Consequences of ship noise for camouflage, anti-predation, and movement in crabs.

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Signature ……………………………………………………………

Abstract

The marine environment is becoming increasingly polluted, with unprecedented levels of anthropogenic noise changing the marine soundscape. Mounting evidence shows that exposure to this noise can cause numerous adverse effects across taxa. However, invertebrates, juveniles, and behaviours not dependent on acoustics have received relatively little attention. Furthermore, research into how individuals may cope with these pressures is lacking. I address these knowledge gaps through a series of laboratory-based playback experiments focussed on juvenile shore crabs (*Carcinus maenas*), using three noise treatments: ship noise, ambient underwater sounds (control), and ambient underwater sounds played at the same amplitude as the ship treatment (loud control).

In chapter 2, I examined the effects of ship noise on brightness change; a strategy employed by juvenile shore crabs to increase their level of camouflage and reduce predation risk. Individuals were repeatedly exposed to one of the aforementioned noise treatments for 8 weeks. Photographs of individuals, taken regularly throughout, were analysed using a predator vision model to determine the level of brightness change and camouflage in an ecologically relevant context. Ship noise reduced the overall brightness change and camouflage, though it did not affect the change in brightness per moult. The level of growth per moult was reduced by ship noise however, and the timing of moulting events was delayed. In chapter 3 I investigated the effects of noise on antipredator behaviour (using the response to a simulated predator) and locomotion, including the frequency of pausing and directionality of movement. By comparing the effects between individuals with varying levels of previous noise exposure, I also tested for signs of acclimatisation. Ship noise reduced the likelihood of individuals responding to a predator and increased their latency of response. Locomotion was not disrupted, but individuals moved away from ship noise, positioning themselves in quieter areas. These findings were consistent for all individuals, regardless of their previous level of noise exposure.

The negative consequences of anthropogenic noise in the marine environment are clearly not constrained to species or behaviours reliant on acoustics, as juvenile shore crabs exposed to ship noise suffered decreased levels of camouflage and reduced growth. Individuals also displayed maladaptive behavioural responses to a simulated predator when exposed to ship noise. There is no evidence that acclimatisation occurred, but individuals did attempt to physically avoid noisy areas. Loud natural sounds did not affect any behaviours studied, suggesting the type of noise is important in determining how individuals may be affected. Overall, this thesis shows that juvenile shore crabs suffer multiple negative effects from noise pollution, including the disruption of critical behaviours that are pervasive in the marine environment, with potential implications for survival.

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Chapter 1 – Introduction:

Underwater anthropogenic noise as a global pollutant

There are several widespread anthropogenic activities with cause for concern regarding the potential environmental impacts (e.g. Wiedinmyer, Yokelson & Gullett, 2014; Lawrence & Vandecar, 2015; Li, Tse & Fok, 2016; Ding, Chen, Chen & Tian, 2017), and numerous pollutants associated with each (e.g. McCain *et al.*, 1988; Derraik, 2002; Longcore & Rich, 2004; Simmonds, Dolman, Jasney, Weilgart & Leaper, 2014); this thesis focusses on underwater noise pollution from shipping activity. Although this has received increasing levels of attention in recent years (e.g. Peng, Zhao & Liu, 2015; Williams *et al.*, 2015; Weilgart, 2018), several knowledge gaps remain, primarily pertaining to it's effect on individuals and behaviours whose reliance on acoustics is minimal (Peng *et al.*, 2015). In this thesis I use laboratory-based playback experiments to explore the effects of underwater noise pollution on colour change, antipredator behaviour, and locomotion in juvenile shore crabs, including their movement-based response to noise.

Environmental Change

Anthropogenic Activity and Environmental Change

Ecosystems and environments impervious to human activity are scarce. Natural resources are being exploited at unprecedented levels, the climate is changing as a result of anthropogenic activity, and both terrestrial and marine systems are suffering high levels of pollution (Barnes, Galgani, Thompson, & Barlaz, 2009; Cole, Lindeque, Halsband, & Galloway, 2011; Derraik, 2002; Hölker, Wolter, Perkin, & Tockner, 2010; Li *et al*., 2016; Longcore & Rich, 2004; Wiedinmyer *et al*., 2014). This is often drastically changing the environment on a global scale, with potentially severe consequences for both humans and other species. For example, overexploitation has led to the collapse of commercial fish stocks (Ding *et al*., 2017; Pedersen *et al.*, 2017), several population and species extinctions (Brook, Sodhl, & Ng, 2003; Castello, Arantes, Mcgrath, Stewart, & De Sousa, 2015; Dulvy, Sadovy, & Reynolds, 2003; Turvey & Risley, 2006), and the direct destruction of certain habitats (Gaveau *et al*., 2014; Mayaux *et al*., 2005; Mertens, Forni, & Lambin, 2001). The latter has led to physical changes to the landscape and the alteration of ecosystem services and processes, including the carbon cycle (Hansen, 2005; Kauffman *et al*., 2017; Lawrence & Vandecar, 2015; Mayaux *et al*., 2005; Mertens *et al.*, 2001; Song, Huang, Saatchi, Hansen, & Townshend, 2015). Associated with this, human-induced climate change is responsible for an increase in extreme weather events, ocean acidification, increased oceanic temperatures, and a rise in sea-level, among other things. These issues, including pollution, are not mutually exclusive, and often arise in conjunction with, or as a result of, another. For example, activities responsible for overexploitation (e.g. commercial fishing), often pollute the surrounding areas or release CO_2 which contributes to climate change. The obvious, direct consequences for humans (e.g. loss of valuable resources due to unsustainable harvesting (Cook, Sinclair, & Stefánsson, 1997; Myers, Hutchings, & Barrowman, 1997; Pauly *et al*., 2002)), and the clear global scale of the issues and effects has led to entire fields of research dedicated to investigating this further.

There are several internationally recognised global pollutants, including light (e.g. from street lighting, well-lit buildings, and fishing boats (Longcore & Rich, 2004)), chemical (e.g. crude oil polluting water bodies and harmful gases contributing to atmospheric pollution (McCain *et al.*, 1988; Kan, Chen & Tong, 2012; Kostianoy & Carpenter, 2018)), plastic (e.g. microplastics (Cole *et al*., 2011; Derraik, 2002)) and noise (e.g. from shipping, construction, and seismic surveys (Firestone & Jarvis, 2007; Simmonds *et al.*, 2014)). As well as affecting terrestrial ecosystems, each of these pollutants penetrate the marine environment as by-products of anthropogenic activity. Here, I focus on underwater anthropogenic noise, which has only been recognised as a major global pollutant since the early 21st century (e.g. European Commission Marne Strategy Framework and US National Environment Policy Act) (Simmonds *et al*., 2014).

There are many sources of underwater noise pollution (Hatch & Wright, 2007; Hildebrand, 2009). For example, during geophysical seismic surveys to identify fossil fuel reservoirs beneath the seabed, airguns are towed from marine vessels and fire highly intense sound signals approximately every 10-20 seconds for several hours (Goold & Fish, 1998). Military vessels often use low- and mid-frequency sonar to detect submarines and other vessels during naval operations, and even civilian and commercial vessels use sonar (albeit less intense) to detect and classify underwater objects (Deng *et al*., 2014; Hatch & Wright, 2007; Hildebrand, 2009). Industrial activities, such as piledriving construction and resource extraction (e.g. drilling for oil), produces large amounts of low frequency noise. Although these activities are stationary and consequently concentrated in certain areas, low frequency noise travels great distances (Bailey *et al.*, 2010). Shipping activity (including military vessels, cargo ships, oil tankers, and cruise ships) is however, one of the most prominent sources of underwater noise, particularly of low frequency (Andrew, Howe, Mercer, & Dzieciuch, 2002; McDonald, Hildebrand, & Wiggins, 2006; McDonald, Hildebrand, Wiggins, & Ross, 2008), and is the focal source used in this thesis.

The majority of underwater noise produced by ships originates from the engine or at the site of the propellers due to cavitation (Hatch & Wright, 2007; Hildebrand, 2009; Sharma, Mani, & Arakeri, 1990; Wittekind & Schuster, 2016). This refers to the quick collapse of bubbles produced by the propellers, which can generate large amounts of noise, differing in frequency based on the size of the bubble. The highly variable nature of noise from shipping activity means it can span a range of 12-40,000Hz, though the peak is typically relatively low (below 200Hz), particularly for larger vessels (Hatch & Wright, 2007; Hildebrand, 2009; McKenna, Ross, Wiggins, & Hildebrand, 2012; Veirs, Veirs, & Wood, 2016). In the past 50 years, ship noise has elevated average ocean ambient levels by approximately 10-15dB (Andrew *et al*., 2002; McDonald *et al*., 2006, 2008), with popular traffic routes, shipping lanes, and coastal ports experiencing more pronounced increases due to the higher concentration of activity (Andrew, Howe, & Mercer, 2011; Garrett *et al*., 2016; Kinda, Le Courtois, & Stéphan, 2017; McDonald *et al*., 2006). Recent trends, including population growth and an increasing demand for the transportation of goods, suggest that the commercial shipping industry will continue to grow in the coming years, including an increase in the size and number of vessels active in the oceans (Kaplan & Solomon, 2016; Tran & Haasis, 2015). Therefore, it is vital we increase our understanding of the consequences of noise generated by these activities for marine ecosystems.

Noise pollution and invertebrates

Much of the previous work investigating the effects of anthropogenic noise on marine ecosystems focusses on vertebrates, particularly echolocating cetaceans and fish (e.g. Gordon *et al.*, 2003; Jensen *et al.*, 2009; Finneran, 2015; Peng *et al*, 2015; Blair, Merchane, Friedlaender, Wiley & Parks, 2016) because of their obvious reliance on the auditory system, their commercial value, or their status as charismatic species. This leaves invertebrates generally overlooked regarding the impacts of noise pollution (Peng *et al*., 2015). However, the auditory capabilities of invertebrates, including their frequency sensitivity, means they too will be able to detect large amounts of underwater noise, leaving them potentially vulnerable to the negative effects associated (Horch, 1971; Popper, Salmon, & Horch, 2001; Salmon, Horch & Hyatt, 1977). Furthermore, invertebrates have high ecological importance, being key components of food webs and often acting as ecosystem engineers (Leal, Puga, Serôdio, Gomes, & Calado, 2012). They are also highly important economically, not only as major parts of the commercial fishing industry, but also in the development of new drugs using products synthesised by such species (Leal *et al*., 2012). This necessitates our understanding of the nature and extent of effects experienced by invertebrates, as the consequences may be severe and far-reaching.

Invertebrates rely on the production and detection of acoustic cues and signals for a variety of activities, including larval settlement (Stanley, Radford, & Jeffs, 2010), predator detection (Hughes, Mann & Kimbro, 2014), communication and mate acquisition (Popper *et al*., 2001). Unlike most vertebrates, invertebrates tend to detect the majority of sounds through means of particle motion (Mooney *et al*., 2010; Nedelec, Campbell, Radford, Simpson, & Merchant, 2016). The mechanisms and organs directly responsible for this have yet to be conclusively identified, however several organs are potentially involved. Decapod crustaceans, for example, have multiple mechanoreceptors, including hair-like cells on the body surface, chordotonal organs associated with the joints of appendages, and statocyst organs in the cephalothorax (Edmonds, Firmin, Goldsmith, Faulkner, & Wood, 2016; Popper *et al.*, 2001; Salmon *et al*., 1977), but their relative importance regarding sound detection is unknown. Generally, invertebrates are most sensitive to low frequency noise, although there is a great deal of variation between species. For example, longfin squid (*Loligo pealeii*) are most sensitive to 100-200Hz (Mooney *et al.*, 2010), whereas fiddler crabs (*Uca spp.*) are most sensitive to 300-700Hz (Popper *et al*., 2001; Salmon *et al*., 1977), and ghost crabs (*Ocypode spp.*) are most sensitive to 1,000-2,000Hz (Horch, 1971; Popper *et al.*, 2001).

Despite the relatively few studies investigating the effects of anthropogenic noise on marine invertebrates, there is a growing body of evidence suggesting that they suffer in numerous ways as a result of exposure. Most obviously, this occurs in relation to behaviours that rely on an acoustic component. However, research shows that anthropogenic noise elevates stress levels (Filiciotto *et al*., 2014; Sierra-Flores, Atack, Migaud, & Davie, 2015; Wale, Simpson, & Radford, 2013b) which can lead to hormonal changes (Webster, 1996), altered energy budgets (Thompson & Bayne, 1974; Wale *et al*., 2013b), and impaired cognitive function (Berglund, 1993; Mendl, 1999). As a result, noise-induced stress has been theorised as the mechanism behind the disruption of several behaviours in the presence of anthropogenic noise, including locomotion (Filiciotto *et al*., 2014, 2016), reproduction (Sierra-Flores *et al.*, 2015) and antipredator behaviour (Spiga, Aldred, & Caldwell, 2017). Similarly, noise has been demonstrated to distract individuals, shifting attention away from primary tasks, including predation risk assessment (Chan, Giraldo-Perez, Smith, & Blumstein, 2010) and foraging (Purser & Radford, 2011). As a result of these two mechanisms in particular (stress and distraction), it is clearly possible for behaviours not associated with the auditory system to be adversely impacted by anthropogenic noise. Other research shows that survival can be more directly reduced by exposure to anthropogenic noise, with one study demonstrating that sea hare (*Stylocheilus striatus*) embryonic development is reduced by 21% and mortality of recently hatched larvae is increased by 22% (Nedelec *et al.*, 2014). Similarly, another study shows that noise delays development and causes physical malformations in scallop larvae (*Pecten novaezelandiae*) (De Soto *et al.*, 2013). Therefore, the effects of noise on invertebrates can clearly be severe.

The variety of behaviours utilised by invertebrates to maximise their survival may all have the potential to be adversely affected by anthropogenic noise, even those with no obvious link to the acoustic system (i.e. it could affect species in ways that sound is not directly involved). However, many of these behaviours are yet to be studied in relation to noise pollution so the extent to which this may be the case is unclear. It is important behaviours central to survival, and widespread among species, are assessed regarding their success in the presence of anthropogenic noise. This will enable us to better understand how individuals may be impacted by human activity and the possible consequences for the ecosystems and processes with which they are most heavily linked. Behaviours and activities of particular importance are discussed below.

Activities and behaviours important for survival

Colour Change

Changing appearance by altering body colouration or patterning is common in nature, particularly the marine environment. This strategy is utilised for a variety of functions across different timescales, all closely tied with survival. For example, a fiddler crab species, *Uca pugilator,* changes from dark to light in colouration in response to temperature, probably functioning in thermoregulation (Wilkens & Fingerman, 1965). Other fiddler crab species, like *Uca panacea*, have a circadian rhythm of change becoming darker during the day, which is believed to function in UV protection (Darnell, 2012). A variety of other species are believed to utilise colour change for communication and signalling purposes, including mate choice and warnings to conspecifics (Stevens, 2016; D. Stuart-Fox & Moussalli, 2008; Umbers, Fabricant, Gawryszewski, Seago, & Herberstein, 2014).

Perhaps most commonly, colour change is used as a way of enhancing camouflage, primarily to reduce detection by predators. This is typically achieved through either disruptive colouration or background matching (Stevens & Merilaita, 2009). Disruptive colouration is a form of camouflage often involving striking colours or markings, whereby an individual's patterning distorts the appearance of their body, breaking up the body outline so predators cannot detect and recognise their shape as efficiently (Cuthill *et al.*, 2005; Stevens & Merilaita, 2009). For example, rock gobies (*Gobius paganellus*) change their patterning in such a way when on patterned substrates that the markings touch the edge of the body, potentially distorting the outline and creating the illusion of false edges (Smithers, Wilson, & Stevens, 2017; Stevens & Merilaita, 2009). This makes it harder for predators to detect or identify the individual's body outline or key features.

Background matching, on the other hand, refers to instances where the individual's colour, brightness, or pattern matches that of the substrate upon which they are positioned (Stevens & Merilaita, 2009). A similar effect is seen when individuals change their brightness (luminance) to reflect the lighting conditions, becoming brighter under lighter conditions (i.e. during the day) and darker when conditions are darker (i.e. at night) (Duarte, Flores, & Stevens, 2017). For example, ghost crabs exhibit a circadian rhythm of colour change, increasing in brightness during the day and becoming darker at night, as well as increasing in brightness when on pale substrates (Stevens, Rong, & Todd, 2013). This enables them to maximise their camouflage in varying conditions and at different time points. Similarly, juvenile shore crabs (*Carcinus maenas*) alter their luminance to match that of the substrate, becoming brighter on light backgrounds and darker on dark backgrounds, enhancing their levels of camouflage through background matching, making them less visible to predators (Stevens, Lown, & Wood, 2014). Cuttlefish (*Sepia officinalis*) are able to rapidly change both their colour and patterning to match that of the substrate with high levels of accuracy when viewed through the visual system of fish predators (Chiao, Wickiser, Allen, Genter, & Hanlon, 2011). This strategy of enhancing camouflage through colour change is pervasive in the marine environment, clearly employed by a range of species.

The type of physiological colour change outlined here involves the dispersion and aggregation of pigments within chromatophore cells (Duarte *et al.*, 2017; Stevens, 2016; Umbers *et al*., 2014). The physiological mechanism through which this is achieved is related to the temporal scale over which the change occurs. Rapid change, like that of rock gobies and cuttlefish, is initiated by neuromuscular action directly on chromatophore cells. Relatively slow change, however, like that of ghost crabs and shore crabs, is mediated endocrinologically (Duarte *et al*., 2017; Umbers *et al.*, 2014). There is often also a morphological component to slower change (Stuart-Fox & Moussalli, 2009; Umbers *et al*., 2014), with individuals changing in colouration quite significantly upon moulting, as is the case with the shore crab. Although it has never been directly tested, colour change is deemed energetically costly due to the nature of these mechanisms (Duarte *et al*., 2017). Despite this, there should be a high fitness advantage associated with efficient camouflage as it can reduce the likelihood of detection by predators, consequently reducing predation risk of individuals and enhancing survival (Chiao *et al.*, 2011; Duarte, Stevens, & Flores, 2018; Stuart-Fox, Moussalli, Marshall, & Owens, 2003). Therefore, it is unsurprising that so many species adopt this technique, or that it is considered an important survival strategy with severe consequences if affected.

There are several studies assessing camouflage efficacy in the face of human-induced environmental change. For example, animals that undergo seasonal moulting to promote camouflage under differing temporal conditions, like the snowshoe hare, have been the subject of multiple studies (e.g. Mills *et al.*, 2013; Zimova, Mills, Lukacs & Michael, 2014; Zimova, Mills & Nowak, 2016). Similarly, the effect of climate-induced coral bleaching on reef fish camouflage is gaining more attention as the loss of coral colour can increase the conspicuousness of individuals, increasing predation risk or driving species away from bleached reefs (Coker, Pratchett, & Munday, 2009). Although the effects of anthropogenic activity on the level of camouflage in various species have been investigated, there is virtually no evidence in the literature suggesting how the mechanisms responsible for camouflage (i.e. colour change) may be impacted by human-induced environmental change, certainly anthropogenic stimuli such as noise pollution. However, the pervasiveness of colour change, its importance for survival in many species, and its capacity to be adversely affected, necessitates such research.

Response to Predator

Unless a species is an apex predator, positioned at the top of the food web, it’s survival will be largely based on it’s ability to evade predation. Regardless of the specific strategy employed, there are multiple components to successful antipredation behaviours. First, an individual must be able to detect and recognise the threat of predation. This requires a certain level of vigilance, risk assessment, and potentially even cognitive processing (Ferrari, Mitchell, Ramasamy, McCormick, & Chivers, 2014; Kelley & Magurran, 2003, 2006; Shettleworth, 2010). Often, individuals will rely on visual, chemical, or acoustic cues from the predator to be alerted to its presence, and in some species, acoustic alarm signals are used to warn conspecifics of such threats (Smith, 1992; Winn *et al*., 1964; Zuberbühler, 2009). Once an individual has detected a predator and categorised it as a threat, they must then respond, particularly if the predator has also detected and recognised the individual as potential prey.

The response behaviour is highly variable between species and life-stages. Some freeze, which likely reduces their chances of being detected and/or identified further, as objects that are motionless are less conspicuous (Hall *et al*., 2013). Although remaining stationary increases the effectiveness of camouflage techniques such as background matching or disruptive colouration (Hall *et al.*, 2013), this is not sufficient for all species, particularly those with a more conspicuous appearance. For some individuals, physically defending themselves is the only feasible option, with individuals using body armour or weaponry such as claws to fend off an attack. For example, when attacked by a conger eel, individual spiny lobsters (*Palinurus elephas)* strike the predator and attempt to scratch it with their antennae to cause harm and deter further attack (Buscaino *et al*., 2011). Directly fleeing from predators is perhaps a more common response. Although movement may make individuals more noticeable, it affords them the opportunity to retreat to a safer environment and take refuge in a shelter.

The obvious importance of antipredation behaviours for individual survival has attracted a lot of research into understanding how these responses may be impacted by anthropogenic activity. For example, evidence suggests that ocean acidification can reduce risk assessment and predator detection in fish (Dixson, Munday, & Jones, 2010; Ferrari *et al*., 2012). Elevated temperatures associated with human-induced climate change can reduce the intensity of antipredator responses in European seabass (*Dicentrarchus labrax*), with decreased shoal cohesion, shorter distances between individuals and the predator, and a quicker recovery to normal activities indicating a tendency to take higher risks *(*Malavasi *et al.*, 2013). A growing body of evidence suggests that underwater noise pollution can also adversely affect antipredator responses in marine species, including: decreasing the distance at which hermit crabs (*Coenobita clypeatus*) initiate their escape response (Chan, Geraldo-Perez, Smith & Blumstein, 2010), increasing the latency of response in shore crabs (*Carcinus maenas*) (Wale, Simpson, & Radford, 2013a), reducing the frequency and speed of response in damselfish (*Pomacentrus amboinensis*) (Simpson *et al*., 2016) and reducing predator inspection behaviour in European seabass (*Dicentrarchus labrax*)

(Spiga *et al.*, 2017). This does not mean that further work investigating these effects are not warranted, as the variation in antipredation techniques and general ecology and physiology between species and even life-stages means the effects may vary.

Locomotion

Many behaviours crucial for survival or the success of an individual or population rely heavily on the ability to move unhindered. Perhaps most obviously, locomotion is critical for an efficient escape in response to threats from predators. In this instance, individuals must be able to move with a directional purpose, and in such a way that they do not enhance their detectability further by becoming more noticeable. For example, if individuals frequently pause and resume movement then this can enhance detection further than if individuals move with continuity, as the onset of movement can attract more attention (Abrams & Christ, 2003). Furthermore, individuals must move at an appropriate speed to avoid capture, without using so much energy that they are unable to travel the required distance to reach safety.

Other activities, such as reproduction, also involve a strong locomotion component in some species. For example, individuals must often travel to breed, like in the case of the humpback whale (*Megaptera novaeangliae*), where females travel up to 10,000km to reach breeding grounds (Stevick *et al*., 2011). For some, successful reproduction involves moving to search for mates. For example, in some fiddler crabs species, females move in search of males who remain static to defend burrows used for copulation or incubation (DeRivera & Vehrencamp, 2001). Similarly, female sperm whales show strong site fidelity along coastal basins, with males exhibiting high levels of movement among these populations in order to reproduce (Engelhaupt *et al.*, 2009).

Of course, relying on locomotion for reproduction is exclusive to adults. That does not mean, however, that juveniles are less dependent on locomotion for success, as, in addition to antipredation, they must often rely on movement for recruitment into adult populations (Moksnes, 2002). This is because in many species, particularly invertebrates, offspring reside and develop in nursery sites which tend to be at a different location (Dahlgren *et al*., 2006; Vasconcelos *et al.*, 2010).

