Introductory Research Essay

Impact of anthropogenic noise on fish behaviour and ecology

Kajsa Johansson

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Department of Wildlife, Fish, and Environmental Studies
Swedish University of Agricultural Sciences
901 83 Umeå, Sweden

Introduction

Visual orientation can be restricted in aquatic environment and then, the auditory system is particularly important. For example, in dark water and at night, is fish getting information at a greater distance with sound rather than with vision (Popper, 2003; Popper and Hastings, 2009). Fish gets information with the auditory system from abiotic and biotic sound sources, and alter their behaviour accordingly. Biotic sound sources is sound produced by fish for inter- and intra-specific communication (Pitcher, 1993) and other marine organisms such as certain kinds of shellfish (*Crustacea*) and marine mammals (*Cetacea*) (Urick, 1983). Crunching noise produced when feeding and low frequency noise by hydrodynamic turbulence produced by swimming fish are other biotic sound sources (Simmons and MacLennan, 2005). Sound waves have the ability to travel long distance in water and many fish species utilize sound as a source to communicate. However, not all species seem to use sound production for communication, but it is clear that all is able to receive acoustic stimuli (Tavolga, 1971). The goldfish, an ostariophysan has extraordinary hearing abilities for fish, but no sound production for communication is known (Schwarz, 1985). Abiotic sound sources are important for fish survival as well. Fish receive information about the surroundings that helps them to orientate in the area (Codarin *et al.*, 2009). Waves breaking on the shore, current moving over reef, rain on the ocean surface and sound produced by seaquakes and volcanoes are examples of abiotic sound sources (Urick, 1983; Popper, 2003).

Activities associated with human benefits, such as fisheries and exploitation of natural resources may have severe impact on fish populations, by causing collapsed fish stocks and habitat degradations (Jackson *et al.*, 2001; Munday, 2004). Also, other human activities not associated with commercial use of the ocean resources can often have severe effects. Different kinds of pollution, such as trash and urban runoff as well as nutrient runoff causing eutrophicated water (Teck *et al.*, 2010) affect the oceans. The effects anthropogenic (human-made) noise may have on fish is a relatively new concern (Popper, 2003) and arise after attention of the effect noise has on marine mammals. Change in resting and vocalizing behaviour and migrating routes have been observed in certain whale species (Richardson *et al.*, 1995; NRC, 2000; NRC, 2003), due to the anthropogenic noise. The marine ecosystem includes many other species other than marine mammals, which are depending on the ability to detect sound for their survival (McCauley *et al.*, 2003). If there is an interference with the detection of the auditory scene there might be significant effects on fishes that use sound to orientate, to detect predator and prey and on those fish that use sound for communication (Amoser *et al.*, 2004; Popper and Hastings, 2009).

Anthropogenic noise is any sound produced by human activities and consists of a wide range of frequency and durations, from high-intensity acute noise to chronic low-frequent noise (Codarin *et al.*, 2009). Due to the type of anthropogenic source, the effects on fish and other aquatic animals may be different (Richardson *et al.*, 1995; NRC, 2000). Shipping, seismic exploitation and sonar are frequently cited in publication, to affect marine mammals (Richardson *et al.*, 1995; NRC, 2003) and are also likely to affect other marine organisms as well. Anthropogenic noise may cause:

- Behavioural effects where noise is causing an avoidance reaction, startle response and it may also exclude fish from otherwise preferred areas.

- Physiological stress response with a metabolic change (production of the stress hormone cortisol and other primary and secondary stressors) and a cardiovascular reaction.

- Temporary or permanent hearing loss by causing hearing threshold shifts and damage of the inner ear hair cells.

- Auditory masking, where sound produced in inter- and intraspecific communication are masked. The noise might also decrease the detection range and therefore reduce fish's ability to detect predator/prey.

Aims

Increased amount of anthropogenic noise in the oceans may have negative effects on marine animals. High frequency sound can harm nearby fish, lower and more moderate noise from vessels may also have impact on fish and has also the potential of affecting a bigger area and a larger number of fish. The aim of this paper will therefore be to review the current knowledge of effects anthropogenic noise have on fish. The paper begins with some basic information about underwater sound and the auditory system in fish, following with ambient and anthropogenic sound sources in the ocean. Current knowledge on effects of anthropogenic noise on fish behaviour and ecology is reviewed and future research areas in need of more investigation are discussed.

