Fish Hearing: New Perspectives from Two ‘Senior’ Bioacousticians¹

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The classic paper discussed in this essay:

Popper AN, Fay RR (1993): Sound detection and processing by fish: critical review and major research questions. *Brain Behav Evol* 41:14–38.

Our 1993 paper was written 20 years after our 1973 review [Popper and Fay, 1973] that critically examined our knowledge of fish hearing up to that time. Our goal in 1993 was to examine the field 20 years after our first paper, see where advances had taken place and provide our thoughts as to future research in the field.

It is now almost 40 years since our first review (and our first paper together²). We are not going to review the literature in this essay [see the papers in Webb et al., 2008], but we will look back briefly at a few issues that particularly interest us. We do this in the context of a new perspective of fish bioacoustics that has arisen in the past 20 years and that will, in our view, shape the future of the field. This context is the increasing societal and scientific concerns about the effects of the substantial increases in man-made (or anthropogenic) sounds on fishes (as well as on marine mammals, aquatic turtles and invertebrates). This perspective enables us to apply what we have learned about fish hearing and bio-

acoustics to a ‘real world’ issue [e.g. Slabekoorn et al., 2010; Popper and Hawkins, 2012]. Moreover, this ‘translational’ issue causes us to stretch what we know about fish hearing and leads us to focus on old and new questions that can help us better mitigate issues resulting from exposing animals to man-made sounds.

In the following sections, we consider a few of the issues that we think are most important 20 years after our 1993 paper. In each case, we provide our sense of the role for each issue in understanding the newer issue of the effects of man-made sounds on fishes.

Particle Motion versus Pressure for Sound Detection

Fishes have, in the past, been often classified as ‘hearing specialists’ or ‘hearing generalists’ based, to a large degree, on their hearing range and sensitivity. It is now generally accepted, however, that fishes fall on a broad continuum with respect to particle motion sensitivity versus pressure sensitivity [Popper and Fay, 2011]. The elasmobranchs and flatfishes (and many other species) fall at one end of the continuum in having no swim bladder or equivalent, and they are therefore likely to be purely motion sensitive. At the other

end of the continuum, primarily detecting pressure, are the Otophysi (goldfish, catfish and relatives) that have Weberian ossicles connecting the swim bladder to the ears. Most other fishes fall somewhere in between with an unknown ratio of dual sensitivities to pressure and particle motion.

Beyond developing the concept of a hearing continuum, we also argued that fishes cannot be placed on this continuum on the basis of anatomy alone [Popper and Fay, 2011]. Instead, to place fishes on a continuum of the relative importance of pressure versus particle motion in individual species, we need to have functional experiments that reveal fish hearing sensitivity in terms of both pressure and particle motion.

To do this, it is imperative that a single, reasonably priced, readily available and ‘off-the-shelf’ system for simultaneously measuring both pressure and particle motion be developed, and that this be accompanied by broadly acceptable standards for its use and interpretation. Such a device would make both lab tank and field studies on hearing much more interpretable and would render moot many of the issues related to ‘near’ and ‘far’ fields that have inhibited workers since the 1960s. Moreover, to understand man-made sound sources and how they affect fishes, it will be critical

¹ We dedicate this paper to our friend, colleague and mentor Prof. William N. Tavolga, in honor of his 90th birthday.

² For those who might be curious, this is our 25th paper together. We have also co-edited 50 books (and counting!) and organized several international meetings together.

for scientists and regulators monitoring the effects on fishes to have simple methods for measuring particle motion as well as pressure, perhaps using the same device developed for lab use.

Sound Source Segregation and Auditory Scene Analysis

Sound source segregation was noted in our 1993 review but is now a major consideration in interpreting hearing studies in fishes with respect to the question of 'What do fishes listen to?' Traditionally, the answer was 'They listen to fish vocalizations, of course.' We now know that fishes are capable of auditory scene analysis [e.g. Fay, 1998], and the answer to the question is probably much wider and more general than listening to vocalizations. Fishes could well be listening to many features of their local soundscape, including abiotic weather-generated sounds, sounds of predators and prey, and sounds, reflected and direct, that provide information about the structure of local environments that could be useful for soundscape orientation [Slabbekoorn et al., 2010].

Auditory scene analysis among fishes has not been investigated beyond its demonstration in psychophysical studies on goldfish [Fay, 1998]. At the same time, auditory scene analysis is an important topic with respect to the effects of natural and man-made noise on fish behavior because a major concern is how fishes perceive their acoustic environment for their livelihood and also how man-made sounds interfere with the perception of these sounds. However, because there has been very little empirical investigation of auditory scene analysis in fishes, it is hard at this point to evaluate how severely man-made sound interferes with auditory scene analysis and if any interference impacts fish fitness.