Once mature, individuals must then leave the juvenile habitat and move to the adult population. Therefore, locomotion plays a key role in recruitment, which is important for the success of the population as a whole, not just the individual.

As with colour change, investigations into the effects of anthropogenic stimuli on locomotion and general movement are scarce. Exposure to water contaminated with crude oil impairs locomotor activity in some marine invertebrates and fish by reducing the swimming speed, with the effects persisting post-exposure (Johansen & Esbaugh, 2017; Percy & Mullin, 1977). On the contrary, limited evidence suggests that locomotion is increased in the spiny lobster in response to noise, with grouped individuals moving a greater distance and at a higher velocity (Filiciotto *et al.*, 2014). Clearly, the effects of prominent anthropogenic stressors, such as noise, on locomotor activity and capability need to be investigated, as in general there is a severe lack of research. Furthermore, the limited evidence that does exist indicates that the effects may be highly variable across species and stimuli and therefore direct assessments are required to provide clarity.

Coping with exposure to anthropogenic noise

As previously discussed, a variety of negative effects have already been documented as a result of exposure to anthropogenic noise, with the potential for many more that are simply unknown at present. The ubiquitous nature of human activity in the marine environment, coupled with the rising human population density and consequent demand for such activities, means it is unlikely our presence in the oceans will subside in the near future (Kaplan & Solomon, 2016). If individuals are to be successful in such a changing world then they must compensate for or counteract the negative effects imposed on them. Alternatively, attempts could be made to contain or limit the levels of anthropogenic noise in the oceans.

It is possible for individuals to cope with the pressures of anthropogenic noise if they are able to acclimatise or develop a tolerance. This would enable individuals to remain in the presence of noise without suffering the full extent of negative effects. Although this is documented in response to changes in temperature

(Donelson, Munday, McCormick, & Pitcher, 2012; Tepolt & Somero, 2014) and ocean acidification (Form & Riebesell, 2012), it remains unclear whether this transpires in response to anthropogenic noise. There is limited evidence indicating that it may occur (Holmes, McWilliam, Ferrari, & McCormick, 2017; Wale *et al.*, 2013b), but it is possible that the intermittency of noise and inconsistency/variability of noise sources may prevent it (Wysocki & Gavin, 2006).

If acclimatisation is not possible, then individuals may be able to mitigate the adverse effects by avoiding or reducing their exposure to anthropogenic noise. There are many documented cases of this occurring in response to noise from seismic surveys (Castellote, Clark, & Lammers, 2012) and piledriving (Dähne *et al.*, 2013; Würsig, Greene, & Jefferson, 2000), with individuals being displaced, leaving the area for an extended period. This enables them to avoid injury or hearing loss (e.g. damage to the ears (McCauley, Fewtrell, & Popper, 2003) or temporary threshold shifts (Finneran, 2015)) and reduce the severity of other effects as the intensity or duration of exposure will be reduced. In some instances, this type of avoidance is temporary, with individuals returning during quieter periods (Rako *et al*., 2013; Stone & Tasker, 2006). However, some individuals may leave an area permanently and migrate to a new location (Bejder *et al.*, 2006). Of course, in either case this can only occur if the individual's locomotor capability and physical environment permits it, i.e. if the physiological tolerance of the individual matches that of the surrounding area or if there are no physical barriers such as trenches.

It is, however, possible for us to relieve some of the pressure and reduce the necessity for acclimatisation or the physical avoidance of certain areas. This could be achieved through the introduction of quieter Marine Protected Areas (MPAs) (Rob Williams, Erbe, Ashe, & Clark, 2015), the use of quieter vessels (Leaper, Renilson, & Ryan, 2014; Rao, 2002), or the introduction of legislation restricting the number of vessels and/or intensity of noise in certain areas, e.g. by diverting traffic routes to ensure minimum disruption (Roman *et al.*, 2013; Silber *et al.*, 2012). Regardless of whether we hope to reduce the severity of consequences associated with anthropogenic activity in the marine environment through human intervention (i.e. reducing noise) or simply by allowing individuals to acclimatise or avoid exposure, we must first understand the nature and extent of these effects, including how individuals respond to noise as a stimulus.

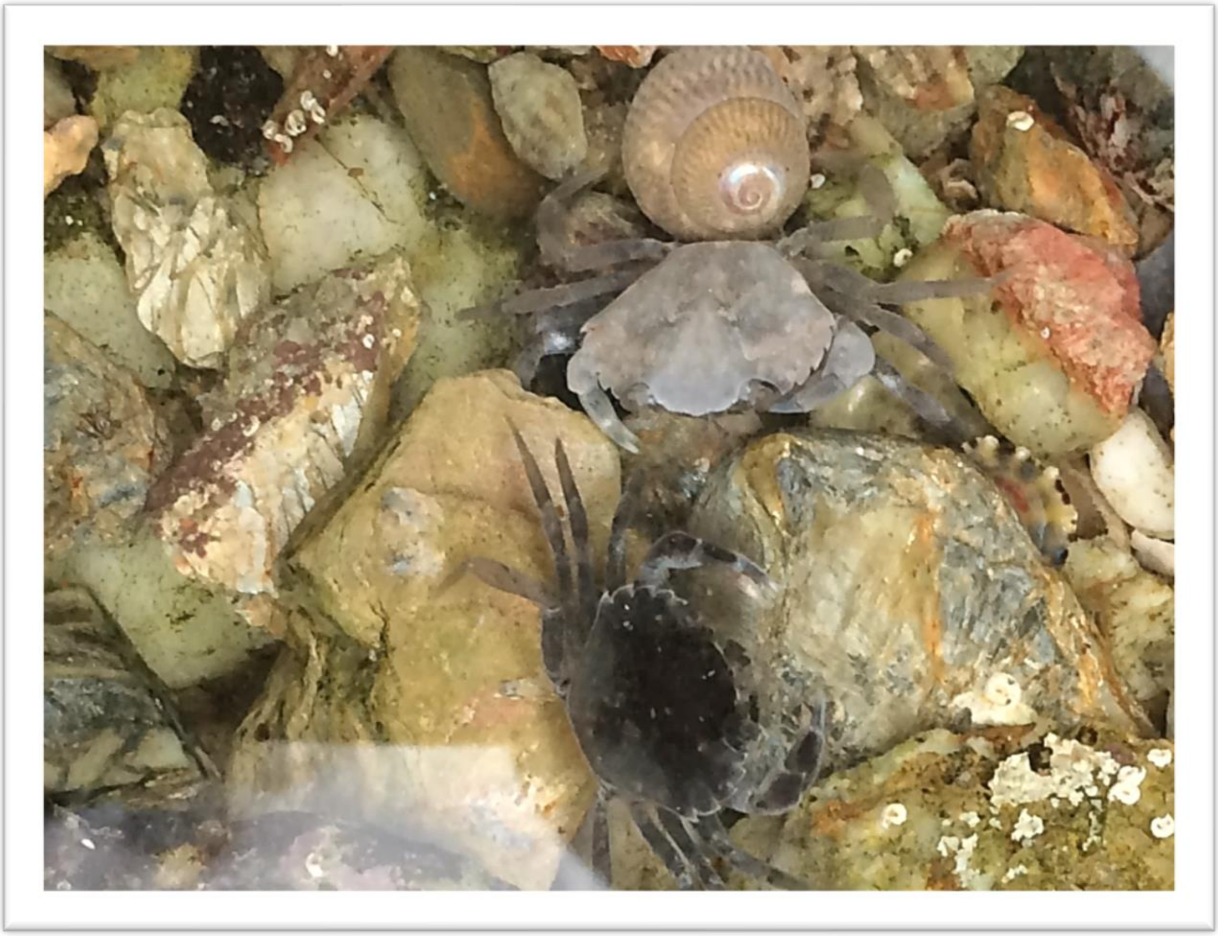
Purpose and aims of this thesis

As discussed above, there is little work investigating the consequences of underwater noise pollution for marine ecosystems beyond the effects on vertebrates and behaviours closely associated with acoustics. Colour change in particular is yet to be directly studied in relation to global pollutants or anthropogenic stimuli. Similarly, locomotion has received little attention in this regard. The effects of noise pollution on antipredator behaviours however have been researched, but as previously discussed, there are many variations of this activity, each containing multiple components with the potential to be adversely affected and consequently in need of comprehensive investigation. The importance of these behaviours for success at both the individual and population level is clear (see above), and therefore, research directly investigating the impact of anthropogenic noise on colour change, locomotion and antipredation is warranted.

Using the juvenile shore crab (*Carcinus maenas*), I address these knowledge gaps in a series of tank-based playback experiments in a laboratory setting. The general ecology of the shore crab is well documented (Crothers, 1968). Shore crabs are an intertidal species, common along European coastlines (Crothers, 1966, 1968). Although adults have been the focus of previous research regarding the effects of noise pollution (e.g. Wale *et al.*, 2013a, 2013b), juveniles have received much less attention (Peng *et al*., 2015). However, evidence suggests that juveniles can be differentially affected by stressors (Dissanayake, Galloway, & Jones, 2008). Furthermore, juveniles often utilise different strategies or must perform different activities in order to survive. For example, juveniles occupy different habitats and therefore must move to be recruited into the adult population (Dahlgren *et al.,* 2006; Vasconcelos *et al.,* 2010). Additionally, juvenile shore crabs use colour change to enhance their levels of background matching by altering their appearance as a way of reducing their detectability to predators (Hogarth, 1978; Stevens, 2016; Stevens *et al.*, 2014). This, along with their size and ease of maintenance, in addition to their ecological and economic importance, makes them ideal as the focus of this study into the effects of noise pollution.

In the first chapter, I aim to explore the effects of shipping noise on both long and short-term brightness change. As the strategy of colour change is likely employed by juvenile shore crabs as a way of reducing their predation risk, I use digital image analysis and a predator vision model to determine the level of change and consequent camouflage (Hart, 2002; Stevens, 2007; Troscianko & Stevens, 2015). I also examine the impact on moulting as this is closely tied with the colour change behaviour, being responsible for the morphological aspect of longer-term change. In the second chapter, I focus on antipredator behaviour and movement. The response of individuals to a simulated predator in the presence of ship noise is examined via a method adapted from previous work (Wale *et al*., 2013a), using individuals with varying levels of experience with noise to also assess if the effect of noise changes with exposure. In an additional experiment, I also directly explore how locomotion is affected and whether individuals move away from noise and consequently avoid intense exposure. In each experiment across both chapters, three noise treatments are used: ship, loud control and control. The use of the loud control enables the effects of anthropogenic noise to be disentangled from that of loud or additional noise in general. In the final chapter, I discuss the implications of these findings and suggest areas for future research.

Chapter 2: The effect of ship noise on colour change, camouflage, and growth



Abstract

Underwater noise pollution, like that from shipping activity, can cause widespread disturbance, with a variety of negative effects on marine taxa. Much of the previous work investigating this is, however, bias towards species and behaviours typically dependent upon the auditory system, with little work assessing the effect of anthropogenic noise on behaviours that rely on alternative sensory modalities. The variety of mechanisms through which individuals can be affected by noise pollution (e.g. stress, distraction) means even behaviours with no obvious link to acoustics may be impacted, and therefore warrant investigation. Here, I examine the effect of ship noise on the luminance change and consequent camouflage of juvenile shore crabs, a strategy employed to reduce detection by predators. In a tank-based playback experiment, individuals were housed on white backgrounds and exposed to either ship noise, loud natural noise or ambient sounds repeatedly for eight weeks and photographed regularly. Digital image analysis using a predator vision model was used to determine the level of luminance change and camouflage. Individuals were also photographed after moulting, and the carapace width measured at this time as this is when individuals typically undergo the biggest change in both luminance and size. The results demonstrated that although the amount of luminance change per moulting event was unaffected, individuals exposed to ship noise changed in luminance significantly less over both two and eight weeks, leaving them less camouflaged. Furthermore, those exposed to ship noise also suffered a reduction in growth and delayed timing of moults. The loud natural noise had no effect, suggesting the type of noise to which individuals are exposed plays an important role in determining how they will be impacted. The pervasiveness of colour change in the marine environment and its importance as a survival strategy highlights the severity and potential magnitude of implications associated with a reduction in its efficacy. Furthermore, this chapter highlights the extensiveness of consequences associated with anthropogenic noise, as even a long-term physiological behaviour with no obvious link to the auditory system is adversely affected.

Introduction

With the development of technology, urban expansion and increased transportation networks, anthropogenic activity in the marine environment is at an all-time high. From piledriving and seismic surveys to shipping and recreational boating, each activity comes with a variety of environmental implications (e.g. Gordon *et al*., 2003; Bailey *et al.*, 2010; Dähne *et al*., 2013; Merchant, Pirotta, Barton, & Thompson, 2014; Eriksson, Sandström, Isæus, Schreiber, & Karås, 2004; Zieman, 1976). Here I focus on anthropogenic noise, primarily from shipping, as this is a major global pollutant but has only been recognised as such in the last two decades (e.g. European Commission Marine Strategy Framework Directive and US National Environment Policy Act) (Simmonds *et al*., 2014).

Shipping activity is a major source of underwater noise pollution, increasing ambient ocean sound levels by 10-15dB (McDonald *et al*, 2006; 2008; Andrew *et al.*, 2002). Typically, noise from shipping spans a frequency range of 12-40,000Hz (Veirs *et al.*, 2016). This overlaps with the hearing ability of many marine species (Table 1), meaning there is potential for widespread disturbance across several taxa. In recent years, substantial experimental work, both laboratory and field-based, has been undertaken to understand the effects of such noise pollution. There is however a strong bias toward species known to be reliant upon acoustic cues (e.g. Rako *et al.*, 2013; Norris, 1994; Sarà *et al*., 2007; Simpson *et al*., 2016), particularly adult fish and mammals, making up to 50% and 20% of the focal taxa in these studies, with very little attention given to invertebrates or juveniles (Peng *et al*., 2015).

Most obviously, additional noise in the environment can mask acoustic cues and signals that animals may rely upon. This can affect communication ranges (Jensen *et al*., 2009), settlement success (Simpson *et al.*, 2016), success in territorial encounters that rely on acoustic warning signals (Sebastianutto, Picciulin, Costantini, & Ferrero, 2011) and even cause total displacement (Rako *et al*., 2013). Noise can also distract individuals, taking their attention away from other behaviours. This can disrupt foraging (Wale *et al*., 2013a), and allow predators to approach individuals more closely before they respond (Chan *et al*., 2010).

Table 1: Frequency sensitivity of different marine taxa.

Taxa	Frequency Sensitivity (Hz)
Mammals (e.g. beluga whale, fur seal, harbour porpoise etc.)	7-180,000 (Ketten, 2004; Southall *et al.*, 2007)
Fish (e.g. Atlantic Cod, Goby, Bull Shark, Clownfish and other hearing generalists)	20-5,000 (Hastings & Popper, 2005; Ladich & Popper, 2004; Mann, Wilson, Song, & Popper, 2009; Parmentier, Colleye, & Mann, 2009)
Decapod Crustaceans (e.g. ghost crab, fiddler crab)	300-2,000 (Horch, 1971; Popper *et al*., 2001; Salmon *et al.,* 1977)

Generally, species whose survival and key behaviours do not obviously depend on their hearing ability have been overlooked in regard to noise pollution, despite such noise overlapping with their hearing sensitivity (Popper *et al*., 2001). More recently, a growing body of evidence has emerged suggesting that these species also experience negative effects from shipping noise, with potential survival consequences both at an individual and population level. For example, in sea hares (*Stylocheilus striatus*), shipping noise directly affects reproductive success, reducing embryonic development by 21% and increasing mortality in recently hatched larvae by 22% (Nedelec *et al.*, 2014). Noise has also been found to affect other sensory modalities entirely, such as in cuttlefish (*Sepia officinalis)*, who alter their visual display during anthropogenic noise playback, swimming, raising their arms and changing colour more frequently (Kunc, Lyons, Sigwart, McLaughlin, & Houghton, 2014). Additionally, Wale *et al.* (2013) demonstrated that in the shore crab (*Carcinus maeanas*), individuals are slower to retreat to a shelter to avoid predation under anthropogenic noise than ambient noise (Wale *et al*., 2013a), which they suggest may be a result of the increased stress levels also found to arise from exposure to shipping noise (Wale *et al*., 2013b). It is therefore clear that the consequences of anthropogenic noise reach beyond behaviours traditionally associated with acoustics, affecting success in numerous ways. This chapter aims to explore this in relation to a behaviour that is vital for the success of many species but has not previously been studied in this anthropogenic context: colour change for camouflage.

The ability to change colour is widespread across several taxa and serves a variety of functions (Duarte *et al*., 2017). Cuttlefish use rapid colour change facilitated by electrical impulses to aid in communication, among other things (Holmes, 1940; Chiao, Wickiser, Allen, Genter, & Hanlon, 2011). Rock gobies (*Gobius paganellus)* rapidly change their patterning when on marked or patterned backgrounds to break up their body outline, potentially acting as a form of disruptive colouration, to reduce the likelihood of detection from predators (Smithers *et al.*, 2017). Fiddler crabs (*Uca.)* have a circadian rhythm of colour change mediated by the expansion and dispersion of pigments (Abramowitz, Hole, & Laboratories, 1937; Brown & Webb, 1948), becoming lighter at night and darker during the day (Atkins, 1926; Abramowitz *et al.*, 1937; Brown & Webb, 1948) to enhance UV protection (Darnell, 2012). Ghost crabs (*Ocypode ceratophthalmus)* also have a circadian rhythm of colour change, becoming lighter during the day and darker at night to better match sand. This cyclical camouflage is fine-tuned by changing to match the brightness of the substrate upon which they are positioned (Stevens *et al*., 2013), known as background matching.

Due to the high reward and survival advantage they afford individuals, it is unsurprising that so many species undergo such processes, despite the high energetic costs believed to be involved (Stuart-Fox & Moussalli, 2009; Stevens, 2016; Rodgers, Gladman, Corless, & Morrell, 2013). Such costs however, mean that when stressed or even distracted by external factors, behaviours like this may suffer or be impaired. This is because limited energy reserves may be depleted or diverted from these processes to others, additional stress hormones may be released, or attention may be taken away from these behaviours. Here, I explore whether anthropogenic noise from shipping has the capacity to affect colour change behaviour and consequent camouflage. I focus on the shore crab (*Carcinus maenas)*, a species that relies on its ability to change colour, primarily it’s brightness, to avoid detection by predators (Hogarth, 1978; Stevens *et al*, 2014). Shore crabs are an intertidal species, widely distributed and occupying a variety of habitats along several coastlines, including the UK and other parts of Europe (Crothers, 1966; 1968). Shore crabs, in particular juveniles, adjust the distribution of black and white pigments within special chromatophore cells to alter their brightness and increase their level of background matching (Stevens, 2016; Stevens *et al,* 2014). They disperse black pigments and concentrate white pigments when on a dark background, and vice versa on a light background (Powell, 1962a). This is likely to be crucial for the survival of juveniles, who are subject to a range of predators, including shore birds, fish and cephalopods (Crothers, 1968), and do not have the same level of physical defence that larger, stronger adults have.

In a series of laboratory tank-based playback experiments, I explored this crucial behaviour further, in the context of underwater noise pollution. Here, I test the hypothesis that ship noise either reduces crabs' capacity to acquire energy, or causes them to waste more energy, and so they do not change in luminance or grow as much as they have less energy available to do so. Alternatively, if individuals habituate over a relatively short time period, then I do not expect these effects of noise to persist for the full duration of the experiment. I also hypothesise that as individuals have evolved in the presence of natural noises they have consequently acclimatised and therefore will be unaffected by high intensity natural noises.

Methods

Ethical Note

All work was conducted with the approval of the University of Exeter Biosciences ethical committee (applications 2018/2106 and 2018/2494). All individuals used in the preliminary trial were returned to their original rockpool area unharmed following the experiment. Those used in the main experiment were used in a further, short, experiment (see Chapter 3 for details) before being returned. Shore crabs are not endangered or protected and therefore no additional licences were required.

Preliminary experiment

To develop the most appropriate experimental setup and procedure, a preliminary trial was conducted. 54 juvenile shore crabs collected from the upper intertidal zone of Gyllyngvase Beach, Falmouth, UK, were housed individually for four weeks in either a black or white PVC pots with the corresponding colour gravel in a laboratory setting. The 54 pots were split into two tanks measuring 900x445x300mm, one for the control noise treatment (natural ambient underwater tracks playing continuously) and one for the ship noise treatment (natural ambient underwater tracks with the sound of a ship passing every hour); see below for details. Each tank contained a total of 27 crabs (13 on a white background and 14 on black) arranged in a checker-board style, with the speaker suspended from above, submerged in the water facing downward. Individuals were photographed immediately upon returning to the lab (within 3 hours of collection), 24 hours later and then every 2 weeks. Individuals were also photographed 48 hours after moulting. The carapace width of each individual was measured at the beginning, after each moult, and then again at the end of the experiment. Images were analysed using ImageJ and a predator vision model (peafowl); see specific details below.

Unfortunately, due to unavoidable circumstances in the lab at the time, the two tanks were adjacent to one another during the preliminary trial, and as full soundproofing was not possible, there was some overlap in the noise treatments, with noise spreading among tanks. Therefore, when interpreting the results, the noise was treated as a continuum based on distance from the ship noise source (speaker). This issue was rectified for the main experiment, where the noise treatments were discrete and could be treated as such. Preliminary analyses indicated that after 24 hours the amount of luminance change exhibited by individuals was too minor for any substantial differences based on noise to be detected. Therefore, it was decided that photographing individuals after 24 hours would cause unnecessary stress and consequently this step would be excluded from the main experiment. In order to assess short-term effects, the images from the 2-week interval would be used instead. In past work, when assessing luminance change, both black and white backgrounds were used (e.g. Stevens *et al.*, 2014). However, as the individuals were already dark in coloration upon collection, very little change occurred in those positioned on a black background, even in those in the quietest conditions. As a result, I opted to only use white backgrounds in order to maximise the sample size and clarity of results, as we were not testing how crabs change in brightness on different background per se, but rather how this type of change is affected by noise. From this trial it was evident that exposure to noise was affecting the luminance change and consequent background matching, despite the limited change seen across individuals. After 4 weeks, many of the individuals were yet to moult and therefore had not had the opportunity to undergo their most considerable change in luminance. It was consequently decided that the experimental period would be extended to 8 eight weeks for the main experiment. For results from the preliminary trial, see Appendix A.

Main experiment

Procedure overview

143 wild-caught juvenile shore crabs were housed on white backgrounds in a laboratory setting for eight weeks and exposed to one of three noise treatments: control, loud control, or ship. Individuals were photographed after collection and then every two weeks (to assess initial effects and in case a sufficient number did not survive for the full eight weeks). Photographs were also taken 48 hours after moulting. In addition, the carapace width of each individual was measured at the start, after moulting and again at the end of the eight weeks. Images were analysed to determine the effect of additional noise in general, as well as anthropogenic noise specifically, on the rate and magnitude of luminance change, as perceived by a predator, as well as overall background matching and camouflage. The level of growth per moult was also analysed.

Study species and collection

This study was conducted in February/March and June/July 2018. 71 juvenile shore crabs were collected from the upper intertidal zone of Gyllyngvase Beach, Falmouth, UK (50°08’33.4690”N, −005°04’07.9716”W) on 11th and 12th February 2018 and a further 72 were collected on 3rd and 4th June. Individuals were collected from the rockpools by hand within 3 hours of low tide and transported back to the University of Exeter’s Penryn Campus in neutral grey buckets. In shore crabs, the most notable change in colour occurs in juveniles approximately 12mm in diameter (or smaller), as above 30mm there is an increase in thickness of the cuticle and deposition of calcium carbonate (Powell, 1962b; Crothers, 1968). Therefore, these smaller individuals were targeted during collection for the experiment. Upon arrival in the lab, the carapace width of each individual was measured, with an overall range of 7-23mm. Individuals were assigned to one of three noise treatments in such a way that they were evenly distributed based on size.

