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

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Thesis summary & General discussion

Over the last decades, increasing amounts of studies on the effects of sound on marine life have been conducted (Erbe et al., 2019; Popper and Hawkins, 2019; Williams et al., 2015). Nevertheless, quantification of behavioural effects relevant to fitness consequences at individual and population level is still in its infancy (Slabbekoorn et al., 2019) and factors that modulate the effects of sound on animals are relatively unknown (Ellison et al., 2012). In this thesis, I addressed both knowledge gaps using captive and field studies on various marine animals from multiple trophic levels. For the quantification of behavioural responses relevant to fitness, I examined the changes in time budgets of Atlantic cod in a net pen in response to sound (chapter 2, Hubert et al., 2020), and conducted a similar experiment in a basin to be able to include quantification of foraging behaviour (chapter 3, Hubert et al., 2020b). To increase insight into factors that modulate sound impact, I examined the effect of variation in acoustic characteristics of the sound stimulus and the environment on European seabass in a net pen (chapter 4, Hubert et al., 2020c), the interspecific interaction between foraging shore crabs and common shrimps during sound exposure (chapter 6, Hubert et al., 2018), the cross-sensory interference by sound in foraging shore crabs (chapter 7, Hubert et al., 2021), and habituation to repeated sound exposures by blue mussels (chapter 8). Here, I summarize and discuss the main findings of all chapters and explore directions for future research.

Effects of sound on cod time budgets

A modelling study on Atlantic cod population growth indicated that reduced food intake and additional energy expenditure more easily lead to population-level effects than additional direct mortality and reproduction failure (Soudijn et al., 2020). So, to gain insight into population level consequences of acoustic disturbance, data on the energy budget of cod seems most relevant. Since it has not yet been possible to measure energy intake and expenditure directly in free-ranging cod that are exposed to sound, a first step may be to quantify the time spent in several behavioural states, which can later be linked to energy intake and expenditure. I quantified the time spent in various behavioural states by cod during and without sound exposure in two complementary experiments. In the net pen experiment (chapter 2), I used the swimming tracks of individual fish as input for Hidden Markov Models (HMMs), which allowed inference of behavioural states throughout the sampling period. The results indicated that some individuals tended to spend more time transiting and less time being locally active or inactive during sound exposure, which may indicate increased energy expenditure. The latter two states may include foraging behaviour, which is a proxy for energy intake and is critical to gain insight into population level effects. Future studies may be able to discriminate foraging behaviour as a separate behavioural state by HMMs using additional data streams, for example from accelerometers.

Another way to quantify foraging behaviour is to record fish on video. I, therefore, designed a second experiment in basins in which the behavioural state of the fish could be manually scored from video footage (chapter 3). Despite several problems, resulting in a low sample size, time spent foraging, swimming and being stationary was scored in three pairs of cod. These fish spent more time swimming and less time being stationary on days with sound exposures, similar to the results from the net pen experiment, and no differences in time spent foraging were found. Qualitative observation of the videos showed that foraging typically involved low or intermediate swimming speed and a lot of turning. This confirmed that the behavioural states 'locally active' and 'inactive' might indeed include foraging behaviour. Future experiments are needed to examine how changes in time budget translate into changes in energy budget.

Time spent in various behavioural states can potentially be translated to energy expenditure and intake using swim tunnel experiments and various foraging experiments. The classification of behaviour into behavioural states in chapter 2 relied on swimming speed and turning angle. Swimming speed has been linked to oxygen use in fish, which is a proxy for energy use (Metcalfe et al., 2016; Tudorache et al., 2008). Such data can be used to translate swimming speed, derived from position data over time, to energy use. We still lack swim tunnel experiments that link oxygen use with swimming speed in Atlantic cod. Additionally, experiments are needed to also include additional energy use from potentially elevated stress levels and directional changes while swimming. Translating time spent foraging into energy intake requires data on the success rate of prey capture and on the energy content of the prey. The success rate can either be determined by an exposure experiment with video observations, such as in chapter 3, or by quantifying the fish' stomach content (e.g. Reubens et al., 2014). The energy content of the captured prey can be determined with a calorimeter (Benoit-Bird, 2004). Several earlier studies examined the effects of sound on swimming and foraging behaviour and found changes in swimming patterns including brief increases in swimming speed (e.g. Neo et al., 2014), reduced feeding attempts, and/or increased food handling errors (e.g. Bracciali et al., 2012; Shafiei Sabet et al., 2015). However, studies that examined both swimming patterns (or another proxy for energy use) and foraging behaviour simultaneously are scarce.

