The noisy underwater world : the effect of sound on behaviour of captive zebrafish

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Chapter 6

General discussion

Summary of thesis results

Human generated sound (anthropogenic noise) is now widely recognized as an environmental stressor, which may affect aquatic life (Slabbekoorn et al. 2010; Radford et al. 2014). Over the last few decades, there is increasing interest of policy makers, animal welfare communities, behavioural biologists and environmental managers to understand how man-made sound may lead to negative consequences on terrestrial (Patricelli & Blickley 2006; Barber et al. 2010; Kight & Swaddle 2011) but also underwater animals (Slabbekoorn et al. 2010; Ellison et al. 2012; Williams et al. 2015). Aquatic animals can be negatively affected by anthropogenic noise in many ways (Popper et al. 2003; Popper & Hastings 2009; Slabbekoorn et al. 2010; Richardson et al. 2013). Therefore, we need to understand how anthropogenic noise may affect individuals to eventually be able to assess the impact of anthropogenic noise on populations, communities, and ecosystems. In my thesis, I have addressed several fundamental aspects of the potential impact of anthropogenic noise by experimental sound exposure studies in captive fish. Below, I first briefly summarize the findings of each of the four data chapters to then address some general concepts in a broader context.

In **Chapter 2,** I focused on the potential effects of sound exposure on predator –prey interactions in captive zebrafish preying on water fleas. I investigated how sound exposure may affect not only zebrafish as predator but also water fleas as prey. I tested sound exposure conditions that varied in temporal pattern: continuous, regular and irregular intermittent, and I also included a control condition with no additional sound exposure. I checked for a sound impact on: 1) waterflea swimming behaviour; 2) zebrafish swimming behaviour, and 3) foraging behaviour and efficiency of zebrafish hunting for waterfleas. My findings indicate: 1) no significant effects of sound exposure on waterfleas; 2) that temporal pattern affected the response to sound exposure in the fish and 3) that the detrimental impact of sound exposure on feeding efficiency was independent of temporal pattern. These data suggest that the direct impact of sound seems to be on the predator, but that will not exclude an indirect impact of sound exposure on the prey. Therefore, the impact on foraging efficiency in predator fish feeding on invertebrate prey in outside natural conditions may alter the balance in abundance between the two taxa. The results of this chapter confirm the possibility of noise impact beyond single species effects and future studies may reveal sound impact at community level under water as has been reported for terrestrial systems (Francis et al. 2009; 2012; Slabbekoorn & Halfwerk 2009). I therefore think that more studies are warranted on other species and other frequency ranges to explore the generality of findings beyond the current species and test conditions.

In **Chapter 3,** I compared the potential effects of sound exposure on two different fish species; zebrafish and cichlids, with different swimming behaviour and different hearing abilities. The findings revealed significant effects on behaviour in response to the elevated sound levels in both species, sometimes in the same way but sometimes in a different way. After the initial seconds, both species reduced their swimming speed during the "prolonged" period of sound exposure. At the onset of sound exposure the zebrafish immediately increased their swimming speed due to startle or initial acceleration responses, which were not observed for cichlids, which occasionally even started to swim backwards. Moreover cichlids went even further down the water column and spent significantly more time in the bottom layer of the tank during both sound exposure conditions, while zebrafish remained at the same level. These responses are likely to be anxiety-related behaviour and are similar to response patterns in other species during acoustic exposure experiments (Andersson et al. 2007; Bui et al. 2013; Neo et al. 2014; Neo et al. 2015). However, we suggest that care should be taken for any interpretation in terms of relative severity for the two species. Understanding impact and underlying mechanism(s) behind the observed behavioural changes requires more studies including physiological measurements and investigations of real long-term effects (at least weeks or months and addressing development, growth, survival, reproduction).