Tank setup and husbandry

Individuals were housed separately in white 60x60x60mm PVC pots to prevent cannibalism or agonism. Both the lid and base of each pot was made of a fine mesh to aid in water-flow and sound transmission. The base of each pot was lined with white gravel (Natural White Aquarium gravel, Pets at Home, Cheshire, UK) to ensure the physical structure of the environment was as natural as possible. Individuals were split between three tanks measuring 900x445x300mm, one for the control noise, one for the ship noise and one for the loud control noise treatment, with each tank containing a total of 22-25 crabs/pots. Individuals were kept under natural white light (TMC GroBeam Ultima Strip natural daylight; AquaRay, Hertfordshire, UK) with a lighting regime that followed that of a natural day. Lights gradually came on at approximately 0700h for sunrise and gradually turned off at 1900h for sunset. A UW30 Underwater Loudspeaker (Electro-Voice; effective frequency range 100-10,000Hz) was attached to a PVC pipe and suspended from above each tank so that the speaker itself was submerged below the waterline, 200mm above the crabs, facing downward (Figure 1).

The inside surfaces of the tanks were lined with bubble-wrap to reduce the amount of noise reflection. Polystyrene sheets measuring 25mm in thickness were attached to the outer surfaces of the tank, and sheets of 50mm in thickness underneath the base to reduce the transmission of any external noise into the tank. Thicker layers were used for the bases as the water pumps and filters situated beneath the tanks generated the most noise creating vibrations through the tables upon which the tanks were positioned.

Each tank was fitted with an external filter (Eheim Classic 600 Filter, EHEIM GmbH & Co KG, Stuttgart, Germany) that filtered 620L/hour. The inflow pipe was placed directly into the water at one end of the tank. The outflow was connected to a piping network suspended above the tank, with holes at regular intervals allowing filtered water to flow evenly into the tank. 50% of the water was siphoned out of the tank and replaced twice a week when the tank was cleaned. The gravel was replaced every 2 weeks when individuals were removed for photographing to ensure that the colour of the gravel remained consistent and was not affected by the growth of any algae. Additionally, treatment groups were rotated between the tanks every 2 weeks to reduce any tank effects. The water was kept at a salinity of 34-35ppt, with a temperature of 13-15°C and quality within safe parameters (NO_3^-:<0.2mg/L, NH_3^+:<0.25mg/L, NO_2^- <0.3mg/L, pH=8). Individuals were fed 2-3 aquarium pellets (Ocean Free Super Crustanorish sinking pellet) every 48 hours.

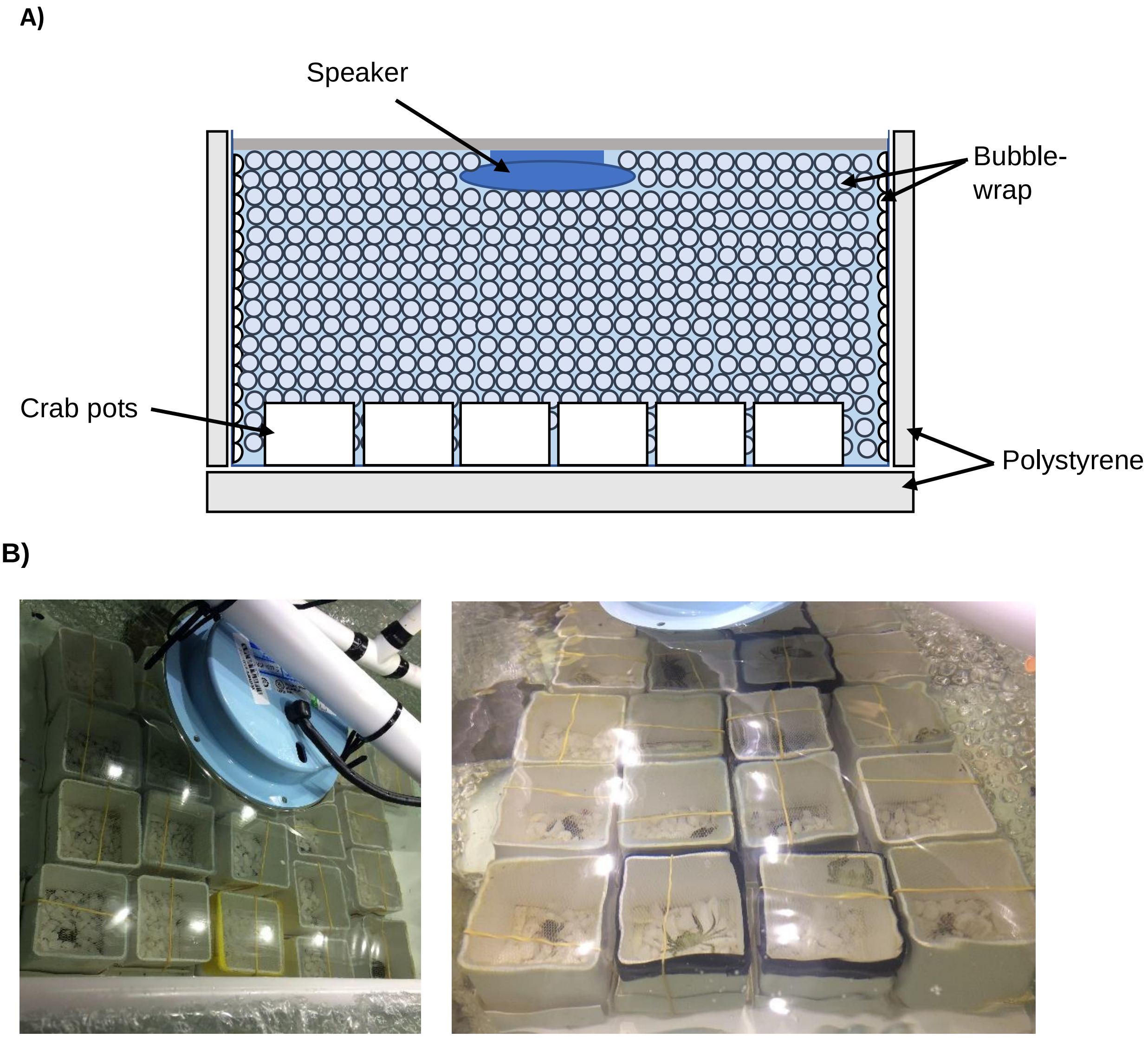


Figure 1. Experimental setup used in the main colour change experiment. A) Diagram showing a cross-section of the tank, as viewed from the side. B) Photographs of tank during experiment.

Care should always be taken when extrapolating the results of a tank-based study as the conditions vary to that of a natural system. This is particularly true when dealing with sound, as the physical structure and size of the tank causes sound to propagate differently than it would in a larger expanse of ocean (Pan, 2012), including in shallow intertidal zones. However, an in-situ experiment was not feasible for this study due to the necessity of a consistent substrate, periodic photographs and sufficient, discrete noise treatments. Necessary precautions were taken to ensure the environment reflected that of a natural setting as closely as possible (e.g. gravel-lined base to match the topography and allow individuals to burrow, textured walls/surfaces to reduce direct noise reflection, and regulated light intensity and regime) to enhance the applicability of the results to a real-world scenario.

Noise Treatments

All sounds used were recorded at 3 major UK ports (Plymouth, Portsmouth and Gravesend) by Wale, Radford and Simpson (2013a). At each location, one ambient recording and the recording of one ship (an LPG tanker, a container ship and a ferry, respectively) passing at ca. 200m distance was made; see Wale *et al*., 2013a for details of recordings and track normalisation/amplitude modification. Sound samples of 45-120 seconds, incorporating the highest amplitude of the ship and the most stable levels of ambient noise, were looped in Audacity 2.2.1.0 (www.audacityteam.org) to create the tracks used in the experiment. Each track included a 30s fade in, 5 minutes of either ship or ambient noise and a 30s fade out. Tracks were played back as MP3 files using a WAV/MP3 player (FecPecu; Digital MP3 Player X20) connected to a UW30 Underwater Loudspeaker (University Sound Diatran Omni-directional Underwater Loudspeaker; effective frequency range: 100-10,000Hz) via an amplifier (Kemo Electronic; 18W; frequency response: 40-20,000Hz).

The control treatment consisted of 3 ambient tracks (one recording from each location) played continuously for the duration of the experiment. Each track followed and was proceeded by each of the other tracks, with the overall order changing regularly so the order could not be learnt, and each track played an equal number of times to reduce the effect of any one specific track. For the ship treatment, the ambient tracks played in the same way as for the control treatment, but once an hour one of the 3 ship tracks played. To make the loud control tracks, the ambient recordings were modified in Audacity 2.2.1.0 (www.audacityteam.org) to play at a similar amplitude as the ship (Figure 2). The loud control treatment mimicked the structure of the ship treatment, with continuous ambient noise playing but the once per hour one of the loud control tracks played. The way in which the ship and loud control tracks were ordered reflected that of the control tracks.

To measure the mean amplitude of each noise treatment, the playbacks were recorded from the centre of the tank approximately 60mm above the tank floor, in line with the height of the crab pots, using a hydrophone (D-Series Hydrophone, JrF Audio Supplies) and recorder (ZOOM Handy H1 Recorder; 44.1kHz sampling rate). The WaveStats function in Audacity was used to determine sound levels. The sound level of the original ship recording (recorded ca. 200m distance) is also given to provide a reference point for real-world context; the ship and loud control noises were played at a level that matched this 200m distant large ship as closely as possible in the lab setting (Table 3). SPL measurements other than our measure of amplitude were not used as crustaceans mainly detect sound through particle motion rather than pressure, and these are sufficient in allowing a comparison of intensity between treatments. Calibrated measurements, such as those used by Wale, Radford and Simpson (2013), were unfortunately not available due to insufficient funds to purchase the necessary equipment and software (e.g. SPL meter, AviSoft) for this study. However, while this may pose some limitations in interpretation it is not a significant issue for our direct findings (see Discussion Chapter).

The use of multiple tracks reduces the effect of pseudoreplication. In this case, each track was also used individually in a predator response trial and the results showed that the 3 control tracks all had the same effect as each other, as did the 3 ship tracks and the 3 loud control tracks (see Chapter 3 for more detail). Therefore, observed effects of ship noise relative to control noise appear to be general features of this type of noise pollution rather than something specific to a particular recording.

***Table 2: Mean sound levels** of each noise treatment, as well as that of the original ship recording for real-world context/reference. Recordings of the noise treatment playbacks, and ambient noise level of tank, taken from the centre of the tank approximately 6cm above the tank base, in line with the top of the crab pots. Original ship recordings taken at a distance of ~200m from the ships. RMS= Root Mean Squared Average; (A) = A-weighted; FS = relative to a full scale where the maximum possible amplitude is 0; Peak = maximum observed amplitude.*

Noise	*RMS(A) dBFS*	*RMS dBFS*	*Peak dBFS*
Control	-61.8	-62.1	-35.7
Loud Control	-29.2	-29.9	-2.2
Ship	-22.4	-23.1	-3.9
Ship Original	-14.8	-13.6	-0.2
Ambient level of tank	-68.4	-67.9	-39.6

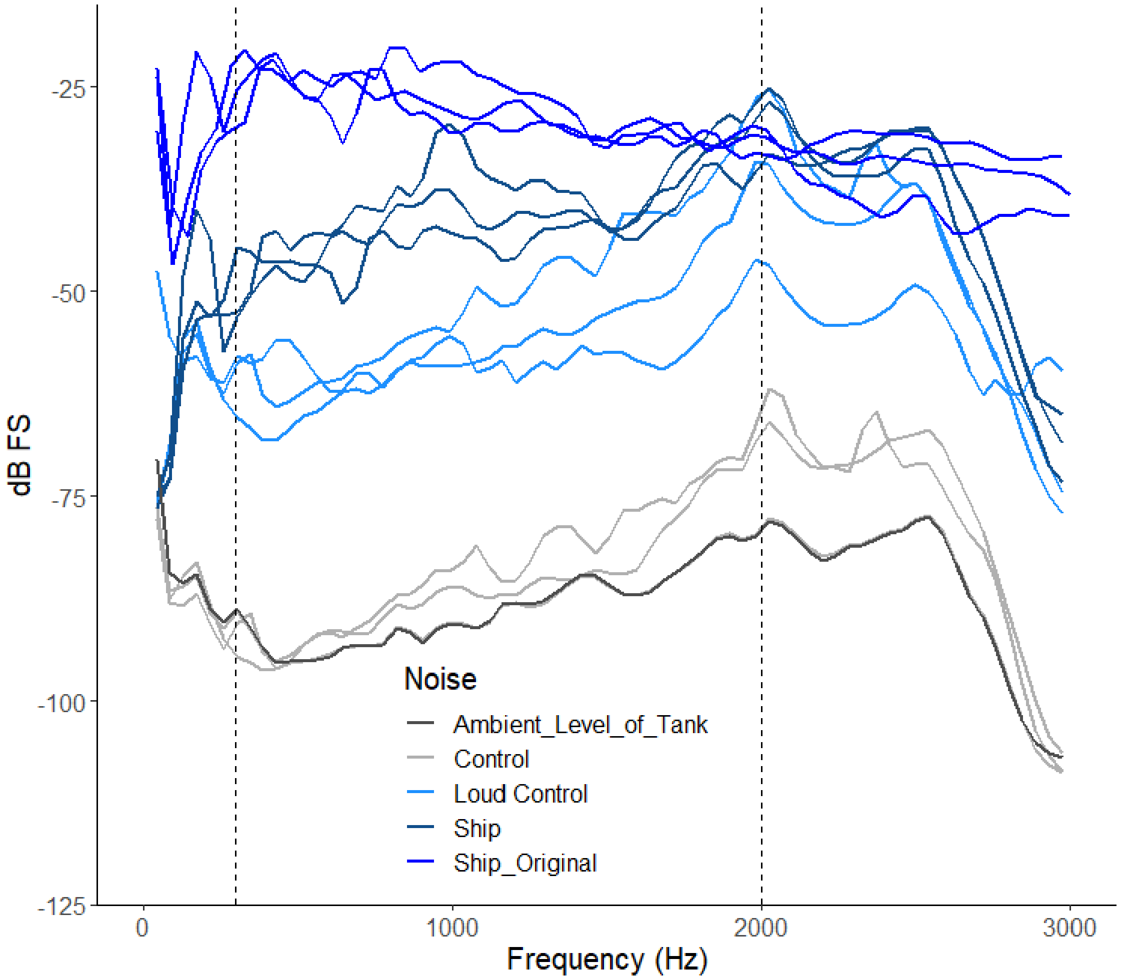


Figure 2: Average sound profile for each noise treatment. Average power spectrographs are shown for recordings of the ship, control and loud control playbacks, as well as the original ship recording for a real-scenario context, and the ambient noise level of the tank (FFT analysis; Hanning evaluation window, FFT size 1024). Recordings were made at the centre of the tank, in line with the top of the crab pots, while the relevant noise played. Dotted lines represent the estimated lower and upper bounds of crab frequency sensitivity (Salmon *et al.*, 1977*;* Horch, 1971). The total plot was cropped to enlarge and highlight this area, as anything outside of these bounds is highly unlikely to be detected by crabs.

Photography and image analyses

All crabs were photographed out of water and were dried beforehand to prevent any reflection from residual water. In order to reduce stress and any additional colour change as a result (Detto, Hemmi, & Backwell, 2008), individuals were photographed as quickly as possible and only removed from the tank immediately before photographing.

All photographs were taken using a Nikon D7000 digital camera which had undergone quartz conversion to make it sensitive to ultraviolet (UV) light. It was also fitted with a Nikon 105mm Nikkor lens. Two photographs were taken of each individual: one human visible photo using a UV/IR blocking filter which transmits wavelengths 400-700nm (Baader UV/IR Cut filter) and one UV photograph using a UV pass and IR blocking filter which transmits 300-400nm (Baader U filter). All photography was conducted under a UV and human visible Arc Lamp (70W 1.0A power source; EYE Colour Arc Lamp with Ventronic, Venture Lighting Europe Ltd. Hertfordshire, UK). Photographs were taken with a fixed aperture and manual white balance, in RAW format. Each photograph included a black and white reflectance standard with 7% and 93% reflectance respectively, and a scale bar.

All image analyses were carried out in ImageJ (version 1.8.0_112) using the Multispectral Image Calibration and Analysis Toolbox (Mica Toolbox version 1.22) developed by Troscianko & Stevens, (2015). Visible and UV images were first combined ensuring maximum alignment, to create a single multi-spectral image for each individual at each time point to be analysed. Due to the nonlinearity of the camera's response to light intensity, the images were first linearised (Stevens, 2007) before any analyses could be performed. Within each image, as much of the individual's carapace was selected as possible (avoiding areas where light reflected directly back – known as specular reflectance) by hand as a region of interest (ROI), and the 93% and 7% reflectance standards selected. Images were calibrated with regards to the reflectance standard, with the image wavelength channels scaled so a value of 65535 on a 16-bit scale equals 100% reflectance.

To assess and compare the extent of background matching and camouflage in an ecologically relevant context, individuals should ideally be viewed and analysed using the visual system of one of their most common predator groups – in this case shore birds (Crothers, 1968). This study, as with most previous studies (e.g. Stevens *et al.*, 2014), uses visual system data of the peafowl (*Pavo cristatus*) as a model species. Like many other shorebirds which regularly prey on crustaceans, the peafowl has a violet-sensitive (VS) visual system (Hart, 2002). This means that their sensitivity is shifted into the violet part of the spectrum, but they are still able to detect UV (Hart & Hunt, 2007; Ödeen & Håstad, 2003). The mean luminance (brightness) of the individual for each ROI is measured by the predicted response of the double cones, which is widely thought to underpin achromatic vision on birds (Osorio & Vorobyev, 2005). This was determined by undertaking a widely implemented mapping approach, converting the images from camera colour space to that of the peafowl vision model using the Batch Multispectral Analysis Tool (Troscianko & Stevens, 2015). This method is highly accurate for modelling predicted photoreceptor stimulation compared to approaches that rely on reflectance (Pike, 2011; Stevens, 2007; Troscianko & Stevens, 2015), The output cone catch values is represented by a value between 0 and 1, as is convention for vision modelling. The same process was used to determine the mean luminance of the background, using Visible and UV photographs of the gravel. As the background upon which individuals were housed was white, we did not have any specific or relevant predictions about colour change, and therefore colour change was not analysed, only luminance. Just noticeable differences (JNDs) were not used as a measure of background matching as this unit is less accurate (and therefore less appropriate) when dealing solely with luminance. Instead, to ascertain the accuracy of background matching achieved by the individuals, the absolute difference in luminance between the crab and the background was calculated, following that of previous work (e.g. Stevens *et al.,* 2013).

Statistical Analyses

16 individuals died and 7 escaped during the first 8-week experiment, and 12 died and 10 escaped during the second; escaping refers to cases where individuals either fully escaped from the tank or regularly escaped from their individual pots and were therefore not on the white, colour-change-inducing background. Consequently, these individuals were excluded from the analyses. This leaves a total of 98 crabs; 30 in the control treatment, 36 in the loud control and 32 in the ship. In the cases of luminance change, background matching and growth, GLMs were used to test for the effect of noise. In each case, a maximal model controlling for relevant variables including trial number, size, moulting and a noise-size interaction (previous studies have shown that in adult shore crabs individuals are affected differentially based on their size (Wale *et al*., 2013b)) was generated. Then using the model simplification method, non-significant terms were removed in turn, comparing the model with and without each variable (Crawley, 2011).

Terms that did not significantly affect the model's deviance were removed entirely, until the minimum adequate model was created. The same technique was adopted to analyse the time taken and likelihood of moulting, but rather than a GLM, a Cox proportional-hazard model was fitted (Fox & Weisberg, 2011). The Cox proportional-hazard model is a form of survival analysis, examining certain factors simultaneously (in this case noise, size, trial number and a noise-size interaction) and how they affect the rate of an event occurring (Cox, 1972, 1984). Here, the occurrence of moulting was set as the 'event', with 'censored' individuals being those that did not moult during the experiment. All statistical analyses were carried out using RStudio (R v.3.4.3) (R Core Team 2017).

Results

The mean luminance of individuals at the start did not differ between treatment groups (Kruskal Wallis; $\chi^2_{(2)}$=0.59, p=0.75) (Figure 3).

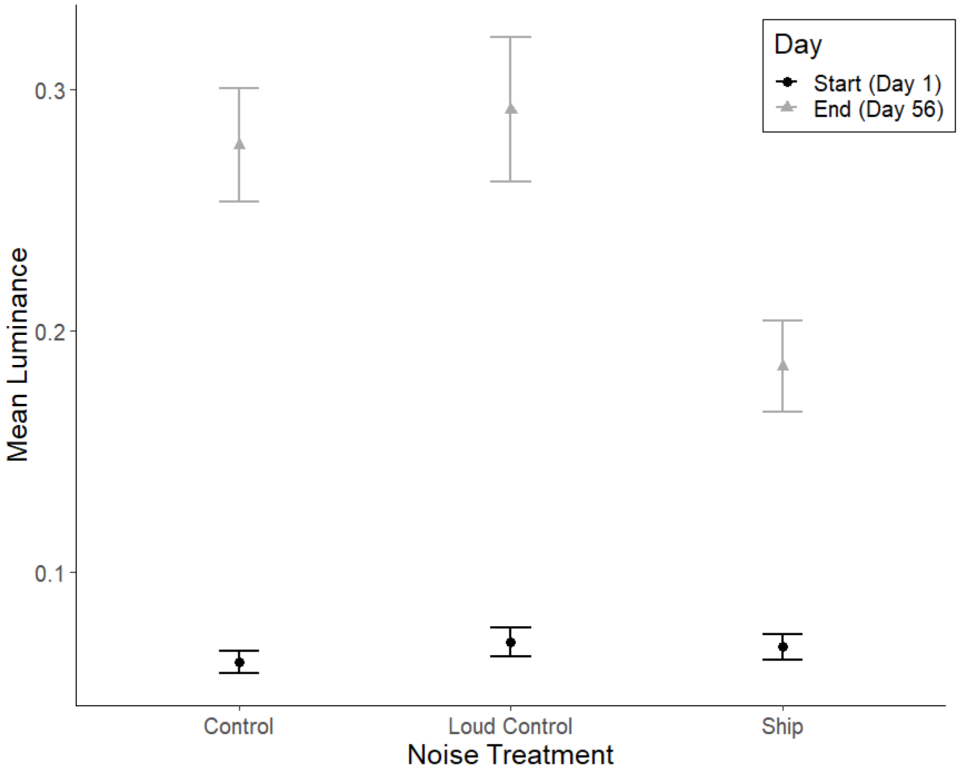


Figure 3: Mean luminance of individuals exposed to each noise treatment; both at the start of the experiment and after 8 weeks of exposure.

Two Weeks

Luminance Change

Noise significantly affected how much individuals changed in luminance in the first 2 weeks of exposure (GLM, $\chi^2_{(2,97)}=0.025$, $p=0.029$), with those exposed to the ship noise changing less (Figure 4a). Size and moulting were controlled for in the model, both significantly affecting the change in luminance ($\chi^2_{(1,96)}=0.03$, $p=0.003$ and $\chi^2_{(1,95)}=0.08$, $p<0.05$ respectively), with larger individuals, and individuals that moulted during this time changing in luminance more. An interaction between noise and size was initially included but removed as it had no significant effect on the model's deviance ($\chi^2_{(2,92)}=0.002$, $p=0.81$), as was the trial number ($\chi^2_{(1,94)}=1.12\times10^{-6}$, $p=0.99$).

