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The Importance of Sounds to Fishes

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Abstract

Fishes can detect underwater sounds and use them to obtain key information about the environment around them. Sounds travel rapidly over great distances in water and can provide detailed information on the presence of prey, predators, and related fishes, while the overall acoustic scene provides the fishes with key information about their environment. Although they do not have the external ears that many vertebrates have, all fish species have effective internal ears. Many fish species engage in making sounds themselves. Their calls are often produced when they are approached by other fish species, and they can be used to startle and deflect their opponents. Sounds are also produced during reproductive activities. There are often differences in the sounds made by fish species, even between closely related species. The sounds of individuals may also differ, and this may play a role in sexual selection, as males compete with one another and aim to attract females that are looking for the best males to mate with. The sounds that fishes can hear are confined to low frequencies, although this is species-dependent. It is evident that fishes can distinguish between sounds that differ in their amplitude and frequency, and also discriminate between sounds that have different temporal characteristics.

They can also distinguish between sounds that arrive from different directions and distances, in some cases enabling them to locate the sources of sound. Detecting sounds may enable fishes to navigate and move to particular habitats, search for prey, move away from predators, and communicate during spawning. However, a particular problem in sound detection is the masking of those sounds that interest the fishes by high and variable levels of background noise. Although some of the background noise is generated by natural sources, including the precipitation of rain and snow, and wind and waves, many underwater sounds now come from anthropogenic sources. Some of these human-made sounds can kill or injure fishes, impair their hearing, and alter their behaviour. Interference with the detection of sounds can have especially adverse effects upon the lives of fishes. There is a need for more work on the impact of human- made underwater noise upon the fitness of fishes, and the strength of fish populations.

Key Words: Fishes; Underwater Sounds; Aquatic Soundscapes; Hearing, Communication; Behavior

Introduction

As fishes live in water, we cannot observe their behaviour easily, and we have little knowledge of their sensory abilities and the importance of various stimuli to them, especially underwater sounds. It is generally assumed that fishes are simple, unsophisticated animals. However, it was pointed out by Balcombe [1] that fishes are sentient, aware, and social animals, capable of interacting with one another. There has always been interes t in whether fishes canhear. Sounds are eas ily generated in water, and are provided with a wide range of characteristics by variations in their temporal patterning and frequency composition. Aristotle, the Greek Philosopher born in 384BC, examined fishes (reviewed by Leroi [2]), and suggested that fishes can hear, although he was not able to see any organs resembling ears. Many years later, the Roman author Pliny the Elder (23-79 CE), in his Natural History books, reached the same conclusion: that fish could hear but did not seem to have a hearing organ.

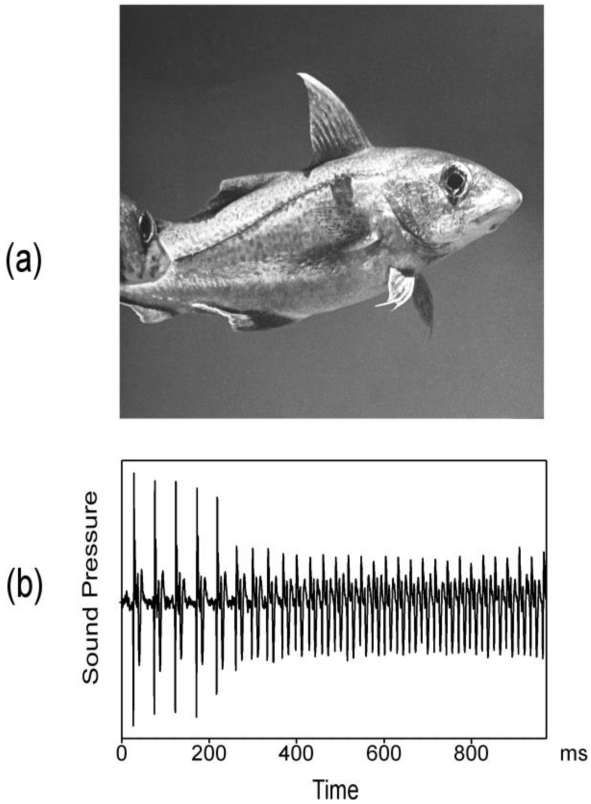
Actually, all fish species, including bony fishes, sharks, skates and rays, lampreys, and hagfishes, have internal ears, although they do not have the external ears that we have. We now have data on the hearing abilities of a number of species (reviewed by Popper et al. [3]). It has been known for many years that some fishes produce sounds themselves, and use them to communicate with one another. Some fishes make sounds, audible to humans, when held out of water, and some make some sounds in the water that can be heard above the surface. There have been reports of fishermen using underwater listening methods to detect fishes and improve their catches (Marshall, 1962 [4]). Fishes use sounds to maintain contact with one another, defend home territories, select breeding mates, and synchronise their behaviour while they are mating (Hawkins and Myrberg, 1983 [5]; Hawkins, 1993 [6]; Ladich and Winkler, 2017 [7]). All fishes are also likely to monitor the underwater soundscapes to obtain key information that may be important for their health and survival [3]. The term "soundscape" is used to describe the physical sound field in terms of the spatial, temporal, and spectral distribution of sound at a particular time and place. The sound field experienced or perceived by living organisms, and used to provide them with environmental information, is often described as the "acoustic scene".

