Swimming bass under pounding bass : fish response to sound exposure

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CHAPTER 6

Synthesis & General Discussion

This thesis set out to investigate potential modulating factors that influence behavioural impacts of underwater man-made sounds on European seabass. The investigation comprised four complementary experiments. The first two experiments were performed in an indoor basin, where groups of European seabass were exposed to a series of four sound treatments and their behaviour was analysed with a video-tracking system. I first examined the influence of sound intermittency and amplitude fluctuation on the behavioural impacts (chapter 2). I found the fish to recover from behavioural changes within an exposure session, so I subsequently investigated if the recovery was due to habituation, while testing the influence of pulse repetition interval on sound impacts (chapter 3). The next two experiments were performed in a large outdoor floating pen using the same experimental design, while the fish swimming trajectories were visualised with a 3D acoustic telemetry system. Using this semi-natural set-up, I examined the efficacy of a 'ramp-up' procedure, as well as the effects of sound intermittency and pulse interval regularity (chapter 4). Next, I tested whether European seabass habituated to repeated exposure sessions, and whether sound exposures at different times of the day affected the behavioural response (chapter 5).

Influence of temporal structure of sound

In the two indoor basin studies, I showed that the temporal structure of sound influenced the behavioural impacts of sound exposure. In the first experiment where I tested sound intermittency and amplitude fluctuation, the fish swimming depth recovered more slowly under impulsive sound than under continuous sound (chapter 2). Moreover, there was a trend that group cohesion recovered more slowly under fluctuating amplitude than under consistent amplitude. In the second experiment, I showed that longer pulse repetition interval of impulsive sound caused fish to swim higher up in the water column after the end of sound exposure (chapter 3). Although the mechanisms for these differential effects are unknown, I showed that European seabass are sensitive to temporal characteristics of sound exposure and may behave differently depending on what sound they are exposed to. However, the temporal effects were not as clear when we tested sound intermittency and pulse interval regularity in the outdoor setting (chapter 4). Although impulsive sound seemed to affect fish behaviour more strongly compared to continuous sound, the effects were not statistically significant.

Nonetheless, this thesis shows that behavioural impacts cannot be sufficiently explained by the standard acoustic metrics (e.g. SPL or SEL), which only consider the sound level and duration. In contrast, the severity of sound impacts may be influenced by the temporal structure of sound. As a result, temporal structure needs to be assessed when evaluating potential impacts, by for example assigning appropriate weighting to different temporal parameters. The temporal structure of sound exposure may also be used to devise mitigating strategies. For example, our results suggest that fish may habituate more easily to continuous pile-drilling than impulsive hammer pile-driving, implying that the former method may be more favourable. However, since temporal parameters tested so far are qualitative in nature, impact assessments may still be complicated. To overcome this complication, some quantitative temporal parameters still need to be developed and tested, such as using temporal entropy or kurtosis[1]. Furthermore, the timescale of temporal variability may also influence sound impacts but still largely unexplored. For example, although pulse interval irregularity of 2 s on average did not influence behavioural impacts (chapter 4), exposure interval irregularity of 1 h on average has been shown to affect the growth of larval Atlantic cod (*Gadus morhua*)[2].

Bridging indoor and outdoor studies

In both the basin and net pen studies, the fish changed their swimming behaviour upon sound exposure. The immediate behavioural changes were rather consistent between the two settings, where the fish startled and dived deeper in a tighter shoal. However, with the outdoor net pen set-up, I revealed sound source avoidance that was absent in the basin studies (chapter 4). The absence of this horizontal avoidance behaviour in the basin set-up could be due to the restricted space or a lack of directional cues in the sound field of the experimental arena. Comparing these two approaches allowed us to evaluate which behaviours are more robust and generalisable than others. For example, the immediate diving behaviour, which is typically associated with anxiety[3], seems to occur readily in all experiments. Using such robust behavioural response, noise impact studies can maintain behavioural validity when conducted indoors, which are generally easier to control and perform than outdoor experiments. On the other hand, some behaviours may be hindered by the size of the experimental enclosure and have limited extrapolative values. Therefore, findings from indoor set-ups can only be extrapolated to outdoor conditions after deliberate evaluation.