Underwater acoustics

Physics of sound

Sound is a form of mechanical energy that causes a change in pressure and gives rise to particle motion. The sound energy is transmitted as a periodic compression and expansion of the water molecules and is travelling as a wave through the medium (Simmons and MacLennan, 2005). The oscillations of the wave can be described as a sinusoid, with a periodic change in amplitude around a baseline (Figure 1). The frequency (f) of the sound wave is the number of cycles/seconds defined in hertz (Hz), the period (T) is $1/f$ and is the duration of one cycle measured in seconds. The wave length (λ) is the distance covered by one full cycle and can be described as c/f or cT, where c is the speed of sound propagation (Simmons, 2002). Sound speed is 1450-1550 ms^{-1} in water and 343 ms^{-1} in air and a sound wave is therefore travelling about 4.5 times faster in water than in air (Hawkins and Sand, 1977; Finfer *et al.*, 2008). Sound speed in water is not constant and varies with temperature, depth and salinity (Simmons, 2002). The intensity of sound (sound level) in water as in air is quoted in decibel (dB), with a logarithmic scale due to the capability of huge range in amplitudes. A measured sound intensity (I_1) is compared to a reference value (I_2), which for water is 1µPa and the ratio in decibel can be described by the formula $r_{dB}=10\log(I_1/I_2)$. However, bioacousticans do not measure intensity but rather sound pressure level. Intensity is related to effective sound pressure (P_e) by the equation; $I=p^2_e/2p_0c$, applied to a sound wave in a homogenous and boundless medium and where p_0 is the density of the medium, c is the propagation velocity of the sound wave, and p_0c is the medium's characteristic acoustic impedance. The pressure described in dB is therefore $dB=10*\log_{10}(p_1^2/2p_0c)/(p^2_2/2p_0c)$ or just $dB=20*\log_{10}(p_1/p_2)$, where p_1 is the measured pressure value and p_2 are the reference pressure value (Simmons, 2002). The reference pressure for water is 1µPa and 20 µPa for air which means that sound pressure in water and air are not directly comparable (Simmons, 2002; Simmons and MacLennan, 2005). Particle displacement is the local oscillation of the molecule and the rate of one particle, called particle velocity (v) is measured in m/s (Simmons and MacLennan, 2005). The relation between particle velocity (v) and sound pressure (p) is the acoustic impedance (Z) and can be described with the equation $p=vZ$ in a free field. Acoustic intensity and pressure are for a plane and spherical wave related by the characteristic impedance Z of the medium; $I=p^2/Z$. (Hildebrand, 2009). However, close to the sound source or in shallow waters is the impedance different from the impedance in a free field which makes the relationship between particle velocity and pressure complicated (Wahlberg and Westerberg, 2005).

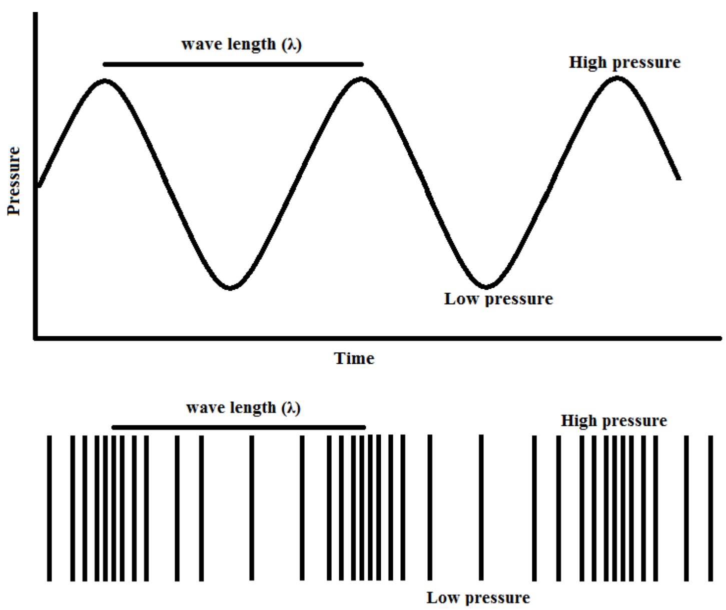

Figure 1. Sound wave propagation in water can be illustrated as a sinusoid (top), with a periodic change in amplitude (high and low pressure) with the wavelength λ, but also as a periodic compression and expansion of the water (bottom). Based on the outline of Simmonds and MacLennan (2005).

Sound waves in water have the ability of long distance travel, and both light and radio waves are attenuated faster than sound energy (Urick, 1983; McCarthy, 2004). The wave is travelling through both water and air as vibration of the fluid particles. When sound travels from one point to another it diminish in amplitude or intensity due to spreading in space, reflection and absorption (Richardson *et al.*, 1995). Energy is removed or scattered from the wave by suspended solids, biota, and entrained gas or converted to heat by physical absorption (Simmons and MacLennan, 2005). People have applied underwater sound to a variety of purposes in different areas, for example in exploitation of the sea with so called sonar system (Urick, 1983). It is also used in acoustic studies with marine animal where data on the sound source, attenuation on the propagation path and the ambient noise in the area have to be received. Sound spectra are used to describe the distribution of sound power as a function of frequency. An animal's sensitivity to a sound varies with frequency and the response to a sound is depended on the presence and levels of sound in the frequency band to which the animal is sensitive to (Richardson *et al.*, 1995).