Even though some fishes do not use sounds of their own to communicate, it is likely that all fishes use sound to learn about their environment by detecting and using the acoustic scene. In effect, sound detection provides fishes with three-dimensional information from a larger space around them than may be possible using vision, olfaction (the sense of smell), or electro- reception, as sound travels especially well through water. The limitations of these other senses in the aquatic environment make sound an exceptionally important stimulus for fishes.

Sound Communication by Fishes

Making sounds is important to some fishes. The nature of fish sounds depends on the sound-producing mechanisms. More than 50 families of fishes make sounds (Myrberg, 1981 [8]). Many of the sounds are produced by fast contracting muscles attached to the gas-filled swim bladder, which is an acoustically resonant organ (Sand and Hawkins, 1973 [9]). The gas within the swim bladder can undergo volume changes and it can, therefore, serve as an effective radiator of sound in all directions. The muscles can repeatedly contract, resulting in the fish sounds consisting of sequences of low-frequency impulses [5], often repeated at different rates and in different patterns. Other sounds can be generated by stridulation, with the fishes pressing their bones or teeth together or rubbing their fins together to make the sounds. The contexts in which the sounds are produced can vary in different species (Hawkins and Picciulin, 2019 [10]; [4]; [6]). They are often produced when fishes are approached by other fish species, that they may be competing with, and the sounds can be used to startle and deflect their opponents. Sounds may also be made by fishes that are swimming in schools, and these may keep the fishes together. Sounds are also produced during reproductive activities. Males are usually the most active sound producers, although females and juveniles may also produce sounds. Females that are ready to spawn may approach the sources of the sounds, and then select particular males to spawn with, based on the characteristics of their sounds. The chosen males may then use their sounds to synchronise their activities with the females (Figure 1), leading up to the simultaneous release of eggs and sperm into the water.

Figure (1) The humming sounds of haddock are made up of a series of rapidly repeated sound pulses (b), produced when the male fish flaunts its fins in front of its female mate, attracting her towards him (a). The male then mounts the female, and they insert their eggs and sperm into the water. The fertilised eggs then develop into small pelagic fish larvae.



There are often differences in the sounds made by fishes, even by closely related species. For example, the cod and haddock, and other gadoid fishes, have consistent differences in their sounds [10]. In addition, the sounds of individuals may also differ, and this may play a role in sexual selection through male-male competition and female mate choice. Other known sources of variability are related to the context of the sounds, including motivation and recent social status, season, and time of day [5]. The sound variability is mainly based on the temporal patterning of pulses within the sounds and on frequency variation. Such variability has been found to play a role in the social life of fishes [5].