All the experiments in this thesis only tested hatchery-reared European seabass in confined environments. The behavioural repertoire of the fish might differ from free-ranging fish, as fish in the wild have a very different experience with their environment and may respond to an acoustic stressor differently[4,5]. Therefore, future studies should reveal whether wild-caught and free-ranging fish react in a similar way as what has been observed in this thesis. Furthermore, the fish in this thesis were exposed to sound playbacks that were artificially generated and acoustically different from real man-made sounds. There is a need to test the impacts of man-made sounds in situ in order to reveal the generalisability of the observed behavioural responses in this thesis. Nonetheless, the acoustic characteristics of natural outdoor conditions may still vary considerably, from open water to shallow water, coral reefs and rocky habitats. In this thesis, I measured the soundscapes of my set-ups, and revealed that sounds produced under tank-based and open-water conditions varied substantially in the ratios of sound pressure and particle motion. The interplay between sound pressure and particle motion may play an important role in fish hearing, although the exact contribution of each component is still largely unclear[6]. Hence, there is a need for future studies to describe the variability of the relationship between sound pressure and particle motion in various natural or unnatural environments, and how it influences fish acoustic sensitivity.

Efficacy of 'ramp-up' procedure

'Ramp-up' procedures have often been implemented before pile driving and airgun shootings as a mitigating measure, in order to repel marine mammals and fish from the loud sound source. However, the efficacy of such practice was only tested for the first time in our study (chapter 4). I used a 'ramp-up' procedure that gradually increased amplitude from the ambient level to the standard exposure level over 20 min. The onset of the 'ramp-up' caused the fish to change behaviour in the same way as when they were exposed to sound treatment directly without a 'ramp-up'. However, the fish did not swim away from the sound source as expected. Moreover, they seemed to habituate to the sound more quickly. These observations suggest that a 'ramp-up' may not necessarily achieve its conventional goal in deterring fish from the proximity of an impact site. In fact, our findings suggest that a 'ramp-up' may enhance fish habituation to the sound exposure.

The failure of 'ramp-up' in repelling fish may result in negative consequences, such as hearing loss or acoustic masking. However, this absence of spatial deterrence may sometimes be favourable, especially if the site is critical for foraging or mating. Therefore, mitigating strategies of either increasing deterrence or enhancing habituation should always be critically evaluated before being implemented. Nevertheless, different 'ramp-up' scenarios may vary in their efficacies. These still need to be tested using 'ramp-up' procedures of different temporal structures, such as a decrease in pulse repetition intervals, different rates of amplitude rise, different lengths and starting sound levels of the 'ramp-up'.

Habituation to sound exposure

Upon sound exposure, European seabass typically increased their swimming speed, swimming depth and group cohesion. Within the 30 or 60 min exposure trials, the fish behaviour recovered back to baseline levels. This recovery was shown to be habituation instead of sensory adaptation or motor fatigue, as the fish could still respond to novel acoustic stimuli (chapter 3). Habituation is a simple form of learning that helps animals ignore irrelevant stimuli in order to focus selectively on biologically significant ones[7,8]. Apart from intra-session habituation, I also revealed inter-session habituation, where the fish habituated to repeated exposure trials within eight sessions over two days (chapter 5). Although both intra-session and inter-session habituation may serve the same adaptive function[8–10], they likely reflect different neurobiological processes. Intra-session habituation is related to working memory and adjustability to the surrounding, whereas inter-session habituation measures long-term memory of previous exposure[8,11].