Ambient noise

The natural background noise (ambient noise) in the ocean can be divided into three different frequency bands; low (10 to 500 Hz), medium (500 Hz to 25 kHz) and high (>25 kHz). Low frequency sound has the potential to long distance propagation since it experience little attenuation, compared to high frequency sound (Hildebrand, 2009). There exists frequencies of ambient noise in the infrasonic range (below 10 Hz) in the oceans and it may be of great importance to fish. For example, Sand and Karlsen (1986) suggest that migrating fish utilize infrasound to orientate. Intermittent sources of noise are sound that do not persist over hours and days, but are of transient occurrence. The ambient noise in the deep sea are created by tides and hydrostatic effects of waves, seismic disturbance, oceanic turbulence, ship traffic, surface waves and thermal noise (Urick, 1983). In general, human industrial activities and shipping are not considered as ambient noise, however, "aggregated traffic noise" from all distanced ship of more than 10 km are included in ambient background noise and is dominated by frequencies of 20-300 Hz (Richardson *et al.*, 1995). Sources of ambient noise in coastal areas, additional from that in the deep sea are human industrial activities and biological noise. Wind speed, biological organisms and shipping are the largest contributor to the ambient noise over the continental shelves. The ambient noise in coastal area is highly variable in both time and place and at a given frequency. The variability of ambient noise is due to change in wind speed, amount of shipping and also because of better sound transition during the winter season. Tidal and human activities are sources of variability of the ambient noise in harbours and bays (Urick, 1983).

Biological noise produced by marine animals can in some waters be one of the dominant sources of ambient noise. The snapping shrimp (*Alpheus* spp. and *Synalpheus* spp.), for example produces mid-frequency sound (Everest *et al.*, 1948) with its claw. Also, many fish species produce sound for inter- and intraspecific communication. There are different mechanisms of sound production between different kinds of fish species (Helfman *et al.*, 2009). One type of sound production is created by vibration of the swim bladder by muscular force, cod (*Gadidae*) is one species that produce sound like this. Other fish species produce sound by rubbing hard parts of the body together. Some catfishes use the pectoral girdle, while some cichlids (*Cichlidae*) use their pharyngeal teeth in sound production (Ladich and Yan, 1998; Simmons and MacLennan, 2005). There are fish species that use sound for communication during the reproduction period, for example mature cod produce a grunting sound in spawning shoals (Brawn, 1961). Acoustic exchange can also be part of an aggressive behaviour (Schwarz, 1985).

Anthropogenic noise

There is a variety of human activities that produces anthropogenic noise in the oceans. The amount of anthropogenic noise in coastal areas as well as in the open ocean has increased in the last decades (Andrew *et al.*, 2002; McDonald *et al.*, 2006). The noise can be categorized into two different groups; high-intensity and acute noise and low-frequent chronic noise. High-intensity noise is produced by military sonar, pile driving and seismic explorations while low-frequent and chronic noise is produced by different kinds of ship and vessels (Codarin *et al.*, 2009). The amount of recreational boats is increasing in high populated coastal areas (Graham and Cooke, 2008) and might be a possible growing threat. Increase in national shipping with low-frequent noise has also been seen (Ross, 2005). Other sources of low frequent noise are public transport and fishing vessels. However, the amount of fishing vessels have not grown much since the 1960s but still include 1.2 million vessels (Slabbekoorn *et al.*, 2010). High intensity low-frequent sonar, mid-frequent sonar, seismic air guns and pile driving are human activities that have raised concerns about the effects on marine mammals and fishes (NRC, 2003; Popper, 2003). Recreational activities and drilling (Richardson *et al.*, 1995; Popper, 2003) are other human activities that produces noise in the oceans and the relatively new and growing concern is the exploitation of offshore windmills, which produces noise under both construction phase and operational phase (Wahlberg and Westerberg, 2005).

Auditory system in fish

Sensitivity to sound in fish is relatively well studied and there are numerous studies on the morphology of inner ear of fish (Popper, 1976; Popper and Coombs, 1982). Fish have two sensory systems for detection of water motion, the inner ear and the lateral line. The lateral line system detects water motion and low frequent sound on short distances while the inner ear detects higher frequencies and from greater distances (Slabbekoorn *et al.*, 2010).

