The noise of the hunt: Effects of noise on predator-prey relationships in a marine ecosystem

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General discussion and summary

The effects of anthropogenic noise on interactions between predators and their prey are still little understood. This thesis aims to fill pressing knowledge gaps on this topic by studying how anthropogenic noise affected various stages in the prey-hunting of predators and the predator-avoidance of prey. For predators, I investigated whether anthropogenic noise could influence habitat choice (chapters 2 and 3), foraging efficiency (chapter 3) and communication between foraging group members (chapter 4). For prey, I studied how anthropogenic noise affected prey behaviour outside of predation contexts (chapter 5) and if current and previous vessel noise exposure affected anti-predator behaviour when a simulated predator attacked (chapter 6). Next to novel insights, my results provide a proof of concept and point to promising avenues of further research on this recently emerging field. Below, I will discuss the conclusions from the various chapters and will indicate the implications for conservation of marine communities in the oceans. Finally, I will discuss what further research is needed to further improve our understanding of the effect of anthropogenic noise on predator-prey relationships.

The effects of sound on predators

As shown in chapters 2 and 3, an increase in ambient noise conditions can induce avoidance of a preferred area by harbour porpoises (*Phocoena phocoena*). The results of this study do not only corroborate earlier observations of harbour porpoises leaving noise-disturbed areas, such as pile-driving construction sites (Carstensen et al. 2006; Tougaard et al. 2009; Dähne et al. 2013), but also match studies on other marine mammals: Blainville's beaked whales (*Mesoplodon densirostris*), for example, stopped prey-search and likely avoided areas with sonar exercises (McCarthy et al. 2011). Nevertheless, whether or not animals will avoid an area, as well as the extent of avoidance, will be influenced by more than just the presence of sound. If the area is the only suitable foraging habitat in the surrounding waters, animals will have limited capacity to avoid it completely, as was observed for Cuvier's beaked whales (*Ziphius cavirostris*) in a Navy training range (Southall et al. 2019).

If predators decide to stay and forage in a noisy area, they may face consequences on foraging efficiency. Zebrafish (*Danio rerio*) preying on water fleas made more handling errors when catching prey under noisy conditions than under ambient conditions (Shafiei Sabet et al. 2015). In contrast, the harbour porpoises in my study (chapter 3) did not show a decreased performance in prey searching. This could be due to the set-up of the experiment, which is likely to have been easier than searching for prey in a natural context. Interestingly, a study that showed that Ambon damselfish (P*omacentrus amboinensis*) were more likely to be predated in noisy conditions, implicitly also showed that their predator was not detrimentally affected by the noise in its foraging performance (Simpson et al. 2016). Predators caught the damselfish with fewer attempts under boat noise playback than under ambient noise playback. This could be explained by a change in behaviour of the damselfish, as they were less likely to startle to a simulated predator attack. Whether anthropogenic noise influences foraging efficiency of predators therefore not only depends on the direct impact on the predator, but also the indirect impact on the behaviour of the prey.

For group-living predators, communication during and after foraging may be affected by increased ambient noise levels. For long-finned pilot whales (*Globicephala melas*), acoustic communication after a deep foraging dive is a potential mechanism for relocating group members (chapter 4). Ambient noise levels affected call detectability, but calls produced in a noisier environment were also louder and longer, possibly to cope with the noise. In bottlenose dolphins (*Tursiops truncatus*), calls produced in low-frequency noisy conditions were found to be of higher frequency and with fewer changes in frequency (Heiler et al. 2016; Fouda et al. 2018; van Ginkel et al. 2018). These changes in call characteristics are hypothesized to counteract decreases in the range of call detectability, and are similar to changes found for vocalisations in terrestrial taxa (Halfwerk and Slabbekoorn 2009; Luther and Gentry 2013). Also, for the terrestrial species, it remains to be proven that the benefits of masking avoidance outweigh the potentially detrimental consequences of signal modification in terms of energy budget and compromised signal value (Slabbekoorn 2013; Read et al. 2014).