Background Matching

The level of background matching after 2 weeks of exposure was significantly affected by noise (GLM, $\chi^2_{(2,97)}=0.108$, $p=0.031$), with those in the ship treatment being less camouflaged (Figure 4b). Moulting and size were controlled for in the model as they both significantly affect the level of background matching ($\chi^2_{(1,95)}=0.245$, $p<0.05$ and $\chi^2_{(1,96)}=0.109$, $p=0.008$ respectively), with larger individuals and those that moulted during this period matching the background more closely. An interaction between noise and size was also included initially but removed as it did not affect the model's deviance ($\chi^2_{(2,92)}=0.008$, $p=0.77$), as was the trial number ($\chi^2_{(1,94)}=0.001$, $p=0.76$).

Eight Weeks

Luminance Change

Noise significantly affected the change in luminance exhibited by individuals between week 2 and 8 (GLM, $\chi^2_{(2,97)}=0.08$, $p=0.03$) (Figure 4). Moulting during this time period was also controlled for as it significantly affects luminance change ($\chi^2_{(1,96)}=0.21$, $p<0.05$), with those that moulted changing in luminance more than those that did not. A noise-size interaction, size and trial number were initially controlled for but were removed as they did not affect luminance change or significantly improve the model's deviance ($\chi^2_{(2,94)}=0.001$, $p=0.96$; $\chi^2_{(1,96)}=0.034$, $p=0.09$; and $\chi^2_{(1,95)}=0.0002$, $p=0.896$ respectively).

Background Matching

After 8 weeks, individuals exposed to shipping noise were less camouflaged (Figure 4d), as noise significantly affected how closely individuals match the background at this time point (GLM, $\chi^2_{(2,99)}$=0.364, p=0.001). Moulting and size were controlled for in the model as they both significantly affect the level of background matching ($\chi^2_{(1,98)}$=0.332, p=0.0005 and $\chi^2_{(1,97)}$=0.256, p=0.002 respectively), with larger individuals and those that moulted matching the background more closely. An interaction between noise and size was also included initially but removed as it did not affect the model's deviance ($\chi^2_{(2,94)}$=0.003, p=0.95), as was the trial number ($\chi^2_{(1,96)}$=0.002, p=0.78).

Moulting

Luminance Change

There was no effect of noise on how much individuals changed in luminance when they moulted (GLM, $\chi^2_{(2,69)}$=0.032, p=0.409). Size, trial number and a noise-size interaction were originally controlled for but were removed from the model as none had a significant effect ($\chi^2_{(1,67)}$=0.001, p=0.84; $\chi^2_{(1,68)}$=0.012, p=0.41 and $\chi^2_{(2,65)}$=0.057, p=0.20 respectively).

Size change

Noise affected how much individuals grew when they moulted (GLM, $\chi^2_{(2,69)}$=2.63, p=0.003), with those exposed to shipping noise changing in size significantly less (Figure 5). Size before moulting, trial number, and an interaction between noise and size were originally controlled for in the model but were removed as none had a significant effect ($\chi^2_{(1,69)}$=0.355, p=0.22; $\chi^2_{(2,65)}$=0.680, p=0.47; and $\chi^2_{(1,68)}$=0.125, p=0.24 respectively).

Time to Moult

Noise significantly affected the rate and probability of moulting at any particular time point (Cox proportional hazard, $\chi^2_{(2)}$=6.75, p=0.034), being significantly reduced by ship noise (Figure 6). Ship noise had a hazard ratio (effect size) of

0.49. Trial was originally controlled for but was removed as it did not significantly improve the model's deviance ($\chi^2_{(1)}$=2.13, p=0.15).

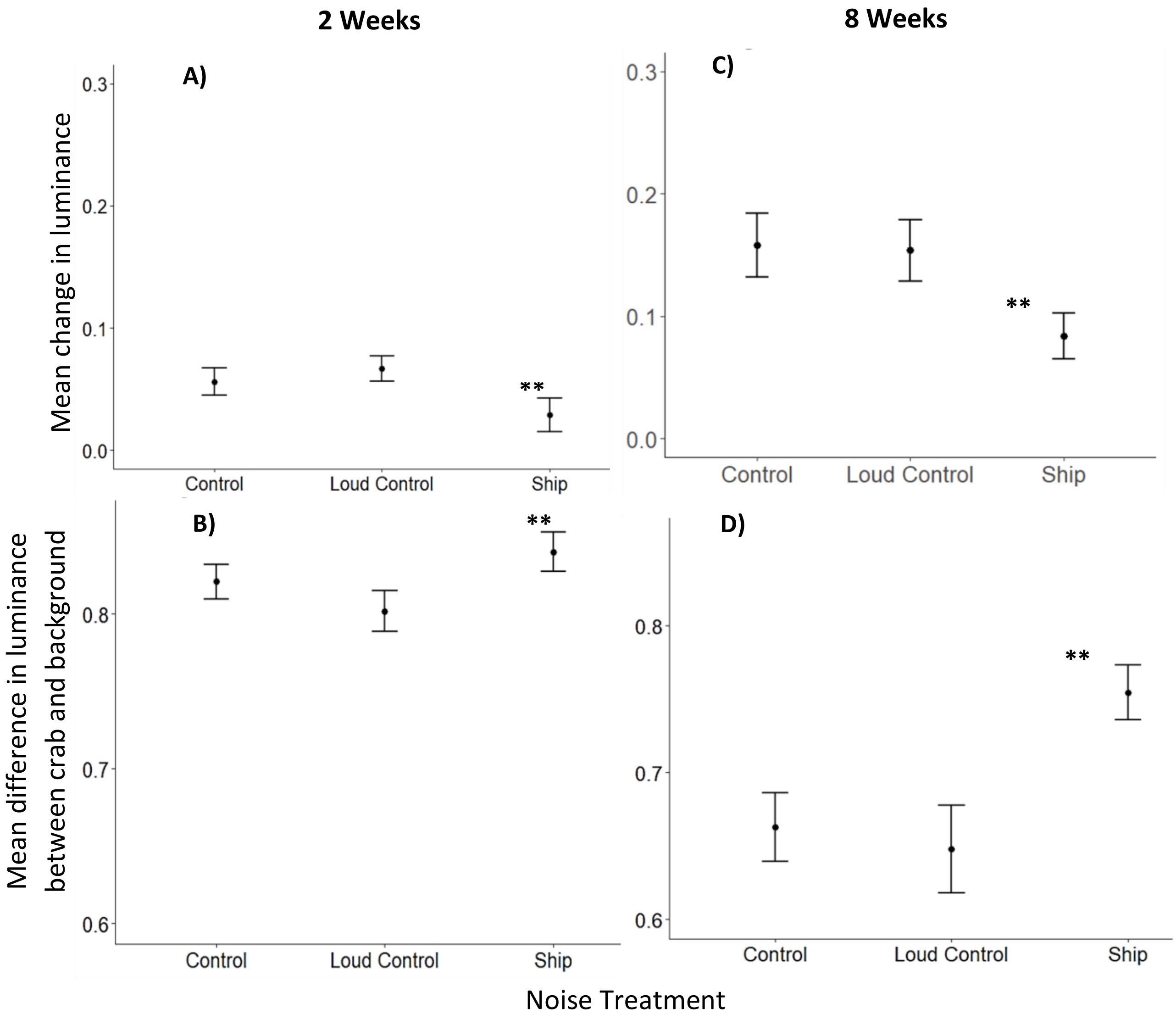


Figure 4: Shipping noise reduces luminance change and consequent background matching after both 2 and 8 weeks of exposure, but loud control has no effect. Mean change in luminance for each noise treatment, with standard error shown, after 2 weeks (**A**) and from 2-8 weeks (**C**) of exposure. Mean difference in luminance between the crab and the background, used as a measure of background matching, with standard error, after 2 weeks (**B**) and 8 weeks (**D**), as a result of the change in luminance. Lower values indicate better matching and consequently a greater level of camouflage. Ship n=32; Loud Control n=36; Control n=30. ** = p<0.05

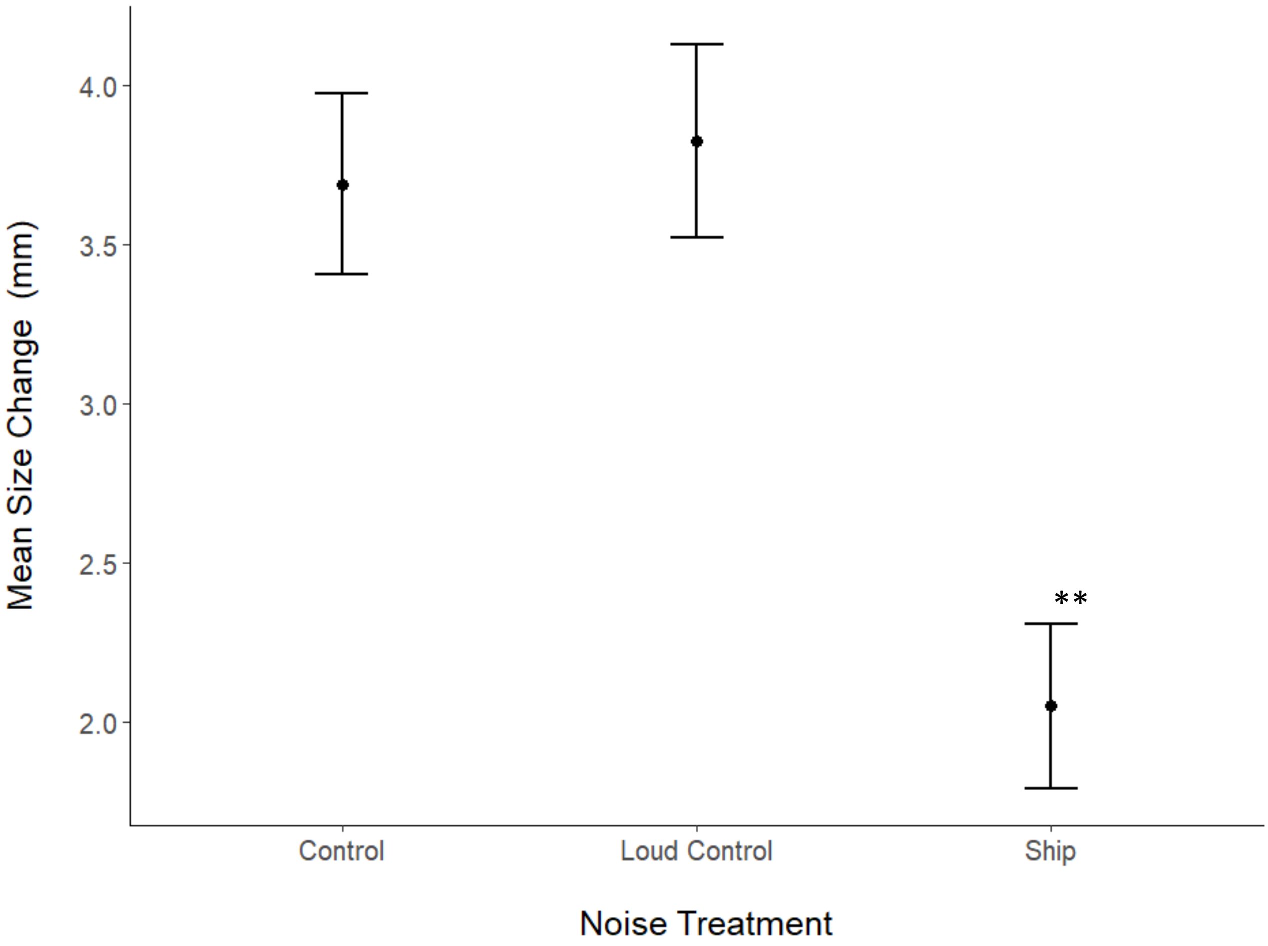


Figure 5: Ship noise reduces the size change per moult, but loud control has no effect. Mean change in size per moult (mm), with standard error. Ship n=20; Loud Control n=23; Control n=29. **=$p<0.05$

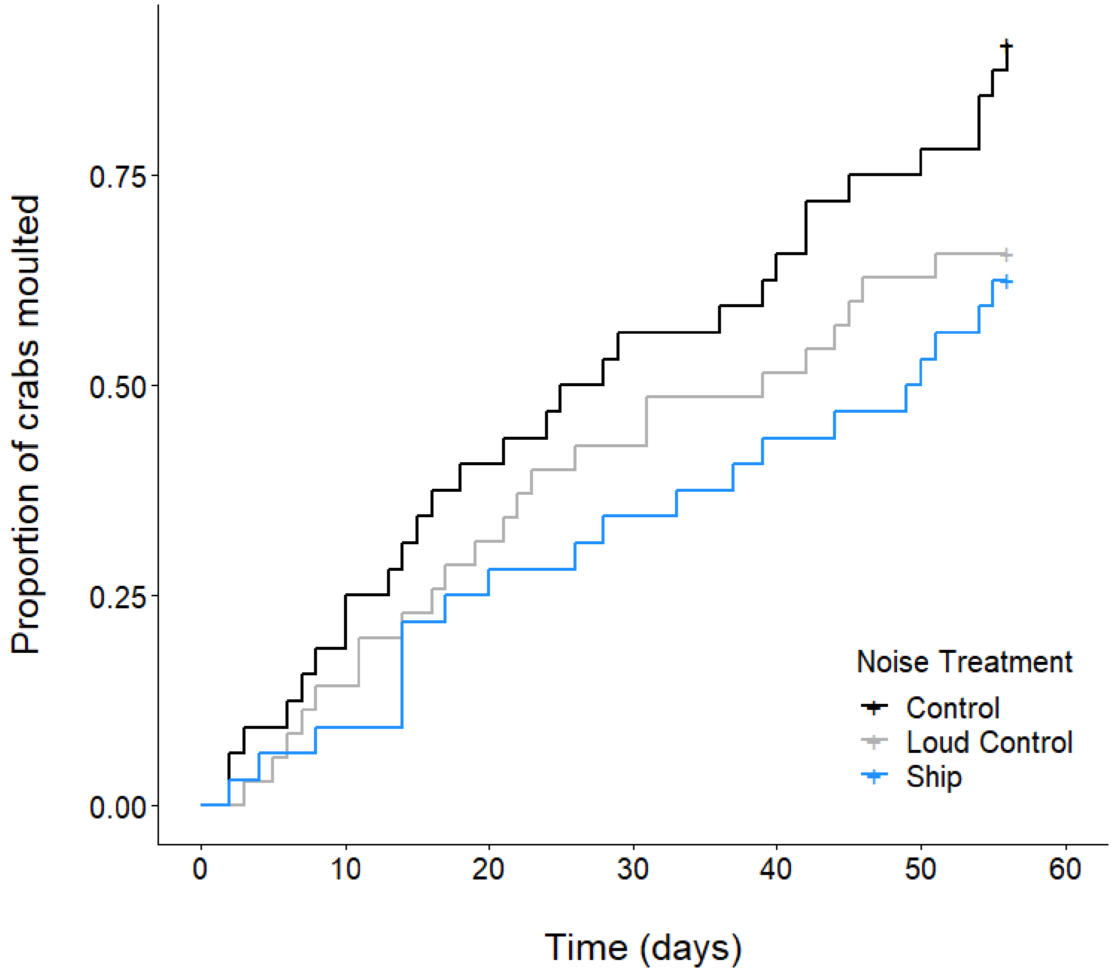


Figure 6: Ship noise increases the time taken for individuals to moult and consequently reduces the likelihood of moulting. Proportion of crabs moulted by each time point (day), culminating in the total proportion of crabs that moulted within each noise treatment by the end of the experiment (day 56). A + at the tip of the line indicates that the group contains ‘censored’ individuals (i.e. individuals that did not moult).

Discussion

Repeated exposure to ship noise resulted in multiple physiological and morphological effects in shore crabs, each with the potential to reduce individual survival. Ship noise reduced the amount of luminance change, leading to decreased levels of background matching, both initially and over a longer time period. It is likely that this limited change in luminance occurs primarily before/between moulting events, as individuals still became significantly brighter when they moulted, though not enough to counteract the reduction and ‘catch up’. The delayed timing of moults seen in individuals exposed to ship noise, coupled with their reduced luminance change within moults will leave such individuals mis-matched for longer periods. This likely has serious implications for predation risk and consequent survival (Stuart-Fox *et al.*, 2003; Merilaita & Lind, 2005). Due to the pervasiveness of colour change across marine species, these implications are not limited to shore crabs.

The type of noise clearly plays a key role in determining how an individual may be impacted. Here we demonstrated that negative effects were only displayed in individuals exposed to loud anthropogenic noise from shipping, not in those exposed to loud natural ambient sounds, suggesting artificial noise in particular creates problems for individuals. This distinction likely matters a great deal, but in previous studies could not be made, as often, the intensity of noise (i.e. loud or quiet) differed between the experimental treatment and the control treatment, along with the type of noise (i.e. anthropogenic or natural). Based on the findings presented in my study, many of the already documented effects of noise (particularly those related to stress (e.g. Filiciotto *et al*., 2014, 2016 Wale *et al.,* 2013b, 2013a)) are likely a result of intense anthropogenic noise specifically, rather than additional noise to the environment in general. As discussed, this is a distinction that, to the best of my knowledge, has not been made in previous studies due to the lack of sufficient loud natural controls.

There may be multiple explanations for the differential effect of anthropogenic sounds compared to natural sounds of similar high amplitudes. Perhaps the most obvious is the novelty of anthropogenic noise, which regardless of the source, has only been present in the ocean for the last few decades. Natural sounds, particularly those that make up the ambient soundscape of the ocean, even at high amplitudes are a feature that individuals will be much more accustomed to and species will have evolved alongside. This ultimately restricts the extent to which such noise will impact individuals. High amplitude sounds are not uncommon in nature, particularly in marine settings like the intertidal zone, where wave action can generate relatively high levels of noise (Coers, Bouton, Vincourt, & Slabbekoorn, 2008). Alternatively, the strong negative effects seen in response to the ship but not the loud ambient sounds could relate to the structure of the noise itself. As with many anthropogenic noises, the sound produced by ships has an artificial consistency, with a continuous, highly intense ‘hum’. Natural sounds however are more varied in their structure, with components of both high and low intensity (see Appendix B for waveform). It is possible that these intervals of less intense noise may provide some relief or break up the higher intensity components enough to alleviate any potential effects.

Our study did not explicitly examine the mechanistic basis of the effects of anthropogenic noise that we observed. However, since luminance change does not rely on acoustic cues, masking can be ruled out. This refers to instances where individuals are unable to detect acoustic cues or signals because additional noise in the environment conceals them. Alternatively, exposure to noise has been suggested to shift attention away from primary tasks as individuals become distracted and their capacity for paying attention is limited (Dukas, 2002; Mendl, 1999). Evidence indicates this can affect predator detection *(*Chan *et al*., 2010) and foraging (Purser & Radford, 2011). However, it is unlikely that this is the case with the luminance change exhibited by shore crabs as this occurs due to physiological and morphological changes over different timescales (Duarte *et al*., 2017), and is therefore generally not considered to require the type of attention that may be reduced if an individual becomes distracted. However, shore crabs are already known to have elevated stress levels when exposed to ship noise (Wale *et al*., 2013b). Stress can affect the behaviour of individuals in two ways; by reducing energy availability and consequently altering the investment in certain behaviours or physiological mechanisms (Kooijman, 2000; Sokolova, Frederich, Bagwe, Lannig, & Sukhotin, 2012), or by altering the balance of particular hormones and disrupting endocrine-regulated processes (e.g. growth and moulting). Noise-induced stress is the most likely explanation for the results demonstrated in this study, however it is unclear which stress-related mechanism in particular (i.e. energy consumption or hormone imbalance) is responsible for the observed disruptions to luminance change, growth and moulting; both possibilities will now be discussed further.

A stress-related hormone imbalance may be responsible for the reduced size increase with moulting, as well as the delayed timing of moults and overall reduced luminance change exhibited by individuals exposed to ship noise. For example, one hormone associated with stress in crustaceans is crustacean hyperglycaemic hormone (CHH) which functions primarily in regulating sugar levels in the hemolymph (Chung & Zmora, 2008; Keller, 1992; Lorenzon, Edomi, Giulianini, Mettulio, & Ferrero, 2005; Webster, 1996). CHH also plays a role in the moult cycle, associated with both the uptake of water and consequent swelling during ecdysis (this is involved in the size increase seen in individuals) (Chung, Dircksen, & Webster, 1999) and the inhibition of ecdysteroid synthesis (hormones that induce moulting) (Keller, 1992; Webster & Keller, 1986). Although the effect of stress on the hormonal and mechanistic aspects of the moult cycle are not fully understood, it is possible that an alteration in the production, release or uptake of CHH, ecdysteroids or other hormones such as the moult inhibiting hormone (MIH) may occur. This could consequently be responsible for, or at least contribute to, the delayed timing of moults or the reduced size change during moulting demonstrated here in response to anthropogenic noise (Mclay, 2015). Furthermore, hormones involved in regulating the contraction or dispersal of pigments and consequent change in brightness or colour (Duarte *et al*., 2017) may be affected in a similar way, disrupting the individual's ability to control the pigment distribution and overall appearance.

Alternatively, reduced energy availability may explain these results. In shore crabs, an increase in metabolic rate, which is often associated with stress, has been observed during exposure to anthropogenic noise (Wale *et al.*, 2013b). Given the potentially high energetic demand of prolonged luminance change (Duarte *et al*., 2017; Rodgers *et al.*, 2013), it is likely that individuals simply do not have sufficient energy to maintain this fully under stressful conditions. The change in luminance when individuals moult, however, is unaffected by exposure to shipping noise, but comes at the cost of reduced growth, suggesting the presence of an energetic trade-off and limited energy budget. Typically, juveniles undergo a considerable size increase upon moulting, in addition to the substantial change in luminance (as was the case with individuals in the control groups in this experiment). Previous work suggests that in juvenile shore crabs, the energy from up to 73% of digested material is normally spent on tissue growth (Breteler, 1975), with a limited ability to increase in size unless food consumption is increased to match the elevated energy expenditure associated with a high metabolic rate, particularly if other energy-demanding behaviours are favoured (Thompson & Bayne, 1974). Therefore, it is possible that this is the case here.

Like many species, crabs rely on their size for a variety of defence-based actions (e.g. success in aggressive interactions (Sneddon, Huntingford, & Taylor, 1997) and protection from predators (Moksnes, Pihl, & Van Montfrans, 1998)) and may consequently suffer as a result of restricted size. Therefore, the investment in luminance change over growth when moulting under stressful conditions suggests strong selection in favour of this camouflaging behaviour. This highlights the severity of implications associated with the overall reduction in luminance change in the presence of anthropogenic noise, as, if favoured above a large size increase during moulting, it is clearly an important aspect in ensuring the success of an individual.