Although habituation may mean that fish become less disturbed by the sounds, it does not necessarily entail the absence of negative impacts. Ongoing sound exposure may still cause chronic stress[12,13], acoustic masking[14,15] and attentional shift[16,17]. These impacts may in turn affect other critical life processes, such as foraging and anti-predatory behaviour. Future studies need to explore how such activities are influenced by long-term sound exposure. Moreover, it will be useful to know if wild fish growing in the presence of man-made sounds also suffer fitness consequences. Whether habituation leads to positive, neutral or negative fitness consequences still needs to be demonstrated. In each scenario, habituation may be deliberately enhanced or prevented as a mitigating strategy by manipulating the temporal characteristics of sound exposure.

Sound exposure at night

Offshore pile driving can take place day and night, exposing fish to sound throughout their diurnal cycles. I exposed European seabass to a series of eight sound exposures over two days, where 46% of the trials took place at night (chapter 5). Comparing baseline swimming patterns before sound exposure at night to during the day, the fish typically swam slower, closer to the surface and less close to each other. These behaviours were probably related to the resting or sleep-like state of the European seabass. When exposed to sound, the behavioural changes were larger at night than during the day, which was either due to sleep disruption or previous experience with sound exposure.

The diel variations in sound impact sensitivity may differ between diurnal and nocturnal species. This species-specific effect warrants more noise impact studies on various species groups. Moreover, since fish alter their behaviour and physiology depending on their experience with the environments, their sensitivity and responsiveness to sound exposure may also vary accordingly. Fish with different ontogenetic backgrounds, such as hatchery-reared or wild-caught, still need to be compared to see how their prior experiences affect their vulnerability to sound exposure. These differences should also be considered when assessing sound impacts and devising mitigating strategies. Moreover, wildlife management should also take into account how sound impacts and human interventions may affect the whole assemblage of fish community.

Future research

The four experiments in this thesis showed that behavioural assessments of sound impacts are more complex than previously assumed. While this thesis answered many important fundamental questions, it also revealed other critical gaps in our knowledge. Many new questions can only be answered with continued interdisciplinary collaborations. As a successful attempt, this thesis collaborated with two other subprojects under a larger project entitled 'The effects of underwater noise on fish and marine mammals in the North Sea', funded by the Dutch National Ocean and Coastal Research Programme (NWO-ZKO). By collaborating with underwater acousticians (primary researcher: Őzkan Sertlek), we can now use sound maps and propagation models to assess the area and diversity of fishes experiencing man-made noise pollution[18,19]. Furthermore, collaboration with marine mammal researchers (primary researcher: Geert Aarts) has inspired the use of individual-based models to evaluate survival and distributional changes of fish upon sound exposure, as well as predator-prey interactions between fish and marine mammals[20,21].

This thesis also highlights the need for more sound impact studies looking beyond effects at individual level, and examining potential impacts at population, community and ecosystem levels. It is crucial to study impacts at different ecological levels, since it would provide insights into effects at different scales and potentially aid in choosing the right focus for wildlife conservation or stock management. For example, animal welfare biologists may be concerned about the different coping strategies of a species to noise pollution, while fisheries biologists may be more interested in the health and stability of fish stocks as a whole. Furthermore, the links between the different ecological levels need still to be explored, in order to improve our understanding of the underlying mechanisms and the scale of underwater sound impacts.

Besides extending our understanding by viewing from broader perspectives, it is also useful to zoom into the mechanistic relationship between various acoustic parameters and sound sensitivity. In fact, our understanding of fish hearing is still rather limited[6,22]. Most audiograms that have been developed so far still suffer from several limitations, such as the exclusion of infrasound sensitivity (< 100 Hz), measurements at various background noise levels, and acoustically and behaviourally unnatural experimental settings[22,23]. Furthermore, most hearing studies focused on the pressure component of sound, while ignoring the particle motion component that is the principal hearing component for many species. There is currently a need to discern the interplay between sound pressure and particle motion in fish hearing. Only then can we use the acoustic information at a particular site to predict the susceptibility of a particular species. Although many questions remain, this thesis addressed an important area that was previously unexplored, and thereby opened up many venues for future research.

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