The effects of sound on predator-avoiding prey

Anthropogenic noise may induce or elevate the level of vigilance in prey animals, because it is perceived as a risk (Frid and Dill 2002). Schooling fish around wind farms increased their cohesion and swam higher in the water column in relation to exposure to a seismic survey and pile driving activity. Nevertheless, response type and strength were within the natural behavioural variation observed outside the exposure period (chapter 5). Due to the small sample size of this study, no general conclusions should be taken from the patterns found. However, both parameters have been found to change in other studies where fish were exposed to noise, albeit that most fish dive down instead of swim up in the water column (Doksæter et al. 2012; Fewtrell and McCauley 2012; Hawkins et al. 2014b; Neo et al. 2014; Neo et al. 2015a). Future studies should strive for replicated experimental design to be able to assess causal relationships between seismic noise and prey behaviour and how resulting changes in the prey field would affect foraging predators.

When a predator attacks a prey under noisy conditions, the prey might have an altered perception of risk and thereby change the degree of its anti-predator response (Frid and Dill 2002). In chapter 6, I investigated how long-term exposure to boat noise influenced the anti-predator behaviour of sand gobies (*Pomatoschistus minutus*) under ambient and short-term boat noise exposure conditions. Sand gobies were less likely to leave the site of the predator attack under playback of boat noise than under playback of ambient noise. Hence, short-term boat noise suppressed the goby avoidance response. This effect became more pronounced in noisy habitats, where gobies exposed to ambient noise also stayed on site after a predator attack. The decreased perception of risk may be detrimental for the prey, if the foraging performance of the predator does not diminish. However, since the predator is often also affected by the noise, general predictions for the impact of anthropogenic noise require research on the community level.

Community effects

Sand gobies are a common prey species of harbour porpoises (Leopold 2015). The cryptic defence strategy of gobies is ineffective against harbour porpoises, which are acoustic (active echolocation) predators (Magnhagen and Forsgren 1991; DeRuiter et al. 2009). Since sand gobies are predicted to be less likely to flee away from an attacking predator under boat noise conditions (chapter 6), harbour porpoises are likely to have more of an advantage when ambient noise levels are higher. This is strengthened by the lack of effect of noise found on prey-searching behaviour of harbour porpoises (chapter 3). Although a subsequent study with the same individuals on prey-catching behaviour during exposure to pile-driving noise showed increased termination of prey-catching attempts under high noise levels of one individual (Kastelein et al. 2019), gobies may respond differently to this sound source. Nevertheless, the benefit for harbour porpoises under noisy conditions only holds true for those porpoises that will stay in noisy areas, which they will likely tend to avoid (c.f. chapter 3). Thus, the resulting predator-prey dynamics will become more complex, as noise adds one more layer to the existing layers of behavioural trade-offs, physical conditions and species distributions (Gaynor et al. 2019).

Pilot whales hunting deep-water prey that are exposed to sonar can stop foraging (Miller et al. 2012). However, the duration of the response was unknown and not all animals responded in the same manner. Supposing pilot whales would not stop their foraging bout, would there be changes in their hunting efficiency due to changes in prey behaviour? Both pelagic fish and squid can be behaviourally affected by sound (chapter 5, Doksæter et al., 2012; Hawkins et al., 2014b; Mooney et al., 2016), but effects of sound on anti-predator behaviour of either taxon have not been studied. Exposure to sound itself induced increased school cohesion and deeper swimming in fish and jetting and inking in squid. These behaviours are also seen in response to predator attacks, so could be regarded as escape or at least increased vigilance (Malavasi et al. 2004; Langridge 2009; Rieucau et al. 2014). However, whether these behavioural changes will be beneficial for the prey depends on timing in relation to foraging bouts of the pilot whales, duration of the change, which type of anthropogenic noise induces the changes and how the pilot whales are affected by that same noise in their foraging performance. Future studies on foraging behaviour of free-ranging pilot whales under noisy conditions can provide insight and may be conducted using suction-cup tags for the whales, combined with a visualisation method for the prey.