The Nature of Underwater Sound

Sound can be propagated through gases, liquids and also solids, and is associated with mechanical disturbance of these media. The nature of underwater sound is fully described at the Discovery of Sound in the Sea website: www.dosits.org and is discussed, in relation to fishes, in a number of papers (Nedelec et al., 2016 [11]; Popper and Hawkins, 2018[12]; [3]; [6]) Acoustic energy can be generated by the movement or vibration of any immersed objects, and is accompanied by changes in both the pressure and motion of the elastic medium in contact with the source. The motion of the sound source forces kinetic energy into the water, which travels away as an acoustic wave. Within the wave, parts of the water move forwards and backwards (termed the "particle motion"). This oscillation of the water is accompanied by pressure changes, including compression and rarefaction, (termed the "sound pressure"). The acoustic wave propagates away from the source at a speed which depends upon the density and elasticity of the medium. In water, sound is propagated 4.5 times faster than in air, although the speed is dependent upon the actual temperature and salinity. Underwater sounds are most commonly monitored using hydrophones sensitive to sound pressure. However, all fishes can detect and use particle motion, and only a subset can detect sound pressure (reviewed by Nedelec et al., 2016; and Popper and Hawkins, 2018). The particle motion can be monitored in terms of the particle displacement, velocity or acceleration [11, 12], and since these are vector quantities it is important to monitor their direction. The sound pressure and particle motion are related to one another, their relative magnitudes depending upon the acoustic impedance of the medium.

The levels of the sound pressure and particle motion decline as sounds propagate away from a source. The particle motion is proportional to the sound pressure at long distances from the source (in the far field), whereas close to the source (in the near field) the magnitude of the particle motion is higher for a given sound pressure. The sound intensity, the power carried by the sound wave, is a product of both the sound pressure and the particle motion. Since particle motion is a vector quantity, it can be used by fishes to determine the direction of the sound source (reviewed by Hawkins and Popper, 2018 [13]), whereas sound pressure is a scalar quantity, acting in all directions, although it is used by terrestrial mammals to determine the source direction by comparing the amplitudes and times of arrival at the two spaced ears. This is more difficult for fishes, if they are only detecting sound pressure, as their ears are close together, and sound travels faster through the water and their tissues [13].

Sound measurements in water are often made at a single location, and the sound levels at other locations estimated by modelling the three dimensional propagation of sound, using an acoustic wave equation, based on the acoustic properties of the water. An example of such a model is provided by Lin et al., (2019) [14], for the sounds generated during construction of an offshore wind farm. As sounds travel through water they may be degraded or altered as a result of reflections from the substrate and the water surface. The temperature and density of the water itself may also vary at different locations, and sounds may be propagated along multiple pathways. Propagation of sound in shallow water environments like rivers can be especially complex as a result of the presence of many discontinuities and complex topography. Sound in the water is also often associated with substrate vibration. It can therefore be quite difficult to predict or model sound propagation in water, especially close to the substrate or water surface.

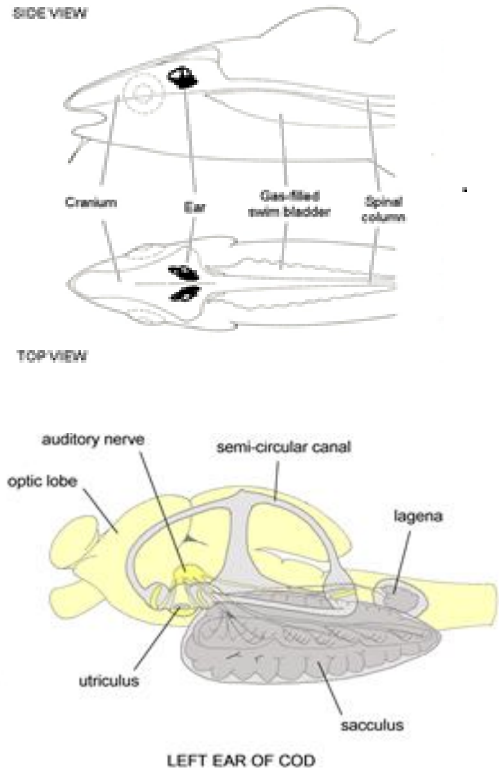
A particular problem in detecting underwater sounds is the masking of the sounds by high and variable levels of background noise. Noise is the term used to describe background sounds that are loud, unpleasant, and which may be harmful to both humans and animals. Noise can be generated in water by a variety of natural sources, including surface waves, rain and ice, water flowing and turbulence, often dependent upon prevailing wind and weather conditions. Hawkins and Chapman (1975 [15]) measured the hearing abilities of the Atlantic cod in a Scottish sea loch. Under calm sea conditions there was very little background noise. However, as the weather conditions varied the ambient noise level in the sea also changed, and was accompanied by a change in the hearing thresholds of the cod. The threshold-to-noise ratio remained constant at a particular frequency. Nowadays, there are many underwater sounds generated by humans – anthropogenic sounds – and the noise that is being generated can affect fishes and other aquatic animals adversely (Hawkins and Popper, 2016 [16].

