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

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General introduction

Pollution in the marine environment

Animals living in today's marine environment face many threats. Many fish populations are in danger of collapse due to overfishing (Madin et al. 2016), while the various effects of climate change have the potential to affect all trophic levels in the ocean (Yao and Somero 2014). Oxygen levels in the oceans have decreased, leading to an expansion of oxygen minimum zones that can affect marine organisms and change predator-prey interactions (Breitburg et al. 2018). Another prominent threat is that of pollution. The accumulation of micro-plastics in marine waters is a familiar example (e.g. Zhang et al. 2019), but other forms of pollution do not leave any physical trace. One of those forms of pollution is sound pollution.

Awareness of sound pollution has emerged over the last decades. Since the invention of motorized ships, marine ambient noise levels have started increasing (Andrew et al. 2002) and have continued to rise as human activities in and above water have spread (Frisk 2012). Sound propagates well in water, so anthropogenic sound sources can affect ambient noise levels of large areas. A moored hydrophone at Ascension Island (equatorial Atlantic Ocean), picked up seismic air gun sounds year-round, possibly from seismic surveys thousands of kilometres away (Haver et al. 2017). In the Dutch part of the North Sea, anthropogenic sources constitute a large proportion of the sea's ambient noise levels (Sertlek et al. 2019). Although the increase in ambient noise levels has slowed down and even stopped in some areas – due to quieting of ships and little increase in ship movements (Andrew et al. 2011; Miksis-Olds and Nichols 2016) – ambient noise levels are still substantially higher than pre-industrial noise levels.

Effects of sound on marine life

These increasing levels of ambient noise affect marine animals (Slabbekoorn et al. 2010; Radford et al. 2014; Kunc et al. 2016). Direct detrimental effects include physiological changes, such as temporary or permanent hearing threshold shifts, to even mortality close to the sound source (Popper 2012). In addition, many animals are potentially affected in their behaviour, as effects of sound on behaviour may already occur at slight increases in ambient noise level (e.g. from 100 to 120 dB re 1 μPa, de Jong et al. 2018). Anthropogenic sound has been shown to affect a range of behaviours: from early-life events such as reef-settlement in larval reef fish (Simpson et al. 2016) to fitness-altering strategies such as mate choice in gobies, thereby also indirectly affecting the next generation (de Jong et al. 2018). The effects of noise span all trophic levels. Cetaceans, many fishes and even invertebrates have shown changes in behaviour in response to noise exposure (Sebastianutto et al. 2011; Blair et al. 2016; Hubert et al. 2018). Since all trophic levels can be affected, it is likely that marine ecosystems will be affected by noise exposure.

Sound characteristics such as level, frequency and amplitude all influence the potential impact of sound pollution. The frequency of the sound influences whether an animal can detect the sound and can potentially be affected by it. Many of the sounds produced by human activities are low in frequency, which overlaps with the hearing range of most fishes and invertebrates (Slabbekoorn et al. 2010). Frequency and sound level can also interact, as the frequency at which the greatest hearing threshold shift occurred for a harbour porpoise (*Phocoena phocoena*) changed with increasing exposure sound level of a sound that did not change in frequency (Kastelein et al. 2014). Furthermore, temporal structure of the sound influences the behavioural response. Impulsive sounds generate different response intensities than continuous sounds (Neo et al. 2014; Nichols et al. 2015; Shafiei Sabet et al. 2015; Radford et al. 2016; Kok et al. 2018). However, at the moment governmental policy makers only focus on trying to decrease the amplitude of ambient sound in the marine environment and disregard other acoustic parameters that might influence the effect on animals (PCEU 2008; Dekeling et al. 2016; Gomez et al. 2016).