Implications for conservation

In recent years, there has been increasing realisation that effects of anthropogenic noise in the ocean should be mitigated. The European Union has added increased ambient noise levels as a pollutant that should be addressed to achieve Good Environmental Status in European waters (Dekeling et al. 2016). Non-governmental organisations such as WWF have asked attention for the effects of anthropogenic noise on marine life (https://www.wwf.nl/kom-in-actie/arctic-noise-petitie) and legislation is in place that requires noise mitigation efforts to take place during construction of wind farms and other offshore activities in national waters (2012). At the same time, mitigation efforts can only be successfully designed and implemented under scientific support.

The current mitigation measures that are being applied mostly focus on decreasing the received level of noise by animals in the vicinity of human activity. Examples of this are bubble curtains around piles that are being driven into the ground that block the sound emitted from the hammer strikes and ramp-up procedures before the start of noisy activities to alert and deter animals from the area. The concept behind these measures is that lower noise levels will have a lower impact on the marine community than higher noise levels (Gomez et al. 2016). Although higher noise levels can induce effects beyond altered behaviour (e.g. hearing threshold shifts, physical damage), the large spatial scale of lower noise levels will affect a lot more individuals and behavioural changes due to low levels of noise can have a similar fitness impact (Slabbekoorn et al. 2010; Popper 2012).

In relation to science-guided mitigation and conservation efforts, my results indicate that conservation should not only focus on protecting or creating pristine environments in terms of noise, but also include more noise-polluted areas. Animals living in noise-polluted areas may show changes in behavioural strategies even when the noise has ceased, which could be detrimental to their survival. For example, long-term increased levels of ambient noise in sand goby habitats led to changes in anti-predator behaviour even under quiet conditions (chapter 6). This indicates that sand gobies in noise-polluted areas did not have altered tolerance levels to the disturbance, but rather had a permanently different behavioural strategy than gobies living in quiet habitats.

Other studies did show that animals increased their tolerance to longer-term noise exposure, either by going back to baseline behaviour during exposure (Neo et al. 2018) or by showing no change in physiology when the noise started after a period of quiet (Harding et al. 2018). However, my study signifies that this will not be the case for every species. Moreover, as sound attenuates little in water, finding entirely noise-pollution-free environments will be difficult. Creating protected marine areas that exclude human activity can, however, improve the ambient noise levels in the centre of that area (Herrera-Montes 2018). Besides that, technological innovation can reduce noise pollution levels, as the quieting of ship engines over the past years has already led to a stagnation in ambient noise level rises in some areas of the world (Miksis-Olds and Nichols 2016).

Additionally, when deciding which areas to designate as nature reserves, focus on those areas that are preferred foraging spots of predators. Predators, especially apex predators, often control the dynamics of the ecosystem and their disappearance can lead to trophic cascades (Estes et al. 2011). Even if ambient noise levels are high, some predators might stay in those areas, if alternative habitats are not available or of much lower quality. However, this might have possible detrimental consequences for foraging efficiency. For example, foraging Cuvier's beaked whales stayed in a naval training area despite naval exercises, which was also the area with the highest prey abundance in the vicinity (Southall et al. 2019), but the same species is also known to stop foraging in response to sonar (DeRuiter et al. 2013; Falcone et al. 2017). Moreover, foraging spots are usually preferred because of a high abundance of prey, so protecting those areas will also lead to protection of more prey animals (Wirsing et al. 2010).

Current knowledge gaps and suggestions for further research

In this thesis, I have described several possible effects of anthropogenic noise on both predator and prey, in various stages of the predator-prey interaction. My results clearly indicate that anthropogenic noise may impact predator-prey dynamics. However, for effective conservation measures we need to understand how these impacts translate into effects on the ecosystem. Therefore, further research is needed to elucidate how these changing dynamics may alter the balance between predator and prey population and how it translates to effects on food web dynamics.