The inner ear

The fish ear consists of a paired structure embedded on each side of the head in the cranial cavity with no obvious external structure. The inner ear consists of endolymph filled canals, sacs and ducts (Pitcher, 1993; Slabbekoorn *et al.*, 2010). There are three semicircular canals and three otolith organs, the saccule, utricle, and lagena (Popper *et al.*, 1982; Popper and Fay, 1999; Popper *et al.*, 2003) often containing one single calcareous stone (the otolith) in teleost fish (Carlström, 1963). The body of a terrestrial animal are an effective barrier to sound, while fish have almost the same density as the surrounding water and is therefore almost acoustically transparent (Hawkins and Sand, 1977). However, the otolith are about three times denser than the fish body (Popper and Coombs, 1982) and lays on top of a sensory macula which consist of a large number of sensory hair cells and supporting cells (Figure 2) (Popper and Fay, 1973; Popper and Coombs, 1982). In a sound field, both the fish body including sensory epithelia and the otolith are set into motion. Due to differences in density between otolith and epithelia, different phase and amplitude of the oscillation are produced. The hair cells undergo a shearing force that results in deflection of the hair cells and a physiological response is produced in respond to the sound (Popper and Fay, 2010). The otolith can therefore be seen as a particle motion detector and there the maculae responds to sound, gravity and to linear acceleration (Bone *et al.*, 1999).

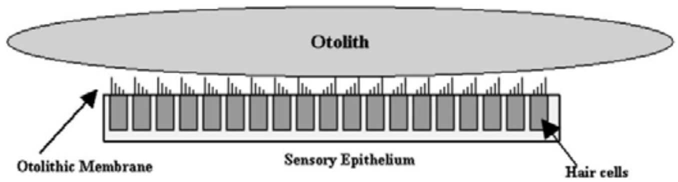

Figure 2. Schematic illustration of the sensory epithelium and the overlying otolith in the fish inner ear. The ciliary bundles from the sensory hair cells are in contact, or come close to contacting the otolith. The otolithic membrane separates, and connects, the otolith and the sensory epithelium (Popper and Lu, 2000).

The lateral line

The lateral line system is a mechanosensory system comprising of hair cell receptors that detect an object by the water disturbance it cause (Montgomery *et al.*, 1995). The lateral line can be described as a sophisticated canal system recessed in the skull or scales. The line is typically found on each side of the body and extends up on the head (Pitcher, 1993). The lateral line system responds to the motion of the water relative to the body of the fish and is able to detect low-frequency (generally below 50 Hz) movements such as surface and flowing water (Montgomery *et al.*, 1995). However, a fish has to be relatively close to the sound source and is only then able to detect an acoustic field. The limited detection range of the lateral line system is of one or two body lengths (Slabbekoorn *et al.*, 2010) but may be important in predator and prey detection as well as in schooling synchrony (Pitcher, 1993; Montgomery *et al.*, 1995). The lateral line system may also be particularly important in waters where visual orientation is deteriorated (Montgomery *et al.*, 1995).

Hearing ability in teleost fish

The swim bladder has several different functions in fish, for example, buoyancy control and sound production. It has also the function as a secondary sound source that radiates sound pressure variation as near-field particle motion (Popper and Fay, 1973; Yan *et al.*, 2000). Swim bladder shape and size and its physical relationship to the ear differ between species which might affect the fish hearing ability (Popper and Fay, 1973). Fish with no accessory hearing structure are often referred as hearing generalists or non-specialists, are sensitive to particle motion and are only able to detect low-frequency sound. Hearing specialists have accessory structures, a series of bones (Weberian ossicles) that connect the swim bladder to the inner ear and enables pressure detection (Popper and Clarke, 1976). Hearing specialists have therefore improved hearing ability with an enhanced detectable frequency range and a lowered hearing threshold (Hawkins, 1972; Popper and Fay, 1973; Popper and Clarke, 1976; Ladich and Popper, 2004). Gas has higher compressibility than water and the swim bladder has the ability to respond to sound pressure fluctuation. The motion from sound pressure is transformed to particle motion and then transmitted to the otolith organs of the inner ear (Popper and Fay, 1999). Eurasian perch (*P. fluviatilis*), Atlantic salmon (*Salmo salar*) and Atlantic cod (*Gadus morhua*) are examples of hearing generalists while cyprinids like roach (*Rutilus rutilus*) and the goldfish (*Carassius auratus*) are two examples of hearing specialists (Schwarz, 1985; Amoser and Ladich, 2005; Wysocki *et al.*, 2006). However, recent suggestions are that the terms of "hearing generalists" and "hearing specialists" should be dropped. There are data showing evidence of fish being sensitive to both sound pressure and particle motion that is frequency dependent and they could therefore neither be termed hearing generalist nor hearing specialists (Popper and Fay, 2010).

