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Driven to distraction? Behavioural impacts of anthropogenic noise on the European hermit crab *Pagurus bernhardus* from individual to group level

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Driven to distraction? Behavioural impacts of anthropogenic noise on the European hermit crab *Pagurus bernhardus* from individual to group level

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**UNIVERSITY OF
PLYMOUTH**

Driven to distraction?

Behavioural impacts of anthropogenic noise on the

European hermit crab

Pagurus bernhardus

from individual to group level

By

Svenja Tidau

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

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In collaboration with

Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology
(Ireland)

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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- SeaBASS – Marine Bioacoustics Summer School 2018 (Durham, USA): “Ship noise playbacks distract European hermit crabs – From the lab to the field” *poster*
- 15th Marine Biological Association Postgraduate Conference 2018 (Plymouth, UK): “To group or not to group? Effects of anthropogenic noise on the grouping behaviour in the European hermit crab” *oral presentation*

- Association for the Study of Animal Behaviour Easter Meeting 2018 (Plymouth, UK): “To group or not to group? Effects of anthropogenic noise on the grouping behaviour in the European hermit crab” *oral presentation*

2017

- XXVI International Bioacoustics Council Meeting (Haridwar, India): “Noisy Neighbours – Behavioural impacts of ship noise on the European hermit” *oral presentation*
- Behaviour 2017 Conference (Estoril, Portugal): “Noise distracts hermit crabs – But how important is it?” *oral presentation*
- 3 Minute Thesis Competition (Plymouth UK) “Noisy neighbours –How ship noise changes the behaviour in hermit crabs” *oral presentation*
- 14th Marine Biological Association Postgraduate Conference (Penryn, UK): “Driven to distraction? Behavioural impacts of ship noise on the European hermit crab” *oral presentation* (highly recommended)
- PlyMSEF Making Waves Postgraduate Conference 2017 (Plymouth, UK): “Driven to distraction? Behavioural impacts of ocean noise on the European hermit crab” *poster*

2016

- The Effects of Noise on Aquatic Life Conference (Dublin, Ireland): “Driven to Distraction: Behavioural Impacts of Ocean Noise on the European Hermit Crab” *poster*
- BBC Radio Wales Science (UK): “The effects of noise on animals” *interviewee*

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Abstract

Human activities are altering the planet at an unprecedented scale and pace, ranging from effects on global systems such as climate and carbon cycles to localised but globally wide-spread exposure to anthropogenic pollution such as noise.

Anthropogenic noise is an example of human-induced rapid environmental change (HIREC) which can mask, distract and disrupt natural stimuli and sensory-cognitive processes. Since HIREC can alter the sensory environment of animals, and how they detect and process information from their biotic and abiotic environment to make accurate decisions, this process has been termed sensory pollution. While growing evidence shows detrimental effects on across taxa, behavioural contexts and situations, invertebrates are understudied despite contributing to global faunal biodiversity to a vastly greater extent than vertebrate animals.

In this thesis, I study how anthropogenic noise as a form of HIREC affects a marine crustacean using the European hermit crab *Pagurus bernhardus* as a model organism. For hermit crabs, empty gastropod shells are a crucial resource affecting growth, reproduction and survival. Crabs are known to have a preferred, optimal shell weight (% PSW) relating the occupied shell weight to the crab's own body weight but the shell size they occupy in nature can diverge from the optimal shell size. First, I exposed hermit crabs over 10 days to low-intensity ship noise playbacks (chapter 2). The sound treatment had no effect on assessment behaviour until the last day of the experiment whereby individuals under noise showed longer latency to assess the new, optimal shell. Crabs in small shells under the noise treatment accepted the new shell more frequently than crabs under ambient sound. This pattern was reversed for crabs in larger shells. This experiment suggests that properties of anthropogenic noise

beyond the intensity affect animals. Besides the noise effects, I show that shell assessment is a repeatable behaviour.

Next, I demonstrate that the effects of noise are modulated by natural factors (chapter 3). I exposed hermit crabs not only to noise and different sized shells but also to a visual predator cue of the common shore crab *Carcinus maenas*. Overall, the interaction between noise, predator presence and shell size influenced the mean duration for the final decision to accept or reject the optimal shell. Hermit crabs in shells of 50% optimal size took less time for their final decision when exposed to both ship noise and predator cue while crabs in shells of 80% optimal size showed shorter decision time only when the predator cue was absent. Moreover, crabs are less likely to accept an optimal shell in the presence of ship noise, suggesting that exposure to ship noise disrupted the information gathering ability of the crabs.

In addition to the noise effects on solitary animals, I examined its effects on intraspecific behavioural interactions (chapter 4 and 5). Under ambient sound, crabs in optimal shells spent most of their time close to a single crab and crabs in suboptimal shells showed no clear preference. Under ship noise, however, this pattern was reversed (chapter 3). Furthermore, noise reduced the aggregated benefit of the arrival of a new shell resource unit to a group of crabs exposed to noise for 24 h (chapter 5) showing that noise effects can accumulate over time. After crabs have been exposed to noise for 24 h I measured the direct effects on their oxygen consumption. In addition, I accounted for the influence of the % PSW of the occupied shell on the oxygen consumption of crabs. Since crabs obtained those shells during the 24 h group process under ship noise (chapter 5), this measure allows to quantify the indirect physiological costs of decisions made under noise (chapter 6). While there was no

direct effect of the sound treatment on oxygen consumption, crabs in shells that were too small in relation to their body size had a higher oxygen consumption than hermit crabs in shells closer to the optimal size. Finally, in a field experiment, I found that the mean startle response duration increased with observation number and that the mean startle response duration was repeatable over the observation period. There was no effect of ship noise, presumably because other natural factors such as wind and water turbulence overrode the effects of noise exposure.

My results indicate that noise affects shell assessment decisions and that the effects can be modulated by natural factors such as predation threat, resource quality and potentially abiotic variables. This suggests that noise can disrupt across multiple sensory channels. In addition, noise can alter not only individual behaviour but the disruption of individual decisions go beyond a single exposure and scaled up to population levels. I discuss the implications of my findings and suggest avenues for future research to gain a more complete picture of the effects of anthropogenic noise on animals.

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Chapter 1: General introduction

In this chapter, I review the current literature on the behavioural effects of anthropogenic underwater noise set in the wider context of human-induced rapid environmental change (HIREC; Sih, 2013; Sih et al., 2011). To provide a framework in which to understand the effects of anthropogenic noise, I begin with a sensory ecology approach to human-induced rapid environmental change. This is followed by a brief overview of sound as a cue, the characteristics of sound and anthropogenic noise, with a focus on aquatic environments. I provide a primer in sound detection abilities of adult aquatic crustaceans before I review the effects of anthropogenic noise on animals to identify research gaps, which I address in this thesis. I present the model organism, the European hermit crab *Pagurus bernhardus*, and finish the chapter with the aims of this thesis and the subsequent chapters.

1.1 A sensory ecology approach to human-induced rapid environmental change

Human activities are altering the planet at an unprecedented scale and pace, ranging from effects on global systems such as climate and carbon cycles to localised but globally wide-spread modification of habitats through fragmentation, destruction and pollution (Sih et al., 2011). HIREC, including anthropogenic noise, has been discovered all over the world from the Arctic to the Antarctic (Haver et al., 2017). In addition to the global scale, HIREC exposes populations to environmental change of an evolutionary unprecedented pace (Palumbi, 2001). While HIREC can have direct and sometimes lethal effects (e.g. exposure to toxic chemicals and heavy metals), in many cases animals are subject to indirect impacts such as altered sensory environments.

Organisms acquire information from their biotic and abiotic environment to make accurate decisions via sensory-cognitive systems developed over generations (Bradbury and Vehrencamp, 2011). HIREC can interfere with the information detection, processing and assessment by creating evolutionary novel environmental conditions (Sih et al., 2011) that mask, distract and disrupt natural stimuli and sensory-cognitive processes; a process termed sensory (information) pollution (Briffa et al., 2012; Halfwerk and Slabbekoorn, 2015; Longcore and Rich, 2004; Lürling and Scheffer, 2007; Shannon et al., 2016b). Most animals experience naturally fluctuating environmental conditions during an individual's life-time or on the population level on an evolutionary time scale. However, the rate of phenotypic change (both from phenotypic plasticity and genetic variation) due to anthropogenic perturbations of the environment is greater compared to natural environmental perturbations (reviewed by Hendry et al., 2008). This finding illustrates the severity that humans have on animals both on the time scale of an individual lifespan and in an evolutionary sense across generations.

Populations might adapt to new conditions (Ghalambor et al., 2007) and hence eventually do so in response to pollution of the sensory environment (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011). However, one of the initial responses of animals to HIREC appears to be via behavioural changes in individuals (Nagelkerken and Munday, 2016; Tuomainen and Candolin, 2011). For instance, individuals may choose to avoid disturbed and polluted but otherwise suitable habitats (Bayne et al., 2008; Blickley et al., 2012a; Blickley et al., 2012b; Francis et al., 2009; Schaub et al., 2008). Alternatively, animals may remain in those areas or are simply unable to escape them, such as sessile marine invertebrates. The behavioural response of individual organisms

to HIREC can have knock-on effects on intra- and interspecific interactions and ecological processes making the study of behaviour an entry point to understanding and eventually predicting the effects of HIREC on populations and communities (Nagelkerken and Munday, 2016). HIREC is almost certainly one of the largest changes for organisms to cope with in the so-called Anthropocene (Crutzen, 2002) and likewise challenging researchers, policy makers and conservationists.

1.1.1 Trade-offs in information gathering and processing

To understand the effects of HIREC on animals in their behaviour and decision-making requires an understanding of how organisms acquire and process information from their environment. Sensory ecology thus offers an insightful approach into the mechanisms by which HIREC can affect information gathering, processing and assessment of natural and anthropogenic stimuli (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011; Tuomainen and Candolin, 2011). Assessing information and making decisions inherently exposes individuals to uncertainties, particularly those associated with heterogeneous and unpredictable environments (Dall, 2010; Shettleworth, 2010). Those uncertainties stem from events and factors that are usually out of an individual's control and, moreover, that are unpredictable (Dall, 2010). While some of these events and factors are irreducible (i.e. they cannot be influenced by the individual) others can be reducible for instance by anticipation and prior experience of the environment. In these cases, an individual may decide to invest in gathering information to reduce uncertainty. Deciding on whether or not to acquire information subjects animals to trade-offs among various intrinsic and extrinsic factors. To begin with, animals need sensory and cognitive systems to detect, process, store and evaluate information such as the neural capability to perform cognitive tasks (Shettleworth, 2010). The

performance of these systems is influenced by an individual's state such as its energy reserves but also its attention. From a cognitive perspective, attention is the neuronal activation at any given time limiting the amount of information which can be processed at this given time (Dukas, 2004; Shettleworth, 2010). Therefore, making appropriate decisions, requires an individual to invest attention to filter information (relevant/ irrelevant). To further complicate this process, attention is required to integrate stimuli from multiple sensory pathways ('top-down mechanism') (Talsma et al., 2010). In fact, sensory stimuli not only require the decision to dedicate attention to them but equally can capture an individual's attention ('bottom-up mechanism'). As a consequence of this bottom-up mechanism, any additional stimulus can divert attention away from one stimulus or task to another one (Shettleworth, 2010). Once individuals decide to acquire information about their environment, another major trade-off is to balance the accuracy and pace of gathering and assessing information (Bradbury and Vehrencamp, 2011). That is, fast information assessment may require less investment in time and energy and hence be cheaper. However, less accurate information can yield too erroneous assessment of that information, and hence suboptimal decisions. Alternatively, slow but more accurate assessments will be more costly to perform. In addition, some cues might be rapidly assessable but hold imprecise information while the better sources of more accurate information can be impossible or too costly to attain (Bradbury and Vehrencamp, 2011). Besides the trade-off between pace and accuracy, individual also have to balance the information assessment against other requirements such as growth and reproduction. Nevertheless these trade-off in decision-making, mistakes in the information assessment are inevitable (Dall, 2010; Shettleworth, 2010). For example, despite

balancing those costs and benefits, individuals can respond with false alarms or divert attention away from pertinent cues so that animals miss out opportunities or in the worst-case fail to detect predators.

1.1.2 Sensory pollution: Disruption of information gathering and assessment

Pollution of the sensory environment can interfere with the described cognitive information processing incorporating all sensory-cognitive stages from stimuli detection, processing, filtering, storing and evaluation (Dukas, 2004; Shettleworth, 2010) through various mechanisms. An animal's sensory ecology is influenced through two main routes (Halfwerk and Slabbekoorn, 2015). First, sensory pollution can have unimodal effects on the detection and assessment of cues that is usually referred to as masking. For instance human-induced chemicals have been shown to disrupt chemical information (Lürling and Scheffer, 2007; Zala and Penn, 2004), artificial light to override visual cues (Duarte et al., 2019; Gaston et al., 2013; Gaston et al., 2012) and noise can interfere with acoustic signals and communication (Brumm and Slabbekoorn, 2005; Clark et al., 2009; Erbe et al., 2016). Second, sensory pollution can disrupt information detection and assessment across modalities. Instead of processing relevant information in one sensory modality, the sensory pollutant can divert an individual's limited attention away from the pertinent cue to another modality (Halfwerk and Slabbekoorn, 2015). For instance, global processes such as climate change causes the acidification of marine ecosystems which has been demonstrated to alter the sensory assessment of olfactory and auditory cues (Ashur et al., 2017; Castro et al., 2017; Rossi et al., 2018). More localised sources of sensory pollution are anthropogenic chemical or physical (noise, light) pollutants. One such case is

anthropogenic noise which has been shown to interfere with visual, chemical or tactile information assessment (Hasan et al., 2018; Kunc et al., 2014; Morris-Drake et al., 2016; Tidau and Briffa, 2019; Tidau and Briffa, In Press; Walsh et al., 2017). Sensory pollution can induce more mistakes or suboptimal behaviour and trade-off to invest time and energy in information assessment. Cross-modal mechanisms are particularly important for understanding the behavioural effects of pollutants which lie outside the primary sensory pathways animals rely on. Specifically, anthropogenic noise has been demonstrated to affect behaviours for which animals do not primarily use acoustic cues and signals (Hasan et al., 2018; Kunc et al., 2014; Tidau and Briffa, 2019; Tidau and Briffa, In Press; Walsh et al., 2017). Besides these uni- and cross-modal effects, in the wild natural and anthropogenic sensory stimuli co-occur and interact affecting animals on multimodal pathways simultaneously (Halfwerk and Slabbekoorn, 2015). Shipping, for instance, not only emits noise, but also light and chemicals in addition to the pollution of the sensory environment through global processes.

In addition to the interference of sensory pollution with the information detection and assessment of environmental cues, anthropogenic stimuli can also affect animals by causing stress. Stress research across taxonomic groups shows that more unpredictable and uncontrollable stimuli are more stressful for organisms (reviewed by Koolhaas et al., 2011). Accordingly, anthropogenic stimuli are in many ways novel and different from natural cues animals have evolved from (Sih et al., 2011). Physiological stress responses in response to HIREC are widespread and are likely to trigger behavioural change in animals (for review on non-behavioural effects Kight and Swaddle, 2011). In nature, all these mechanisms, through which anthropogenic pollution can affect animals, are not mutually exclusive but rather work in conjunction.

Although behaviour is often referred to as the most plastic phenotypic trait which enables learning and responding to changing and novel environments (Gross et al., 2010) such plasticity can be costly and limited (DeWitt et al., 1998). Notably, the costs of plasticity emerge from energetic input required to maintain an adequate sensory system, energetic effort involved in gathering information. In addition to these costs, there will also be limits on the benefits of behavioural plasticity arising from the degree of unreliability that surrounds any source of information, lost opportunities and increased risks while acquiring of information rather than dedicating time and energy to other tasks. Since mistakes in decisions are likely in such environments, plastic behaviour can be difficult to achieve or costly to maintain (Sih et al., 2004). In addition, if behavioural plasticity would be unlimited, why does non-optimal behaviour occur rather than being selected against towards a single phenotype with maximum plasticity (Bell, 2007; DeWitt et al., 1998; Sih et al., 2004)? These limits and the costs of plasticity can explain why selection can favour consistent inter-individual differences in behaviour within and between populations rather than driving towards population wide optimal strategies (Bell, 2007; Dall et al., 2004; Sih et al., 2004) such consistent behaviour across time, situation or context is described as personality (Bell et al., 2009; Dall et al., 2004; Dingemanse and Réale, 2005; Réale et al., 2010). While plasticity and personality might appear contradictory at first, Dingemanse et al. (2010) integrate them in their approach of behavioural reaction norms. Behavioural reaction norms are sets of phenotypic traits produced by a single genotype leading to consistent inter-individual variation in plasticity within populations. Therefore, we may expect animals to exhibit plastic behaviour under sensory pollution or, due to the limitations and costs of plasticity, to display consistent inter-individual differences. Behavioural reaction

norms thus define the scope of possible responses of animals to cope with the pollution of their sensory environment.

1.2 Sound as a cue: Characteristics of sound and anthropogenic noise

Light and vision, while being one of the most important sensory channels on land, are of more limited use underwater. As a consequence of the attenuation of light underwater, it only travels a few hundred meters before its absorption and scattering (Marshall, 2017; Slabbekoorn et al., 2010). In contrast, sound underwater propagates quickly over large distances. In water, the speed of sound is nearly five times faster than in air also be expressed by the velocity which is 1500 m s^{-1} in water versus 334 m s^{-1} in air (Ainslie et al., 2009; Hatch and Wright, 2007; Tasker et al., 2010). Hence, many marine animals have developed sensory systems that are well adapted to acoustic signals and cues, making sound one of the most important sources of information and mode of communication underwater (Bradbury and Vehrencamp, 2011; Slabbekoorn et al., 2010; Wartzok and Ketten, 1999).

1.2.1 Characteristics of sound

In its broadest sense, sound is a mechanical disturbance that travels through an elastic medium such as air, solids or water. Sound is generated by an external force (energy) which displaces the particles (i.e. the matter) in that medium and causes them to oscillate around their original position (Götz et al., 2009). When these oscillating particles set other particles in motion, energy propagates through the medium and causes pressure fluctuations in the form of waves where particles are compressed and expanded (Figure 1-1a; Götz et al., 2009).

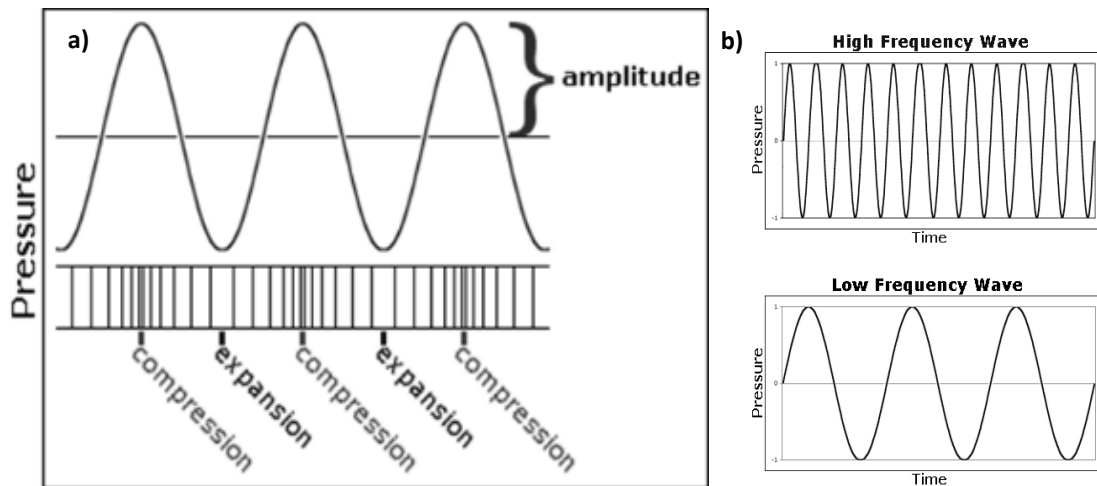


Figure 1-1 Graphical display of a) compression and expansion of sound waves and b) comparison of high and low frequency sound waves (figures taken from DOSITS, 2016a; DOSITS, 2016b).

The perceived characteristics of sound are soft or loud intensity and low or high pitched (DOSITS, 2019). To measure its physical properties and the energy it carries, sound is quantified in terms of frequency (pitch) and amplitude (intensity) (Götz et al., 2009; Tasker et al., 2010). Both, frequency and amplitude relate to how sound travels whereby frequency describes *how often* it moves (the number of a sound wave) and amplitude *how much* (the height of a sound wave) (DOSITS, 2019). More precisely, frequency expresses the number of cycles of a sound wave as a function of time i.e. the number of cycles in 1 s measured in Hertz (Hz = 1 cycle per s; 1 kHz = 1 000 cycles per s). The frequency can also be described as the rate of change of pressure fluctuations spatially expressed by the wavelength (Figure 1-1b; Figure 1-2b; Götz et al., 2009). The wavelength (λ in m) is the distance a wave travels in 1 cycle respectively 1 m and is calculated as a function of velocity (v in m s^{-1}) and frequency (f in Hz) (Götz et al., 2009):

$$\lambda = v / f \text{ (velocity/ frequency).}$$

Thus, wavelength and frequency are inversely related depending on the speed of sound (Figure 1-1b). As an example, the wavelength in water at 100 Hz is approximately 15 m (velocity: 1 500 m s⁻¹ /frequency: 100 Hz). As the energy of low frequency sound is absorbed more slowly, it can travel further than high frequency waves (Hatch and Wright, 2007).

The amplitude measures the energy of a soundwave, which is the change in pressure from the original state in a specified direction over time measured in decibels (dB) (Götz et al., 2009). High pressure compresses particles and carries high levels of energy while low pressure allows waves to expand and carries a relatively small amount of energy (Figure 1-1b). Amplitude is commonly referred to as intensity or loudness, namely the higher amplitude (or intensity) the louder the sound (Götz et al., 2009). Amplitude is often displayed as a wave on a relative scale between an equilibrium (no sound, usually expressed as 0) and a crest (usually + 1 = maximum pressure, -1 = minimum pressure). The amplitudes of these wave cycles can be measured in three ways (Figure 1-2a): first, as the difference between the minimum negative and the maximum positive pressure of the waveform (peak-to-peak between 1 and -1), second, as the difference between the equilibrium (0) and the maximum positive peak pressure (0-peak), and third, as the root of the mean of the squares (RMS) of the amplitudes across cycles (Götz et al., 2009). Sound spectrum encapsulates the amplitude as a function of frequency and bandwidth describes the range of frequencies of a sound (Götz et al., 2009).

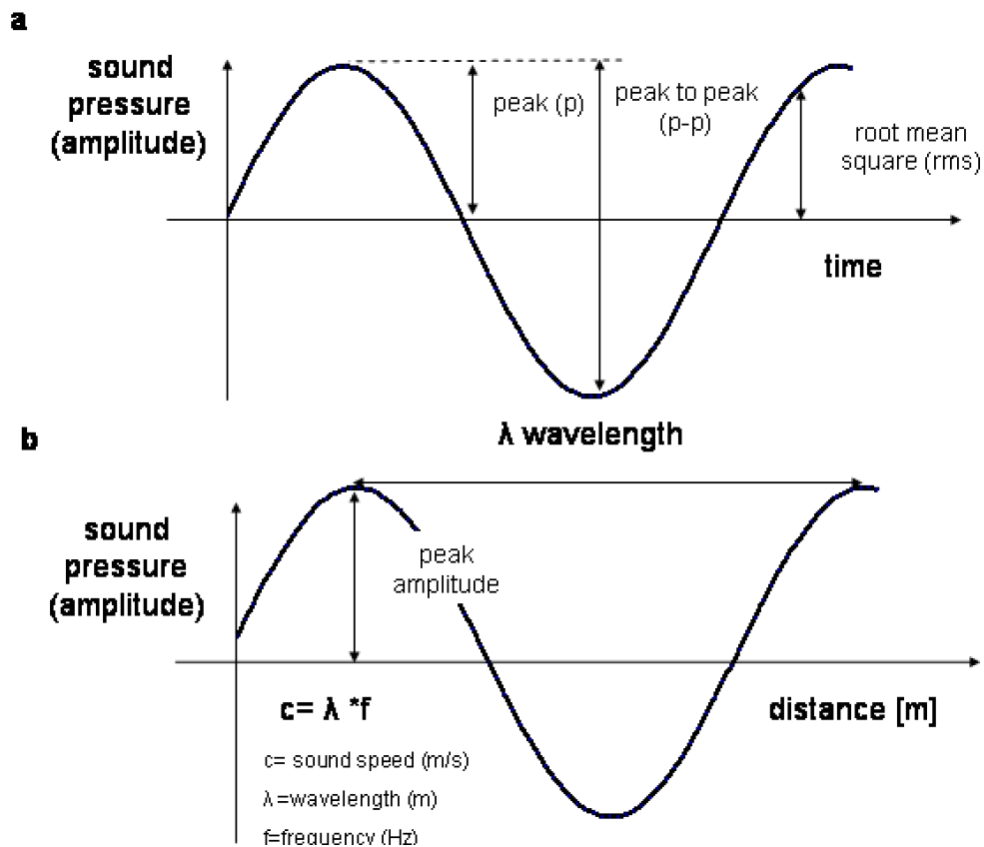


Figure 1-2 Variation of sound pressure on a) temporal scale including most common amplitude measurements and b) spatial scale characterised by wavelength (figures taken from Götz et al., 2009).

Sound pressure and particle motion are quantified in different ways. Pressure is a scalar quantity measured on a logarithmic scale, expressed in decibels (dB) and referenced to 1 micropascal (μ Pa) in underwater acoustics as compared to 20 micropascals (μ Pa) in air (Hatch and Wright, 2007; Tasker et al., 2010). Due to these different reference levels, sound intensities in water cannot be compared directly to those in air (Ainslie et al., 2009). Particle motion is the vibrations of the molecules around an equilibrium state and is quantified by a 3-dimensional vector of displacement (nm), velocity (m s^{-1}) and acceleration (m s^{-2}) of the particles at a certain location in the medium (Götz et al., 2009; Southall et al., 2007; Tasker et al., 2010).

The relation between pressure and particle motion varies with the distance from the source and the properties of the medium (elasticity and density) which is also called acoustic impedance (Tasker et al., 2010). Distant from the sound source, the ratio between sound pressure and particle motion is constant whereas close to the source and over short distances the ratio changes rapidly due to reflections such as by the sea surface or substrate (Tasker et al., 2010) making sound measurements particularly difficult in shallow, coastal areas (Ainslie et al., 2009; Cato, 2008; Hildebrand, 2009; Ma et al., 2005). Most sounds cause relatively low particle motion in water; except in the so-called nearfield to the source or close to the sea surface which generate high particle motion (Tasker et al., 2010).

The particle motion component of sound is particularly relevant for the sound detection in most invertebrates and fishes (André et al., 2016; Hawkins et al., 2015; Hawkins and Popper, 2016; Tasker et al., 2010). However, understanding its full role to these taxa is still limited among others because of its physical complexity which is particularly complex in small tanks in the laboratory (Akamatsu et al., 2002; Gray et al., 2016; Hawkins and Popper, 2016). However, the complexity of measuring particle motion is not limited to laboratories alone but also challenging in the field due to the availability of equipment (for an excellent discussion on the importance and current limitations of measuring particle motion for instance Nedelec et al., 2016a).

1.2.2 Sources and characteristics of anthropogenic underwater noise

The importance of sound to marine life can at least partially explain the rapid growth of research on the impacts of anthropogenic underwater noise in the last two decades (Williams et al., 2015). In contrast to the “The Silent World” as postulated by Jacques

Cousteau in his documentary film (1956), the ocean is anything but quiet.

Technological advancements have generated a boost in soundscape analyses improving our understanding of the ecological diversity of deep sea, polar, temperate and tropical reefs and marine and freshwater ecosystems and helping to monitor environmental change (Archer et al., 2018; Ceraulo et al., 2018; Gervaise et al., 2019; Gordon et al., 2018; Gottesman et al., 2018; Lillis and Mooney, 2018). The analysis of soundscapes reveals an incredible diversity of natural sounds from the so-called geophony of braking of wave, rain fall, the eruption of underwater volcanos and breaking of ice alongside the so-called biophony of grunts, croaks, clicks, and snaps which animals use to attract mates respectively ward off predators (Slabbekoorn et al., 2010). Besides the biotic and abiotic sounds, anthropogenic noise has become a major acoustic ingredient of aquatic soundscapes. Human society has utilised the seas for centuries and probably never more so than in the last decades (for an overview of the sources of anthropogenic noise in aquatic ecosystems see Table 1-1; Götz et al., 2009; Hatch and Wright, 2007; Tasker et al., 2010).

Urban development, the extraction of resources and extensive transportation networks around the globe have changed the soundscapes of terrestrial (Barber et al., 2010; Pijanowski et al., 2011) and aquatic ecosystems (Haver et al., 2017; Hildebrand, 2009; McDonald et al., 2008) making anthropogenic noise a chronic source of pollution. However, there is very little long-term data to quantify overall marine noise pollution among others due to challenges in monitoring and measuring standards (Dekeling et al., 2016). Despite the lack of a global noise monitoring system, monitoring stations in the Pacific Ocean provide clear evidence for significantly increased noise levels over the last decades (Andrew et al., 2011; Andrew et al., 2002).

Table 1-1 Anthropogenic noise sources, source levels (in dB re 1 μ Pa 1 m), measurement unit (RMS = Root Mean Square; 0-P = zero to Peak; P-P = Peak-to-Peak), frequency bandwidth, maximum amplitude and duration (based on Götz et al., 2009).

Noise source	Source level (dB re 1 μ Pa 1 m)	Unit	Frequency bandwidth (in Hz)	Maximum Amplitude (in dB)	Duration (in ms)
Continuous noise sources					
<u>Shipping</u>					
Small boats and ships	160 - 180	RMS	20 - > 20 000	> 1 000	Continuous
Large vessels	180 - 190	RMS	6 - > 30 000	> 200	Continuous
<u>Offshore industrial activities</u>					
Dredging	168 - 186	RMS	30 - > 20 000	100 - 500	Continuous
Drilling	145 - 190	RMS	10 - 10 000	< 100	Continuous
Wind turbines	142	RMS	16 - 20 000	30 - 200	Continuous
Tidal and wave energy devices	165 - 175	RMS	10 - 50 000	-	Continuous
Impulsive noise sources					
<u>Offshore construction</u>					
TNT (1 - 100 lbs)	272 - 287	0-P	2 - 1 000	6 - 21	~ 1 - 10
Pile driving	228/ 243 - 257	0-P/ P-P	20 - > 20 000	100 - 500	50
<u>Sonar</u>					
Military sonar (low-frequency)	215	0-P	100 - 500	-	600 - 1 000
Military sonar (mid-frequency)	223 - 235	0-P	2 800 - 8 200	3 500	500 - 2 000
Echo-sounders	235	0-P	Variable	1 500 - 36 000	5 - 10
<u>Seismic survey</u>					
Airgun array	260 - 262	P-P	10 - 10 000	10 - 120	30 - 60
<u>Other</u>					
Acoustic deterrents	132 - 200	0-P	5 000 - 30 000	5 000 - 30 000	15 - 500

Commercial ships, ferry boats and boats for fishing and recreational purposes are the dominant noise sources in coastal regions and harbours (Barlett and Wilson, 2002). Ships significantly contribute to anthropogenic noise due to their large

numbers, wide distribution and mobility (Hildebrand, 2009; Jasny et al., 2005; Richardson et al., 1995). The global fleet has increased in size, speed (Ainslie et al., 2009) and number from around 30 000 vessels in 1950 to over 85 000 vessels in 1998 (see Figure 1-3; Tasker et al., 2010). This rise primarily reflects past global economic growth which allows to predict that oceans are unlikely to become less busy in the future unless ships become more efficient and less loud (Frisk, 2012).

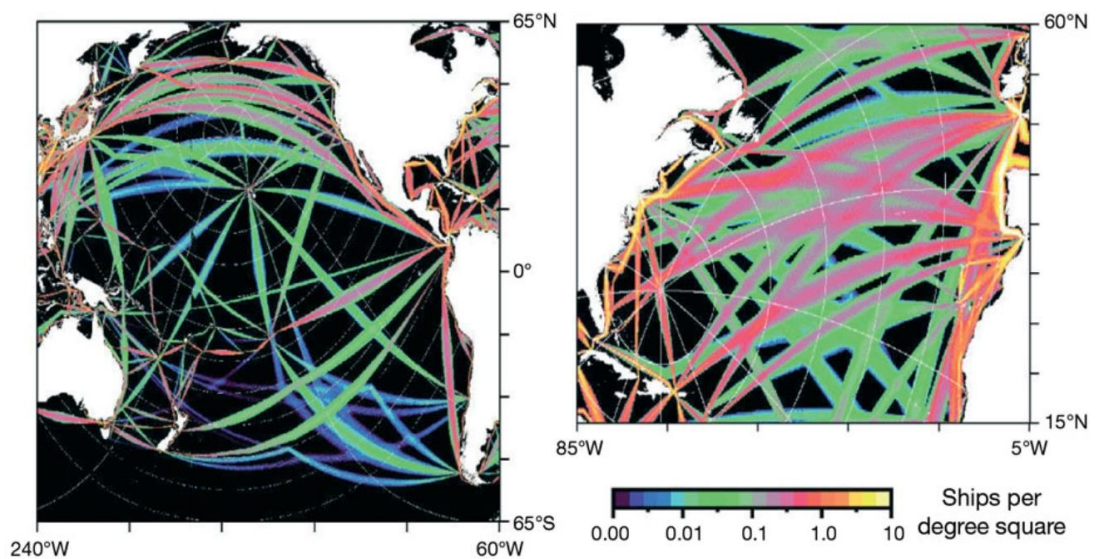


Figure 1-3 Shipping densities and propagation in the Pacific Ocean (left side) and the Atlantic Ocean (right side) based on shipping statistics released in 2003 (figure taken from Hildebrand, 2009).

Ships produce unique acoustic signals depending on factors like speed and load (Hildebrand 2009). Rotating propellers generate quickly cavitating bubbles, these burst and create noise (continuous buzzing and humming sound) and the faster a propeller rotates, the more cavitation noise ships produce reaching sound amplitudes of up to 160 and 180 dB re 1 μ Pa at 1 m at frequencies usually concentrated below 200 Hz (Hatch and Wright, 2007; Richardson et al., 1995). Since ship noise is continuous, its

sound pressure is commonly measured as the root-mean-square (RMS) (Tasker et al., 2010).

1.3 Effects of anthropogenic noise on animals

Recent decades have seen mounting evidence for the detrimental effects of anthropogenic noise on humans and non-human animals ranging from avoidance of noise, masking, distraction and stress. The aim here is not to give an exhaustive review on this vast topic which has been done elsewhere (for instance Kunc et al., 2016; Shannon et al., 2016b) but to provide an overview of the behavioural effects of anthropogenic noise on adult aquatic crustaceans, so as to identify the research gaps that I address in this thesis.

In their systematic review on the effects of noise on wildlife, Shannon et al. (2016b) identified that the majority of noise related studies focussed on vocal communication in songbirds and marine mammals. This is not surprising given the importance of acoustic communication for these taxa and thus the apparent negative fitness consequence anthropogenic noise can induce (Richardson et al., 1995; Slabbekoorn, 2013; Slabbekoorn and Ripmeester, 2008; Southall et al., 2007). As research on anthropogenic noise is growing, so is the taxonomic scope providing evidence concerning fishes (reviewed by Cox et al., 2018; Slabbekoorn et al., 2010). Yet, noise effects on invertebrates and among them crustaceans remain understudied (Hawkins et al., 2015; Morley et al., 2014). Understanding the impacts on crustacean will be crucial if we are to develop a rounded view of how noise pollution alters ecosystems. A version of a published review on the behavioural effects of anthropogenic noise on crustaceans (Tidau and Briffa, 2016; attached in the appendix of the thesis) will be summarised and complemented by recent studies here (for an

overview see Table 1-2), after discussing the mechanisms of sound detection in adult aquatic crustacean.

1.3.1 Sound detection in adult aquatic crustaceans

Though the auditory system of crustaceans has been studied for more than 150 years (see for instance Farre, 1843), overall it is still relatively poorly understood (Popper et al., 2001). While sound production by aquatic crustaceans has been found only in few species (for an overview see Tidau and Briffa, 2016), sound detection is widespread and well documented (Budelmann, 1992). In a narrow sense, most adult aquatic crustaceans are unlikely to hear as they lack an air-filled chamber to detect changes in sound pressure (Breithaupt, 2002; Breithaupt and Tautz, 1990; Budelmann, 1992; Goodall et al., 1990; Popper et al., 2001). However, three anatomical structures equip crustaceans to detect particle motion via hydrodynamic receptors (Breithaupt, 2002; Budelmann, 1992; Popper et al., 2001). This sensory system is comprised of setae hair-like cells on the body surface, a statocyst receptor system and chordotonal organs (Breithaupt, 2002; Budelmann, 1992; McCauley and Fewtrell, 2008). Thus, contrary to the narrow definition of hearing regarding sound pressure, in the broadest sense almost all crustaceans are able to detect the particle motion component of underwater sound (Budelmann, 1992).

Sound detection can be studied using behavioural measures and electrophysiological techniques such as auditory evoked potentials.

Electrophysiological techniques provide audiograms and sensitivity thresholds (e.g. detectable frequencies range bandwidth and the lowest detectable stimulus intensity) which are generated relatively rapid and easy but those results can contrast behavioural measurements (for review and discussion of these two approaches, the

different sensitivity levels they produce see for instance Ladich and Fay, 2013; Sisneros et al., 2016; Stanley et al., 2011). Lovell et al. (2005) used this approach for the first time for a crustaceans and found that the common prawn *Palaemon serratus* can detect sounds in frequencies between 100 – 3 000 Hz at sound pressure level between 105 to 132 dB re 1 μ Pa at 1 m. Although electrophysiological measurements may differ from behavioural responses and are not applicable to all crustaceans (see published review for a more detailed discussion), they can serve as a starting point to determine a reasonable frequency range for investigating the impacts of anthropogenic noise on hermit crabs for this thesis.

1.3.2 Behavioural effects of anthropogenic noise on adult aquatic crustaceans

Experiments on the behavioural effects of anthropogenic noise on adult aquatic crustacean reveal changes in individuals concerning foraging, locomotion, antipredator behaviour and altered intra- and interspecific interactions (for an overview see Table 1-2). Three field surveys assessed the effects of airguns (for instance employed for seismic surveys) on the catch rates of economically important crustaceans (shrimps, rock lobster and snow crab), which could be indicative for avoidance of noise or mortality. While none of the studies found altered catch rates (Andriguetto-Filho et al., 2005; Morris et al., 2018; Parry and Gason, 2006), both Andriguetto-Filho et al. (2005) and Morris et al. (2018) discuss significant challenges in isolating the effects of the sound treatment from other factors in the field and suggest complementary laboratory experiments. For instance, contrary to the field, American lobster *Homarus americanus* increased its food intake when exposed to airgun noise in laboratory experiments (Parry and Gason, 2006).

Table 1-2 Overview about peer-reviewed articles on behavioural effects of anthropogenic noise on adult aquatic crustaceans.

Author	Common name	Scientific name	Noise source	Response
Andriguetto-Filho et al. 2005	Southern white shrimp Southern brown shrimp Atlantic seabob	<i>Litopenaeus schmitti</i> <i>Farfantepenaeus subtilis</i> <i>Xyphopenaeus kroyer</i>	Airguns	No significant decrease in density or catch rates ~ 36 hours after air-gun employment
Celi et al. 2013	Red swamp crayfish	<i>Procambarus clarkii</i>	White noise	Fewer encounters of grouped individuals, fights and tail flips
Filiciotti et al. 2014	Mediterranean spiny lobsters	<i>Palinurus elephas</i>	Ship, boat	Increased locomotion time, distance moved in grouped animals, increased velocity in grouped animals but lowered proximity in grouped lobsters
Filiciotti et al. 2016	Common prawn	<i>Palaemon serratus</i>	Ship, boat	Fewer encounters between individuals, more time outside shelter and resting
Filiciotti et al. 2018	Semi-terrestrial crab	<i>Neohelice granulata</i>	Sweep tone	Unreceptive females lower distance and duration moved, receptive females and males higher distance, but lower duration
Hubert et al. 2018	Common shore crab Common shrimp	<i>Carcinus maenas</i> <i>Crangon crangon</i>	White noise	Fewer crabs and more shrimps at foraging site
Meyer-Rockow et al. 1982	Rock lobster	<i>Panulirus longipes</i>	Pure tone	Slightly longer to antennular flicks, longer time to emerge from hide, longer to search for food
Morris et al. 2018	Snow crab	<i>Chionoecetes (species not named)</i>	Airguns	No effect on catch rates within days or weeks
Nousek-McGregor and Mei 2016	European hermit crabs	<i>Pagurus bernhardus</i>	Ship, boat	Longer latency of first antipredator response to ship noise, more variable response latency and emergence time in both treatments
Parry and Gason 2006	Rock lobster	<i>Not provided</i>	Airguns	No statistical effect on catch rates

Author	Common name	Scientific name	Noise source	Response
Payne et al. 2008	American lobster	<i>Homarus americanus</i>	Airguns	Increased food consumption, in some cases several weeks post-exposure
Solan et al. 2016	Norwegian lobster	<i>Nephrops norvegicus</i>	Pile-driving, ship, boat	Repressed burying, bioirrigation, locomotion
Spiga 2016	Snapping shrimps	<i>Athanas nitescens</i> <i>Alpheus macrocheles</i> <i>Alpheus glaber</i>	Pile-driving	More snaps and increased amplitude during exposure but not after
Wale et al. 2013	Common shore crab	<i>Carcinus maenas</i>	Ship, boat	Disrupted feeding after first onset, slower retreat into shelter to simulated predator, righted up faster after being turned on back
Walsh et al. 2017	European hermit crab	<i>Pagurus bernhardus</i>	White noise	Took less time to approach, investigate and enter a shell
Zhou et al. 2018	Mud crab	<i>Scylla paramamosain</i>	Linear sweeps	Increased locomotion

Altered feeding patterns in response to anthropogenic noise appear to be a commonality in crustaceans although findings differ in direction. American lobster *H. americanus* displayed increased food intake presumably as a stress response to airguns (Parry and Gason, 2006). A recent field study reports modified feeding competition between common shore crab *Carcinus maenas* and common shrimp *Crangon crangon* under white noise (Hubert et al., 2018). While *C. maenas* dominated the sites in the absence of noise, in its presence, *C. maenas* avoided noisy sites resulting in higher numbers of *C. crangon*. Somewhat contrary to this, Meyer-Rochow et al. (1982) found delayed search for food in rock lobster *Panulirus longipes* under white noise and Wale et al. (2013a) reported disrupted feeding *C. maenas* under ship noise. Missed foraging

opportunities due to noise could result in energetic costs. Increased energetic costs are also likely for more intense communication in snapping shrimp. The animals escalated the amplitude and number of snaps under pile-driving playbacks (Spiga, 2016).

Noise also influences locomotion behaviour. Single and grouped Mediterranean spiny lobster *Palinurus elephas* and common prawn *P. serratus* exposed to ship and boat noise (Filiciotto et al., 2016; Filiciotto et al., 2014) and the mud crab *Scylla paramamosain* exposed to linear sweep tones (Zhou et al., 2018) all increased their locomotion activity under noise. As for disrupted foraging, increased locomotion under noise can cause higher physiological demand. However, increased locomotion is not a unequivocal response as exemplified in two experiments. Norwegian lobster *Nephrops norvegicus* decreased locomotion under pile-driving, ship and boat noise (Solan et al., 2016) and in the semi-terrestrial crab *Neohelice granulata* locomotion was modulated by the sexual maturity Filiciotto et al. (2018). Unreceptive females showed a lower distance and duration moved during exposure to sweep tones whereas receptive females and males moved longer distances but for a shorter duration.

Anthropogenic noise has also been shown to affect predator defence. The European hermit crab *Pagurus bernhardus* increased the latency to withdraw into its shell in response to a dummy predator under ship and boat noise (Nousek-McGregor and Mei, 2016) and shore crab *C. maenas* showed slower response to predator induced event and righted up faster during ship noise playbacks (Wale et al., 2013a). Increased latency in antipredator behaviour can lower the likelihood of survival for prey; presumably a consequence of distraction. Such delayed or distracted response to predators has also been shown for semi-terrestrial crabs exposed to noise in air and thus termed 'distracted prey hypothesis' (Chan et al., 2010a; Chan et al., 2010b).

Somewhat contrary to the studies above, European hermit crabs in suboptimal sized shells approached, investigated and entered empty shells of better fit faster under white noise (Walsh et al., 2017). The authors propose that, since better shells offer better protection against predators, crabs may have perceived noise as a threat from which they wanted to seek better protection as quickly as possible.

Besides solitary animals, noise can alter intraspecific behaviour. Spiny lobster showed suppressed social behaviour under noise (Filiciotto et al., 2014) and crayfish *Procambarus clarkii* reduced agonistic encounters indicated by reduced fights and tail flips under white noise (Celi et al., 2013). In another experiment, lobster took longer to emerge from a hide when exposed to a pure tone, which was set at the same frequency and amplitude to sounds from conspecifics (Meyer-Rochow et al., 1982). In some crustacean species altered behaviour under anthropogenic noise could have ecological consequences. For instance, Norwegian lobster *N. norvegicus* repressed bioirrigation and burying in the presence of pile driving and ship noise both of which are important for nutrient cycling (Solan et al., 2016).

Though research on crustacean behaviour under noise appears to be growing (Filiciotto et al., 2018; Hubert et al., 2018; Morris et al., 2018; Walsh et al., 2017; Zhou et al., 2018) many questions remain unanswered. The main aim of this thesis is to contribute to widen the taxonomic scope in noise research using the European hermit crab *P. bernhardus* as a model organism as well as examining questions of wider biological relevance such as the repeated exposure to noise.

1.3.3 Chronic noise pollution and repeated exposure

Despite being a chronic source of pollution in nature (Haver et al., 2017; Hildebrand, 2009; McDonald et al., 2008; Pijanowski et al., 2011), anthropogenic noise is

predominantly tested for its immediate, short-term effect on animals (Kunc et al., 2016; Morley et al., 2014; Shannon et al., 2016b). Repeated and long-term noise experiments can investigate whether animals learn to cope with anthropogenic stimuli over time for instances by ignoring those stimuli and thus avoiding inappropriate behaviours and potentially maladaptive decisions (Sih et al., 2011; Tuomainen and Candolin, 2011). In its most simple forms, animals learn either as they weaken their response to repeated, disturbing stimuli (= habituation) or, alternatively, as they increase their response (= sensitisation) (Commins, 2018). Habituation can be beneficial if animals ignore irrelevant cues but detrimental if the persistent presence in noisy habitats causes reduced reproductive success as shown in bird communities (Injaian et al., 2018; Kleist et al., 2018). However, experiments on the repeated exposure to anthropogenic noise found contrasting results. For instance, prolonged exposure to motorboat playbacks led to increased offspring mortality in the spiny chromis *Acanthochromis polyacanthus* (Nedelec et al., 2017) but juvenile coral reef fish *Dascyllus trimaculatus* no longer increased hiding times after one and two weeks of exposure (Nedelec et al., 2016b). More experiments on repeated exposure to noise can help to identify more general patterns.

1.3.4 Effects of anthropogenic noise on intraspecific relationships

Large parts of noise research seem to study isolated individuals on single exposure to noise. Such behaviour includes movement, foraging and responses to predators (Bruintjes et al., 2016; Chan et al., 2010b; Luo et al., 2015; Neo et al., 2015; Schaub et al., 2008; Shafiei Sabet et al., 2015; Shafiei Sabet et al., 2016; Siemers and Schaub, 2011; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a; Wisniewska et al., 2018). By comparison, the effects of noise on intraspecific interactions and group

processes have not yet received the same attention. Studies on social behaviour have focussed on the potential masking of acoustic communication (reviewed for different taxa in Brumm and Slabbekoorn, 2005; Clark et al., 2009; Dooling et al., 2015; Erbe et al., 2016). However, many animals interact with conspecifics based on non-vocal social signals and behaviour such as shoaling in fish. Choosing to join groups by assessing the benefits and costs requires animals to gather cues from their environment (reviewed in Krause and Ruxton, 2002). While noise has been shown to alter grouping (Bas et al., 2017; Fewtrell and McCauley, 2012; Filiciotto et al., 2014; Herbert-Read et al., 2017; Neo et al., 2018), its effect appears to be highly variable across study systems and noise regime. For instance, the Mediterranean spiny lobster *P. elephas* (Filiciotto et al., 2014) and bottlenose dolphin *Tursiops truncatus* (Bas et al., 2017) exhibited reduced grouping behaviour when exposed to boat noise. In contrast, noise from a single air-gun led to increased grouping in the trevally *Pseudocaranx dentex* (Fewtrell and McCauley, 2012). Divergent social responses to noise can even be seen within the same species, such as the European sea bass *Dicentrarchus labrax* exposed to different noise source and playback regimes. Fish shoals were less coordinated (in cohesion, direction, speed and directional changes) when exposed to pile-driving (Herbert-Read et al., 2017) but increased grouping activities under ship noise (Neo et al., 2018). Although less intensively studied (compared to aquatic examples), anthropogenic noise can also affect non-vocal social behaviour in terrestrial species. In Carolina chickadees *Poecilie carolinensis* and tufted titmice *Baeolophus bicolor* flocking density was enhanced in the presence of traffic noise (Owens et al., 2012).

In addition to the effects of joining a group, an important consequence of intraspecific interactions is the distribution of resources. Resource distribution is

frequently thought to result from competition over the ownership of limited and indivisible resource units (Briffa and Hardy, 2013a; Briffa and Hardy, 2013b). However, when a resource within population is reusable, such as gastropod shells in hermit crab populations, an alternative resource distribution processes can take place known as vacancy chains (Chase, 1991; Chase and DeWitt, 1988; Weissburg et al., 1991). In vacancy chains the abandonment of a resource unit like a shell frees that resource for the conspecifics in the population. If the arrival of one new resource unit prompts one individual to accept the new resource, it will vacate its previously occupied resource and thereby can initiate the redistribution of resource within a population. To the best of my knowledge such population level effects of noise on crustaceans remain to be explored.

1.3.5 Behavioural and physiological effects of anthropogenic noise

Since behaviour and physiology have been shown to correlate when coping with environmental challenges and stress (reviewed by Koolhaas et al., 2011), investigating both in conjunction can provide a more complete insight into the impacts of noise and its proximate consequences (Halfwerk and Slabbekoorn, 2015). Anthropogenic noise has been shown to alter a variety of proximate mechanisms that underpin behaviour (Kight and Swaddle, 2011) ranging from altered genes and cells, damages of the auditory system (André et al., 2011; Guerra et al., 2011; McCauley and Fewtrell, 2008; Solé et al., 2013), endocrine changes and biochemical stress responses (Anderson et al., 2011; Blickley et al., 2012b; Buscaino et al., 2010; Crino et al., 2013; Filiciotto et al., 2018; Rolland et al., 2012; Smith et al., 2004; Wysocki et al., 2006), altered oxygen demand (Bruitjens et al., 2016; Dunlop et al., 2017; Harding et al., 2018; Isojunno et al.,

2018; Purser et al., 2016; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a), delayed development (Aguilar de Soto et al., 2013; Nedelec et al., 2014; Nedelec et al., 2015; Pine et al., 2012) and reduced survival and recruitment (Blas et al., 2007; Ferrari et al., 2018; MacDougall-Shackleton et al., 2009; Nedelec et al., 2017; Nedelec et al., 2014). However, few experiments have tested the possibility that behavioural and physiological responses to noise correlate (Buscaino et al., 2010; Injaian et al., 2018) or at least co-occur (Anderson et al., 2011; Blickley et al., 2012b; Celi et al., 2013; Day et al., 2017; Filiciotto et al., 2018; Filiciotto et al., 2016; Filiciotto et al., 2014; Simpson et al., 2015).