It is important to investigate the mechanisms that underlie the effect of noise on behaviour of predator and prey, so it will become possible to predict how species outside of the study system will be affected by noise (Slabbekoorn et al. 2018). For instance, what mechanism underlies if a prey species will be distracted or become more vigilant due to the noise (Chan and Blumstein 2011; Voellmy et al. 2014b)? It could be related to the association of the presented noise to a predatory threat, but if so, would that change with experience? Even long-term exposure does not always lead to increased tolerance levels (chapter 6). Understanding mechanisms like these are needed to extrapolate the effect of noise on one predator-prey combination to other possible predator-prey combinations of the two study species. Only then can we start to paint a picture of how the ecosystem is affected.

Another topic that deserves further investigation is the effect of long-term exposure to noise. The results of chapter 6 show that habituation does not always occur when animals are exposed to noise over longer periods. Are there indicative parameters that could predict how animals will react in the long-term? And is it possible to reverse changes in behaviour that are induced by long-term exposure to noise? Answers to these questions are necessary to understand fundamental behavioural processes, but also to be able to guide conservation efforts. If behavioural effects of long-term exposure to noise turn out to be non-reversible, this might change how conservation efforts should be focused.

These and other questions should be answered through a combination of theoretical modelling, experiments in captivity and field studies (Slabbekoorn et al. 2018). Only when combining these techniques will it be possible to really understand all aspects of the problem. The study on captive harbour porpoises in chapters 2 and 3 showed that it is possible to provide a proof of concept of the mechanisms underlying behavioural responses seen in the wild. The study on free-ranging pilot whales in chapter 4 proved that combining theoretical modelling with field observations can lead to insights that are otherwise difficult to acquire. The results of the study on pelagic and benthic fish in chapters 5 and 6 stressed the need for thorough replication in field studies, as the response of free-ranging animals most closely approaches how individuals will respond in their natural environment. And finally, the experimental field study of chapter 6 showed that when an easily observable study organism is chosen, a field experiment can produce high sample size data sets on individuals in their own environment – and thus provide information on how individuals will actually respond.

Conclusion

The multi-disciplinary studies of this thesis combine to unravel more insight into the influence of noise on predator-prey relationships in the marine environment. This thesis showed that: 1) harbour porpoise swimming speed and surfacing rate can be used as independent metrics to analyse porpoise spatial behaviour (chapter 2); 2) two captive harbour porpoises avoided noisy areas, but when forced to search for prey in noise, did not lower their search performance (chapter 3); 3) long-finned pilot whales that were separated vertically when part of the group is foraging had the potential to keep in contact through acoustic communication, but fewer calls were detected in higher ambient noise levels at the receiver (chapter 5); 4) sound from a seismic survey and from pile driving could potentially disturb spatial behaviour of pelagic fish schools at wind farms in the North Sea; 5) exposure to long-term acoustic disturbance by boat noise interacts with the effect of short-term boat noise playback on the anti-predator behaviour of sand gobies.

Further investigations should focus on revealing the mechanistic underpinning of noise effects on behaviour of both predator and prey. However, effective noise mitigation measures will not only depend on thorough knowledge of the impacts but also on economic and political interests. Trade-offs exist, for instance, with the still-increasing demand for green energy. For conservation measures to be effective, therefore, collaboration between stake holders is necessary, preferably on an international scale. Noise does not respect nation boundaries and changes that could have a large impact, such as silencing ship engines, need to be applied by many countries before any improvement will be visible. To properly conserve marine ecosystems from noise, we do not only need to study the effects on a higher scale of species interactions, but we should also zoom out when considering mitigation measures to find out if they are not counteracted by other processes affecting the animals. Only then will we be able to reduce the impact of noise on marine ecosystems.