Hearing in Fishes

The main sound receptors in fish are the otolith organs of the inner ears

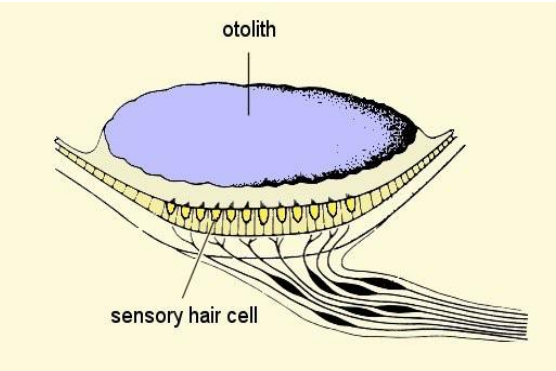
[3]. The ears are paired structures embedded in the skull on each side of the head, close to the brain. There are no obvious external structures to indicate their presence. Each ear is composed of three semi-circular canals that respond to rotational motion of the head, together with three sacs filled with fluid. Each of these sacs contains an otolith, a dense calcareous stone, that sits upon a sensory membrane, or macula, composed of many mechanoreceptive hair cells (Figure 1). Each hair cell is directional in its response to mechanical stimulation. In many fishes the inner ears stand alone, with no ancillary structures or attachments. In some species, however, there are structural linkages with gas-filled cavities, including the swim bladder, an organ that increases the buoyancy of the fish [9].

(Figure 2) The ear of the cod Gadus morhua. There are two inner ears, each composed of three semi-circular canals and three otolith organs, the utriculus, sacculus and lagena. The dense calcareous otoliths are sitting on sensory maculae of hair cells, connected by nerve fibres to the brain.



Each otolith organ has several functions. The organ serves as a gravity receptor, allowing the fish to determine its orientation with respect to the Earth's gravitational field. It is also sensitive to linear acceleration, lagging behind as the fish accelerates, or moving forward when the body comes to rest, stimulating the hair cells. The otolith organ also plays a role in sound reception, responding to the particle motion that is transmitted through the tissues of the fish head, which are mostly of similar density to the surrounding water. The otolith itself is denser than the surrounding tissues, and it moves differently, mechanically stimulating the sensory hair cells (Figure 2). It has been consistently shown that the otolith organs of fishes are sensitive to particle motion, rather than the sound pressure [11, 12]. However, in those fishes that have a gas-filled cavity close to an otolith organ, the gas in the cavity acts as an acoustic transformer, contracting and expanding in response to the sound pressure, and thereby generating much higher levels of particle motion at the otolith organs. Otophysan species (many families of freshwater fishes, including the carps and goldfishes) have a series of small bones, the Weberian ossicles, connecting the swim bladder to the inner ears. There are three pairs of these small bones connect the front of the swim bladder to a perilymphatic space within the inner ear (Boyle and Herrel, 2018 [17]). The Clupeids (herring fishes), and some other fishes, have narrow extensions from the swim bladder that end in a gas-filled bulla, close to the utriculus. Some other species, including the Gadidae (cod fishes), have their swim bladders positioned quite close to the ear. The proximity or connection of gas-filled cavities to the inner ears results in such fishes being sensitive to sound pressure, even though the otolith organs themselves are sensitive to particle motion [3, 12]. Many fishes without swim bladders (e.g. the plaice), or fishes where the swim bladders are positioned well away from the ears (e.g. the salmon), are sensitive only to particle motion.

(Figure 3) The saccular otolith organ of the cod. The calcareous otolith is connected through an auditory membrane to the hair cells. Motion of the fish body, which can be created by passage of a sound wave, results in lagging of the otolith, which stimulates the hair cells. Groups of the hair cells are orientated in different directions.