As pointed out above, changes to metabolic rate are indicative of a stress response to anthropogenic noise and the oxygen consumption one of the most widely measured physiological traits (Pettersen et al., 2018) allowing us to measure the direct physiological costs of anthropogenic noise. An alternative and seemingly less well studied aspect of anthropogenic noise is that behavioural responses under noise can cause subsequent physiological costs after the immediate exposure. For instance, noise can reduce foraging performance and efficiency (Purser and Radford, 2011; Shannon et al., 2014; Siemers and Schaub, 2011; Wale et al., 2013a) which will in all likelihood be energetically costly. In hermit crabs, the ultimate costs of decisions made under noise can be assessed by the fit of the occupied shell since shells which are too large can be energetically costly to carry and conversely, shells which are too small do not provide optimal protection against predators and environmental extremes (Taylor, 1981; Vance, 1972). Indeed, decisions about shell occupation under noise could be physiologically costly such as indicated by the oxygen consumption which allows us to quantify the costs of decisions made under noise.

1.3.6 Effects of anthropogenic noise in the field

A 'reductive' approach in the laboratory whereby all variables except the ones of interest can be kept constant facilitates isolation of the effects of anthropogenic noise from other presumably confounding factors and identification of effects that could otherwise be masked. However, sounds in small tanks can be highly distorted by reverberations of tank walls that trigger stronger particle motion than in natural settings under the same sound pressure level (Akamatsu et al., 2002; Slabbekoorn, 2016). The particle motion component of sound is particularly important to crustaceans making field studies a desirable step forward to assess the effects of anthropogenic noise under more natural sound conditions. While there is a growing number of noise exposure experiments under more natural sound conditions in semi-controlled and field settings (Harding et al., 2018; Maxwell et al., 2018; McCormick et al., 2018; Nedelec et al., 2017; Nedelec et al., 2014; Neo et al., 2016; Radford et al., 2016a), to the best of my knowledge there is only one study in which the behaviour of adult crustaceans under noise has been tested in the field (Hubert et al., 2018).

1.4 The model organism European hermit crab *Pagurus bernhardus*

Hermit crabs are a globally abundant decapod crustaceans inhabiting shallow coastal waters as well as the deep sea from the poles to the tropics (Balazy et al., 2015; Kim and Barry, 2016). The European hermit crab *P. bernhardus* is one of the most common crustacean species at the European coast and can be found at the rocky intertidal shore of the UK and Ireland. Common characteristics of hermit crabs are their calcified carapace covering the cephalothorax and the soft, weakly calcified abdomen. Hermit

crabs rely on gastropod shells for protection against predators (Vance, 1972) and environmental extremes (Taylor, 1981; Young, 1978). Furthermore, the optimal shell allows for growth (Angel, 2000) and reproduction as females carry their eggs inside the shells (Bertness, 1981a). Small shells can inhibit growth, reproductive success and exposes crabs to predators since they cannot fully withdraw into their shelter. On the other hand, shells that are too large impose energetic costs for carrying unnecessary weight (Elwood and Neil, 1992).

While hermit crabs prefer any empty gastropod shell over none, crabs can have distinct shell preferences such as concerning quality, species and size. Usually hermit crabs obtain gastropod shells either when discarded by others or through shell fights with other crabs (snail predation is rare) (Elwood and Neil, 1992). The motivation of crabs to search for shells or to engage in shell fights depends on the quality of the occupied shell such as regarding size and species. Hermit crab behaviour has been extensively studied shell assessment and motivational changes (Briffa and Elwood, 2001; Elwood, 1995), crypsis (Briffa and Twyman, 2011), aggression (Briffa and Elwood, 2000a; Briffa and Elwood, 2000c; Briffa and Elwood, 2004; Briffa and Elwood, 2007; Briffa et al., 1998), and inter-individual behavioural plasticity and consistency (Briffa, 2013a; Briffa et al., 2013; Briffa et al., 2008b; Velasque Borges, 2017) in solitary and group situations (Briffa, 2013a; Briffa and Austin, 2009; Edquist and Rotjan, 2012; Rotjan et al., 2004). Moreover, hermit crabs vary their behaviour in response to various biotic (predation risk: Briffa, 2013b; Briffa and Austin, 2009; shell fit: Briffa and Bibost, 2009; crypticity of the shells: Briffa and Twyman, 2011), abiotic (temperature: Briffa et al., 2013; oxygen level: Briffa and Elwood, 2000b) and anthropogenic (copper pollution: White and Briffa, 2017) factors. Taken together, that body of research

provides a comprehensive behavioural baseline against which to examine in the effect of anthropogenic noise on these crustaceans.

Shell assessment and decision-making processes in hermit crabs can be readily probed, distinguished by their assessment steps (rather than only behavioural outcomes, see Table 1-3) and quantified (Elwood, 1995). Motivational models have been developed to investigate relatively complex activities such as shell assessment, where the size of the occupied shell is linked to motivation to assess and choose shells and engage in agonistic contests (Elwood and Neil, 1992). For instance, hermit crabs have an optimal or preferred shell weight (% PSW), and for a given size of crab the optimal shell size can be estimated from regression equations that relate preferred shell weight to the crab's body weight, obtained from various shell selection experiments (Briffa et al., 2013; Dowds and Elwood, 1983). Based on the % PSW, crabs occupying smaller shells have a larger motivation to assess new shells compared to crabs in better fitting shells. Since the behaviour of hermit crabs can be manipulated easily for instance by manipulation the occupied shell, this model organism allows to add biological complexity to investigating the effects of anthropogenic noise on crustaceans.

Table 1-3 Ethogram of shell assessment activities of *P. bernhardus* (based on Elwood and Neil, 1992)

Behavioural measurement and description

Antennae contact

- Contacts the new shell with at least one antenna
- Usually this is the first contact with the new shell

External shell assessment

- Contacts the exterior of the new shell usually with at least one chelipeds and moves it over the surface
- Uses sometimes also the walking legs and antennae at the same time
- Grasps the new shells and moves chelipeds over the surface
- May hold the new shell (on its aperture) without moving which it often does before and after inserting chelipeds or walking legs into the aperture or turning shell

Turning the shell

- Turns the new shell, often done before/ in between inserting chelipeds and/ or walking legs into the interior of the shell
- Does it more often when the aperture is blocked

Internal shell assessment

- Inserts at least one cheliped and sometimes also walking leg into the new shell
- Can alternate external and internal assessment of the new shell

Entering the new shell

- Grabs new shell, releases the grip on the old shell and swings abdomen out of the occupied shell and swings it over into the new shell
- Exposes its abdomen

Shell assessment after entering the new shell

- Holds onto the old shell and repeats same shell assessment steps as for the new shell
- Withdraws into the new shell
- Swings the new shell of the substrate
- Runs the walking legs over the exterior of the new shell

Swapping back into the old shell

- Grabs old shell & swings back
 - Exposes its abdomen
 - Potentially holds onto the just vacated new shell and assesses it again
-

1.5 Thesis aims and outline

Using the European hermit crab *Pagurus bernhardus* as a model system, this thesis aims to investigate the impacts of anthropogenic noise on crustaceans from individual behaviour to group level. By incorporating naturally occurring factors such as resource

quality, predator cue and the social environment in the laboratory as well as conducting in a field study, I aim to build a rounded picture on the effects of noise on crustaceans. Furthermore, I employ different noise regimes such as single and repeated exposure to noise (over 10 days), short-term and prolonged, continuous exposure (over 24 h). Since hermit crabs primarily rely on chemical, tactile and visual cues rather than acoustic ones, this work will also contribute to understanding better the effects of noise across sensory modalities.

Specifically, I begin by observing hermit crabs in their shell assessment behaviour over 10 days while exposing them to ambient sound and ship noise (chapter 2). By repeating the exposure to noise and alternating the sound treatment order, I can examine if crabs habituate or sensitise to noise. In addition, as the ship noise will be of similar amplitude to the ambient sound, I can investigate if other characteristics than amplitude influence hermit crabs. In chapter 3, I identify if high intensity ship noise affects shell assessment and decision-making and if noise effects are modulated by naturally occurring stimuli i.e. a visual predator cue and the size of the occupied shell. In chapter 4, I ask whether hermit crabs prefer to group (with single conspecific or group of five conspecifics) or not and if the group preferences are influenced by the size of the occupied shell and ship noise. Next, I study the effects of anthropogenic noise on resource distribution in groups via vacancy chains allowing us to examine group level impacts of noise (chapter 5). Moreover, observing vacancy chains after 1 h and 24 h will give an insight into how the prolonged and continuous exposure to anthropogenic noise affects animals. In addition to the behavioural experiment, I will also measure oxygen consumption after 24 h of group process and noise exposure (chapter 6). Since hermit crabs will have gained their occupied shell from the group

process in the preceding experiment, I can quantify the costs of on decision-making in grouped animals under noise. Finally, I conduct a field experiment in Galway Bay, Ireland, on the startle response of hermit crabs (the re-emergence from the shell after withdrawing) over two days of exposure to ship noise and ambient control allowing to measure whether the behaviour is repeatable and affected by noise (chapter 7).

The following data chapters were created in collaboration with those mentioned in the 'Authors declaration' section of this thesis. I use the term "we" throughout the data chapters as per publication standard practice and for consistency. It is not intended to suggest that any part of this thesis is not my own.

Chapter 2: Effects of repeated exposure to anthropogenic noise on resource assessment

2.1 Abstract

The use of information from environmental cues and signals is crucial for decision-making of animals. However, anthropogenic pollution can interfere with information gathering and processing by altering the sensory ecology of animals. One of those examples is anthropogenic noise which has become a chronic source of pollution. Despite noise being chronic, experiments often examine effects of short, single exposures. Furthermore, studies which test noise properties beyond its intensity seem to be rare. We measure the effects of 10 days repeated exposure to sound on shell assessment behaviour and decision-making in the European hermit crab *Pagurus bernhardus*. By manipulating the ambient sound and the ship noise treatments to be played back at similar intensities, we can investigate whether other noise properties influence hermit crabs. Crabs are known to have a preferred shell weight based on their own weight. Crabs occupied shells of different quality (50%/ 80% of the optimal size) and were given an optimal shell leading to four treatment groups (sound treatment * occupied shell). To stop crabs from entering shells, the shells apertures were physically blocked internally, except for the last day of the experiment. We found that shell assessment was repeatable across sound and shell treatments. The sound treatment had no effect on the assessment behaviour except on the last day of the experiment. When shells were unblocked so that crabs could enter them, individuals under noise showed longer latency to assess the shell. Crabs in small shells under ship noise accepted the shell more frequently than crabs under ambient sound. The pattern

was reversed for crabs in larger shells. These findings suggest that noise properties beyond intensity affect animals in their information gathering and assessment under noise.

2.2 Introduction

Animals use and produce cues and signals across a broad range of modalities to make decisions (Blumstein and Munoz, 2012; Partan and Marler, 1999). However, anthropogenic pollution can alter the natural sensory ecology of wild animals exposing them to novel stimuli at an evolutionarily unprecedented pace (Palumbi, 2001; Sih et al., 2011). Urban development, the extraction of resources and extensive global transportation networks have changed the soundscapes of terrestrial and aquatic ecosystems making anthropogenic noise a pervasive source of pollution to humans and other animals (Haver et al., 2017; Hildebrand, 2009; McDonald et al., 2008; Pijanowski et al., 2011). Though populations can adapt to new environments (Ghalambor et al., 2007) and thus presumably to human-induced rapid environmental change (HIREC; Sih et al., 2011), the initial response is thought to be behavioural (Tuomainen and Candolin, 2011). Studying how animals encounter, detect and respond to anthropogenic stimuli can enable us to understand and eventually predict how anthropogenic pollution like noise impacts animals (Sih et al., 2011).

While carefully manipulated experiments ensure that animals will encounter the anthropogenic cue, cue detection is species specific and influenced by the sound properties such as frequency composition, sound intensity or the temporal and spatial features (Bradbury and Vehrencamp, 2011; Gill et al., 2014; Sih et al., 2011). Research on anthropogenic noise has examined in detail the role of frequency and intensity on how animals respond to noise but other properties such as the temporal structure

appear to be rare (Gill et al., 2014; but see for exception Neo et al., 2016; Neo et al., 2014; Shafiei Sabet et al., 2015). The temporal structure of sound can vary for instance regarding its intensity onset (slow/ sudden), consistency (continuous/ intermittent) and regularity (consistent or random length of interval in the same amplitude) (Neo et al., 2016; Neo et al., 2014). For instance, sound amplitude may be consistent (such as noise from motors) or fluctuate over time with high intensity peaks which dissipate with time (such as from pile-driving and seismic airguns). Alternatively, the amplitude might be consistent over time but can be continuous without silent periods or with intermittent quiet periods (for a graphic display and comparison see Figure 2-1 from Neo et al., 2014).

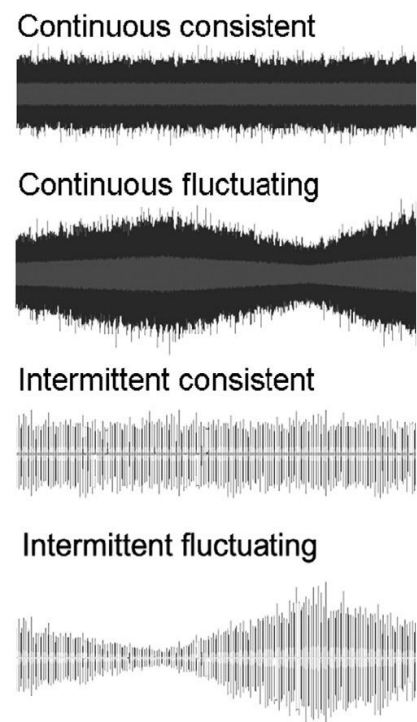


Figure 2-1 Different temporal patterns of sound treatments (figure taken from Neo et al., 2014)

Behavioural changes to noise can be linked to physiological stress responses whereby stress can be the proximate mechanisms for observed behavioural changes. Since the stress response of animals to stimuli is highly linked to its predictability and controllability (Koolhaas et al., 2011), the temporal structure of a sound stimulus could influence the effects of anthropogenic noise on animals. Accordingly, some studies compared the effects of anthropogenic noise sources with different temporal patterns such as the consistency or intermittency of noisy and quiet periods. For instance, giant kelpfish *Heterostichus rostratus* exposed to random intermittent noise had higher cortisol concentrations than fish exposed to continuous noise (Nichols et al., 2015).

Similarly, Radford et al. (2016a) report that European seabass *Dicentrarchus labrax* reacted more strongly to intermittent, impulsive noise from pile-driving and airguns than to the more continuous noise from ships (but see Nedelec et al., 2015 for the opposite result). Similar results have been found in other, non-aquatic, habitats. greater sage-grouse *Centrocercus urophasianus*, for instance, attended lekking sites exposed to relatively continuous noise from natural gas drilling more frequently than sites exposed to intermittent road noise (Blickley et al., 2012b). Another approach is to observe responses to artificially generated noise such as white noise and noise from an anthropogenic source. White noise is characterised by equal energy intensity across frequencies (Barber et al., 2010) whereas vessels such as ships produce unique acoustic signals depending on factors like speed and load (Hildebrand, 2009). Consequently, ships are likely to produce more unpredictable sounds to animals than artificial white noise. The few studies that compared artificial white noise and anthropogenic noise indicate that anthropogenic noise tends to be similarly (Bermúdez-Cuamatzin et al., 2018) if not more behaviourally distractive than artificial white noise (Bent et al., 2018; Holles et al., 2013). For instance, more coral reef fish larvae moved away from the reef in the presence of boat playbacks compared to natural reef sound but no significant response was found during white noise (Holles et al., 2013). Similarly to the coral reef fish, female field cricket *Gryllus bimaculatus* spent less time attending to male calls under road noise whereas white noise had no effect on female behaviour (Bent et al., 2018). These examples indicate that the two noise stimuli, which are similar in frequency and amplitude, can nevertheless elicit different behavioural responses and thus act as different cues for animals. Understanding which sound features alter behaviour could help to better manage anthropogenic noise.

Another temporal effect of anthropogenic noise relates to the exposure duration. In nature, animals are often chronically exposed to noise, yet in experiments they are predominantly tested in their immediate, short-term response to noise (Kunc et al., 2016; Morley et al., 2014; Shannon et al., 2016b). Repeated and long-term exposure to noise can test whether animals can cope with anthropogenic stimuli over time such as by ignoring or escaping them and thus avoid inappropriate and potentially maladaptive behaviours (Sih et al., 2011; Tuomainen and Candolin, 2011). In its most simple forms, animals learn by habituating to a repeated disturbance stimulus (i.e. they show reduced responsiveness) or, alternatively, sensitising (i.e. increased responsiveness) (Commins, 2018). Habituation can be beneficial if animals ignore irrelevant cues but detrimental if a stimulus has negative fitness consequence such as reduced reproductive success in noisy habitats (Injaian et al., 2018; Kleist et al., 2018). Experiments on repeated exposure to anthropogenic noise yield contrasting results. In the spiny chromis *Acanthochromis polyacanthus* 12 days of repeated boat noise led to increased offspring mortality presumably as males got distracted in their brood guarding either by chasing fish that were not predators or threatening predatory fish less efficiently (Nedelec et al., 2017). Males of the Greater sage grouse *C. urophasianus* avoided noisy but otherwise suitable leks when exposed to natural gas drilling and road noise and continued to do so in the following years (Blickley et al., 2012b). Juvenile coral reef fish *Dascyllus trimaculatus* increasingly hid as an initial response to boat noise but this response disappeared over two weeks of exposure (Nedelec et al., 2016b) indicating that the fish first sensitised and then habituated to noise.

Although behaviour is a plastic trait that enables learning and adjusting the immediate behaviour to fluctuating stimuli from the environment such as

anthropogenic noise, behavioural plasticity is also subject to constraints (Sih et al., 2004). Typically, any individual will display a subset of the full behavioural range present at the population level. The resultant consistent among individual differences in behaviour across time are usually described as repeatability or animal personality (Bell et al., 2009; Briffa, 2017; Dall et al., 2004; Dingemanse and Réale, 2005; Réale et al., 2010). Repeatability, which provides an effect size estimate, expresses the proportion of total behavioural variance that is due to differences between individuals (V_{BI}) in addition to behavioural variance that is due to differences within the individual (V_{WI}) (Nakagawa and Schielzeth, 2010):

$$R = V_{BI} / V_{WI} + V_{BI}$$

A number of explanations have been put forward for this type of phenotypic variation. A key hypothesis is that such phenotypic variation may represent adaptive constraints around a mean way of behaving, allowing individuals to behave with 'approximate appropriateness'. Fully appropriate behaviour in unpredictable environments requires reliable information. To detect and process this information, animals need a sufficiently complex sensory-cognitive system that has become adapted to their environment (Shettleworth, 2010). In addition, individual animals have to trade-off the investment of time, energy and attention for information assessment and decision-making to reduce the uncertainty arising from uncontrollable and unpredictable environments against other benefits such as growth and reproduction (Dall, 2010). Besides the constraints that result from the balancing of those costs and benefits, appropriate behaviour is also limited by inevitable mistakes during information gathering and processing (Dall, 2010; Shettleworth, 2010). Given the costs and limits of behavioural plasticity, it is unsurprising that individuals instead

behave in consistent ways ultimately leading to consistent inter-individual differences in behaviour. As a result, although there can be a broad behavioural range at the population level, a given genotype may only display a narrow subset of the population level phenotypic variance, in this context equating to a limited behavioural diversity so that animals within a population show consistent inter-individual differences in behaviour. To predict the response of animals to chronic anthropogenic noise we can therefore expect both behavioural plasticity as well as changes to the degree of repeatability expressed across time.

In order to study the effects of repeated exposure to noise, we observed the European hermit crab *Pagurus bernhardus* for 10 days under ship noise and ambient sound as a control. Noise effects on shell assessment in *P. bernhardus* have been reported under high intensity white noise (Walsh et al., 2017). Here, ambient sound and ship noise are of similar low intensity allowing us to test if other properties beyond the amplitude (such as their temporal structure) affect hermit crabs in their shell assessment. Hermit crabs protect their weakly calcified abdomen by occupying empty gastropod shells and under normal circumstances latency and duration to assess shells is related to the potential shell gain i.e. the size of the occupied shell compared to the optimal shell weight. Since the optimal, preferred shell weight in *P. bernhardus* is correlated with its own body weight (Briffa and Elwood, 2007), the manipulation of the occupied shell allows us to also test whether noise effects depend the quality of the shell. Thus, we can compare the strength of anthropogenic noise with the one of the naturally occurring variable of shell optimality. We predict that hermit crabs in small shells will show shorter latency to assess the optimal shell and will allocate more time to shell assessment than individuals in larger shells. If the time exposed to noise affects

behaviour, we would expect the assessment duration to change with day of observation. On the last day of the experiment, hermit crabs will be able to enter the optimal shell and we expect that more crabs in smaller shells will accept the optimal shell than crabs in larger shells. However, if noise distracts hermit crabs from shell assessment, this pattern should be altered in the presence of noise.

2.3 Methods

2.3.1 Collection and husbandry of hermit crabs

We collected *P. bernhardus* from the rocky intertidal of Hannafore Point, Cornwall, UK (50° 20' 42'' N, 4° 28' 0'' W) between February and May 2016 and transported the animals directly to temperature controlled room at the University of Plymouth, UK. The room was set at 15 °C with a 12:12 h light:dark cycle and crabs were kept in a single holding tank containing 125 l of continuously filtered and aerated seawater (Briffa and Elwood, 2007). The seawater for the laboratory supply was obtained from the seaward side of Mount Batten pier (50° 21' 34'' N, 4° 8' 8'' W) in Plymouth Sound, UK, at spring tides. We fed crabs *ad libitum* with white fish. At least 22 hours before the observation, crabs were carefully removed from their shell with a bench vice, sexed and weighed. Crab weight ranged from 0.27 to 1.35 g (mean weight \pm SE = 0.72 \pm 0.022 g; $N = 18$). Each crab was assigned a *Littorina littorea* shell of 50% or 80% of its preferred shell weight based on a regression line relating preferred shell weight (PSW) to body weight obtained from previous shell selection experiments (Briffa and Elwood, 2007; Dowds and Elwood, 1983). Crabs were individually housed in white plastic dish of 15 cm diameter containing continuously aerated seawater to a depth of 5 cm and kept in a 15 °C temperature controlled room. Since the breeding season is likely to affect the behaviour of egg-carrying females, only male crabs without damaged

appendages, visible parasites or recent moulting were included in the study (Briffa and Elwood, 2007). After the observations the animals were given an optimal shell and brought back to the collection point.

2.3.2 Tank set-up and sound analysis

The observations were conducted in a tank (65 x 40 x 30 cm) filled up to 20 cm with seawater (~ 52 l). The tank was placed on a trolley in the middle of the room to avoid vibration from the walls (Figure 2-2). The trolley was cushioned with a foam mat (1 cm thick) and the tank with pipe insulation (2 cm diameter). The speaker was submerged from a bar cushioned with a 2 cm thick pipe insulation at 5 cm distance to the tank wall facing towards the observation arenas. The observation arenas for the hermit crabs (plastic dish of 15 cm) were glued to the bottom of the tank at 40 cm distance to the speaker measured from the centre of the arenas.

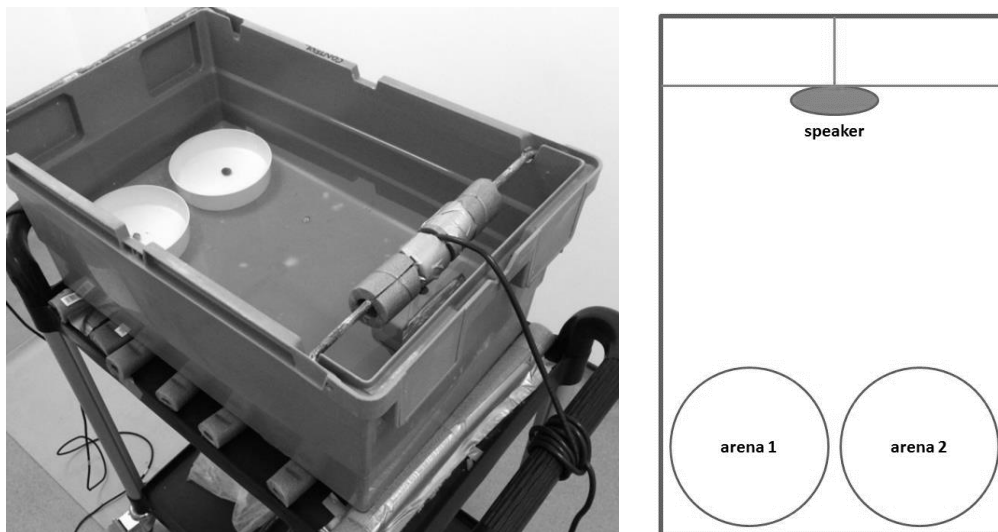


Figure 2-2 Tank set-up and observation arena. Left: The cushioned tank sits on a cushioned trolley. The speaker is submerged from a cushioned bar. Right: Two observation arena opposite to the speaker at 40 cm distance. The empty shells were placed in centres of the arenas.

For the sound set-up, we used an underwater speaker (DNH Aqua-30 underwater speaker, effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway) connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping Town, China). We played back the sound tracks from a Toshiba Portégé R830-13C laptop (Tokyo, Japan). For the sound treatment, we used three ship noise playbacks and three corresponding ambient sounds from the same sites recorded at three major UK harbours (for details on recordings such as ship size and speed see Simpson et al., 2015; Wale et al., 2013a). We used Audacity 2.1.2 (Audacity Team, 2016) to create a total of six audio tracks. In case of the ship noise tracks, we alternated 2 min of ship noise with 2 min of ambient sound including 15 s fading in and out to simulate noise of passing by ships.

While hearing in a narrowly defined sense to detect sound pressure is unlikely in crustaceans (they lack an air-filled chamber to detect changes in pressure), sound detection of particle motion has been widely demonstrated in Decapoda (Breithaupt, 2002; Breithaupt and Tautz, 1990; Budelmann, 1992; Goodall et al., 1990; Hawkins et al., 2015). Auditory thresholds i.e. frequency range and sound intensity can be retrieved using electrophysiological techniques. Lovell et al. (2005) used this technique for the first time for an invertebrate (where two subcutaneous electrodes were positioned in the carapace close to the supraesophageal ganglion and the statocyst), demonstrating that the common prawn *Palaemon serratus* can detect sounds in the frequency range of 100 – 3 000 Hz measured at sound pressure levels from 105 – 132 dB re 1 μ Pa at 1 m. Since there is no similar study for *P. bernhardus* we conducted the sound pressure analysis for this frequency range.

In line with previous noise exposure studies in the laboratory (Herbert-Read et al., 2017; Simpson et al., 2015; Wale et al., 2013a), we analysed the power spectrum of the sound pressure to confirm that we exposed crabs to two distinctive sound conditions, namely ship noise and ambient sound. We are aware of the unresolved challenges of tank acoustics (Rogers et al., 2016; Simpson et al., 2015). In nature, the relationship between sound pressure and particle motion is complex in the nearfield of a sound source and even more so in small tanks where reflecting objects or surfaces change this ratio particularly close to the sound source (Akamatsu et al., 2002; Tasker et al., 2010). Thus, the spectral analysis in the pressure domain of the sound treatment does not allow us to infer exactly what *P. bernhardus* perceived and we do not attempt to establish absolute noise sensitivity levels for hermit crabs. However, measuring the power spectrum in the pressure domain allows us to assess the sound intensity of the two sound treatments for our experiment.

For the power spectrum analysis, we re-recorded the six audio tracks at the centre of the observation arena at 40 cm distance to the speaker (where the crabs were placed at the beginning of the experiment) at 1 – 2 cm distance to the bottom of the arena with an omnidirectional hydrophone HTI-96-MIN (with inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V μ Pa; frequency range 0.002 – 30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave signals from a function generator with a measured voltage recorded in line on an oscilloscope). We analysed the sound power spectrum similar to Simpson et al. (2015) with the Fast Fourier Transform (FFT) analysis of sound between 1 – 3 000 Hz using Avisoft-SASLab Pro version 5.2 (Avisoft Bioacoustics, 2016). The spectrum level

units were normalised to 1 Hz bandwidth and we applied Hann evaluation window, 50% overlap, FFT size 1024, averaged from a 60 s sample of each recording (Figure 2-3; Figure 2-4; Table 2-1; Table 2-2).

The three original ambient sound tracks had an average sound pressure level of 43.86 dB RMS re 1 μ Pa (ambient A: 40.91, ambient B: 46.38, ambient C: 44.29) and the original ship noise sound tracks an average of 90.62 dB RMS re 1 μ Pa (ship A: 89.53, ship B: 90.81, ship C: 91.50) across the frequency bandwidth 1 – 3 000 Hz (Figure 2-3; Figure 2-4). The playbacks of the ambient sound re-recorded in the tank had an average sound pressure level of 50.53 dB RMS re 1 μ Pa (ambient A: 50.25, ambient B: 52.43, ambient C: 48.91) and the ship noise an average of 52.85 dB RMS re 1 μ Pa (ship A: 48.65, ship B: 60.45, ship C: 49.46) across the frequency bandwidth 1 – 3 000 Hz (Figure 2-4). Therewith, the sound tracks were played back so that they had a similar average intensity.

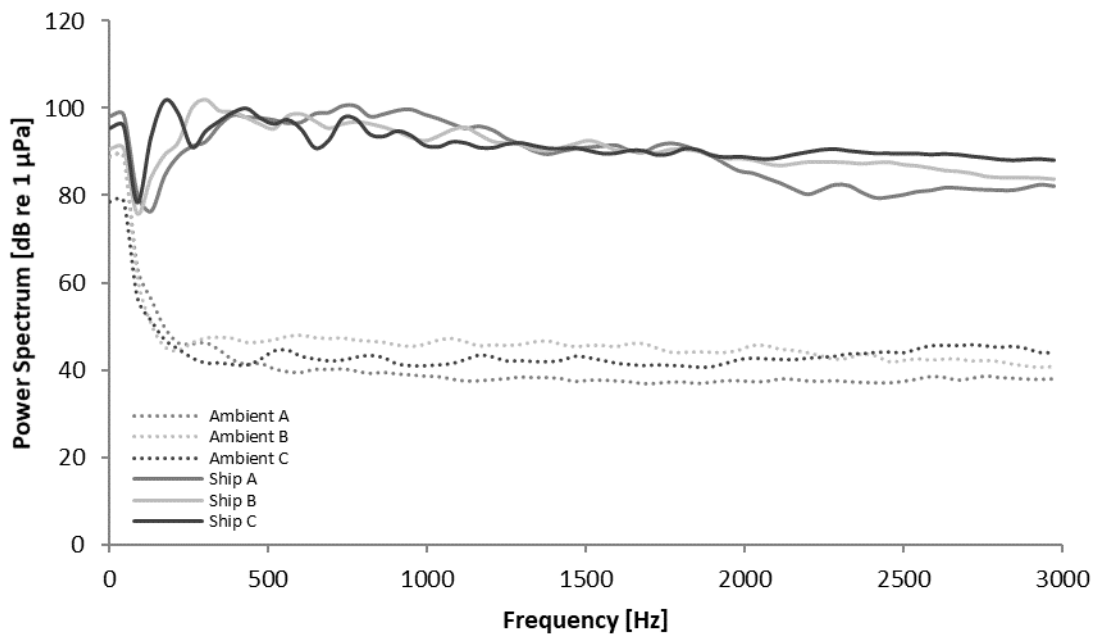


Figure 2-3 Power spectrum of the six original sound tracks (ambient control sound A, B, C; ship noise A, B, C). Filtered for 1 – 3 000 Hz frequency bandwidth.

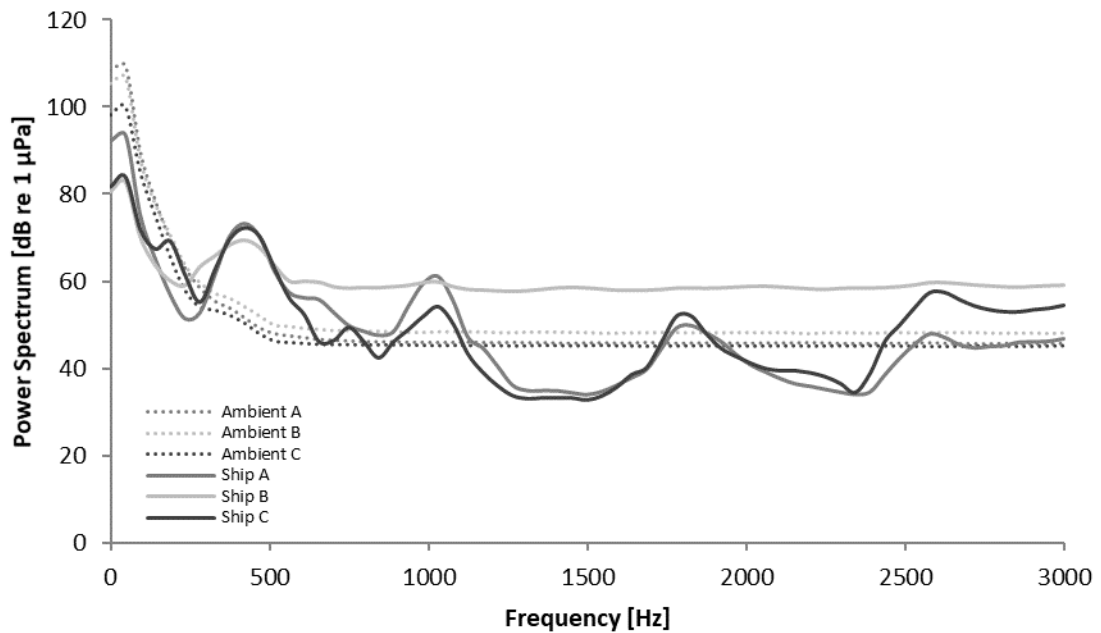


Figure 2-4 Power spectrum of the six playbacks (ambient control sound A, B, C; ship noise A, B, C) recorded in the centre of the arena at 40 cm distance to the speaker. Filtered for 1 – 3 000 Hz frequency bandwidth.

Table 2-1 Sound intensities of the six original sound tracks: Minimum amplitude, maximum amplitude, average amplitude across 1 – 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa.

Sound track	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1 000 Hz
Ambient recording A	36.86 at 1679.59 Hz	88.93 at 43.07 Hz	40.91	38.62
Ambient recording B	40.54 at 2928.52 Hz	89.06 at 43.07 Hz	46.38	45.78
Ambient recording C	40.74 at 1851.86 Hz	78.67 at 43.07 Hz	44.29	41.03
Ship noise recording A	76.32 at 129.20 Hz	100.54 at 732.13 Hz	89.53	98.56
Ship noise recording B	75.93 at 86.13 Hz	101.99 at 301.46 Hz	90.81	92.60
Ship noise recording C	78.26 at 86.13 Hz	101.64 at 172.27 Hz	91.50	91.40

Table 2-2 Sound intensities of the six playbacks: Minimum amplitude, maximum amplitude, average amplitude across 1 – 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa at 40 cm distance to the speaker.

Playback	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1 000 Hz
Ambient playback A	45.58 at 2765.63 Hz	109.33 at 46.88 Hz	50.25	45.92
Ambient playback B	48.09 at 2203.13 Hz	106.81 at 46.88 Hz	52.43	48.38
Ambient playback C	44.96 at 2578.13 Hz	99.90 at 46.88 Hz	48.91	45.23
Ship noise playback A	34.10 at 1500.00 Hz	93.52 at 46.88 Hz	48.65	59.52
Ship noise playback B	57.75 at 1265.63 Hz	82.70 at 46.88 Hz	60.45	59.75
Ship noise playback C	32.74 at 1500.00 Hz	84.03 at 46.88 Hz	49.46	51.97

To investigate whether the two sound treatments (ambient sound/ ship noise) differed in other properties such as the temporal structure we visualised all six sound tracks (Figure 2-5) in Audacity 2.1.2 (Audacity Team, 2016). The visual inspection shows that both sound treatments are continuous but differ in their regularity. While the temporal pattern of the ambient sound appears to be regular, the ship noise seem irregular. Ships produce unique acoustic signals depending on factors such as speed and load (Hildebrand, 2009) and their associated noise is characterised by repeated intervals with sharp tonal pulses (Hatch and Wright, 2007; Hildebrand, 2009). Compared to the ambient sounds, the ship noises appear to be temporarily intermittent with pulses of higher amplitude interchanged with phases of relatively low amplitude and thus represent a temporally more irregular stimulus. In addition, the ships also differed among each other.

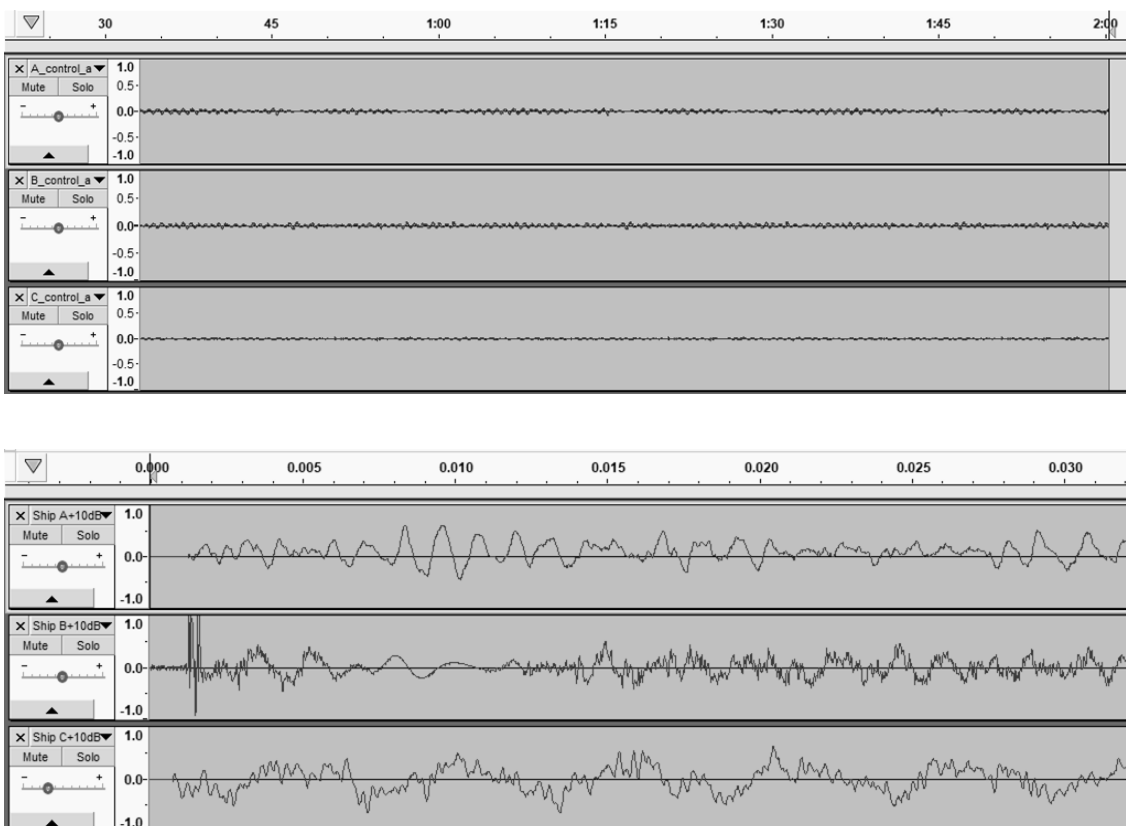


Figure 2-5 Temporal pattern of the three original ambient control sound tracks A – C (top) and the three original ship noise sound tracks A – C (bottom).

2.3.3 Experimental design and behavioural analysis

We designed a fully orthogonal experiment to test the effect of sound treatment (ambient sound/ ship noise) and occupied shell size (50%/ 80% PSW) on repeated shell assessment behaviour in *P. bernhardus*. The combination of these two factors led to four treatment groups and we collected data over 10 observation days (Table 2-3): 5 observations over 5 days of the same individuals in the same sound treatment (observation days 1 – 5), 2 days of break and another 5 observations over 5 days (observation days 6 – 10) in which the crabs were exposed to the opposite sound treatment compared to days 1 – 5 (i.e. a crossover design was used). Crabs were randomly assigned to either of the four treatment group.

Table 2-3 Experimental design and sample size in each treatment group. Factors and their interaction: Sound treatment order, occupied shell and day of observation.

Sound treatment order	Occupied shell	Day of observation										
		1	2	3	4	5	Break	6	7	8	9	10
Ambient control + ship noise	50%	A	A	A	A	A		N	N	N	N	N
Ship noise + ambient control	50%	N	N	N	N	N		A	A	A	A	A
Ambient control + ship noise	80%	A	A	A	A	A		N	N	N	N	N
Ship noise + ambient control	80%	N	N	N	N	N		A	A	A	A	A
	<i>n</i> =	15	13	15	18	16		18	17	18	16	16

On each observation day we collected data in all four treatment groups. We observed two individuals concurrently with each crab in a separate arena so that they were unable to interact with one another. To avoid the effect of shell size being confounded by time of day, we always observed concurrently a crab starting the observation in 50% and 80% adequate shell. To avoid confounding the data through any directional bias the position (left or right arena) we alternated the two shell size treatments between arenas across consecutive observations. To reduce the handling

stress for hermit crabs, each individual received a shell of a 100% PSW, which was blocked internally with modelling clay. That allowed us to observe the shell assessment behaviour without having to remove the crabs from the shell each time they would swap into the optimal sized shell. On the last observation day, day 10, crabs were given an unblocked optimal shell of 100% PSW to quantify their shell assessment choice.

The crabs were video recorded for 20 min with a Canon Legria HF R47 (Tokyo, Japan) and their behaviour was coded blind to the sound treatment and the occupied shell size, with the event logger software The Observer version 12 (Noldus IT, Wageningen, The Netherlands). Before the start of the observation we placed the blocked shell of 100% PSW in the middle of the arena with the aperture facing downwards. Once the sound playback was switched on, we placed the focal crab in their allocated arenas with the aperture of the gastropod shells facing upwards. The observation started when the crab had emerged from its shell and placed at least one of its appendages on the bottom of the tank. For all behaviours we measured the latency and duration in s.

The coding included the following mutually exclusive and exhaustive state responses for days 1 – 9 (based on Elwood and Neil, 1992): (1) first contact with the optimal shell (since crabs do not always have clear antennal contact), (2) contact with the optimal shell with the antennae, (3) assessment of the external shell, (4) turning the shell, (5) assessment of the internal shell, (6) sum of the total assessment duration and (7) other behaviour. On the last day 10, when the new optimal shell of a 100% PSW was unblocked so that crabs could enter shells, we also measured the latency and duration of crabs to (8) enter the optimal shell, (9) assess the previously occupied shell after entering the optimal shell, (10) swap back into the previously occupied shell and

(11) total decision time for crabs to accept or reject the optimal shell. The final decision was made either when the crab entered the optimal shell and moved at least as far away from the previously occupied shell as the length of its body (“optimal shell accepted”) or the crab contacted the optimal shell but did not enter it and moved away at least as far as the length of its body (“optimal shell rejected”). Due to moulting and technical problems, the sample sizes varied for each day (Table 2-3) and we only had crabs under ship noise playback A and ambient sound A.

2.3.4 Statistical analysis

We tested the effects of the interaction between sound and occupied shell, sound and shell as main effects, treatment order, observation day and crab weight on the latency and duration of the different shell assessment steps as outlined above. To determine whether sound treatment and occupied shell influenced the shell assessment behaviour we used general and generalised linear mixed effect models implemented in the R-package lme4 (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2015). We analysed the shell assessment latency and duration for the days 1 – 9 separately from day 10 since the shell was not blocked on the last day. For the latency response on days 1 – 9 (contact the optimal shell, contact the optimal shell with their antennae, external shell assessment, turn the shell, internal shell assessment) we included the interaction between sound (ambient/ noise) and occupied shell (50%/ 80% PSW), treatment order (noise + ambient/ ambient + noise) and observation number (day 1 – 9) as fixed factors in the model. Body weight (in g) was included as a covariate. To account for the repeated observation of the same individual, we included crab ID as a random factor. For the sum of the shell assessment duration measurements (antennae contact, external shell assessment, turning the shell, internal shell assessment) we

used the same model as described above. Where necessary the data was log transformed to improve normality.

For days 1 – 9 we analysed whether the shell assessment behaviour was repeatable using the rpt package (Stoffel et al., 2017). We assessed the repeatability of eight measurements: (1) latency to contact the optimal shell, (2) latency to assess the external shell, (3) latency to turn the shell, (4) latency to assess the internal shell, (5) the total assessment duration, (6) duration to assess the external shell, (7) duration to turn the shell and (8) duration to assess the internal shell. To account for the experimental design, we also calculated the adjusted repeatability by including all factors as described above (i.e. the full model) into the analysis. A behaviour was deemed to be repeatable if *P*-values were below 0.05 and 95% confidence intervals (CIs) did not span zero. Since the duration measurements were repeatable (see 5 – 8 above), we also tested whether repeatability differed between the treatment levels i.e. if the repeatability differed within the sound treatment between ambient and noise and within the shell treatment between crabs occupying shells of 50% and 80% PSW. We subsetted the data between ambient and noise and between 50% and 80% PSW respectively. We then added the remaining factors into the model and compared the *R*-values. Differences between the treatment levels were deemed to be significant if *P*-values were below 0.05 and 95% confidence intervals (CIs) did not overlap.

Finally, to test the effect of sound treatment and occupied shell on the shell assessment of the unblocked, optimal shell on the last day, day 10, we used linear regression models for shell latency and duration measurements (contact the shell, assess the external shell, turn the shell, assess the internal shell, enter shell, assess the old shell after swapping, total assessment duration). We included the interaction

between sound (ambient/ noise) and occupied shell (50%/ 80% PSW) as fixed factors and crab weight as a covariate in the model. For the final decision outcome on day 10 of whether or not crabs accepted the optimal shell, we used accept/ reject as the binary response variable using a generalised model with the interaction between sound (ambient/ noise) and occupied shell (50%/ 80% PSW) as fixed factors and crab weight as a covariate. We used post-hoc residual plots to assess the fit of each model. Where necessary we natural log transformed the data to improve fit to normality.

Ethical note: No animals were harmed during the experiment. After the experiment each crab was supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences or permits were required for this study.

2.4 Results

The latency to contact the optimal shell was not affected by the interaction between sound and occupied shell ($\chi^2_{1} = 1.07, P = 0.30$), sound ($\chi^2_{1} = 0.97, P = 0.33$), occupied shell ($\chi^2_{1} = 1.74, P = 0.19$) or any of the other factors and covariates (Table 2-4 in the appendix to this chapter as all other results tables). There was a tendency for heavier crabs to display a shorter latency to contact the optimal shell with their antennae ($\chi^2_{1} = 3.78, P = 0.05$; Figure 2-6 for illustrative purposes) (note this may be an artefact of the fact that larger crabs have larger antennae which can be more easily seen). Though there was tendency that crabs in larger shells took longer to begin assessing the interior or the shell ($\chi^2_{1} = 3.49, P = 0.06$; Figure 2-7 for illustrative purposes), none of the other factors influenced the latency of assessing the exterior of the shell, of turning the shell or of assessing the interior of the shell (Table 2-4).

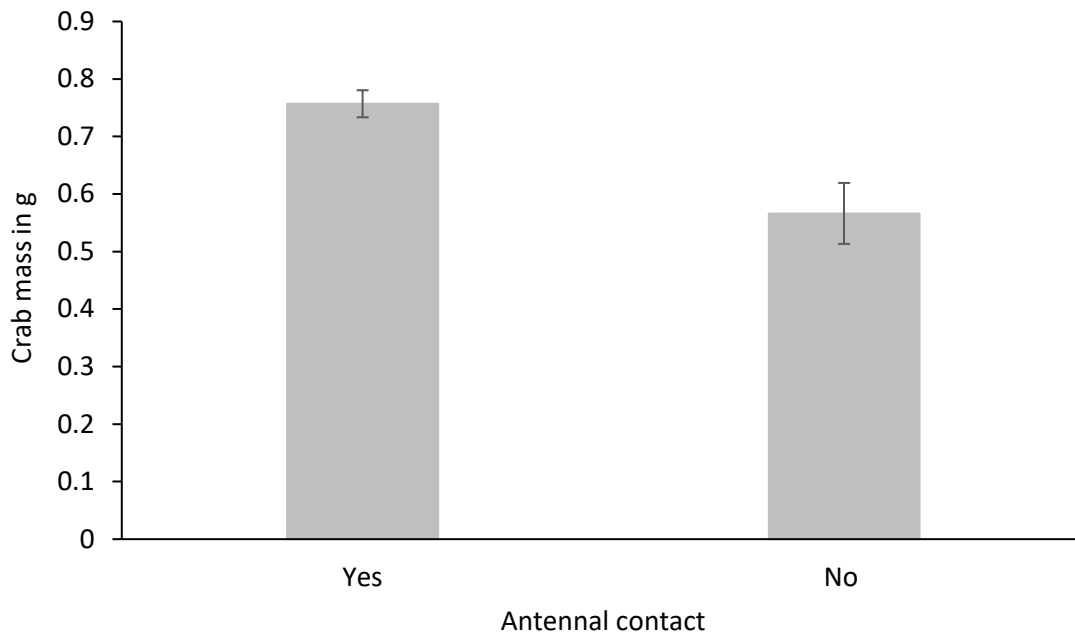


Figure 2-6 Effect of crab weight on the occurrence of antennal contact with the optimal shell (for illustrative purposes). Error bars show standard errors.

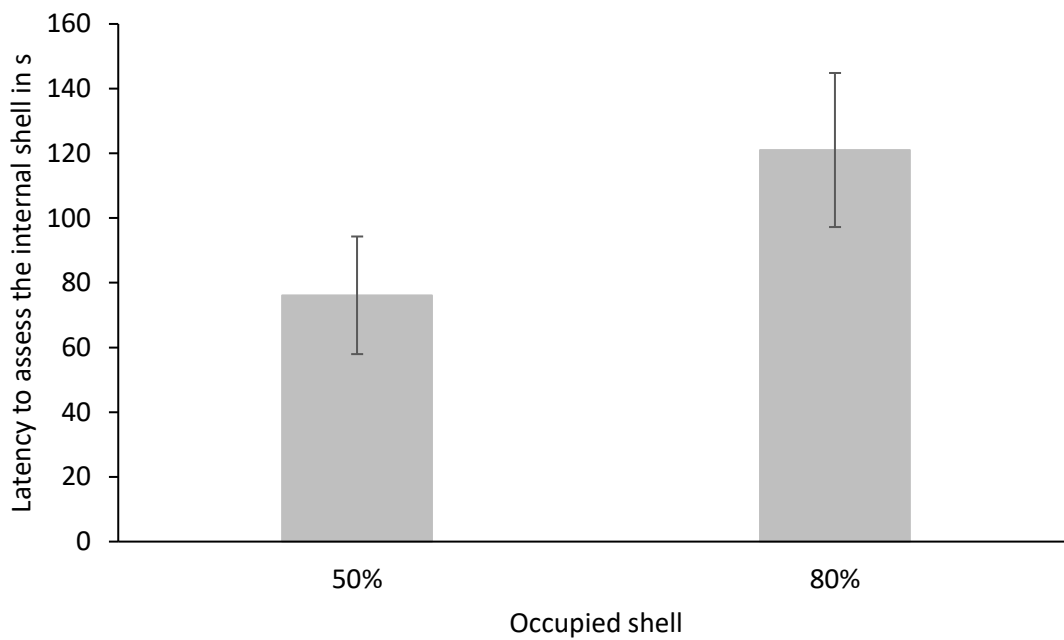


Figure 2-7 Effect of the occupied shell on the latency to assess the internal shell (for illustrative purposes). Error bars show standard errors.

