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Sound investigation: effects of noise on marine animals across trophic levels

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Citation

Hubert, J. (2021, September 9). *Sound investigation: effects of noise on marine animals across trophic levels*. Retrieved from <https://hdl.handle.net/1887/3209242>

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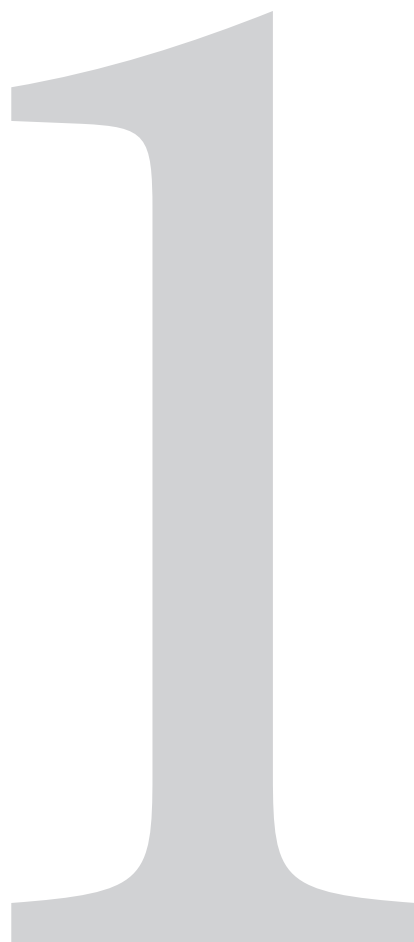
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Issue Date: 2021-09-09

General introduction



The marine environment is filled with a cacophony of sound. Ambient sound originates from water surface roughness as a function of weather conditions and waves (Carey and Browning, 1988; Wenz, 1962), and many marine animals produce sounds to communicate (e.g. Vasconcelos et al., 2007; Wilson et al., 2014). Over the past decades, there are also increasing amounts of anthropogenic sound sources in the marine environment (Andrew et al., 2002; Hildebrand, 2009). In the Dutch part of the North Sea, shipping is the most prominent sound source (Sertlek et al., 2019). Shipping produces continuous low-frequency sound, and at larger distances, it is impossible to discriminate this from other ambient noise (Wright et al., 2007). Nevertheless, it does elevate the ambient noise levels in the marine environment, especially around harbours and shipping routes (Haver et al., 2018; Sertlek et al., 2016). Seismic surveys are another prominent sound source. Seismic surveys are explorations of the geological structure beneath the seafloor using airguns (Gisiner, 2016; Landrø and Amundsen, 2018). A third prominent source is pile driving for offshore constructions such as wind turbines (Matuschek and Betke, 2009). Both, seismic surveys and pile driving, produce high intensity, low-frequency impulsive sounds at a regular interval, and can persist for weeks to months (McCauley et al., 2000; Sertlek et al., 2019). Sounds from the above-mentioned sources are audible to most – if not all – marine animals, however, relatively little is known on the effects of anthropogenic sound on marine life, especially for fish and invertebrates (Hawkins et al., 2015; Slabbekoorn et al., 2010; Williams et al., 2015).

Fish use sound to orient, for example by finding suitable habitat and detecting prey or predators, and to communicate, for example to find a partner (Gordon et al., 2019; Popper and Hawkins, 2019; Wilson et al., 2014). Many fish species are known to produce sound (Amorim et al., 2015; Fine and Parmentier, 2015; Ladich, 2008), while all are expected to be able to hear sound (Popper and Hawkins, 2018). Fish can produce sound by a variety of mechanisms, such as by drumming the swim bladder with the sonic muscle, or rubbing bones or teeth together (stridulation) (Webb et al., 2008). Fish detect sound with their inner ear and lateral line system (Engelmann et al., 2000; Popper and Fay, 2011). The inner ear consists of three otoliths surrounded by sensory hair cells. Otoliths have a higher density than the fish and water. Hence, the otoliths move at a different amplitude and phase than the rest of the fish in response to the particle motion aspect of sound. This movement is subsequently detected by the hair cells. Many fish have a gas-filled swim bladder which fluctuates in volume in response to sound pressure waves, this contributes to sound perception if the swim bladder oscillation results in otolith motion. The role of the swim bladder in hearing depends on the proximity of the swim bladder to the inner ear and the presence of a connection between the swim bladder and inner ear, for example by the

Weberian ossicles. The lateral line system consists of hair cells in the skin of the fish which also detect low-frequency particle motion (Popper and Fay, 2011; Popper and Hawkins, 2019; Popper and Higgs, 2010).