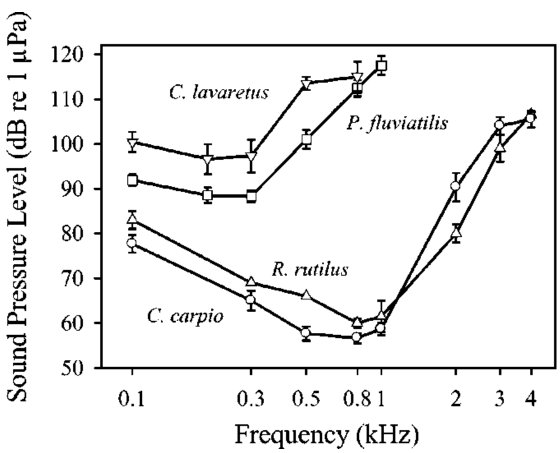

Figure 3. Audiograms (mean ± SE) of the four selected fish species; *C. lavaretus*, *P. fluviatilis*, *R.rutilus* and *C. carpio*, determined using the AEP-recording technique (Amoser *et al.*, 2004).

Hearing threshold can be measured by using physiological methods or conditioning techniques (Popper and Fay, 1973). Auditory evoked potential (AEP), also called auditory brainstem response (ABR) is a non-invasive technique where neural responses to auditory stimuli is measured (Corwin *et al.*, 1982). The threshold level is determined by the point when fish is responding in 50 % of the trials at the sound level (Popper, 1970; Simmons and MacLennan, 2005). The hearing threshold data are used in audiograms and provide good basic data for description of auditory function (Figure 3) (Popper and Fay, 1973; Amoser *et al.*, 2004). Auditory threshold varies with frequency and is generally high at low frequencies, diminishes to a frequency with an optimal sensitivity, and with further increase in frequency, the threshold is again increasing (Richardson *et al.*, 1995). There are fish that have been tested and are able to detect sounds with frequencies over 3,000 Hz, these are fishes with evolved specializations that enhance the hearing capabilities (Popper and Fay, 1999) while other species have the ability to detect sound in infrasonic range (below 20 Hz) (Sand and Karlsen, 1986; Karlsen *et al.*, 2004).

Effects of anthropogenic sound on fish behaviour and ecology

Possible effects of anthropogenic noise on fish might be no effects at all till severe damage on the auditory organs and behavioural effects. Fish might swim away from the sound source and by doing that also leaving feeding or reproduction area (Engås *et al.*, 1996). On the other hand, if fish stays in a noisy area other consequences might have both long and short term effects, e.g. causing stress responses, auditory masking and cause damage on auditory organs.

Behavioural effects

Avoidance reaction and startle responses

There are few but diverse studies on behavioural effects of noise on fish. Most research has been made on the effects boat noise produced by fishing vessels have on fish behaviour, with the aim of better management of catch rate (Figure 4) (Wahlberg and Westerberg, 2005; Wysocki *et al.*, 2006). Engås *et al.*, (1996) found that seismic shooting severely affected fish distribution, local abundance and catch rate in their investigated area. Avoidance behaviour of fish could be a problem since avoiding boats could result in misleading estimation in acoustic stock assessment (Drastik and Kubecka, 2005). An another example is the study by Sarà *et al.*, (2007) who studied the behavioural effect different types of boats have on bluefin tuna (*Thunnus thynnus*). They observed a concentrated, coordinated school structure with unidirectional swimming in the absence of boat noise while a changed behaviour with directional and increased vertical movement towards surface or bottom was found when a boat was approaching. An unconcentrated structure and uncoordinated swimming behaviour of the school was also observed. The reaction to the boat noise did elicit an escape response similar to the response to a predator. Avoidance reaction to noise is referred to as a conspicuous and rapid escape in order to evade predatory attack and therefore increase probability of survival. The escape can be seen as an abrupt stereotyped movement triggered with minimum delay (Korn and Faber, 1996; Karlsen *et al.*, 2004). Differences in amount of movement at a given time span can also be studied as a consequence of a reaction to noise disturbance. Buscaino *et al.* (2010) exposed European sea bass (*Dicentrarchus labrax*) and gilthead sea bream (*Sparus aurata*) to acoustic stimuli with frequencies of 0.1-1 kHz and a maximum sound pressure level of 150 dB_{rms} re 1 µPa and measured the motility (the sum of the movement across the x, y and z axis). They found that noise-exposed sea bream and sea bass had a significantly higher motility ($p < 0.0001$ and $p < 0.001$, respectively) than the control group with no noise exposure.