The duration of the overall shell assessment was not affected by the interaction between sound and occupied shell ($\chi^2_{1} = 1.38, P = 0.24$; Table 2-5), sound ($\chi^2_{1} = 1.14, P = 0.29$) or shell ($\chi^2_{1} = 1.84, P = 0.17$). There was no interaction between sound and occupied shell ($\chi^2_{1} = 1.28, P = 0.26$) and no effect of any of the other predictors on the external assessment. However, the treatment order was close to significantly affect the time spent assessing the exterior of the shell ($\chi^2_{1} = 3.76, P = 0.05$; Figure 2-8 for illustrative purposes). The trend suggests that crabs in the “ambient + noise” sound treatment order assessed the exterior shell longer than crabs in the “noise + ambient” treatment order.

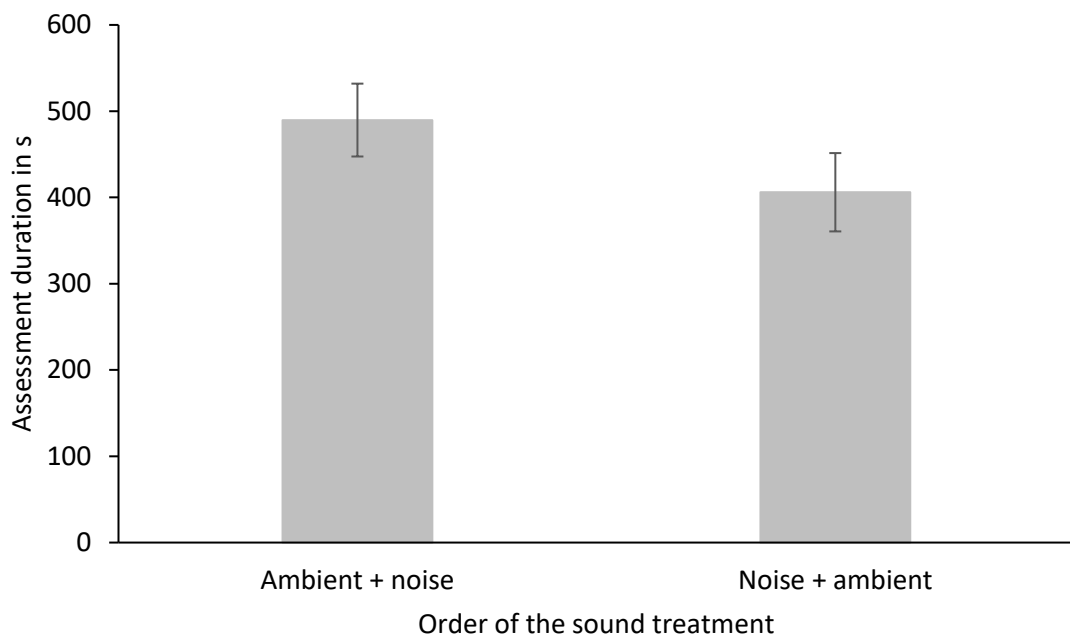


Figure 2-8 Effect of the order of sound treatment on the total shell assessment duration (for illustrative purposes). Error bars show standard errors.

The time spent to turn the shell was not altered by the interaction between sound and shell ($\chi^2_{1} = 0.16, P = 0.69$) or sound ($\chi^2_{1} = 0.002, P = 0.97$). Crabs in smaller shells, however, took significantly more time to turn the shell ($\chi^2_{1} = 9.07, P = 0.003$;

Figure 2-9). While neither the interaction nor any of the main factors influences the internal assessment time, heavier crabs spent less time assessing interior of the shell ($\chi^2_1 = 6.28, P = 0.01$; Figure 2-10).

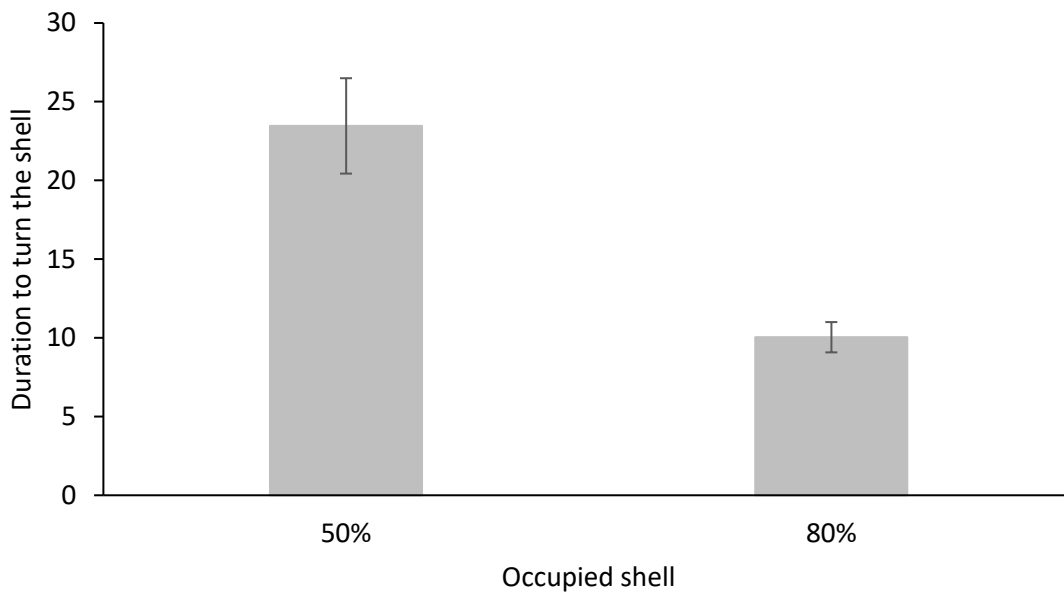


Figure 2-9 Effect of the occupied shell on the duration to turn the shell. Error bars show standard errors.

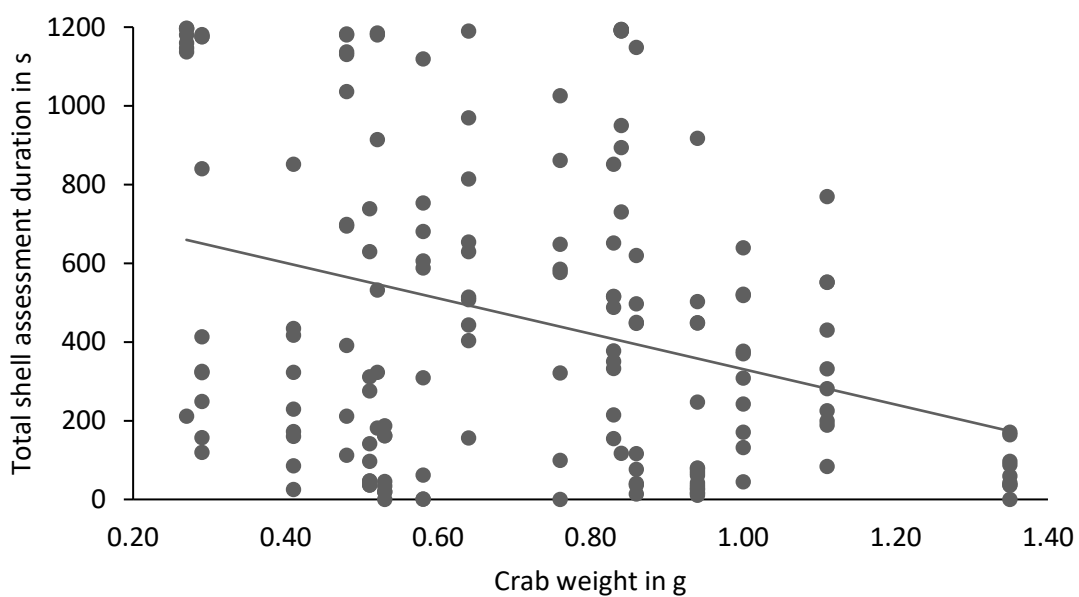


Figure 2-10 Effect of crab weight on the total assessment duration.

We tested the repeatability of the latency and duration of the shell assessment behaviours adjusted by the predictors included in the full model (latency: Table 2-6; duration: Table 2-7). Though the unadjusted repeatability was higher than the adjusted repeatability for all behaviours, the latter all remained significant. None of the latencies was repeatable except for the unadjusted external assessment ($R = 0.11$, 95% CIs = 0.0, 0.27, $P = 0.04$). The total shell assessment duration was moderately repeatable ($R = 0.47$, 95% CIs = 0.23, 0.67, $P > 0.0001$; Figure 2-11), as was the duration of the external assessment ($R = 0.20$, 95% CIs = 0.04, 0.40, $P = 0.002$) and of turning the shell ($R = 0.39$, 95% CI = 0.18, 0.62, $P > 0.0001$). Most repeatable was the internal shell assessment duration ($R = 0.51$, 95% CIs = 0.29, 0.71, $P > 0.0001$; Figure 2-12).

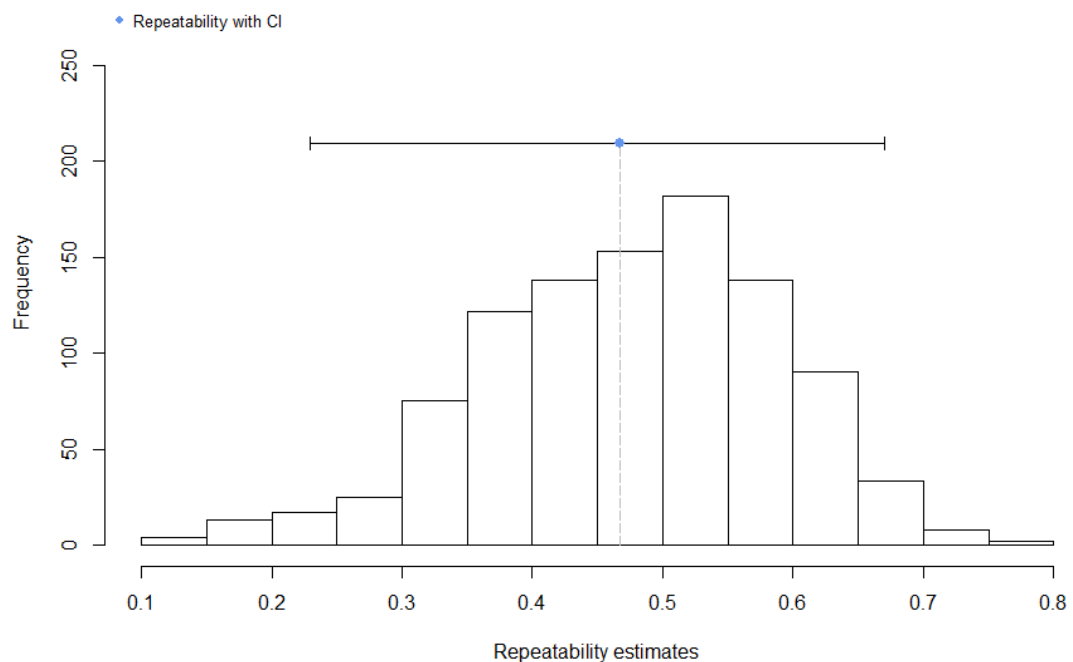


Figure 2-11 Repeatability of the total shell assessment duration. Error bar shows 5% and 95% confidence intervals.

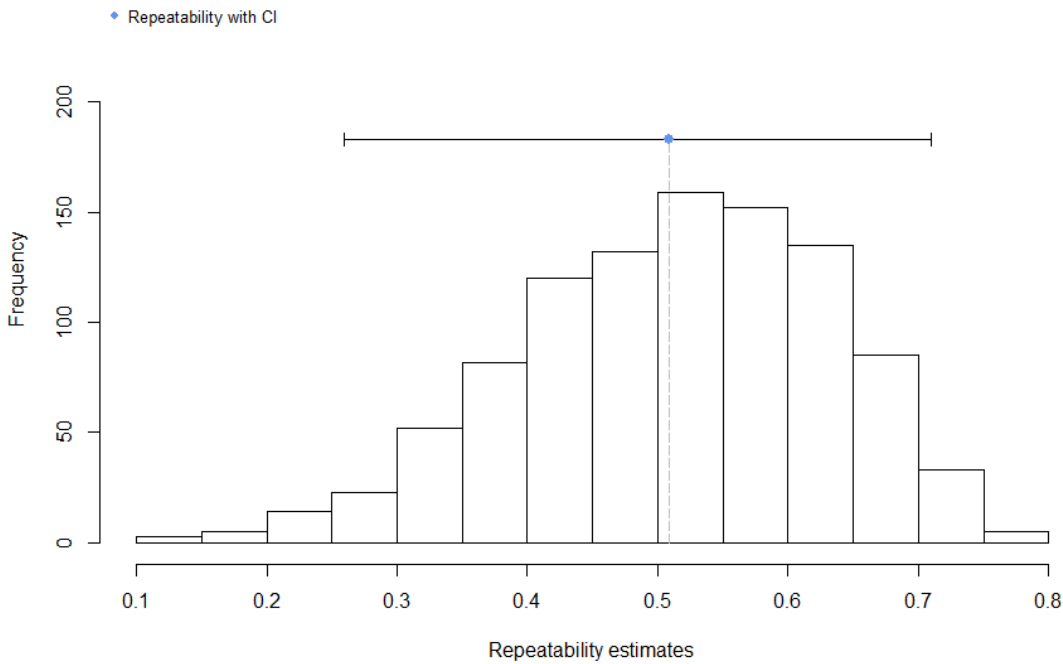


Figure 2-12 Repeatability of the internal shell assessment duration. Error bar shows 5% and 95% confidence intervals.

There was no difference in repeatability between occupied shell (small shells: $R = 0.63$, $CIs = 0.16, 0.88$, $P > 0.0001$; large shells: $R = 0.37$, $CIs = 0.09, 0.64$, $P > 0.0001$) since the confidence intervals overlapped (Figure 2-13 for illustrative purposes). Similarly, the repeatability estimates between the sound treatments did not differ statistically from each other (Table 2-7). If there is an effect of any treatment (sound or shell) on the repeatability there is not enough statistical power to detect this.

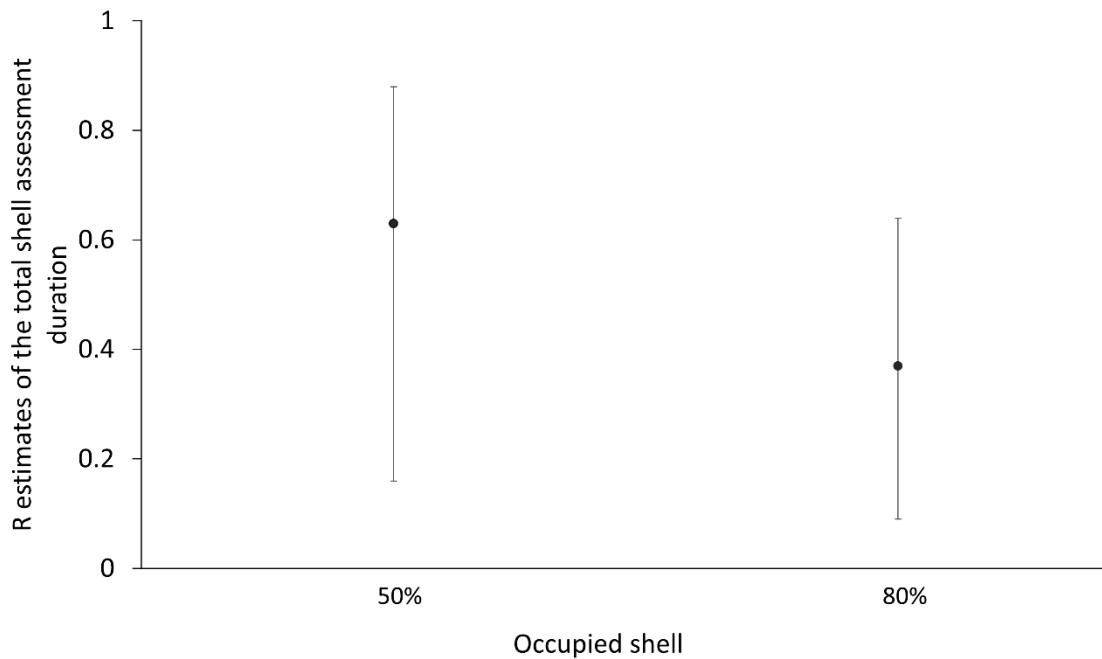


Figure 2-13 Repeatability of total shell assessment duration comparing crabs in small and large shells (for illustrative purposes). Error bars show 5% and 95% confidence intervals.

On the last day (day 10), none of the predictors or the interaction between sound and occupied shell affected the latency to contact the shell (Table 2-8). However, compared to ambient sound crabs under noise took longer to assess the external surface of the shell ($\chi^2_{1} = 9.0$, $P = 0.01$; Figure 2-14a), turn the shell ($\chi^2_{1} = 6.14$, $P = 0.03$; Figure 2-14b) and to assess the interior of the shell ($\chi^2_{1} = 8.62$, $P = 0.01$; Figure 2-14c) on the last day. Crabs in smaller shells also spent less time turning the optimal shell ($\chi^2_{1} = 6.14$, $P = 0.03$; Figure 2-15a) and assessing the interior of the optimal shell ($\chi^2_{1} = 6.14$, $P = 0.03$; Figure 2-15b). There was a trend for crabs in small shells to assess the exterior of the shell longer than crabs in larger shells (Table 2-9). Once crabs assessed the shell, those in small shells showed shorter latencies to enter the optimal shell ($\chi^2_{1} = 8.54$, $P = 0.01$; Figure 2-16a) and to re-assess the old, initially occupied shell after swapping ($\chi^2_{1} = 8.11$, $P = 0.01$; Figure 2-16b).

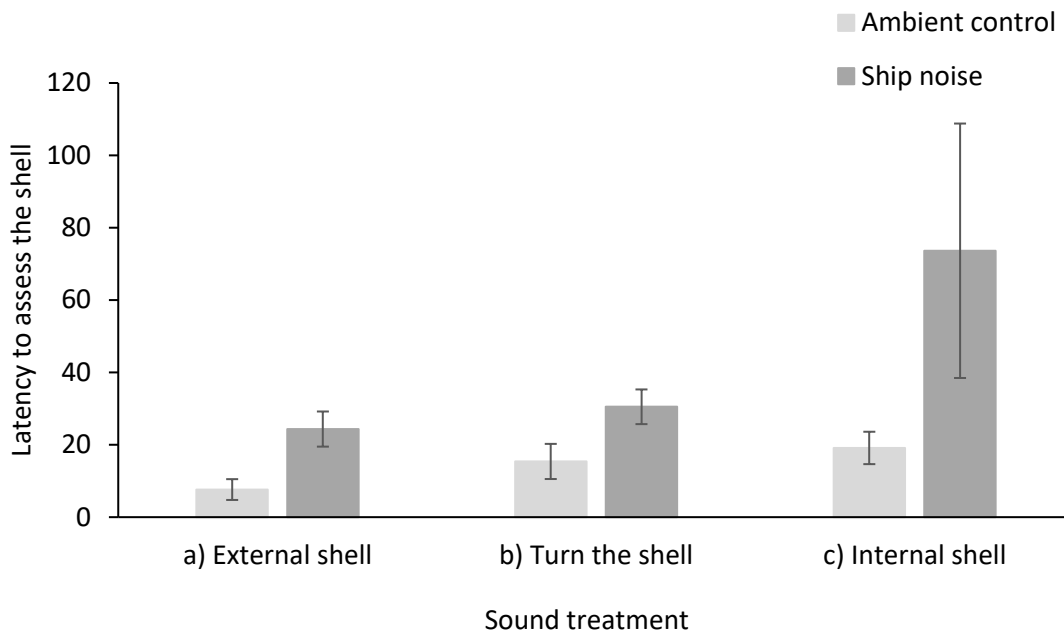


Figure 2-14 Effect of the sound treatment on the latency to assess the a) external shell, b) turn the shell and c) assess the internal shell on the last observation day (unblocked shell). Error bars show standad errors.

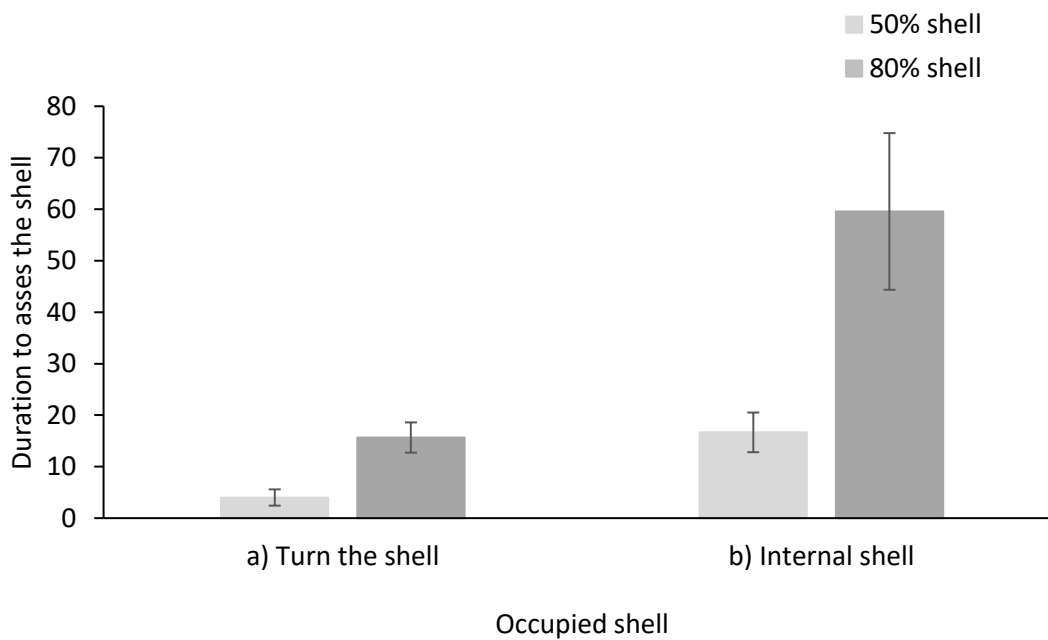


Figure 2-15 Effect of occupied shell on the duration to a) turn the shell and b) assess the internal shell on the last observation day (unblocked shell). Error bars show standad errors.

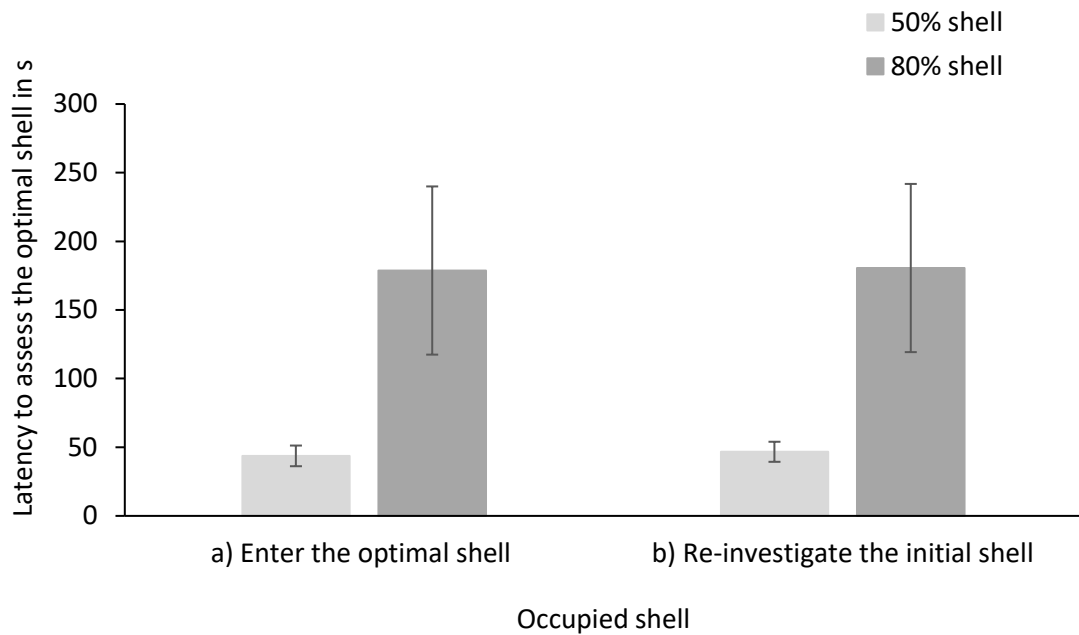


Figure 2-16 Effect of the occupied shell on the latency to a) enter the optimal shell and b) re-investigate the initially occupied shell after swapping on the last observation day (unblocked shell). Error bars show standard errors.

The final decision on day 10 whether to accept or reject the optimal shell was altered by the interaction between sound and occupied shell ($\chi^2_{1} = 6.14, P = 0.03$; **Error! Reference source not found.**). Crabs that were supplied with 50% adequate shells were more likely to accept the optimal shell on day 10 if they were exposed to ship noise than if they were exposed to ambient noise. For crabs supplied with 80% adequate shells this difference between sound treatments was reversed but less more marked. Crabs accepting the optimal shell had a lower mean weight than crabs rejecting the optimal shell ($\chi^2_{1} = 6.14, P = 0.03$; Figure 2-18).



Figure 2-17 Effect of the internaction between sound treatment and occupied shell on the proportion of crabs accepting the optimal shell on the last observation day (unblocked shell).

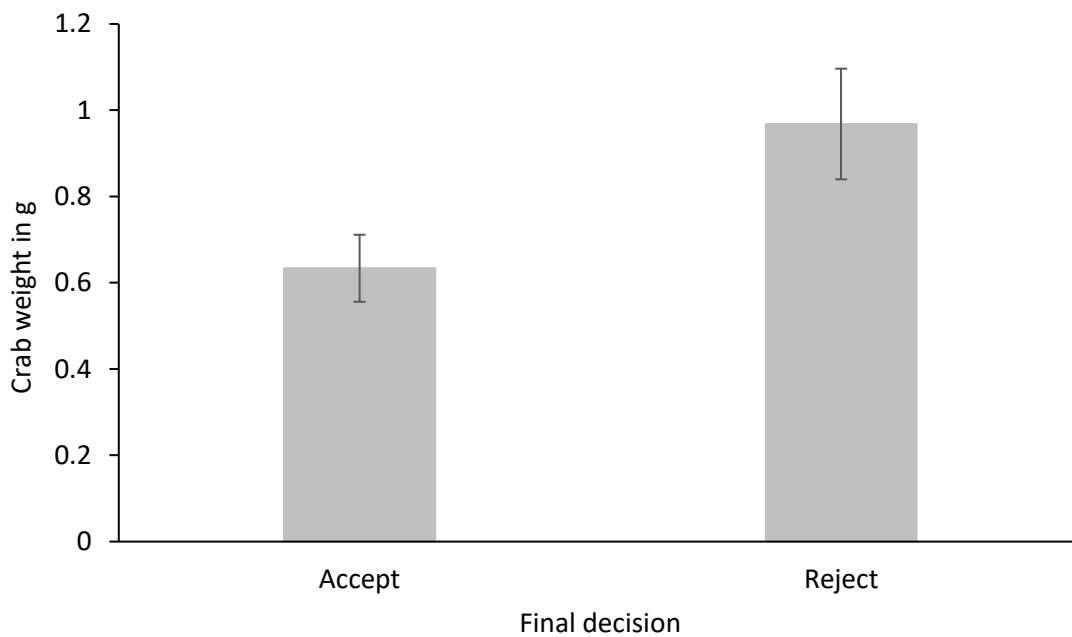


Figure 2-18 Effect of crab weight in g on the final decision to accept or reject the optimal shell on the last observation day (unblocked shell). Error bars show standad errors.

2.5 Discussion

To assess the quality of shells, hermit crabs use tactile, visual and chemical cues (Elwood, 1995; Gherardi and Tiedemann, 2004; Hazlett, 1982). For hermit crabs shell assessment and selection are crucial decision-making processes that drive differences in survival and fitness. Shells that are too small can inhibit growth (Angel, 2000) and reproduction (Bertness, 1981a) and reduce protection against predators (Vance, 1972) and environmental extremes (Taylor, 1981; Young, 1978), whereas shells that are too heavy are energetically costly to carry (Briffa and Elwood, 2005; Osorno et al., 1998). Our findings show that the shell assessment behaviour of *P. bernhardus* is repeatable across the sound treatments (ambient sound/ ship noise) and the size of the occupied shell (50%/ 80%). We also show that even in the absence of a difference in sound intensity, anthropogenic ship noise can affect specific stages of this critical decision-making process.

Shell assessment behaviour of hermit crabs is considerably influenced by the occupied shell and repeatable across shell and sound treatments. In contrast to our initial prediction that hermit crabs in 50% optimal shells will show shorter latencies and longer shell assessment duration, the latency for the first shell contact and the subsequent steps was not significantly affected by occupied shell. There was a tendency that crabs in smaller shells assessed the interior of the shell more quickly than crabs in 80% shells. Similarly, the total shell assessment duration was not affected by any of the tested factors but crabs in 50% shells turned the shell for longer. Given that hermit crabs turn shells to remove obstacles from them (Elwood and Neil, 1992), this behaviour was to be expected indicating higher motivation to enter better fitting shells of crabs in 50% shells compared to crabs in 80% shells. Hermit crabs showed

repeatable total shell assessment duration and particularly so in assessing the interior of the shell. When investigating the surface of the shells, hermit crabs can gain information on the gastropod species and assess the integrity of the shell (e.g. holes, epibiont cover). More detailed, and presumably more complex, information on the width, depth and concavity of the aperture is gained through the internal assessment (Elwood and Neil, 1992) which could explain the longer and more repeatable assessment duration for that part of the shell. Evidence across taxa and contexts shows that behaviour is a highly repeatable phenotypic trait (an average repeatability estimate of 0.37, see Bell et al., 2009). Repeatability over time (i.e. personality) has been suggested to be advantageous in unpredictable environmental conditions since maintaining plastic behaviour (e.g. for gathering and processing information) is costly and mistakes in decision are nevertheless inevitable (Sih et al., 2004). One explanation could be that noisy conditions enhance environmental unpredictability if anthropogenic noise is of a certain intensity which could be the most important sound property. *P. bernhardus* previously showed repeatable behaviours over time (animal personality) and across situations or contexts such as startle responses, exploration and aggression (behavioural syndromes) in the laboratory (Briffa, 2013a; Briffa et al., 2013; Briffa et al., 2008b; Mowles et al., 2012) and in the field (chapter 7). Shell assessment appears to be another repeatable behavioural trait in *P. bernhardus*.

On the last day 10, when the individuals were presented with an unblocked optimal shell, the behaviour differed not only with the occupied shell but now also with the sound treatment. As expected, hermit crabs in 50% shells showed shorter latency to enter the optimal shell and to assess the previously occupied shell after entering the new, optimal shell. As on the previous days, crabs in 50% shell took less

time to start turning and internally assessing the optimal shell compared to crabs in 80% shells which coincides with the known differences in motivation in hermit crabs (Elwood and Neil, 1992). While there was no effect of noise on any behavioural measure (latency, duration, repeatability) on the first 9 days of the experiment, on day 10 hermit crabs altered their behaviour and final decision-making under noise. Individuals showed longer latency to assess the exterior shell, turn the shell and assess the interior of the shell under noise compared to ambient sound. In addition to the latency, crabs in small shells under the noise treatment accepted the new shell more frequently than crabs under ambient sound. For crabs in larger shells this pattern was reversed but less marked. The only difference between shells on days 1 – 9 and day 10 was that shells on day 10 was not blocked with modelling clay. Hermit crabs can gain some information before contacting the shell such as by visual and chemical cues (Elwood, 1995; Gherardi and Tiedemann, 2004; Hazlett, 1982). Since the optimal shells were placed in the tank with the aperture facing downwards, we confidently exclude the possibility that crabs gained visual information on the different shell aperture. Crabs could have taken longer to start assessing shells if they detected that the unblocked shells were different to those on previous days. For instance, the unblocked shells on day 10 may have emitted a different chemical cue profile compared with the shells blocked with modelling clay. We cannot rule out that chemical cues from the modelling clay distracted hermit crabs from shells. However, this does not explain the interaction between occupied shell and sound on accepting the optimal shell on day 10. Rather, the decision to accept the optimal shell seems to be influenced by an effect of ship noise modulated by the occupied shell.

Effects of anthropogenic noise on animals largely depend on three types of possibly interacting factors: the biology of the species in question, the similarity to relevant biological sounds and the properties of the anthropogenic stimulus (Ellison et al., 2012; Francis and Barber, 2013; Gill et al., 2014; Shannon et al., 2016b). *P. bernhardus* has been shown to alter the timings of their behaviour under high intensity anthropogenic noise (chapter 4, Tidau and Briffa, 2019; chapter 3, Tidau and Briffa, In Press) and white noise (Walsh et al., 2017). Here we show that also low intensity anthropogenic noise alters decision-making in hermit crabs. In previous experiments, *P. bernhardus* showed shorter latency when exposed to high intensity white noise (Walsh et al., 2017) and accepted the optimal shell less frequently under anthropogenic noise (chapter 3, Tidau and Briffa, In Press). Since the results within this experiment appear to oppose those from the other studies, the initial explanation could be the different sound intensities. Though the exact sound detection abilities of *P. bernhardus* are unknown, research on the common prawn showed that crustaceans can detect sounds in the frequency range between 100 – 3 000 Hz in amplitudes from 132 dB SPL re 1 μ Pa down to 90 dB SPL re 1 μ Pa (Lovell et al., 2005). High intensity sounds cause stronger particle motion (Tasker et al., 2010) which might explain why low intensity noise only affects crabs when they have to make decisions with strong fitness consequences, i.e. whether or not to enter better fitting shells.

Since the sound intensity between the anthropogenic noise and the ambient sound was of similar magnitude, this sound property alone cannot explain why there was an effect of noise. Our results suggest that crabs were influenced by the other differences in the sound stimuli such as a different temporal pattern. This explanation would be supported by the general pattern that more unpredictable stimuli can cause

more stress to animals (Koolhaas et al., 2011). In accordance with the review by Koolhaas et al. (2011), juvenile European seabass *D. labrax*, the giant kelpfish *H. rostratus* and the greater sage-grouse *C. urophasianus* reacted more strongly to intermittent, impulsive noise (pile-driving and seismic survey respectively road noise) than to comparatively more continuous noise (drilling noise in Blickley et al., 2012b; ship noise in Nichols et al., 2015; Radford et al., 2016a) illustrating how noise can affect animals depending on its characteristics beyond intensity like the temporal pattern.

The importance of advancing from a focus on sound intensities alone, towards temporal and spatial heterogeneity of noise has been discussed (Gill et al., 2014) and tested in some cases (Neo et al., 2016; Neo et al., 2014; Shafiei Sabet et al., 2015). This experiment provides further evidence that exposure to anthropogenic noise with similar intensity to ambient sound can still alter behaviour. This effect could be caused by a range of features of the novel sound such as its frequency in and other characteristics such as the temporal structure and onset. A more precise characterisation of the noise properties which impact animals would also allow to better target management measures by regulating noise. Further research to formally compare different sound intensities and temporal structure known to be in the detection range of an organisms would provide valuable insight into understanding the complexity of the effects of anthropogenic noise and allow to determine whether our observations can be generalised. Moreover, since we found no effect of low intensity noise over time, the influence of chronic high intensity on crustaceans remains to be explored.

2.6 Appendix to the chapter

Table 2-4 Latencies to start the different steps in the shell assessment process: First contact, antennal contact, external assessment, turning the shell and internal assessment on days 1 – 9 (blocked shell; bold indicates significant effects).

Behaviour and effects of factors	χ^2	df	P
Latency to contact the shell			
Sound * occupied shell	1.07	1	0.30
Occupied shell	1.74	1	0.19
Sound	0.97	1	0.33
Sound treatment order	0.27	1	0.60
Observation	10.10	8	0.26
Crab weight	0.52	1	0.47
Latency to show antennal contact			
Sound * occupied shell	2.58	1	0.11
Occupied shell	0.69	1	0.41
Sound	0.02	1	0.88
Sound treatment order	0.06	1	0.80
Observation	8.73	8	0.37
Crab weight	3.78	1	0.05
Latency to show external shell assessment			
Sound * occupied shell	0.92	1	0.34
Occupied shell	2.39	1	0.12
Sound	1.39	1	0.24
Sound treatment order	0.15	1	0.70
Observation	9.15	8	0.33
Crab weight	0.10	1	0.75
Latency to turn the shell			
Sound * occupied shell	1.31	1	0.25
Occupied shell	2.73	1	0.10
Sound	0.54	1	0.46
Sound treatment order	0.44	1	0.51
Observation	8.25	8	0.41
Crab weight	0.70	1	0.40
Latency to show internal shell assessment			
Sound * occupied shell	1.38	1	0.24
Occupied shell	3.49	1	0.06
Sound	0.007	1	0.93
Sound treatment order	0.30	1	0.58
Observation	9.13	8	0.33
Crab weight	1.92	1	0.17

Table 2-5 Duration spent with different steps in the shell assessment process on days 1 – 9 (blocked shell; bold indicates significant effects; bold and italics trends).

Behaviour and effects of factors	χ^2	df	P
Overall shell assessment			
Sound * occupied shell	1.38	1	0.24
Occupied shell	1.84	1	0.17
Sound	1.14	1	0.29
Sound treatment order	2.98	1	0.08
Observation	9.48	8	0.30
<i>Crab weight</i>	3.29	1	0.07
External shell assessment			
Sound * occupied shell	1.28	1	0.26
Occupied shell	1.99	1	0.16
Sound	1.03	1	0.31
<i>Sound treatment order</i>	3.76	1	0.05
Observation	5.43	8	0.71
Crab weight	0.33	1	0.56
Turning the shell			
Sound * occupied shell	0.16	1	0.69
Occupied shell	9.07	1	0.003
Sound	0.002	1	0.97
Sound treatment order	0.13	1	0.72
Observation	10.82	8	0.21
Crab weight	0.15	1	0.70
Internal shell assessment			
Sound * occupied shell	0.32	1	0.57
Occupied shell	1.88	1	0.17
Sound	1.06	1	0.30
Sound treatment order	0.39	1	0.53
Observation	12.61	8	0.13
Crab weight	6.28	1	0.01

Table 2-6 Repeatability of latency to assess the shell: First contact, external assessment, turning the shell and internal assessment on days 1 – 9 (blocked shell; bold indicates significant effects).

Latency measure	Model	R	Bootstrapping (LTR)*	
			CI	P
To contact the shell	rpt(lat.sh ~ (1 crab.ID))	0.03	0, 0.14	0.31
	rpt(lat.sh ~ (1 crab.ID)) + full model*	0.02	0, 0.16	1.00
To external assess	rpt(ext.lat ~ (1 crab.ID))	0.11	0.0, 0.27	0.04
	rpt(ext.lat ~ (1 crab.ID)) + full model	0.08	0, 0.27	0.17
To turn the shell	rpt(turn.lat ~ (1 crab.ID))	0.06	0, 0.19	0.19
	rpt(turn.lat ~ (1 crab.ID)) + full model	0.05	0, 0.21	0.32
To internal assess	rpt(int.lat ~ (1 crab.ID))	0.04	0, 0.18	0.27
	rpt(int.lat ~ (1 crab.ID)) + full model	0.04	0, 0.20	0.43

Note: Bootstrapping is based on * Likelihood ratio test

Table 2-7 Repeatability of duration to assess the shell: Total assessment duration, external assessment, turning the shell and internal assessment on days 1 – 9 (blocked shell; bold indicates significant effects).

Duration measure	Model	R	Bootstrapping (LTR)*	
			CI	P
Total assessment duration	rpt(assess.dur ~ (1 crab.ID))	0.54	0.29, 0.7	> 0.0001
	rpt(assess.dur ~ (1 crab.ID) + full model)	0.47	0.23, 0.67	> 0.0001
Small shells	rpt(assess.dur ~ (1 crab.ID) + full model – occupied shell, data=small.sh)	0.63	0.10, 0.88	> 0.0001
Large shells	rpt(assess.dur ~ (1 crab.ID) + full model – occupied shell, data=large.sh)	0.37	0.09, 0.64	> 0.0001
Ambient control	rpt(assess.dur ~ (1 crab.ID) + full model – sound, data=ambient)	0.50	0.26, 0.75	> 0.0001
Ship noise	rpt(assess.dur ~ (1 crab.ID) + full model – sound, data=noise)	0.50	0.25, 0.76	> 0.0001
External shell assessment	rpt(ext.dur p ~ (1 crab.ID))	0.24	0.06, 0.41	> 0.0001
	rpt(ext.dur ~ (1 crab.ID)) + full model	0.20	0.04, 0.40	0.002
Small shells	rpt(ext.dur ~ (1 crab.ID) + full model – occupied shell, data=small.sh)	0.22	0.0, 0.58	0.05
Large shells	rpt(ext.dur ~ (1 crab.ID) + full model – occupied shell, data=large.sh)	0.24	0.0, 0.52	0.004
Ambient control	rpt(ext.dur ~ (1 crab.ID) + full model – sound, data=ambient)	0.19	0.0, 0.48	0.07
Ship noise	rpt(ext.dur ~ (1 crab.ID) + full model – sound, data=noise)	0.35	0.08, 0.65	0.003
Turning the shell	rpt(turn.dur ~ (1 crab.ID))	0.50	0.26, 0.67	> 0.0001
	rpt(turn.dur ~ (1 crab.ID)) + full model	0.39	0.18, 0.62	> 0.0001
Small shells	rpt(turn.dur ~ (1 crab.ID) + full model – occupied shell, data=small.sh)	0.57	0.04, 0.85	> 0.0001
Large shells	rpt(turn.dur ~ (1 crab.ID) + full model – occupied shell, data=large.sh)	0	0.0, 0.0	0.5
Ambient control	rpt(turn.dur ~ (1 crab.ID) + full model – sound, data=ambient)	0.49	0.23, 0.73	> 0.0001
Ship noise	rpt(turn.dur ~ (1 crab.ID) + full model – sound, data=noise)	0.22	0.0, 0.58	0.10
Internal shell assessment	rpt(int.dur ~ (1 crab.ID))	0.58	0.35, 0.73	> 0.00001
	rpt(int.dur ~ (1 crab.ID)) + full model	0.51	0.27, 0.71	> 0.00001
Small shells	rpt(int.dur ~ (1 crab.ID) + full model – occupied shell, data=small.sh)	0.69	0.19, 0.90	> 0.00001
Large shells	rpt(int.dur ~ (1 crab.ID) + full model – occupied shell, data=large.sh)	0.38	0.10, 0.67	0.0001
Ambient control	rpt(int.dur ~ (1 crab.ID) + full model – sound, data=ambient)	0.55	0.32, 0.77	> 0.00001
Ship noise	rpt(int.dur ~ (1 crab.ID) + full model – sound, data=noise)	0.47	0.21, 0.74	0.0002

Note: Bootstrapping is based on * Likelihood ratio test

Table 2-8 Latency to assess the shell: First contact, external assessment, turning the shell and internal assessment on the last observation day (unblocked shell; bold indicates significant effects).

Behaviour and effects of factors	df	Residual df	F	P
Latency to contact the shell				
Sound * occupied shell	1	11	1.30	0.28
Sound	1	13	1.51	0.24
Occupied shell	1	14	2.01	0.18
Crab weight	1	12	0.19	0.67
Latency to assess the external shell				
Sound * occupied shell	1	11	0.31	0.59
Sound	1	14	9.00	0.01
Occupied shell	1	12	0.24	0.63
Crab weight	1	13	1.60	0.23
Latency to turn the shell				
Sound * occupied shell	1	11	0.4	0.85
Sound	1	14	6.14	0.03
Occupied shell	1	12	0.09	0.77
Crab weight	1	13	1.11	0.31
Latency to assess the internal shell				
Sound * occupied shell	1	11	0.76	0.40
Sound	1	14	8.62	0.01
Occupied shell	1	12	0.85	0.38
Crab weight	1	13	3.12	0.10
Latency to enter shell				
Sound * occupied shell	1	10	0.07	0.80
Sound	1	11	0.82	0.39
Occupied shell	1	13	8.54	0.01
Crab weight	1	12	3.33	0.09
Latency to assess the old shell after swapping				
Sound * occupied shell	1	10	0.12	0.73
Sound	1	11	0.64	0.44
Occupied shell	1	13	8.11	0.01
Crab weight	1	12	2.81	0.12

Table 2-9 Duration to assess the shell: First contact, external assessment, turning the shell and internal assessment on the last observation day (unblocked shell; bold indicates significant effects; bold and italics trends).

Behaviour and effects of factors	df	Residual df	F	P
Duration to assess the shell				
Sound * occupied shell	1	11	0.06	0.81
Sound	1	13	1.45	0.25
Occupied shell	1	14	2.90	0.11
Crab weight	1	12	0.59	0.46
Duration to assess the external shell				
Sound * occupied shell	1	11	0.01	0.91
Sound	1	13	1.53	0.24
<i>Occupied shell</i>	1	14	4.52	0.05
Crab weight	1	12	0.44	0.52
Duration to turn the shell				
Sound * occupied shell	1	11	1.33	0.27
Sound	1	13	1.86	0.20
Occupied shell	1	14	11.37	0.005
Crab weight	1	12	0.63	0.44
Duration to assess the internal shell				
Sound * occupied shell	1	11	0.02	0.90
Sound	1	12	0.01	0.91
Occupied shell	1	14	7.89	0.01
Crab weight	1	13	0.98	0.34

Table 2-10 Final decision outcome on the last day (unblocked shell; bold indicates significant effects).

Factors and their interactions	df	χ^2	P
Sound * occupied shell	1	5.68	0.02
Crab weight	1	9.73	0.002

Chapter 3: Distracted decision-makers: Ship noise and predation risk change shell choice in hermit crabs

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3.1 Abstract

Human-induced rapid environmental change such as noise pollution alters the ability of animals to integrate information cues. Many studies focus on how noise impacts single sensory channels but in reality animals rely on multi-modal sources of information. In this study, we investigated the effect of anthropogenic noise and the visual presence of a predator on tactile information gathering during gastropod shell assessment in the European hermit crab *Pagurus bernhardus*. For hermit crabs, empty gastropod shells are a crucial resource affecting growth, reproduction, and survival. We measured shell assessment behaviour and manipulated (1) the shell size (50% or 80% of the optimal), (2) sound condition (ship or ambient), and (3) visual predator cue (absence/ presence). Overall we found that crabs were less likely to accept an optimal shell in the presence of ship noise, suggesting that exposure to ship noise disrupted the information gathering ability of the crabs. We also found a significant interaction between noise, predator presence, and shell size on the mean duration for the final decision to accept or reject the optimal shell. Hermit crabs in 50% shells took less time

for their final decision when exposed to both ship noise and predator cue while crabs in 80% shells showed shorter decision time only when the predator cue was absent. Our results indicate that anthropogenic noise can interact with predation threat and resource quality to change resource acquisition, suggesting that noise pollution can disrupt behaviour in a non-additive way, by disrupting information use across multiple sensory channels.

3.2 Introduction

Human-induced rapid environmental change (HIREC; Sih et al., 2011) encompasses global processes such as climate change as well as examples of more localised and transient pollution such as ship noise (Tuomainen and Candolin, 2011). HIREC can either affect behaviour directly by impacting whole organism performance capacities (via changes to development or physiological state) or indirectly by altering the sensory environment and disrupting the information gathering and decision-making processes that underpin behaviour. Both routes have potential implications for survival and fitness. Noise has been shown to affect the detectability (and recognisability) of cues both through masking of sound (Barber et al., 2010; Brumm, 2004; Clark et al., 2009; Foote et al., 2004; Halfwerk et al., 2012; Heiler et al., 2016; Lampe et al., 2012; Spiga, 2016; Sun and Narins, 2005) and by distracting an animal's limited attention (Chan et al., 2010a; Chan et al., 2010b; Kunc et al., 2014; Nedelec et al., 2017; Simpson et al., 2015; Tidau and Briffa, 2019; Wale et al., 2013a; Walsh et al., 2017). Since animals perceive and have to process information across various modalities, their limited attention is a cognitive constraint (Dukas, 2004). As a consequence, the 'distracted prey hypothesis' (Chan et al., 2010b) suggests that since animals have to divide their attention they may no longer respond appropriately to predator cues in

the presence of noise. Thus, noise might not only distract attention from acoustic cues but also from non-acoustic cues across visual, chemical and tactile channels and in addition can also disrupt the integration of information across sensory modalities (Halfwerk and Slabbekoorn, 2015).

Recent decades have seen mounting evidence for effects of anthropogenic noise pollution across a range of taxa, habitats, and behavioural contexts (Barber et al., 2010; Kight and Swaddle, 2011; Williams et al., 2015). This includes shifts in the amplitude, duration, timing, and patterns of acoustic communication as possible means of compensating for noise, with examples in birds (Brumm, 2004; Halfwerk et al., 2012), amphibians (Sun and Narins, 2005), insects (Lampe et al., 2012), marine mammals (Foote et al., 2004; Heiler et al., 2016) and snapping shrimp (Spiga, 2016). However, there is also evidence that behaviours in contexts other than communication can be impacted by noise, and in these cases, the scope for animals to compensate may be more limited. Furthermore, due to distraction effects disruption is not limited to behaviour that relies on acoustic sources of information only. Examples of the wide range of impacted behavioural contexts include reduced foraging performance in the common shore crab *Carcinus maenas* (Wale et al., 2013a), the Greater mouse-eared bat *Myotis myotis* (Siemers and Schaub, 2011), and the Black-tailed prairie dog *Cynomys ludovicianus* (Shannon et al., 2014), decreased parental care in the spiny chromis *Acanthochromis polyacanthus* (Nedelec et al., 2017), impaired shoaling in the Bluefin tuna *Thunnus thynnus* (Sara et al., 2007), and reduced predator avoidance in the European eel *Anguilla anguilla* (Simpson et al., 2015).

Anthropogenic noise not only disrupts the sensory environment of animals along acoustic, unimodal sensory channels but also across non-acoustic channels for

information gathering and processing, such as the visual and tactile sensory systems (Kunc et al., 2014; Morris-Drake et al., 2016; Tidau and Briffa, 2019). It has been suggested that such cross-sensory interference can distract organisms, thus explaining behavioural changes in response to anthropogenic pollution in vertebrates and invertebrates alike (Halfwerk and Slabbekoorn, 2015). However, different sources of information used by animals tend to be studied in isolation. In contrast, few studies have taken a multi-sensory approach to investigate the effects of anthropogenic noise on behaviours that (in nature) are likely to be dependent on information from several channels (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011). For example, the European hermit crab *Pagurus bernhardus* integrates tactile and visual information when assessing the value of an empty gastropod shell. This is a critical resource that provides protection for their weakly calcified abdomen and crabs are known to choose new shells based on information about their weight, species, condition (Elwood and Neil, 1992), and colour (Briffa and Twyman, 2011). During the process of exchanging an old shell for a new one, hermit crabs are vulnerable to attack and hence they adjust their shell assessment behaviour in the presence of predators (Briffa et al., 2008b). Hermit crabs rely on a range of tactile, visual, and chemical cues to compare the quality of a potential new shell with that of the currently occupied shell. Like other coastal species, however, hermit crabs are subject to noise pollution caused by the motors of ships and boats. While *P. bernhardus* is found in coastal intertidal rock pools, as they grow, these hermit crabs prefer to occupy *Buccinum undatum* shells and are increasingly found in subtidal areas such as the English Channel. Thus, for *P. bernhardus* noise from ships represents a relevant anthropogenic stimulus. A recent laboratory study has shown that the time taken for *P. bernhardus* to choose a new

shell decreases significantly in the presence of white noise (Walsh et al., 2017). While the effects of noise on shell assessment (Walsh et al., 2017) and antipredator behaviour (Chan et al., 2010b) have been analysed in isolation in different species of hermit crabs, the effects of noise on the ability to integrate information about the shell resource and predation threat has yet to be investigated.