The effects of sound on behaviour of marine animals have been studied with various methods. They have been studied with theoretical methods, for instance by creating acoustic propagation models and combining those with animal movement models (Aarts et al. 2016). Others have used indoor experiments, often by exposing fish in a tank to sound and recording their behavioural response, for instance in relation to foraging (Voellmy et al. 2014a; Shafiei Sabet et al. 2015). Increasingly, outdoor experiments have been used with controlled sound exposure (e.g. Miller et al. 2012; Neo et al. 2016) or behavioural observations of free-ranging animals that were exposed to uncontrolled anthropogenic sound events are conducted (e.g. McCarthy et al. 2011; Dyndo et al. 2015). All these types of study have their merits and pitfalls. Theoretical studies are useful for exploring effects of sound that would be logistically challenging to study otherwise, but the predictive value of the model relies on the accuracy of its assumptions (Starfield 1997). Indoor experiments are a great way to closely observe the behavioural response of the animal, but animals in captivity may behave differently than they would in free-ranging conditions (Garton et al. 2005). Outdoor experiments or observations record the natural behaviour of animals, but can be logistically challenging, often leading to incomplete datasets and small sample sizes, and in the case of observations, can only rarely show cause-effect relationships (Garton et al. 2005).

Impact of sound on predator-prey interactions

Sound does not only affect single species, but is likely to also cause shifts in the ecosystem (Francis and Barber 2013). This can be caused by differences in sound impact between species. For example, species composition of a bird community in New Mexico changed in the presence of noise, from 32 species present at the quiet control site to 21 species at the noisy site (Francis et al. 2009). Similar results have been found for an avian community in Puerto Rico (Herrera-Montes and Aide 2011), although the anuran community in that area did not change its composition. In a marine environment, the call rate and call complexity of a fish community in the Mediterranean Sea was significantly lower at a noisy location than at a nearby pristine location (González Correa et al. 2019). The mechanisms underlying these changes in species composition can likely be related to species differences in behavioural impacts of noise. These could for instance be differences in avoidance of noisy areas between species, sound-related changes in competition strength of a species to competitor species at the same trophic level, or a sound-related shift in the balance between predator and prey species at multiple trophic levels.

The influence of sound on predator-prey interactions is a potentially important driver for ecosystem effects. Changes in predator-prey interactions may cascade through the food-web, thereby affecting not one but multiple species (Rao 2018). There are multiple aspects to the predator-prey interaction that can be influenced by sound (Fig. 1). The encounter rate between predators and prey depends on the spatial behaviour of both, which is influenced by habitat choice. Noisiness of the environment can influence this choice. Harbour porpoises, for instance, were temporarily excluded from certain parts of their habitat, due to pile-driving activities in that area (Carstensen et al. 2006; Tougaard et al. 2009; Dähne et al. 2013). When predators hunt prey, sound may directly influence the performance of the predator (Voellmy et al. 2014a; Shafiei Sabet et al. 2015) or the anti-predator behaviour of the prey (Voellmy et al. 2014b; Simpson et al. 2016). Many cetacean predators are highly social animals, while groups split up when foraging. Sound may decrease the communication range of group members (Janik 2000; David 2006; Miller 2006), making it more difficult to relocate the group at the end of the foraging bout. Finally, the changes in behaviour caused by sound may alter time-budgets for other behaviours (Isojunno et al. 2017), for instance such that prey that become more vigilant have less time for other behaviours, such as foraging (Voellmy et al. 2014a).

Despite this general knowledge, there are many gaps in understanding the effects of sound on predator-prey interactions. In cetaceans, effects of sound are difficult to study, because controlled indoor experiments are generally not possible. Controlled outdoor experiments have been increasing in number and have led to great advances in understanding the effects of sound on marine animal behaviour (Miller et al. 2012; Dunlop et al. 2016), but still are logistically challenging and costly. Furthermore, it becomes more and more evident that responses to sound differ between sound types, as well as between species. In fish, effects of noise on anti-predator behaviour fall into two categories: fish get distracted or oppositely, increase their vigilance. It is unclear how these processes relate to each other, let alone why one species gets distracted while the other does not (Rosa and Koper 2018). The largest prey taxon, invertebrates, has hardly been studied at all, even though this group is likely to be sensitive to low-frequency sound, which is the frequency range of most anthropogenic sound sources (Slabbekoorn et al. 2010; Morley et al. 2014).