Marine invertebrates can also detect and utilize sound. Many invertebrates (including crustaceans) have statocysts, just like with otoliths in the inner ear of fish. A statocyst consists of a mass, whose movements are detected by sensory hairs (Lovell et al., 2005). Just like the lateral line system in fish, crustaceans (e.g. crabs and shrimps) also have sensory hairs on their body that can detect low frequency sound (Derby, 1982). Both sensory systems detect the particle motion component of sound, and since crabs and shrimps do not have gas filled cavities, they are likely not sensitive to sound pressure (Edmonds et al., 2016). Crabs and shrimps in their pelagic life stage have been shown to orient to particular soundscapes to find suitable habitat (Jeffs et al., 2003; Simpson et al., 2011), and crabs in later life stages have been shown to alter foraging behaviour after playbacks of sounds from predatory fish (Hughes et al., 2014). Several bivalve families have a specialized hearing organ, the abdominal sense organ (ASO), a large mechanosensory organ which also detects particle motion. Bivalves that do not have the ASO possess structurally similar organs, possibly also for sound detection (Haszprunar, 1985; Zhadan, 2005). Pelagic larvae of eastern oyster (*Crassostrea virginica*) show increased settlement behaviour during the playback of sound from suitable habitat, and swash-riding clams (*Donax variabilis*) jump out of the sand during playback of wave sound to surf on the waves and maintain a position at the shoreline, along with the moving tides (Ellers, 1995; Lillis et al., 2013).

Since marine animals can hear sound and animals use sound for activities critical to their survival and reproduction, it is likely that they are affected by anthropogenic sound (Slabbekoorn et al., 2010). Close to a high-intensity sound source, fish may get physically injured, for example by swim bladder rupture and damaged capillaries, due to the high-amplitude pressure fluctuations around the swim bladder (Casper et al., 2013; Halvorsen et al., 2012). At larger distances from the sound source, anthropogenic sound may still mask biologically relevant sound, this may decrease the distance from which suitable habitat, potential mates, or predators and prey are detected (Codarin et al., 2009; Radford et al., 2014; Wysocki and Ladich, 2005). Anthropogenic sound may also affect behaviour and physiology. It has been shown to disrupt swimming patterns, change activity patterns, and elevate stress related physiological parameters (Filiciotto et al., 2016; Neo et al., 2014). Impact to fish close to a high-intensity sound source may seem most severe, but only applies to relatively small numbers of fish. Moderate effects at larger distances apply to many more individuals, and therefore have

more potential to be relevant for population level effects (Slabbekoorn et al., 2010; Soudijn et al., 2020). For this reason, it is especially important to study behavioural and physiological effects of sound on marine life.

There is a wide variety of factors that may influence the response of an animal to anthropogenic sound. Anthropogenic sound varies in amplitude, frequency, and temporal fluctuations in both domains, which may all influence the animals' response (Neo et al., 2014; Vetter et al., 2015; Wysocki et al., 2006). Not only the characteristics of the – potentially disturbing – stimulus may matter, but also the acoustic characteristics of the environment may modulate the nature and strength of a response. For example, higher ambient noise levels will decrease the signal to noise ratio of the stimulus and may therefore reduce the response (Wells, 2009). Other external factors, such as temperature, season, time of the day, may all influence behaviour and thereby also the behavioural response of animals (Bejder et al., 2009). Not only abiotic factors, but also biotic factors such as conspecific and heterospecific individuals, and their response to sound, may affect the response of an individual (Francis et al., 2009; Slabbekoorn and Halfwerk, 2009). Furthermore, the internal state of an individual will also determine its response to sound. A hungry, migrating or reproducing individual may face a different trade-off than when it has eaten well (Croy and Hughes, 1991; Schadeegg and Herberholz, 2017). Previous experiences to sound may have led to habituation, desensitization or motor fatigue (Neo et al., 2018). Lastly, sound may not only affect animals through auditory masking or anxiety, but processing of the sound may also interfere with the processing of other relevant stimuli (Halfwerk and Slabbekoorn, 2015). Altogether, there is a great variety of factors and mechanisms that may determine the effects of sound on animals, knowledge about these mechanisms is critical to understand the impact of anthropogenic sound on animals (fig. 1).