Here, we investigate the effects of ship noise on the ability of hermit crabs to use tactile and visual information to choose a shell of optimal quality and to adjust their shell assessment behaviour in the visual presence of a predator. A common predator of *P. bernhardus* is the common shore crab *C. maenas* and previous studies have shown that hermit crabs respond to their chemical cues (Briffa et al., 2008b; Rotjan et al., 2004). Under normal circumstances the duration of shell investigation and chance of a hermit crab exchanging shells increases with the potential gain in shell quality (Elwood, 1995; Elwood and Stewart, 1985; Tricarico and Gherardi, 2007; Turra and Gorman, 2014) but decreases with predation risk (Briffa and Austin, 2009; Rotjan et al., 2004), reflecting a trade-off between the costs and benefits of changing shells. If this trade-off between shell quality and predation risk is altered by the presence of noise, this would indicate that anthropogenic noise reduces the ability of hermit crabs to integrate pertinent information across different sensory channels. We predict that hermit crabs will respond to the visual predator cue by altering their shell assessment and that this is influenced by the quality of shell a hermit crabs occupies, that is, crabs in small shells (50% of its preferred shell based on the crabs own body weight) will have a large shell gain (50%) but are also more exposed to predators while crabs in larger shells (80% of its preferred shell) have a lower shell gain (20%) but are less exposed to a predator. We predict that crabs in small shells will therefore show greater

responses to the predator cue. Moreover, if noise disrupts information gathering across sensory channels, we expect crabs to alter their shell dependent predator response in the presence of noise. Thus, the effect of original shell size on responses to a predator cue should be reduced in the presence of noise. Thereby, we aim to address a current gap in knowledge about how the effects of anthropogenic noise might impact the integration of behaviour across the different sensory channels that animals rely on in nature.

3.3 Materials and methods

3.3.1 Collection and husbandry of hermit crabs

P. bernhardus inhabits subtidal as well as intertidal marine habitats. For practically of sampling, we collected *P. bernhardus* from the rocky intertidal of Hannafore Point, Cornwall, UK (50° 20' 42'' N, 4° 28' 0'' W) adjacent to the English Channel and next to a local fishing harbour between November 2016 and January 2017. We transported the animals directly to a temperature-controlled room at the University of Plymouth. The room was maintained at 15 °C with a 12:12 h light:dark cycle and hermit crabs kept in a single holding tank containing 125 l of continuously filtered and aerated seawater (Briffa and Elwood, 2007) taken from the laboratory supply obtained from the seaward side of Mount Batten pier (50° 21' 34'' N, 4° 8' 8'' W) in Plymouth Sound at spring tides. We fed crabs in this stock tank once a week with white fish.

At least 16 hours before the observation, we removed crabs with a bench vice from their shell, sexed and weighed each individual. Crab weight ranged from 0.18 to 1.61 g (mean weight \pm SE = 0.798 \pm 0.32 g, $N = 59$). Each crab was assigned a *Littorina littorea* shell of either 50% or 80% of its preferred shell weight based on a regression

line relating preferred shell weight to body weight (Briffa and Elwood, 2007; Dowds and Elwood, 1983). We housed the crabs in individual white plastic dishes of 15 cm diameter containing continuously aerated seawater to a depth of 5 cm. Since the shell weight preferences of females are subject to change during the breeding season, we used only male crabs without damaged appendages, visible parasites or recent moulting in the study (Briffa and Elwood 2007). After the observations we returned the animals unharmed to the sea at the collection point.

3.3.2 Tank set-up and sound analysis

We carried out the observations in an 80 x 50 x 50 cm sized glass tank filled with ~ 130 l (to a depth of 40 cm) of seawater from the laboratory supply (Figure 3-1). We placed the tank on a free-standing trolley and cushioned it with at least 1 cm Styrofoam plates between tank and trolley as well as the trolley and floor.

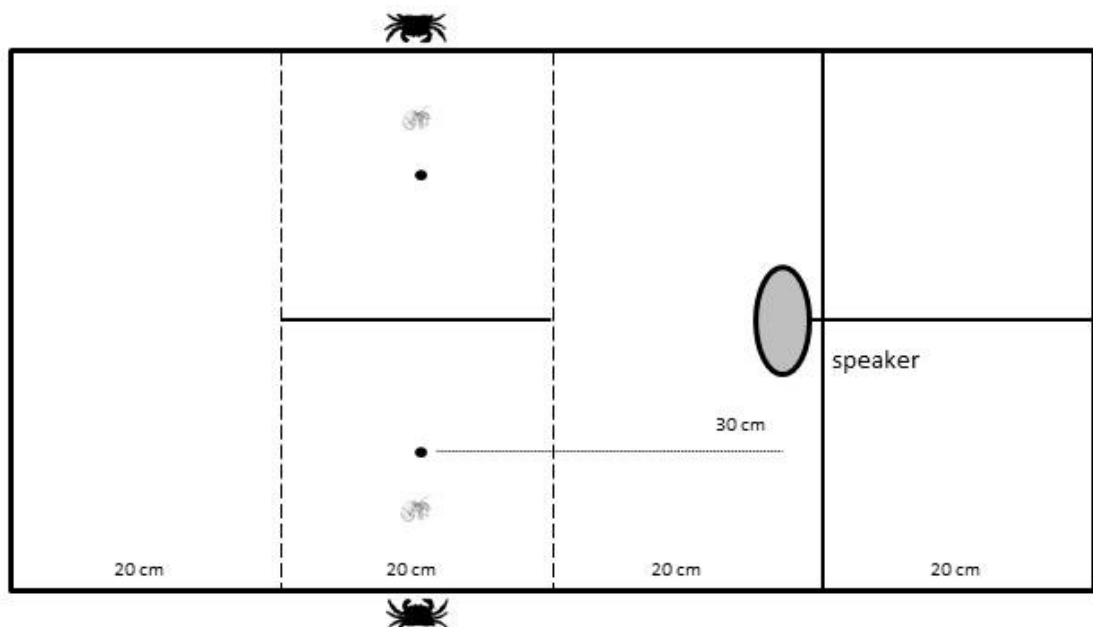


Figure 3-1 Tank set-up and observation arena (plan view). The dotted lines represent the mesh to separate the arena from the rest of the tank. The blank line represent the opaque plastic sheet to separate the hermit crabs. The empty shells were placed in the centre of the arena at 30 cm distance to the speaker. The visual predator cue was placed outside the tank and hermit crabs were placed between the shell and the predator cue.

The speaker was suspended in the tank from a cushioned bamboo stick at 20 cm distance to one end of the tank, such that it was fully submerged in the seawater. To ensure that crabs were exposed to similar sound conditions, we designed two 20 x 20 cm arenas within the larger tank at equal distances from the speaker. The centre of each arena was 30 cm from the centre speaker and the other end of the tank. No substrate was provided on the arena floors, as this is known to interfere with the locomotion and general activity of hermit crabs and other non-swimming crustaceans (Tidau and Briffa, 2019; Wale et al., 2013a; Walsh et al., 2017). The arenas were divided by an opaque 15 cm high plastic sheet. To disrupt the particle motion resulting from the sound playbacks as little as possible while preventing the crabs from directly escaping from the arena, we constructed the walls of each arena from 1 x 1 cm mesh-size plastic mesh. For the predator cue, we placed a plastic model crab of approximately 10 cm width in an upright position outside of the tank and cantered to the arena such that it was visible from inside the arena imitating the natural predator *C. maenas* (Briffa et al., 2008b; Rotjan et al., 2004).

While some studies use white noise as a substitute sound source to test the effect of anthropogenic noise pollution on animals (Chan et al., 2010a; Stahlman et al., 2011; Walsh et al., 2017), most noise studies utilise playbacks of actual anthropogenic pollutants, for example, ships. Ship noise and white noise playbacks not only differ in their spectral properties (frequency, amplitude) but also in their temporal pattern and predictability. Compared with white noise, which is characterised by equal energy intensity across frequencies (Barber et al., 2010), ships produce unique acoustic signals depending on factors such as speed and load (Hildebrand, 2009). Consequently, ships produce a more unpredictable signal compared with artificial white noise. It is known

that the stress induced by a stimulus is linked to its predictability (Francis and Barber, 2013; Koolhaas et al., 2011) and that for this reason less predictable stimuli are likely to be more distracting to animals. Relatively few studies have formally compared the effect of artificial white noise and playbacks of anthropogenic noise pollutants (Bent et al., 2018; Bermúdez-Cuamatzin et al., 2018; Holles et al., 2013), but where this has been done noise from anthropogenic pollutants tends to be similarly (Bermúdez-Cuamatzin et al., 2018) if not more distracting than white noise in terms of behaviour (Bent et al., 2018; Holles et al., 2013). For these reasons, we used three ship noise playbacks along with corresponding ambient control sounds from the same sites recorded at three major UK harbours. These recordings were used in previous studies in which the sample location, ship size and speed were detailed (Simpson et al., 2015; Wale et al., 2013a). We used Audacity 2.1.2 (Audacity Team, 2016) to create a total of six sound tracks for playback to the crabs, of either ambient control sound or ship noise. In the case of ship noise tracks, we alternated 2 min of ship noise with 2 min of ambient sound including 15 s fading in and out to simulate noise of passing ships. We assigned the crabs randomly to one of the two sound treatments (ambient control/ship noise). Within each of these treatments crabs received one of three alternative sound recordings of ship noise or ambient sound, as appropriate for their treatment group. These recordings were alternated between the successive observations (for details on the noise exposure and behavioural observation see section below).

For the playbacks of the sound tracks, we used a Toshiba Portégé R830-13C laptop (Tokyo, Japan) connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping Town, China) and an underwater speaker (DNH Aqua-30 underwater speaker, effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway). To

characterise the acoustic properties of our playbacks within the laboratory aquarium we undertook a spectral analysis as follows. We re-recorded the six sound tracks at the centre of the arena at 30 cm distance to the speaker and 10cm to the tank wall at 1 – 2 cm distance to the bottom of the tank with an omnidirectional hydrophone HTI-96-MIN (with inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V μ P; frequency range 0.002 – 30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave signals from a function generator with a measured voltage recorded in line on an oscilloscope). We used PAMGuide (Merchant et al., 2015) for MATLAB R2015b (MathWorks, 2015) to perform a power spectrum analysis of 60 s recording with Hann evaluation window, overlap 50%, 0.25 s window length, 100 – 3 000 Hz bandwidth normalised to 1 Hz. The three ambient sound tracks were played back so that they had an average sound pressure level of 80.03 dB RMS re 1 μ Pa (ambient A: 76.97, ambient B: 82.95, ambient C: 80.17) and the ship noise had an average of 123.5 dB RMS re 1 μ Pa (ship A: 127.5, ship B: 122.7, ship C: 120.5) at 1 000 Hz (Figure 3-2; Table 3-1).

Table 3-1 Sound intensity of the six playbacks and system’s self-noise: Minimum amplitude, maximum amplitude, average amplitude between 100 – 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa recorded in the centre of the arena and 30 cm distance to the speaker. Filtered for 100 – 3 000 Hz.

Playback	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1 000 Hz
Ship noise playback A	97.15 at 625 Hz	147.6 at 100 Hz	118.8	127.5
Ship noise playback B	98.4 at 2305 Hz	148.0 at 100 Hz	118.3	122.7
Ship noise playback C	97.66 at 625 Hz	148.7 at 100 Hz	119.1	120.5
Ambient playback A	51.26 at 2324 Hz	123.9 at 100 Hz	75.43	76.97
Ambient playback B	56.05 at 2325 Hz	128.3 at 100 Hz	80.9	82.95
Ambient playback C	54.93 at 2320 Hz	123.6 at 100 Hz	79.18	80.17
System self-noise	49.15 at 2320 Hz	110.7 at 100 Hz	57.66	57.55

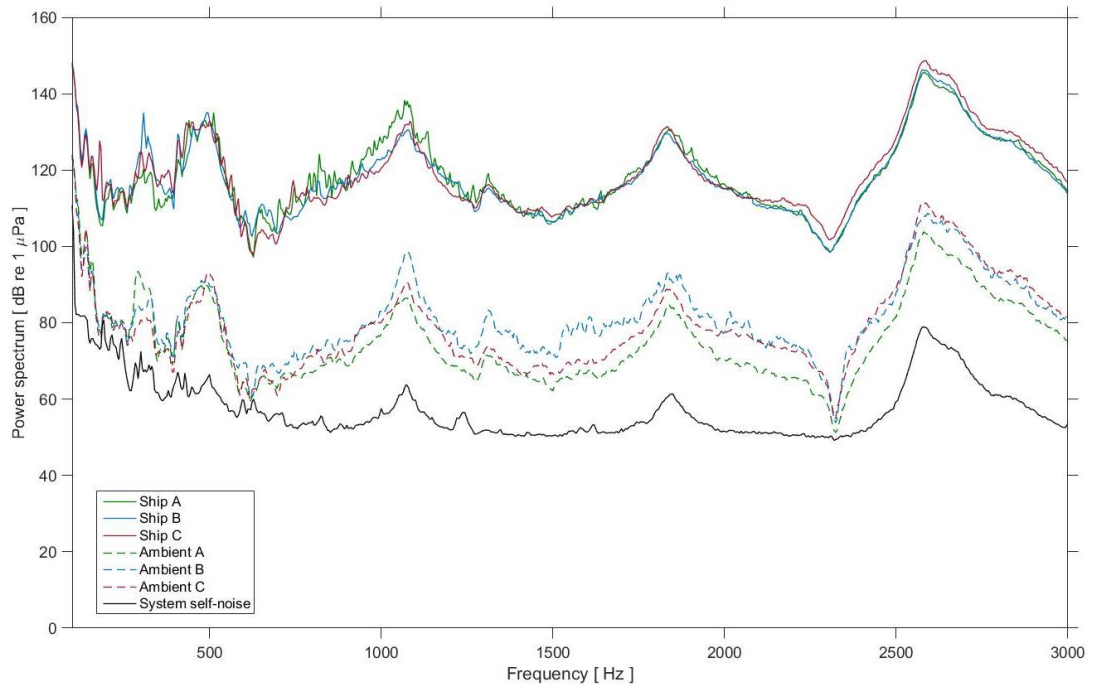


Figure 3-2 Power spectrum for three ship noise playbacks and three corresponding ambient sound playbacks recorded at 30 cm distance to the speaker. The system self-noise characterises the sound output by the equipment without playbacks. Filtered for 100 – 3 000 Hz frequency bandwidth.

These sound levels were similar to those in previous studies on crustaceans (Wale et al., 2013a; Wale et al., 2013b). We note that hermit crabs are likely to perceive the particle motion component of sound rather than the measured sound pressure levels (Breithaupt, 2002; Popper et al., 2001). However, as in previous studies (for instance, Herbert-Read et al., 2017; Wale et al., 2013a; Wale et al., 2013b), and due to unresolved challenges of tank acoustics (Rogers et al., 2016) we analysed the power spectrum of the sound pressure for each playback to make sure that we exposed crabs to two distinctive sound conditions namely ship noise and ambient control, rather than attempting to establish absolute noise sensitivity levels for hermit crabs.

3.3.3 Experimental design and behavioural analysis

We designed a fully orthogonal experiment with the three factors; sound condition (ambient control/ ship noise), predator cue (absent/ present) and initial shell size (50% PSW/ 80% PSW). The combination of these treatments resulted in 8 treatment groups. During each observation session, our set-up containing two arenas allowed us to concurrently expose two individuals (that were unable to interact with one another) to the same sound track. At the start of the session, we placed a shell of 100% preferred size for the crab allocated to each arena with the aperture facing downwards in the middle of each arena. After starting the sound playback, we placed the crabs in their allocated arenas with the aperture of their gastropod shells facing upwards. To avoid the effect of shell size being confounded by time of day, we always observed concurrently a crab starting in the observation in a 50% adequate shell and a crab starting the observation in an 80% adequate shell, one in each of the two observation arenas. To avoid confounding the data through any directional bias the position (left or right arena) we alternated the two shell size treatments between arenas across consecutive observations. On each day of observation, we collected data from a similar number of crabs from each of the four ship noise and predator cue combinations, and the order of treatment combinations was varied from day to day.

The shell assessment behaviour was recorded with a Canon Legria HF R47 (Tokyo, Japan) for a maximum of 25 min (up to 5 min were allowed for crabs to emerge from their gastropod shell at the start of the observation and 20 min of behaviour were then quantified). The videos were scored using The Observer version 12 (Noldus IT, Wageningen, The Netherlands) event logger software blind to the sound and predator cue treatments. We scored the frequency, duration, and latency

for each of the behaviours. The observation started when the crab had emerged from its shell and placed at least one of its appendages on the bottom of the tank. During the 20 min of observation the crabs were continuously exposed to either ambient control sound or ship noise playback as described above. We recorded the total decision time defined by the time from the start of the observation when crabs contacted the bottom of the tank with at least one walking leg to the point where the crabs had made a clear decision to reject either the new, optimal shell or the initially occupied shell. We designated the final decision point as that time at which crabs had moved one body length away from either the rejected optimal shell or the previously occupied shell. We also recorded whether crabs contacted the optimal shell with their antennae, whether they entered the optimal shell. For those crabs that did enter the optimal shell we recorded whether or not they finally accepted the optimal shell. Observations were terminated when one of the following conditions was met: The crab swapped into the optimal shell and moved at least as far away from the old shell as the length of its body (“optimal shell accepted”), the crab had contact with the 100% shell but did not swap into it and moved away at least as far as the length of its body (“optimal shell rejected”) or after 20 min, if the crab had no shell contact (“no decision”). Of the initial 77 observations conducted, 18 crabs made no contact with the optimal shell. Since their decision was not affected by any of the predictors (sound: $\chi^2_1 = 0.34$, $P = 0.56$; predator cue: $\chi^2_1 = 1.17$, $P = 0.28$, occupied shell: $\chi^2_1 = 0.02$, $P = 0.89$) or their interaction (see supplemental files for a complete results table), we excluded those 18 crabs from the analysis. This left a sample size of $N = 59$ crabs (Table 3-2).

Table 3-2 Experimental design and sample size in each treatment group. Summary of number of observations in each treatment combination: Sound treatment, predator cue and occupied shell. The number of crabs that changed shell in each case given in parentheses.

Sound treatment	Predator cue and occupied shell					
	Predator absent					
	50% shell			80% shell		
	<i>n</i>	entered	accepted	<i>n</i>	entered	accepted
Ambient sound (<i>n</i> = 32)	6	(6)	(6)	10	(8)	(7)
Ship noise (<i>n</i> = 27)	7	(5)	(5)	7	(4)	(2)
	Predator present					
	50% shell			80% shell		
	<i>n</i>	entered	accepted	<i>n</i>	entered	accepted
Ambient sound (<i>n</i> =32)	8	(8)	(8)	8	(4)	(4)
Ship noise (<i>n</i> =27)	6	(5)	(4)	7	(4)	(2)

3.3.4 Statistical analysis

To determine the effects of noise condition, predator cue and shell size on shell assessment behaviour we used general and generalised linear mixed effect models, as appropriate, implemented in the R-package lme4 (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2015). The fixed effects were sound treatment (ambient control/ ship noise), predator cue (absent/ present) and initial occupied shell size (50%/ 80%), and their interactions. Crab body weight was included as a covariate. To account for the potential pseudo-replication that might arise from re-using each of the three ship noise and three ambient control recordings across multiple observations, we included playback identity as a random (intercept) effect. Furthermore, we included a second random intercept to account for the paired observations within each observation session. Where necessary, the data (i.e. latency to contact the optimal shell, total decision time to accept or reject the optimal shell) were log transformed to improve normality, so that the assumption of the linear models would be met. For the binary response variables (displaying antennal contact, entering the optimal shell, accepting

the optimal shell), we used a binomial distribution and for continuous data (duration and latency), we used a Gaussian distribution. For models with non-Gaussian data we used likelihood ratio tests. To assess model fit we visually inspected the distribution of residuals.

Ethical note: No animals were harmed during the experiment. After the experiment each crab was supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences or permits were required for this study.

3.4 Results

There was no effect of the interaction between sound, predator cue and occupied shell size ($\chi^2_1 = 3.08$, $P = 0.08$) or any of the main effects, i.e. sound ($\chi^2_1 = 2.11$, $P = 0.15$), predator cue ($\chi^2_1 = 0.34$, $P = 0.56$) or initially occupied shell size ($\chi^2_1 = 0.99$, $P = 0.32$) on the latency to contact the optimal shell (Table 3-3, see appendix to this chapter for all result tables). Larger hermit crabs approached the optimal shell faster than smaller crabs ($\chi^2_1 = 7.44$, $P = 0.006$; Figure 3-3).

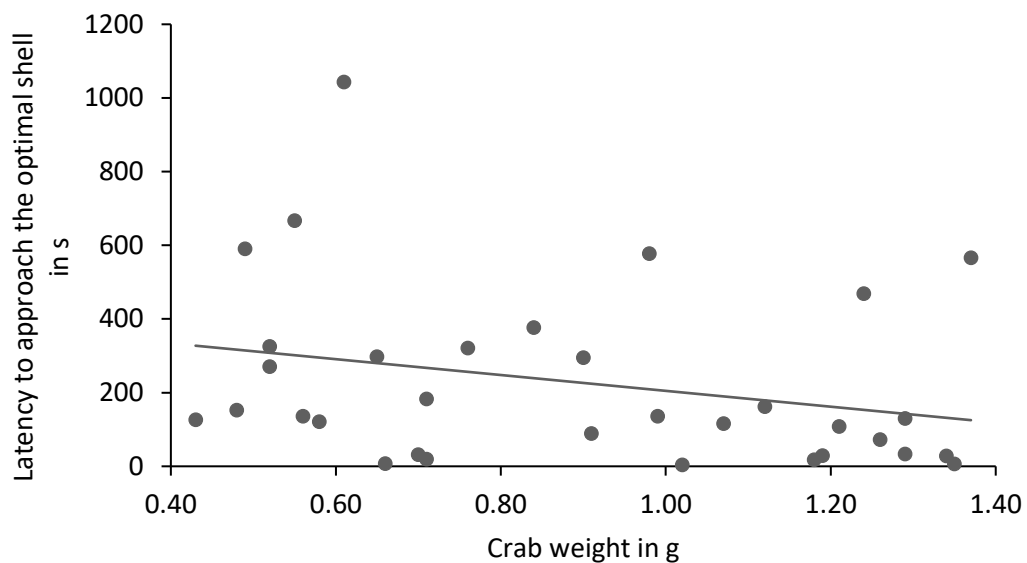


Figure 3-3 Effect of crab mass on latency to first contact the optimal shell.

For crabs that contacted the optimal shell, we analysed the effect of the predictors on the occurrence of antennal contact. Since not every crab decided to contact the optimal shell, we did not have sufficient data on the occurrence of antennal contact to calculate the three-way interaction. For those crabs that did contact the optimal shell, there were no significant two-way interactions: sound and predator cue ($\chi^2_1 = 1.51, P = 0.22$) or predator cue and occupied shell ($\chi^2_1 = 3.08, P = 0.08$; Table 3-4). However, under ambient sound conditions, hermit crabs in 50% shells were less likely to contact the optimal shell with their antennae compared to crabs in 80% shells whereas this pattern was absent in the presence of ship noise ($\chi^2_1 = 10.0, P = 0.002$; Figure 3-4). In the presence of a predator cue, more crabs displayed antennal contact with the optimal shell ($\chi^2_1 = 4.07, P = 0.04$; Figure 3-5).

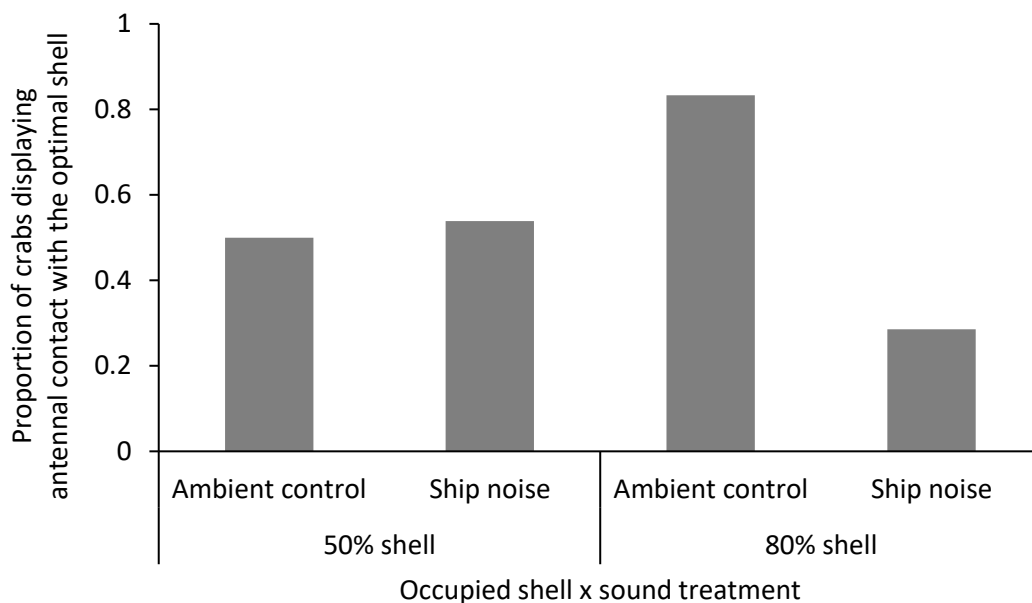


Figure 3-4 Effect of the interaction between sound treatment and occupied shell on the proportion of crabs that contacted the optimal shell with their antennae.

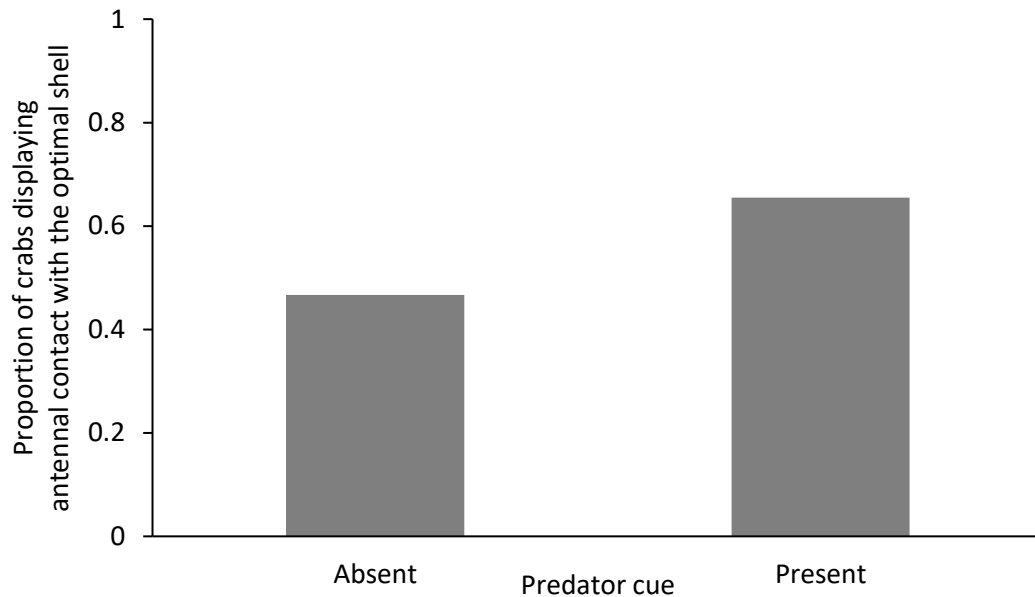


Figure 3-5 Effect of a visual predator cue on the proportion of crabs that contacted the optimal shell with their antennae.

Crabs which occupied a 50% shell were more likely to enter the optimal shell than crabs in 80% shells ($\chi^2_1 = 5.46$, $P = 0.02$; Figure 3-6; Table 3-5). We could not reliably calculate the three-way interaction for this decision since relatively few crabs with an 80% shell that were exposed to ship noise decided to enter the optimal shell (Table 3-5). None of the two-way interactions between sound and predator ($\chi^2_1 = 1.57$, $P = 0.21$), sound and occupied shell ($\chi^2_1 = 3.15$, $P = 0.08$), predator cue and occupied shell ($\chi^2_1 = 0.67$, $P = 0.41$) or the main effects other than occupied shell (sound: $\chi^2_1 = 2.58$, $P = 0.11$; predator cue: $\chi^2_1 = 0.17$, $P = 0.68$) had a significant effect on whether crabs entered the optimal shell. None of the factors or their interaction affected the latency to swap into the optimal shell.

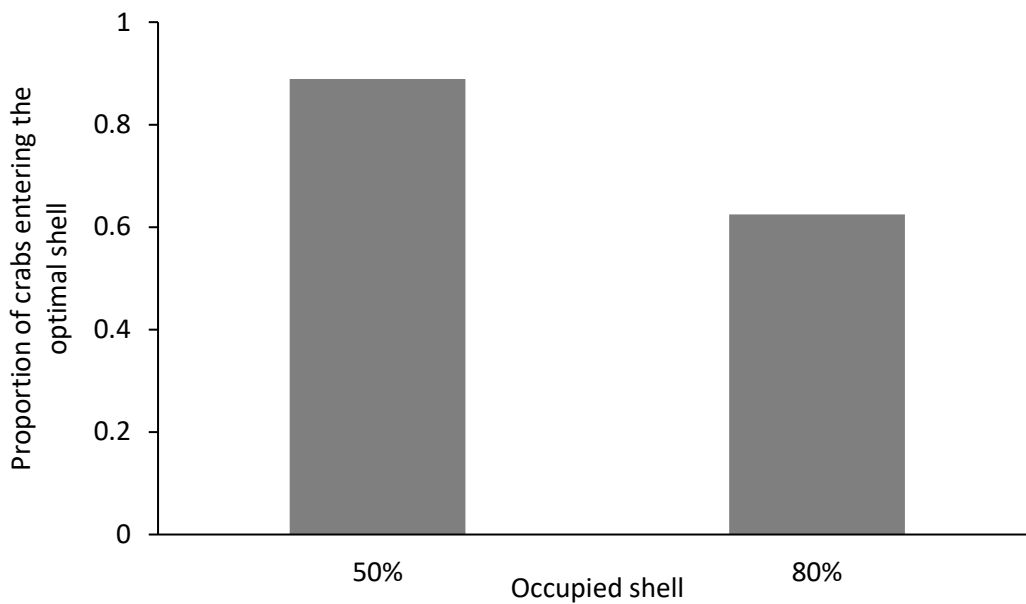


Figure 3-6 Effect of initially occupied shell on the proportion of crabs that swap and did not swap into the optimal shell.

For the final decision to accept the optimal shell, we could not calculate the three-way interaction as relatively few individuals with an 80% adequate shell that were exposed to noise chose to enter the optimal shell (Table 3-7). The decision was not affected by the interactions between sound and predator cue ($\chi^2_1 = 0.34, P = 0.56$), sound and occupied shell ($\chi^2_1 = 2.19, P = 0.14$), predator and occupied shell ($\chi^2_1 = 0.005, P = 0.94$) or predator cue ($\chi^2_1 = 0.38, P = 0.54$). However, under ambient sound conditions, crabs accepted the optimal shell more frequently than under noise conditions ($\chi^2_1 = 8.0, P = 0.005$; Figure 3-7). Crabs in a 50% shell accepted the optimal shell more often than crabs in an 80% shell ($\chi^2_1 = 11.67, P = 0.0006$; Figure 3-8).

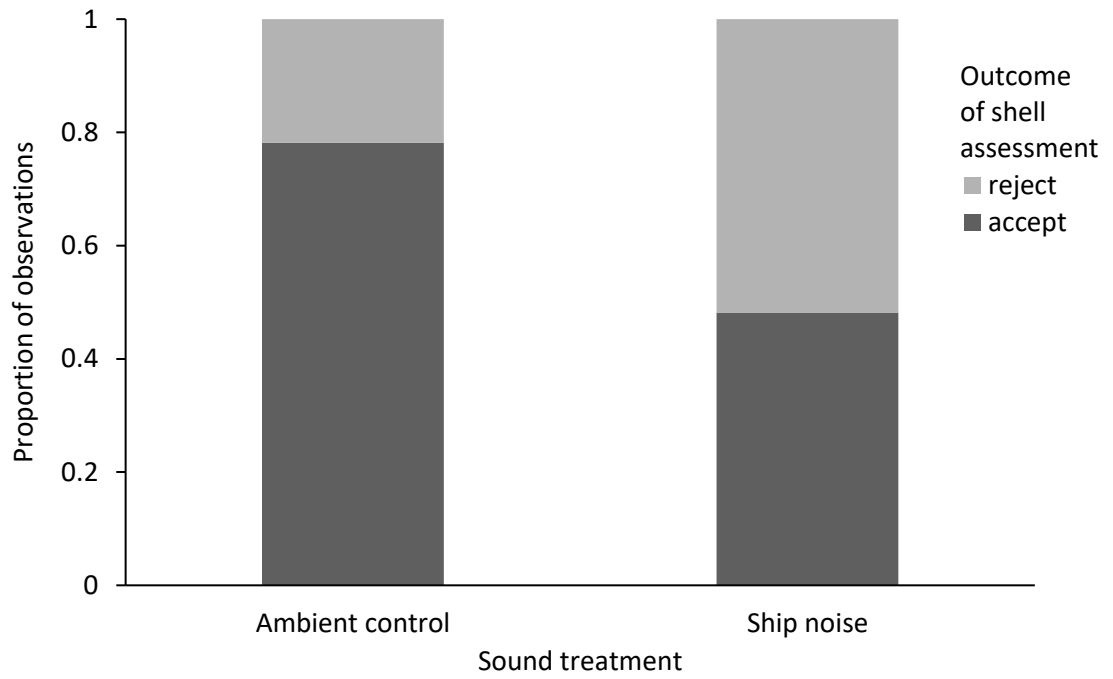


Figure 3-7 Effect of sound treatment on the decision of crabs to accept or reject the optimal shell.

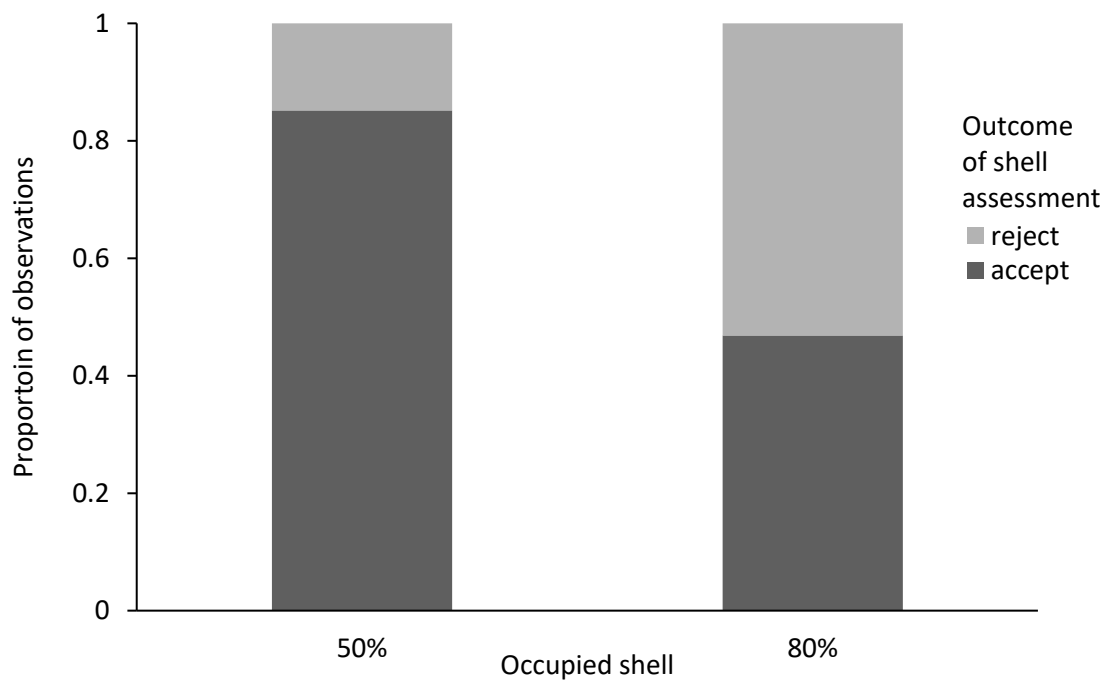


Figure 3-8 Effect of occupied shell on the decision of crabs to accept or reject the optimal shell.

There was a three-way interaction effect between sound, predator cue and occupied shell on the total decision time to accept or reject the optimal shell ($\chi^2_1 = 5.0$, $P = 0.03$; Figure 3-9; Table 3-8). Crabs in a 50% adequate shell and exposed to a predator took a longer total decision time under ambient control compared to ship noise. Crabs in 80% shells showed the opposite pattern, taking more time to decide under ambient sound than ship noise when the predator was absent, but being unaffected by the sound treatment when the predator was present. The total decision time decreased with crab weight ($\chi^2_1 = 7.23$, $P = 0.007$).

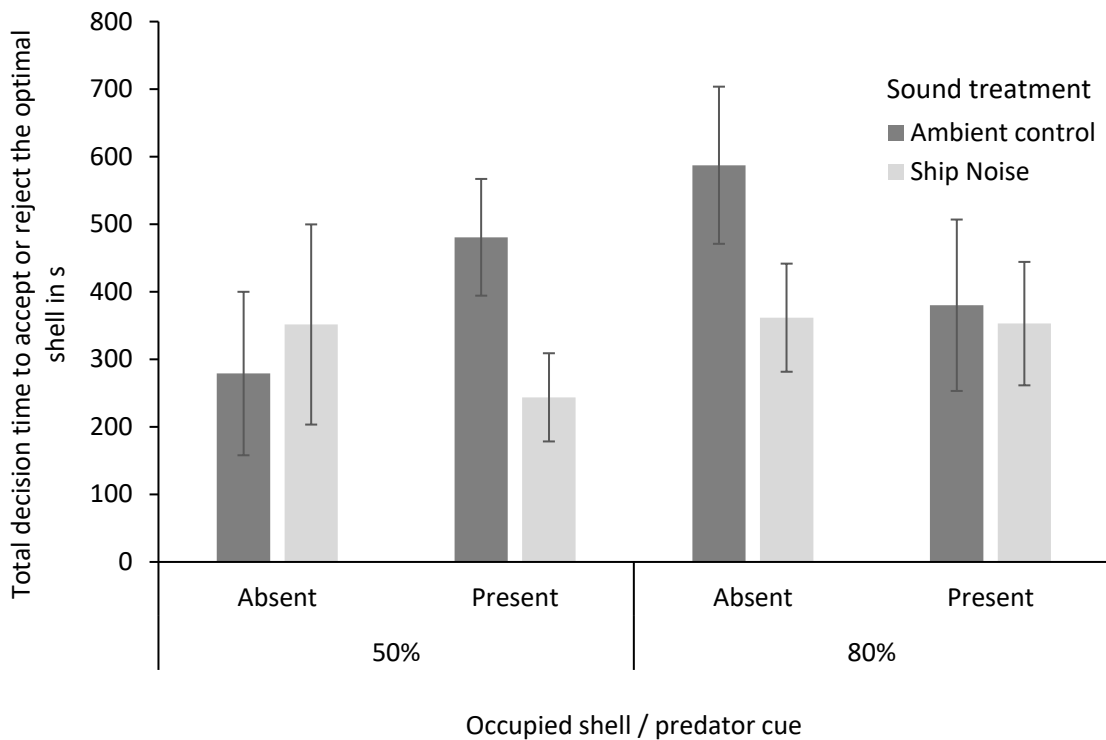


Figure 3-9 Effect of the three-way interaction between sound treatment, predator cue and occupied shell on the total decision time to accept or reject the optimal shell. Error bars show standard errors.

3.5 Discussion

Noise exposure significantly influenced the shell assessment behaviour of hermit crabs, disrupting both activities during shell assessment and the final decision to accept or

reject the optimal. *P. bernhardus* responded to noise in interaction with other (naturally occurring) cues in the case of shell assessment activities but also in isolation in the case of the final decision to accept the optimal shell. For hermit crabs, gastropod shells represent a critical resource, which determines not only survival but also growth and fecundity. Therefore, the assessment process and decision to exchange the current shell for an optimal one will directly influence an individual's fitness. These decisions can be complex because the benefits of swapping into a better shell must be balanced against the temporary predation risk during the assessment process, which might attract the attention of predators. On swapping shells, the weakly calcified abdomen is briefly exposed. Thus, crabs are usually less likely to swap shells when the risk of predation is high (Briffa et al., 2008a). The current data show that the way hermit crabs use information on these benefits and risks can be disrupted by changes to the sensory environment caused by anthropogenic noise.

The total decision time taken to find, assess, and then finally accept or reject the optimal shell was influenced by a complex three-way interaction between sound treatment, size of the initially occupied shell, and the visual predator cue. That crabs in a 50% shell show shorter decision time than crabs in an 80% shell under the control conditions (without predator cue and noise) is in line with previous studies demonstrating that the potential gain in shell quality influences the motivation for changing shells (Elwood, 1995). Further, predator cues affected crabs differently depending on the shell quality they hold and generally crabs exposed to predation risk tend to behave more cautiously (Briffa et al., 2008a). Here, crabs showed more cautious shell assessment steps such as the antennal contact in the presence of a predator cue. For crabs in a low quality 50% adequate shells, the visual predator cue

led to an increase in decision time under ambient sound but this effect was absent when ship noise was present. Thus, for crabs with the potential for a large increase in shell quality, ship noise appears to negate the normal effect of predator presence. Compared with crabs in a 50% shell, crabs in 80% shells took longer to assess shells in the absence of a predator cue than in its presence and the normal pattern observed under ambient sound was absent in the presence of ship noise (as in the case of crabs in 50% shells). A recent study on the hermit crab *Clibanarius vittatus* showed that the shell quality affects the response time to a predator cue and that crabs in better quality shells show longer startle response without predation risk than crabs exposed to a predator cue (Gorman et al., 2018) as we observed. Here, the decision-making duration of hermit crabs was influenced by two naturally occurring cues, shell quality and predation risk, as well as anthropogenic noise. Therefore, the present data show that anthropogenic noise can lead to changes in behaviour through interactions with other sources of information. Previous studies on the response to noise in crustaceans suggest that they adjust the timing or duration of their behaviour when noise is the only factor animals were exposed to. The common shore crab *C. maenas* retreated more slowly into shelters exposed to ship noise playbacks (Wale et al., 2013a) and the hermit crab *P. bernhardus* investigated shells more quickly under white noise (Walsh et al., 2017). Likewise exposed to white noise, the marine rock lobster *Panulirus longipes* took longer to emerge from shelter (Meyer-Rochow et al., 1982) and the Caribbean hermit crab *Coenobita clypeatus* let a predator approach closer before hiding (Chan et al., 2010a). Expanding on those studies, our results indicate that rather than acting in isolation, noise effects are also influenced by at least two other, naturally occurring factors, shell size and predation risk, both of which hermit crabs are likely to

experience frequently in nature (as pointed out in the introduction on the natural habitat of *P. bernhardus*). The shell quality has been shown to determine behaviour and physiological state in hermit crabs (Briffa and Elwood, 2000b; Briffa and Elwood, 2005). One of the few examples on the effects of ship noise and predation risk in interaction with physiological condition was on the European eel *A. anguilla*. Here, juveniles in poor condition decreased their startle response to ship noise (Purser et al., 2016). Even though the exact mechanisms remain unknown, the differences observed between hermit crabs in 50% (poorer condition) and 80% (better condition) adequate shells seem similar. Future research on examining the mechanisms underpinning interactions between noise and physiology could help to better explain these observed behavioural responses.

Further we found evidence that noise affects animals differently depending on the resource quality they hold and the complexity of the task. Under ambient conditions, crabs initially in 80% shells (which had relatively little to gain) employed more antennal contact during shell investigation compared to crabs initially in 50% shells (which could make a relatively large gain). This difference is likely to reflect the fact that those crabs in 80% shell had been presented with a more difficult choice than those in 50% shells and hence made greater efforts to assess the empty shell. In the presence of ship noise, however, this difference between crabs presented with easy and difficult choices (in terms of potential gain in shell quality) was absent, with no difference in the amount of antennal contact shown by crabs supplied with 50% and 80% adequate shells. Although it is difficult to disentangle the effects of motivation from those of task complexity it is likely that animals with more difficult decisions to make are susceptible to distraction by anthropogenic noise. As animals possess a finite

amount of attention and hence any attention directed towards a novel cue (e.g. ship noise) is unavailable for other tasks (Dukas, 2004). Thus, routine tasks that require attention, such as assessing empty shells, can be disrupted by novel stimuli. Blue jays *Cyanocitta cristata* have been shown to divert their attention from a predator stimulus under more difficult and complex foraging tasks (Dukas and Kamil, 2000). That the difficulty of a task has an impact on the ability to detect and respond to a stimulus (such as a predator) is known from other studies on several bird species and the three-spined sticklebacks *Gasterosteus aculeatus* (for an overview see Lawrence, 1985). In humans it has been shown that with increasing difficulty of a task less attention was spent on a second stimulus; the perception of the distracting stimulus depends on the cognitive load of the focus task (Rees et al., 1997). Therefore, the fact that crabs with less motivation and a more difficult decision were more susceptible to the effects of noise provides additional support for the distracting effect of noise (such as in the distracted prey hypothesis) which has been shown across humans and non-human vertebrates and invertebrates. Future research on the cognitive processes underlying these observations will allow to better understand the causes and consequences of noise.

Anthropogenic noise exposure can also alter the final outcome of critical decision-making. Under anthropogenic noise fewer crabs accepted the optimal shell; a similar result to that recently obtained in crabs exposed to white noise (Walsh et al., 2017). Rather than being affected by noise in interaction with the additional factors of predator cue and shell size, the final decision to accept or reject the optimal shell was influenced by noise itself. Suboptimal shells can inhibit growth and reproductive success as females carry their eggs within the shell (Bertness, 1981a). Furthermore,

shell fit is important for protection against predators. When shells are too small hermit crabs cannot withdraw fully into the shell and hence are most exposed (Angel, 2000). As a consequence, anthropogenic noise could have implications beyond individual crabs at the population level. This effect could also be multiplied as vacated shells serve as a resource for smaller crabs and cascade through the population, a process known as vacancy chain previously described in hermit crabs (Briffa and Austin, 2009; Lewis and Rotjan, 2009). Thus, noise appears to make it more difficult for hermit crabs to utilise information about predation risk and shell quality. The decisions that are underpinned by such information are also dependent on motivational state, and here, we also investigated whether noise might interact with the motivation of crabs to change shells.

Our findings are broadly in line with the “distracted prey hypothesis” which suggests that animals seem to get distracted by noise when assessing the potential threat of a predator, allocating part of their limited attention away from the threat towards the distracting stimulus (Chan et al., 2010b). For instance, prey showed decreased anti-predator response (Bruitjes et al., 2016; Bruitjes and Radford, 2013; Purser et al., 2016), were slower to be startled by a stimulated predator attack (Simpson et al., 2015) and were caught more efficiently and quickly (Nedelec et al., 2015). What we now show is that these patterns of altered responses to information concerning predation threat interact with altered responses to other cues, in this case tactile and visual information gathering concerning resource quality. Moreover, distraction appears to alter the ability of crabs to integrate this information on resource value with information on the risk of predation. Thus, anthropogenic noise pollution alters the multisensory integration of cues during the information gathering,

assessment and decision-making process surrounding utilisation of a critical resource in the European hermit crab. To the best of our knowledge, there are no other studies that have compared the effect of noise (an anthropogenic pollutant) with the effects of variation in the complexity of a cognitive task (driven in this case by the size of the initial occupied shell) and the visual presence of an external threat (visual presence of a predator). As animals live in complex environments with competing information and attention demands (Talsma et al., 2010), it is important to understand the interactive effect of anthropogenic noise with biologically relevant factors such as predator cue and resource value. Under noise, stimulus-selective attention, where less relevant information is ignored (Dukas, 2002), seems to be compromised. The result that hermit crabs choose an optimal shell less often under anthropogenic noise is likely a consequence of distraction of their limited attention away from the pertinent natural cues towards the anthropogenic stimuli. The decision to accept or reject an optimal shell has not only implications for the fitness and survival of an individual but potentially cascades up to the population level by reproduction, exposure to predators and freeing resources for conspecifics. Our results provide evidence that pollutants such as noise can act across sensory modalities (Halfwerk and Slabbekoorn, 2015) and distract information gathering and decision-making of animals, here in using tactile and visual cues for resource assessment. Cross-modal distraction from noise is not limited to the predation context such as in the common cuttlefish *Sepia officinalis* which changed its colour more frequently during a playback of anthropogenic noise (Kunc et al., 2014) or animals but has been shown in humans as well (Ljungberg and Parmentier, 2012; Parmentier et al., 2011). Here, we demonstrate multi-modal effects of HIREC on the sensory environment of animals and compromise the use of

biologically relevant cues, specifically that ship noise disrupts both tactile and visual information gathering under predation risk in the European hermit crab by interacting with these information channels.

3.6 Appendix to the chapter

Table 3-3 Latency to contact the optimal shell (bold indicates significant effects).

Factors and their interactions	χ^2	df	P-value
Sound * predator cue * occupied shell	3.08	1	0.08
Sound * predator cue	0.02	1	0.88
Sound * occupied shell	0.01	1	0.91
Predator cue * occupied shell	2.11	1	0.15
Sound	1.95	1	0.16
Predator cue	0.34	1	0.56
Occupied shell	0.99	1	0.32
Crab weight	7.44	1	0.006

Table 3-4 Occurrence of antennal contact with the optimal shell (bold indicates significant effects).

Factors and their interactions	χ^2	df	P-value
Sound * predator cue * occupied shell	NA	NA	NA
Sound * predator cue	1.51	1	0.22
Sound * occupied shell	10.0	1	0.002
Predator cue * occupied shell	3.08	1	0.08
Predator cue	4.07	1	0.04
Crab weight	1.91	1	0.17

Note that since not every crab decided to contact the optimal shell, we did not have sufficient data on the occurrence of antennal contact to calculate the three-way interaction.

Table 3-5 Occurrence to enter the optimal shell (bold indicates significant effects).

Factors and their interactions	χ^2	df	P-value
Sound * predator cue * occupied shell	NA	NA	NA
Sound * predator cue	1.57	1	0.21
Sound * occupied shell	3.15	1	0.08
Predator cue * occupied shell	0.67	1	0.41
Sound	2.58	1	0.11
Predator cue	0.17	1	0.68
Occupied shell	5.46	1	0.02
Crab weight	0.88	1	0.35

Note that since relatively few crabs with an 80% shell that were exposed to ship noise decided to enter the optimal shell, there was not sufficient data to calculate the three-way interaction.

Table 3-6 Latency to enter the optimal shell (bold indicates significant effects).

Factors and their interactions	χ^2	df	P-value
Sound * predator cue * occupied shell	1.62	1	0.20
Sound * predator cue	0.20	1	0.66
Sound * occupied shell	0.41	1	0.52
Predator cue * occupied shell	0.91	1	0.34
Sound	0.30	1	0.59
Predator cue	1.88	1	0.17
Occupied shell	0.56	1	0.45
Crab weight	0.95	1	0.33

Table 3-7 Final decision to accept the optimal shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
Sound * predator cue * occupied shell	NA	NA	NA
Sound * predator cue	0.34	1	0.56
Sound * occupied shell	2.19	1	0.14
Predator cue * occupied shell	0.005	1	0.94
Sound	8.0	1	0.005
Predator cue	0.38	1	0.54
Occupied shell	11.67	1	0.0006
Crab weight	0.48	1	0.49

Note that since relatively few individuals with an 80% adequate shell that were exposed to noise chose to enter the optimal shell, there was not sufficient data to calculate the three-way interaction.

Table 3-8 Total decision time to assess the optimal shell (bold indicates significant effects).

Factors and their interactions	χ^2	df	P-value
Sound * predator cue * occupied shell	5.0	1	0.03
Crab weight	7.23	1	0.007

Note that results were obtained using a model simplification approach, and as such reporting is restricted to the highest order effects, where significant interactions are present.