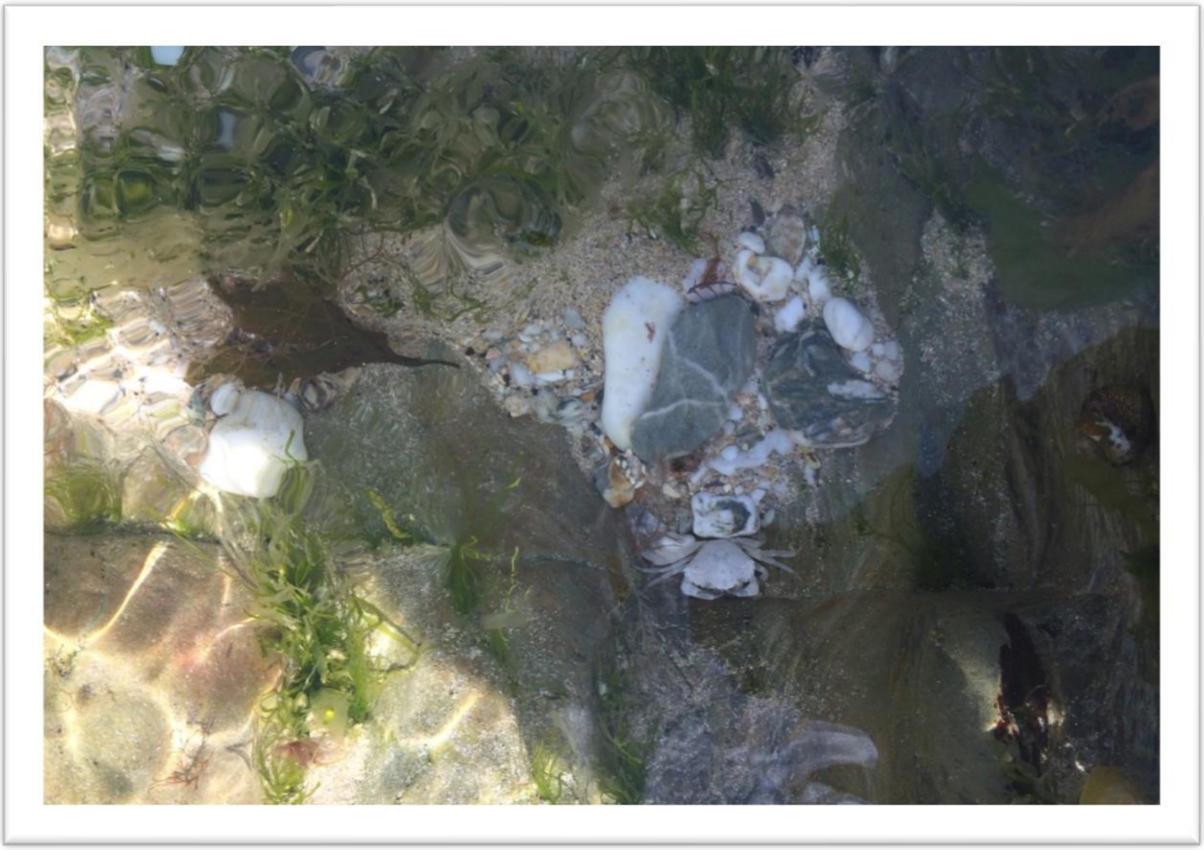
Given more time, individuals may acclimatise or desensitise to noise (Wale *et al.*, 2013b; Holmes *et al.*, 2017), reducing the negative effects seen, and in this case affording them the opportunity to catch up, increasing their camouflage and consequently reducing their predation risk. There are, however, multiple caveats to this suggestion. First, due to the difference in the rate of luminance change, individuals exposed to ship noise are increasingly disadvantaged, meaning the more time goes on, the further they are from the luminance they would otherwise be at that point. Therefore, even if the negative effects were reduced, a considerable change in luminance would still be required for them to become sufficiently camouflaged and resemble their appearance had they not been subject to such noise. Due to the possible energetic costs likely involved (Rodgers *et al.*, 2013), it may be unlikely that this would occur rapidly enough to prevent any further additional predation risk arising from prolonged mismatching. Second, little work has been done to explore the possibility of acclimatisation, with indications that it may only occur in cases where individuals are exposed to continuous bouts of the same noise (Bejder, Samuels, Whitehead, Finn, & Allen, 2009; Smith, 2004). Limited evidence suggests the occurrence of novel or variable noise such as that from different boats or ships could prevent acclimatisation or any reduction in effects (Wysocki & Gavin, 2006). A previous study found that the stress response of shore crabs repeatedly exposed to ship noise did not increase over time as it did with those exposed to ambient noise (the increase with ambient noise in their study likely a result of repeated handling). The authors hypothesise this could be a result of acclimatisation, with the increase in stress from handling counteracted by a reduced response to the ship noise (Wale *et al*., 2013b). However, it is also possible that upon first exposure to the ship noise individuals exhibited a maximal stress response and therefore the same positive relationship between stress and exposure found with ambient noise could not be seen, as the peak had already been reached. Further experiments assessing acclimatisation are warranted to ascertain a clearer understanding regarding its conceivability and gain insight into the future prospects of this and other species subject to intense anthropogenic noise; the following chapter explores this further.

The lack of any size-dependent differences contradicts that of previous work assessing the effects of noise pollution on shore crabs (Wale *et al*., 2013b), which found that larger individuals were more affected by noise exposure regarding their stress response. The discrepancy in results is likely due to the differing life stages and span of sizes; here we studied only small juveniles with a much narrower size range whereas Wale *et al.* focussed only on adults with a much broader range of sizes.

Generally speaking, the attention given to invertebrates when attempting to understand the impacts of anthropogenic noise has been disproportionate with their abundance, diversity and importance, both ecologically (e.g. for their role in food webs and as ecosystem engineers (Leal *et al.*, 2012)) and economically (not only in the commercial fishing industry but also as a source of natural products for the development of new drugs (Leal *et al.*, 2012)). To begin to rectify this, more studies such as this one, using an invertebrate as the focal species must be carried out to prevent a vital contributor to the marine ecosystem being overlooked and consequently a major part of the picture missed (Morley, Jones, & Radford, 2013).

As this is a tank-based study care should be taken when applying the results to a real-world setting due to the differences in sound propagation between small, enclosed spaces and larger expanses of water. Additionally, crustaceans likely detect sound through means of particle motion (Popper *et al*., 2001) which could not be quantified here. However, our study is not only the first to investigate how anthropogenic noise impacts camouflage behaviour, but to also use a loud natural control treatment to disentangle the effect of elevated noise levels from that of novel anthropogenic noise specifically. It further demonstrates the vast extent of the consequences associated with our increasing activity in the ocean, and that the effects of anthropogenic noise are in no way limited to species and behaviours reliant upon audition. It is clear how vitally important it is that we treat anthropogenic noise in the marine environment as a major pollutant and begin to consequently monitor and regulate it as such, to have any chance at alleviating this additional pressure on an already stressed ecosystem.

Chapter 3: The effect of noise pollution on antipredator behaviour and movement



Abstract

Anthropogenic noise has been shown to adversely affect a range of behaviours, even those with no obvious link to the auditory system, as demonstrated in the previous chapter. In this chapter, I present two experiments to examine the effect of noise on two activities important for success in juvenile shore crabs: the antipredator response and movement. It has been demonstrated that ship noise disrupts antipredator behaviours in adult shore crabs, increasing their retreat time but not affecting their ability to detect the predator. However, evidence suggests that individuals of different life-stages can be differentially impacted by certain stimuli and are therefore worthy of specific investigation. Movement is a major component of the antipredator response and plays an important role in several other activities including foraging and transference into adult populations. Therefore, I also examined mobility separately, specifically the continuity of movement in the presence of noise, as few studies have been conducted to investigate this. Additionally, I assessed whether individuals attempt to move away from, and consequently avoid exposure to anthropogenic noise. In each experiment, I used three noise treatments (ship, loud natural control, and control) to distinguish between the effects of ship noise specifically and that of additional noise in general. In the first experiment I tested the antipredator response and found that unlike adults, juveniles were less likely to respond to a predator, as well as being slower to retreat, in the presence of ship noise. In the second experiment, investigating the effect of noise on mobility and movement, I found that there was no effect on the frequency of pausing during movement. I also found that individuals moved away from ship noise, positioning themselves further from the speaker, consequently avoiding intense exposure. Furthermore, each experiment was conducted on individuals with varying levels of experience with noise to determine if those exposed previously had developed a tolerance. This was, however, not the case as for each behaviour all individuals were affected by ship noise in the same way regardless of their previous level of exposure. The loud natural control had no effect on any behaviour investigated, suggesting that many documented effects may be a result of anthropogenic noise specifically, and that the type of noise is important in determining the impact. Overall, ship noise disrupted crucial antipredator behaviours with serious

implications for survival, but evidence suggests individuals may be able to alleviate some of these additional pressures by avoiding noisy areas.

Introduction

Anthropogenic noise in the marine environment has the potential to cause widespread disturbance, with negative impacts affecting a wide spectrum of species. As well as disrupting communication by masking signals (Sebastianutto *et al*, 2011; Jensen *et al*., 2009) or altering the calling rate of individuals (de Jong, Amorim, Fonseca, Fox, & Heubel, 2018), noise also reduces settlement (Simpson *et al.*, 2016), predator response (Chan *et al.*, 2010; Wale *et al*., 2013a) and foraging (Wale *et al*, 2013a; Voellmy *et al.*, 2014), by masking cues, increasing stress or distracting individuals (Chan *et al.*, 2010). Additionally, evidence suggests that noise not only disrupts behaviours, but also has the capacity to directly reduce survival by increasing mortality through stress or barotrauma and causing developmental behaviour in embryos (Nedelec *et al*., 2014). The previous chapter demonstrated that even a long-term physiological behaviour with no obvious link to the auditory system can be severely impacted by anthropogenic noise. Many behaviours are yet to be directly explored in relation to shipping noise (e.g. movement/locomotion), or, as with antipredator responses, warrant further investigation due to their significance or complexity regarding the number of components to be considered. In order to understand the full extent at which anthropogenic noise affects marine ecosystems, such behaviours must be investigated, and the physical response of individuals to noise itself must be identified.

Antipredator Behaviours

If individuals are to be successful during predator-prey encounters, then they must first be alerted to the predator’s presence. As many species rely on acoustic cues from the predator or acoustic alarm signals from conspecifics, anthropogenic noise may impede their ability to detect such threats by masking these sounds (Erbe, Reichmuth, Cunningham, Lucke, & Dooling, 2016). Even if this is not the case, the presence of anthropogenic noise may still increase predation risk by interfering with the prey’s response behaviour or ability to recognise the predator as a threat. For example, noise can distract individuals, reallocating their limited attention, which can affect risk assessment and ultimately prevent prey from responding to predators (Chan *et al*., 2010; Dukas, 2002, 2004). Furthermore, exposure to noise can elevate stress levels (Sierra-

Flores *et al.*, 2015; Smith, 2004; Wale *et al.*, 2013b; Wysocki & Gavin, 2006) which can lead to hormone-based physiological responses (Chang, Ernest, 2005; Lorenzon *et al*., 2005) and reduced energy availability (Kooijman, 2000; Sokolova *et al*., 2012), which may alter overall activity and locomotor behaviour (Mendl, 1999), including the escape response of prey. Wale *et al*. (2013) demonstrated that while exposed to anthropogenic noise from shipping, adult shore crabs were slower to retreat during a simulated predator attack, although their ability to detect the predator and likelihood of responding was not affected (Wale *et al*., 2013a). Conversely, in addition to responding less rapidly, damselfish also respond less often to predators in the presence of noise (Simpson *et al.*, 2016). Furthermore, Voellmy *et al* (2014) demonstrated that, although they share similar predator ecologies, the predator response of two sympatric fish species was differentially affected by exposure to ship noise.

Anthropogenic noise, therefore, has the capacity to affect antipredator responses through a variety of mechanisms (e.g. acoustic masking, distraction, stress), affecting multiple species in different ways, regardless of which antipredator strategies they employ. This, coupled with the significance of implications associated with the disruption of such behaviours, highlights the importance of gaining a thorough understanding of how individuals across different species and life-stages may be affected regarding their antipredator behaviour.

Movement

In mobile species, movement is an important aspect of many crucial behaviours, and being able to move with unhindered fluidity can be vital for success. For example, many species, particularly invertebrates, must move between sites in order to leave nurseries or juvenile habitats and join adult populations (Dahlgren *et al*., 2006; Vasconcelos *et al.*, 2010). If movement is disrupted in any way (e.g. if individuals are slower, pause more frequently or movement becomes uncoordinated) then recruitment into the adult population may be reduced. Similarly, efficient movement can be crucial for successful reproduction, particularly when individuals must search for partners (DeRivera & Vehrencamp, 2001; Engelhaupt *et al*., 2009). Hindered movement may not only affect mate acquisition and reproductive success, but also individual survival if search time increases, as this increases exposure to predators (Pomiankowsklt, 1987).

Additionally, disrupted movement may have more direct consequences regarding predation risk if individuals are less efficient in their escape movement. Alternatively, if movement is increased, with individuals swimming faster, more regularly or pausing less often, then an individual's energy budget may be depleted more rapidly which can compromise other biological activities.

Investigations into the effect of noise on the movement/mobility of marine species is lacking, but studies are certainly warranted due to the aforementioned potential implications if altered. Noise has been shown to increase locomotor activity in spiny lobsters, suggested to be a form of disturbance response associated with the presence of a threat *(*Filiciotto *et al*., 2014). Alternatively, Wale, Radford and Simpson (2013a) theorise that, in shore crabs, the increase in pausing whilst feeding in the presence of shipping noise may be a result of increased vigilance. If this is the case, then the continuity of movement may be disrupted as well. Furthermore, noise-induced stress (Wale *et al.*, 2013b) could alter an individual's energy budget resulting in similar effects. Exposure to stressful situations has been known to change locomotor activity, reducing the extent of movement as well as individuals' orientation and speed (Mendl, 1999; Metcalfe, Huntingford, & Thorpe, 1987).

As well as fluidity and continuity, directionality is also an important aspect of movement. Many species use movement as a way of avoiding suboptimal conditions, by leaving an area either temporarily or permanently; the temporal scale of movement often depends on the type of stressor. When a harmful stimulus is intermittent in its occurrence, as is often the case with underwater anthropogenic noise, individuals might move away during periods of disturbance but return soon after. Evidence suggests this is often the case with marine mammals whose ranges overlap with areas undergoing seismic surveys (Castellote *et al.*, 2012) or piledriving (Dähne *et al.*, 2013; Würsig *et al.*, 2000). This temporary relocation allows species to remain in their environment in the long term without being severely impacted by periodic disturbances. In instances where the environmental stressor is constant however, the distribution of species may be altered to allow individuals to reside under conditions most closely resembling their original habitat (Perry, Low, Ellis, & Reynolds, 2005). This can lead to the permanent migration and displacement of individuals, populations or even whole species (Walther *et al.*, 2002), but would enable them to avoid exposure to unfavourable stimuli and minimise the harmful effects they would otherwise suffer.

In response to shipping noise, species could adopt this avoidance technique on either temporal scale (temporarily moving away or permanently migrating) due to the varied regularity and intensity of shipping activity across different locations, i.e. continually busy shipping lanes or ports could be abandoned entirely, but areas utilised less frequently by ships could simply be avoided while ships are present. For example, in response to the noisy conditions caused by leisure boat activity during the peak tourism period in Cres–Lošinj archipelago (northern Adriatic Sea, Croatia), seasonal displacement has been recorded in bottlenose dolphins (Rako *et al*., 2013), but in Shark Bay (Australia), where leisure boat activity is persistent throughout the year, there has been a long-term decline in bottlenose dolphin abundance (Bejder *et al.*, 2006). Few studies have been conducted to directly assess these avoidance practices in marine species, particularly in relation to noise from shipping, with current work focussing on marine mammals (e.g Richardson, Würsig & Greene, 1990; Bejder *et al.*, 2006; Rako *et al.*, 2013). Species not restricted physiologically to narrow regions or specialised conditions, with the ability to actively swim or move, certainly have the capacity to exhibit these behaviours. Understanding whether physical avoidance is implemented in response to anthropogenic noise, particularly from shipping activity, is vital to understanding not only how individuals will cope in the face of this pressure, but also how populations and whole ecosystems will look in the future regarding their structure and consequent success.

In some cases, repeated exposure to particular stressors enables individuals to develop a tolerance to such stimuli. Although existing literature on this is scarce, evidence suggests it can occur in response to elevated temperatures (Donelson *et al*., 2012; Tepolt & Somero, 2014) and ocean acidification (Form & Riebesell, 2012). Limited evidence indicates that this type of adaptation may also be possible in response to anthropogenic noise (Holmes *et al.*, 2017; Wale *et al.*, 2013b), but ultimately this remains unclear. As this may be the only strategy available for some individuals, particularly in instances where the type of movement described above is not possible, it certainly warrants investigation.

Invertebrates are understudied regarding noise pollution (Morley *et al.,* 2013), despite a heavy overlap in the frequency of anthropogenic noise and their hearing sensitivity. Here, we focus on the shore crab (*Carcinus maenas*), an intertidal species found in abundance along European coastlines. Previous work has demonstrated that noise from shipping can elevate stress levels (Wale *et al*., 2013b) and disrupt foraging and antipredator responses in adults (Wale *et al*., 2013a), in addition to the reduced camouflage ability and impeded growth of juveniles demonstrated in the previous chapter. Like adult shore crabs, juveniles rely on a physical escape behaviour to retreat to a shelter once detected by a predator. The effect of anthropogenic noise on this behaviour in juvenile shore crabs (and on juveniles in general (Peng *et al.*, 2015)) has not been studied, but as previously mentioned warrants specific investigation as the variety of mechanisms through which individuals can be affected by noise may result in differential effects across life-stages. Furthermore, their high mobility (relying on it for foraging, predator avoidance, and transference into adult populations), small size and directional sensitivity to noise (Popper *et al.*, 2001) makes them ideal for studying the effects of noise on movement in a laboratory setting.

Using a series of laboratory tank-based playback experiments, this chapter aims to explore the effect of ship noise on antipredation behaviour and movement (directionality, i.e. do individuals avoid noisy areas?, and fluidity) in juvenile shore crabs, and ascertain whether individuals develop a tolerance to ship noise with repeated exposure. Based on previous findings, I hypothesise that exposure to ship noise causes maladaptive behaviour in response to a simulated predator, with the speed at which individuals respond being reduced. Additionally, I test the hypothesis that ship noise disrupts the fluidity of movement and so individuals pause more frequently when moving. Furthermore, I test whether individuals actively avoid intense exposure to ship noise, spending less time in close proximity to and positioning themselves further away from the noise source. Finally, I hypothesise that juvenile shore crabs habituate to noise over time and consequently individuals who have been repeatedly exposed to the ship noise previously do not suffer the same negative effects as those experiencing it for the first time.

Methods

Ethical Note

All experiments were approved by the University of Exeter Bioscience ethics committee (applications eCORN000380 v2.1 and 2018/2495). All individuals used in these experiments were used in a prior experiment for 8 weeks (see previous chapter for details), and following testing all remaining crabs were returned unharmed to their original rockpool area at Gyllyngvase beach. Shore crabs are not a protected or endangered species and therefore no additional licences were required.

Experiment 1: Antipredator Behaviour

Experimental setup

The 115 individuals remaining at the end of the brightness change experiment (Chapter 2) were used in this experiment, including those that were not included in the analyses for the brightness change experiment because they did not consistently remain on the colour-change-inducing background. However, as they were still exposed to the noise treatment, they could still be used here. This afforded us the ability to compare responses between individuals based on their experience with noise, as 39 individuals had been exposed to the ship treatment for 8 weeks, 39 to the loud control treatment and 37 to the control treatment. Therefore, I could ascertain whether individuals had acclimatised to their noise treatment during this time. My prediction was that during the predator response experiment, individuals would not respond to their respective noise in the same way as those individuals hearing it for the first time.

The setup of the arena and general experimental procedure was adapted from that of (Wale *et al*., 2013a), who conducted a similar experiment on large adults. They demonstrated that shipping noise increases the time taken for individuals to retreat from a simulated predator. This knowledge meant this experiment could be used to test for acclimatisation as we already know that this behaviour is likely disrupted to some extent in individuals hearing shipping noise for the first time. Therefore, we could replicate this result and compare the response with that of individuals who had been repeatedly exposed to ship noise. The experimental arena measured 400x290x90mm. The base was coated with a thin layer of fine gravel (Sand Mix Aquarium Gravel, Pets at Home) varying in colour from cream to dark brown, broadly matching that of a natural rockpool. The varied intermediate colours reduced the likelihood that any individuals perceived themselves to be more/less threatened based on their level of background matching and therefore responded differently. At one end of the arena two large rocks were positioned which acted as shelter, under or behind which individuals could hide (Figure 1).

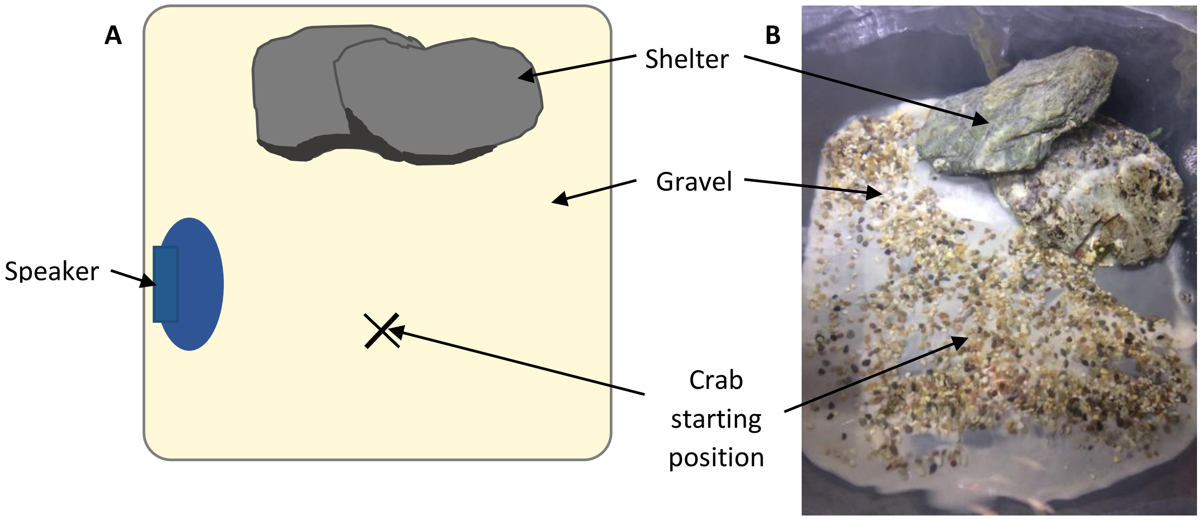


Figure 1: Diagram (A) and photograph (B) of the experimental arena used in experiment 1.

<u>Procedure overview</u>

Individuals were placed inside a plastic chamber in the centre of the experimental arena for one minute to acclimatise. After 15 seconds, the noise treatment - either one of the three control tracks, one of the three ship tracks or one of the three loud control tracks (see Chapter 2 methods for track details) - was started. At the end of the minute, the chamber was removed releasing the crab into the arena. Ten seconds later, a wooden dowel was plunged into the water in front of the individual three times consecutively, to simulate a predation attempt by a shore bird. Once this occurred, the amount of time it took for the individual to retreat to the shelter was recorded. For this to be the case, the individual’s full body and legs on at least one side of the body had to be under or behind the rock, and the individual had to remain there for three seconds. This was to avoid including instances where the individual was simply exploring the tank and walked along the edge behind the rock as a result. If the individual had not retreated within 60 seconds of the simulated attack it was recorded as not having retreated. During preliminary trials, individuals were given three minutes to retreat. Any individual that had not retreated after one minute failed to do so completely, and therefore this was set as the cut-off for the experiment. In addition, it was deemed that after this time, any positioning behind/under the shelter that occurred would not have been a direct response to the predator attack and therefore irrelevant.

The experiment was repeated three times for each individual; once for each noise treatment (ship, loud control or control). The order in which each individual was exposed to each noise treatment was randomised so that individuals did not undergo the three experiments in the same order. Individuals were left for three minutes between trials. The tracks used for each noise treatment were alternated, so individuals were not all exposed to the same sounds.