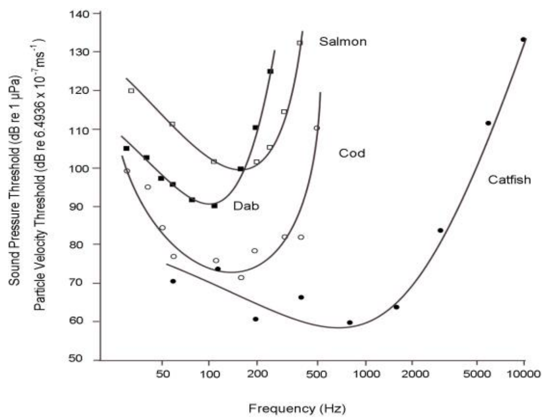


Fish Hearing Experiments

Hearing can vary greatly between different species of fish. However, relatively few experiments on fish hearing have been carried out under appropriate acoustic conditions (Hawkins, 2014 [18]). Many of the measurements made in aquarium tanks are unreliable, as the presence of reflecting surfaces changes the relationship between the sound pressure and particle motion, altough the measurements themselves are often expressed solely in terms of sound pressure. There are several different ways of determining hearing thresholds for fishes. Fish may habituate to the repeated presentation of sounds, making it difficult to present a full range of sound stimuli and fully explore responses to a range of sounds. However, various training and conditioning techniques have been developed to ensure that fish will always respond to those sounds that they can hear [3]. Thus, fish have been trained to press a lever or swim through an aperture when they hear a sound, in anticipation of a subsequent reward of food. Or the electrocardiograph of the fish is monitored and the fish is conditioned to show a delay in the heartbeat when presented with a sound, in anticipation of a mild electric shock.

Once a fish is trained to respond to sound, the sound level can be reduced progressively until the fish no longer responds. Raising the sound level if the fish does not respond, and reducing it when the fish does respond, may then bracket the threshold for detection. Although application of these techniques is very labour intensive, the thresholds obtained are often repeatable and reliably reflect the full hearing abilities of the fish. The thresholds are usually determined for a range of different pure tones (single frequencies) and then plotted against frequency to provide an audiogram. Audiograms for a number of fish species are provided in (Figure 4).90

Figure (4): Audiograms for four species of fish: Atlantic cod (Gadus morhua): Chapman and Hawkins 1973 [19]; the dab (Limanda limanda): Chapman and Sand 1974 [20]; the Atlantic salmon (Salmo salar): Hawkins and Johnstone 1978 [21]; and the catfish (Ictalurus nebulosus): Poggendorf 1952 [22]. Each audiogram plots the auditory thresholds (the minimum sound levels that can be detected), determined using conditioning techniques. It has been shown that the dab and salmon are sensitive to particle motion, whereas the cod and catfish are sensitive to sound pressure. These threshold studies were carried out under controlled acoustic conditions.



Physiological recording technique s may also be used to examine the hearing capabilities of fishes [3], as they are for other animals. An auditory electrical response (AEP) is recorded from the nervous system of the animal when a sound is presented. For example, microphonic potentials may be detected from the hair cells of the ear using an inserted electrode; or an auditory brainstem response (ABR) may be monitored by surface electrodes placed on the head of the fish, as is done with mammals. It is possible to determine thresholds at different frequencies by reducing the sound level until the potentials can no longer be detected against the background of electrical noise. Alternatively, frequency response curves may be prepared by comparing the sound levels that yield a given level of electrical response. With fishes, AEP and ABR audiograms often require comparison with behavioural audiograms, to help establish their usefulness as a possible description of a species' hearing abilities (Sisneros et al., 2016 [23]). AEPs and ABRs simply monitor the electrical signals generated within the ear, by the hair cells, or by groups of cells within the brain. That do not necessarily demonstrate that the fish is obtaining information that results in changes in its behaviour. Nevertheless, AEPs can be used to investigate the effects of sound exposure, by monitoring hearing abilities before and after noise exposure [23].

In general, fishes have a more restricted frequency range than mammals or birds. However, both frequency range and hearing sensitivity vary from one species to another. Recently, fishes have been classified as follows in terms of their hearing abilities (Popper and Hawkins, 2019 [24]):

- Fishes without a swim bladder can show relatively poor hearing, and they detect particle motion only. They include sharks, skates, and rays; sturgeon; and many species of flatfish.
- Fishes with a swim bladder that is not involved in hearing and which have relatively poor hearing, detecting particle motion only. They include species like the salmon, trout, and eels.
- Fishes with a swim bladder involved in hearing, which show more acute sensitivity and a wider frequency range, as they can detect the sound pressure as well as the particle motion. They include the cod, and its relatives, where the swim bladder is relatively close to the inner ear. Other species have physical connections between the swim bladder and the ear, including the goldfish, while others have other gas-filled organs close to the ear, including the herring, and shad (Alosinae). Some of these fishes are able to detect ultrasonic frequencies (above 20 kiloHertz).
- Fish eggs and larvae, for which little information is available.