Chapter 4: Anthropogenic noise reverses grouping behaviour in hermit crabs

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4.1 Abstract

Noise is a form of human-induced rapid environmental change, and mounting evidence suggests that it can affect the sensory environment and consequently the decision-making ability of animals. However, while the effects of anthropogenic noise on individual organisms in the context of movement patterns, foraging and predation risk have been reported, relatively little is known about how noise impacts groups and intraspecific interactions. Here we investigated the effects of anthropogenic noise on grouping preference (i.e. being with conspecifics or alone) in the European hermit crab *Pagurus bernhardus*. Hermit crabs live in empty gastropod shells and frequently fight with each other to gain an optimal-fitting shell. Thus, crabs' grouping preference may depend on the optimality of their own shell and thus on their motivation to gain another. To test the effect of shell size and its interaction with noise exposure on grouping preferences, crabs were housed in either suboptimal or optimal shells before being exposed to playbacks of either ship noise or an ambient sound (control) and given the choice to group with one or five conspecifics or to remain alone in a neutral zone. Crabs occupying suboptimal shells had a longer latency to enter the zone with a single crab than crabs in optimal shells. This difference was only seen in the ambient

sound treatment, disappearing completely under ship noise. Under ambient sound, crabs in optimal shells spent most of their time close to a single crab, while crabs in suboptimal shells showed no clear preference. However, exposure to ship noise reversed the effect of shell quality on grouping preference. Our results demonstrate that exposure to anthropogenic noise can alter not only individual behaviour but also social behaviour.

4.2 Introduction

Assessing diverse cues from the environment is an essential component of animals' decision-making. However, human-induced rapid environmental change (HIREC) (Sih et al., 2011), caused by noise, chemicals or light, can disrupt information gathering, processing and assessment in animals both by inducing physiological stress (for review Kight and Swaddle, 2011) and by changing animals' sensory environment (for review Halfwerk and Slabbekoorn, 2015; Tuomainen and Candolin, 2011). An example of unimodal interference by noise is the masking of acoustic cues and signals documented in terrestrial and aquatic taxa (Barber et al., 2010; Brumm, 2004; Clark et al., 2009; Foote et al., 2004; Halfwerk et al., 2012; Heiler et al., 2016; Lampe et al., 2012; Spiga, 2016; Sun and Narins, 2005). This has been demonstrated across behavioural contexts such as territory defence (Brumm, 2004), mating (Sun and Narins, 2005) and the detection of habitats (Pine et al., 2012), conspecifics (Codarin et al., 2009) and predators (Curé et al., 2013). In addition to these unimodal effects, noise can also have cross-modal effects, disrupting information processing and assessment of non-acoustic cues (Halfwerk and Slabbekoorn, 2015). For instance, underwater noise has been shown to alter behaviours related to visual and chemical cues used in predator avoidance and detection (Hasan et al., 2018; Kunc et al., 2014; McCormick et

al., 2018). Such effects have been explained by distraction (Chan et al., 2010b) due to limited attention in animals (Dukas, 2004), which modulates the multisensory integration (Talsma et al., 2010). This effect has also been termed 'info-disruption' (Lürling and Scheffer, 2007) and 'sensory pollution' (Halfwerk and Slabbekoorn, 2015). In addition to these sensory effects noise has been shown to cause physiological stress (Kight and Swaddle, 2011) which could also alter animal behaviour. Cross-modal noise pollution might therefore adversely affect animals even though they do not use acoustic communication.

The behavioural effects of anthropogenic noise have frequently been studied in two contexts. First, many studies have focused on individual behaviour, including impacts on movement, foraging and responses to predators (Chan et al., 2010b; Luo et al., 2015; Shafiei Sabet et al., 2015; Siemers and Schaub, 2011; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a; Wisniewska et al., 2018). Second, studies on social behaviour have focused on the potential masking of acoustic communication in insects, anurans, birds and mammals (Brumm and Slabbekoorn, 2005; Erbe et al., 2016). In contrast, the effect of noise on non-vocal social behaviour, such as shoaling, has received relatively little attention. Noise exposure experiments on intraspecific interactions have found altered parental care (Maxwell et al., 2018; Nedelec et al., 2017) and social interactions (Bas et al., 2017). A basic aspect of social behaviour is that individuals choose to join groups such as flocks or shoals, which requires animals to assess cues from their environment. Groups are associated with a range of benefits (reviewed by Krause and Ruxton, 2002) such as decreased vigilance (Powell, 1974; Ward et al., 2011), finding and exploiting resources (Bazazi et al., 2012; Childress and Herrnkind, 2001) and conservation of heat (Wilson, 2009). On the other hand, there

are also costs associated with group membership such as increased attack rates (for large groups Mooring et al., 2004), elevated parasite burden (Côté and Poulinb, 1995; Daviews et al., 1991) and foraging competition (Rieucau and Giraldeau, 2009). Noise has been shown to alter grouping (Fewtrell and McCauley, 2012; Herbert-Read et al., 2017) and appears to be highly variable across study systems and noise regime. Mediterranean spiny lobsters *Palinurus elephas* (Filiciotto et al., 2014) and bottlenose dolphins *Tursiops truncatus* (Bas et al., 2017) exhibited reduced grouping behaviour when exposed to boat noise. In contrast, noise led to increased grouping in the trevally *Pseudocaranx dentex* (Fewtrell and McCauley, 2012). Divergent social responses to noise can even be seen within the same species. In the European sea bass *Dicentrarchus labrax* the social behaviour differed with the noise source and regime: fish shoals were less coordinated (in cohesion, direction, speed and directional changes) when exposed to pile driving (Herbert-Read et al., 2017) but they increased grouping activities under ship noise (Neo et al., 2018). In the Atlantic bluefin tuna *Thunnus thynnus* noise led to less concentrated and coordinated shoals, but individuals increasingly swam towards one another and seemed more likely to join a group (Sara et al., 2007). Although less intensively studied (compared to aquatic examples) anthropogenic noise can also affect non-vocal social behaviour in terrestrial species. In Carolina chickadees *Poecile carolinensis* and tufted titmice *Baeolophus bicolor* flocking density increased in the presence of traffic noise (Owens et al., 2012). Thus, as well as changing the propensity to join groups, noise can influence interactions within groups.

In marine environments, grouping is common among cetaceans and fish (i.e. shoaling) but has also been demonstrated in crustaceans as a response to predation risk (Evans et al., 2007; Ratchford and Eggleston, 1998). Owing to their association with

gastropod shells, hermit crabs represent an ideal model organism for studying the effects of underwater noise on the drivers of grouping behaviour. They are globally distributed crustaceans characterised by a weakly calcified abdomen which they protect from predators (Vance, 1972) and environmental extremes (Taylor, 1981; Young, 1978) by occupying empty gastropod shells. They usually obtain these either when discarded by others or through shell fights with other crabs (predation of snails is rare; Elwood and Neil, 1992). Hermit crabs need to search for empty shells of increasing size to allow for growth or, in the case of females, during the reproductive season to accommodate their eggs (Angel, 2000; Bertness, 1981a). The extent of grouping in hermit crabs differs between species, from those that are solitary (Hazlett, 1979) to those that form aggregations of hundreds or even thousands of individuals as in *Clibanarius erythropus* (Gherardi, 1991). The drivers for grouping can differ widely between species. These include attraction to foraging sites (Hazlett, 1979; Hazlett, 2015; Hazlett and Winn, 1962), shell exchange (Gherardi and Vannini, 1993; Hazlett, 1978; Hazlett and Herrnkind, 1980) and predator defence (Bertness, 1981b). The need to obtain new shells could also influence grouping. Shell exchange markets as observed in the mangrove-dwelling hermit crab *Clibanarius laevimanus* and the thinstripe hermit crab *Clibanarius vittatus* (Gherardi and Vannini, 1993; Hazlett and Herrnkind, 1980), and vacancy chain processes in the European hermit crab *Pagurus bernhardus* (Briffa, 2013a), predict that associating with other crabs may increase the chances of finding an optimal shell (Gherardi and Vannini, 1993). In addition, the larger the group the lower the likelihood at the individual level of being preyed upon, an effect known as the dilution effect (Foster and Treherne, 1981; Gherardi and Benvenuto, 2001). On the other hand, larger groups can be more detectable (Krause and Ruxton, 2002) and for

hermit crabs their individual defence mechanisms, primarily withdrawing into their gastropod shell (Gherardi and Benvenuto, 2001) or fleeing (Mima et al., 2003; Rosen et al., 2009; Scarratt and Godin, 1992), might be a better responses to a predator attack than joining a group. Given this array of the potential costs and benefits of grouping, to make decisions on whether to join a group hermit crabs need to assess information from their environment across different sensory modalities, including tactile information on the size of the shell relative to their own size (smaller shells offer less protection).

As in other hermit crabs, *P. bernhardus* are frequently found in aggregations, and the factors described above are all likely to contribute to this (Elwood and Neil, 1992). Here we aimed to determine whether the decision to join a group in *P. bernhardus* is influenced by information on risk level (i.e. shell fit) and on the number of conspecifics in a group. We then asked whether the grouping patterns were altered in the presence of anthropogenic noise using ship noise playbacks and ambient controls. We predicted that, owing to a combination of shell exchange markets and the dilution effect, crabs in suboptimal shells would be more likely to join a group than crabs in optimal shells. Furthermore, if noise distracts hermit crabs and reduces their ability to use information on shell and group size, we expected these different grouping preferences of crabs in suboptimal and optimal shells (described above) to be altered by noise.

4.3 Methods

4.3.1 Collection and husbandry of hermit crabs

We collected *P. bernhardus* from the rocky intertidal of Hannafore Point, Cornwall, U.K. (50° 20' 42'' N, 4° 28' 0'' W) in May and July 2017 and transported them directly to the laboratory at the University of Plymouth, U.K. We kept the crabs in a temperature-controlled room at 15 °C with a 12:12 h light:dark cycle in a single holding tank containing 125 l of continuously filtered and aerated sea water (Briffa et al., 2008b). The laboratory sea water was obtained from the seaward side of Mount Batten pier (50° 21' 34'' N, 4° 8' 8'' W) in Plymouth Sound, U.K., at spring tides. We fed crabs *ad libitum* with white fish. To remove focal crabs from their original gastropod shells (at least 22 h prior to observations) we carefully cracked the shell with a bench vice, which allows the crab to be removed from its shell without injuring the crab. Afterwards the crabs were sexed and weighed. The crab weight ranged from 0.36 to 1.61 g (mean weight \pm SE = 0.84 \pm 0.045 g, $N = 45$). Based on a regression line relating preferred shell weight to body weight obtained from a previous shell selection experiment, where crabs across a range of sizes were provided with free access to a range of different-sized shells (Briffa and Elwood, 2007), we assigned a *Littorina littorea* shell of either 75% or 100% of its preferred shell weight to each crab. Although a range of other shell features might also influence preferences, the relation between crab weight and shell weight is the primary predictor of shell preference. To optimise the reliability, the shell selection experiment (Briffa and Elwood, 2007) was conducted using shells collected from the same location as the hermit crabs used in this study to minimise the effect of factors such as shell internal volume to weight ratio, which can differ between study sites. Furthermore, following a standard approach, only clean and intact shells, without

encrusting organisms, holes or damage to the aperture were used. Afterwards we housed crabs individually in a white plastic dish of 15 cm diameter containing continuously aerated sea water to a depth of 5 cm. Since the breeding season is likely to affect the behaviour of egg-carrying females, we used only male crabs without obviously damaged appendages, visible parasites or recent moult (Briffa and Elwood, 2007). After the observations we returned the animals to the sea at the collection point.

4.3.2 Tank set-up and sound analysis

We carried out the observations in glass tank (80 x 50 x 50 cm made of 1 cm thick aquarium glass) filled to a depth of 40 cm with sea water from the laboratory supply (~160 l). We placed the tank on a free-standing trolley and cushioned the set-up with 1 cm Styrofoam plates between tank and trolley as well as between the trolley and floor. We suspended an underwater speaker from a cushioned bamboo stick 20 cm from one end of the tank, facing towards an observation arena (Figure 4-1).

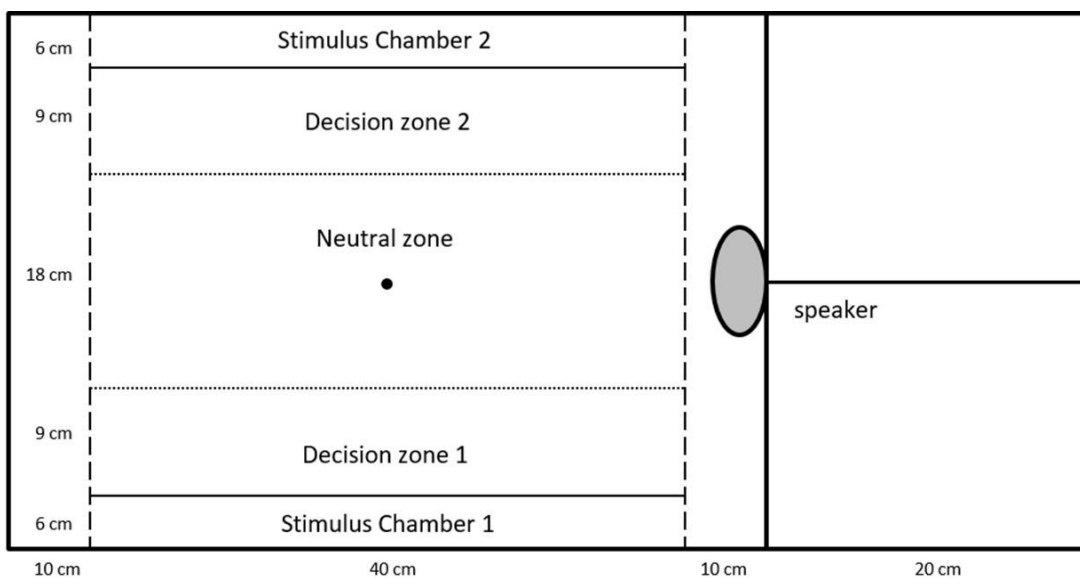


Figure 4-1 Tank set-up and observation arena. Thick solid lines represent the tank walls and speaker supports, the dashed lines represent the mesh separating the arena from the rest of the tank, the thin solid lines show the walls of the stimulus chambers and the dotted lines show the decision zones marked at the bottom of the tank.

At 10 cm from the speaker we divided the observation arena (50 x 40 cm) from the rest of the tank with 1 x 1 cm mesh. Along either side of the glass walls we separated two 'stimulus chambers (6 cm wide) for the two groups of stimulus crabs (see details below). The chambers were custom-made of 3 mm transparent acrylic sheets. Adjacent to each of these stimulus chambers, we defined 'decision zones' (9 cm wide) marked by a line on the base of the arena so that the focal crab could freely enter either decision zone. We designated a 'neutral zone' (18 cm width) at the centre of the tank. At the beginning of each observation, we placed the focal crabs in the centre of the neutral zone 30 cm from the speaker and equal distance to the walls of the stimulus chambers. At this location (the point in Figure 4-1) we analysed the sound pressure levels of the two sound treatments (ship noise and ambient control).

While hearing in a narrow definition seems to be absent in nearly all aquatic crustaceans, sound detection has been widely demonstrated in Decapoda (Budelmann, 1992). Few auditory thresholds have been established for invertebrates but in an experiment the common prawn *Palaemon serratus* showed an auditory brain response to acoustic stimuli at a frequency range of 100 – 3 000 Hz with amplitudes varying between 105 – 130 dB SPL re 1 μ Pa at 1 m (Lovell et al., 2005). There has been no similar study conducted for *P. bernhardus* but behavioural sensitivity (antennae flicks) to substrate-borne vibration in this species has been demonstrated for frequencies between 5 and 410 Hz at a particle acceleration of 0.02 – 0.44 m s⁻² RMS (Roberts et al., 2016).

For the sound playbacks we used an underwater speaker (DNH Aqua-30 underwater speaker, effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway) connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping

Town, China). We played back the sound tracks from a Toshiba Portégé R830-13C laptop (Tokyo, Japan). For the sound treatment we used three ship noise playbacks and three corresponding ambient control sounds from the same sites recorded at three major U.K. harbours (for details on recordings such as ship size and speed see Simpson et al., 2015; Wale et al., 2013a). We used Audacity 2.1.2 (Audacity Team, 2016) to create six audio tracks. For ship noise tracks we alternated 2 min of ship noise with 2 min of ambient crabs randomly to one of the two sound treatments (ambient sound/ ship noise) and to one of the alternative three audio tracks within these sound treatments (ambient A, B, C; ship A, B, C) and alternated the sound treatment between consecutive observations.

To make sure crabs were exposed to two distinct sound treatments we analysed the power spectrum as a proxy as in previous studies on crustaceans (e.g. Wale et al., 2013a). We are aware of the challenges of measuring noise in small tanks (Rogers et al., 2016; Simpson et al., 2015) and that hermit crabs are likely to perceive the particle motion component of sound rather than the measured sound pressure levels (Breithaupt, 2002; Popper, Salmon & Horch, 2001). However, as pointed out in previous studies (e.g. Herbert-Read et al., 2017; Simpson et al., 2015; Wale et al., 2013a), we did not aim to establish absolute noise sensitivity levels for hermit crabs but analysed the power spectrum to confirm that we exposed crabs to two different sound treatments, namely ship noise and ambient control. To do that, we rerecorded the six audio tracks at the centre of the arena at 30 cm from the speaker and 25 cm from the glass walls (where the crabs were be placed at the beginning of the experiment) at 1 – 2 cm from the bottom of the tank with an omnidirectional hydrophone HTI-96-MIN (with inbuilt preamplifier, manufacturer-calibrated sensitivity

-165 dB re 1 V μ Pa; frequency range 0.002 – 30 kHz, High Tech Inc., Gulfport, MS, U.S.A.) and Linear Sony PCM-M10 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave signals from a function generator with a measured voltage recorded in line on an oscilloscope). We used PAMGuide (Merchant et al., 2015) for MATLAB R2015b (MathWorks, 2015) to perform a power spectrum analysis of 60 s recording with Hann evaluation window, overlap 50%, 0.25 s window length, 100 – 3 000 Hz bandwidth normalised to 1 Hz. The three ambient control sounds had an average sound pressure level of 74.5 dB RMS re 1 μ Pa (ambient A: 70.8, ambient B: 76.2, ambient C: 76.6) and the ship noise an average of 119.4 dB RMS re 1 μ Pa (ship A: 124.4, ship B: 118.7, ship C: 115.2) both measured at 1 000 Hz (Figure 4-2; Table 4-1).

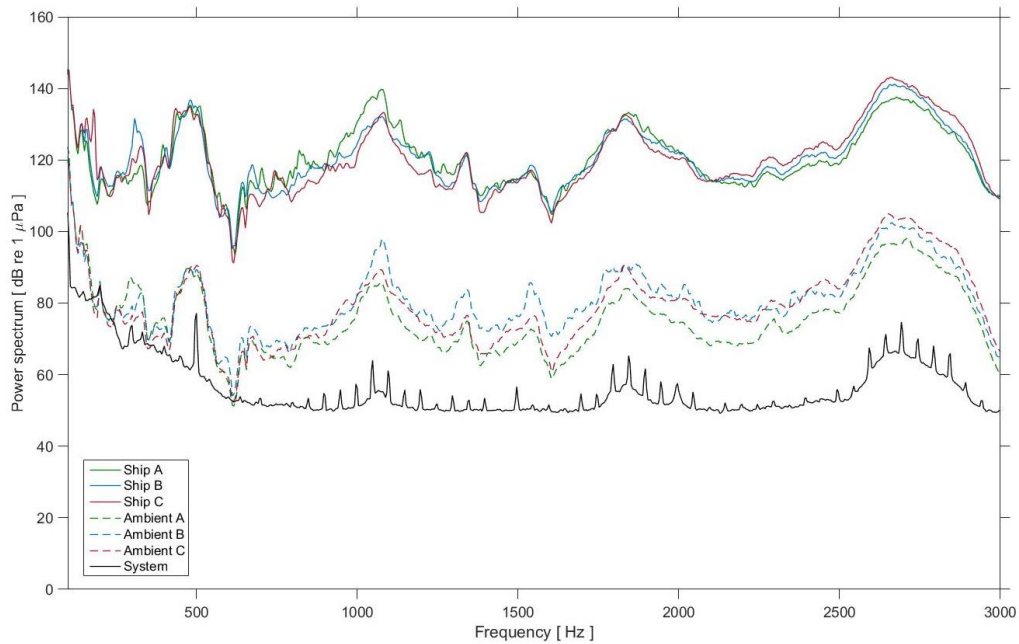


Figure 4-2 Power spectrum for three ship noise playbacks and three corresponding ambient sound playbacks recorded at 30 cm distance to the speaker. The system self-noise characterises the sound output by the equipment without playbacks. Filtered for 100 – 3 000 Hz frequency bandwidth.

Table 4-1 Sound intensity of the six playbacks and system's self-noise: Minimum amplitude, maximum amplitude, average amplitude between 100 – 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa recorded in the centre of the arena and 30 cm distance to the speaker.

Playback	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1000 Hz
Ship noise playback A	94.99 at 620 Hz	145.9 at 100 Hz	121.6	124.4
Ship noise playback B	96.81 at 615 Hz	145.5 at 100 Hz	121.6	118.7
Ship noise playback C	92.27 at 615 Hz	145.0 at 100 Hz	121.4	115.2
Ambient playback A	52.24 at 615 Hz	123.9 at 100 Hz	76.63	70.8
Ambient playback B	55.06 at 615 Hz	121.3 at 100 Hz	81.92	76.2
Ambient playback C	53.42 at 615 Hz	120.2 at 100 Hz	80.38	76.6
System self-noise	49.16 at 2128 Hz	105.2 at 100 Hz	56.22	56.24

4.3.3 Experimental design and behavioural analysis

We designed a classic choice experiment with three zones (Krause and Ruxton, 2002; Figure 4-1), which has previously been applied to shoaling in crustaceans (Evans et al., 2007). We placed a single crab in one of the stimulus chambers (SSC) and five crabs in the other (the group stimulus chamber, GSC) as in a previous study (Evans et al., 2007). To remove the possibility of directional bias we alternated the sides of the SSC and GSC between each day of observations. After being placed in a stimulus chamber, the stimulus crabs had 20 min to acclimatise to the tank before any of the six sound tracks was played. We ran the experiment in blocks of observations where the same stimuli crabs (one and five individuals in each observation) were used repeatedly for eight observations of focal individuals (thus an experimental block = eight observations of unique focal crabs per day, reusing the same stimuli crabs across these eight observations). Observations within each block consisted of four observations in the presence of ship noise and four under ambient control conditions). We visually matched focal and stimulus crabs for size as closely as possible. After observations were completed, we removed the stimulus crabs from their shells and sexed and weighed them to test the effectiveness of matching focal and stimulus crabs by

calculating the relative weight differences between them. The weight of the focal crabs was positively correlated with the weight of SSC crabs (Spearman rank correlation: $r_s = 0.67$, $N = 45$, $P < 0.0001$) and the average weight of crabs in the GSC group ($r_s = 0.63$, $N = 45$, $P < 0.0001$).

Immediately following the start of the playback of either ship noise or ambient control, we placed the focal crab in the centre of the neutral zone (equidistant from the boundary of each of the two associated decision zone) and in an inverted position with the aperture of the shell facing upwards. Once the focal crab had recovered from the startle response (it emerged from its shell and contacted the bottom of the tank with a walking leg), we recorded its behaviour for 20 min (Canon Legria HF R47 digital video camera; Tokyo, Japan). We assigned focal crabs to be in association with either the single conspecific or the group of five conspecifics when the whole of their occupied shell had crossed the outer boundary of the appropriate decision zone. We excluded crabs that climbed up the mesh and escaped the arena or did not emerge from their shell after 5 min from the analysis. We coded the behaviour with The Observer version 12 (Noldus IT, Wageningen, the Netherlands) event logger software blind to the sound treatment and the occupied shell size. We recorded whether each decision zone was entered, the latency to enter each decision zone and the average proportion of the total observation time spent in each of the three zones. Thus, the experiment contained two factors, sound treatment and shell size, and four treatment combinations (Table 4-2).

Table 4-2 Experimental design and sample size in each treatment group. Interaction between sound treatment and occupied shell. The values in each cell of the table indicate the % preferred shell weight of shells supplied to crabs in each group prior to observations.

<i>n</i> = 45		Sound treatment	
		Ambient control	Ship noise
Initially occupied shell	75 % (suboptimal)	<i>n</i> = 9	<i>n</i> = 10
	100 % (optimal)	<i>n</i> = 11	<i>n</i> = 15

4.3.4 Statistical analysis

To determine whether ship noise and shell size influenced the chance of crabs entering the single and group stimulus zones we used general and generalised linear mixed-effect models implemented in the R package lme4 (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2015) with a binary response variable. For the response variable of whether, or not, crabs entered a zone (yes/ no), sound (ambient sound/ ship noise) and occupied shell (suboptimal = 75%/ optimal = 100%) were the fixed factors and body weight was included as a covariate. To account for the repeated use of three different sound playbacks for both sound treatments (ambient sound/ ship noise) we included playback as a random factor. To account for the fact that each set of stimuli crabs was used for eight observations of focal crabs per day, block was also treated as a random factor. To determine the effects of sound treatment and shell size on the latency and average proportion of time spent in each zone, we used linear mixed-effect models, again implemented using the lme4 package. As above, we included playback ID and block of the experiment as random factors. Finally, to determine whether shell size and noise treatment influenced the average proportion of time spent in all three zones, we used a single linear mixed-effects model and to account for the fact that we took three measurements from each focal crab to analyse the average proportion of time spent in each zone (single/ neutral/ group), we added zone as a

fixed factor and the focal crab ID as a third random factor. We used post hoc residual plots to assess the fit of each model. Where necessary we natural log transformed the data to improve normality, such that the assumption of the linear models would be met.

Ethical note: No animals were harmed during the experiment. After the experiment each crab was supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences or permits were required for this study.

4.4 Results

There was no interaction between sound treatment and shell size ($\chi^2_1 = 1.27, P = 0.26$; see Table 4-3 in the appendix to the chapter) and no main effects of sound treatment ($\chi^2_1 = 0.003, P = 0.96$), shell size ($\chi^2_1 = 1.25, P = 0.26$) or crab weight ($\chi^2_1 = 2.5, P = 0.11$) on whether crabs entered the single zone (see Table 4-3 in the appendix to this chapter for complete statistics). Similarly, there was no interaction between sound treatment and shell size ($\chi^2_1 = 0.06, P = 0.81$) and no main effect of sound treatment ($\chi^2_1 = 0.03, P = 0.87$), shell size ($\chi^2_1 = 1.04, P = 0.31$) or crab weight ($\chi^2_1 = 0.13, P = 0.72$) on whether crabs entered the group zone.

There was no interaction between sound treatment and shell size ($\chi^2_1 = 0.4, P = 0.55$) and no main effect of sound treatment ($\chi^2_1 = 0.06, P = 0.81$), shell size ($\chi^2_1 = 2.45, P = 0.11$) or the weight of the focal crab ($\chi^2_1 = 0.8, P = 0.38$) on the latency to enter the group zone.

There was, however, a significant interaction between sound treatment and shell size on the latency to enter the single zone ($\chi^2_1 = 5.6, P = 0.02$; Figure 4-3). Under the ambient control treatment, crabs in suboptimal shells showed a longer latency to

enter the single crab decision zone compared with crabs in optimal shells, but in the presence of noise this pattern was absent. The weight of the focal crab had no effect on the latency to enter the single zone ($\chi^2_1 = 2.0, P = 0.16$).

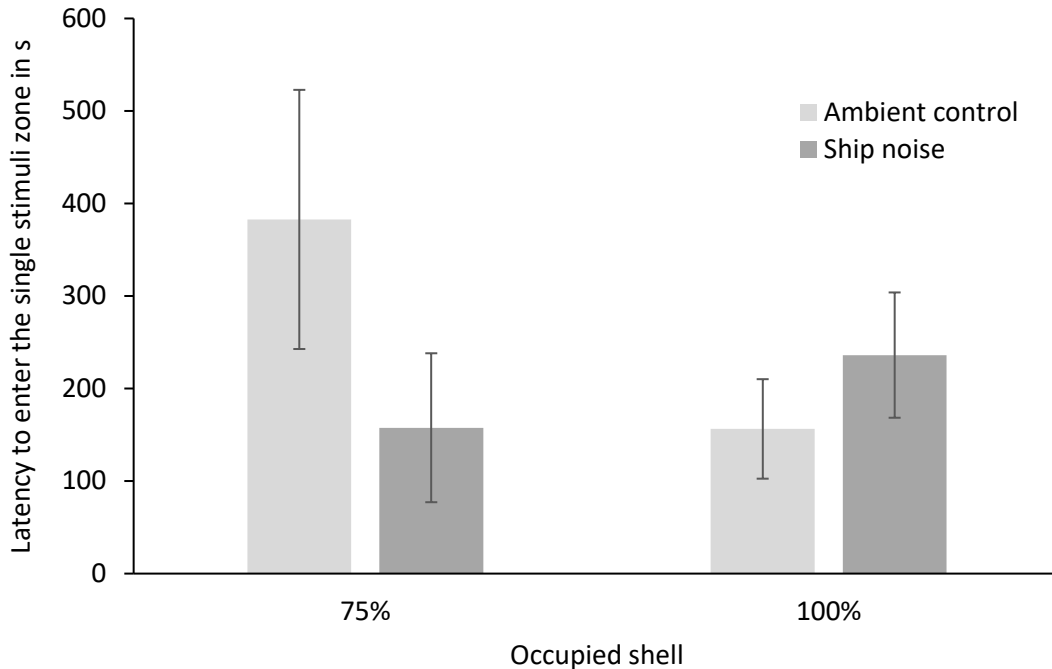


Figure 4-3 Effect of the interaction between sound treatment and shell size on the latency to enter the single stimulus zone. Error bars show standard error.

There was a significant three-way interaction between sound treatment, shell size and zone on the average proportion of time spent in each zone ($\chi^2_1 = 7.1, P = 0.03$; Figure 4-4). Under ambient sound, crabs in suboptimal shells showed no discernible preference for any of the three zones while crabs in optimal shells spent more time with conspecifics; mostly with a single crab. Under ship noise this pattern was reversed. Crabs in a suboptimal shell strongly preferred the zone adjacent to a single crab and spent very little time in the neutral zone whereas for crabs in optimal shells the preference for the zone adjacent to a single crab was reduced under noise and the crabs spent their time more evenly in all three zones compared to ambient sound.

Crabs in suboptimal shells spent significantly less time in the neutral zone than crabs in optimal shells. The weight of the focal crab had no effect on the average proportion of time spent in each zone ($\chi^2_1 = 0.4, P = 0.51$).

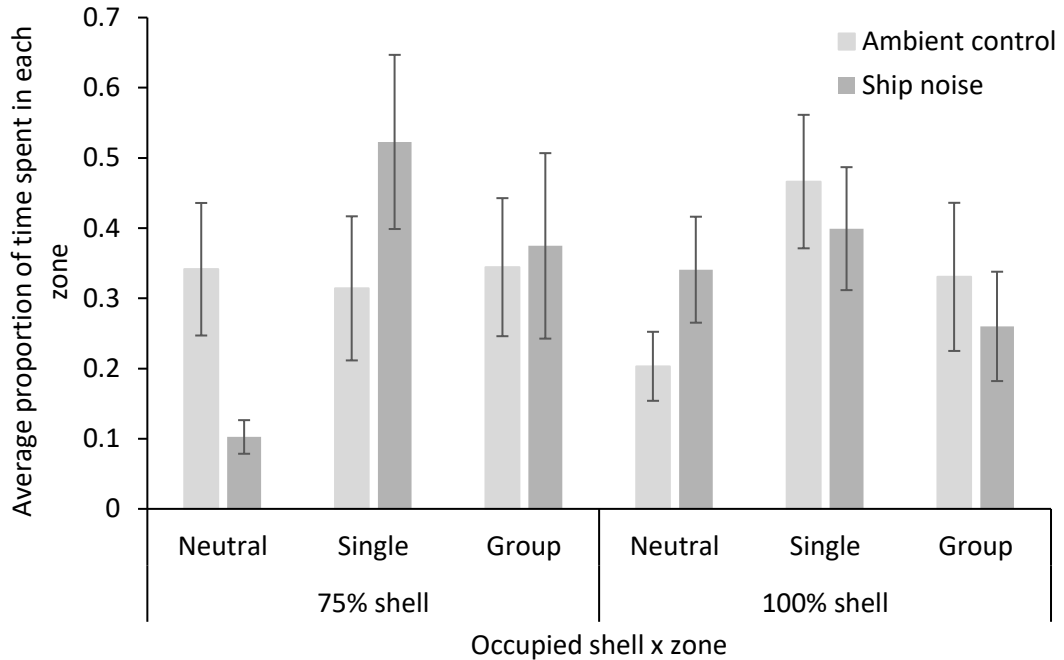


Figure 4-4 effect of ambient control and ship noise on the proportion of time (out of a maximum of 20 min) spent in each of the three zones. Error bars show standard errors.

4.5 Discussion

We predicted, based on the ideas of shell exchange markets and predator dilution, that hermit crabs in suboptimal shells would show a stronger preference for joining groups than crabs in optimal shells. Furthermore, we predicted that noise would disrupt this behaviour. Surprisingly, we found the opposite pattern under ambient control, where crabs in suboptimal shells did not show a preference for either zone but crabs in optimal shells preferred to group with a single conspecific. Noise, however, reversed the grouping pattern. While crabs in suboptimal shells now preferred to

group with conspecifics and particularly with a single crab, crabs in optimal shells showed no clear preference and spent their time more evenly across all three zones. Thus, although our overarching prediction that noise pollution would disrupt the grouping behaviour of hermit crabs (expressed under ambient conditions) was upheld, the direction of that effect differed from what we expected.

The unexpected pattern under ambient sound that crabs in small shells showed longer latency than crabs in optimal shells might be explained by considering some wider behavioural consequences of shell size. In hermit crabs the latency to emerge from the shell after a short disturbance, also called the startle response, is a common measure for boldness (Briffa et al., 2008b; Gherardi et al., 2012). Previous experiments have shown that hermit crabs in a 100% optimal shell showed a shorter startle response than individuals in 75% shells (Briffa and Bibost, 2009). Furthermore, bolder crabs were also more inquisitive and more likely to investigate empty shells than shy crabs (Mowles et al., 2012). Thus, the relative lagging of crabs in suboptimal shells to join another individual might be driven by the effect of shell size on inquisitiveness, rather than by the relative costs and benefits of joining a group as we initially hypothesised. Indeed, grouping behaviour has been shown to be influenced by personality (such as shy – bold) in a wide range of species (for reviewed by Webster and Ward, 2011) and gregarious species show stronger personality differences (von Merten et al., 2017).

The grouping pattern we found under ambient sound suggests that shell exchange markets or the dilution effect do not lead to the clusters we observed in *P. bernhardus* in the wild (S. Tidau, personal observation) and which have been reported in other species (Hazlett, 1966; Hazlett, 1979; Tricarico and Gherardi, 2006). One factor

could be that under ambient sound crabs in suboptimal shells perceived greater costs from grouping than being solitary. As shown by Briffa and Bibost (2009), crabs in suboptimal shells stay hidden for longer than crabs in optimal shells indicating that they perceive a greater level of risk from conspecifics. This risk could stem from cannibalism which has occasionally been observed in *P. bernhardus* (S. Tidau, personal observation) and is also known for other hermit crab species (Tran et al., 2014). While some species form groups of up to hundreds or thousands (Gherardi, 1991), solitary behaviour has been reported in others (Hazlett, 1966; Hazlett, 1979) and demonstrated in the field in the long-clawed hermit crab *Pagurus longicarpus* (Tricarico and Gherardi, 2006). As grouping behaviour varies widely between hermit crab species, the clustering and grouping preferences observed in *P. bernhardus* might be species specific. Alternatively, for the baseline behaviour under ambient sound conditions we cannot rule out that our groups (here of two or six crabs) could have been too small to provide predator protection as predicted by the 'dilution effect' (Foster and Treherne, 1981). Indeed, being in small groups might make crabs more apparent to predators than being single. If a predator detects the group, the crab in a suboptimal shell would be particularly vulnerable to that predator, and if that crab has a smaller apparent body size than other group members, it may be easier to detect due to 'standing out' (Krause and Godin, 1994). To withdraw into the shell (Gherardi and Benvenuto, 2001) or flee (Mima et al., 2003; Rosen et al., 2009; Scarratt and Godin, 1992) thus might be the better strategy to avoid predation. Finally, we cannot eliminate the possibility that crabs might be attracted by something else in the field or their behaviour might be driven by abiotic factors such as water currents (Pallas et al., 2006) which raises questions for further research.

Although the grouping pattern of hermit crabs under ambient sound differed from our initial expectations, grouping behaviour was clearly altered by exposure to noise. Indeed, the usual (i.e. under ambient sound) pattern was reversed in the presence of noise. One explanation for why noise reversed decisions about joining a group is that crabs were distracted by the noise so that their ability to make appropriate decisions was impaired leading to the opposite decision made under ambient sound. Thus, crabs in suboptimal shells that would normally behave cautiously failed to adjust their behaviour to match the size of their shell in the presence of noise, that is, crabs in suboptimal shells showed more cautious behaviour by taking longer to encounter a single conspecific. This distraction effect of noise on crustaceans has been observed under predation risk (Chan et al., 2010b) and suggested as a mechanism to explain behavioural changes in other taxa under noise (Simpson et al., 2015). An alternative explanation is that crabs exposed to noise might have perceived the noise itself as a threat. Besides functioning as a novel and unpredictable stimulus for animals, some sound properties of noise could also be biologically similar to relevant stimuli, that is, elicit similar responses (Francis and Barber, 2013; Shannon et al., 2016b). For instance, Blainville's beaked whales *Mesoplodon densirostris* responded in similar ways to simulated military sonar and to playbacks of predatory killer whale *Orcinus orca* calls (Tyack et al., 2011). In our study, crabs in suboptimal shells may have weighed the potential benefits of associating with another crab (e.g. the dilution effect) higher than the costs (e.g. attacks by other hermit crabs). Under acute predation threat, animals are expected to join larger shoals (e.g. Hager and Helfman, 1991). Here crabs that were both exposed to noise and supplied with suboptimal shells (and were therefore at a high risk of predation) chose

to avoid the neutral zone. Our results do not allow us to distinguish between these two possibilities (distraction and perception of threat) directly. However, we note that crabs in optimal shells also changed their preference, that is, associating with another individual was reduced under ship noise compared with ambient noise. This implies that noise disrupted the usual decision-making process in both groups, crabs in suboptimal and optimal shells alike. Furthermore, the size of the shell did not seem to protect from the impacts of noise.

Our results add to the growing body of evidence that anthropogenic noise can clearly influence group dynamics from crustaceans to mammals. As noted above, the direction and intensity of changes in behaviour and the consequences for survival and fitness are far less obvious. When exposed to noise, groups of *Mediterranean spiny lobsters* (Filiciotto et al., 2014), European sea bass (exposed to pile driving see Herbert-Read et al., 2017), bottlenose dolphins (Bas et al., 2017) and red swamp crayfish *Procambarus clarkii* (Celi et al., 2013) were less cohesive, decreasing cooperative interactions among conspecifics, and cichlid fish *Neolamprologus pulcher* were more aggressive (Bruitjes and Radford, 2013). On the other hand, trevally (Fewtrell and McCauley, 2012), European sea bass (exposed to ship noise see Neo et al., 2018), Carolina chickadees and tufted titmice (Owens et al., 2012) formed tighter groups under anthropogenic noise. These effects could be due to stress and distraction of attention, stimulus perception and filtering or a combination of these mechanisms. Since an animal's ability to perceive and process stimuli is limited (Dukas, 2004) and since noise and other pollutants have been shown to affect animals across sensory channels (Halfwerk and Slabbekoorn, 2015), it has been suggested that anthropogenic noise acts as a distracting stimulus (Chan et al., 2010b; Simpson et al., 2015).

Our study is one of a few that have looked at cross-modal effects of anthropogenic noise on grouping behaviour, showing that this occurs in hermit crabs. Specifically, in *P. bernhardus*, exposure to ship noise caused crabs that occupied a suboptimal resource (a shell that was too small) to behave as if they possessed an optimal resource in terms of their interactions with other individuals. Further work is warranted to investigate the underlying causes of the behavioural changes (e.g. lack of caution or risk avoidance). Nevertheless, given that survival in hermit crabs is strongly tied to the quality of their gastropod shell, any changes to shell-mediated behaviour could impact individual survival and hence population structure. Grouping behaviour is a common phenomenon in nature with consequences for survival and fitness and potential noise effects should be further investigated.

4.6 Appendix to the chapter

Table 4-3 Effects of the interaction between and main effect of sound treatment, occupied shell and crab weight on grouping behaviour (bold indicates significant results).

Behaviour and effects of factors	χ^2	P
Occurrence to enter the single zone		
Sound treatment : occupied shell	1.27	0.26
Sound treatment	0.003	0.96
Occupied shell	1.25	0.26
Crab weight	2.5	0.11
Occurrence to enter the group zone		
Sound treatment : occupied shell	0.06	0.81
Sound treatment	0.03	0.87
Occupied shell	1.04	0.31
Crab weight	0.13	0.72
Latency to enter the single zone		
Sound treatment : occupied shell	5.6	0.02
Crab weight	2.0	0.16
Latency to enter the group zone		
Sound treatment : occupied shell	0.4	0.55
Sound treatment	0.06	0.81
Occupied shell	2.45	0.11
Crab weight	0.8	0.38
Average proportion of time spent in each zone		
Sound treatment : occupied shell : zones	7.1	0.03
Crab weight	0.4	0.51

Note that results were obtained using a model simplification approach, and as such reporting is restricted to the highest order effects, where significant interactions are present.

Chapter 5: Effects of anthropogenic noise on the structure and benefits of vacancy chains

5.1 Abstract

While animals have adapted to environmental perturbations over their evolutionary history, human-induced rapid environmental changes, such as noise pollution, expose animals to novel stimuli at an unparalleled pace of change. Effects of anthropogenic noise have been investigated across habitats, behaviours, and taxa but relatively little is known about how noise alters group-level processes. Here we tested the effect of anthropogenic noise on vacancy chains. These chains describe a process in which the arrival of a discrete, reusable and vacant resource unit to an animal population can initiate a cascade of re-allocation of ownership according to ranks in the population leading to aggregated benefits. We investigated the effect of anthropogenic noise on vacancy chains in groups of European hermit crabs *Pagurus bernhardus*, where the arrival of a single empty gastropod shell (which serves as a portable shelter) can cause a cascade of upgrades in shell quality as swapping into this new shell means that an individual will vacate its previously occupied shell which is freed up for other group members. We found that noise had no effect on the sequence of vacancy moves to be closely tied to the linear size hierarchy of groups. However, noise reduced the multiplier effect, which quantifies the number of chain participants that benefit from the arrival of a new resource unit. Furthermore, noise altered the structure of vacancy chains. Chains after 24 h of ambient sound and ship noise showed the largest dissimilarity in their structure suggesting that the differences observed in the multiplier effect developed over 24 h of noise exposure. These findings show that

noise alters the decision-making and resource assessment in individuals and these individual decisions scales up to group levels after 24 h. Since gastropod shells are crucial for survival and fitness in this species such scaling up of suboptimal decisions could have negative consequences for populations.

5.2 Introduction

Anthropogenic noise is one pollutant out of an array of human-induced rapid environmental changes (HIREC; Sih et al., 2011) and has been shown to affect animals in their decision-making across modalities by changing animals sensory ecology (Halfwerk and Slabbekoorn, 2015). Though most populations have experienced environmental perturbations in their evolutionary past to which they have adapted (Ghalambor et al., 2007), HIREC denotes that animals are not only exposed to novel conditions and stimuli but also at an unexperienced pace (Sih et al., 2011; Tuomainen and Candolin, 2011). The impacts of HIREC range from the molecular- and cellular-level, to impacts on individual fitness and reproductive success and ultimately up to community structure, species density and biodiversity (Barber et al., 2010; Francis and Barber, 2013; Francis et al., 2017; Kight and Swaddle, 2011; Radford et al., 2012; Williams et al., 2015). However, the initial response of an individual to these rapid changes is expected to be behavioural (Tuomainen and Candolin, 2011), such that by focussing on behavioural responses we can gain an early indication of potential broad-scale effects. Indeed, mounting evidence shows that anthropogenic noise affects animals in their movement, foraging and predator-prey interactions (Chan et al., 2010b; Luo et al., 2015; Shafiei Sabet et al., 2015; Siemers and Schaub, 2011; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a; Wisniewska et al., 2018). By comparison, how noise influences intraspecific interactions and group-level processes

(which are all underpinned by the behaviour of multiple individuals) has received relatively little attention in noise research.

Some recent studies on noise impacts on grouping and shoaling patterns reveal a wide range of responses whereby the propensity to join groups was reduced in some cases but enhanced in others (Bas et al., 2017; Fewtrell and McCauley, 2012; Filiciotto et al., 2014; Herbert-Read et al., 2017; Neo et al., 2018; Sara et al., 2007).

Anthropogenic noise can also have a negative effect on a range of other intraspecific interactions like nest guarding in the largemouth bass *Micropterus salmoides* (Maxwell et al., 2018), feeding and offspring interactions in the spiny chromis *Acanthochromis polyacanthus* (Nedelec et al., 2017) and agonistic interactions in the red swamp crayfish *Procambarus clarkii* (Celi et al., 2013). In addition to these contexts, an important function of intraspecific interactions is the distribution of resources.

Resource distribution is frequently thought of as resulting from competition over the ownership of indivisible resource units. Accordingly, pairwise agonistic contests usually take place because resources cannot be re-used and are limited in supply (Briffa and Hardy, 2013a; Briffa and Hardy, 2013b). However, when a resource is reusable, alternative processes to exploitative competition could govern the resource distribution within populations such as vacancy chains (Chase, 1991; Chase and DeWitt, 1988; Weissburg et al., 1991). Vacancy chains describe a resource allocation system in which a new, discrete and limited but *reusable* resource unit of higher quality arrives in a group or population and initiates a process of redistributions of current ownerships (Chase, 1991; Chase and DeWitt, 1988; Chase et al., 1988; Weissburg et al., 1991). Originally developed to understand the effects of job retirements and promotions (White, 1970; White, 1971), the concept of vacancy

chains has been applied to various human and non-human social contexts and resources. In humans, vacancy chains are used to study the distribution of resources such as homes (Ben-Shahar and Sulganik, 2011; Briggs et al., 2010; Persky and Felsenstein, 2008), jobs (Rosenfeld, 1992) and cars (Chase, 1991). In non-human animals, the predominant contexts are the distribution of mates (Forsgren, 1997), territory (Benson et al., 2004; Eikenaar et al., 2009; Fox et al., 1981; Frank et al., 2018) or shelter (Fayed et al., 2008). Besides the living world, robotics research applies vacancy chain theory to understand task allocation processes (Dahl et al., 2009). While reusable resources occur in many taxa like fish (Forsgren, 1997), reptiles (Fox et al., 1981), mammals (Benson et al., 2004; Frank et al., 2018) and birds (Eikenaar et al., 2009), due to their use of empty gastropod shells as portable shelters, hermit crabs are the ideal model organism to study the shell allocation through vacancy chains (Briffa, 2013a; Briffa and Austin, 2009; Chase and DeWitt, 1988; Edquist and Rotjan, 2012; Laidre, 2012; Lewis and Rotjan, 2009; Rotjan et al., 2010). Hermit crabs are characterised by a weakly calcified exoskeleton (Briffa and Mowles, 2008) and therefore seek empty gastropod shells to protect them from predators (Vance, 1972) and environmental extremes (Shumway, 1978; Taylor, 1981; Young, 1978). Besides increasing the chance of survival, crabs search for (larger) shells to allow for growth (Angel, 2000) and reproduction (Bertness, 1981a). Hermit crabs usually obtain shells from conspecifics through contests or by encountering an unoccupied empty shell although snail predation is rare and rather anecdotal (Brightwell, 1953; Brightwell, 1951; Elwood and Neil, 1992). But the primary driver in vacancy chains is the arrival of a new unoccupied shell of high quality.

In hermit crabs and other systems, an ideal vacancy chain describes a hierarchical system (for instance based on income, age or size) in which the introduction of a vacant resource unit (a shell in the case of hermit crabs) allows the top-ranked individual ("rank 1") to move into that better quality resource unit (Chase, 1991; Chase and DeWitt, 1988; Weissburg et al., 1991). If this individual decides to move, it will vacate the initially occupied unit and therewith frees up a unit now available to other group members. Conversely from the perspective of the occupants, the *vacancy* has moved from the new resource unit down to the unit initially occupied by the highest ranked individual. Hence, the first move of the vacancy chain has been completed. Since vacancy chains assume a hierarchical resource distribution, the abandoned resource unit initially occupied by the highest ranked individual will now be available to the next ranked individual ("rank 2"). If the second ranked individual decides to move into this recently abandoned unit (because it is likely to represent an increase in value of this individual's initially occupied resource unit), the vacancy will now move from the second level (stratum) of the chain to the third, and the second move of the vacancy chain has been completed. Thus, a vacancy chain describes a sequence of vacancy moves down through several strata, such that the arrival of a single new re-useable resource unit can lead to aggregate benefits that ramify down a hierarchically structured population. Taken together, these decisions can create a cascade of aggregated benefits where more than just one individual benefits (as opposed to dyadic pairwise competition) and the value of the initial new vacant shell can potentially propagate through the whole chain over time. Note that vacancies move down the chain as chain participants move up the chain from smaller into larger units (Weissburg et al., 1991). In an ideal system, vacancy chains end either when a

new recruit arrives (e.g. a naked crab enters the group so that all vacancies are filled) or when all chain participants own a resource unit which is of higher value than the lowest value unit available, known as the absorbance state (so that no individual would benefit by occupying it) (Chase and DeWitt, 1988).

Laboratory and field experiments with hermit crabs provide evidence that both intrinsic and extrinsic factors can cause deviations from ideal vacancy chains. These factors include the personality traits of chain participants (Briffa, 2013a), predation risk (Briffa and Austin, 2009), different habitats (rocky shore and mudflats), shell fit, and damage (Edquist and Rotjan, 2012), and the introduction of non-native gastropod snails (van Oosterhout et al., 2013). To the best of our knowledge, however, group processes and resource distribution such as vacancy chains have not been studied in the context of anthropogenic pollution such as noise. Nevertheless, there is the potential for anthropogenic noise to disrupt this resource allocation process because vacancy chains in hermit crabs are dependent on a series of assessments (of shell quality) and subsequent decisions (to exchange shells) made by the chain participants using visual, tactile and chemical cues (Elwood, 1995; Gherardi and Tiedemann, 2004; Hazlett, 1982). Recent studies have demonstrated how these processes are disrupted by anthropogenic noise (chapter 3, Tidau and Briffa, 2019; chapter 2, Tidau and Briffa, In Press; Walsh et al., 2017).

The aim of this study is to determine if and how anthropogenic noise affects the resource distribution in groups using the vacancy chain concept as a model relevant to hermit crabs (Briffa, 2013a; Chase, 1991; Chase and DeWitt, 1988). In vacancy chains, time has been shown to increase the number of moves between shells in hermit crabs. Hence, we expect more moves between shells after 24 h compared to

1 h. Under noise, however, *P. bernhardus* accepts optimal shells less frequently (chapter 3, Tidau and Briffa, In Press). Therefore, we predict that noise will lead to fewer moves between vacant shells thus reducing the aggregate benefits derived from the arrival of a single new resource unit. We also predict that noise should change ranked based hierarchies of vacancy chains whereby fewer chains will conform to the ideal vacancy chains under ship noise compared to ambient sound (control). With this experiment, we aim to contribute to a better understanding of the effects of noise on group-level processes. Moreover, our model system represents an understudied taxa in noise research despite their globally widespread distribution (Morley et al., 2014; Tidau and Briffa, 2016; Williams et al., 2015).