Ideally, sound impact studies are conducted in the wild during anthropogenic sound exposure from a real source. Although proper replication in time and space is still required, both the possibility for animals to express natural behaviour and the acoustic exposure optimally resemble the conditions of real noisy human activities (Rogers et al., 2016; Slabbekoorn, 2016). However, fieldwork at sea also entails limitations and challenges. It is difficult to track individual animals for an extended period of time, and such experiments are expensive and logistically challenging, which often results in limited replication, making it hard to control for natural fluctuations in behaviour or confounding variables such as the weather. Hence, many sound impact studies are conducted in a captive environment, e.g. a tank, basin, or net pen. However, behaviour of animals, including their response to sound, likely differs from free-ranging

animals in situ (Wright et al., 2007). For example, captive fish are limited in their ability to swim away from a sound source and there is typically less inter- and intra-species interaction. Additionally, the animals' enclosure and sound source will also affect the sound field. Both sound pressure and particle motion are affected by the proximity of tank walls and water surface (Campbell et al., 2019; Parvulescu, 1967; Rogers et al., 2016). Additionally, speakers are often used to play back sound, even though speakers typically have frequency limitations and are point sources, in contrast to many anthropogenic sound sources – such as ships and pile driving – which are not (Lippert et al., 2018). The extent to which such limitations pose a problem for sound impact studies depends – among other things – on the research question, experimental design, and study species.

Despite the limitations of controlled experiments in tanks or net pens, there are also several benefits of such experiments. Controlled experiments typically enable replicated and independent trials and there is typically more control over environmental variables such as background noise, light intensity, temperature, and weather conditions. Additionally, the (recent) life history of the animals is sometimes known and can be standardized. Altogether, such experiments likely yield data with limited (unexplained) variance which makes it easier to compare treatment groups. Besides, it is also possible to manipulate environmental variables, previous experiences or the internal state of the animals. This allows to examine such characteristics without being confounded by other characteristics. This will increase our understanding of the mechanisms that underly the response of animals to sound, which will aid the interpretation of other experiments and the extrapolation of results from experiments to the wild. Finally, controlled experiments can be used as proof of concept to test and gain insight in particular methodology or (potential to change) behaviour, which can later be used or examined in situ. Altogether, both field and captive experiments can provide complementary insights into the effects of sound on animals. All studies thus have their own benefits and limitations, and we should interpret results accordingly. Despite all potential benefits and opportunities of controlled experiments, some experiments can only be conducted in the field, for example experiments aiming to quantify absolute response levels.

For this thesis, and together with colleagues and students, I conducted five experiments using captive animals and one experiment using free-ranging animals. I examined factors that modulate the effects of sound on animals and the quantification of behavioural effects that may ultimately be used to gain insight into fitness and population consequences. We collected data on Atlantic cod (*Gadus morhua*), European seabass (*Dicentrarchus labrax*), shore crabs (*Carcinus maenas*), common shrimps (*Crangon crangon*), and blue mussels

(*Mytilus edulis*). Both cod and seabass are demersal and shoaling fish (Frimodt and Dore, 1995). Cod and seabass hear best up to 400 and 1000 Hz respectively, and cod is also known to produce sound (Chapman and Hawkins, 1973; Lovell, 2003; Wilson et al., 2014). Cod and seabass forage – among other prey species – on crabs and shrimps (Reubens et al., 2014; Whitehead, 1984). Both shore crabs and common shrimps are epibenthic crustaceans and live in a wide range of shallow marine habitats (Campos et al., 2012; Carlton and Cohen, 2003). The hearing curves of shore crabs and shrimp are not known, but another crab and shrimp species hear up to at least 1600 and 3000 Hz respectively (Hughes et al., 2014; Lovell et al., 2005). The blue mussel is a major prey species of the shore crab (Matheson and McKenzie, 2014). Mussels adopt a sessile lifestyle in intertidal areas and play an important role in ecosystems as filter-feeders and reef-builders (Borthagaray and Carranza, 2007; Jørgensen, 1990). Mussels hear up to at least 410 Hz (Roberts et al., 2015). Altogether, these species represent multiple trophic levels and many of them are of commercial interest (fig. 2).

Thesis outline

This thesis describes six sound exposure studies on marine animals from multiple trophic levels. In the first two data chapters, I aimed to quantify behavioural responses to sound relevant to fitness. In chapter 2, I examined the time expenditure in several behavioural states of Atlantic cod in a floating pen and changes in time budget due to the playback of seismic airgun sound. In chapter 3, I conducted a similar sound exposure experiment in a basin and using video observations to be able to quantify foraging behaviour, in addition to swimming and stationary behaviour, which are all relevant to energy budgets of Atlantic cod. In the next four chapters, I studied factors that may modulate the effects of sounds on different marine animals. In chapter 4, I examined the effects of the acoustic characteristics: pulse rate interval, signal to noise ratio, and elevated background level on the response of European seabass on sound exposures. In chapter 5, I studied species interactions during sound exposures by examining aggregation of shore crabs and common shrimps at a food item in the field. In chapter 6, I examined whether reduced aggregation at a food item by crabs can be explained cross-sensory interference. For this, I studied whether olfactory-mediated food finding by shore crabs was affected by sound exposures. Since short-term effects of sound may not be indicative of long-term effects, I also studied habituation. In chapter 7, I examined the habituation of blue mussels to repeated sound exposures, and their recovery to baseline levels during or after single pulses and pulse trains. In chapter 8, I summarized and discussed the results from the previous chapters and suggested follow-up steps.