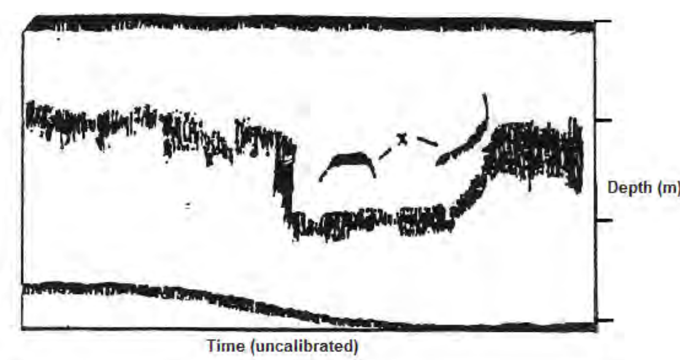

Figure 4. Echo sounder track of herring school, which is diving when a trawl (x) from a fishing vessel is approaching (Mohr, 1964 in Wahlberg and Westerberg, 2005).

Exclusion of fish from otherwise preferred areas

The effect noise has on one individual may be measurable or observable but the effect on a whole population or community is more difficult to evaluate. One question you may ask is, if anthropogenic noise causes negative effects on fish, are there less fish in noisy areas than in less noisy areas? Wardle *et al.* (2001) found no or little effect of sound from seismic triple G. airgun on the day-to-day behaviour of resident fish and invertebrates on an inshore reef on the west coast of Scotland. However, Picciulin *et al.* (2010) investigated the behavioural responses to boat noise exposure of red-mouth goby (*Gobius cruentatus*) and chromis (*Chromis chromis*) living in a marine protected area in the northern Adriatic Sea. Noise from a 26 m tourist ferry and a 5 m fibreglass boat were recorded and played back *in situ* to the experimental fish. They did not found any short termed behavioural effects such as avoidance reaction or startle responses. However, the amount of time *G. cruentatus* and *C. chromis* did spend in their nests and inside their shelter respectively was significant higher when exposed to noise. These results indicate the importance of research about long-termed effects of noise on fish behaviour.

Physiological stress

Metabolic changes

Environmental changes (stressors) both natural and human (Santulli *et al.*, 1999) can cause stress responses in humans. Several studies have shown that noise also can cause stress and stress induced responses in animals, for example fish, where stress is causing a metabolic change (Smith *et al.*, 2004b; Wysocki *et al.*, 2007; Buscaino *et al.*, 2010). The primary reaction to stress is a rapid change in concentration of plasma catecholamines and corticosteroids (Mazeaud *et al.*, 1977). Cortisol is a corticosteroid hormone or glucocorticoid and is involved in responses to stress and anxiety and is therefore often referred as a stress hormone (Slabbekoorn *et al.*, 2010). An increased level of cortisol concentration in the blood plasma and tissue of the fish indicates a physiological stress (Pickering, 1992; Wysocki *et al.*, 2006) and the transient spike in plasma cortisol can often be seen within 10 minutes after the stress exposure (Smith *et al.*, 2004b). Analysing cortisol production is a common way of studying physiological stress in fish, however, other primary and secondary stressors such as blood glucose and lactate can also be analysed (Buscaino *et al.*, 2010). For example, a research on acoustic stress induced by air gun blast did cause biochemical responses in European seabass (*Dicentrarchus labrax*). The variation in cortisol, glucose, lactate, AMP, ADP, ATP and cAMP concentrations in different tissue were primary and secondary responses to the noise. The biochemical parameters had returned to physiological values within 72 h after the acoustical stress exposure, which indicates a rapid homeostasis (Santulli *et al.*, 1999). Wysocki *et al.* (2006) studied the effect of ship noise recorded in field (L_{Leq} average 153 dB re µPa, 30 min) on Eurasian perch (*P. fluviatilis*), common carp (*Cyprinus carpio*) and gudgeon (*Gobio gobio*). Cortisol was extracted from water and showed significant increased concentration compared to control level for all three fish species tested. The results indicate that boat noise with amplitude and frequency fluctuation may be a potential stressor and that also *P. fluviatilis,* with its poor hearing capabilities is affected.

Cardiovascular response

A response of the cardiovascular system can also be used as an indicator of stress responses in fish (Cooke *et al.*, 2003). In the study of Ashley and Cooke (2008) largemouth bass (*Micropterus salmoides*) were exposed to noise from either 9.9 hp combustion engine, an electric motor and a canoe paddle and cardiac output and its components (heart rate and stroke volume) were monitored. Exposure to all three types of activities resulted in increased cardiac output with an increase in heart rate and a slight decrease in stroke volume. Most extreme response was measured in fish exposed to the combustion engine treatment; there also cardiovascular variables recovery was the longest (~40 min). The result indicates that fish experience physiological disturbance in response to noise from recreational boating activities.