5.3 Methods

5.3.1 Collection, husbandry and preparation of hermit crabs

We collected hermit crabs from the rocky intertidal of Hannafore Point, Cornwall, UK (50° 20' 42'' N, 4° 28' 0'' W) in January and February 2018 and transported the animals directly to the laboratory at the University of Plymouth, UK. Crabs were maintained in a temperature controlled room at 15 °C with a 12:12 h light:dark cycle in a single holding tank containing 125 l of continuously filtered and aerated seawater from the seaward side of Mount Batten pier (50° 21' 34'' N, 4° 8' 8'' W) in Plymouth Sound, UK, collected at spring tides (Briffa, 2013a). Crabs in the stock tank were fed once a week with white shell fish. The morning before we initiated the vacancy chains, we carefully removed the crabs from their shells with a bench vice, sexed and weighed them (Briffa, 2013a). Since the breeding season is likely to affect the shell preference behaviour of egg-carrying females, we used only male crabs without damaged appendages, visible parasites or recent moult (Briffa and Elwood, 2007). As in Briffa and Austin (2009),

each vacancy chain contained five crabs of the following five weight classes: (1) 0.99-0.9 g, (2) 0.89-0.8 g, (3) 0.79-0.7 g, (4) 0.69-0.6 g and (5) 0.59-0.5 g. Hereafter, crabs are referred to as rank 1 (largest crab) to 5 (smallest crab). To identify each individual crab within their group of five, the major cheliped of each crab was marked with a distinct colour of nail polish. Each crab was assigned a labelled *Littorina littorea* shell of 50 % of its preferred shell weight (PSW), calculated from a regression line relating preferred shell weight to body weight obtained from previous shell selection experiments (Briffa and Elwood, 2007; Dowds and Elwood, 1983). After this preparation, each crab was housed individually in a white plastic dish of 15 cm diameter containing continuously aerated seawater to a depth of 5 cm until the vacancy chain was initiated on the following day (see Experimental Design, below). During the isolation period each crab was fed with white fish and kept in a 15 °C temperature controlled room. At the end of the experiment, all crabs were supplied with larger shells and returned to the sea at the collection point.

5.3.2 Tank set-up and sound analysis

The vacancy chain observations were carried out in a 80 x 50 x 50 cm sized glass tank (with 1 cm thick aquarium glass) filled to a depth of 40 cm (~ 130 l) with seawater from the laboratory supply. We placed the tank on a free-standing trolley and cushioned the set-up with 1 cm Styrofoam plates between tank and trolley as well as the trolley and floor. An underwater speaker (see below for details) was suspended from a cushioned bamboo stick at 20 cm distance to one end of the tank, facing towards two observation arenas (Figure 5-1). For the arenas, we used two acoustically transparent plastic dish of 15 cm diameter which were glued to bottom of the tank at 30 cm distance from the centre of the dish to the speaker.

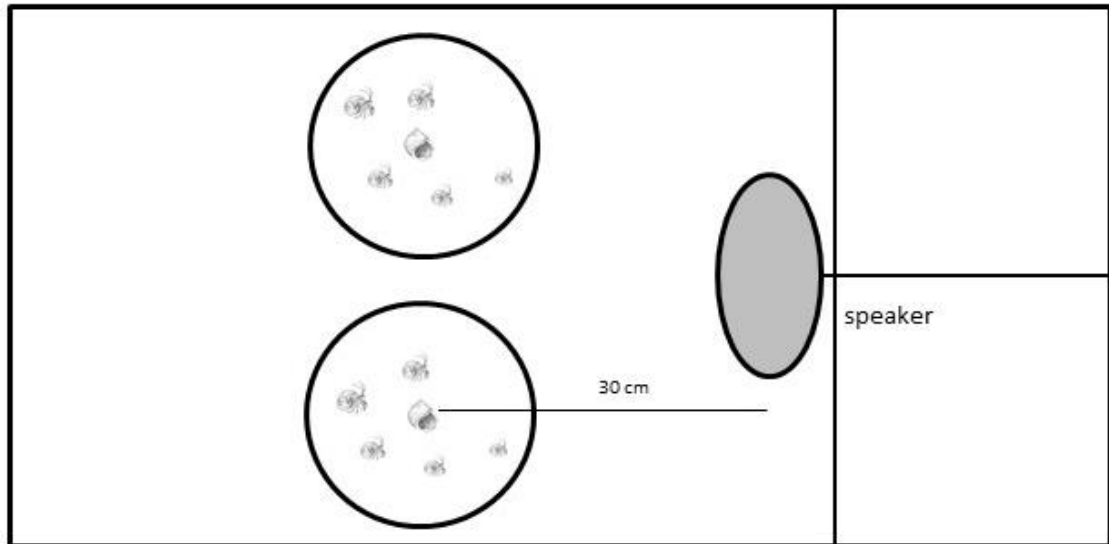


Figure 5-1 Tank set-up and observation arena. The arenas are made of acoustically transparent white plastic dishes of 15 cm diameter and placed at 30 cm distance to the speaker (measured from the centre of the arena). Each arena contained one group of 5 hermit crabs and the empty gastropod shell was placed in the centre of the dish.

The underwater speaker (DNH Aqua-30 underwater speaker, effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway) was connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping Town, China) and sound tracks were played back from a Toshiba Portégé R830-13C laptop (Tokyo, Japan). For the sound treatment we used three ship noise playbacks and three corresponding ambient control sounds from the same sites recorded at three major UK harbours (for details on recordings such as ship size and speed see Simpson et al., 2015; Wale et al., 2013a). We used Audacity 2.1.2 (Audacity Team, 2016) to create a total of six audio tracks of either ambient control or ship noise to be played back to the crabs. For the ship noise tracks, we alternated 2 min of ship noise with 2 min of ambient control sound including 15 s fading in and out to simulate the passing by of a ship. The ambient control sounds consisted of the ambient sounds recorded at the same site as the ships.

To characterise the acoustic properties of the playbacks in the tank, we undertook a spectral analysis of the six audio tracks which we re-recorded at the centre of the arenas at 30 cm distance to the speaker and 1 – 2 cm distance to the bottom of the tank. For those recordings, we used an omnidirectional hydrophone HTI-96-MIN (with inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V μ Pa; frequency range 0.002 – 30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave signals from a function generator with a measured voltage recorded in line on an oscilloscope). To obtain those sound pressure levels, we used PAMGuide (Merchant et al., 2015) for MATLAB R2015b (MathWorks, 2015) and performed a power spectrum analysis of 60 s recordings with Hann evaluation window, overlap 50%, 1 s window length, 100 – 3 000 Hz bandwidth normalised to 1 Hz. We chose a filter of 3 000 Hz since the only known auditory thresholds for a similar crustacean has been received for the common prawn *Palaemon serratus* which showed an auditory brain response to acoustics stimuli at a frequency range of 100 – 3 000 Hz with amplitudes varying between 105 and 130 dB SPL re 1 μ Pa at 1 m (Lovell et al., 2005). Based on these parameters, the three ambient control tracks were played back so that they had a mean spectral density of 73.25 dB RMS re 1 μ Pa (ambient A: 68.5, ambient B: 77.38, ambient C: 73.88) and the ship noise tracks had a mean maximum of 119.83 dB RMS re 1 μ Pa (ship A: 123.4, ship B: 119.6, ship C: 116.5) at 1 000 Hz (Figure 5-2; Table 5-1). Those sound levels were similar to the ones in previous studies on crustaceans exposed to noise in the laboratory (Wale et al., 2013a).

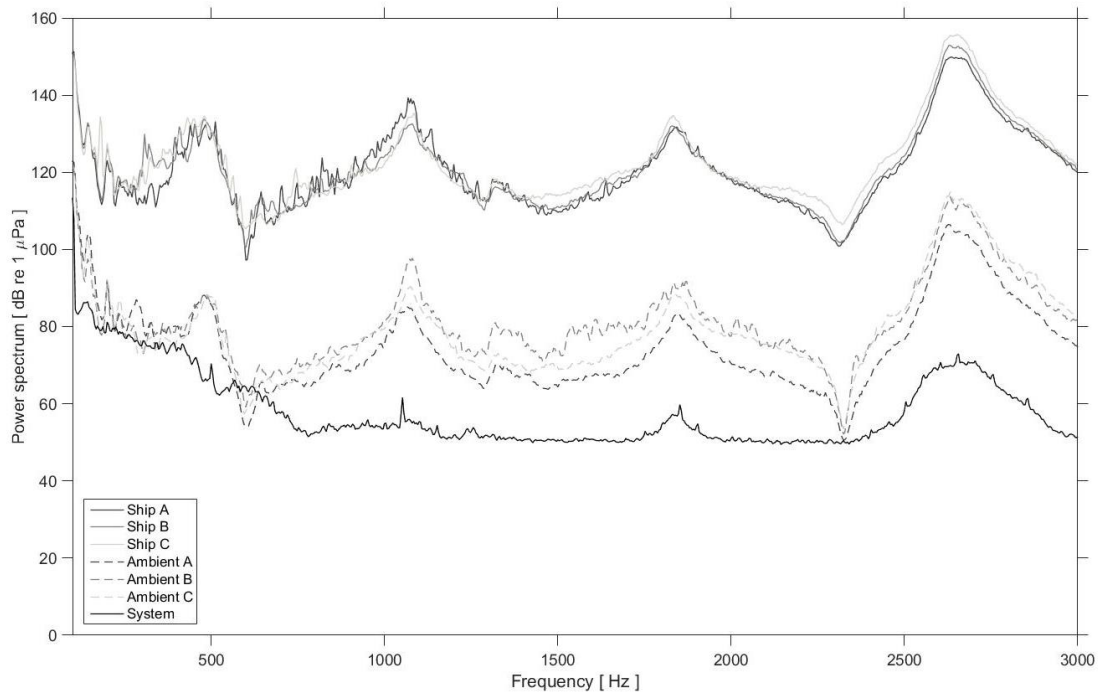


Figure 5-2 Power spectrum for three ship noise playbacks and three corresponding ambient sound playbacks recorded at 30 cm distance to the speaker. The system self-noise characterises the sound output by the equipment without playbacks. Filtered for 100 – 3 000 Hz frequency bandwidth.

Table 5-1 Sound intensity of the six playbacks and system’s self-noise: Minimum amplitude, maximum amplitude, average amplitude between 100 - 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa recorded in the centre of the arena and 30 cm distance to the speaker.

Playback	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1000 Hz
Ship noise playback A	101.9 at 2310 Hz	149.9 at 100 Hz	122	123.4
Ship noise playback B	104.7 at 2315 Hz	149.2 at 2650 Hz	124	119.6
Ship noise playback C	102.7 at 625 Hz	150.4 at 2650 Hz	123.7	116.5
Ambient playback A	60.22 at 2315 Hz	120.1 at 100 Hz	81.06	68.5
Ambient playback B	62.65 at 2315 Hz	120.5 at 100 Hz	84.64	77.38
Ambient playback C	59.91 at 720 Hz	120.5 at 100 Hz	80.66	73.88
System self-noise	49.15 at 2320 Hz	110.7 at 100 Hz	57.66	57.55

We note that hermit crabs are likely to perceive the particle motion component of sound rather than the measured sound pressure levels (Breithaupt, 2002; Popper et al., 2001). In line with previous noise exposure studies in the laboratory (Simpson et

al., 2015; Wale et al., 2013a), however, we analysed the power spectrum of the sound pressure to confirm that we exposed crabs to two distinctive sound conditions namely ship noise and ambient control. We are aware of the unresolved challenges of tank acoustics (Rogers et al., 2016) and do not attempt to establish absolute noise sensitivity levels for hermit crabs.

5.3.3 Characterising vacancy chains

Vacancy chains are typically characterised by a set of measures that describe (a) the extent to which aggregate benefits from the arrival of a single resource unit spread down the chain and (b) the structure of the chain in terms of the pattern of vacancy moves from stratum to stratum quantified by four measurements (for review see Briffa, 2013a; Briffa and Austin, 2009; Chase, 1991; Weissburg et al., 1991). First, the *multiplier effect* describes the extent to which multiple chain participants benefit from the arrival of the single new resource unit. This measure can be quantified in two ways. We can sum up the total number of moves that the vacancy has made i.e. how the shell moves down the chain (Chase and DeWitt, 1988), which would have a maximum of 6 moves here. Alternatively, we can sum the total number of observed moves of the chain participants (Briffa, 2013a; Briffa and Austin, 2009), which has a maximum of 5 possible moves in this study. For consistency with other studies on hermit crabs, we retained to the latter approach. Second, while multiplier effect expresses the length of the chain, it does not inform about the shell distribution in relation to the hierarchy of the chain participants. This is measured by the second property, the chain *linearity* (Briffa, 2013a) which is the correlation between the hierarchical rank of the chain participants (crab rank 1 – 5) and the rank of the resource unit they occupy. Since there are 6 shells (one per crabs plus 1 new vacancy)

the shell ranks range between 1 – 6. Third, while these measures describe that individuals benefited from the vacancy chain, they do not quantify these benefits directly. Individual resource improvement in hermit crabs can be expressed as the percentage of the *preferred shell weight* (PSW, as mentioned above) of the shell occupied by each crab after 1 h and 24 h (Briffa and Elwood, 2007). Fourth, to investigate the structure of the vacancy chains, all vacancy moves were summed up in *transition matrices* (Chase, 1991). These matrices include all the vacancy moves within a treatment (see below for details) and can be expressed as the frequency or proportion of all possible moves based on the total number of vacancies in a treatment group. Those grand transition matrices, which represent the sum of all vacancies, can be (1) tested for randomness, (2) assessed by the proximity to an ideal vacancy chain and (3) compared against each other to assess differences between treatments.

While randomness assumes that there is no underlying pattern in the vacancy moves, an ideal vacancy chain predicts that all vacancies are occupied according to the rank of the chain participants (the largest crab 1 moves into the new vacancy shell rank 1, crab 2 moves into the vacancy initially occupied by crab 1, etc.). As a result, in an ideal vacancy chain, all moves would occur along the main diagonal of transition matrices. These measurements allow us to determine whether the different treatments affect the structure of the chains and hence the resource allocation system as a whole. However, since the chains can be disrupted by imperfect information gathering (i.e. the chance to encounter empty shells), vacancy chains are rarely ideal; some individuals make greater benefits than predicted gains while others may even experience reduced resource quality (Briffa and Austin, 2009) due to ‘backwards moves’ and ‘skipping’ of strata (Edquist and Rotjan, 2012; Rotjan et al., 2010).

5.3.4 Experimental design

We designed a fully orthogonal experiment comprised of the two factors time (1 h/ 24 h) and sound (ambient sound/ ship noise) (Table 1 for sample sizes). Vacancy chains were initiated in the morning between 10:00 am and 11:00 am. First, the individually housed crabs were grouped and placed into one of the two arena (15 cm diameter) in the larger tank. Both groups of crabs had 5 min acclimation time to settle in the arena without sound treatment. After 5 min, we started the sound playback and placed a vacant shell of a 100% PSW of the largest crab ranked 1 in the centre of the arena. Placing the shell in the centre marked the initiation of the vacancy chain. After 1 h, we recorded the first set of data required for calculating the benefits and structure of each vacancy chain described above. Specifically, we recorded the level (i.e. stratum) of the vacant shell and the stratum of each shell occupied by crabs. The crabs were then left undisturbed in their groups of five conspecifics for a further 23 h. After a total of 24 h from initiation of the vacancy chain, we recorded the same information again, enabling us to compare the benefits and structure of vacancy chains across two sound treatments at two time points (1 h/ 24 h). We initiated 42 vacancy chains (crabs: $N = 210$) but had to exclude chains or crabs due to technical problems such as that the sound treatment did not work over the full 24 h, crabs did not occupy a shell or moulted either prior to initiating a chain or overnight during the chain process (Table 5-2). We assigned each vacancy chain randomly to one of the two sound treatments and one of the three alternative sound tracks which we alternated between the subsequent observations.

Table 5-2 Experimental design and sample size in each treatment group. Summary of number of observations in each treatment combination sound and time for 42 initiated chains with 5 hermit crabs in each chain.

		Time	Sound treatment		N
			Ambient sound	Ship noise	
Chains	initiated	0 h	23	19	42
	analysed	1 h	22	19	41
		24 h	18	17	35
Crabs	exposed	0 h	115	95	210
	analysed	1 h	110	95	205
		24 h	90	85	175

5.3.5 Statistical analysis

The first set of analyses assesses the aggregate benefits of vacancy chains. To test for the effects of sound and time on the multiplier effect, linearity and occupied % PSW, we used general and generalised linear mixed effect models implemented in the R- packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) in R version 3.4.3 (R Core Team, 2017). Since the multiplier effect (the number of crabs that exchanged their original shell for a new one) was bound by a maximum of five possible crabs that could change shell, we converted the frequencies into the proportion of possible moves and applied a binomial error structure. Sound (ambient control/ ship noise) and time (1 h/ 24 h) were the fixed factors while we accounted for other elements of the experimental design by including a number of random effects. First, we accounted for the fact that we observed each group of five crabs on two occasions (1 h/ 24 h) by including chain identity as a random factor. Second, since we collected data in blocks of two vacancy chains that ran simultaneously, we accounted for this source of non-independence by adding block as a second random factor. Finally, since we re-used each of the three different sound playbacks for each of the two sound treatments, we added playback identity as a third random factor. To provide an index

of the linearity of the vacancy chains, we first calculated the Pearson's correlation coefficient between the crab rank and the shell rank for each chain at each of the two time points (1 h/ 24 h). The effects of time and sound treatment on this index were then analysed using a similar analysis to that described above, but in this case using a Gaussian error distribution. The response variable was log-transformed to improve normality. To analyse effects of time and sound on % PSW, we applied a third similar model but added crab rank as an additional fixed factor so that we could test for the effect of hierarchical position of crabs within their chain on the occupied resource quality. Here, time had three levels with 0 h indicating the start of the observation (when all crabs occupied a shell of 50% PSW) compared against 1 h and 24 h. Again, this response variable was log-transformed to better fit normality.

The second set of analyses examined the structure of the vacancy chains. First, we collated the observed vacancy moves across all chains within each sound treatment into a single grand transition matrix. This was done for each treatment group i.e. the two factors sound and time producing four grand transition matrices (Chase and DeWitt, 1988). To test whether the collated moves in the chains differed from random moves (i.e. an equal number of moves in each cell of the matrix), we subjected each matrix to Fisher's exact test (Briffa, 2013a). Since Fisher's tests does not work well for matrices with table larger than 2 x 2 we chose to calculate a simulated *P*-value with 8 000 simulations. This is sufficient to determine whether or not the chains are non-random but that does not allow us to compare the signal strength. A non-random distribution of vacancy moves does not directly test deviation from an ideal vacancy chain, where all moves are expected to occur along the main diagonal. To test how closely the chains conformed to an ideal vacancy chain, we subjected each matrix to

Bartlett's test of sphericity (Bartlett, 1951), which compares the observed moves to the predicted moves based on an ideal vacancy chain (Chase, 1991). For this test, we transformed the frequency counts to proportions. Since the test cannot be performed with a determinant = 0, we added 1 to every cell on the main diagonal of each matrix (Wothke, 1993). Finally, to analyse whether the vacancy chains in the four groups differed from each other, we made pair-wise comparisons of matrices using a procrustean randomization test (Dray et al., 2003; Jackson, 1995). While Fisher's test can be found in the R base package, Bartlett's test is in the psych package (Revelle, 2017) and the procrustean randomisation test is in the R-package ade4 (Dray et al., 2007).

Ethical note: No animals were harmed during the experiment. After the experiment each crab was supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences or permits were required for this study.

5.4 Results

There was no significant interaction between sound and time on the multiplier effect ($\chi^2_1 = 0.002$, $P = 0.96$). However, under noise, the multiplier effect was smaller compared to ambient control ($\chi^2_1 = 6.45$, $P = 0.01$; Figure 5-3) indicating that fewer moves occurred under ship noise (mean per chain = 1.97 moves; Table 5-3) compared to ambient control (mean per chain = 2.48 moves). In addition, the multiplier effect was greater after 24 h compared to 1 h ($\chi^2_1 = 5.55$, $P = 0.02$; Figure 5-4) meaning that more moves occurred after 24 h (2.46 moves) compared to 1 h (2.05 moves).

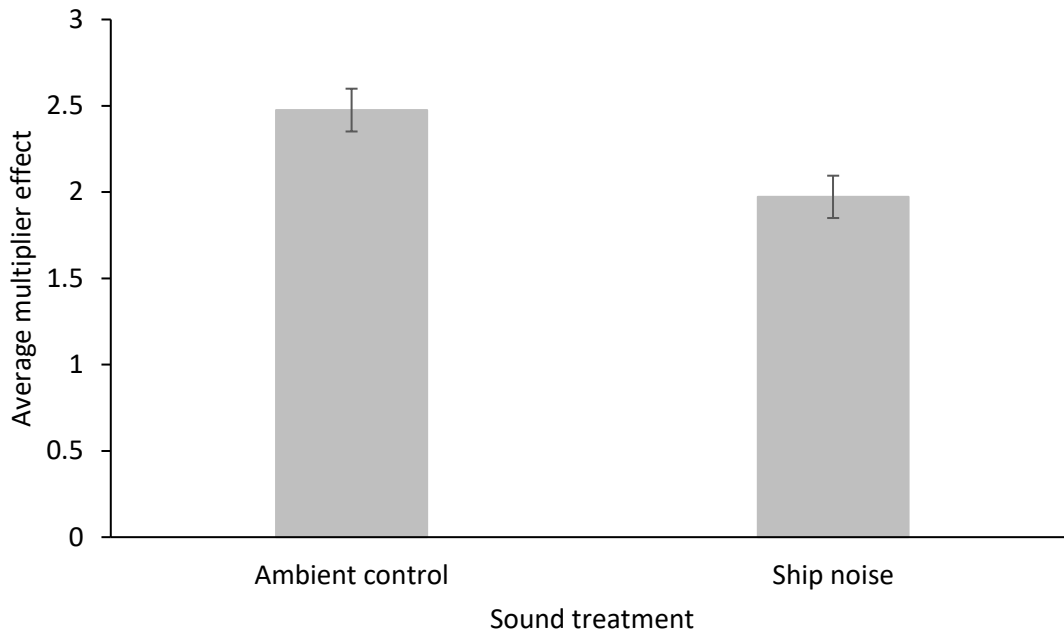


Figure 5-3 Effect of sound treatment on multiplier effect. Error bars show standard errors.

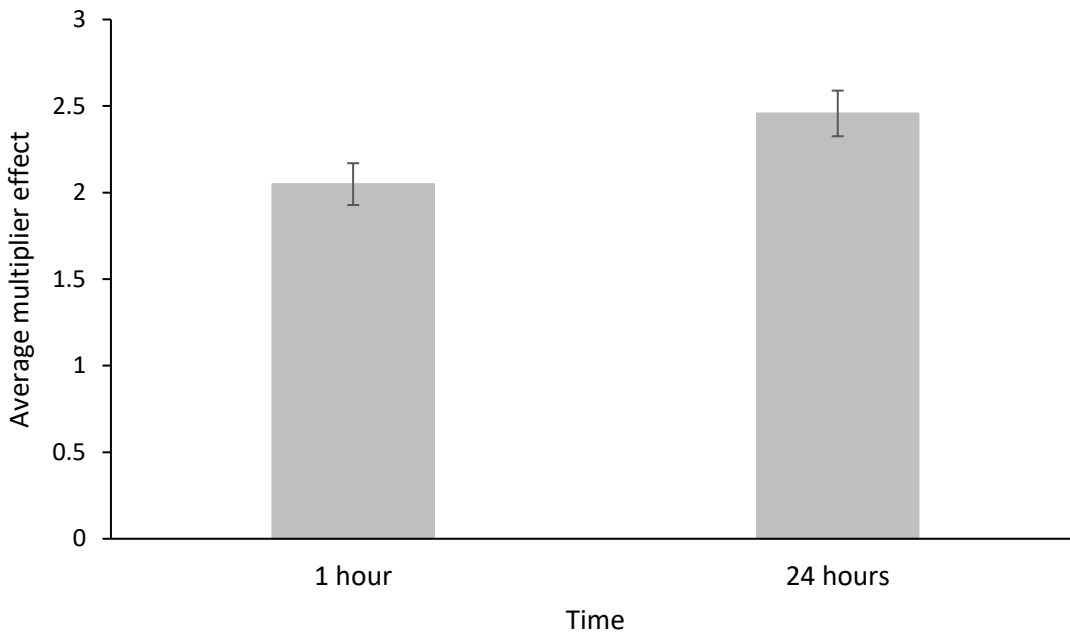


Figure 5-4 Effect of time on multiplier effect. Error bars show standard errors.

Table 5-3 illustrates that, out of all observed vacancy moves occurring during the experiment, most vacancy chains exposed to noise had 1 or 2 moves whereas the vacancy chains under ambient control had a higher frequency of longer chains with 2 or 3 moves. No vacancy chain showed the possible maximum number of 5 moves.

Table 5-3 Multiplier effect as a proportion of all observed chains in the sound treatment across the two time points (1 h and 24 h).

Sound treatment	Multiplier effect as a proportion of all observed chains					
	Mean	One	Two	Three	Four	Five
Ambient control	2.48	0.08	0.48	0.35	0.10	0.00
Ship noise	1.97	0.25	0.56	0.17	0.03	0.00

Linearity was not influenced by the interaction between sound and time ($\chi^2_1 = 1.13, P = 0.25$), or by the main effects of sound ($\chi^2_1 = 0.49, P = 0.48$) or time ($\chi^2_1 = 0.004, P = 0.95$). The percentage preferred shell weight (% PSW) was not affected by the interaction between sound, time and rank ($\chi^2_8 = 2.92, P = 0.94$), sound and time ($\chi^2_2 = 0.2, P = 0.89$), sound and rank ($\chi^2_4 = 1.65, P = 0.80$) or sound as a main factor ($\chi^2_1 = 0.03, P = 0.87$). However, the % PSW was influenced by the interaction between time and rank ($\chi^2_8 = 31.47, P = 0.0001$; Figure 5-5). After 1 h, on average all ranks increased their % PSW, with a tendency for greater average increase of higher ranked crabs compared with lower ranked crabs. This pattern was more marked after 24 h whereby crabs of higher ranks (particularly rank 1) increased their % PSW to a greater extent than those of lower ranks. The greater increase in % PSW for crabs in rank 1 was, in part, due to the opportunity for those crabs to gain their optimal shell of 100% PSW, whereas all other ranks (assuming an ideal vacancy chain) could increase their % PSW by 10% (i.e. giving a maximum of 60% PSW for those crabs). Thus, the lower increase in % PSW for ranks 2 – 4 does not necessarily mean that no vacancy moves occurred in those strata.

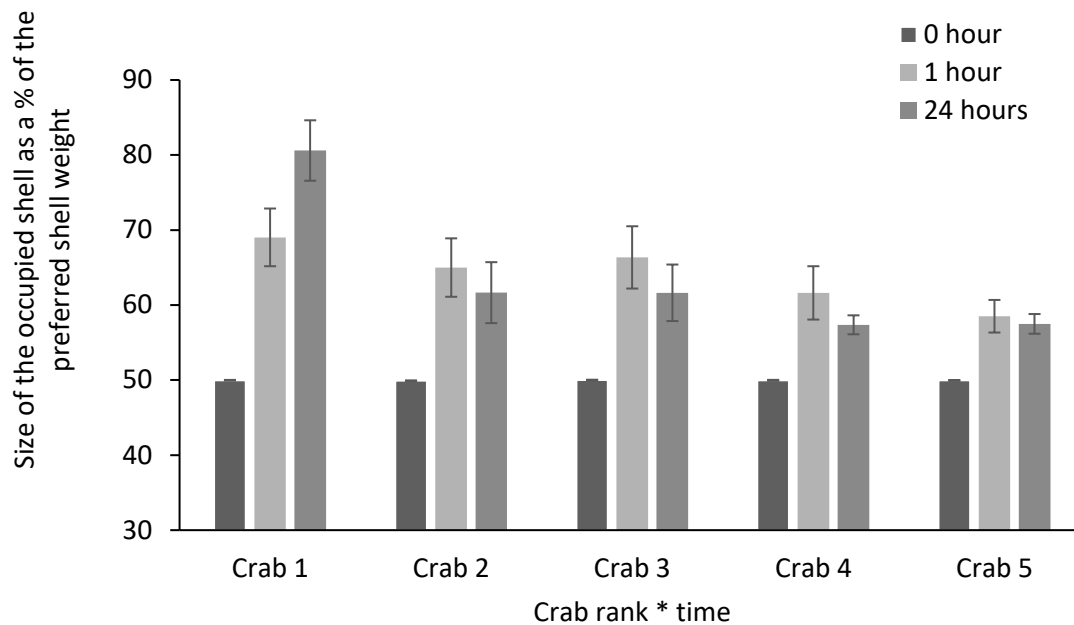


Figure 5-5 Effect of the interaction between time and crab rank on the size of the occupied shell as a % of the preferred shell weight. Error bars show standard errors.

The analysis of the chain structure provides insights into the patterns of vacancy moves in each treatment group as summed up by the four transition matrices (Table 5-4, bold diagonal). All matrices were significantly different from random (Fisher's exact test: $P = <0.0001$, in all four matrices). However, each matrix also differed from the predicted ideal vacancy chain (Bartlett's test: ambient 1 h: $\chi^2 = 48.9$, $P < 0.0001$; ambient after 24 h: $\chi^2 = 41.4$, $P = 0.0003$; noise 1 h: $\chi^2 = 34.6$, $P = 0.003$; noise 24 h: $\chi^2 = 34.0$, $P = 0.003$) indicating that a significant number of moves occurred off the main diagonal at each of the sound treatments and two time points.

These results suggest that the vacancy chains exposed to 1 h ambient control had the most moves away from the ideal chain while the vacancy chains exposed to ship noise for 1 h and 24 h had more moves along the main diagonal and hence were closer to an ideal vacancy chain. A comparison of the matrices across all four

combinations of sound treatment and time shows that all four vacancy chains differed in their structure (Procustean random test based on 9 999 replicates). Vacancy chains under 1 h and 24 h of noise exposure differed the most from each other in their structure ($P = 0.007$) while chains after 1 h and 24 h of ambient sound diverged the least in their structure (both $P = 0.01$). Chains after 24 h ambient sound compared to 24 h ship noise also highly differed in their structure ($P = 0.003$). Chains exposed to 1 h ambient compared to 1 h noise diverged the least from each other in their structure (both $P = 0.01$).

Table 5-4 Transition matrices. The frequencies of vacancy moves from original state to destination state under ambient sound and ship noise and after 1 h and 24 h. ABS is the absorption state (all chain participants own a resource unit higher than the lowest). The bold numbers illustrate the ideal vacancy chain along the main diagonal.

Sound treatment	Time	Original state	Destination state					
			2	3	4	5	6	ABS
Ambient sound	1 h	1	8	6	6	2	0	0
		2	11	1	3	3	2	2
		3	0	13	3	5	1	0
		4	0	1	9	3	5	4
		5	2	1	0	9	2	8
		6	1	0	1	0	12	8
	24 h	1	10	4	4	0	0	0
		2	4	1	4	5	2	2
		3	3	8	2	4	1	0
		4	0	2	7	2	6	1
		5	1	2	1	6	4	4
		6	0	1	0	1	5	11
Ship noise	1 h	1	7	5	4	2	1	0
		2	11	1	1	2	3	1
		3	1	10	1	1	3	3
		4	0	2	13	1	1	2
		5	0	1	0	10	1	7
		6	0	0	0	3	10	6
	24 h	1	11	4	2	0	0	0
		2	6	1	1	6	2	1
		3	0	9	1	2	3	2
		4	0	1	13	1	1	1
		5	0	2	0	5	2	8
		6	0	0	0	3	9	5

In summary, significantly non-random patterns of vacancy movement indicate that vacancy chain processes were underway 1 h after initiation and this pattern had continued to develop over the ensuing 23 h in both sound treatment whereby more move occurred under ambient sound than under ship noise. Since a significant number of moves occurred away from the main diagonal in each case, the observed chain structures also differed from what would be expected under ideal vacancy chains. The extent to which this happened differed significantly between the sound treatments. Crabs exposed to ship noise performed fewer unexpected moves than those exposed to ambient sound i.e. vacancy chains under ambient sound were further away from the ideal chain, more spread and less often occurred below the main diagonal (30/108; 28%). In contrast, in chains under noise considerably more moves occurred below the main diagonal (42/102; 41%).

5.5 Discussion

Vacancy chains describe a pattern of resource allocation where the benefit of the arrival of a single new and reusable resource unit spreads through a group or population. This spreading can lead to a chain of redistributions and thus can create aggregated benefits for more than one individual. The length of a chain, i.e. its multiplier effect, expresses the number of individuals that benefit from the new resource unit and a multiplier effect of ≥ 1 is the key indicator that a vacancy chain has occurred (Chase, 1991; Weissburg et al., 1991). Previous studies have shown that the multiplier effect increases over time and is influenced by a range of factors including the personality types of chain participants, predation risk and social context and in both humans and non-human animals (Briffa and Austin, 2009; Edquist and Rotjan, 2012; Ferrari, 2011; Persky and Felsenstein, 2008). Here, we have shown for the first

time that anthropogenic factors also influence the structure and benefits of vacancy chains. While vacancy chains occurred under both sound treatments, the presence of ship noise lowered the multiplier effect and this effect persisted over time. As we predicted based on previous experiments, the multiplier effect was higher after 24 h compared to 1 h and the average chain length of 2.48 moves is similar to the one seen in previous studies of vacancy chains in hermit crabs observed over similar time-scales (Briffa, 2013a; Briffa and Austin, 2009; Chase et al., 1988; Lewis and Rotjan, 2009; Rotjan et al., 2010). Out of all the observed chains under noise, most had only 1 move (25%) or 2 moves (56%). In contrast, the chains under ambient sound conditions were longer i.e. with a greater proportion of chains having 2 or (48%) or 3 moves (35%).

Since an optimal shell is crucial for predator protection (Bertness, 1981b), growth (Angel, 2000) and reproduction (Bertness, 1981a), staying in a suboptimal shell is a costly decision for hermit crabs. However, when hermit crabs swap shells, they expose their weakly calcified abdomen, which makes them vulnerable to predator attacks. Hence, hermit crabs have to assess their environment for threats and balance the benefits of gaining a better shell against the cost of this short period of elevated risk by swapping shells. In chapter 3, hermit crabs have been shown to choose optimal shells less frequently under ship noise (chapter 3, Tidau and Briffa, In Press). In fact, noise has been suggested to affect animals by distracting them and diverting their limited attention away from pertinent cues (Chan et al., 2010b), by changing their sensory environment (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011) and by inducing stress (Kight and Swaddle, 2011). Since there was no interaction between sound and time, the effect of noise seems both immediate and persistent, and there was no indication of habituation to noise over the course of the experiment.

Changes in shell fit (% PSW) quantify the individual benefit that crabs obtained from the vacancy chain. For all crabs, % PSW increased over time as reported in previous vacancy chains with hermit crabs (Briffa and Austin, 2009; Chase and DeWitt, 1988; Chase et al., 1988; Rotjan et al., 2010) which was largely influenced on crab rank. After 1 h of observation, the % PSW was more evenly distributed among crabs compared to 24 h indicating that there were more mismatches between crab rank and shell rank after 1 h than after 24 h. Overall however, the largest crabs benefited the most from the new shell resource unit (highest % PSW) after 1 h and 24 h. That chain participants of the highest rank benefit the most while those on the lowest ranks benefited the least has also been shown for *Pagurus longicarpus* suggesting a general pattern across hermit crab species (Chase and DeWitt, 1988). However, there was no effect of the sound treatment on the % PSW although the lower multiplier effect signalled fewer moves under ship noise compared to ambient sound. Contrary to our prediction, we found no evidence that noise caused a mismatch between crab rank and shell rank. That the correlation of crab rank and shell rank i.e. the linearity of the vacancy chains was maintained under both sound treatments and at both time points is indicative for a stable group hierarchy in hermit crabs based on the crabs' body weight. This result concords with previous studies where linearity has also remained unaffected by other contexts (Briffa, 2013a; Edquist and Rotjan, 2012).

The structure of the vacancy chains can give more insight into the potential mechanisms underlying the effects of anthropogenic noise on the vacancy chain process. The structure is expressed in a grand matrix and sums up all moves in for each of the four treatment groups. As predicted, time and sound influenced the vacancy chain structure and none of the matrices was random or ideal. All four grand matrices

differed significantly from each other in their structure. Resource improvements through vacancy chains can occur within 30 min in *P. bernhardus* (Briffa and Austin, 2009) and after 24 h and 48 h in the terrestrial hermit crab *Coenobita compressus* (Laidre, 2012). Thus, it is not surprising that there were differences in chain structure between 1 h and 24 h for crabs exposed to the ambient sound. Vacancy chains after 1 h exposure to ambient sound and ship noise were the least different while those after 24 h of ambient control and noise treatment showed the largest dissimilarity. This pattern suggests that the differences observed in the multiplier effect developed over the course of the 24 h of exposure.

In accordance with previous studies, none of the vacancy chains was ideal, none showed 5 moves and approximately 80% of the crabs in rank 1 occupied the largest shell (Briffa, 2013a). Even though vacancy chains occur in nature and some species such as the terrestrial hermit crab *C. compressus* tend to form tightly matched size based hierarchies (Osorno et al., 1998), ideal chains seem to be rare (Briffa, 2013a). Rather mismatches, backward moves and skipping are common characteristics in vacancy chains of hermit crabs (Briffa, 2013a; Briffa and Austin, 2009; Edquist and Rotjan, 2012; Rotjan et al., 2010). Although none of the chains was ideal, the two chains under ship noise (1 h and 24 h) were both closer to the ideal vacancy chain than the two sets of chains under ambient sound. The more ideal behaviour under noise could be due to the underlying physiological effects. Humans and animals have shown increased attention and cognitive performance in behavioural response when exposed to noise which has been explained by noise stimulate the neurotransmitter release (Prior, 2002; Smith and Nutt, 1996). For instance, laboratory rats naïve to a T maze made less errors and finished their trial faster when exposed to noise presumably

because of a higher choline uptake and activity in the prefrontal cortex and hippocampus (Prior, 2002). The same could be true for hermit crabs if noise causes analogous physiological changes. However, as noted by Prior (2002) this effect might only occur under moderate sound intensity (68 dB in this case) and also varies with the duration of exposure. Furthermore, previous studies have shown that the characteristics of the noise exposure regime (e.g. intermittent sound from pile driving versus continuous noise from ships) can have different behavioural impacts even on the same species (Herbert-Read et al., 2017; Neo et al., 2018). To confirm or reject such a mechanism further studies would be necessary.

Alternatively, a similar pattern observed under noise has been shown for vacancy chains exposed to a predator cue in which vacancy chains in the presence of that cue were closer to ideal chains than in the absence of predator cues (Briffa and Austin, 2009). While boldness, i.e. the willingness to take risks, had no effect on aggregated benefits and the structure of vacancy chains (Briffa, 2013a), the exposure to and risk perception of predation is a mechanism which can suppress the otherwise seemingly natural disruption of vacancy chain processes leading to chains closer to ideal as shown by Briffa and Austin (2009). Animals tend to trade-off speed over accuracy under risky situations (Sih, 2013) and the decision to change shells is based on individuals to trade-off the benefits and the costs of shell swapping. The sum of these individual decisions can lead to aggregated benefits for a population. To swap into a new shell is an essential assessment for hermit crabs to gain better information on the internal shell fit (Elwood and Neil, 1992) likely to be observed also in nature. While in the absence of risk or threat, swapping shells more frequently might be beneficial for hermit crabs, under risk that could have been perceived as too costly.

Since the pattern observed here is similar to the one observed for vacancy chains under predation risk (Briffa and Austin, 2009), crabs could have perceived sound as a threat and consequently suppressed their natural behaviour of swapping between shells more frequently.

Anthropogenic noise has been suggested to not only function as a novel and unpredictable stimulus for animals (which could explain the similar structure of vacancy chains observed under predation threat) but that noise could also be similar to biologically relevant stimuli i.e. elicit similar responses (Shannon et al., 2016b). For instance, the Blainville's beaked whales *Mesoplodon densirostris* showed similar response under the controlled exposure to simulated military sonar and playbacks of their predator call, the killer whale *Orcinus orca* (Tyack et al., 2011). With regard to the more general effects of noise on group behaviour, there is evidence that animals seem to alter intraspecific grouping behaviour, shoal structure and group preferences under anthropogenic noise (Dunlop et al., 2017; Fewtrell and McCauley, 2012; Filiciotto et al., 2014; Herbert-Read et al., 2017; Sara et al., 2007; Visser et al., 2016). Experiments have shown that fish formed more cohesive shoals and increased grouping activity under ship noise (Fewtrell and McCauley, 2012; Neo et al., 2014). Individuals of bluefin tuna *Thunnus thynnus* increasingly swam towards one and another and seemed more likely to join a group under noise (though the shoals were less concentrated and coordinated see Sara et al., 2007). However, the response to noise by groups is not uniform and in some species or under different sound regimes less grouping was observed (Bas et al., 2017; Filiciotto et al., 2014; Herbert-Read et al., 2017).

To the best of our knowledge, there are only few experiments on the effects of noise or other environmental stimuli explicitly on social hierarchies. For instance,

under noise dominant individuals of the cichlid fish *Neolamprologus pulcher* showed more aggression towards subordinates (Bruintjes and Radford, 2013) while animals of the red swamp crayfish *P. clarkii* encountered each other less frequently and reduced engagement in agonistic interactions (Celi et al., 2013). Since our data suggests that the social hierarchy remained stable, our results do not conform to either of these studies. Studies on the effects of other environmental stressors such as drought on social hierarchies obtain similarly opposing results. For instance in the brown trout *Salmo trutta* broke down the initial social structures which had benefited dominant conspecifics with higher growth rates (Sloman et al., 2001), but in the Eastern mosquitofish *Gambusia holbrooki* droughts did not change the overall social organization or rank stability but induced higher level of conflict (Flood and Wong, 2017). Ultimately, the mechanisms based on which crabs under noise behaved more similar to crabs under predation threat requires further research.

The experiment shows that anthropogenic noise alters the benefits and structure of resource allocation through vacancy chains in hermit crabs. That is, fewer crabs benefited from the arrival of a new resource unit. On the other hand, the hierarchies within the groups, as measured by the linearity, were stable under noise. Hierarchies among hermit crabs are size dependent. Thus, in contrast to other sources of information such as shell quality, perception of the body size of conspecifics is presumably unaffected by noise. Vacancy chains represent one approach to studying the effects of noise on intraspecific interactions, which in this case determines access to resources. Given the crucial role of shell fit for survival, growth and reproduction in hermit crabs, this study demonstrates how disruption of decision-making at the

individual level (as a result of exposure to noise) has the potential to scale up and impact on populations.

Chapter 6: Decisions made under anthropogenic noise can be physiologically costly

6.1 Abstract

Anthropogenic noise has been shown to alter a range of behaviours and physiological processes in humans and non-humans. Yet, both are often studied in isolation.

Behavioural and physiological impacts can be linked for instance as physiological stress responses can be a proximate mechanism behind observed behavioural changes. An alternative route is that decisions made under noise can be have indirect physiological consequences and be costly for animals. We use the European hermit crab *Pagurus bernhardus* to quantify the physiological costs of decisions made under noise by measuring the oxygen consumption. In a preceding behavioural experiment, crabs were in groups of five and could freely interact with one another including the exchange of shells for 24 h while being exposed to two distinct sound treatments (ambient sound/ ship noise).As a result, fewer crabs obtained better fitting shells in the group process under noise. Afterwards, we measured the oxygen consumption to quantify the physiological costs of decisions made under noise. There was no direct effect of the sound treatment on the oxygen consumption. However, crabs in shells that were too small in relation to their body size had a higher oxygen consumption than hermit crabs in shells closer to the optimal sized shells. The experiment shows that, while anthropogenic noise did not directly alter the oxygen consumption in crabs exposed to noise for 24 h, behavioural decisions made under noise can be physiologically costly. Future work examining whether behavioural and physiological

responses under noise are correlated would give valuable insight into proximate causes of behavioural change under noise.

6.2 Introduction

Mounting evidence demonstrates the adverse effects of human-induced rapid environmental change (HIREC; Sih et al., 2011) such as anthropogenic noise on the behaviour and physiology of humans and other animals (for reviews see Kight and Swaddle, 2011; Kunc et al., 2016; Shannon et al., 2016b). Urban development, extraction of resources and extensive global transportation networks have changed the soundscapes of terrestrial and aquatic ecosystems around the globe making anthropogenic noise a chronic source of pollution to animals (Haver et al., 2017; Hildebrand, 2009; McDonald et al., 2008; Pijanowski et al., 2011). Anthropogenic pollution has been recognised to disrupt information gathering, processing and assessment changing the sensory ecology of animals (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011). Though populations can eventually adapt to new environments (Ghalambor et al., 2007) and the sensory pollution (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011), the initial response of organisms is thought to be behavioural (Tuomainen and Candolin, 2011). One of the most immediate responses would be to avoid noisy but otherwise suitable habitats (Bayne et al., 2008; Blickley et al., 2012a; Blickley et al., 2012b; Francis et al., 2009; Schaub et al., 2008). However, if animals decide to remain in noisy areas or cannot escape them, noise can interfere with information gathering and processing and act as a sensory pollutant.

The pollution of the sensory environment of animals can act along three main routes (Halfwerk and Slabbekoorn, 2015). First, unimodal effects describe the masking of natural cues and signals by an anthropogenic pollutant which disrupts the

information detection such as noise can mask acoustic cues (Brumm and Slabbekoorn, 2005; Clark et al., 2009; Erbe et al., 2016), light can confound visual cues (Gaston et al., 2013) and anthropogenic chemicals can alter natural chemical cues (Lürling and Scheffer, 2007). Second, anthropogenic noise has been shown to disrupt the information gathering, processing and assessment across modalities and interfere for instance with visual, chemical or tactile stimuli (Kunc et al., 2014; Morris-Drake et al., 2016; chapter 3, Tidau and Briffa, 2019; chapter 2, Tidau and Briffa, In Press; Walsh et al., 2017). In those cases, noise is thought to affect animals in their information gathering and processing capacity as a result of their limited attention (Dukas, 2002). Since attention and the multisensory integration of stimuli interact (reviewed by Talsma et al., 2010), the addition of anthropogenic noise can distract animals' attention away from pertinent cues (Chan et al., 2010b). This mechanism is of particular interest to understand behaviours in animals that do not primarily rely on acoustic cues and signals for their decision-making. Moreover, anthropogenic pollution often contributes to multimodal impacts, as human activities produce various stimuli simultaneously such as ships are not only emitting noise, but also light and chemicals. Besides altering their behaviour to cope with changing and potentially stressful natural environmental conditions and anthropogenic pollution, a third route is that organisms can adjust their physiology (for a comprehensive review on the mechanistic effects of noise see Kight and Swaddle, 2011). Such non-behavioural effects can range from alterations or damage to genes, cells and tissues, the immune and neuroendocrine system but also injuries to the auditory system and the impairment of cognitive, cardiovascular, reproductive, developmental and metabolic processes.

Metabolic rate is one of the most widely measure physiological traits and most often estimated from measuring the oxygen consumption (Pettersen et al., 2018) indicative for acute and chronic stress responses. Most experiments measuring the oxygen consumption of animals during or immediately after being exposed to anthropogenic noise show an acute elevation (Bruintjes et al., 2016; Dunlop et al., 2017; Harding et al., 2018; Purser et al., 2016; Radford et al., 2016b; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a but see Isojunno et al., 2018 who found reduced breathing rates in long-finned pilot whales *Globicephela melas*). Physiological noise effects appear to vary according to a range of factors including exposure duration (i.e. a short-term or repeated and over longer time) and with the point of measurement (i.e. during the exposure, immediately after or following a resting period). For instance, juvenile European eels *Anguilla Anguilla* and European seabass *Dicentrarchus labrax* rapidly recovered from short-term exposure to ship noise (Bruintjes et al., 2016). When exposed over a prolonged duration, fish can habituate (Nedelec et al., 2016b; Neo et al., 2018; Neo et al., 2014; Neo et al., 2015) some of which even within a day (Neo et al., 2015). Regulating the metabolic rate can be a short-term response to noise which appears to dissipate with time as animals habituate.

Since behaviour and physiology have been shown to correlate when coping with environmental challenges and stress (reviewed by Koolhaas et al., 2011), investigating behavioural and physiological responses to anthropogenic noise in conjunction can reveal mechanistic insights. Few experiments, however, have tested for correlation between behavioural and physiological responses under noise. In the European sea bass *D. labrax* and the gilthead sea bream *Sparus aurata*, motility and

haematological parameters like lactate and haematocrit were positively correlated under linear sweep noise (Buscaino et al., 2010). In sea bream under the noise, however, blood glucose levels were negatively correlated with swimming suggesting that there are species specific sensitivities to sound. Injaian et al. (2018) show that even though parents of the tree swallow *Tachycineta bicolor* reduced vigilance and increased feeding rates of nestlings in noisy territories (traffic noise), this behaviour did not compensate for lower growth rates and higher oxidative stress in nestlings exposed to noise. Thus, the decision of parents to nest in noisy habitats incurs long-term physiological costs for the nestlings and reduced reproductive success despite the parent's increased feeding rates. These examples demonstrate that physiological and behavioural approaches can reveal similar conclusions on the detrimental noise effects and that physiological responses to noise can provide a proximate cause for understanding behavioural changes, in particular when behaviour and physiology are correlated (Buscaino et al., 2010; Injaian et al., 2018). Direct or even causal correlation can be difficult to assess but changes in behaviour and physiology often co-occur. The co-occurrence of behavioural and physiological changes under noise has been shown in the scallop *Pecten fumatus* (Day et al., 2017), several aquatic and semi-terrestrial crustacean species (Celi et al., 2013; Filiciotto et al., 2018; Filiciotto et al., 2016; Filiciotto et al., 2014), the lined seahorse *Hippocampus erectus* (Anderson et al., 2011), the European eel *A. Anguilla* (Simpson et al., 2015) and the greater sage-grouse *Centrocercus urophasianus* (Blickley et al., 2012b). For instance, the greater sage-grouse was less abundant in areas experimentally exposed to noise and males, which remained at the mating site, had elevated levels of the stress hormone corticosterone (Blickley et al., 2012b). Despite being unable to identify a causal direction, this study

exemplifies that habitat avoidance and a physiological stress response in animals can appear simultaneously.

An alternative and seemingly less studied aspect of noise impacts is that behavioural responses under noise can cause subsequent physiological costs after the immediate exposure. For instance, noise can reduce immediate foraging performance and efficiency, which is energetically costly. Examples of altered foraging under noise includes the common shore crab *Carcinus maenas* (Wale et al., 2013a), the three-spined sticklebacks *Gasterosteus aculeatus* (Purser et al., 2016), the Greater mouse-eared bat *Myotis myotis* (Siemers and Schaub, 2011) and the Black-tailed prairie dog *Cynomys ludovicianus* (Shannon et al., 2014). Measuring the subsequent physiological costs of such behavioural changes cause by noise exposure can help to better quantify the full consequences of anthropogenic noise for animals.

Here, we use the European hermit crab *Pagurus bernhardus* to assess and quantify the direct and indirect physiological costs of decisions made under noise after 24 h of exposure. Since hermit crabs have a weakly calcified abdomen, they rely on empty gastropod shells for their protection and shelter for instance against predators and environmental extremes. Prior to measuring oxygen consumption, crabs underwent the re-allocation of new gastropod shells by participating in vacancy chains comprising groups of five crabs (chapter 5). After 24 h of this group process, fewer crabs were in the better fitting shells under noise compared with ambient sound. Since the shell hermit crabs occupied is the result of a group process under noise, we can quantify the metabolic costs of this group behaviour. First, if the prolonged exposure to noise (for 24 h) is stressful for *P. bernhardus*, we expect to see an increased oxygen consumption under noise. Second, if the behavioural decisions under noise are

physiologically costly, we would see a lower oxygen consumption for crabs which gained better fitting shells than crabs in lower quality shell.