Ideally, behavioural and physiological effects of noise are quantified over a time window that resembles the actual duration of anthropogenic disturbance or over the life time of the animal. Many sound impact studies examined behaviour over a relatively short time scale, at the onset of the sound or for a short period after the onset. However, anthropogenic sound is omnipresent, pile driving and seismic surveys can last for months and shipping is ongoing (Duarte et al., 2021; Slabbekoorn et al., 2019). Behavioural responses may change over time due to processes like habituation (chapter 7) and physiological stress levels may accumulate and only become problematic over time. Short-term responses are therefore likely not representative for long-term responses and short-term behavioural responses can be expected to be less likely than long-term responses to change individual fitness or population levels. So, to quantify effects of sound relevant to fitness and populations, more long-term experiments are needed. There seems only one study that examined the relatively long-term effects of increased vessel activity on both swimming activity and food intake in free-ranging fish. Tagged mulloways (Argyrosomus japonicus) were less active during the weekend, and other individuals had less full stomachs and fewer fish in their diet over the weekend. These differences were likely due to higher boat activity in the weekends (Payne et al., 2014). Such studies may aid to parametrization of changes in energy expenditure and intake due to sound exposure.

Effects of acoustic characteristics on seabass

Responsiveness of fish and other animals to sound may be partially modulated by acoustic characteristics of both the ambient noise and the sound stimulus. In efforts to mitigate the effects of anthropogenic sound, most attention is given to the amplitude of various sources. However, previous studies have shown that temporal patterns are modulating responses as well (Neo et al., 2014; Wysocki et al., 2006) and the same may apply to variation in the frequency distribution of exposure conditions (Marvit and Crawford, 2000; Slabbekoorn et al., 2010), and signal-to-noise levels associated with a particular disturbing sound (Kastelein et al., 2011; Wells, 2009). Ambient noise levels vary in amplitude due to weather conditions and distant boat noise (Carey and Browning, 1988; Wright et al., 2007). I tested the effect of experimentally elevated artificial background sound levels, various impulsive sound levels, and intervals between impulsive sound on European seabass in a net pen (chapter 4). The fish increased their swimming depth after the onset of the impulsive sound, but the magnitude of the change in depth could not be linked to any of the experimentally manipulated acoustic characteristics.

Previous studies have found differential effects of continuous versus impulsive sound, different pulse rates, and consistent versus fluctuating amplitude in fish behaviour and physiology (Neo et al., 2014; Neo et al., 2015a; Wysocki et al., 2006). Additionally, increased background levels have been shown to increase hearing thresholds in cod (Hawkins and Chapman, 1975), and other vertebrates have also been shown to be sensitive to pulse intervals and elevated background levels (Davis, 1970; Gatchel, 1975; Schlittmeier et al., 2008). Since these other studies indicate that pulse interval and signal to noise ratio influence behaviour and sound detection (Davis, 1970; Gatchel, 1975; Hawkins and Chapman, 1975; Neo et al., 2015b), I call for further testing with wider ranges of all acoustic characteristics which may add to the current results. Complementary studies should be done using artificial sounds with specific ranges of acoustic variation, and realistic sounds that are relevant to occurrence in the field, for example pile driving sound with and without bubble screen, and different types of airguns or ships. Insights into the variable effects related to acoustic characteristics will aid in understanding and predicting behavioural responses, which can be used to mitigate and increase effects (for deterrence purposes).

Effects of sound on foraging crustaceans

Fish are relatively often subject of sound impact studies, probably mostly due to commercial interest. Invertebrates, including decapod crustaceans, still received limited attention, whereas their abundance is critical for higher trophic levels as food or through ecosystem services (Morley et al., 2014; Solan et al., 2016). Just like with fish, successful foraging behaviour in crustaceans is vital for growth, reproduction, and survival. So, impact of sound on foraging may negatively affect fitness at individual level and growth rate at population level. I examined the effects of sound on foraging crustaceans in two complementary studies: an in-situ experiment with free-ranging animals to allow interspecies interactions, and an indoor experiment to focus on a mechanism that might explain the results from the in-situ experiment. For the in-situ experiment, I used a baited camera to attract and film shore crabs and common shrimps (chapter 5). During sound exposure, fewer crabs aggregated around the food item than during a silent control. The increased shrimp numbers, however, could be explained by crab numbers rather than by the sound treatment. This means that shrimps could indirectly benefit from the sound exposure through competitive release (Slabbekoorn and Halfwerk, 2009). This shows that animals do not only respond directly to sound, but may also respond to the response to sound by other animals. Ultimately, we should be interested in the effects of sound on free-ranging animals in situ. So, more experiments that allow species interactions are needed on animals under natural conditions.