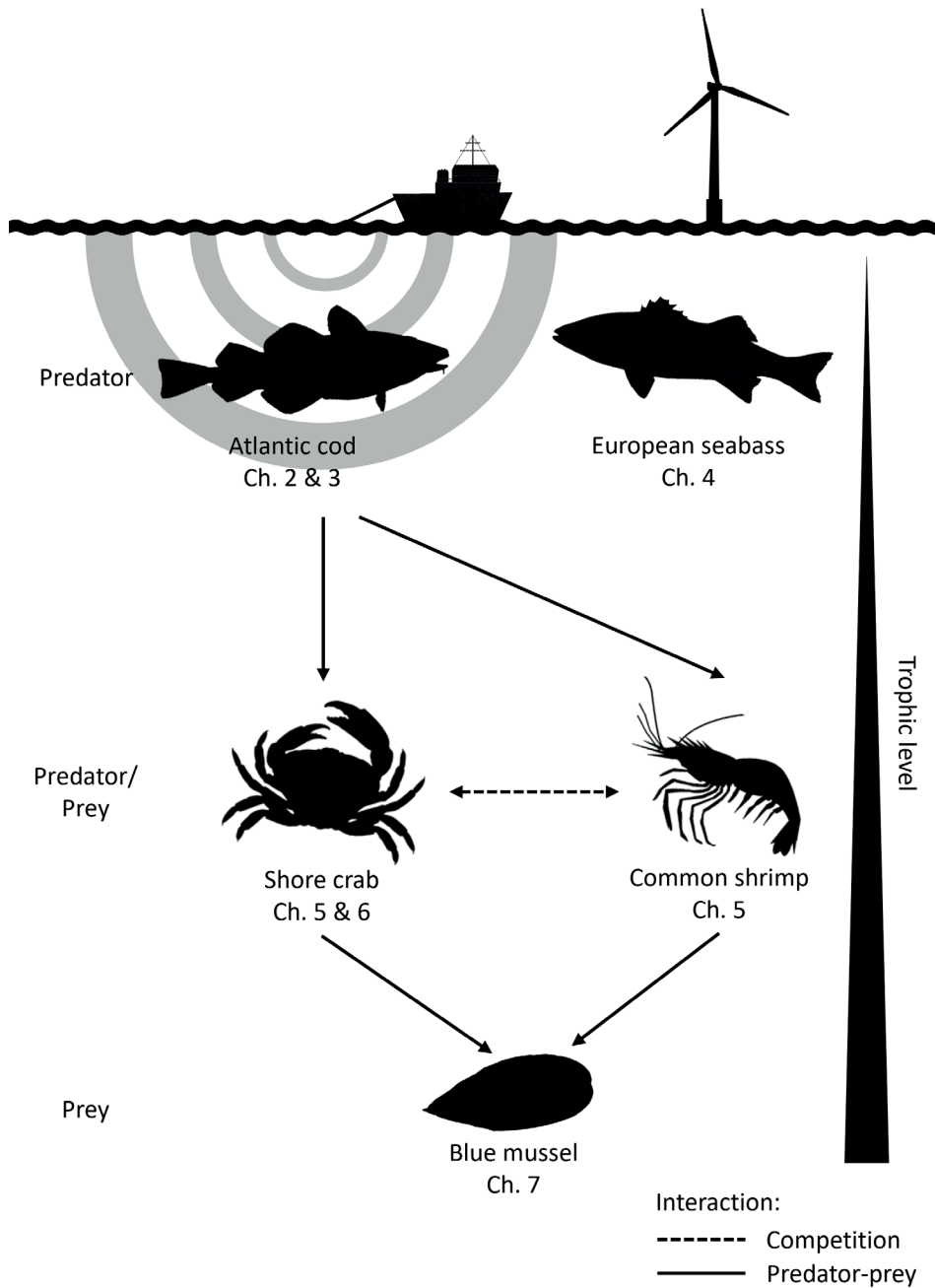


Fig. 1: Schematic of the study species that are used in the experiments described in this thesis. The effects of sound on marine animals from various trophic layers and the interaction between some of them were studied. The arrows indicate the interactions that were part of the studies. 'Ch. #' indicate the chapters in that describe experiments on this study. Note that crabs and shrimp only ate dead mussels in these experiments, common shrimps do not predate on live mussels.

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