Statistical Analyses

All statistical analyses were carried out in RStudio (R v.3.4.3) (R Core Team 2017). GLMs were fitted to test for the effect of noise on whether or not individuals responded to a simulated predator and, for those that responded, the time it took them to retreat to a shelter. An interaction between noise and previous noise exposure (i.e. which treatment group they belonged to for 8 weeks prior to this experiment) was included to determine whether an individual's experience with noise determined how it responded to a particular noise treatment in the future, and consequently if individuals had acclimatised to ship noise and suffered reduced effects in the future as a result. Additional variables were controlled for, including a noise-size interaction, size, trial and audio track. The model simplification method was then used, removing non-significant terms in turn and comparing the model with and without (Crawley, 2011). Those that did not significantly affect the model's deviance were removed from the model entirely until the minimum adequate model was generated. A GLM with binomial family was used to determine the effect of noise on whether or not individuals respond to a perceived predator. Individuals that responded were assigned the number 1, and those that did not were assigned 0. When testing for differences in retreat time, only individuals that responded to the simulated predator were included in the analysis. A Cox proportional-hazard model was fitted to analyse the time taken and likelihood of retreating combined (Fox & Weisberg, 2011). The Cox proportional-hazard model is a form of survival analysis, analysing the effect of multiple factors simultaneously (in this case noise, size, audio track, trial number, a noise-size interaction and an interaction between current and previous noise treatment) on the rate of an event occurring, accounting for individuals for whom the event failed to occur (censored individuals) (Cox, 1972; 1984). The occurrence of retreating was set as the ‘event’, with ‘censored’ individuals being those that did not retreat from the simulated predator. The model simplification method was used as outlined above.

Experiment 2: Mobility and Movement (Noise Avoidance)

Experimental setup

The same individuals used in experiment 1 (predator response) were used in this experiment. As discussed previously, this allows comparisons to be made between the response of individuals based on their previous exposure to the noise and consequently any level of acclimatisation to be determined. As the individuals in the control noise treatment for the 8 weeks prior were only subject to the ship and loud control sounds for no longer than 1 minute 45 seconds during the predator response experiment, and this experiment was conducted at least 48 hours later, they were still considered to be ‘naïve’ and the treatments novel.

The experimental arena measured 1200 x 300 x 445 mm. The external surfaces were surrounded by sheets of polystyrene measuring 25 mm in thickness, apart from the base which was positioned on top of sheets with a thickness of 50 mm, to reduce the transmission of external noise into the tank. The internal tank walls were lined with bubble-wrap to reduce sound reflection. A thin layer of sand covered the base of the tank. A speaker was positioned at each end of the tank, so they were the greatest distance apart and faced the centre. A divider made of a fine-mesh was placed in front of each speaker to prevent individuals from approaching too closely and walking behind it. A piece of string the same length as the tank was attached to the base on each of the long edges, with 8 even sections marked out (Figure 2).

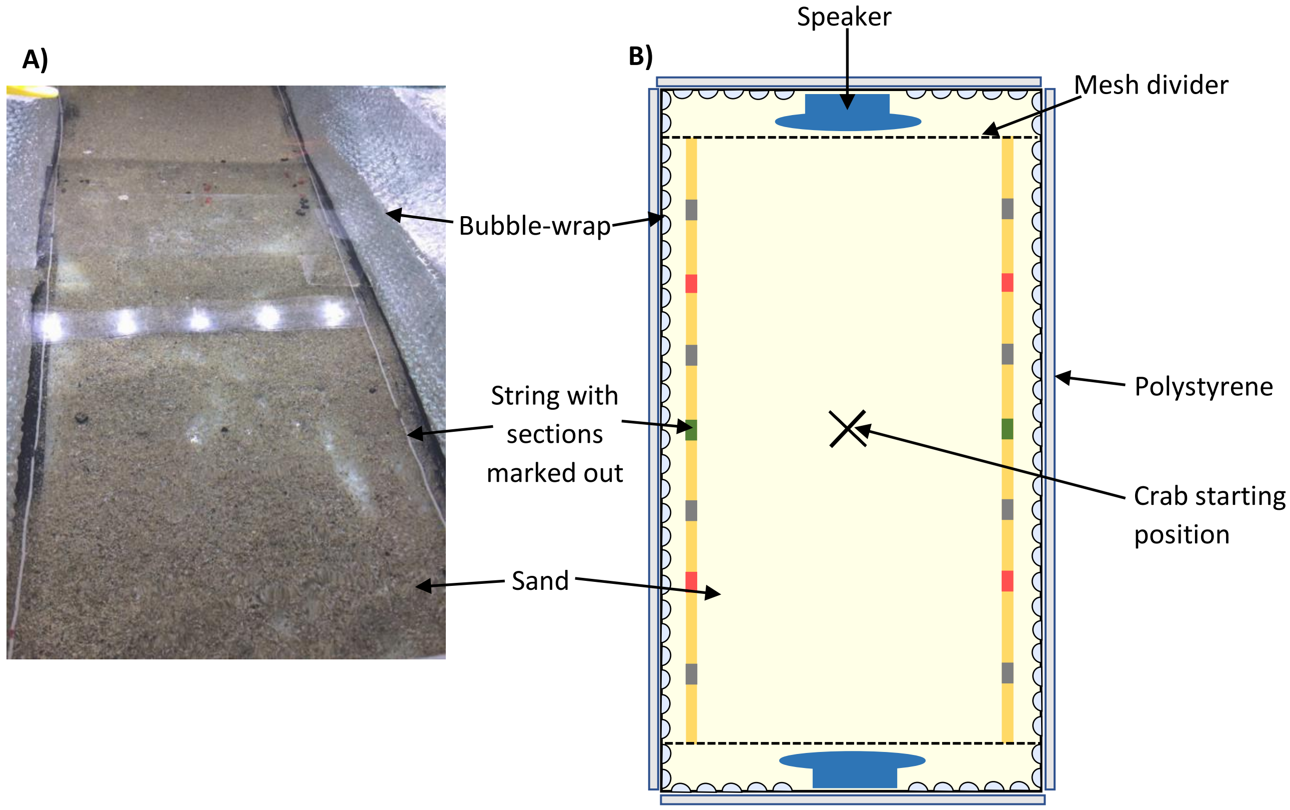


Figure 2: Photograph (A) and diagram (B) of the experimental arena used in experiment 2.

Noise Treatments

The same sound recordings used to create the tracks used in the previous chapter and in the predator response experiment were used here. For this experiment, the tracks created were 11 minutes in duration, with a 30 second fade in. To determine the sound level in the regions of the tank closest to the noise source, recordings were taken in front of the speaker through which the noise was playing. The hydrophone was not positioned immediately in front of the speaker, but instead was approximately 200 - 250 mm away, in the region within which the crabs would be closest to the noise. To determine the sound level furthest from the noise source, recordings were made in the same way, but in relation to the region at which they would be furthest from the noise, approximately 950 -1000 mm away.

(Figure 3). In both cases, the hydrophone was positioned in front of the mesh divider, at the closest point the crabs could position themselves. The WavStats function in Audacity 2.2.1.0 (www.audacityteam.org) was used to measure the amplitude (Table 1). Noise treatments were played at levels that matched that of the previous experiment at the closest point to the noise source so that crabs were never exposed to noise levels greater than that of the original ship recording. SPL measurements other than our measure of amplitude were not used as crustaceans mainly detect sound through particle motion rather than pressure. Calibrated measurements, such as those used by Wale, Radford and Simpson (2013), were unfortunately not available due to insufficient funds to purchase the necessary equipment and software (e.g. SPL meter, AviSoft) for this study. However, while this may pose some limitations in interpretation it is not a significant issue for our direct findings (see Discussion Chapter).

Table 1: Mean sound level *of each noise treatment closest to and furthest from the noise source, at points accessible to the crabs, as well as the original ship recording and the ambient noise level of the tank. RMS= Root Mean Squared Average; (A) = A-weighted; FS = relative to a full scale where the maximum possible amplitude is 0; Peak = maximum observed amplitude.*

Noise	*Distance*	*RMS (A) dBFS*	*RMS dBFS*	*Peak dBFS*
Control	Near	-92.8	-78.1	-62
	Far	-93.3	-77.9	-61.6
Loud Control	Near	-20.2	-21.1	-0.25
	Far	-44.8	-42.4	-19.1
Ship	Near	-17.2	-17.6	-2.7
	Far	-41.1	-40.1	-22.8
Original Ship Recording	~200m	-14.8	-13.6	-0.2
Ambient Level of Tank	N/A	-94.5	-77.3	-63.1

Procedure

Individuals were placed inside a plastic chamber in the centre of the tank for 2 minutes to acclimatise. The noise was gradually started after 1 minute, the animal was held for a further 1 minute until the noise had reached its full intensity. This was to ensure any response measured from the individual was not simply a startle response to the sudden onset of noise and was in response to the full measured noise level, not any of the softer initial intervals. After the full 2 minutes, the divider was removed, and the individual released into the tank. The individual's position within the tank (sections 1-8 as marked on the string, 1 being closest to the noise source, 8 being furthest away) was recorded every 30 seconds for 10 minutes.

Each individual was only assigned one noise treatment, of which they were exposed to one of the three tracks, so not all individuals assigned to the same noise treatment were exposed to the same sound. Treatments were assigned in such a way that one third of the individuals exposed to the ship treatment for 8 weeks before the experiment were exposed to the control, one third the ship and one third the loud control; and so on for the other two groups. Therefore, individuals of varying levels of experience were exposed to each noise. The noise was played through alternate speakers for each individual.

Statistical Analyses

All statistical analyses were carried out using RStudio (R v.3.4.3). GLMs were used to test for the effect of noise on each of the response variables used to measure noise avoidance and movement (given below). An interaction between noise treatment during the experiment and previous noise exposure was included to test for acclimatisation. If individuals developed a tolerance to the noise treatment they had been exposed to for 8 weeks prior to the experiment, then we would expect them to respond differently to this noise compared to those experiencing it for the first time. Maximal models controlling for relevant variables including trial number, audio track (i.e. which of the three ship noises, which of the three loud control noises and so on), size and a noise-size interaction were generated. The model simplification method was used, and non-significant variables were removed in turn and the model's deviance compared with and without. Terms that did not significantly affect the model's deviance were removed entirely until the minimum adequate model was created (Crawley, 2011).

Noise avoidance

The position in which an individual remained for the longest duration, with a minimum of three consecutive recordings, was considered its position of settlement. The proportion of time spent closest to the noise source (sections 1 and 2) was also calculated to establish whether individuals actively avoided the noise or were unbiased during their exploration of the tank.

Movement

The number of times an individual paused (remained in the same section for two or more consecutive recordings) and the proportion of time spent stationary (the proportion of recordings in the same position) were calculated to determine if movement was continuous or disrupted.

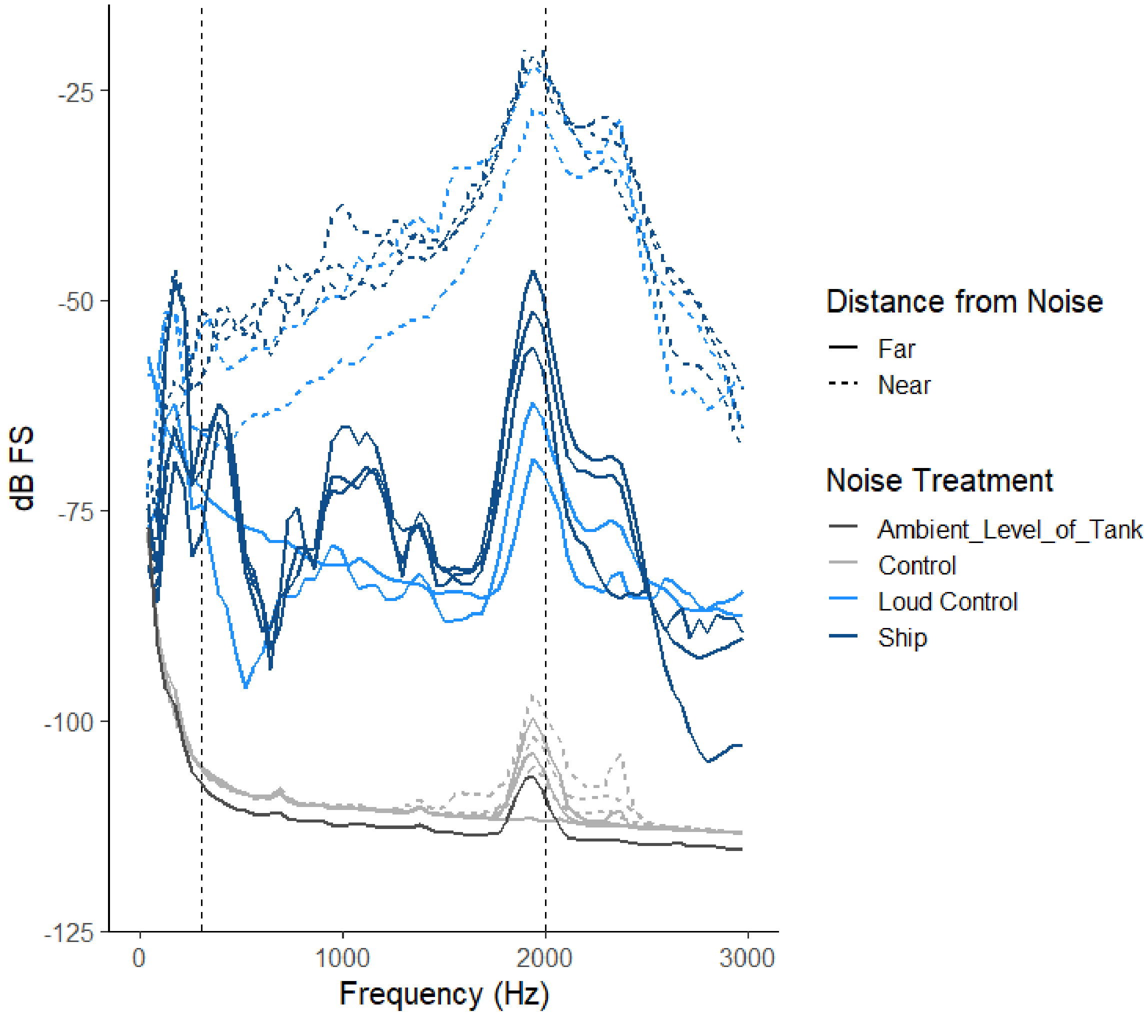


Figure 3: Average sound profile for the three noise treatments, both closest to the noise source and furthest from the noise source. Average power spectrographs are shown for recordings of the ship, ambient (control) and loud control playbacks, as well as ambient recording of the tank (FFT analysis; Hanning evaluation window, FFT size 1024). 'Near' recordings were taken in front of the speaker through which the noise was playing. The hydrophone was not positioned immediately in front of the speaker, but instead was approximately 250 – 300 mm away, at the furthest edge of the region within which the crabs would be closest to the noise. The 'far' recordings were made in the same way, but in relation to the region at which they would be furthest from the noise, approximately 950 – 1000 mm away. Dotted lines represent the estimated lower and upper bounds of crab frequency sensitivity *(*Salmon *et al.*, 1977*;* Horch,

1971). The total plot was cropped to enlarge and highlight this area, as anything outside of these bounds is highly unlikely to be detected by crabs.

Results

Experiment 1

Did individuals respond to the predator?

Noise affected whether or not individuals responded to a predator during a perceived attack (GLM with family binomial, $\chi^2_{(2,339)}$=43.9, p=2.88x10^{-10}), with those exposed to ship noise during the attack responding significantly less (Figure 4). These individuals only responded 62% of the time compared to 93% and 91% for individuals exposed to control and loud control respectively. An interaction between the noise treatment during the attack and the noise treatment individuals were exposed to for 8 weeks prior to the predator trial was originally included to understand if individuals are more/less likely to be affected by noise if they have been previously exposed and therefore if there is any level of acclimatisation. This was however removed from the model as it did not have a significant effect on the model's deviance ($\chi^2_{(4,324)}$=6.14, p=0.19). Therefore, there was no indication of acclimatisation as an individual's previous experience with noise did not affect the way it behaved in the presence of noise in the future. This means crabs were still affected by ship noise to the same degree even if they had been exposed to it previously, in this case for 8 weeks. A noise-size interaction, track, size and trial were also initially included but removed due to the lack of significance ($\chi^2_{(2,324)}$=1.06, p=0.59; $\chi^2_{(7,330)}$=6.65, p=0.45; $\chi^2_{(1,337)}$=1.80, p=0.18 and $\chi^2_{(1,338)}$=2.06, p=0.15 respectively).

Retreat Time

Individuals that did respond were significantly slower to do so if exposed to ship noise during the attack (GLM, $\chi^2_{(2,278)}$=31.09, p=5.19x10^{-11}; log-transformed) (Figure 5). The interaction between previous noise exposure and noise treatment during the attack did not affect the model's deviance ($\chi^2_{(6,261)}$=4.83, p=0.29), and therefore the interaction term was removed from the model. This indicates that individuals did not acclimatise to the noise, as those exposed to the ship noise for the first time during the attack were still affected to the same degree as those who had been exposed to the noise previously. A noise-size interaction, track and size were originally controlled for but removed as they did not significantly affect the model's variance ($\chi^2_{(2,267)}$=2.98, p=0.11, $\chi^2_{(7,269)}$=1.80, p=0.91 and $\chi^2_{(1,276)}$=0.001, p=0.97 respectively). Trial number significantly affected retreat time, with individuals in the first cohort being faster, and therefore remained in the model to control for this (GLM, $\chi^2_{(1,277)}$=11.02, p=4.18x10^{-5}).

Probability of individuals retreating

Noise significantly affected the rate of retreating during a perceived predator attack (Cox proportional-hazard, $\chi^2_{(2)}$=74.3, p<2.2x10^{-16}) (Figure 6). The hazard ratio of ship noise specifically was 0.30, meaning that, holding the other covariates constant, ship noise reduced the retreat behaviour by 70%. The hazard ratio refers to the effect size of the covariate. Trial also significantly affected this (Cox proportional-hazard, hazard ratio = 1.54, $\chi^2_{(1)}$=12.8, p=3.48x10^{-4}) and therefore was controlled for. The interaction between noise treatment during the attack and previous noise exposure was removed as it did not affect the model's variance ($\chi^2_{(6)}$=4.64, p=0.59). Therefore, there is no indication of acclimatisation. Size, track and a noise-size interaction were initially controlled for in the model but were removed as they did not have a significant effect ($\chi^2_{(1)}$=1.52, p=0.22; $\chi^2_{(7)}$=6.17, p=0.52 and $\chi^2_{(2)}$=0.087, p=0.96 respectively).

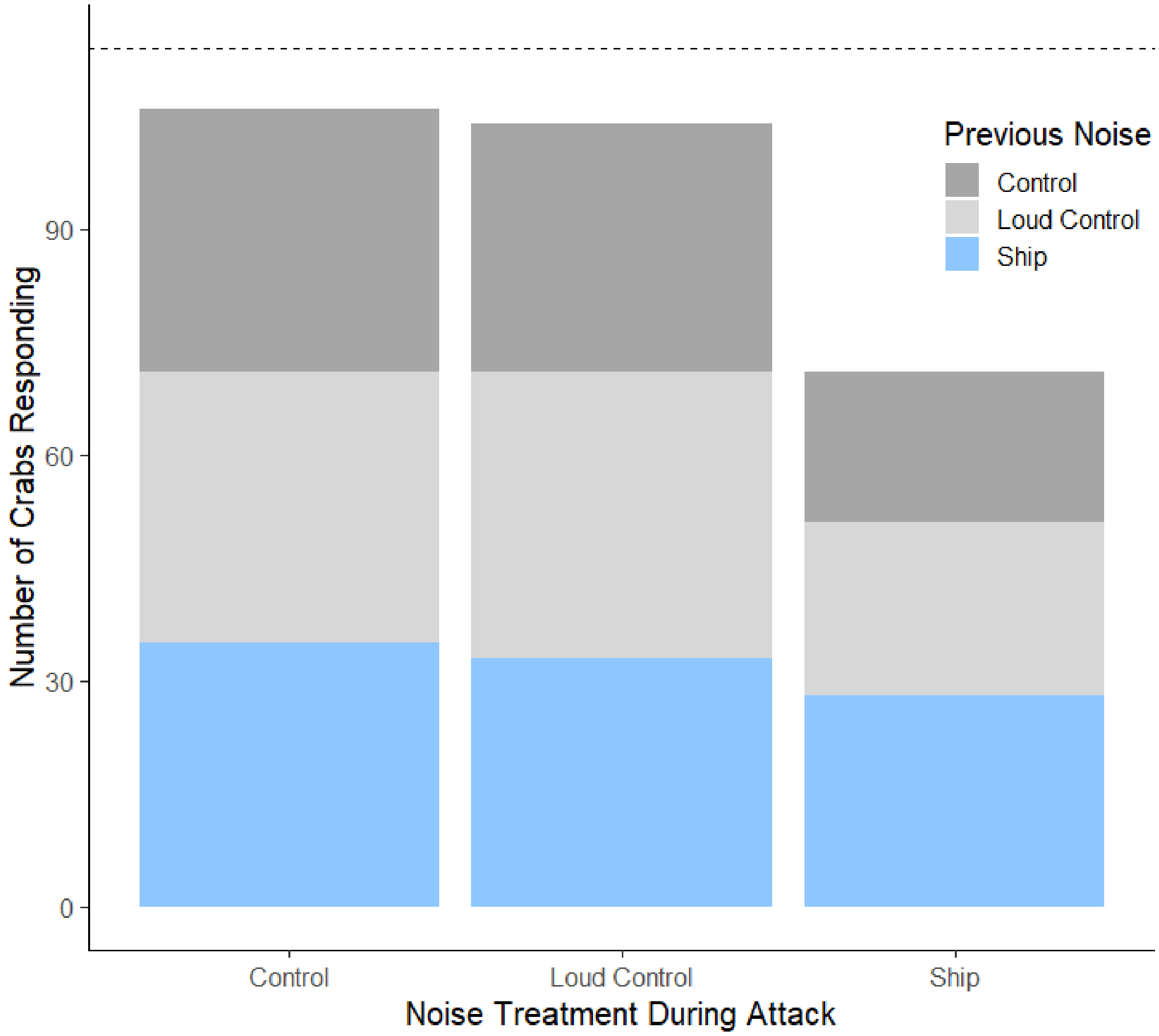


Figure 4: Fewer individuals responded to the predator attack when exposed to the ship noise during the predation attempt, but previous exposure to noise had no effect. Number of crabs retreating from the simulated predator when exposed to each noise treatment, separated within each group to show the number of individuals from each previous noise treatment. The dotted line represents the total number of individuals.