Outline of the thesis

This thesis specifically investigates the effects of noise on predator-prey relationships. Using a multidisciplinary approach, I investigated various stages in the process of predator-prey interactions that can be influenced by sound (Fig. 1). The thesis is subdivided in two sections. The first section investigates how noise affects foraging predators (Chapters 2 to 4), while the second section investigates how noise affects prey (Chapters 4 & 5). I studied two cetacean predator species: harbour porpoises (*Phocoena phocoena*) and long-finned pilot whales (*Globicephala melas*). As prey species, I studied

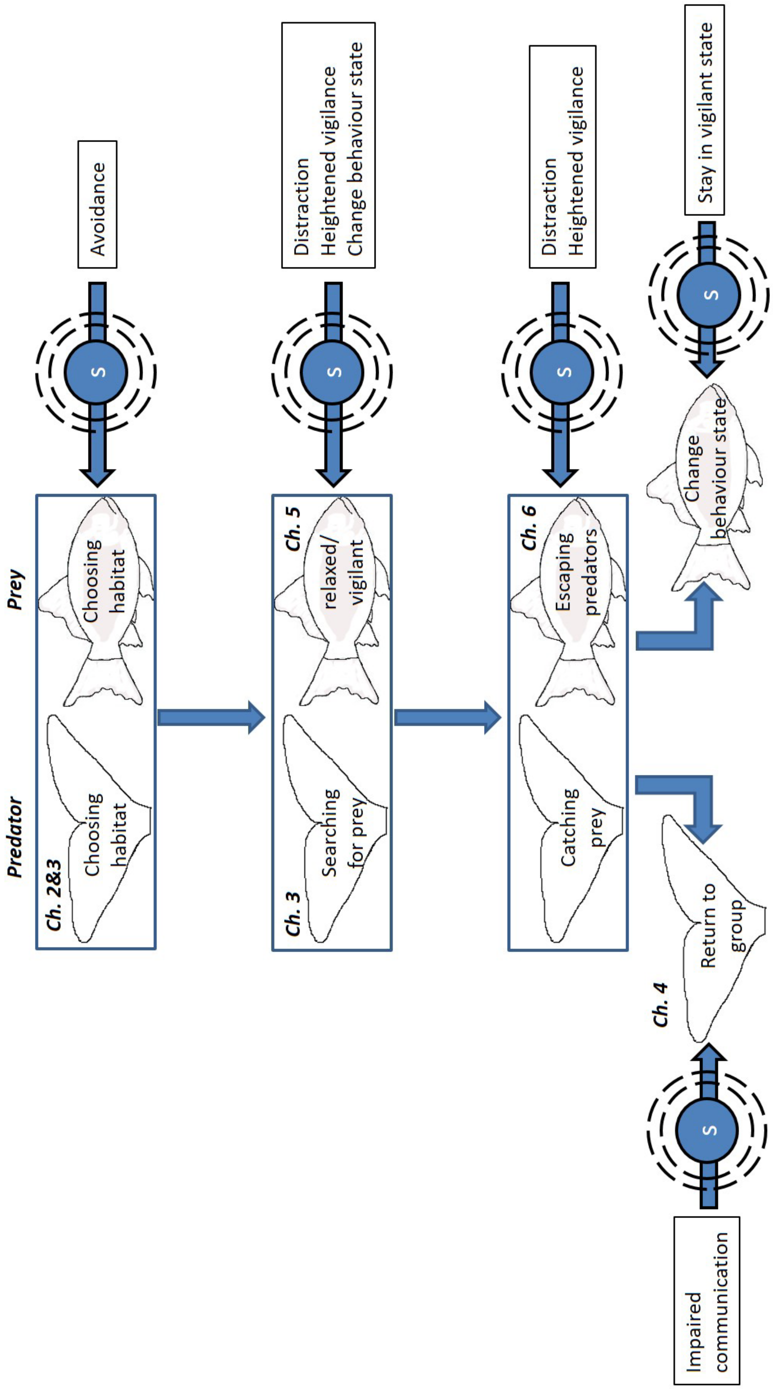

Figure 1: Schematic overview of the stages in predator-prey interactions in which anthropogenic noise can have an influence.

sand gobies (*Pomatoschistus minutus*) and pelagic fish of the North Sea. Because of the varying demands of each study, I combined indoor and outdoor experiments with behavioural observations and theoretical modelling, thereby benefitting from the specific advantages of each method. Combined, these studies aim to advance insight in the behavioural responses of predators and prey to anthropogenic noise.