In **Chapter 4,** I tested zebrafish behavioural changes in response to experimental sound and light conditions. My aims were to investigate the effect of two modalities and study whether sound and light exposure affect spatial distribution and swimming behaviour of zebrafish. The experimental fish had a choice between two fish tanks: a treatment tank and a quiet and light escape tank. The findings of this chapter showed that elevated sound levels did not cause any tank preference in terms of the overall time the zebrafish spent in the treatment tank. Furthermore, although dark conditions in the treatment tank reduced the crossing activity between tanks, it also did not result in a spatial bias to the dark or light tank. The elevated sound levels clearly changed zebrafish behaviour when they were within the treatment tank; they increased freezing time and decreased the percentage of time spent near the active speaker. Dark conditions in the treatment tank also affected their behaviour and resulted in less time spent close to the tube and more time spent in the upper layer. In addition, we did not find any interaction effects of sound and light conditions on zebrafish behaviour. Overall, these data suggest that each modality has its own specific and qualitatively distinct impact independent of the conditions in the other modality (see Kunc et al. 2014; Halfwerk & Slabbekoorn 2015). Dim light may be a trigger to relax and make fish less hesitant to get close to the water surface, while loud sound clearly induces anxiety-indicating interruption of activities.

In **Chapter 5**, I conducted two experiments together with MSc-student James Campbell in which we measured the acoustic field inside a standard 1-meter fish tank, including sound pressure level and sound particle velocity level. We quantified the confined area available to the fish within an enclosure cage to explore the relationship between the two sound components and the potential relevance to fish behavioural responses. The first experiment examined how the ratio of pressure to particle motion in a small enclosure cage varies in response to the spatial location within the cage, as compared to theoretical open-water conditions. In the second experiment, we further examined the pressure and particle velocity levels within the context of an acoustically induced behavioural response by zebrafish. The findings of this chapter provide new insights into the sound field complexity of relatively small fish tanks and into the challenging exploration of the link between sound field parameters and fish behaviour.

Effects of sound on feeding efficiency

I found detrimental effects of sound exposure on food intake and subsequently in overall foraging performance in captive zebrafish, which confirms the results of several other studies on different fish species (Purser & Radford 2011; Bracciali et al. 2012; Voellmy et al. 2014a; Payne et al. 2015; McLaughlin & Kunc 2015) and other vertebrates (Croll et al. 2001; Aguilar Soto et al. 2006; Miller et al. 2009) but also invertebrates (Chan et al. 2010; Wale et al. 2013; Hughes et al. 2014). These studies all show an impact of sound on non-auditory tasks, which may be caused by visual distraction or attentional shift (Mendl 1999; Dukas 2002). It is unclear whether animals can habituate to this, but it may have an impact that is easily overlooked when animals stay in a noisy area (no impact on distribution) and keep on showing natural behavior (no apparent impact on welfare or fitness consequences).

Sound, anxiety, stress and behaviour

In all four of the experimental exposure studies I have observed the same types of behavioural changes. These behaviours are typically characterized by an initial increase in swimming speed and a downward shift toward the bottom of the tank and a prolonged swimming speed decrease, which were interpreted as anxiety/fear-related behavioural responses to sound exposure (c.f. Neo et al. 2015). This interpretation was in line with reports on similar responses to chemical alarm pheromone (Egan et al. 2009) and visual threat stimuli (Bass & Gerlai 2008; Luca & Gerlai 2012a; Luca & Gerlai 2012b). Other indoor studies on other species find either the same types of responses (Pearson et al. 1992; Andersson et al. 2007; Bui et al. 2013; Neo et al. 2014; Voellmy et al. 2014b) or additional ones such as reduced food searching, lower feeding rates and increased hiding time in a shelter (Bracciali et al. 2012; Løkkeborg et al. 2012; McLaughlin & Kunc 2015).

Outdoor studies report similar (Blaxter et al. 1981) and or different fish behaviour such as sound-related horizontal escape behaviour (Ona & Godø 1990; Engås & Løkkeborg 1996; Engås & Løkkeborg 2002; Draštík & Kubečka 2005). Even though several studies have reported physiological effects of sound exposure in terms of stress-hormone levels (Santulli et al. 1999; Wysocki et al. 2006; Buscaino et al. 2010; Filiciotto et al. 2014) and also growth and survival rate (Wysocki et al. 2007; Davidson et al. 2009; Debusschere et al. 2016), there is limited data on long-term effect from studies in aquaculture (Bart et al. 2001; Smith 2004) and complete lack of data where specific behavioural response patterns are linked to physiology or long-term effects. Although it appears clear that sound exposure can induce anxiety-related responses, future studies should focus on the effects of sound exposure on both behavioral and physiological measures to explore both immediate and prolonged anxiety/fear related behavioural response in free-ranging and captive fish species.