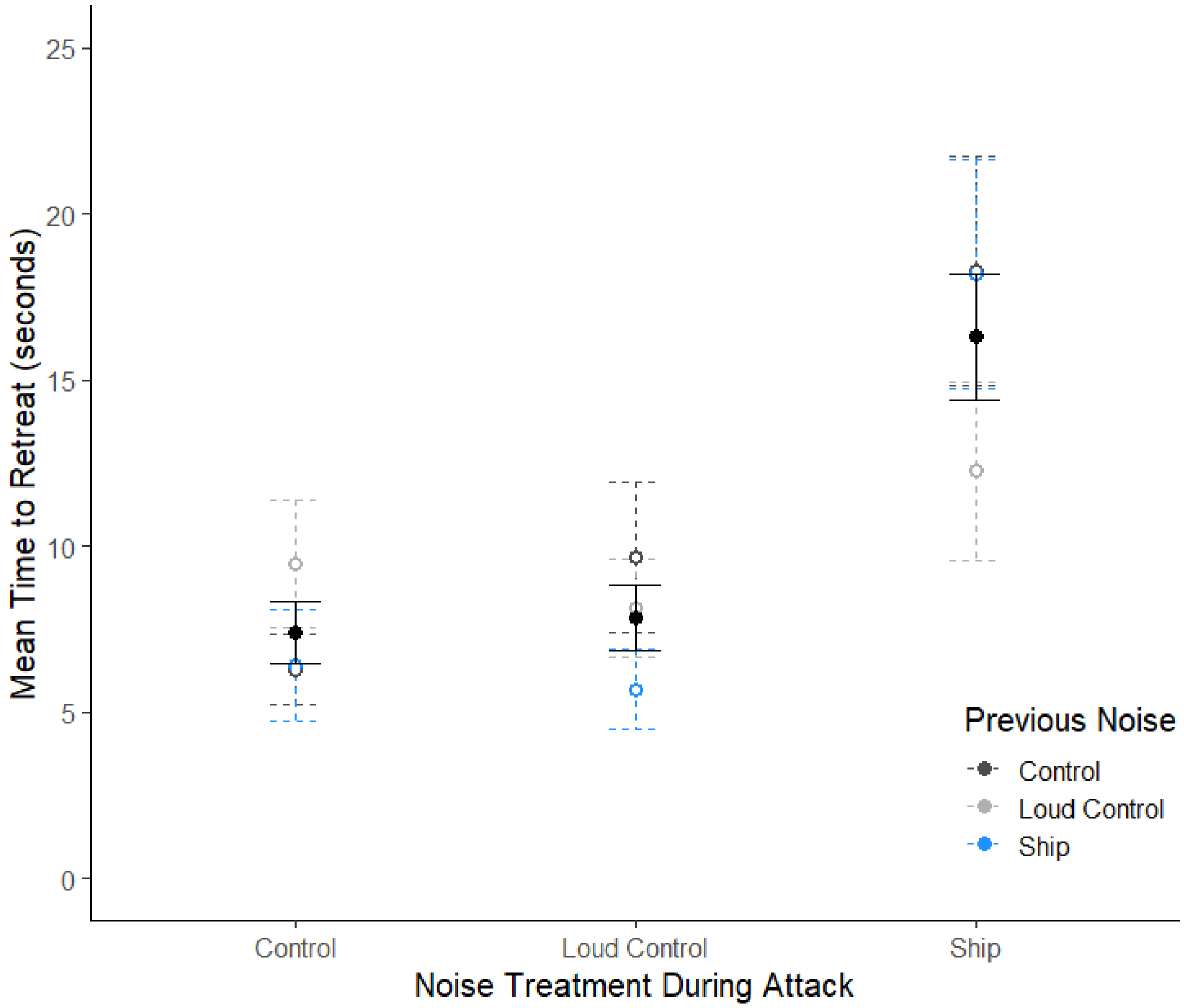


Figure 5: Among individuals that retreated from the predator, those exposed to the ship noise during the attack were slower to retreat, but their previous noise exposure had no effect. Mean time taken to retreat fully into the shelter among those individuals that responded, when exposed to each noise treatment during the attack, separated to show the previous noise treatments individuals were exposed to, with standard error. Black points represent the combined response of individuals across all three previous noise treatments.

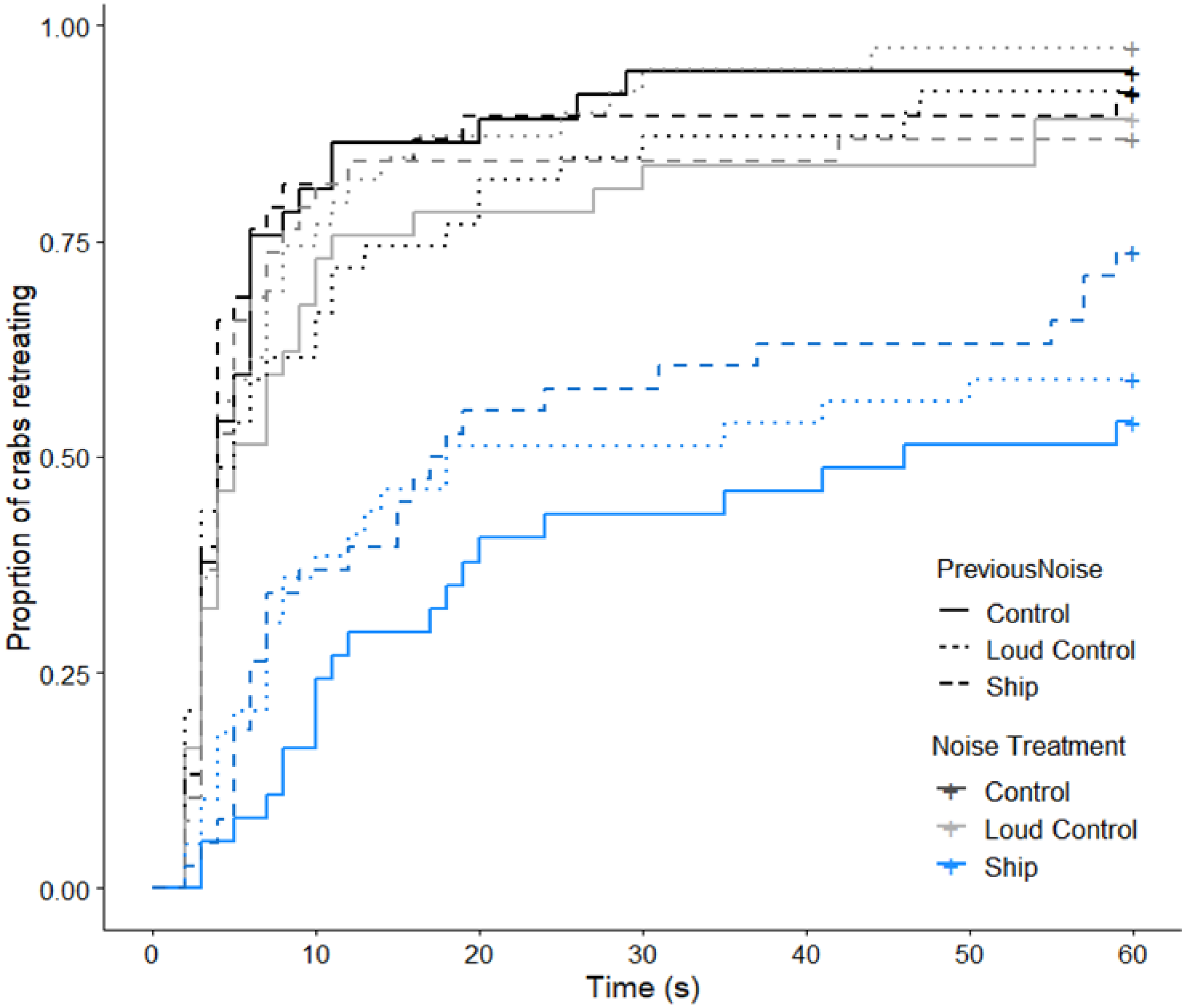


Figure 6: Exposure to ship noise during a perceived predator attack reduces the probability and rate of retreating, but previous noise exposure has no effect. A + at the end of a line indicates that group contains censored individuals (i.e. individuals that did not respond were removed).

Experiment 2

Noise Avoidance

Proportion of time nearest to noise

Noise did not significantly affect the proportion of time individuals spent closest to the noise source (GLM, $\chi^2_{(2,109)}$=0.70, p=0.13; arcsine transformed). There was also no evidence of acclimatisation as the interaction between noise treatment during the experiment and previous noise exposure did not have any effect on the proportion of time spent near the noise, nor on the model's deviance and was therefore removed from the model ($\chi^2_{(6,99)}$=1.10, p=0.38). A noise-size interaction, size, audio track and trial number were also controlled for originally but removed as they did not improve the model's deviance ($\chi^2_{(2,93)}$=0.17, p=0.61; $\chi^2_{(1,100)}$=0.02, p=0.72; $\chi^2_{(8,100)}$=1.22, p=0.52 and $\chi^2_{(1,108)}$=0.38, p=0.13 respectively).

Position of settlement

Noise significantly affected the settlement position of individuals during exposure (GLM, $\chi^2_{(2,109)}$=7.20, p=0.02), with those exposed to ship noise positioning themselves further away from the noise source (Figure 7). The interaction between noise treatment during the experiment and previous noise treatment was removed from the model as it did not affect the model's deviance ($\chi^2_{(6,99)}$=6.58, p=0.36). Therefore, there was no indication that individuals had acclimatised to the noise. A noise-size interaction, audio track, size and trial number were all included in the original model but removed as they did not affect the model's deviance ($\chi^2_{(2,93)}$=1.84, p=0.40; $\chi^2_{(8,99)}$=5.14, p=0.74; $\chi^2_{(1,107)}$=1.46, p=0.23 and $\chi^2_{(1,108)}$=1.46, p=0.23 respectively).

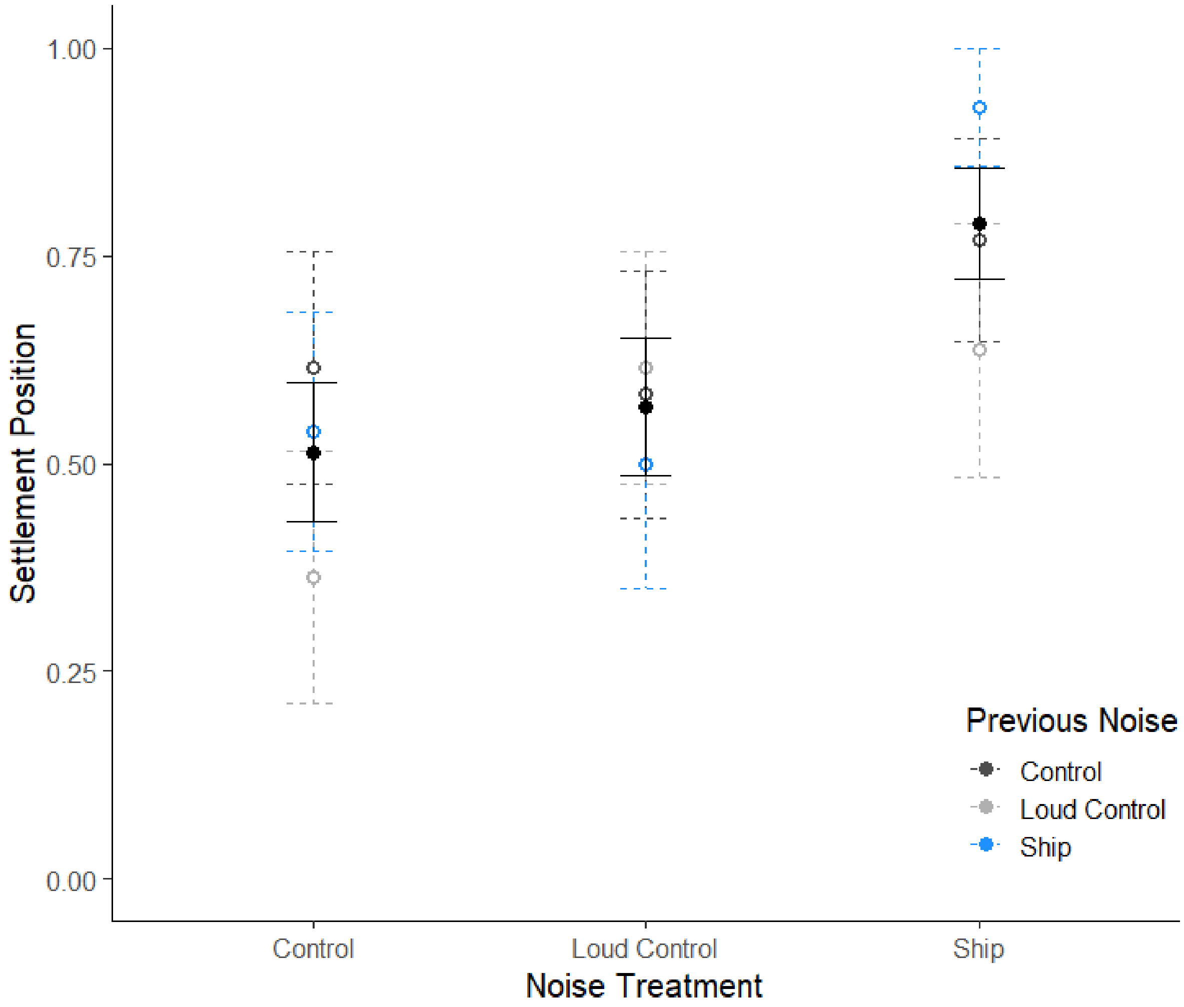


Figure 7: Individuals positioned themselves further away from the noise source during the ship noise treatment. Individuals responded in the same way regardless of their previous noise exposure. Mean settlement position during each noise treatment, with settlement position defined as the section in which individuals were recorded for the longest consecutive duration, with a minimum of 2 consecutive recordings. Settlement positions 1-4 were grouped and assigned 0 (close to the noise), positions 5-8 were grouped and assigned 1 (further from the noise) to generate a binomial distribution. Black points represent the combined response of individuals across each previous noise exposure group.

Movement

Number of times paused

Noise did not affect the number of times individuals paused whilst exploring the tank (GLM, $\chi^2_{(2,109)}$=0.64, p=0.73). The interaction between noise treatment and previous noise exposure did not significantly affect the model's deviance and was consequently removed ($\chi^2_{(6,92)}$=2.37, p=0.88). A noise-size interaction, track, trial number and size were all initially controlled for but each removed as they did not significantly affect the model's deviance ($\chi^2_{(3,90)}$=4.38, p=0.22; $\chi^2_{(8,98)}$=1.65, p=0.99; $\chi^2_{(1,106)}$=0.11, p=0.74; and $\chi^2_{(1,107)}$=3.24, p=0.07 respectively). The proportion of time spent stationary was controlled for as it correlates with the frequency of pausing (i.e. individuals that settled right away were stationary for a high proportion of time and therefore had little scope to pause frequently), (GLM, $\chi^2_{(1,108)}$=25.4, p=4.64x10^{-7}).

Proportion of time spent still

Noise did not significantly affect the proportion of time spent still (GLM, $\chi^2_{(2,109)}$=0.19, p=0.09). The interaction between noise treatment and previous noise exposure was removed from the model as it did not significantly affect the model's deviance ($\chi^2_{(4,92)}$=0.11, p=0.66). A noise-size interaction, trial and audio track were originally included but removed as they did not significantly affect the model's deviance ($\chi^2_{(2,90)}$=0.003, p=0.97; $\chi^2_{(1,96)}$=0.007, p=0.70; and $\chi^2_{(8,97)}$=0.02, p=0.99 respectively). Size and the number of times the individual paused were controlled for (GLM, $\chi^2_{(1,108)}$=2.09, p=4.40x10^{-12} and $\chi^2_{(1,105)}$=2.54, p=1.92x10^{-14} respectively).

Discussion

Despite not affecting mobility, individuals were slower to retreat from a simulated predator in the presence of ship noise, with many failing to respond entirely. The severity of implications associated with this diminished survival response necessitates a reduction in exposure to anthropogenic noise. This may be achieved through the avoidance of noisy areas, highlighting the importance of the avoidance behaviour demonstrated in this study, and consequently the significance of individuals being able to move unhindered in the presence of anthropogenic noise.

Exposure to shipping noise caused maladaptive behavioural responses in juvenile shore crabs. Prior to this study, Wale *et al*. demonstrated this in adults regarding their antipredator behaviour (Wale *et al.*, 2013a). Here I show for the first time that juveniles are similarly (and perhaps more severely) impacted, with an additional distinction between the effect (or lack of effect) of loud natural noise compared with that of ship noise. In adults, ship noise did not affect the likelihood of individuals responding to a predator, only the time it took for individuals to retreat (Wale *et al.*, 2013a). However, our study demonstrates that for juveniles both aspects of the response are adversely impacted, with individuals not only being slower to retreat from a simulated predator but also less likely to respond at all. The same effect was demonstrated in damselfish (*Pomacentrus amboinensis*) in the presence of boat noise, who were consequently captured more readily by their natural predator (Simpson *et al.*, 2016), highlighting the severe implications this disruption has for individual survival.

The differential effect of noise on the likelihood of adults and juveniles responding to a predator in the presence of ship noise suggests that juveniles may be affected through an additional mechanism, or simply more extremely. As the simulated predator carried no acoustic cues, an inability to detect the predator due to masking by the ship noise can be ruled out. Crustaceans have a limited capacity for paying attention (Dukas, 2002; Mendl, 1999), and therefore anything that may act as a distraction can take attention away from and consequently impede other behaviours (Chan *et al.*, 2010; Purser & Radford, 2011). Given their immaturity, juveniles may be more prone to distraction and therefore more strongly affected. Alternatively, noise causes stress (Wale *et al.*, 2013b) which is known to impair cognitive function, consequently diminishing decision-making and awareness (Berglund, 1993; Mendl, 1999). It is possible that juveniles experience stress more significantly than adults, consequently resulting in a greater magnitude of effects. Stress levels resulting from anthropogenic activity have not been directly compared between adults and juveniles, so it cannot be stated with certainty that this is the case. Previous work has demonstrated that certain environmental contaminants affect juvenile shore crabs but not adults, suggesting the existence of physiological differences between these life-stages

(Dissanayake *et al.*, 2008), which could account for the differential responses observed regarding antipredator behaviour in the presence of ship noise. Regardless of the mechanism through which it occurs, exposure to anthropogenic noise disrupted the antipredator response of juvenile shore crabs, completely diminishing it in some individuals, with serious implications for their survival.

Despite being slower in their physical retreat from a simulated predator, the fluidity of movement and locomotion was not disrupted in the presence of ship noise. However, individuals did show a directional preference. Actively favouring quieter conditions, as demonstrated here, will likely alleviate the additional pressures faced by individuals exposed to intense anthropogenic noise. However, physical limitations associated with this tank-based study restrict the extent to which we can extrapolate to the behaviour of wild shore crabs, particularly regarding the distance and frequency of movement. For example, it is unclear whether individuals attempt to permanently migrate to quieter areas or if they simply choose to move during noisy periods, returning soon after. Although both types of movement might serve to benefit the individual by affording them the opportunity to cope with anthropogenic disturbance, they can pose a variety of potential issues. If such movement is permanent, and individuals consequently migrate to a new area, this could lead to complicated community dynamics as species compositions will be altered both at the newly occupied and original sites (Berg *et al*., 2010; Francis, Ortega, & Cruz, 2009; Sorte, Williams, & Carlton, 2010). Additionally, if the movement is only temporary then individuals may be regularly expending additional energy (Masden, Haydon, Fox, & Furness, 2010). My study provides a basis for future work to investigate this further and ascertain whether individuals migrate permanently to quieter areas or simply move short distances in search of quieter conditions while ships are present, something which may be determined by the location of the individual and consequently the density of ship traffic.

In some cases, avoidance through movement may not be possible. This occurs when physical environmental barriers prevent individuals from moving (e.g. ocean currents or trenches, (Gaines & Bertness, 1992; Gaylord & Gaines, 2000)), when individuals are restricted to specific environmental conditions for their survival (Somero, 2002; 2005), or when individuals lack the mobility required to travel longer distances or move with a directional purpose (e.g. larvae or juveniles (Gaines & Bertness, 1992)). Therefore, although my results provide evidence that marine invertebrates can attempt to avoid noise through movement, it may not necessarily occur in a natural setting if environmental conditions prevent it. My results demonstrate however, that exposure to noise does not disrupt mobility in terms of its continuity, and therefore individuals may not suffer further movement restrictions as a direct result of exposure to noise.

I found no evidence to suggest that individuals acclimatised or developed a tolerance to noise as for each behaviour, all individuals were affected in the same way regardless of which noise treatment they had been previously exposed to. This is unsurprising as only a few studies suggest this transpires in the presence of anthropogenic noise, with the evidence often being limited or weak (Holmes *et al.*, 2017; Wale *et al*., 2013b). Although there may be several reasons for this, it is likely that the variability and intermittency of noise inhibits individuals from acclimatising or developing a tolerance (Wysocki & Gavin, 2006). It is possible that because of this, individuals may simply require more time or increased exposure to the stimuli to acclimatise. A study, similar to the one presented here, occurring over a longer time-frame could elucidate this further.

The lack of effects induced by the loud control treatment across all behaviours is consistent with my findings described in the previous chapter. This further confirms that many of the negative effects documented as a result of intense noise arise from exposure to anthropogenic noise in particular, rather than just additional noise to the environment. Of course in instances where behaviours are impeded as a result of acoustic cues and signals being masked, any form of additional noise above ambient levels could be responsible, although anthropogenic sources are often chronic and more disruptive (Clark *et al.*, 2009). Other mechanisms that alter behaviours and are brought on by noise (e.g. stress (Wale *et al*., 2013b)) are likely specific to anthropogenic noise.

It is possible that some of the noise treatment recordings from this study, particularly the ‘near’ recordings from the movement experiment, were taken in the acoustic near-field due to the relatively small size of the tanks. This refers to the sound field close to the sound source, where the sound pressure and acoustic particle velocity are not in phase. Therefore, soundwaves behave differently in the near-field compared to the far-field. In the acoustic far field, the sound field is much more stable as the soundwave propagation is more uniform. The mixture of circulating and propagating waves in the near-field means that accurately measuring sound intensity in the near-field is difficult without the use of multiple hydrophones. Therefore, measurements taken in the near-field with a single hydrophone may not be as reliable or repeatable as those taken in the more stable far-field. Therefore, comparisons between recordings taken in the near-field and those in the far-field should be made with caution as the exact difference in intensity between noise in these areas cannot accurately be determined using a single hydrophone. However, the measurements taken here do provide us with an indication that the level of noise furthest from the speaker in the movement experiment in chapter 3 was much lower than that nearest the speaker, suggesting that a difference in noise intensity is the reason for the directional preference of individuals, as all factors other than noise remained the same between these two areas.

Anthropogenic noise has become ubiquitous in the marine environment, with many species suffering effects potentially detrimental to their survival (e.g. Purser & Radford, 2011; Wale, *et al.*, 2013a; Kunc *et al.*, 2014; Nedelec *et al.*, 2014; Simpson, Purser & Radford, 2015; Spiga *et al.*, 2017). I have demonstrated that exposure to ship noise causes maladaptive behaviour in response to predators, but individuals remain unaffected by loud natural sounds. Furthermore, locomotion/mobility is unaffected by noise regarding its continuity, however, individuals move away from ship noise, actively avoiding intense exposure by settling at greater distances. Care should be taken when extending the results of a laboratory-based study to a real-world context, particularly when dealing with noise due to the differential propagation of sound in large open spaces compared to that of a tank. Furthermore, shore crabs likely detect sound through means of particle motion rather than pressure which could not be quantified here (Popper *et al.*, 2001). However, this study highlights that crustaceans are adversely affected by ship noise in many ways, but have the capacity to actively move away from sources of anthropogenic noise, potentially limiting the extent of negative effects they may be subject to. Further work is required to understand the extent to which this movement occurs, and consequently the effect this may have at the population and community level.

Chapter 4: General Discussion

The developing picture: overall findings and implications

This thesis explores the effect of anthropogenic noise on juvenile shore crabs, investigating a range of behaviours employed over different timescales to maximise survival in various situations. This includes both long and short-term luminance change for camouflage, antipredator behaviour, mobility, and avoidance of noise through movement. Exploring each of these behaviours in juvenile shore crabs allows us to not only understand the extent to which this species may be affected by noise pollution, particularly during this early life-stage, but also how other species that utilise the same survival strategies may be impacted. Invertebrates are often overlooked regarding noise pollution, as are juveniles in general (Peng *et al.*, 2015), but the results of this study when compared to similar work on adult shore crabs (e.g. Wale *et al.*, 2013) highlight the differential effect among life-stages and consequently the importance of assessing impacts across multiple demographics (including, for example, between sexes and populations). This is evident from the adverse effect on the likelihood of juveniles responding to a predator in the presence of noise but lack of effect in this regard in adults who utilise the same antipredator behaviour. Furthermore, it demonstrates the extent of negative effects suffered as a result of anthropogenic noise compared with loud natural noise, and the significant parts of the picture that may be missed if behaviours with no obvious link to acoustics are overlooked.