How noise may affect a foraging predator

When a predator starts foraging, it first has to locate a suitable habitat. Foraging habitat quality is regulated by many factors, such as the availability of prey and the risk of being predated. Anthropogenic noise can alter habitat choice by deterring animals from a particular area. Harbour porpoises have been observed to evade wind farm construction sites during pile driving events (Carstensen et al. 2006; Tougaard et al. 2009; Dähne et al. 2013). However, these were correlational studies that did not investigate whether the observed avoidance was a direct deterrent effect of the noise on the porpoises, or an indirect consequence of other noise-induced changes, such as prey leaving the area. In chapters 2 and 3, I investigated swimming behaviour of two captive harbour porpoises in control conditions (chapter 2) and under artificial noise exposure (chapter 3). Furthermore, I studied the influence of sound pressure level (SPL) and temporal sound structure on the probability of avoidance.

After finding a suitable habitat to forage, a predator has to search for a specific prey item. This process can be disturbed by sound in multiple ways. First, anthropogenic noise can cause a change in behavioural state, meaning the predator stops foraging and starts an alternative behaviour, such as travelling. This response type has been documented for several cetacean species (Miller et al. 2012; DeRuiter et al. 2013). Second, anthropogenic noise can cause distraction from prey searching, lowering performance levels. In chapter 3, I studied how noise affected prey searching in harbour porpoises that were trained to perform a prey search task by locating a dead fish in one of three possible cages. By varying temporal structure and sound level of the noise, I investigated the influence of these sound characteristics on the probability of distraction.

Finally, when a predator has finished foraging it will return to another behavioural state. Many odontocetes are deep-diving marine predators, which forage individually at depth but form stable social groups at the surface after foraging is over. In order to relocate their group at the surface, odontocetes are likely using acoustic communication. Increasing ambient noise levels might disrupt communication between separated individuals. In chapter 4 I tested the potential for pilot whale calls to be used for acoustic relocation when animals were vertically separated and investigated whether environmental variables such as ambient noise level at the receiver, as well as call characteristics, influenced communication potential.

How noise may affect prey

The prey must be vigilant for a sudden encounter with their predator. This vigilance for predation has a trade-off with other behaviours, such as foraging, and can therefore be altered under the influence of noise in two ways. On the one hand, prey could be distracted by the noise, thereby becoming less vigilant (Chan et al. 2010). On the other hand, prey could perceive the sound as a risk to be predated and respond as if a predator was close (Frid and Dill 2002). In chapter 5, I investigated whether the behaviour of North Sea pelagic fauna changed during exposure to a seismic survey and pile driving. I recorded whether pelagic biomass showed vertical displacement during sound exposure and whether schooling organisms changed their cohesion, both behavioural traits that also change as part of anti-predator behaviour (Rieucau et al. 2014).

At the moment of a predator attack, prey will try to escape the predator. Again, prey can be distracted by the noise and react more slowly to the predator than they would otherwise. A direct consequence is an increase in mortality (Simpson et al. 2016), thereby favouring selection for individuals that show little distraction by noise, or are vigilant, vs. those that become distracted . If an exposed individual does not get eaten, an alternative consequence might be habituation to the noise exposure over time. Thus, in areas with long-term exposure to anthropogenic noise animals are likely to be overall less responsive, or more vigilant to the noise than in areas that have not been exposed to noise. I tested this hypothesis in chapter 6 with sand gobies living in areas with varying degrees of exposure to boat noise, which I exposed to a simulated predator under ambient or boat noise conditions.

All the effects on predators and prey together paint a complex picture of the effect of noise on the marine ecosystem. Chapter 7 provides a synthesis of the results of the previous chapters. I summarise the effects that I found on predators and on prey in this thesis and discuss how these results might be put into ecosystem context. Bridging all the knowledge gaps in the effects of noise on predators and prey is impossible with one thesis, so chapter 7 also suggests future directions for this line of research.