Some fishes like the salmon can detect infrasound, at frequencies below 20 Hz (Sand and Karlsen, 2000 [25]). Infrasonic frequencies have been shown to be especially effective for evoking both awareness reactions and avoidance responses. It has also been suggested that salmon may use the ambient infrasound in the ocean, produced by waves, tides, microseisms and other large-scale motions, for orientation during migration. However, the entire importance of sound, including infrasound, to fishes still has to be fully evaluated.

Some species, including the cod, are not limited by their absolute sensitivity at some sound frequencies, but by the masking of the sounds by environmental ambient noise, even under relatively quiet sea conditions [15]. Any increase in the level of ambient noise in the sea results in a decline in the sensitivity of the fishes to other sounds. Indeed, the differences seen in the audiograms of some species may be the result of different levels of ambient noise during the hearing experiments. However, some species like the salmon, which are less sensitive to sounds, only have their hearing limited by ambient noise under very noisy conditions in the sea, lakes and rivers. Where masking takes place, not all frequencies contained within the background noise are equally effective at masking. Experiments with cod [15] and salmon [20] have shown that only the frequencies in a narrow band on either side of a masked tone (the critical band) contribute to the masking. Both the cod and salmon employ auditory filters to remove the masking effect of frequencies that are different from those of the sounds being listened to. The critical bands in the cod are rather narrower than they are in the salmon.

Directional hearing by fishes, and whether they can locate sound sources, has long been controversial [13]. It was originally suggested by Van Bergeijk (1967 [26]) that a fish that effectively had only a single sound pressure detector (the swim bladder) could not locate a sound source, and that no fishes could detect the direction of a source when they were in the far field. However, field observations of freely ranging sharks (which lack a swim bladder) showed that they orientated toward sound sources, often from great distances (Myrberg et al. 1969 [27]). It is now quite clear that some fishes can discriminate sounds from different directions, both in the near-field and far-field (reviewed by Sand and Bleckmann 2008 [28], and Hawkins and Popper, 2018 [13]). Some teleost fishes are able to detect differences in the direction of sound sources in both the horizontal plane (Schuijf et al. 1972 [29]; Chapman and Johnstone 1974 [30]), and vertical planes (Hawkins and Sand, 1977 [31]). It is also possible for the cod to distinguish between sound sources at different distances (Schuijf and Hawkins 1983 [32]). It is evident that fishes can locate sound sources in three dimensions. Their sensitivity to the direction from which sounds are coming also helps them to improve the actual detection of sounds that might otherwise be masked by background noise, which may be non-directional or coming from a different direction.

The otolith organs provide the basis for the detection of the axis of particle motion by functioning as vector detectors. It was Enger et al. (1973 [33]} that first examined the electrophysiological responses of the ear of a fish (the haddock) to particle motion coming from different directions. The fish was shaken in different azimuth directions, and the responses of particular groups of hair cells varied, depending on the direction of stimulation. Within the maculae of the otolith organs of fishes, groups of hair cells can differ in their orientation [13].

The hair cells within the different otolith organs also differ in their orientation. By comparing the responses of different groups of hair cells to the particle motion, fishes are able to distinguish between sounds coming from different directions, and therefore locate the direction of a sound source [13]. Essentially, the response of the otolith organs to particle motion is used to determine the direction along which the sound is propagating. Experiments by Hawkins and Horner (1981 [34]), examined the responses of the separate auditory nerve fibres from the sacculus and utriculus in an Atlantic cod while vibrating the fish in different directions in a horizontal plane. It proved possible to obtain polar diagrams that illustrated the different directional responses of these two otolith organs. The pulsed responses within the auditory nerves were also highly synchronised with the waveforms of the stimuli. Later, experiments, on a range of fish species, confirmed that different parts of the inner ear respond primarily to particle motion from different directions (e.g. Edds-Walton et al., 1999 [35], Meyer et al., 2011 [36]) and it was suggested that there is likely to be separate information provided within the brain by the hair cells within the different macular orientation groups.

