We need to know the levels of sounds that can affect fish, the differentiation between sound levels that cause temporary and permanent hearing loss, and the behavior of fish in response to the loud sounds (will they escape or will they adapt to the sound and stay put, thereby increasing exposure). Moreover, while it is impossible to ascertain the effect of anthropogenic sounds on all fishes, data are needed for a range of different species with different ear structures, different hearing sensitivities, and different behavioral responses and uses of sound.

Conclusions

While there is still a lack of extensive data, the data that we do have on fish and on other animals (including humans) strongly suggest that all animals may be affected by an increase in anthropogenic sound in the environment. The effect may be minimal and have nothing but a short-term effect on the animal. Or the effect may be longer lasting and affect the survival of an individual animal or a group of animals.

Although we most often think in terms of very loud sounds as having the most potential effect on animals (and humans), it is well documented that longer exposures to any anthropogenic sounds may also affect the health and well-being of a human (or an animal). Thus, we need to be concerned about the effect on fish of sounds in aquaria and in other facilities where fish have long-term exposure to sounds that are significantly above the normal ambient acoustic environment in which they evolved. If nothing else, it will be important to ask the right questions to determine if the effects are present and important or if they have little or no long-term consequence to the animal. Moreover, we might consider the effects of long-term acoustic tagging on fishes that can detect the ultrasonic sounds of the tags.

It thus becomes clear that we really have very few answers regarding the effects of anthropogenic sounds on fishes. Many questions posed here have yet to be answered, and there are many other questions that have yet to be considered at all. For example, while there have been a few studies on the effects of anthropogenic sounds on fish eggs and developing fish (e.g., Banner and Hyatt 1973), none of the studies have been over long-term nor have there been more than the most cursory analyses of the structure and physiology of the eggs or developing larvae as a consequence of noise exposure. There have been few studies on the effects of sounds on stress factors in fish, and no studies have systematically looked at the effect on fish of very intense environmental sounds such as pile driving or blowing up off-shore oil rigs. Both low- and high-frequency sonar, especially at the power levels currently in use, may have a considerable effect on fishes, and this area is in serious need of investigation.

Moreover, while this article has concentrated on the effects of sound on the ear, the lateral line of fishes has the same type of sensory cell as found in the ear, and it is possible that this very important sensor could also be affected by sound. In addition, it is possible that other aspects of fish physiology may be affected by exposure to anthropogenic sounds, and so future studies should consider things like stress effects and the physiology of other organ systems.

Finally, it must be remembered that fish make up only a small portion of the aquatic animal biomass. While very little is known about sound detection in invertebrates, many species have mechanosensors that have some resemblance to vertebrate ears (e.g., Popper et al. 2001), and so it would be important to examine the effect of anthropogenic sounds on a wider range of marine fauna.

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