6.3 Methods

6.3.1 Collection, husbandry and preparation of hermit crabs

We measured the metabolic rate in a subset of hermit crabs from the vacancy chain experiment in which crabs had been exposed to a 24 h sound treatment (ambient sound/ ship noise) and the animals were prepared accordingly (chapter 5). We collected hermit crabs from the rocky intertidal of Hannafore Point, Cornwall, UK (50° 20' 42'' N, 4° 28' 0'' W) in January and February 2018 and transported the animals directly to the laboratory at the University of Plymouth, UK. Crabs were maintained in a temperature controlled room at 15 °C with a 12:12 h light:dark cycle in a single holding tank containing 125 l of continuously filtered and aerated seawater from the seaward side of Mount Batten pier (50° 21' 34'' N, 4° 8' 8'' W) in Plymouth Sound, UK, collected at spring tides (Briffa et al., 2013). Crabs in the stock tank were fed once a week with white shell fish. The morning before we initiated the vacancy chains, crabs were carefully removed from their shell with a bench vice, sexed, and weighed (Briffa et al., 2013). Since the breeding season is likely to affect the behaviour of egg-carrying females, we used only male crabs without damaged appendages, visible parasites, or recent moult (Briffa et al., 2013). As in Briffa and Austin (2009), each vacancy chain contained of five crabs and one individual out of the following five weight classes: (1) 0.99–0.9 g, (2) 0.89–0.8 g, (3) 0.79–0.7 g, (4) 0.69–0.6 g and (5) 0.59–0.5 g which are hereafter referred to as ranks 1 – 5. Each crab was assigned a *Littorina littorea* shell of 50% of its preferred shell weight (% PSW) based on a regression line relating preferred shell weight to body weight obtained from a previous shell selection experiment (Briffa

et al., 2013). To identify the crabs and their potential shell gain throughout the observation, each crab was marked with a distinct colour of nail polish and shells were labelled with its weight. After this preparation each crab was housed individually in a white plastic dish of 15 cm diameter containing continuously aerated seawater to a depth of 5 cm until the observation on the following day and fed with white fish. After the observations the animals were supplied with larger shells and returned to the collection point.

6.3.2 Tank set-up and sound analysis

The behavioural observations prior to the metabolic rate measurements (chapter 5) were carried out in an 80 x 50 x 50 cm sized glass tank (with 1 cm thick aquarium glass) filled to a depth of 40 cm (~ 130 l) with seawater from the laboratory supply (Figure 6-1). We placed the tank on a free-standing trolley and cushioned the set-up with 1 cm Styrofoam plates between tank and trolley as well as the trolley and floor.

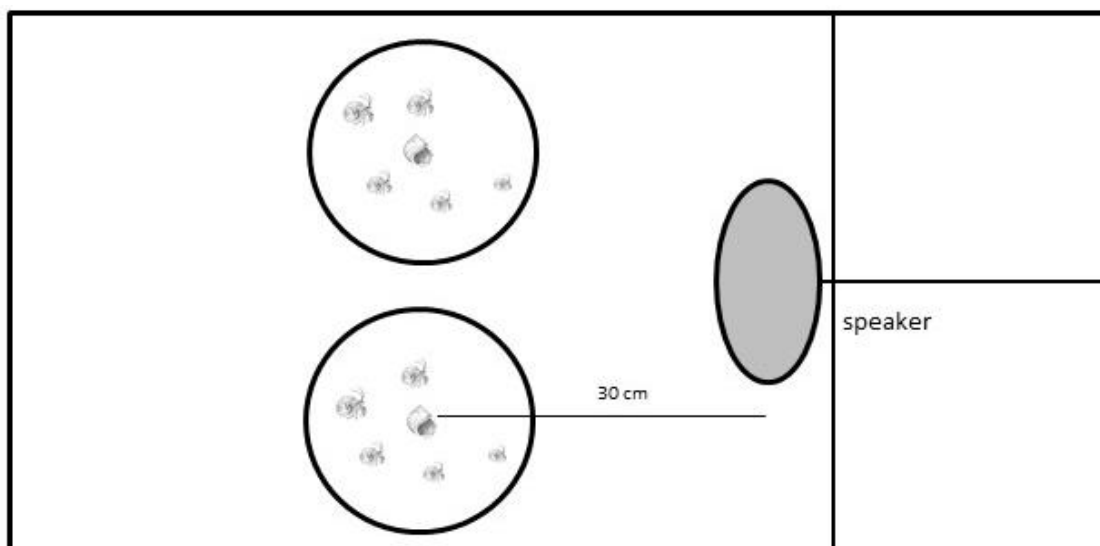


Figure 6-1 Tank set-up and observation arena. The arenas are made of acoustically transparent white plastic dishes of 15 cm diameter and placed at 30 cm distance to the speaker (measured from the centre of the arena). Each arena contained one group of 5 hermit crabs and the empty gastropod shell was placed in the centre of the dish.

An underwater speaker was suspended from a cushioned bamboo stick at 20 cm distance to one end of the tank, facing towards two observation arenas (plastic dishes of 15 cm diameter glued to the tank at 30 cm distance to the speaker measured from the centre). The underwater speaker (DNH Aqua-30 underwater speaker, of effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway) was connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping Town, China) and sound tracks were played back from a Toshiba Portégé R830-13C laptop (Tokyo, Japan). For the sound treatment we used three ship noise playbacks and three corresponding ambient control sounds from the same sites recorded at three major UK harbours (for details on recordings such as ship size and speed see Simpson et al., 2015; Wale et al., 2013b). We used Audacity 2.1.2 (Audacity Team, 2016) to create a total of 6 six audio tracks of either ambient control sound or ship noise for playback to the crabs. For the ship noise tracks, we alternated 2 min of ship noise with 2 min of ambient sound including 15 s fading in and out to simulate noise of passing by ships. The ambient control sounds were composed by the ambient sounds recorded at the same site as the ships.

To characterise the acoustic properties of the playbacks in the laboratory aquarium we undertook a spectral analysis of the six audio tracks re-recorded the playbacks at the centre of the dish which was at 30 cm distance to the speaker and 1 – 2 cm distance to the bottom of the tank. For those recordings, we used an omnidirectional hydrophone HTI-96-MIN (with inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V μ Pa; frequency range 0.002 – 30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave signals

from a function generator with a measured voltage recorded in line on an oscilloscope). We used PAMGuide (Merchant et al., 2015) for MATLAB R2015b (MathWorks, 2015) to perform a power spectrum analysis of 60 s recording with Hann evaluation window, overlap 50%, 0.2 s window length, 100 – 3 000 Hz bandwidth normalised to 1 Hz. We chose a filter of 3 000 Hz since the only known auditory thresholds for a similar crustacean has been received for the common prawn *Palaemon serratus* which showed an auditory brain response to acoustics stimuli at a frequency range of 100 – 3 000 Hz with amplitudes varying between 105 and 130 dB SPL re 1 μ Pa at 1 m (Lovell et al., 2005). the three ambient control tracks were played back so that they had a mean spectral density of 73.25 dB RMS re 1 μ Pa (ambient A: 68.5, ambient B: 77.38, ambient C: 73.88) and the ship noise tracks had a mean maximum of 119.83 dB RMS re 1 μ Pa (ship A: 123.4, ship B: 119.6, ship C: 116.5) at 1 000 Hz (Figure 6-2; Table 6-1). The sound levels were similar to those in previous studies on crustaceans exposed to noise in the laboratory (Wale et al., 2013a; Wale et al., 2013b).

Table 6-1 Sound intensity of the six playbacks and system’s self-noise: Minimum amplitude, maximum amplitude, average amplitude between 100 – 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa recorded in the centre of the arena and 30 cm distance to the speaker.

Playback	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1000 Hz
Ship noise playback A	101.9 at 2310 Hz	149.9 at 100 Hz	122	123.4
Ship noise playback B	104.7 at 2315 Hz	149.2 at 2650 Hz	124	119.6
Ship noise playback C	102.7 at 625 Hz	150.4 at 2650 Hz	123.7	116.5
Ambient playback A	60.22 at 2315 Hz	120.1 at 100 Hz	81.06	68.5
Ambient playback B	62.65 at 2315 Hz	120.5 at 100 Hz	84.64	77.38
Ambient playback C	59.91 at 720 Hz	120.5 at 100 Hz	80.66	73.88
System self-noise	49.15 at 2320 Hz	110.7 at 100 Hz	57.66	57.55

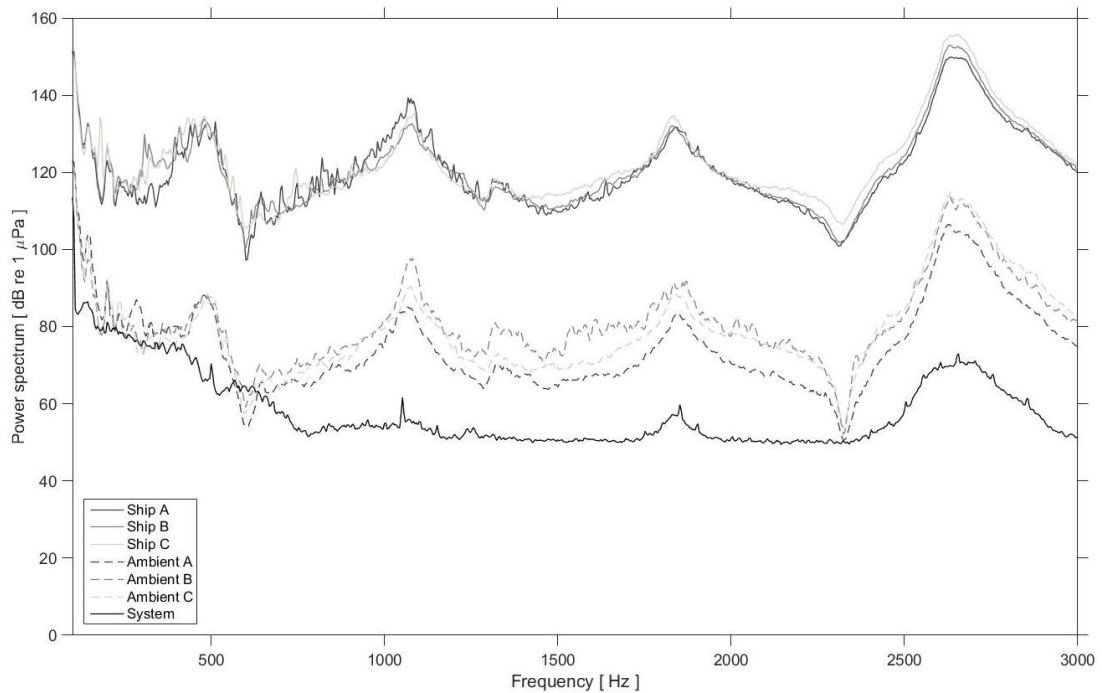


Figure 6-2 Power spectrum for three ship noise playbacks and three corresponding ambient sound playbacks recorded at 30 cm distance to the speaker. The system self-noise characterises the sound output by the equipment without playbacks. Filtered for 100 – 3 000 Hz frequency bandwidth.

We note that hermit crabs are likely to perceive the particle motion component of sound rather than the measured sound pressure levels (Breithaupt, 2002; Popper et al., 2001). In line with previous noise exposure studies in the laboratory (Simpson et al., 2015; Wale et al., 2013a), however, we analysed the power spectrum of the sound pressure to confirm that we exposed crabs to two distinctive sound conditions namely ship noise and ambient control. We are aware of the unresolved challenges of tank acoustics (Rogers et al., 2016) and do not attempt to establish absolute noise sensitivity levels for hermit crabs.

6.3.3 Experimental design

In the behavioural experiment preceding the oxygen measurements (chapter 5), hermit crabs were in groups of five conspecifics over 24 h and subjected to a shell re-allocation process. In this group process, crabs could freely interact including the exchange of shells and were randomly assigned to one of the two sound treatments (ambient control/ ship noise). The results showed that under 24 h noise exposure fewer crabs swapped into better fitting shells supporting the results from shell assessment in a solitary context under noise (chapter 3). As in the vacancy chain experiment (chapter 5), the metabolic rate experiment was designed in a fully orthogonal way with the factor sound (ambient sound/ ship noise) as a main factor (see Table 6-2). We measured and calculated the oxygen consumption similar to the protocol in Velasque Borges (2017) in a sub-set of crabs after 24 h sound exposure. Note that since the vacancy chains were initiated between 10:00 am and 11:00 am the metabolic rate measurements were taken between 10:00 am and 11:00 am the following day. We placed hermit crabs in sealed and blackened out Kilner jars filled with 175 ml autoclaved seawater. We closed the jars underwater to avoid any air bubbles. To prevent oxygen stratification, we put a magnetic flea inside the jar separated from the crab by a mesh glued to the bottom of the jar and placed the jars on a magnetic stirrer. A sensor spot was attached on the inner wall with silicone glue which reacts with an optical oxygen sensor to measure the oxygen consumption (OxySense GEN III 5000 series, OxySense, Dallas, TX, USA). We allowed hermit crabs 10 min to rest in the jar with the stirrer switched on before we took the first oxygen measurement. We measured the oxygen consumption every 5 min between 10:25 am

and 11:10 am generating 10 data points per crab. We calculated the oxygen consumption as follows:

$$O_2 \text{ uptake (ml } O_2 \text{ g h)} = O_2 \text{ consumed ml} \times (\text{pressure in mmHg} - \text{Weiss coefficient}) / 760 \text{ mmHg,}$$

where the O_2 consumption is converted from % to ml adjusted for temperature and salinity (Green and Carritt, 1967; Velasque Borges, 2017) and jar volume where weight equals volume as in Clark et al. (2013). We then corrected the O_2 consumption by the pressure and Weiss coefficient (Weiss, 1970) and finally the individual's crab weight in g (Velasque Borges, 2017).

We measured the metabolic rate in crabs from 14 chains collected over 7 days (two chains were observed per day) leading to an initial sample size of 140 individuals. However, since crabs were exposed to a social environment through which they obtained their shells, we excluded all group members if one out of the five had moulted overnight. In addition, technical problems reduced the sample size to $N = 58$ crabs (Table 6-2).

Table 6-2 Experimental design and sample size in each treatment group. Crabs in the two sound treatments (ambient sound/ ship noise) and five ranks (1 – 5).

Sound treatment	Rank					Sum
	One	Two	Three	Four	Five	
Ambient control	6	5	6	5	6	28
Ship noise	7	7	7	4	5	30

6.3.4 Statistical analysis

For the statistical analysis we used linear models and linear mixed effect models implemented in the R-package lme4 (Bates et al., 2015) in R version 3.4.3 (R Core Team, 2017). In contrast to fully controlled experiments, where crabs obtain a

predefined shell as the percentage of their preferred shell weight (% PSW), in this experiment hermit crabs obtained the shells through a group process. Consequently, crabs were in different sized shells in relation to their optimal shell and had different experience prior to the metabolic rate measurements. Furthermore, crabs in the vacancy chain were ranked by their body weight (1 being the heaviest crabs and 5 the lightest) and had different proportions of optimal shell size. While crabs in rank 1 had the opportunity to gain a maximum 100% optimal shell, crabs in smaller shells could obtain a shell of over a 100% optimal shell fit (heavier than optimal). Since the % PSW was related to the rank by the experimental design (i.e. crabs of rank 1 were expected to occupy the largest shell by the end of the experiment (chapter 5)), we first tested if rank predicts % PSW. We used a linear model with % PSW as the response variable and rank as the only fixed factor, applied model simplification and compared models with and without crab rank. We ran this model twice i.e. once for all crabs including crabs in rank 1 and for a subset of crabs from which we excluded crabs in rank 1. In both models, rank predicted the % PSW (all crabs: $F_1 = 4.32$, $P = 0.004$; crabs rank 2-5: $F_1 = 2.94$, $P = 0.04$) and was hence not included in the consecutive analysis of oxygen consumption.

For the final model, we used a linear mixed effect model with oxygen consumption in ml O₂ g h as the response variable and the interaction between sound treatment (ambient control/ ship noise) and % PSW (continuous variable) as the fixed factors. We also included day, chain ID and playback ID as random factors. Day was included because we exposed two groups of five crabs simultaneously to sound and chain ID accounted for the fact that the five crabs in each chain were not independent. Since we used three different ship playbacks and three different ambient controls we

included playback ID as another random factor. The continuous response variable (oxygen consumption) was log-transformed to improve normality.

Ethical note: No animals were harmed during the experiment. After the experiment each crab was supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences or permits were required for this study.

6.4 Results

There was no interaction between sound treatment and shell fit (% PSW after 24 h: $\chi^2_1 = 2.14$, $P = 0.14$) and oxygen consumption was not affected by sound treatment ($\chi^2_1 = 0.91$, $P = 0.34$). However, oxygen consumption decreased with increasing % PSW of the occupied shell, such that crabs in relatively large shells had lower oxygen consumption than those in relatively small ones ($\chi^2_1 = 11.26$, $P = 0.0008$; Figure 6-3).

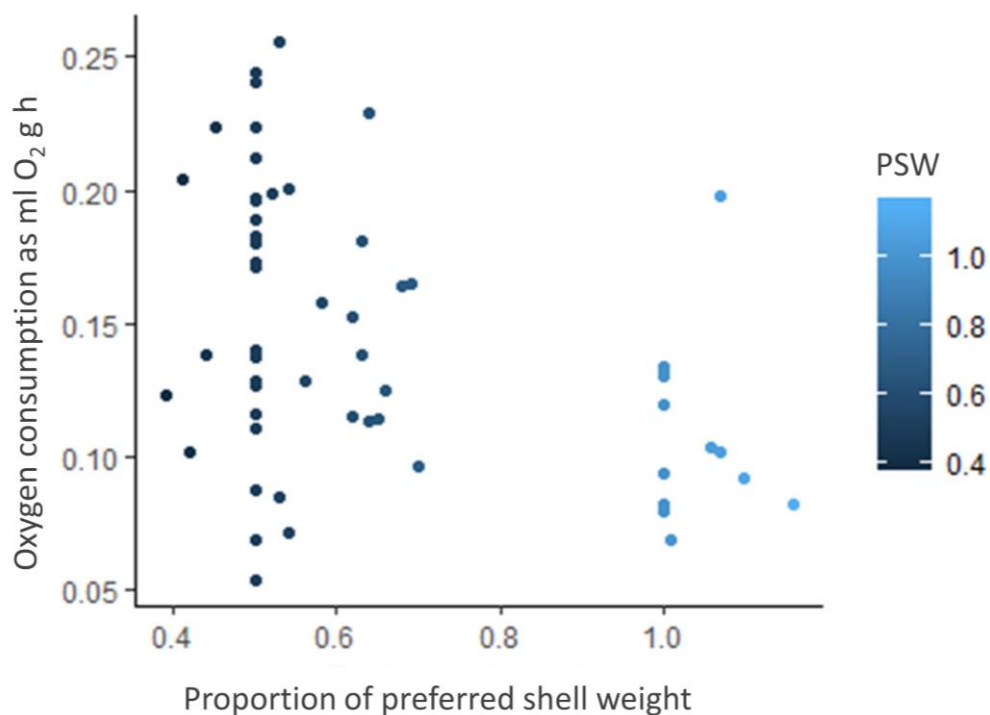


Figure 6-3 Effect of preferred shell weight on the oxygen consumption as ml O₂ g h (corrected for crab weight and time of first measurement).

6.5 Discussion

Organisms can adjust their behaviour and physiological functioning to cope with changing environmental conditions such as anthropogenic noise. In addition to directly regulating their oxygen consumption when exposed to anthropogenic noise, the decisions made under noise can be physiologically costly. Here we measured the oxygen consumption of hermit crabs immediately after being exposed to either ambient control or ship noise for 24 h. This allowed to assess the direct physiological costs of noise beyond a single, short-term exposure. After 24 h of sound treatment, the oxygen consumption did not differ between hermit crabs exposed ambient control from crabs exposed to noise indicating that there were no direct physiological effects of noise. To assess the indirect physiological costs of group behaviour under noise, we measured the oxygen consumption in relation to the % PSW. Hermit crabs in suboptimal shells (< 100% PSW) had a higher oxygen consumption than crabs in either optimal (100% PSW) or supraoptimal (> 100% PSW) shells. Crabs which occupied shells smaller than the optimal size are more exposed to predators (Vance, 1972) and environmental extremes such as desiccation during low tide (Taylor, 1981; Young, 1978). Furthermore, the optimal fit of the shell is crucial for survival and fitness in hermit crabs as it affects growth, reproduction (Bertness, 1981a) and energy budget (Herreid and Full, 1986). The result here adds to the existing evidence that suboptimal resources are detrimental for hermit crabs.

The sound treatment had no effect on the direct oxygen consumption in hermit crabs after 24 h exposure. Since we only measured the animals after 24 h, we do not know if *P. bernhardus* either showed an acute stress response immediately after being exposed to noise for the first as it has been demonstrated in other animals (Bruitjes

et al., 2016; Dunlop et al., 2017; Harding et al., 2018; Purser et al., 2016; Radford et al., 2016b; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a) and habituated (Neo et al., 2015) respectively recovered rapidly (Bruintjes et al., 2016; Neo et al., 2014) or if hermit crabs can tolerate ship noise. To fully understand the physiological effects of noise on crustaceans, future experiments will be needed. These could encompass measurement of oxygen consumption from the first, acute exposure in shorter intervals in organisms where this is feasible. A general conclusion of stress research is that more unpredictable and uncontrollable stimuli are more stressful (for review see Koolhaas et al., 2011). Therefore, future studies should also consider how anthropogenic noise with different temporal and spectral characteristics may affect crustaceans (chapter 2). For instance, juvenile European seabass *D. labrax* increased their ventilation under the impulsive noise sources (pile-driving and seismic survey) but not under ship noise (Radford et al., 2016b). Similarly, the giant kelpfish *Heterostichus rostratus* exhibited an acute increase of the stress hormone cortisol when exposed to intermittent noise but not under continuous noise (Nichols et al., 2015) illustrating how noise can directly affect physiology depending on the characteristic of the noise treatment. A potential difficulty is that handling stress can override any noise effect in animals where the oxygen consumption cannot be measured by observation such as the opercular beat rate in fish (for a detailed discussion about the possibility of handling and habituation on the oxygen consumption in common shore crabs in Wale et al., 2013b). Furthermore, stress responses in crustaceans may be apparent through indicators other than metabolic rate, such as lactate and glucose metabolism (Briffa and Elwood, 2005).

Occupying a suboptimal shell, as the result of group behaviour and decisions under noise (chapter 5), led to an elevated O₂ consumption in *P. bernhardus* and thus appears to be stressful. Though it is known that suboptimal shells are disadvantageous for survival and reproduction in hermit crabs, here we show that when the outcome of social interactions (in this case the acquisition of new shells via participation in vacancy chains) is altered by noise exposure, this change can have subsequent consequences for physiological state. In other words, exposure to noise caused a direct effect on behaviour, which in turn led to an indirect effect of noise on metabolic rate. Combining behaviour and physiology will allow to better understand the proximate mechanisms behind observed behavioural changes under anthropogenic noise and other forms of HIREC (Halfwerk and Slabbekoorn, 2015) but also quantify the costs of decisions made under noise. One of the few studies similar to ours assessing the physiological costs of behaviour under noise demonstrates that breeding in noisy territories decreased the adults' reproductive success and nestlings' growth rates which the parents could not compensate for by increasing their feeding rates (Injaian et al., 2018). Other studies measured the co-occurrence of behavioural and physiological changes under noise at the same time (Anderson et al., 2011; Blickley et al., 2012a; Buscaino et al., 2010; Celi et al., 2013; Day et al., 2017; Filiciotto et al., 2018; Filiciotto et al., 2016; Filiciotto et al., 2014; Simpson et al., 2015). For instance, under aquarium noise lined seahorse *H. erectus* had higher cortisol concentrations, its kidneys were more affected by parasites and animals exhibited signs of behavioural distress like tail adjustments and more time spent stationary (Anderson et al., 2011). Such studies enable us to conclude that both behaviour and physiology are likewise affected by noise. However, they do not allow the direct and subsequent indirect effects of noise to be easily disentangled. Thus, a

clear picture of causal relationships between the behavioural and physiological consequences of noise exposure has yet to emerge, in any general sense. Providing experimental evidence for causal relationships between behaviour and physiology (or how noise alters other, non-behavioural indicators as outlined by Kight and Swaddle, 2011) will allow us to understand if and how altered proximate mechanisms drive behavioural responses to noise. Here we show that decisions made under noise exposure can be physiologically costly in the period following exposure. Future research that examines the behavioural costs of decisions under noise and if behaviour and physiology are correlate would allow us to better understand and predict how and when animals respond to noise and quantify the costs of noise to animals.

Chapter 7: Startle response repeatability in hermit crabs under exposure to anthropogenic noise in the field

7.1 Abstract

Animals need to gather information from their environment to make adequate decisions. Human-induced rapid environmental change such as noise pollution, however, alters the sensory environment for gathering and assessing cues and has become a chronic source of pollution. Behavioural plasticity can help animals adjust to anthropogenic altered environments but there are limits to the degree of plasticity that can occur. In addition, despite gathering information from the environment, animals can make mistakes, particularly under unpredictable environmental conditions. If plasticity is costly and does not allow adequate responses, animals may instead display repeatable, consistent inter-individual variation in behaviour. Here we test the repeated exposure to anthropogenic noise in the field on the repeatability of startle response duration using the European hermit crab *Pagurus bernhardus*. Hermit crabs seek shelter in gastropod shells to protect their weakly calcified abdomen. We exposed hermit crabs to ship noise and ambient control once per day over two consecutive days (4 observations, 2 per sound treatment) in a field site in Galway Bay, Ireland measuring the mean startle response (MSR) which is the time crabs take to re-emerge from their shell after withdrawal. We found that MSR increased with observation. When adjusted for observation, the MSR was repeatable across sound treatments. These results show that behaviour is not only repeatable in the laboratory

as shown in previous experiments, but also in the field. We cannot rule out the possibility that ambient noise caused by wind masked and distorted the sound playbacks in the field. Further research combining laboratory and (semi-controlled) field experiments is necessary to better understand how animals respond to chronic anthropogenic pollution such as noise on crustaceans and other invertebrates.

7.2 Introduction

The effects of human-induced rapid environmental change (HIREC) on animals and their sensory ecology has become a growing field of research (Sih, 2013; Sih et al., 2011; Tuomainen and Candolin, 2011). Anthropogenic noise in terrestrial and aquatic ecosystems increased markedly during the last half century due to intensified traffic networks and increases in the number and size of vessels, making noise a chronic source of pollution in most ecosystems (Andrew et al., 2002; Barber et al., 2010; Hildebrand, 2009). The potential detrimental consequences of anthropogenic noise (and other sources of HIREC) have been experimentally demonstrated in a variety of vertebrate and invertebrate taxa. Studies including humans and non-human animals reveal that noise can alter an organism's genes, physiology, development and immune system (for review see Kight and Swaddle, 2011) as well as behaviour across contexts and situations (for review see Tuomainen and Candolin, 2011). While HIREC may eventually cause animals to adapt to changing environments, its initial response is often behavioural (Shannon et al., 2016b; Tuomainen and Candolin, 2011). Behaviour is commonly referred to as the most plastic phenotypic trait, allowing animals to respond appropriately to changing and novel environments (Gross et al., 2010). However, behavioural plasticity is limited and can be costly. An adequate response to a heterogeneous environment requires animals to have a sufficiently developed sensory

system for information gathering and processing (Briffa et al., 2008b). Such a sensory system can be costly to develop and maintain (DeWitt 1998). Besides these sensory prerequisites, any individual will only display a subset of the full behavioural range present at the population level. In addition, unlimited plasticity would fail to explain why apparently non-optimal behaviour occurs within populations rather than being selected against (Bell, 2007; Sih et al., 2004). Instead, theory suggests that, if environmental conditions are unpredictable such as under HIREC, rather than behaving plastic it can be less costly to behave consistent. As a consequence, individuals can show consistent inter-individual differences between and within populations rather than reaching a population wide optimal strategy (Bell, 2007; Briffa et al., 2008b; Dall et al., 2004; Sih et al., 2004). For instance, bold and explorative individuals may gain more feeding or mating opportunities but are more likely to be detected by predators, whereas shy and less explorative individuals tend to compromise access to those opportunities in favour of staying hidden for longer to avoid predators. Such consistent inter-individual differences in behaviour correlating either across time, situations or contexts and tested on more than one occasion are termed personality in human and non-human animals (Bell et al., 2009; Dall et al., 2004; Dingemanse and Réale, 2005; Réale et al., 2010). Since animals are exposed to environmental conditions altered by HIREC, a major question is how animals trade-off behavioural plasticity and consistency.

Anthropogenic noise has become a chronic source of pollution in nature. Though anthropogenic noise can originate from an acute source limited in time, animals are often subject to repeated, and even chronic noise pollution from motors in vehicles, ships and boats (Barber et al., 2010; Götz et al., 2009; Radford et al., 2012;

Tasker et al., 2010). Hence, most wild animals are potentially exposed to anthropogenic noise over a prolonged period, and the effects of this long term exposure are unlikely to be limited to initial behavioural responses. So far, most studies have tested the effects of noise on animals during a single exposure (Morley et al., 2014; Shannon et al., 2016b) and the few studies in which individuals have been subjected to repeated exposure have yet to reach a consensus on the potential effects. For instance, a laboratory experiment on the common shore crab *Carcinus maenas* showed that exposure to ship noise over 48 h resulted in constantly elevated oxygen consumption compared to the control (Wale et al., 2013b). In a recent field study, motorboat-noise playbacks for 12 days reduced the feeding behaviour and offspring interactions in brood-guarding spiny chromis *Acanthochromis polyacanthus* with some nests having 100% mortality rate (Nedelec et al., 2017). On the other hand, while juvenile coral reef fish *Dascyllus trimaculatus* initially sought shelter for longer during the first two days of boat noise, the fish resumed their previous behaviour after an exposure of a week or two, suggesting that they habituated to noise (Nedelec et al., 2016b). Thus, there is a clear need for more experiments investigating the effects of repeated exposure to noise on animals.

The repeated or continuous exposure of an animal to a stimulus such as anthropogenic noise can create a cumulative experience leading to one of the two most simple learning processes, habituation and sensitisation (Bejder et al., 2006; Commins, 2018). Habituation describes a decreased reaction to a stimulus over time as animals learn that the stimulus holds no significant consequence, whereas sensitisation represents an increased response and reduced tolerance to the repeated, presumably disturbing, stimulus (Bejder et al., 2006; Blumstein, 2016; Commins, 2018).

If animals fail to habituate to a changing environment and rather sensitise their response, this can be disadvantageous for their fitness and survival, being ultimately maladaptive. For instance, animals have been shown to avoid noisy but otherwise suitable habitat for feeding, mating and breeding (Bayne et al., 2008; Blickley et al., 2012b; Francis and Barber, 2013; Francis et al., 2009; Schaub et al., 2008) which can reduce their reproductive success. Unfavourable responses include animals responding to irrelevant stimuli, being distracted from important cues such as predators or food, making energetically costly decisions, and missing out on beneficial opportunities. Thus, the effect of long-term or repeated noise exposure is of interest for conservation biology, policy and management and an urgent question is whether animals habituate to avoid disadvantageous and potentially maladaptive responses to anthropogenic noise (Sih et al., 2011; Tuomainen and Candolin, 2011).

The European hermit crab *Pagurus bernhardus* is a model organism to study personality and behavioural plasticity in invertebrates and has recently been shown to alter its behaviour in response to anthropogenic noise (chapter 4, Tidau and Briffa, 2019; chapter 3, Tidau and Briffa, In Press; Walsh et al., 2017). In hermit crabs, the startle response duration is a measure of personality defined as the time crabs take to re-emerge from their gastropod shell after their withdrawal due to a disturbance stimulus (i.e. latency to re-emerge) (Briffa, 2013b; Briffa et al., 2008b; Gherardi et al., 2012). Hermit crabs are characterised by a weakly calcified abdomen, and empty gastropod shells serve as a portable shelter to protect animals against environmental extremes and predation. *P. bernhardus* adjusts its startle response to diverse biotic (predation risk: Briffa, 2013b; shell fit: Briffa and Bibost, 2009; crypticity of the shells: Briffa and Twyman, 2011), abiotic (temperature: Briffa et al., 2013; oxygen level: Briffa

and Elwood, 2000b) and anthropogenic factors (copper: White et al., 2013). For instance, hermit crabs adjusted their startle response to a predator cue but individuals were also consistently different in their response across the predation situation (Briffa et al., 2008a). Under higher temperatures, crabs were less predictable (higher intra-individual variation) contributing to lower repeatability in their startle response duration (Briffa et al., 2013). Since hermit crabs adjust their startle response to their environmental conditions, respond to noise in the laboratory and represent a generally understudied taxonomic group in noise research (Morley et al., 2014; Shannon et al., 2016b), *P. bernhardus* is an ideal model organism to test the effect of repeated exposure to ship noise. Furthermore, crustaceans have only recently been investigated under field conditions (Hubert et al., 2018) and there is a need to complement laboratory experiments with field experiments to better understand the consequences of anthropogenic noise on animals (Kunc et al., 2016; Simpson et al., 2015; Slabbekoorn, 2016).

Here we test the startle response of *P. bernhardus* in response to ship noise and ambient sound under field conditions. Based on the behaviour of *P. bernhardus* in response to noise in the laboratory and their behaviour under a predator cue (Briffa, 2013b; Briffa et al., 2008a), we predict that individuals will adjust their behaviour to noise and be consistently different in their response across both sound situations. More specifically, we predict that hermit crabs will show longer startle response under ship noise playbacks compared to ambient control. We also test whether startle response is correlated across days and sound treatments.

7.3 Methods

7.3.1 Site, hermit crab collection and preparation

We collected the data in July 2018 at the intertidal rocky shore of the Flaggy Shore, Co. Clare, Ireland (53°09'15.7"N 9°07'03.9"W; Figure 7-1). Since we conducted the noise exposure around the high tide, we collected the hermit crabs during low tide from the same site, transported them to a temperature controlled room at 16 °C, adjusted weekly to the seasonal light cycle (i.e. mid-July 16:8 h light:dark) at Galway-Mayo Institute of Technology, in Galway, Ireland.



Figure 7-1 Field site. Top: Geographical location. Bottom left: at low tide, when the hermit crabs were collected. Bottom right: at high tide, when the experiment was carried out.

We kept the hermit crabs in a single holding tank (60 x 15 x 40 cm) containing filtered and aerated seawater obtained from the National Aquarium of Ireland, Galway, Ireland. We fed the crabs *ad libitum* with white fish. On the day of the experiment, we randomly selected crabs from the tank and transported them back to the Flaggy Shore. For the transport, each crab was kept individually in a numbered screw top jar (7 cm diameter, 9 cm height) which we filled with aerated seawater from the temperature-controlled room. To reduce stress of the transport we blacked out the jars with black insulation tape, cut holes into the lid of the jars and placed the jars in a bucket with extra seawater to maintain as constant a temperature as possible. Between the observation days, we transported the crabs back to the temperature-controlled room at GMIT and kept them individually in numbered buckets (14 cm diameter, 18 cm height) filled with filtered and constantly aerated seawater.

After the second observation day in the field we transported the crabs back to the lab to carefully removed from their shells, sex and weigh them and the shell fraction (Briffa and Elwood, 2007). To calculate the shell fraction, we collected, dried and weighed the shell fragments. All crabs used in the experiment were male and no crabs had missing appendages, but we excluded one individual which had parasites (Briffa and Elwood, 2007). The crab weight ranged from 0.07 to 0.31 g (mean weight \pm SE = 0.19 ± 0.013 g, $N = 23$). Crab weight and shell fraction were strongly correlated ($r_s = 0.90$, $P < 0.001$). We only used crabs in intact *Littorina obtusata* shells since they were the most common at the field site (S. Tidau, personal observation). *L. obtusata* shells occur in different colour morphs varying between dark brown to yellow and an intermediate morph. Since colour morph has been shown to affect hermit crab decision-making (Briffa and Twyman, 2011) and re-emergence time in other species

(Pellitteri-Rosa et al., 2017) we only used crabs in shells of the intermediate colour morph. After cracking the crabs out of their shells, sexing and weighing them, each crab was supplied with a new shell and returned to the sea.

7.3.2 Sound set-up

For the sound playbacks, we designed a custom-made sound set-up on a floating rubber dinghy (Figure 7-2 top). We used an underwater speaker (DNH Aqua-30 underwater speaker, effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway) connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping Town, China) and powered by a 12 v 7 aH lead acid rechargeable battery (RS PRO, S Components Pte Ltd., Singapore). The amplifier and the battery were both placed in a plastic bag and kept dry in a sealable plastic box. This box with the electronic equipment was kept on an inflatable rubber dinghy (Figure 7-2). The sound tracks were played back from an mp3 player (SanDisk Clip Sport, Milpitas, CA, United States).

To make sure that the speaker was always the same distance from the substrate (i.e. that the hermit crabs were 30 cm from the speaker) we tied the speaker to a Styrofoam plate and also attached three dive weights with an adjustable rope to the Styrofoam (Figure 7-2 bottom centre and right, Figure 7-3). Below the floating speaker we placed an observational arena (28 cm diameter, 12 cm height) and placed the crabs in the centre of that arena. An arena was necessary to prevent hermit crabs from escaping the sound exposure (Figure 7-2 bottom right) and other organisms such as the common shore crab *Carcinus maenas* and common shrimp *Crangon crangon* from disturbing the focal animals (S. Tidau, personal observation during pilot study).



Figure 7-2 Sound set-up. Top: Complete sound set-up on the rubber dinghy. Bottom left: Sound equipment in waterproof boxes and bags. Bottom centre and right: Underwater speaker floating on Styrofoam and held at the same distance to the substrate and sea surface by dive weights (30 cm).

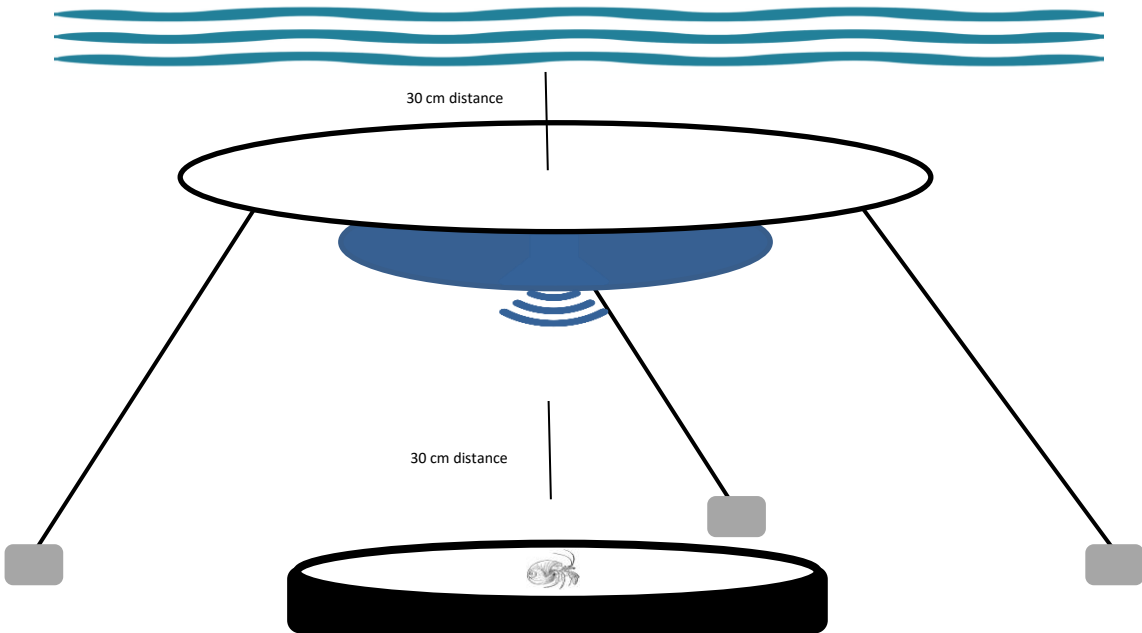


Figure 7-3 Experimental set-up and observation arena. Hermit crab were placed at 30 cm distance to the speaker in the centre of the arena. The speaker was at least 30 cm below sea surface.

For the sound treatment we used a ship noise playback and a corresponding ambient control sound (for details on recordings such as ship size and speed see Simpson et al., 2015; Wale et al., 2013a) and created two continuous noise and ambient sound tracks in Audacity 2.1.2 (Audacity Team, 2016). To make sure crabs were exposed to two distinct sound treatments we analysed the power spectrum as a proxy, as in previous studies on crustaceans (for instance Wale et al., 2013a). We are aware that hermit crabs are likely to perceive the particle motion component of sound rather than the measured sound pressure levels (Breithaupt, 2002; Popper et al., 2001). However, as pointed out in previous studies (see for instance Herbert-Read et al., 2017; Simpson et al., 2015; Wale et al., 2013a), we do not aim to establish absolute noise sensitivity levels for hermit crabs but analysed the power spectrum to confirm that we exposed crabs to two different sound treatments, namely ship noise and ambient control. To do that, we re-recorded the two audio tracks at the centre of the arena, where the hermit crabs would be placed, at 30 cm distance from the speaker, using an omnidirectional hydrophone HTI-96-MIN (with inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V μ Pa; frequency range 0.002 – 30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave signals from a function generator with a measured voltage recorded in line on an oscilloscope). At 30 cm distance to the speaker, the ship noise had a sound pressure level of 126.6 dB RMS re 1 μ Pa, ambient sound playback 71.86 dB RMS re 1 μ Pa and the natural ambient sound 62.16 dB RMS re 1 μ Pa all at 1 000 Hz (Figure 7-4; Table 7-1). We used PAMGuide (Merchant et al., 2015) for MATLAB R2015b (MathWorks, 2015) to perform a power spectrum analysis of 30 s recording with Hann

evaluation window, overlap 50%, 0.2 s window length, 100 – 3 000 Hz bandwidth
normalised to 1 Hz.

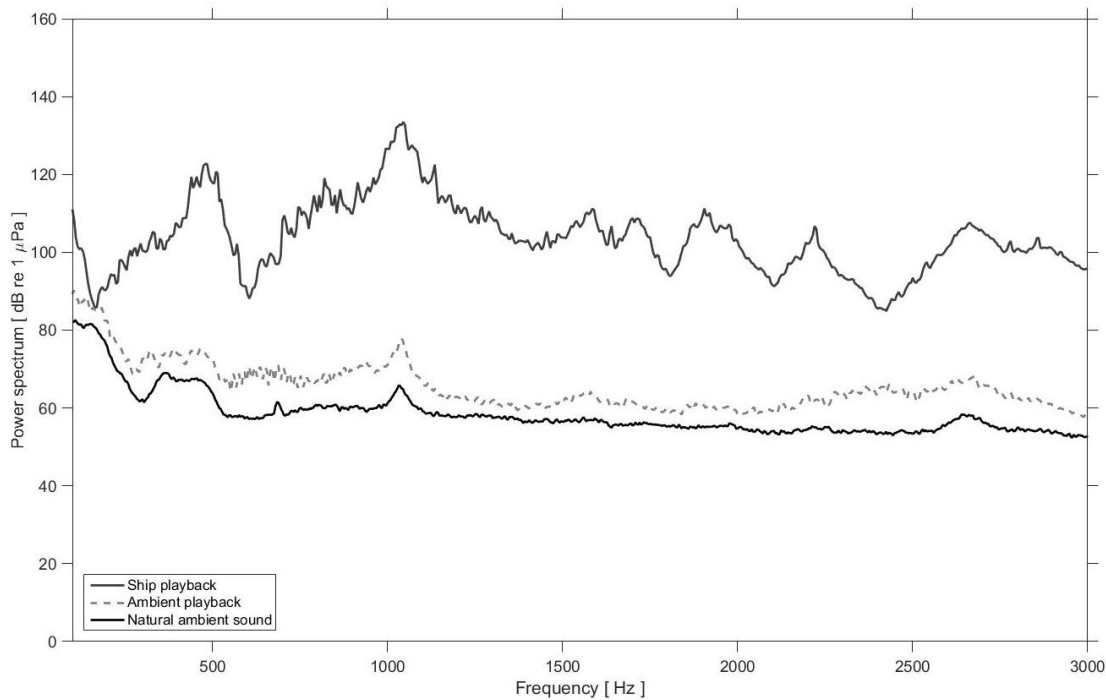


Figure 7-4 Power spectrum the ship noise playback, the ambient control sound playback and the natural ambient sound (equipment switched off) recorded at 30 cm distance to the speaker. Filtered for 100 – 3 000 Hz frequency bandwidth.

Table 7-1 Sound intensity of ship noise playback, ambient sound playback and the natural ambient sound: Minimum amplitude, maximum amplitude, average amplitude between 100 – 3 000 Hz and amplitude at 1 000 Hz all in dB re μ Pa recorded in the centre of the arena and 30 cm distance to the speaker.

Playback	Minimum amplitude	Maximum amplitude	Average amplitude	Amplitude at 1 000 Hz
Ship noise playback A	84.89 at 2 425 Hz	133.4 at 1 045 Hz	103.7	126.6
Ambient playback A	58.35 at 2 055 Hz	91.33 at 100 Hz	66.29	71.86
Natural ambient sound	53.47 at 3 000 Hz	83.2 at 100 Hz	59.44	62.16

An impairment of the experiment is that the sound treatment could not be characterised at the exact same site where the experiment was conducted due to technical problems with the equipment. Instead, the recordings for spectral analysis of

the sound treatment were taken at a nearby site. However, the recordings at this second site were taken under the same conditions e.g. the distance from the hermit crab arena to the speaker and the relevant environmental conditions (i.e. low winds) were the same. This allows us to conclude that using our equipment and experimental set-up, during low wind conditions at the experimental site, we would have been able to establish a sound treatment similar to the one in the laboratory tank with regard to the sound pressure domain, and different from the natural ambient soundscape at the field site (Figure 7-4).

7.3.3 Experimental design and behavioural measures

We used a crossover field experiment (Quinn and Keough, 2002) for the sound treatment (ambient control/ ship noise) with repeated observations (observation 1 – 4) on the same individual over two time periods (day 1/ day 2). Overall, we took up to four startle responses of each hermit crab i.e. two observations per day (Table 7-2). Those crabs which were first exposed to noise followed by ambient control on day 1 received the opposite order of sound treatment on day 2, namely first ambient control followed by noise (treatment order NAAN). The second group of crabs received the opposite treatment order (ANNA). We observed 24 hermit crabs but had to exclude one individual with had parasites ($N = 23$). Due to environmental conditions and associated handling error, the sample sizes varied for each day (Table 7-2).

Table 7-2 Experimental design and sample size in each treatment group. Observation 1 and 3 started 30 min before high tide, observation 2 and 4 started at high tide.

Sound treatment order	Day 1		Day 2	
	Observation 1	Observation 2	Observation 3	Observation 4
NAAN:				
Noise-Ambient-Ambient-Noise	$N = 10$	$N = 11$	$N = 7$	$N = 8$
ANNA:				
Ambient-Noise-Noise-Ambient	$N = 10$	$N = 6$	$N = 11$	$N = 0$

Since the startle response is in most cases a short reaction time and we wanted to make sure that all crabs experienced one of the sound treatments we started the playback before initiating the startle response. The method for inducing and recording startle response durations was based on Briffa et al. (2008b). We took the crab out of the jar and held it inverted for 10 s. This handling usually causes hermit crabs to withdraw so that they close the aperture with their major cheliped. We then placed the crab on the substrate in the centre of the arena with the shell aperture facing upwards. Since the turbidity of the water sometimes did not allow us to see when the crab had first contacted the substrate with a walking leg (as it was measured by Briffa et al., 2008b), we timed the startle response duration from when the crab had been placed on the substrate until it turned around fully. After recording the startle response, the crabs were placed back into their assigned screw top jar filled with seawater. As it has been shown previously that handling increases oxygen consumption but that this stabilises after 20 min in *P. bernhardus* (Velasque Borges, 2017), hermit crabs had at least 20 min resting time between carrying the crabs from to shore onto the rubber dinghy and the start of the first observations.

7.3.4 Environmental conditions

Since this was an *in situ* experiment with many uncontrollable environmental factors, which can potentially confound the results and hence should be avoided particularly for repeatability studies (Nakagawa and Schielzeth, 2010), we recorded wind speed, water temperature and the tidal range (Table 7-3). We also assessed the cloud cover to account for light since both have been shown to affect hermit crab behaviour (Velasque Borges, 2017). Sound properties are particularly difficult to map and characterise in shallow coastal waters such as those where the experiment was

conducted. Wind is a major source of ambient noise (together with rain) originating from oscillating gas bubbles at the sea surface which are entrained as waves break. Wind speed and rain are major sources of ambient noise particularly in shallow and very shallow waters (Ainslie et al., 2009; Cato, 2008; Hildebrand, 2009; Ma et al., 2005). The ambient noise is reflected from the sea floor where it can reach up to 120 dB re 1 μ Pa at very low frequencies of 100 Hz and below, and decays in intensity with increasing frequency (Ainslie et al., 2009; Cato, 2008; Hildebrand, 2009; Ma et al., 2005). In soundscape analysis, where the underwater sound is recorded from boats, wind and shallow water are a well-known confounding factor and hence avoided (McWilliam and Hawkins, 2013). Ambient noise levels correlated best with the speed of wind and can be predicted from the weather forecast (Cato, 2008). Hence, we carefully monitored the weather forecast between July and September 2018 for low wind intensities (ideally at a maximum of 1 Beaufort scale = 1 – 3 knots) to have as little natural interference of wind with the sound playbacks as possible. In addition, we had to exclude all days with rain and days when the high tide was not during daylight hours. Furthermore, we needed at least two consecutive days with these environmental conditions. As a result, we decided to collect data on July 21st and 22nd (Table 7-3).

Table 7-3 Environmental conditions on day 1 and day 2

Observation day	Wind speed			°C		
	Knots	Km/h	Beaufort scale	Jars	Seawater	Cloud cover
Day 1 (21.07.2018)	6	11.1	2	17.0	17.0	90%
Day 2 (22.07.2018)	9	16.7	3	22.0	19.5	90%

To avoid as much interference from the tidal system as possible, we decided to collect the startle response data around high tide, i.e. around 40 min before and after high tide, and we monitored the tidal range during the observation time (Figure 7-5).

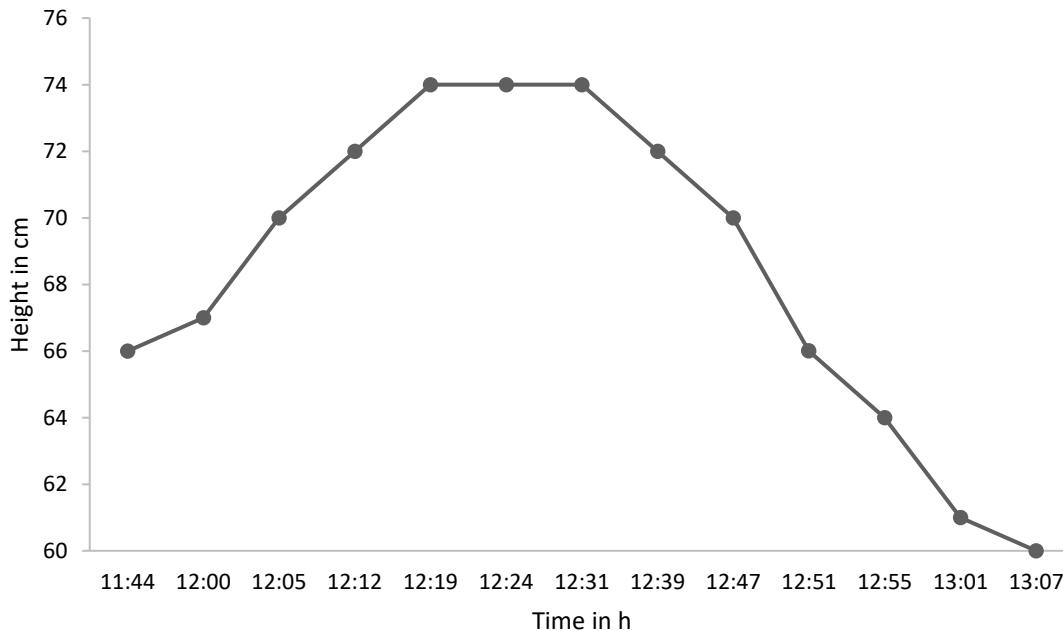


Figure 7-5 Tidal profile of the experimental site around high tide (04.09.2018, HT = 12:38).