The Effects of Anthropogenic Sounds upon Fishes

Natural sounds are present in seas, lakes, and rivers, generated by rain, snow, waves, bubbling and spraying water, cracking ice, and water turbulence, resulting in varying levels of ambient noise. In some areas, lightening strikes, earthquakes, and volcanic eruptions, may generate very intense sounds, that travel great distances. Sounds from animals also add to the ambient noise, including calls from marine mammals, fishes, and crustaceans. Chorusing fishes, snapping shrimps and other animals can generate sounds over a wide band of frequencies, which may mask the communication signals being used by other animals. Such biological sounds, together with sounds from other natural sources, may dominate the ambient noise levels.

In recent years, humans have generated a great deal of underwater noise [16].Anthropogenic sounds from shipping, underwater explosions, seismic exploration, offshore construction, and sonars of various types have raised the levels of ambient noise in the sea. Road traffic and other human activities can result in noise being generated in lakes and rivers. Sounds from ships dominate the ambient noise levels in some parts of the ocean, and also in some rivers and estuaries. The sounds are generated by the engines and other machinery, rotating shafts, propellers, and the interaction of water with the hull. The motion of the ship through the water may create low-frequency sound pressures and water displacements around the ship. Some of the louder sounds from ships result from cavitation – the collapse of air spaces induced by rotating propellers. Ship noise is greatest close to ports and shipping lanes, and it has become much greater as the number of ships on the high seas has increased. In shallow coastal waters, lakes and rivers, the soundscape may be dominated by noise from small boats driven by outboard motors.

Construction and industrial activities, both onshore, inshore and offshore, may generate significant levels of noise in the sea, and also in lakes and rivers. These activities include pile driving, dredging, drilling, the use of explosives in construction and decommissioning, the operation of wind farms, and activities at oil- and gas-production facilities. Percussive pile driving may produce especially intense sounds. This involves a post, sheet, or tube made of steel or reinforced concrete being driven into the substrate to support a superstructure such as a jetty, bridge, oil-platform or wind turbine. The head of the pile is struck repeatedly, driving it downward. Pile driving generates short pulses of sound with most of the energy concentrated at frequencies below 1000 Hz. The sounds that are generated can have adverse effects, especially upon pelagic fishes (Hawkins et al., 2014 [37]). It has been demonstrated that pile driving sounds can disrupt the collective dynamics of fish shoals (Herbert-Read et al., 2017 [38]. Close to the pile, the peak sound pressures associated with each strike may be very high. In addition, compressive, shear, and surface waves are generated within the substrate that may result in large levels of particle motion close to the substrate. The use of explosives in construction and in the removal or decommissioning of structures such as oil platforms, as well as in a military context, also produces very high peak sound levels. The sounds from these activities can travel great distances and may be detected by fishes over tens of kilometers [37].]

Vibrating pile drivers, in contrast to their percussive counterparts, produce continuous sounds, as does trawling by commercial fishing vessels, the drilling of oil and gas wells, and tunnelling beneath the substrate. Dredging at ports and harbours as well as the extraction of sand and gravel from the seabed also create continuous but rather variable levels of sound at low frequencies. Noise is also generated by the operation of offshore wind farms and by oil and gas platforms. However, the sound levels produced during their operation are generally lower than those during the construction phase.

Other human activities deliberately produce underwater sounds. Seismic surveying for oil and gas involves the generation of low-frequency pulses of sound (with most of the energy in the range 10–120 Hz) that travels through water to enter the seabed. A receiver array detects the returning sound. By analysing the reflections, it is possible to identify the properties of the seabed, the underlying geology, and the presence of oil and gas deposits. The surveys are conducted from a ship towing an array of air guns. Each air gun produces a short intense pulse of sound that is focused downward by the configuration of the array. The surveys may cover a wide area and last for several weeks. Sonar systems also generate underwater sounds. They are used to measure depth, to map the seabed, to detect fish, to track subsurface vehicles, or to search for military targets. Sonars operate at a range of sound frequencies and are classified as low- (<1 kHz), mid- (1–10 kHz), and high-frequency (>10 kHz) devices. High-frequency sonars may be detected by only a few fish species, but mid- and low-frequency sonars may operate well within the range of frequencies that can be detected by fishes.