Since olfactory cues are important for foraging in crabs, I hypothesized that the reduced aggregation of crabs in the baited camera experiment could be explained by cross-sensory interference. This entails interference of the sensory processing and interpretation of a stimulus, in this case most likely an olfactory cue, by simultaneous perception of a stimulus in another modality, in this case an auditory cue (Halfwerk and Slabbekoorn, 2015). To study this, I designed an experiment in which shore crabs were allowed to forage on a food item, but could only find it using olfactory cues (chapter 6). Food finding success and foraging efficiency were not negatively affected by the boat sound exposures, so no evidence to support the cross-sensory interference hypothesis was found.

Even though I found reduced aggregation at a food item during sound exposure by shore crabs in-situ, I did not find a lower food finding success rate or increased foraging duration during sound exposure in a T-maze. The seemingly different results in the two experiments may be explained in various ways including differences in sound exposures, experimental set ups, and study subject sizes. Another potential reason is the difference in food-deprivation. The individuals that were scored for the in-situ experiment were free-ranging animals and not tracked until they were in view of the camera, so their hunger levels were unknown. The individuals in the T-maze experiment were food-deprived for three days prior to their trial to standardize hunger levels across individuals in this experiment. Across experiments, it may however be that there were differences in motivation to go to the food item, resulting in different motivation levels to take risks. Various studies have experimentally shown that food-deprived individuals display more behaviour that the authors labelled as risky (Croy and Hughes, 1991; Godin and Crossman, 1994). Insight into such factors that modulate the effects of sound on animals will aid in understanding and the interpretation of sound impact studies, and will also help to extrapolate results from controlled experiments to the real-world and free-ranging conditions.

The aim of the T-maze study was not to determine absolute response levels to sound, but to examine cross-sensory interference as a potential mechanism for the reduced aggregation at a food item in-situ. Since we found no reduced food finding success rate or increased food finding duration, we found no evidence for cross-sensory interference of boat playbacks on olfactory mediated food finding. The seemingly different results across experiments again highlight that absolute response levels to sound can best be tested in-situ, whereas mechanisms underlying certain responses can best be studied in a controlled environment. Additionally, one of the six boat playback stimuli yielded deviating results: excluding this data showed that crabs were faster to reach the food during the remaining five boat playbacks than during the ambient control. This result did not affect our conclusion on cross-modal interference, but emphasised the need of sufficient replication of playback stimuli to prevent that a single stimulus can affect the results substantially. This result also indicated that different boats may elicit different effects. Dedicated studies are needed to confirm and further examine this.

Habituation by mussels

Even sessile invertebrates are able to hear and respond to sound. Sessile animals, or other animals with a small home range, are likely to be exposed to anthropogenic sound repeatedly. Activities such as pile driving and seismic surveys can last for weeks to months in a particular area, and shipping intensity is continuously higher around harbours and shipping lanes (Haver et al., 2018; McCauley et al., 2000; Sertlek et al., 2019). During repeated or continuous exposures, habituation may mitigate part of the responses to sound. I examined whether blue mussels, a semi-sessile bivalve, can habituate to repeated sound exposures (chapter 7). Mussels were exposed to repeated sound exposures, followed by a single exposure to a different sound. After the onset of the first exposure, the mussels partially closed their valve gape. This response decreased in magnitude over repeated sound exposures, but was stronger again during the exposure to a different sound. This latter effect clearly showed that the decrease in response can be attributed to habituation (Bejder et al., 2009; Rankin et al., 2009). Habituation to sound does not necessarily mean the lack of any negative effects (Bejder et al., 2009), as sound may still cause physiological stress, mask relevant sounds, and result in shifting attention (Chan et al., 2010; Wale et al., 2019; Wysocki and Ladich, 2005). Nevertheless, studying the potential for a mitigating impact of habituation on the effects of anthropogenic noise is critical to understand the consequences of repeated sound exposures on animals.