Fitness costs and higher mortality

Studies have shown that swimming activities are drastically reduced during gonadal synthesis and that a reduction of locomotion may compensate for the cost of production of gonadal tissue (Koch and Wieser, 1983). Other studies have also shown that energy budget for muscle activity can be a great deal of total energy costs (Boisclair and Sirois, 1993). There is a possibility that an increased swimming activity may have other consequences as well, such as for food requirements and reproduction. Therefore, increased activity due to a reaction triggered by anthropogenic noise may have additional and long-termed impact other than the initial reaction to the noise, such as on fitness. Other fitness consequences may be related to increased predation costs or decreased mating success. Studies about effects of noise on fish larvae and eggs are scarce. In the study by Banner and Hyatt (1973) eggs and larval fish were exposed to moderate and high level of noise (approximately 20 db higher in noisy tank than in quiet tank). They found lower growth rates of the sheepshead minnow (*Cyprinodon variegates*) and longnose killifish (*Fundulus similis*) in the noisier tank compared to fish in the quiet tank. The viability of eggs and resulting *C. variegates* larvae was also significant reduced in the noisier tank.

Temporary or permanent hearing loss

Several studies have been focused on how noise affects fish hearing capabilities by studying hearing threshold shift (Popper and Clarke, 1976; Smith *et al.*, 2004a). Smith *et al.* (2004b) studied effects of increased ambient sound on hearing in goldfish (*Carassius auratus*), by exposing fish to white noise with a bandwidth ranging from 0.1 kHz to 10 kHz at 160-170 dB re µPa total sound pressure level for either 1, 3, 7, 14, or 21 days. The result showed a significant threshold shift in hearing after 10 minutes of exposure and a linear increase up to 28 dB after 24 h of noise exposure. However, further noise exposure did not increase hearing threshold. It took 14 days for the goldfish to fully recover to control hearing level after 21 days of noise exposure. Studies have also shown that high intensity anthropogenic noise can damage the fish ear. Repetitive use of high energy sources such as air gun arrays, for marine seismic petroleum exploration, is one common source of anthropogenic noise in the oceans. McCauley *et al.* (2003) found that ear of fish exposed to an operating air-gun sustained extensive damage to their sensory epithelia. In the experiment, pink snapper (*Pagrus auratus*) were held in cages and exposed to signal from an air-gun towed toward and away from the cages. Damage of the sensory epithelia was seen as ablated hair cells and still, after 58 days, no evidence of repair or replacement of damaged sensory cells was seen. The amount of sensory hair cells in fish depends on the size of the fish and the number of cells increases with age (Popper and Hoxter, 1990). Other studies on noise exposure to fish have shown that fish have the ability to replace cells that have been damaged or lost. Smith *et al.* (2006) investigated recovery of the goldfish (*C. auratus*) ear following white noise exposure. Fish were exposed to noise with a bandwidth ranging from 0.1 kHz to 10 kHz at 170 dB re. 1 µPa RMS sound pressure level, for 48 h. AEP technique were used to determine hearing threshold and the hair bundle loss and apoptotic cell death were quantified in epithelia. Temporary hearing threshold shift (TTS) was exhibited and ranging from 13 to 20 dB at frequencies tested (0.2-2 kHz). Increased apoptotic activity in the saccule and lagena was observed. Hair bundle density in central saccule had recovered, while bundle in caudal saccule had not recovered at the end of the experiment. This experiment shows that noise exposure can cause damage on the inner ear of goldfish and that they also have a significant regenerative responses.

Auditory masking

It is well known that background noise have the potential of raising the threshold value (Fletcher, 1940) and auditory masking is when a sound source impairs another sound source. It is therefore important to relate the auditory threshold to background noise in order to determine the signal-detecting abilities of animals in the natural environment (Wysocki and Ladich, 2005). For example, noise from small vessels can significantly mask acoustically mediated communication in delphinids (Jensen *et al.*, 2009). Fish can usually detect acoustic signals in the 100-500 Hz band (Popper *et al.*, 2003) and due to increased low-frequent noise (under 1000 Hz) during the last decades, there is a risk that this noise will be masked and have a negative effect on fish welfare (Richardson *et al.*, 1995; Buscaino *et al.*, 2010). It is also insufficient to compare audiograms established under quiet laboratory condition with field sound spectra in order to calculate the detectable distance of boat noise, since hearing can be masked by ambient noise in natural environment (Amoser *et al.*, 2004). Also, most fish produce sound signals in the broad band (>500 Hz) (Kihslinger and Klimley, 2002) and are in risk of being masked by low-frequent anthropogenic noises.