The Effects of Masking

Auditory masking in fishes was discussed in the 1993 review, but at the time, the literature on masking had been motivated primarily by questions of the fundamental mechanisms of masking [Fay, 2012]. Behavioral studies of most aspects of hearing in fishes had all but disappeared from the literature. The questions now posed about masking concern the consequences of natural and anthropogenic

noise for fish fitness and survival. Indeed, since 1998, masking has been studied only using auditory evoked potential methods [e.g. Amoser and Ladich, 2005].

There are two current issues related to masking in fishes. The first concerns the masking of specific, naturally occurring sounds (e.g. fish communication sounds) by noise of arbitrary spectral shape (e.g. ship noise) or, possibly, by repetitive high-intensity sounds (e.g. pile driving, seismic air guns). The second issue concerns the fitness and survival consequences of masking if such sounds impact the ability of fishes to communicate acoustically or perceive the auditory scene. There is agreement that this issue is of high priority [Popper and Hawkins, 2012], but there has been no empirical research on this topic.

Spectral versus Temporal Processing

The issue of spectral versus temporal processing is very old and has motivated some of the first modern era interest in the question of hearing by fishes. This is because the otolith organs of fishes lack the equivalent of a traveling wave on the sensory epithelium and thus, presumably, a 'place principle' of frequency analysis. Therefore, it was initially assumed that whatever capacities fishes had for frequency analysis had to depend on analyzing the temporal waveform of the sound. In 1993, we mentioned the work that evaluated the alternative hypothesis that primary afferents from the goldfish saccule were, in fact, tuned to different frequency regions, raising the possibility that frequency analysis could arise from a sort of place principle after all. Little progress has been made since then, other than the recent work by Smith et al. [2011] on the frequency-dependent tone damage to different regions of the saccule. Thus, the controversy about place versus time coding for frequency analysis in fishes remains, as it does for mammals and other vertebrates. Although less directly relevant to the effects of man-made sounds, greater knowledge in this area will improve our ability to model potential effects of such sounds on fishes.

The New Driving Issue: Effects of Man-Made Sound on Fishes

It is now clear that many parts of the world's aquatic environment are substan-

tially noisier now than they were decades earlier. The source of these sounds includes, among many other things, increased shipping, high-intensity naval sonars, pile driving used in the construction of bridges and wind farms, and the use of seismic air guns for geological exploration for gas and oil [Popper and Hastings, 2009; see papers in Popper and Hawkins, 2012].

The effects of man-made sounds may range from minimal, where fishes ignore the sounds, to the highly consequential, where behavior is altered or death occurs. Although physical harm is likely to occur only when animals are very close to a source [e.g. Popper and Hastings, 2009; Halvorsen et al., 2011], behavioral effects may extend great distances from a source. The sounds may mask the acoustic scene and communication sounds and/or they may prompt fishes to move away from feeding sites.

Despite the growing concern and interest in the effects of man-made sounds on fishes, there is only a very small body of peer-reviewed literature [reviewed in Popper and Hastings, 2009]. The question of how sounds affect fishes is relatively new, and it is very difficult to do field studies on acoustic behavior of wild fishes despite this being a most important question. The few studies that have been done with animals in their natural habitats thus far provide only very limited data.

Conclusions

In this essay, we did not cover a number of the many areas in which we see progress as having been made but in which more progress is needed if we are to truly understand fish hearing and the use of sound by fishes. Areas that we see ripe for future study include understanding the structure and physiology of the auditory central nervous system in fishes, the mechanics of the inner ear and how it processes sound, the significance of the interspecific differences in inner ear structure, the functional significance of differences between different types of inner ear hair cells, the (comparative) function of the lateral line, comparative hearing capabilities, ultrasound detection and, of course, the whole area of sound production and communication among fishes. And we have not discussed a topic that is perhaps closest to both of us, sound source localization.

A major problem in getting needed data on fish bioacoustics is that the number of investigators with appropriate interests has not grown over the past 20 years, and may have even declined. Another problem is that most of the recent studies on hearing rely exclusively on auditory evoked potentials to measure fish hearing and do not examine the behavioral responses to sound or the fundamental mechanisms of hearing such as sound source localization and inner ear signal

processing. These problems are compounded by difficulties in obtaining funding for basic studies on fish bioacoustics, an area that is not traditionally seen as having a great impact on human health or the environment.

At the same time, questions about the effects of man-made sounds on fishes are of great and growing importance because they impact the fitness and survival of fishes, the environment and even human food sources. Funding for studies on the

effects of man-made sound appears to be growing, and one can imagine investigators approaching some of the most interesting and exciting questions about basic mechanisms of fish bioacoustics from the perspective of understanding effects of man-made sound on fishes. Indeed, this is a unique opportunity and one that we both plan to pursue for a while longer (despite retirement). We encourage our colleagues to think in this direction as well.

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