Experimental set-ups and sound exposures

For this thesis, I conducted a variety of experiments that differed in both experimental set-up and sound exposures. The experiments were either conducted 1) indoors, using captive animals; 2) outdoors, using captive animals; or 3) outdoors using free-ranging animals. Indoors, it is easier to shield the experiment from external conditions (e.g., weather or unwanted sound) and typically also easier to perform standardized and high-resolution behavioural measurements. However, both the behaviour of the animals and the acoustic propagation is expected to be very different from the field (Rogers et al., 2016; Slabbekoorn, 2016). It is therefore critical to realize that some research questions can only be answered with the details and replication of measurements from the controlled conditions of an indoor experiment and that some research questions cannot be answered by just indoor studies. Outdoor experiments will have a higher acoustic validity, meaning that the acoustic propagation in the experimental arena can be more easily translated to other outdoor locations. The behaviour of captive animals outdoors may also resemble that of free-ranging animals more. The best behavioural validity can obviously be achieved by using free-ranging individuals in their natural habitat (e.g. van der Knaap et al., 2021). The behaviour that can be measured outdoors is more limited and the resolution will likely be lower. However, again, it will depend on the goal of the experiment what set-up is best suited to answer a specific research question.

To expose the experimental animals to sound, I always used an underwater speaker and playbacks with either artificially generated sound or recordings of actual anthropogenic sound. I used artificially generated sound when highly controlled sound stimuli were required to answer the research questions, often related to the contribution of particular acoustic features to the response of the animals. Recordings of anthropogenic sound were used to increase the realism of the exposures. However, it should be noted that all exposure conditions tested in this thesis, including both indoor and outdoor experiments, were substantially different from actual exposure conditions in the outside world because of speaker limitations (lack of low frequencies: < 150 Hz), sound propagation complexity in tanks (different from outdoors), and a speaker being a point source, which is in contrast to most anthropogenic sources. The limitations in acoustic validity should make us refrain from any extrapolation from the results in terms of absolute sound or response levels. However, this was also not the target in this thesis, as I aimed to answer research questions which were fundamental in nature and did not aim to determine absolute threshold levels. Studies that do aim at absolute dose-response levels are best conducted in the field, using free-ranging animals, with actual anthropogenic sound sources, and taking a wide variety of response-modulating factors into account.

Ecological consequences

I found that animals at various trophic levels were affected by sound and that species interactions might also change due to sound exposures. When competitive or predator-prey balances between species shift, sound can have impact at a community and ecosystem level. There is already some evidence for this from other studies. Anthropogenic sound has been shown to reduce species richness in avian communities and to indirectly facilitate breeding success of particular species because of lower abundance of a nest predator species (Francis et al., 2009; Slabbekoorn and Halfwerk, 2009). Mulloways had an altered diet composition in the weekends, the days with most boating activity (Payne et al., 2014), from which we can infer shifts in predator-prey relationships. In chapter

5, I also showed that less crabs aggregated at a food item during sound, which created an opportunity for shrimps. Through such mechanisms, sound can change the environment beyond a single species. The current study species are all abundant species and play important roles in the ecosystem; as reef builder, water filterer, prey, or predator. If sound changes foraging, growth, reproduction or survival for one or more of these species, this may therefore change the ecosystem substantially. It should be noted, however, that all my experiments were relatively short-term and more without than with species interactions. More studies are therefore needed as also potential ecosystem effects have to be tested empirically. Again, this is best tested in the field, using free-ranging animals, but can be complementary to mechanistic studies in captivity.

Conclusion

The amount of anthropogenic activities at sea is not likely to decrease in the near future. Both the amount of shipping and the amount of offshore wind farms is expected to continue to increase (International Maritime Organization, 2015; Reed, 2020). The amount of seismic surveys is partly linked to the oil price and may be harder to predict. However, seismic surveys are also used to identify sites for carbon sequestration which may increase in popularity in an effort to mitigate global warming (Carroll et al., 2014). Mitigation measures to reduce sound levels of shipping and piling are being developed, and seismic airguns with less loud high frequency components are already available. Nevertheless, the amount of anthropogenic sound in the marine environment is expected to remain substantial (Duarte et al., 2021). So, it remains important to continue studying the effects of anthropogenic sound.

The variety in test conditions, model species, and test results in this thesis, indicates that this area of research remains a growing field of opportunity, for both fundamental studies and investigations of applied value. It is important to continue research that aims to quantify fitness effects for individuals and populations. This thesis may provide a first step, but similar research has to be conducted in-situ, complementary with experiments that will allow translation from changes in time budgets to changes in energy budgets, and consequently to changes in growth, reproduction, and survival. Additionally, studies into the factors that modulate the effects of sound are needed to fully understand the impact of sound. Such studies may be best conducted in captivity with a high level of experimental control and the ability to track individuals at a high resolution. The use of controlled indoor studies is occasionally debated, but in this way, both in-situ and controlled experiments are complementary and both valuable to increase insight into the effects of sound on animals while using the opportunities and being aware of the limitations of both types of experiments.

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