Auditory masking in fish can be studied by comparing auditory threshold under quiet condition and with masking noise. Two studies by Wysocki and Ladich (2005) and Amoser and Ladich (2005) focus on hearing in fishes under noise condition and their adaptation to ambient noise in their habitat. Wysocki and Ladich (2005) investigated the influence of noise level on two hearing specialists and one hearing generalist with the objective to investigate how it affects hearing threshold, to which degree different frequencies is masked and whether fishes with different hearing abilities are affected by similar noise levels. They found that the hearing threshold shifts depends on the hearing abilities of the species, the frequency and noise levels tested. Acoustic communication and orientation in fish may therefore be limited by noise regime in the environment.

Increased amount of anthropogenic noise in the oceans may cause a reduction in active space and decreased detection range. This may cause an increased mortality due to unbalancing predator/prey detection (Codarin *et al.*, 2009; Slabbekoorn *et al.*, 2010), since hearing and localizing of sound might be important for predators finding prey and for prey to avoid predators. This can therefore be restricted in noisy condition since it might lower catch efficiency (Slabbekoorn *et al.*, 2010). Effects of anthropogenic noise on food and escape efficiency have been studied on mammals and birds (Quinn *et al.*, 2006; Schaub *et al.*, 2009), however, research on fish is lacking.

Future research

There are only hearing data for about 100 of the about 29 000 existing fish species (Popper and Hastings, 2009) and extrapolation of the effects of anthropogenic noise between different species should therefore be done with caution. There are several aspects you must keep in mind when working with aquatic organisms not often encountered by investigators working with non aquatic animals (Popper and Fay, 1973). For example, some fish species can detect both particle velocity and sound pressure and it is therefore important to measure both components. Extrapolating between different stimuli should also be done with caution since the characteristics of the source differ significantly from one another (Popper and Hastings, 2009), e.g. high- and low-frequent and acute or chronic noise such as noise from sonar's respectively boat noise. Experiments with captive fish only tell us how they may react, it is not necessary that they will react in the same way when they are not restricted to a cage in a lake or ocean, because fish held in cages have not the ability to avoid loud sounds. Studies in aquatic environments are difficult since observers have difficulties in studying animals over large areas and localizing sound underwater (Slabbekoorn *et al.*, 2010). Another difficult subject to investigate is the habituation to anthropogenic sound, which is important when evaluating the effects sound have on marine wildlife (Wahlberg and Westerberg, 2005). Most studies on sound detection in fishes have been performed in laboratory with the aim of having as quiet background noise as possible (Wysocki and Ladich, 2005). However, the results may be ill-suited since in natural environment, sound detection are depended on ambient noise level and the sound detection may not be as good as in the laboratory. A new research study by Buscaino *et al.*, (2010) presents semi-natural experiments on the effects noise have on fish. They investigated the impact of an acoustic stimulus on the motility and haematological responses in European sea bass (*Dicentrarchus labrax*) and giltheads sea bream (*Sparus aurata*). The experimental sea cages were placed in a circular natural harbour and the effect of ambient noise in the harbour were therefore also included. However, the experimental fish had still not the ability to swim away from the sound source. The effects of anthropogenic sources of sound on fishes have been reviewed by Popper and Hastings (2009) and they conclude that there are still only little known about the effect of pile driving and other anthropogenic sounds on fishes. Slabbekoorn *et al.*, (2010) suggest major targets for future research and highlights the need of noise-dependent fish distribution research, does the distribution vary with sound sources, fish age, physical and biological factors. Other research areas in need of future research are reproductive consequences of noisy condition, masking effects on communicative sounds and masking effects on predator-prey relationships.

Conclusions

Fish use the auditory system to get information about the surroundings, and many fish species utilize sound as a source of communication. An interference with the detection of the auditory scene can therefore have major effects on fish. The amount of anthropogenic noise in the oceans has increased during the last decades and data is indicating that marine animals are affected by the sound. Military sonar, pile driving, seismic explorations and noise from boats and vessels are human activities that produce anthropogenic noise. Studies have shown that loud noise can damage fish auditory organs but there are also indications of that lower, more consistent sound might have impact on fish welfare. Hearing abilities in fish differ between species and the effect anthropogenic noise has on one species might therefore be different from another. Anthropogenic noise can cause behavioural reactions, stress responses, auditory masking and also damage the auditory organs. Still, after years of research of fish hearing and on how fish is affected by noise, little is known about the effects and especially how fish react to noise in the wild.

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