The effects of these anthropogenic sounds upon fishes and other aquatic animals can be very detrimental, both to the individual animals and also their populations. Some sounds may be so intense that they may injure fishes, damage their ears, and even kill them [22]. Lower levels of sound may mask the detection of natural sounds, making the calls of fishes difficult to detect, and making it more difficult for them to orientate and migrate. Exposure to sounds may also accelerate the ageing process in fishes. It has been shown that RNA decay is one of the potential pathways affected by audible sound stimulation in animals. Audible sine wave sounds can induce cellular responses, resulting in sound-induced gene regulation (Kumeta et al., 2018 [39]).

The behavioural effects upon fishes from exposure to noise may operate over substantial distances from some sound sources. As well as simple startle reactions, which may have little importance in terms of effects upon vital functions, significant changes in behaviour may take place, with clear effects upon vital functions. These may include the break-up of fish aggregations, long-term changes in distribution, such as moving from preferred sites for feeding and reproduction, or alteration of navigation or migration patterns. Anthropogenic sounds may have significantly detrimental effects upon the fitness of fishes, affecting their welfare and their survival, with adverse effects at the population level [16]. There is often a need to reduce the production of anthropogenic sounds or to mitigate their impact by reducing their levels. However, few comprehensive studies of their effects upon fish populations have yet been carried out.The use of sounds for communication is especially important to fishes, as is the detection and monitoring of other natural sound sources. Fishes communicate using sounds under ecological constraints, which can damage sound transmission and detection, having adverse effects upon them (Ladich, 2019 [40]). It is very important to find out to what extent fishes can modify their sounds, especially when key ecological factors, such as the levels of ambient noise, and water temperature, are subject to change.

Now that climate change is under way, it is important to investigate the effects of temperature increases on acoustic communication in fishes and to analyse whether changes in sound properties may result in changes in their auditory sensitivity. The relationship between temperature and sound may affect the survival of some fish species. A recent study by Ladich and Maiditsch, (2019) [41] has shown that sound communication by a catfish species can be adversely affected by changes in the ambient temperature. It has also been suggested that temperature variations can result in major changes in the body metabolism of some animals, with higher temperatures associated with increased ageing (Martins, 2019 [42]). It has certainly been shown that that sound production and the hearing abilities of the catfish Platydoras armatulus, can be adversely affected by changes in the ambient temperature (Papes and Ladich, 2011[43]).

There are large gaps in our understanding of the effects of anthropogenic sounds (identified by Hawkins et al., 2015 [44]). Many of the scientific papers dealing with these effects have not been peer reviewed, and are based on poorly performed sound exposure experiments. Our knowledge on the effects of noise on sound communication in fishes is especially poor. The effects of anthropogenic sounds on acoustic communication in fishes especially needs to be investigated. It is extremely difficult at the moment to conclude which anthropogenic sources of sound are most damaging, in terms of adverse effects upon hearing and behaviour, or physical harm to fishes. It is important to identify those sounds that have especially detrimental effects upon fish populations, and to regulate or mitigate the effects of such sounds. Fishes are important species in many aquatic habitats. They constitute a major source of food for marine mammals and also humans!

Conclusions

Fishes obtain a great deal of information about the environment around them by listening to sounds. Many fishes make sounds to communicate with one another. The hearing of fishes is based on internal ears, that are sensitive to particle motion, rather than the sound pressure, although some species can detect sound pressure using gas-filled organs like the swim bladder. Sound propagates rapidly through water, and provides fishes with information from far greater distances than other sensory stimuli. The sounds that most fishes hear are confined to low frequencies compared with the frequenci es detected by most terrestrial animals and aquatic mammals. Fishes are able to discriminate between sounds of different amplitude, frequency, and temporal characteristics. Fishes are also able to locate the directional characteristics of sounds. Underwater sounds play a key role in navigation, foraging for prey, the detection of predators, and communicati on with one another, especially during spawning. Some fishes may also use the detection of natural sound sources to select their habitats. Many underwater sounds are now generated by human sources, including shipping, dredging and trawling, underwater explosions, seismic exploration, offshore constructio n work, and sonar systems. Interference of anthropogenic noise with detection of sounds has the potential of reducing fitness and impacting the lives of individual fishes, with potentially adverse effects upon their populations [22]. There is a need for more research to be carried out on the impact of anthropogenic sounds upon fishes.

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