Species comparisons

My second data chapter already stressed the fact that multiple species may be involved in impact analyses of anthropogenic noise. The third one also confirmed that two different fish species with different hearing abilities may respond to sound exposure, but in different ways. Base line differences in behavior and response, as well as direct and indirect effects of sound on species indicate the complexity of sound impact studies. It is also not clear yet to what degree fish vary individually in sensitivity to sounds in their environment and how factors such as life stage, body condition and behavioural contexts modify this sensitivity (Purser et al. 2016). Moreover, assessments of potential effects of man-made sound go beyond single species and individual fish and eventually we have to address impact in outdoor conditions at the ecosystem level (Slabbekoorn 2016).

Spatial avoidance or lack there-off

In my third and fourth data chapter I found no evidence for spatial avoidance in our long tank or in our dual tank set-up. Only in very close proximity of the active speaker in our dual tank set-up, we found evidence for a directional response away from the sound source. Field studies have reported on spatial responses during ‘natural’ occurrence of man-made sounds (Ona & Godø 1990; Engås & Løkkeborg 1996; Engås & Løkkeborg 2002; Slotte et al. 2004; Draštík & Kubečka 2005; Sarà et al. 2007; Blaxter et al. 1981; Hawkins et al. 2014; Febrina et al. 2015) and spatial avoidance may just be more difficult to induce or assess in captive conditions.

There are some studies that showed horizontal attraction to playback of conspecific sounds in fish tank conditions (Higgs et al. 2007; Rollo & Higgs 2008; Verzijden et al. 2010). This seems in contradiction with the general lack of spatial deterrence responses away from loud sound sources in the variety of fish tank conditions in my thesis. Nevertheless, the spatial avoidance of the area right in front of the active speaker in chapter 3 may reflect a capability of sound source orientation under some condition or in some parts of the fish tank that must also be the explanation for the positive phonotactic studies in captivity.

In outdoor conditions, experimental exposure studies have reported spatial avoidance, but still only to a limited extent (Neo et al. submitted). Consequently, fish tank studies may be useful for investigations on general aspects of potential impact of sound on fish, but not for spatial avoidance studies. Future studies should be done in outdoor conditions with tagged fish or penned fish. I believe such studies would yield important information because there would be less acoustic field complexity and fish in the open field are not confined and therefore may behave more naturally in response to acoustic stimuli.

Perceptual salience of sound components

In my final data chapter, I report about a first empirical exploration of both detailed acoustic properties of sound fields in relatively small fish tanks and whether it is possible to investigate the relative importance of sound components in triggering a behavioural response. I like to draw attention to the potential of using stimuli of different frequency ranges to study fundamental aspects of hearing. Zebrafish are most sensitive to sound of frequencies around 800 Hz, but are likely to hear well above 1000 Hz, up to 4000 Hz (Higgs et al. 2002; Bretschneider et al. 2013). Furthermore, relative sensitivities for particle motion and sound pressure are likely to complement each other, but vary spectrally with a bias to the low end for particle motion and to the high end for sound pressure (Schulz-Mirbach et al. 2012). I believe this concerns an area of research that could yield important insights about auditory functions in fish in general and the potential for disturbance by artificially elevated sound in particular.

My experiments in this thesis addressed fundamental issues of potential sound impact and are not directly applicable to outside conditions nor suitable to extract absolute threshold values for legislation or permits. Nevertheless, my studies are complementing growing evidence in the literature that prolonged sound exposure can also result in long-term modification of behaviour and change spatial habitat use of fishes (Bass & McKibben 2003; Wysocki et al. 2009; Slabbekoorn et al. 2010; Slabbekoorn 2016; Radford et al. 2014; Amorim et al. 2015; Ladich 2015). I believe effective management of fish stocks or wildlife areas requires many more studies, especially into chronic effects of anthropogenic noise (c.f. Slabbekoorn et al. 2010; Francis & Barber 2013; Radford et al. 2014). Policy makers have already set regulations for marine environments to safeguard a so-called good environmental status, but there are no agreements yet for freshwater habitats. This means freshwater fish in a diversity of waterbody types are more or less exposed to man-made sound without any incentive to control impact and without any protection by law. Many freshwater fish species actually have quite well-developed hearing abilities and there is no reason to believe that they are less vulnerable to detrimental effects from anthropogenic noise than their marine counterparts. I hope the studies in my thesis contribute eventually to more general awareness of potential issues with sound pollution in both marine and freshwater habitat. I am sure that, by then, more fundamental insights will come in handy for potential monitoring, protection or mitigation efforts.

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