7.3.5 Statistical analysis

To analyse the effects of treatment (ambient sound/ ship noise), sound treatment order (NAAN/ ANNA) and covariates (observation number, crab weight in g) on startle response duration we used a linear mixed effects model in R version 3.4.1 (R Core Team, 2017) using the lme4 package (Bates et al., 2015). For the fixed effects, we built two interactions into the model, namely sound * day and sound * observation. Since each crab was observed 4 times, random intercepts were used to account for crab ID. To improve normality, we transformed the data ($\log_{10} + 1$). To assess the model fit we plotted the residuals (with the functions qqnorm and qqline). We calculated the repeatability of the startle responses with the rptR package (Stoffel et al., 2017). Since

the lmer model showed that observation had a significant effect, we also calculated the adjusted repeatability (Nakagawa and Schielzeth, 2010) where observation number was included as a fixed effect in the model. To test whether the individual differences in startle responses were consistent across sound treatments and days we used Spearman's rank correlation coefficient which allows missing values and is more conservative for small data set such as ours (Dytham, 2011). More precisely, we analysed the correlations (1) between days, (2) between sound treatments, (3) between days and within sound treatments and (4) between sound treatments and within days.

Ethical note: No animals were harmed during the experiment. After the experiment each crab was supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences or permits were required for this study.

7.4 Results

There was no effect of the interaction between sound and observation number ($X^2_1 = 1.17, P = 0.49$), sound and day ($X^2_1 = 0.48, P = 0.49$), sound ($X^2_1 = 0.71, P = 0.40$) or day ($X^2_1 = 0.71, P = 0.40$) on the duration of the startle response. However, the startle response increased as a function of observation number ($X^2_1 = 8.71, P = 0.003$; Figure 7-6). The startle response was shorter during observation 1 and 2 (day 1) compared to observations 3 and 4 (day 2). The treatment order ($X^2_1 = 1.72, P = 0.19$) or weight ($X^2_1 = 0.69, P = 0.41$) had no effect on the startle response. While we could not analyse the intra-individual variation and hence the behavioural reaction norms, the illustration of the individual startle responses (Figure 7-7) suggests a random slope effect whereby most individuals increased their startle response over the observation number and some decreased their startle response.

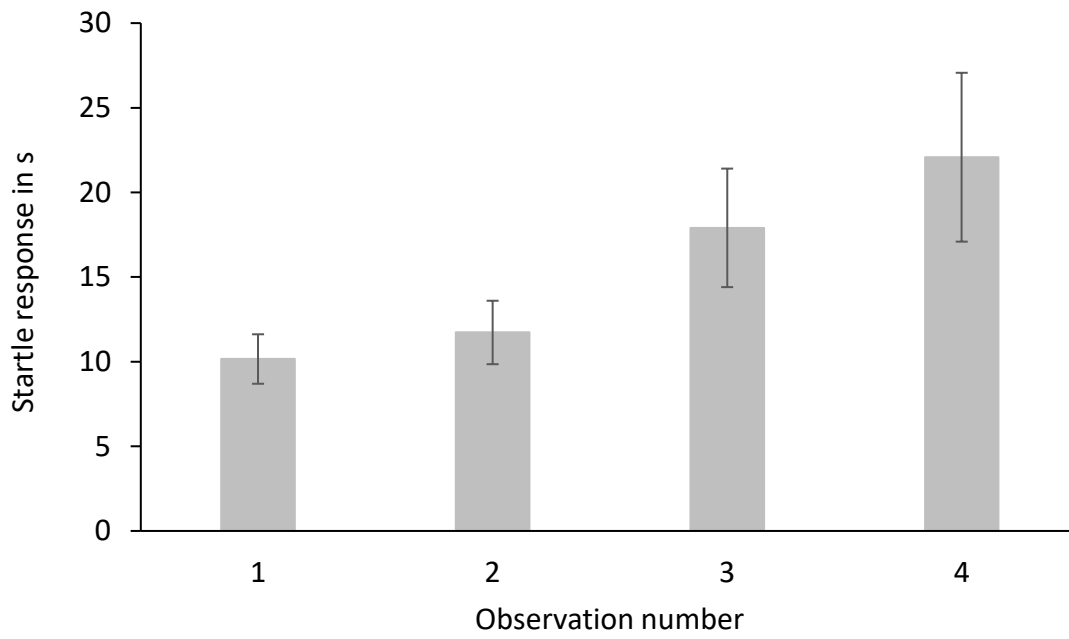


Figure 7-6 Effect of observation number on the startle response in s. Error bars show standard errors.

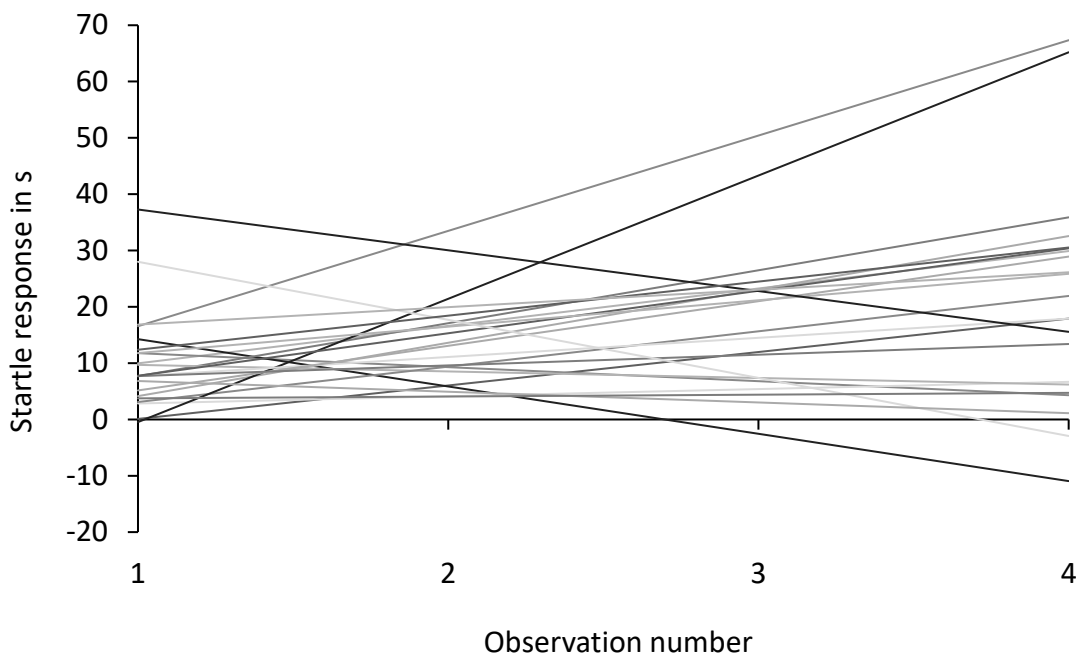


Figure 7-7 Plotted inter-individual variation in change in startle response duration across repeated observations. This plot is for illustrative purposes only.

The (agreement) repeatability was not significant ($R = 0.07 \pm 0.10$, $P_{LTR} = 0.34$; Table 7-4). However, the startle response was repeatable when adjusted for observation ($R = 0.24 \pm 0.14$, $P_{LTR} = 0.048$).

Table 7-4 Agreement repeatability and adjusted repeatability (including the full model) of the startle response based on bootstrapping (bold indicates significance).

Repeatability measure	Model	<i>R</i>	SE	Df	CI	<i>P</i>
Agreement repeatability	rpt(SR ~ (1 crab.ID))	0.07	0.10	1	0, 0.34	0.34
Adjusted repeatability	rpt(SR ~ (1 crab.ID) + obs)	0.24	0.14	1	0, 0.51	0.048

The startle responses were not correlated across days or sound treatments, across days and within sound treatments, or within days and across sound treatments (Table 7-5).

Table 7-5 Correlations of startle responses: (1) between days, (2) between sound treatments, (3) between days and within sound treatment and (4) between sound treatments and within days (bold indicates significance).

Correlation	Level	<i>rho</i>	<i>P</i>
(1) Between days	Day 1, Day 2	0.38	0.08
(2) Between sound treatments	Noise, ambient	0.13	0.59
(3) Between days and within sound treatments	Noise: N1, N2	0.19	0.56
	Ambient: A1, A2*	n.a.	n.a.
(4) Between sound treatments and within days	Day 1: N1, A1	0.30	0.27
	Day 2: N2, A2*	n.a.	n.a.

* Note: Since the ambient sound treatment on day 2 has very few data points, we cannot reliably calculate the correlations for these groups.

7.5 Discussion

The startle response duration of *P. bernhardus* was not affected by the sound treatment (ambient control/ ship noise) in the field. However, our experiment demonstrates that the startle response duration in hermit crabs is repeatable in the field and that it increased over the course of the experiment. The most pronounced difference occurred between observations 1 and 2 (day 1) compared to observations 3

and 4 (day 2). Even though not significant, there was a trend that the startle responses between day 1 and day 2 were correlated. Our startle response measurements largely agree with previous studies on *P. bernhardus* both in the field and in the laboratory (Briffa et al. 2008; Stamps et al. 2012).

The range of the absolute startle response durations we measured at the Flaggly Shore was similar to the overall range shown by three UK populations in the field (Briffa et al., 2008b). Although care needs to be taken when directly comparing findings between the field and laboratory, even for the same behaviour in the same individual (Bell et al., 2009; Osborn and Briffa, 2017), *P. bernhardus* increased its startle response duration as a function of time i.e. observation number, as has also been shown previously in the laboratory (Stamps et al., 2012). The increased mean startle response duration we found here indicates that hermit crabs became sensitised over time which can be advantageous if more cautious behaviour helps to avoid predator attacks (Krause et al., 1998) as was found for *Pagurus acadianus* during a simulated predator attack (Scarratt and Godin, 1992). However, longer startle response i.e. prolonged hiding behaviour can also be costly due to lost opportunities for essential activities such as foraging, mate searching, reproduction or predator detection (Krause et al., 1998; Martin and Lopez, 1999; Scarratt and Godin, 1992). While it is beyond the scope of the analysis to answer whether all individuals behaved the same, the visualisation of the individual startle responses (Figure 7-7) suggests a random slope effect whereby most individuals increased their startle response (although some decreased).

P. bernhardus exhibits both consistent variation between individuals and behavioural plasticity in the lab and in the field. Hermit crabs previously showed

repeatable behaviours over time, across situations, contexts (animal personality) and behavioural traits such as startle responses, exploration and aggression (behavioural syndromes) alongside behavioural plasticity under varying environmental conditions in the laboratory (Briffa, 2013a; Briffa, 2013b; Briffa et al., 2008b; Mowles et al., 2012). Here we demonstrated that consistent variation between individuals accounted for 24% of the observed variance in our experiment and that such a behavioural response is upheld under natural field conditions across two sound treatments. Other invertebrates, like the beadlet anemone *Actinia equina*, also express repeatable startle response across laboratory and field experiments (Osborn and Briffa, 2017). The strength of the effect size shown by *P. bernhardus* here is within the range in published studies across taxa (an average repeatability estimate of 0.37) which suggests that animals are more repeatable under field conditions (i.e. heterogeneous conditions) than in the laboratory (Bell et al., 2009). Even if animals exhibit consistent inter-individual variation in behaviour (animal personality), this does not exclude behavioural plasticity within individuals in how they respond to changing environmental conditions. Changing environments make information assessment more difficult for animals, and while behavioural plasticity can be costly to develop and maintain, it allows more appropriate responses to heterogeneous environments, although it does not lead to entirely faultless behaviours (Sih et al., 2004). In contrast to plasticity, repeatability (i.e. personality) does not require constant reassessment of changing environmental conditions and therefore can be less costly and advantageous over plasticity in unpredictable environmental conditions. In this study, none of the startle responses were correlated, which suggests that hermit crabs adjusted their behaviour to the environmental conditions by behaving in a plastic manner.

Behavioural plasticity in response to a fluctuating environment may have contributed to the lack of effect for noise treatment under natural conditions (as opposed to the laboratory based experiments described in the preceding chapters of this thesis). To test the presence or absence of consistent between individual differences across observations one should aim to avoid environmental fluctuation since this can confound the results (Briffa and Greenaway, 2011; Martin and Lopez, 1999; Nakagawa and Schielzeth, 2010). However, heterogeneous environmental conditions might better reflect the environmental variations animals are exposed to and which are unavoidable under complex natural conditions (Briffa and Greenaway, 2011). The population of *P. bernhardus* sampled here inhabit the rocky shore in proximity to the Atlantic Ocean and thus is naturally exposed to extreme and rapidly changing environmental conditions, for instance wind, rain and tides. Wind and the associated waves and water turbulence are major sources of ambient noise, particularly in shallow waters (Ainslie et al., 2009; Cato, 2008; Hildebrand, 2009; Ma et al., 2005). That hermit crabs exhibited stronger plasticity could be due to crabs responding to the changing environmental conditions over the course of the experiment (stronger wind on day 2 than on day 1). If crabs responded to the naturally changing environmental conditions during the experiment, this does not fully explain the overall pattern of increased startle response duration over the 4 observations. Crabs could have sensitised to the handling for the experiment. Experiments can create a cumulative stress experience (Blumstein, 2016) as shown, for instance, in the Eurasian perch *Perca fluviatilis* in the laboratory (Jentoft et al., 2005). However, sensitising during heterogeneous conditions appears unlikely. Rather, the stronger wind and thus particle motion in the water could have masked and distorted the

detection of other environmental cues by hermit crabs causing them to behave more cautiously (The desired environmental conditions did not occur during the study period and on both observation days the wind was above the intended wind speed level).

Despite the costs to gather, assess and process a variety of information in heterogeneous environments, hermit crabs have been found to modify their behaviour according to a range of biotic (predation risk: Briffa, 2013b; shell fit: Briffa and Bibost, 2009; crypticity of the shells: Briffa and Twyman, 2011) and abiotic factors (temperature: Briffa et al., 2013; oxygen level: Briffa and Elwood, 2000b). For instance, in the laboratory, aquatic crustaceans can detect chemical cues from conspecifics, gastropod snails and predators (Rittschof and Hazlett, 1997; Rittschof et al., 1992) and with their sensory hair-like setae on the body, legs and chelipeds, they can also sense changes in hydrodynamic flows and particles (Budelmann, 1992; Heinisch and Wiese, 1987). However, under laboratory conditions, there is little distortion of such chemical cues compared to turbulent field conditions. If the wind and associated strong particle motion in the water column distorts the direction or intensity of chemical cues, for instance from predators, a longer and more cautious startle response would be beneficial for hermit crabs. In the laboratory *P. bernhardus* adjusts its startle response in response to chemically induced predation risk (Briffa, 2013b) and the same information gathering mechanism should hold under field conditions. At close proximity, crabs could also use mechanoreceptive stimuli to detect approaching predators. If such cues to avoid predators cannot be detected, animals are expected to behave more cautiously (Sih et al., 2004). To adjust the latency to disturbance stimuli, i.e. delayed re-emergence from shelters and prolonged hiding times under predation risk, is a common trade-off among animals, as shown in the tubeworm *Serpula*

vermicularis (Dill and Fraser, 1997), the three-spined stickleback *Gasterosteus aculeatus* (Krause et al., 1998) and the Iberian rock lizard *Lacerta monticola* (Martin and Lopez, 1999).

Besides interfering with the detection of cues, the ambient noise (from the stronger wind causing water turbulence and particle motion) could have increased the cognitive load to process environmental stimuli. Anthropogenic noise can interfere and disturb the integration of sensory stimuli across modalities like visual and tactile cues (Kunc et al., 2014; chapter 3, Tidau and Briffa, 2019; chapter 2, Tidau and Briffa, In Press) and most likely does so with chemical cues (Halfwerk and Slabbekoorn, 2015). Similarly to anthropogenic noise, ambient noise could distract animals across sensory modalities; a hypothesis which would require future experiments to be tested.

Contrary to our initial prediction and previous studies in the laboratory, we did not find an effect of sound on the mean startle response duration in the field. Few studies have tested the effect of repeated or prolonged exposure to anthropogenic noise, and to the best of our knowledge there is only one study in which crustaceans have been exposed to noise in the field (Hubert et al., 2018). Although we cannot disentangle whether there is no effect of sound in the field on *P. bernhardus* from the possibility that the effect was masked by some of the confounding factors discussed above, the results raise general questions about the benefits and limitations of field and laboratory experiments. It is possible that there was indeed no effect of sound on hermit crabs in the field, in contrast to the results of laboratory experiments, as sound in small tanks in the laboratory is highly distorted by reverberations of tank walls which trigger stronger particle motion than in natural settings under the same sound pressure level (Akamatsu et al., 2002; Slabbekoorn, 2016). However, shore crabs and

prawns have recently been shown to change their distribution pattern under white noise in the field (Hubert et al., 2018) indicating that noise does alter the behaviour of crustaceans under more complex natural conditions. Consequently, it appears more reasonable to assume that the environmental conditions during this experiment overrode any noise effect. Analysing the power spectrum of the ambient noise conditions over different wind speeds could have helped to assess the sound intensity of the wind and potentially test if the wind masked the sound treatment (see McWilliam and Hawkins, 2013 for challenges associated with soundscape analysis in shallow waters). Field conditions are complex, often very difficult to account for and not always quantifiable. Laboratory experiments instead allow a 'reductive' approach whereby all variables except the ones of interest can be kept constant. That facilitates isolation of the effects of the experimental variables, from other potentially confounding factors, and the identification of effects that could otherwise be masked. However, it is important to acknowledge that laboratory experiments could give the impression that an effect is large, when in nature it might not be as important as other environmental variables.

In conclusion, laboratory experiments in conjunction with field studies will provide the most insight into the effects of anthropogenic noise and other forms of HIREC on animals. Laboratory experiments can be a valuable starting point to understand how anthropogenic noise can affect animals and which behaviours are affected. A future route for quantifying the effects of noise would be to study if all individuals react to anthropogenic noise in the same way. This means that future research would benefit from investigating behavioural reaction norms across sound treatments to disentangle how much the response to noise can be explained by the

consistent variation between individuals and the variation within individuals (Dingemanse and Réale, 2005). Due to the complexity of such experiments regarding the behavioural assays and the challenges of working in marine environments this would best be studied in the laboratory (first). Building on laboratory experiments, studies under more natural conditions, for instance in semi-natural mesocosms, should yield valuable insight into how anthropogenic noise affects animals in the wild and allow better informed management recommendations by conservationists and policy-makers.

Chapter 8: General discussion

Research studies provide ample evidence for the detrimental effects of anthropogenic underwater noise on the behaviour and physiology of animals. Despite this growing attention, surprisingly little is known about how crustaceans are impacted by anthropogenic noise. This thesis aimed to contribute to expanding our knowledge on the impacts of anthropogenic noise on this taxa using the European hermit crab *Pagurus bernhardus* as a model organism as well as answer questions of wider biological relevance such as noise effects across sensory modalities. Hermit crabs need gastropod shells of optimal fit to allow for growth, reproduction and protection against environmental extremes and predators. This function makes the assessment of shells a crucial behaviour for survival and fitness for hermit crabs. Crabs do not primarily rely on acoustic cues for shell assessment and decision-making, but to a much greater extent on visual, tactile and chemical information (Elwood, 1995; Gherardi and Tiedemann, 2004; Hazlett, 1982). Nonetheless, anthropogenic noise influenced the behaviour of crabs providing evidence for cross-modal impacts of noise. Therefore, it seems clear that a broader variety of taxa than commonly anticipated (i.e. those relying heavily on acoustic information) could be affected by noise and other sources of sensory pollution.

Specifically (see Figure 8-1 for a visual summary of the findings), I found that noise alters the shell assessment behaviour and decisions in solitary individuals (chapter 2 – 3, chapter 7) and groups of crabs (chapter 4 – 5), and that the decisions made under noise can be physiologically costly (chapter 6). In many cases, behaviour under noise was modulated by natural factors such as the quality of the occupied shell resource (chapter 2 – 6), the presence of a visual predator cue (chapter 3), social

(chapter 4 – 6) and natural environment in the field (chapter 7). In addition to these natural factors, effects of noise vary with the characteristics of the noise regime like noise intensity and other properties (chapter 2) and exposure duration ranging from short-term exposure (chapter 3 – 4), short-interval repeated exposure (chapter 2, chapter 7) and continuous exposure over 24 h (chapter 5 – 6). In this final chapter, I will discuss how my research contributes to the field, highlighting the knowledge gained through my work and methodological limitations both of which lead to recommendations for conservation and suggestions for future research.

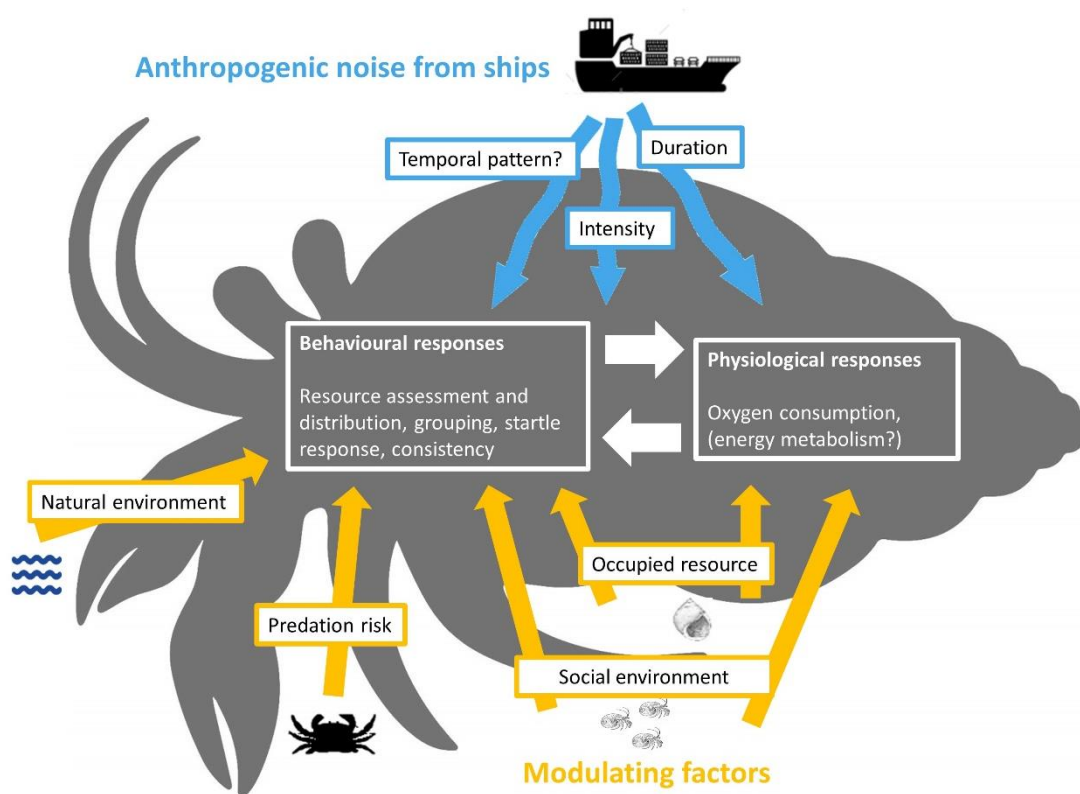


Figure 8-1 Schematic illustration of the effects of ship noise on the behaviour *Pagurus bernhardus*. Different components of ship noise are shown by blue arrows. Natural variables that influence behaviour and potentially interact with ship noise, and modulate its effects, are shown by yellow arrows. Biological responses to ship noise and natural variables are shown in white boxes. Note that these may interact with one another.

8.1 Modulating factors: Anthropogenic noise effects

interact with natural factors

In nature, animals are subject to various natural and anthropogenic stimuli and conditions simultaneously, thus creating multi-sensory environments in which animals have to integrate signals and cues from various modalities (Talsma et al., 2010).

However, investigating the effects of sensory pollution on behaviours that depend on several sensory channels can be complex and so far most experiments have examined noise and other pollutants in isolation (Halfwerk and Slabbekoorn, 2015; Sih et al., 2011). For instance, recent experiments on *P. bernhardus* have shown that hermit crabs in small shells chose optimal shells less frequently in the presence of white noise (Walsh et al., 2017) and that noise can alter anti-predator behaviour (Chan et al., 2010b) in the terrestrial Caribbean hermit crab *Coenobita clypeatus*. In this thesis, I attempted to examine how such effects of anthropogenic noise might interact with those natural cues that also form part of the animal's sensory environment, assessing the influence of noise alongside that of (i) shell quality (chapter 2 – 3), (ii) shell quality and predator cue (chapter 3), (iii) the social environment (chapter 4 – 5) and (iv) natural abiotic environmental conditions (chapter 7).

8.1.1 Quality of the occupied resource

Hermit crabs can occupy shells in varying degree of fit in the wild rather the optimal, preferred shell weight (% PSW) provided in experiments. In the first experiment (chapter 2), I exposed crabs for 10 days to two sound treatments using a crossover design so that all crabs experienced ambient sound and ship noise. On the first 9 days of the experiment, when the optimal shells were blocked so that crabs could not enter

the shell, the low intensity noise had no effect on any behaviour. However, on the last day, when the optimal shells were not blocked so that crabs could enter them, crabs in small shells under ship noise accepted the optimal shell more frequently than crabs under ambient sound. This pattern was reversed for crabs in larger shells and less marked. That ship noise influenced the decision-making in hermit crabs despite being of similar intensity to ambient sound suggests that to hermit crabs the two sound treatments must differ in other properties than just the intensity (for the discussion on the noise properties see further below). It is possible that intensity is the main driver of noise effects but that other properties play a role in decision-making when the consequences for survival and fitness are high (such as swapping into better fitting shells for better protection against predators).

Following this experiment, I decided to change the experimental set-up to create a noise treatment that was also different from ambient sound in sound intensity. In chapter 3, I found that anthropogenic noise and occupied shell interacted but also acted in isolation on hermit crabs. Crabs under high intensity noise chose optimal shells less frequently than conspecifics under ambient sound and crabs in small shells (50% PSW) chose optimal shells less frequently than crabs in larger shells (80% PSW). However, quality of occupied shell was more significant than sound treatment indicating that shell quality could be a better predictor for the behaviour in hermit crabs than high amplitude noise. Likewise, the occupied shell was indicative for the latency to approach the optimal shell but high amplitude noise had no effect. On the other hand, hermit crabs in 50% shells were less likely to contact the optimal shell with their antennae compared to crabs in 80% shells whereas this pattern was absent in the presence of ship noise demonstrating that occupied shell and high intensity

noise can interact depending on the task. Since the set-ups between chapter 2 and chapter 3 were very different, a direct comparison of the results is not straightforward. Nevertheless, together the experiments indicate that the effect of noise can be modulated by resource quality (entering the optimal shell and antennal contact) whereas in some instances natural factors (resource quality) can be more predictive for behaviour than anthropogenic noise. So-called 'ramp-up' experiments could bridge these two studies. In those experiments, animals are gradually exposed to raising noise intensities (Hawkins and Popper, 2016; Neo et al., 2016) which could reveal if hermit crabs change their behaviour at certain intensity thresholds, at which noise intensity natural and anthropogenic factors are decoupled and if or at which noise intensities shell swapping is compromised all together.

8.1.2 Increasing complexity: Noise, resource quality and predator cue

In chapter 3 I asked whether noise interacts with two naturally occurring factors, occupied shell quality and a visual predator cue to affect shell assessment and decision-making. I found that hermit crabs in 50% shells took less time for their final decision when exposed to both ship noise and predator cue while crabs in 80% shells showed shorter decision time only when the predator cue was absent. These results indicate that the effects of anthropogenic noise are modulated by two natural factors (predation threat and resource quality) in a complex three-way interaction.

Besides demonstrating that noise influences resource acquisition (chapter 2 – 3; Walsh et al., 2017), these findings also suggest that noise disrupts information assessment across multiple sensory channels. However, since hermit crabs use a combination of visual, chemical and tactile information gathering and processing when

assessing shells, disentangling the effect of noise on the responses of crabs to information in each sensory channel is difficult. By adding the visual predator cue, I clearly illustrate that noise disrupts the processing of visual cues, which has also been shown for instance in the common cuttlefish *Sepia officinalis* (Kunc et al., 2014), the terrestrial Caribbean hermit crab *C. clypeatus* (Chan et al., 2010b) and in humans (Ljungberg and Parmentier, 2012; Parmentier et al., 2011). In addition to visual cues, there is also recent evidence for disruption of olfactory cues by anthropogenic noise (Morris-Drake et al., 2016) which are particularly important to many crustaceans. Aquatic crustaceans can detect chemical cues from conspecifics, gastropod snails and predators (Rittschof and Hazlett, 1997; Rittschof et al., 1992). Chemical cues can be readily manipulated for *P. bernhardus* by inducing water from tanks containing the predatory *Carcinus maenas* (Briffa, 2013b; Briffa and Austin, 2009; Briffa et al., 2008a; Briffa et al., 2008b). Due to the logistical constraints on water changes arising from the large volume tank used in my experiments investigating chemical cues was not practical; rather, I decided instead to focus on some of the many other unresolved questions in noise research. Nevertheless, future research on cross-modal effects where the modalities can be studied in isolated and combination could examine whether noise is more distractive in some modalities than in others.

8.1.3 Intraspecific interactions

Anthropogenic noise has been widely shown to alter behaviour of individual organisms such as movement, foraging, and anti-predator responses (Chan et al., 2010b; Luo et al., 2015; Shafiei Sabet et al., 2015; Shafiei Sabet et al., 2016; Shannon et al., 2014; Shannon et al., 2016a; Siemers and Schaub, 2011; Simpson et al., 2015; Simpson et al., 2016; Wale et al., 2013a; Wisniewska et al., 2018). A second frequently studied context

is acoustic communication (reviewed by Brumm and Slabbekoorn, 2005; Erbe et al., 2016). However, relatively little is known about how noise impacts social behaviour and intraspecific interactions in animals that do not primarily rely on acoustic communication and I addressed this question in two experiments (chapter 4 – 5).

In hermit crabs, grouping aggregations can reach up to hundreds and thousands individuals (Gherardi, 1991) and *P. bernhardus* is often found in aggregations of at least up to several dozen individuals in rock pools during low tide (S. Tidau, personal observation). The preference of *P. bernhardus* for joining groups, however, was not yet known. Since hermit crabs frequently obtain gastropod shells from their conspecifics via agonistic encounters, it has been hypothesised that they gather to form shell exchange markets (Gherardi and Vannini, 1993; Hazlett and Herrnkind, 1980), or simply because they are attracted to sites where empty shells or other resources (e.g. food) are available in large numbers (M. Briffa, personal communication). In addition, aggregation might be a strategy to dilute the attention of predators (Foster and Treherne, 1981; Gherardi and Benvenuto, 2001). Based on these ideas, I examined whether *P. bernhardus* shows a preference for grouping with a single conspecific, a group of five conspecifics or whether they prefer to remain solitary, and how those preferences might be influenced by noise (chapter 4, Tidau and Briffa, 2019). I found that under ambient sound crabs in optimal shells spent most of their time close to a single crab, while crabs in suboptimal shells showed no clear preference. However, exposure to ship noise reversed the effect of shell quality on grouping preference demonstrating that this anthropogenic stimulus also affects social behaviour.

Next, I conducted an experiment in which conspecifics not only acted as a stimulus but could freely interact and exchange shell resources via a resource distribution system known as vacancy chains (chapter 5). The size hierarchy remained stable under noise but under noise fewer crabs benefited from the arrival of a new shell resource over the course of 24 h compared to ambient sound. Contrary to the stable hierarchy in hermit crabs, two previous studies demonstrate that noise can alter social hierarchies (Bruintjes and Radford, 2013; Celi et al., 2013). The finding that fewer crabs benefited from optimal shells under noise (together with the results from chapter 2 and chapter 3) provides further evidence that decision under noise, which are tightly linked to the optimal shell fit, eventually reduce crabs' survival and fitness. Moreover, this experiment shows that decision-making and resource assessment of individuals exposed to noise can scale-up to group and eventually population level.

8.1.4 Naturally fluctuating environments

Sound playbacks in small tanks suffer from acoustic distortion particularly in the particle motion domain (Akamatsu et al., 2002) which is relevant to the detectability of sound in crustaceans (Budelmann, 1992; Hawkins et al., 2015; Hawkins and Popper, 2016). Therefore, I conducted a field study investigating how noise affects hermit crabs under more natural sound conditions (chapter 7). I found that the mean startle response (MSR) increased with observation and, when adjusted for observation, that the mean startle response was repeatable. After demonstrating repeatable behaviour under laboratory conditions in my first experiment (chapter 2), this final experiment illustrates that their behaviour is also repeatable in the field, although to a lesser extent. However, the ship noise had no effect on mean startle response duration, or on its repeatability under field conditions. These results raise the question if the sound

treatment was masked and distorted by natural factors i.e. wind and waves. Biological sources of ambient noise are comprised of feeding and territorial defence by fish and invertebrates which can reach intensities of up to 80 dB re 1 μ Pa (Holles et al., 2013). Depending on the frequency, ambient noise from wind can reach higher intensities which can mask ship noise (Hildebrand, 2009). Moreover, very shallow waters, such as those where the experiment was conducted, are characterised by complex sound fields resulting from reverberations of the sea surface and substrate (Ainslie et al., 2009; Cato, 2008; Hildebrand, 2009; Ma et al., 2005). Ambient noise reflected from the seafloor can reach up to 120 dB re 1 μ Pa at very low frequencies of 100 Hz (Hildebrand, 2009) and wind and shallow water are a well-known confounding factors in soundscape analysis (McWilliam and Hawkins, 2013).

Under consideration of the acoustic complexity of coastal shallow waters, more exact characterisation of the sound treatment in the field would require measurement of particle motion relevant to most invertebrates and many fish. However, such measurements are currently one of the major limitations in describing how invertebrates perceive noise (see a more detailed discussion below; Hawkins and Popper, 2016; Nedelec et al., 2016a). Nevertheless, since a recent field study has shown that shore crabs responded to noise in semi-natural outdoor conditions (crabs avoided noisy areas) (Hubert et al., 2018), I am confident that my sound set-up created a sound treatment detectable by *P. bernhardus*. Instead, most likely wind masked the playbacks so that for hermit crabs there was no distinguishable sound treatment. As I only had observations from 2 days and hence 2 wind speeds, I did not have enough data to statistically analyse the effect of wind. Although I closely monitored the weather, there were no days with better conditions. Besides those acoustic challenges,

I had to stop the data collection on day 2 (due to the unanticipated arrival of a lion's mane jellyfish in close proximity to my study site), which further reduced the data availability. Despite the obvious logistical constraints on field-based experiments, attempts to characterise the effects of noise under more natural conditions are clearly warranted.

8.2 Behaviour and physiology: A missing link

Anthropogenic noise has been shown to alter behaviour (Kunc et al., 2016; Shannon et al., 2016b) and diverse non-behavioural functioning and mechanisms effects in humans and non-humans (Kight and Swaddle, 2011). Research provides ample evidence that behaviour and physiology can correlate when coping with stress (reviewed by Koolhaas et al., 2011). However, few experiments have studied if and how behaviour and physiology correlate under noise (for exception see Buscaino et al., 2010; Injaian et al., 2018) and some examined co-occurring effects of noise on both behaviour and physiology (Anderson et al., 2011; Blickley et al., 2012a; Buscaino et al., 2010; Celi et al., 2013; Day et al., 2017; Filiciotto et al., 2018; Filiciotto et al., 2016; Filiciotto et al., 2014; Simpson et al., 2015). In chapter 6, I quantify the direct and indirect physiological costs of noise by measuring the oxygen consumption in hermit crabs after 24 h exposure to group processes (chapter 5) and noise.

8.2.1 Direct physiological effects of noise

A physiological measurement taken on a single event as in this experiment can indicate the state of an organisms to human disturbance (Nisbet, 2000) such as an anthropogenic noise stimulus. After 24 h of noise exposure, hermit crabs showed no difference in oxygen consumption between crabs under ambient sound and ship noise

which makes two explanations probable. First, crabs could have shown an acute stress response immediately after being exposed to noise for the first time which would be undetected by my study design. For instance, the common shrimp *Crangon crangon* and the common shore crab *C. maenas* increased the oxygen consumption directly after being exposed to white noise respectively ship noise (Regnault and Lagardère, 1983; Wale et al., 2013a). Also animals from other taxa show an acute stress response immediately after being exposed to noise for the first time (Bruitjes et al., 2016; Dunlop et al., 2017; Harding et al., 2018; Purser et al., 2016; Radford et al., 2016b; Simpson et al., 2015; Simpson et al., 2016). Some animals resume quickly to their previous state immediately after the noise exposure stops (Bruitjes et al., 2016; Chen et al., 2011; Neo et al., 2014). Others habituate over time whereby individuals first showed an increase in physiological response to noise and subsequent weakening (Nedelec et al., 2016b; Neo et al., 2018; Neo et al., 2014; Neo et al., 2015). For instance, European seabass *Dicentrarchus labrax* habituated to noise within an hour (Neo et al., 2015). Since I only measured the animals after 24h, I cannot exclude that *P. bernhardus* showed an initial acute response to noise by an altered oxygen consumption followed by a quick recovery or habituation over 24 h. Repeated sampling over shorter time intervals after the first exposure and in consecutive time intervals would help to clarify if crabs recovered quickly or habituated.

A second, alternative explanation is that hermit crabs may be tolerant of ship noise in terms of oxygen demands but were affected in other ways. For instance, noise could cause other types of physiological stress response such as elevated lactate and glucose levels, caused by the release of crustacean hyperglycaemic hormone (CHH), which is known to be released in potentially stressful situations (Briffa and Elwood,

2005). Indeed, agonistic encounters alter the concentration of metabolites in hermit crabs i.e. lactate in the haemolymph of attackers (Briffa and Elwood, 2001) and muscular glycogen and circulating glucose in defenders (Briffa and Elwood, 2001; Briffa and Elwood, 2004). As for oxygen consumption, these could be acute responses or even sustained up to 24 h.

Ultimately, I cannot rule out that handling stress overrode any noise effects despite giving crabs 10 min to rest before measuring their oxygen consumption. Handling stress is particularly challenging in animals whose oxygen consumption cannot be measured by observation. The prevalence of study organisms where the effects of noise on the oxygen consumption can be assessed visually, such as the opercular beat rate in fish, supports this view. On the other hand, oxygen consumption has been measured successfully in *P. bernhardus* (Velasque Borges, 2017) and a similar protocol has been applied here.

In conclusion, though I cannot unequivocally explain the mechanism, hermit crabs appear to tolerate to ship noise after 24 h in their direct physiological response.

8.2.2 Indirect physiological effects of noise

Despite the limitations to explain the result discussed above, chapter 6 provides evidence for a seemingly less studied effect of noise, namely indirect physiological effects that arise in consequence of the altered decisions made under exposure to noise. I found that crabs in shells smaller than optimal for their body size had a higher oxygen consumption than hermit crabs in shells closer to the optimal size. Since crabs obtained those shells in a previous experiment where crabs could freely interact and redistribute shell resources under noise (chapter 5), we may conclude that behavioural

decisions made under noise can be physiologically costly and that these are indirect effects of noise on the metabolic rate.

The scope of conclusions that may be derived from a single experiment on physiological effects of noise is necessarily limited, and future studies will certainly be required to identify how far this result can be generalised. While an entire project could be dedicated to assess only the physiological effects of noise on crustaceans, research where both behaviour and physiology are studied in combination would allow deeper insights of the proximate mechanisms that underpin behavioural responses to noise. Providing experimental evidence for causal relationships between behaviour and physiology (or how noise alters other non-behavioural parameters as outlined by Kight and Swaddle, 2011) will enable us to better understand if and how altered proximate mechanisms drive observed behavioural changes under anthropogenic noise and other forms of HIREC (Halfwerk and Slabbekoorn, 2015). Despite direct effects, I also advocate to test indirect physiological costs and quantify the consequences of decisions made under noise.

8.3 Biology meets physics: Acoustic considerations

Assessing the effects of anthropogenic noise on animals not only requires knowledge of the biology of the species of interest such as its behaviour and physiology but also careful consideration of the acoustic set-up and the characteristics of the sound regime. That is, noise research involves consideration of exposure duration, characteristics of the noise source as well as technical challenges, and the benefits and limitations of experiments in the laboratory and field.

8.3.1 Duration of noise exposure

In nature, animals are often chronically exposed to noise, yet in experiments they are predominantly tested in their immediate, short-term response to noise (Kunc et al., 2016; Morley et al., 2014; Shannon et al., 2016b). Experiments on chronic noise enable testing of whether animals avoid disadvantageous and potentially maladaptive responses by learning to cope with anthropogenic noise such as through habituation (Sih et al., 2011; Tuomainen and Candolin, 2011). Studies in which animals have been subjected to repeated or long-term exposure have yet to reach a consensus on the potential effects and hence more experiments can contribute to establish a general pattern. Besides single, short-term exposures (chapter 3 – 4), I also assessed impacts of noise during repeated short-term exposure over 5 days in the laboratory (chapter 2) and over 2 days in the field (chapter 7), and continuous exposure over 24 h (chapter 5 – 6). I found that there was neither an effect of low intensity noise over 5 days in the laboratory (chapter 2) nor an effect of high intensity noise over 2 days in the field (chapter 7). However, I found that high intensity noise over 24 h lowered aggregated benefits of resource distribution in groups (chapter 5) leading to indirect physiological costs (chapter 6). The different set-ups and experimental designs make a direct comparison of the results in the two laboratory studies (chapter 2 and chapter 5) difficult. First, the exposure duration varied between those two experiments. Nearly 24 h between the repeated exposure of 20 min are likely to be enough time for hermit crabs to recover between observations and probably that is why I did not find an effect. Instead, the continuous exposure over 24 h might have been more distractive. Second, these two experiments also differed in the sound intensities whereby crabs experienced 20 min in low intensity noise compared to 24 h high intensity noise. Third,

since crabs did not show a preference to group (chapter 4), the social environment (chapter 5) could have been more stressful for hermit crabs than solitary conditions (chapter 2). Whether anthropogenic noise with higher amplitudes would affect crustaceans over time would be worth exploring in a controlled experiment with an orthogonal design allowing to disentangle the role of noise intensity and exposure duration on crustaceans.

8.3.2 Characteristics of the noise source: Sound intensity and other properties

Gill et al. (2014) discuss in detail the ample evidence that noise research extensively focussed on the intensity but rarely characterise and test for other features. I found that even in the absence of sharp differences in sound intensities, ship noise can affect specific stages of decision-making in hermit crabs (chapter 2) suggesting low intensity ship noise and ambient sounds must differ in other properties to hermit crabs as well. The finding that crabs were influenced by low intensity noise in decisions about whether to enter optimal shells allows for speculation about whether the effect of noise may depend on the implication of the decision, i.e. whether the decision has strong fitness consequences.

The visual inspection of the acoustic pattern implies that the two sound treatments differed in their temporal structure, though I do not mean to exclude other sound properties that might have differed as well. In fact, the sound treatments may differ in several properties simultaneously making it difficult to isolate and disentangle which properties crabs were responsive to or whether the combination of factors triggered the observed behavioural responses. Future experiments with carefully controlled varying temporal and spectral characteristics may help to clarify which

characteristics affect crustaceans the most. Disentangling which noise features affect animals the most could allow regulators to better management noise providing an interesting avenue for conservation research.

8.3.3 Experiments in the laboratory and in the field

Sound distortion in small tanks is a widely discussed topic in noise research, particularly for fish and invertebrates which detect the particle motion component of sound (Akamatsu et al., 2002; Gray et al., 2016; Hawkins and Popper, 2016; Rogers et al., 2016; Slabbekoorn, 2016). Particle motion depends on sound pressure whereby high intensity sound pressure causes stronger particle motion than low intensity sound pressure (Tasker et al., 2010). However, the walls of small tanks and the proximity of the surface cause reverberations leading to complex sound properties and particle motion intensities beyond the effects of sound pressure on particle motion found in nature (Akamatsu et al., 2002; Gray et al., 2016; Hawkins and Popper, 2016; Rogers et al., 2016; Slabbekoorn, 2016). As a consequence, results from experiments in laboratories do not allow us to deduce direct conclusions for noise effects on animals in the wild and implications for impact assessments and management. Hence, the need to complement laboratory experiments with field experiments to better understand the consequences of anthropogenic noise on particle motion detecting fish and invertebrates has been widely raised (Hawkins and Popper, 2016; Kunc et al., 2016; Simpson et al., 2015; Slabbekoorn, 2016).

Recent years have seen an increase in outdoor studies by using playbacks (Maxwell et al., 2018; Nedelec et al., 2014; Neo et al., 2016; Radford et al., 2016a; Spiga et al., 2017) or actual sources of noise such as boats (Harding et al., 2018; Jain-Schlaepfer et al., 2018; McCormick et al., 2018; Nedelec et al., 2017). To the best of my

knowledge, noise effects on crustaceans have only recently been investigated for the first time under field conditions (Hubert et al., 2018). Contrary to our initial prediction and the laboratory studies, I did not find an effect of sound on the mean startle response duration in the field (chapter 7). Although care needs to be taken to generalise from small tanks (Akamatsu et al., 2002; Tasker et al., 2010), the findings from the laboratory indicate that hermit crabs are able to detect sounds at low (chapter 2) and high intensities (chapter 3 – 5). A major challenge is that we did not measure the particle motion. Improved availability and affordability of equipment to measure particle motion (Nedelec et al., 2016a) would “open a current black box” in the noise research and help to describe more precisely what fish and invertebrates sensitive to particle motion such as *P. bernhardus* are exposed to in the laboratory and in the field. This would allow to quantify which noise level crustacean detect, distinguish more precisely the characteristic of sound treatments according to the biology of the focal species and replicate more accurately sound conditions in the laboratory and field. These limitations to research are shared with studies on other invertebrates and fish specialised to detect particle motion (Hawkins and Popper, 2016). Despite the possibility that hermit crabs were not affected by the noise, most probably the uncontrollable environmental conditions masked and distorted the sound treatment. Reviewing such environmental conditions animals are naturally exposed can open new avenues for laboratory experiments where these factors can be isolated to study their effect (Briffa and Greenaway, 2011).

Finally, the field experiment also raises general questions about the benefits and limitations of both field and laboratory experiments. Field conditions are complex, often very difficult to account for and not always quantifiable as exemplified here.

Laboratory experiments instead allow a 'reductive' approach whereby all variables except the ones of interest can be kept constant facilitating the isolation of the effects of the experimental variables, from other possibly confounding factors, and the identification of effects that could otherwise be masked. However, it is important to acknowledge that laboratory experiments could give the impression that an effect is large, when in nature it might not be as important as other environmental variables. Future research combining laboratory and (semi-controlled) field experiments is thus necessary to better understand the effects of noise on crustaceans and other invertebrates. For instance, researchers have conducted indoor experiments and then transferred the design to semi-controlled outdoor set-ups revealing similar results in fish exposed to noise in the laboratory and field (Debusschere et al., 2014; Neo et al., 2016). The challenge to bridge field and laboratory experiments is by no means special to noise but has been shown with regard to various aspects of animal behaviour, ecology and physiology (Bell et al., 2009; Calisi and Bentley, 2009; Spicer, 2014). Both, laboratory and field experiments are generally considered complementary approaches (Briffa and Greenaway, 2011; Kunc et al., 2016; Shannon et al., 2016b). Laboratory experiments in conjunction with field studies will provide the most insight into the effects of anthropogenic noise and other forms of HIREC on animals whereby laboratory experiments can be a valuable stepping stone to understand mechanisms of how anthropogenic noise can affect animals and which behaviours are affected.

8.4 Suggestions for future directions

Throughout this thesis, I indicated avenues for future research. Rather than repeating these here, I advocate the following broader questions:

- What do crustaceans perceive when exposed to noise?

A major advanced of the field will be the accessibility of equipment to measure particle motion. Until now, particle motion largely appears to be a “black box”.

Advancements in availability of equipment will allow to directly compare noise characteristics as perceived by the organism of interest and assess how crustaceans and other invertebrates perceive anthropogenic noise.

- What are the noise impacts on behaviours with consequences for survival and fitness and those which have knock-on effects for populations, communities and ecosystems?

To gain a broader picture on noise impacts, more research on diverse functional contexts and intraspecific interactions should be explored for instance regarding the competitive access to resources such as mates and behaviours of animals which provide ecosystem services and functions.

- Noise as a selective force?

A future route for quantifying the effects of noise would be to study if all individuals react to anthropogenic noise in the same way by investigating behavioural reaction norms (Dingemanse et al., 2010). This would allow to assess whether certain behavioural phenotypes benefit or lose out under noise leading towards the broader question if noise acts as an evolutionary force (Swaddle et al., 2015)? This might also be studied in context of developmental plasticity of organisms.

- Behaviour and physiology: A missing link

One of the most fruitful future avenue would be combined projects where both behaviour and physiology are studied in combination to shed light into the proximate mechanisms of noise for animals but also to quantify the costs of noise on animals.

- What do we have to know to regulate and manage noise (for crustaceans)?

Experiments comparing the role of sound intensity and exposure duration on crustaceans (i.e. applying ramp-up procedures) together with studies examining various temporal and spectral characteristics may help to clarify which noise characteristics affect crustaceans the most. Combining laboratory and field studies behaviours with consequences for survival and fitness should be prioritised from an applied perspective. Such findings could then inform regulators to better management noise providing an interesting avenue for conservation research. In this context the question if and to which noise conditions crustaceans can habituate to chronic noise remains to be answered.

8.5 Conclusions

This thesis demonstrates that anthropogenic noise has the potential to alter crucial behaviours in hermit crabs and distract them away from pertinent cues presumably since noise contributes to more complexity for sensory-cognitive processes of animals.

Here I show that anthropogenic noise can disrupt behaviours at the level of individual decisions and at the level of social behaviour in animals that do not rely on acoustic cues and this effect should hold true in nature as well. Moreover, I show that other, naturally occurring factors, such as shell quality, presence of a predator cue and social environment, interact with and modify effects of anthropogenic noise. In some cases,

as in the case of occupied shells, natural factors can have a stronger influence in crab's decision-making than anthropogenic noise. By designing experiments that incorporate naturally occurring factors, I attempted to increase the biological realism and complexity to my thesis. However, this approach does not always provide straight forward answers. Given that survival in hermit crabs is strongly tied to the quality of their gastropod shell, any changes to shell-mediated behaviour could impact individual survival and hence population structure.

Animals live in environments with multiple stressor co-occurring. As climate change and most other forms of HIREC, anthropogenic noise is a globally widespread challenge. However, other than climate change, its sources can be located and accordingly managed. Anthropogenic pollutants such as noise could reduce the resilience of animals decreasing their ability to cope with sources of HIREC which are complex to manage such climate change. Therefore, managing point sources such as noise should be an aim of policy and management and future research to inform appropriate measure is certainly warranted.

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Appendix

List of Publications:

Tidau, S. & Briffa, M. 2016. Review on behavioral impacts of aquatic noise on crustaceans. *Proceedings of Meetings on Acoustics*, **27**, 010028.

DOI <https://asa.scitation.org/doi/abs/10.1121/2.0000302>

Tidau, S. & Briffa, M. 2019. Anthropogenic noise pollution reverses grouping behaviour in hermit crabs. *Animal Behaviour*, **151**, 113-120.

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Tidau, S. & Briffa, M. In Press. Distracted decision makers: ship noise and predation risk change shell choice in hermit crabs. *Behavioral Ecology*.

DOI <https://doi.org/10.1093/beheco/arz064>