Predation

In the first chapter, I found that ship noise decreases luminance change and consequent levels of background matching, with an additional reduction in growth. This occurred within a relatively short time-frame as well as persisting over a longer time period. A reduction in camouflage of this sort will likely lead to an increase in detection by predators and consequent predation risk, as individuals may suffer a greater number of attacks (Bond & Kamil, 2002; Hultgren & Stachowicz, 2008; Stuart-Fox *et al.*, 2003). This amplifies the need for rapid detection and recognition of predators, as well as an efficient escape response following exposure to such threats. However, the results of chapter 3 clearly demonstrate that in the presence of ship noise juvenile shore crabs are slower to retreat and often fail to respond entirely to simulated predators, thus increasing their predation risk further. If juvenile shore crabs are more prone to detection and consequent attacks from predators, and are less likely to respond or flee, then it is possible individuals will have to rely on their physical defence to be successful in predator-prey interactions. In the first chapter, however, I found that in the presence of ship noise, individuals also suffered a reduction in growth. This may further hinder their ability to avoid predation as size plays an important role in predator avoidance, with larger individuals generally being more successful (Moksnes *et al.*, 1998). Therefore, this thesis has demonstrated that ship noise can adversely affect numerous aspects of the antipredator behaviour of juvenile shore crabs, from limiting their ability to camouflage themselves and avoid detection by predators to reducing their capacity to detect and respond to such threats. This has obvious, but potentially severe, implications for their survival, with the potential to alter recruitment and consequently affect the demography of impacted populations. If juvenile survival is reduced, then the number of juveniles developing and joining the adult population may decrease. This could result in a reduction in the number of receptive females, for example, and hence reproductively successful adults. Consequently, the ratio of juveniles to adults may become heavily skewed and the overall population may begin to decline.

Size-related activities

As previously mentioned, being able to grow to a larger size can be important for reducing predation risk, particularly in juveniles (Moksnes *et al.,* 1998). Size also plays a vital role in determining the outcome of aggressive interactions with conspecifics (Sneddon *et al.,* 1997) and, for adults, in various aspects of reproduction, including mate acquisition (Styrishave, Rewitz, & Andersen, 2004), with larger sized individuals often having greater success. If ship noise impedes juvenile growth, then individuals may be disadvantaged during the aforementioned activities when in competition with conspecifics that have not suffered the same negative effects of shipping noise. As juveniles often disperse (Moksnes, 2002), or as demonstrated in chapter 3, likely move away from noisy areas when feasible, it is possible they may encounter and compete with juveniles who have not been subject to the same level of anthropogenic noise. Similarly, upon recruitment into adult populations they may coexist with individuals from quieter locations who have consequently not experienced limited growth. Therefore, as well as the noise-induced stunted growth contributing to an elevated predation risk, it also has implications for individual success in conspecific interactions and competition.

Movement

The third chapter demonstrated that mobility is not disrupted by anthropogenic noise. There are several implications of this finding, the most obvious being the lack of disruption in this regard to behaviours with a strong movement component. This includes the noise avoidance behaviour also demonstrated in the third chapter, suggesting that individuals have the capacity to move away from anthropogenic noise without their ability to do so being physically hindered by it. Furthermore, a lack of disruption to mobility suggests that impeded movement is not responsible for the increased retreat time displayed in response to a predator attack when exposed to ship noise (Wale *et al.*, 2013a). The lack of disruption to mobility also has implications for camouflage and detection by predators. Although movement in general can increase detection and often render camouflage strategies such as background matching ineffective (Hall *et al*., 2013), regularly pausing and beginning movement again can increase the conspicuousness of individuals even further, making them more noticeable to predators. This is because the onset of movement attracts attention (Abrams & Christ, 2003). However, pausing was not increased in the presence of anthropogenic noise, and therefore although ship noise reduces the amount of luminance change and consequent levels of background matching, detection during movement will not be increased further by noise. Although this study demonstrates that individuals do not pause more in the presence of ship noise, mobility may be impacted by noise in other ways. For example, this study did not examine the speed or distance of movement, which have both been shown to increase in spiny lobsters (*Palinurus elephas*) as a result of ship noise exposure (Filiciotto *et al.*, 2014). Therefore, the prospect of anthropogenic noise affecting mobility cannot be ruled out entirely by the findings of this study.

Common trends

Other than mobility, ship noise adversely affected each behaviour assessed. The mechanisms involved in these behaviours and the way in which they were affected suggests that stress may be the primary pathway through which these effects occurred. For example, the reduction in luminance change, growth and likelihood of responding to a predator could all be induced by the physiological basis of a stress response, either through hormonal changes (Webster, 1996), alterations to the energy budget (Thompson & Bayne, 1974; Wale *et al.*, 2013b) or impaired cognitive function and awareness (Berglund, 1993; Mendl, 1999). If stress is largely responsible for these effects, then it is possible that this is something that may decline over time, consequently reducing the magnitude of impacts. Individuals exposed to stressful stimuli over prolonged periods of time have been shown to develop a tolerance, with their stress response gradually decreasing (Requena, Fernández-Borrás & Planas, 1997; Smith, 2004; Johansson *et al* 2016). Although we found no evidence of this during the experiments in chapter 3, it is possible that the period of exposure was not long enough considering the intensity, intermittency and variability of the stimuli. Additionally, as we were not testing the stress response directly, it is possible that this did decrease but some effects were a result of a different mechanism and therefore persisted. For example, distraction and consequent reallocation of attention may contribute to the impacts of noise on the antipredator response (Chan *et al.*, 2010; Dukas, 2002; Purser & Radford, 2011). This is something that may also reduce over time if individuals desensitise to noise, allowing their focus to remain on primary tasks, but the likelihood and extent of this occurring remains unclear. Juvenile damselfish (*Pomacentrus amboinensis*) have been shown to desensitise to boat noise over time, with behaviours that were initially affected returning to normal (Holmes *et al*., 2017). The mechanisms likely involved in the disruption of these behaviours vary and therefore indicate that it is possible for desensitisation or habituation to occur in this context as well as in terms of stress responses.

Another common theme throughout this thesis is the lack of effects on any behaviour elicited in individuals exposed to the loud control treatment. As this noise treatment had the same mean amplitude as the ship treatment, it is highly unlikely that this is due to individuals not being able to detect the sounds. As discussed in previous chapters, it is likely that this is at least in part due to the relative novelty of anthropogenic noise compared to natural ambient sounds, even of high intensities. Loud ambient sounds occur in nature, particularly along coastlines and in the intertidal zone where shore crabs reside, with wave action for example generating relatively high levels of noise (Coers *et al.*, 2008). Therefore, exposure to loud sounds of natural origin is unlikely to be a new experience, and it is widely accepted that often a large proportion of negative effects associated with external stressors arise initially when individuals are unfamiliar with the stimuli. This distinction between the effects of loud natural sounds and anthropogenic noise has, to the best of my knowledge, not previously been made and should be considered in future studies as it may help to disentangle the effects of additional noise in the environment from that of anthropogenic noise in particular.

Limitations

As this was a laboratory-based study, with all experiments conducted in artificial tanks, care must be taken when extrapolating the results to individuals in the wild. Although measures were taken to increase the authenticity of the experimental arenas, both in terms of the physical structure and topography and the abiotic conditions (e.g. light, salinity etc.), certain factors limit the extent to which this is possible. Most prominently, the size of the tank restricts the extent to which the noise treatments will reflect that of a natural setting as sound propagates differently in open expanses of water compared to small enclosed spaces (Pan, 2012).

Although measures were taken to reduce acoustic reflection and reverberation within the tank (e.g. the use of bubble-wrap to line the walls), due to the shape and size of the experimental arenas, it is possible that these were still present. This may consequently have ramifications on the findings of this study. Firstly, certain frequencies will have longer reverberation times, so individuals may be exposed to these for longer. If a certain frequency is dominant in one treatment more than the other, then this could affect how an individual responds to a particular noise treatment. Similarly, acoustic reflection can result in the amplification of certain notes (constructive interference) but can cancel out others (disruptive interference), distorting the sound. This may make sounds appear less favourable resulting in stronger adverse effects or alternatively could soften certain aspects that individuals would normally respond negatively to, consequently reducing adverse effects. Therefore, either disruptive or constructive interference from acoustic reflection could cause individuals to respond differently to the noise than they otherwise would. Finally, if any documented effects were as a result of reverberation or acoustic reflection, rather than the noise treatment itself, then this reduces the applicability of the results to any real-world scenario, as in situ, the nature of the open ocean means that reverberation and acoustic reflection will only be slight. However, as previously discussed in the methods, measures were taken to reduce both issues (e.g. walls lined with bubble-wrap to eliminate parallel flat surfaces that can result in distortion and standing waves), so any of the aforementioned possible ramifications of acoustic reflection or reverberation should be minimal. This can be seen when comparing the spectra of the noise treatments and ambient noise of the tanks (Chapter 2, Figures 2; Chapter 3, Figure 3).

A lack of calibrated noise measurements can come with limitations regarding our ability to interpret the data in a real-world context, because we cannot easily compare the noise levels of these noise treatments with that found in the ocean. Therefore, we cannot say with certainty how extensive/strong the effects of our noise treatments would be *in situ*. Similarly, the noise levels we have are not directly comparable to that of other studies that have used calibrated recordings; since the measurements are not analogous it creates limitations in trying to directly compare results. For example, we cannot say for certain how similar the levels of noise in this study were in relation to that of the antipredator experiment conducted by Wale, Radford and Simpson (2013). In this case, we cannot determine which study uses sounds of higher intensity, or if the studies in fact use similar intensities. Therefore, we can only speculate possible reasons for the discrepancies between the results presented here and the results of Wale, Radford and Simpson, as it is possible there is a difference in noise level that we cannot determine which may be responsible.

There may also be difficulties when attempting to compare the results of this study with that of future studies exploring similar avenues, e.g. if a future study investigates the effect of alternative sources of noise on colour change/camouflage it may not be possible to directly control for or compare the sound intensities and consequently the results. However, the results of this study still unambiguously confirm several effects of noise, and consequently provide a basis for future investigations, opening a new avenue of research that otherwise may not have been explored. In addition, answering the question of what levels of ship noise crabs would perceive in the wild is far from simple – this will depend greatly on the local environment, the type of ship, and the distance of the ship to the crab, all of which will have enormous variation in nature. Therefore, just as with previous work (Wale et al. 2013), our study shows that anthropogenic ship noise has the potential to be detrimental to crabs in multiple ways, but as with any research, only *in situ* experiments or a large number of studies directly replicating a sample size of real-world locations and noise scenarios can reveal to what extent wild crabs will be affected across sites.

Furthermore, crustaceans likely detect the majority of sounds in the environment through means of particle motion rather than sound pressure (Popper *et al*., 2001), therefore, directly measuring particle motion may be more ecologically relevant. However, the ability to do this is hampered by the availability and accessibility of instruments capable of this, and therefore many studies use some measure of sound pressure level or amplitude instead (e.g. Chan *et al.*, 2010; Wale *et al.,* 2013a; Filiciotto *et al.*, 2014, 2016). The measures used in this thesis are sufficient in allowing a comparison between the intensity of noise treatments and that of the original ship recording for real-world context, as well as a comparison among noise treatments to confirm the similarity between the anthropogenic noise and the loud natural noise in this regard.

Future Research

Although this thesis addresses several knowledge gaps, substantial uncertainty regarding the true extent of impacts of underwater noise pollution still remains, and many of the findings presented here give rise to further questions. Perhaps the most prominent in this respect is the strong effect of ship noise on luminance change and consequent camouflage. This disruption brings into question the success of a vast number of other behaviours in the presence of anthropogenic noise that may have otherwise been overlooked due to a lack of obvious connection to acoustics. The focus of future research needs to be unbiased in this respect and prioritise behaviours with the most significance regarding survival and success, and consequently most severe implications, rather than behaviours that simply involve an acoustic component. For example, a range of antipredator behaviours are used across different species, with varying levels of acoustic reliance. However, all are important for survival and therefore should be examined with equal priority regarding noise pollution.

Although the most prominent colour change behaviour utilised by shore crabs is the relatively slow change in luminance to match the substrate, a range of colour change strategies are used by decapod crustaceans, as well as a multitude of other marine taxa, to promote survival. Ghost crabs (*Ocypode ceratophthalmus*) display a circadian rhythm of luminance change to enhance camouflage as the lighting conditions change (Stevens *et al*., 2013), chameleon prawns (*Hippolyte varians*) change from either red, green or transparent during the day to blue in colouration at night (Keeble & Gamble, 1900; Kleinholz & Welsh, 1937), and fiddler crabs (*Uca.*) change in luminance to become darker during the day to function in UV protection (Darnell, 2012). Other marine species undergo more rapid changes in their colouration and patterning, typically mediated by electrical impulses, to serve a variety of functions. For example, cuttlefish (*Sepia officinalis*) utilise this to aid in communication and camouflage (Chiao *et al.*, 2011; Holmes, 1940) and rock gobies (*Gobius paganellus*) rapidly change their luminance and patterning when on patterned backgrounds to break up their body outline and reduce detection by predators (Smithers *et al*., 2017; Stevens, Lown, & Denton, 2014). Although the mechanisms driving these strategies vary based on the temporal scale over which they occur (e.g. change over hours/days/weeks is generally mediated hormonally, whereas rapid change over seconds/minutes tends to occur via nerve impulses (Duarte *et al*., 2017)), they may carry similar levels of energetic costs and are implemented by species with similar auditory capabilities and hearing sensitivities (Kaifu, Akamatsu, & Segawa, 2008; Ladich & Popper, 2004; Popper *et al*., 2001). Therefore, this thesis has demonstrated that they also have the potential to be affected by anthropogenic noise. Hence, research exploring these types of changes in the presence of anthropogenic noise, in addition to other environmental stressors, is certainly warranted, particularly those involved in camouflage as this may have direct survival consequences if impeded.

It is clear from this thesis, as well as previous work, that the antipredator responses of several species are adversely affected by anthropogenic noise (e.g. Chan *et al.*, 2010; Wale, *et al.*, 2013a; Spiga *et al.*, 2017). However, to understand the full extent of implications associated with this, predatory behaviours must also be examined in this context. For example, as well as suffering predation attempts from shore birds, shore crabs are also attacked by fish and shrimp (Moksnes *et al.,* 1998; Moksnes, 2002). The latter will be exposed to the same levels of anthropogenic noise as the shore crab and consequently their behaviour may also be adversely affected. If this is the case, then during predator-prey interactions, as well as the prey not responding as efficiently, the predators may not be as capable regarding their attack. Voellmy *et al.* (2014) demonstrated that in the presence of anthropogenic noise, the foraging behaviour of two sympatric fish species on live prey was adversely affected in two different ways. Minnows (*Phoxinus phoxinus*) shifted away from the foraging behaviour altogether, becoming more inactive and partaking more in social behaviour, whereas sticklebacks (*Gasterosteus aculeatus*) maintained their foraging effort but made more mistakes (Voellmy *et al*., 2014). Alternatively, another study found that damselfish mortality increased in the presence of boat noise as their response to a natural predator was reduced (Simpson *et al*., 2016), suggesting that the predator was either unaffected by noise exposure or was not affected severely enough to counteract the reduced response of the prey. Therefore, it is possible the effect of noise on predatory behaviour varies across species, with some experiencing a reduction in foraging ability in the presence of noise and some potentially benefitting from noise exposure if they remain unaffected but their prey suffers negative impacts. It would be beneficial to directly examine the effect of noise on the predator-prey interaction itself, assessing the behaviour of both the prey and predator simultaneously, and consequently the relative success of each role. Identifying a reduction in the behaviour on one side of the interaction only tells half a story and cannot indicate with any certainty the outcome of such interactions (and consequently the likelihood of prey mortality or predator starvation) unless the effect on both sides is understood.

Another important avenue for future research follows on from the results of the third chapter that demonstrate juvenile shore crabs have the capacity to avoid noisy areas through movement. This is particularly important as human activity in the marine environment is ubiquitous, and the demand for many of the activities is so high, meaning it is unlikely our presence in the ocean, and consequently the high levels of noise associated, will subside in the near future (Kaplan & Solomon, 2016). Attempts to limit or contain the amount of noise produced (e.g. through quieter engines in shipping vessels (Rao, 2002)), are underway but these advances are slow, and it could be some time before any new technologies that soften sound, or policies that limit its presence, are implemented as global mandates (IMO, 2013). Therefore, the pressure falls to species and individuals to compensate for or counteract the negative effects imposed on them.

The avoidance behaviour demonstrated in this thesis is one possible strategy through which this may be achieved. However, it is unclear whether this type of avoidance results in individuals permanently abandoning a site and migrating, or if individuals move temporarily and return once the noise has ceased. Although both strategies may mitigate the harmful effects of ship noise, they each come with potential issues. For example, additional regular movement can impose added energetic costs on individuals (Masden *et al.*, 2010), or leave them exposed to predators more frequently or for longer periods. In cases where anthropogenic noise is a permanent feature of the area, the distribution of species or populations may be altered to allow individuals to reside under conditions most closely resembling their original habitat, as is often the case in response to elevated temperature for example (Perry *et al.*, 2005). This can lead to the permanent displacement of individuals, populations or even whole species (Walther *et al.*, 2002). Although this enables individuals to avoid exposure to unfavourable stimuli and minimise the harmful effects they would otherwise suffer, permanent forced migration can also lead to potential problems. The structure and dynamics of the community both at the newly occupied and original sites are likely to change (Berg *et al.*, 2010; Francis *et al.*, 2009), and in some instances species forced to relocate may act as invasive species (Rahel & Olden, 2008; Sorte *et al.*, 2010). This can result in competitive exclusion, niche displacement and behavioural shifts (Mooney & Cleland, 2001; Sakai *et al.*, 2001). Therefore, it is not only imperative to understand if noise avoidance occurs in a natural setting, but also the frequency and extent to which this occurs and what factors may affect this. This will consequently elucidate the likelihood of individuals avoiding intense exposure to anthropogenic noise and consequently their future prospects for survival. Furthermore, determining the temporal scale over which individuals move away from noise (e.g. temporarily or in forced migration), if at all, may allude to the future composition, structure and consequent success of populations, communities and even whole ecosystems.

Alternatively, individuals have been known to acclimatise and develop a tolerance to certain stressors, reducing the severity of negative consequence (Berg *et al.*, 2010). Existing literature on the latter is scarce, but evidence does exist suggesting it can occur in response to temperature increases (Donelson *et al.*, 2012; Tepolt & Somero, 2014) and ocean acidification (Form & Riebesell, 2012). Although I found no evidence of this occurring in response to ship noise, further work exploring this is warranted as individuals may simply require more time to acclimatise due to the intermittency and variability of the noise. Furthermore, if the factors required to induce acclimatisation can be understood (i.e. the frequency or duration of exposure), then this could inform policies regarding anthropogenic activity to attempt to promote acclimatisation and consequently reduce the negative impacts. This is particularly important for species whose mobility or physiological requirements may restrict them to specific regions, or those whose movement may be hindered by physical environmental barriers.

Reducing the problem at the source: limiting the intensity of noise pollution

It is entirely possible for us to relieve some of the pressure faced by marine ecosystems and reduce the necessity for acclimatisation or the physical avoidance of certain areas. This could be achieved in a variety of ways. For example, quieter shipping vessels would limit the intensity of noise produced and consequently experienced by individuals. Quieter engines are being developed through the use of wake flow devices and energy saving devices which may ultimately increase propeller efficiency and reduce cavitation (a large contributor to ship noise) (Leaper *et al.,* 2014; Rao, 2002). Evidence also suggests noise could be reduced by simply reducing vessel speed (Leaper *et al*., 2014; Veirs, Veirs, Williams, Jasny, & Wood, 2018). However, transitioning to a state where the use of noise-reducing devices and practices (i.e. speed alterations) is common practice would likely be a slow process due to the number of stakeholders within the shipping industry as well as the sheer quantity of vessels and cost of replacing or updating them.

Alternatively, quiet zones could be implemented. Marine Protected Areas (MPAs) are already in existence, but the total area encompassed by these is dwarfed by the areas burdened with human activity. Many of these sites still lack sufficient protection and few lie in international waters where there is no national jurisdiction or governance (Juffe-Bignoli *et al.*, 2014). Furthermore, the location and relatively small size of some MPAs means even if individuals reside within the boundaries, they will likely be exposed to high levels of noise. For example, the Miramare MPA in the Gulf of Trieste is surrounded by high levels of human activity, with the city of Trieste less than 8km away, bringing in more than 48 million tonnes of ship traffic per year. Evidence suggests that ship traffic at the periphery of this MPA can increase noise levels within the reserve and adversely affect the species present (Codarin, Wysocki, Ladich, & Picciulin, 2009). Therefore, the current use of MPAs does not necessarily encompass protection from anthropogenic noise. This could however be achieved through the use of buffer zones around the perimeter. If activity within these buffers were kept to a minimum and noise levels at the periphery were consequently regulated then this would limit the amount of anthropogenic noise penetrating the reserve (Codarin *et al.*, 2009; Williams *et al.*, 2015; Wright, Deak, & Parsons, 2011). In order for such zones to be effectively implemented, it is important we first understand which species and behaviours are affected, as well as which frequencies, noise sources and intensities are responsible, and consequently the level of sensitivity and vulnerability of species and ecosystems (Zacharias & Gregr, 2005). This can help to identify the most appropriate locations and sizes of both the protected area itself and the buffer zones, as well as policies for activity within the buffers.

Similarly, legislation restricting the number of vessels and/or noise within certain areas or along traffic routes could be introduced, forcing companies to adopt quieter practices, or the traffic routes themselves could be altered or diverted to ensure minimum disruption (NOAA 2012; Silber *et al.*, 2012; Roman *et al.*, 2013).

Implementing new legislation can be difficult, particularly when it involves the marine environment due to the political complexities regarding international regulations and a number of stakeholders (e.g. governments, shipping companies etc.) (Firestone & Jarvis, 2007; Lister, Poulsen, & Ponte, 2015). It is often hard to enforce such laws and there can be a strong lack of compliance (Lister *et al.*, 2015; Roman *et al*., 2013). Extensive research and evidence demonstrating the severity of consequences associated with underwater noise pollution may be the most effective way of ensuring such policies are introduced and respected.

In order to implement the best practices regarding anthropogenic activity in the marine environment it is imperative we have a comprehensive understanding of the extent to which individuals are impacted by noise pollution and if/how they are able to mitigate these effects themselves, whether that be through avoidance or developing a tolerance. This could be achieved further through experiments like the ones presented in this thesis, or from the future research suggested above. This understanding will go a long way toward the sustainable management of marine ecosystems as it will assist in determining the most appropriate locations for anthropogenic activity so the least disturbance is caused, encourage the use of the least disruptive equipment (e.g. quieter vessels), and inform effective legal restrictions in order to maximise survival and minimise disturbance across as many individuals and species as possible.

Concluding Remarks

Underwater noise pollution has the potential to affect several aspects of a population, community and even entire ecosystems, including predator-prey interactions, demographics, structure and dynamics. The interconnectedness of the affected behaviours and activities means understanding the full extent of impacts and broader consequences is difficult, with many species and behaviours being affected in different ways through different mechanisms. It is, however, abundantly clear that noise pollution is not a problem simply faced by those reliant on acoustics and therefore should not be treated as such. Behaviours important for survival, including colour change for camouflage and response to predators as demonstrated in this thesis, can also be adversely affected, despite no obvious link to acoustics. Therefore, activities like this are worthy of investigation in the context of noise pollution regardless of their relationship with the auditory system. It is imperative we work to limit noise in the oceans, as it remains unclear whether individuals will be able to acclimatise to such, and the consequences of species avoiding noisy areas are unknown but may be extreme.

Appendices

Appendix A: Preliminary Trial Results

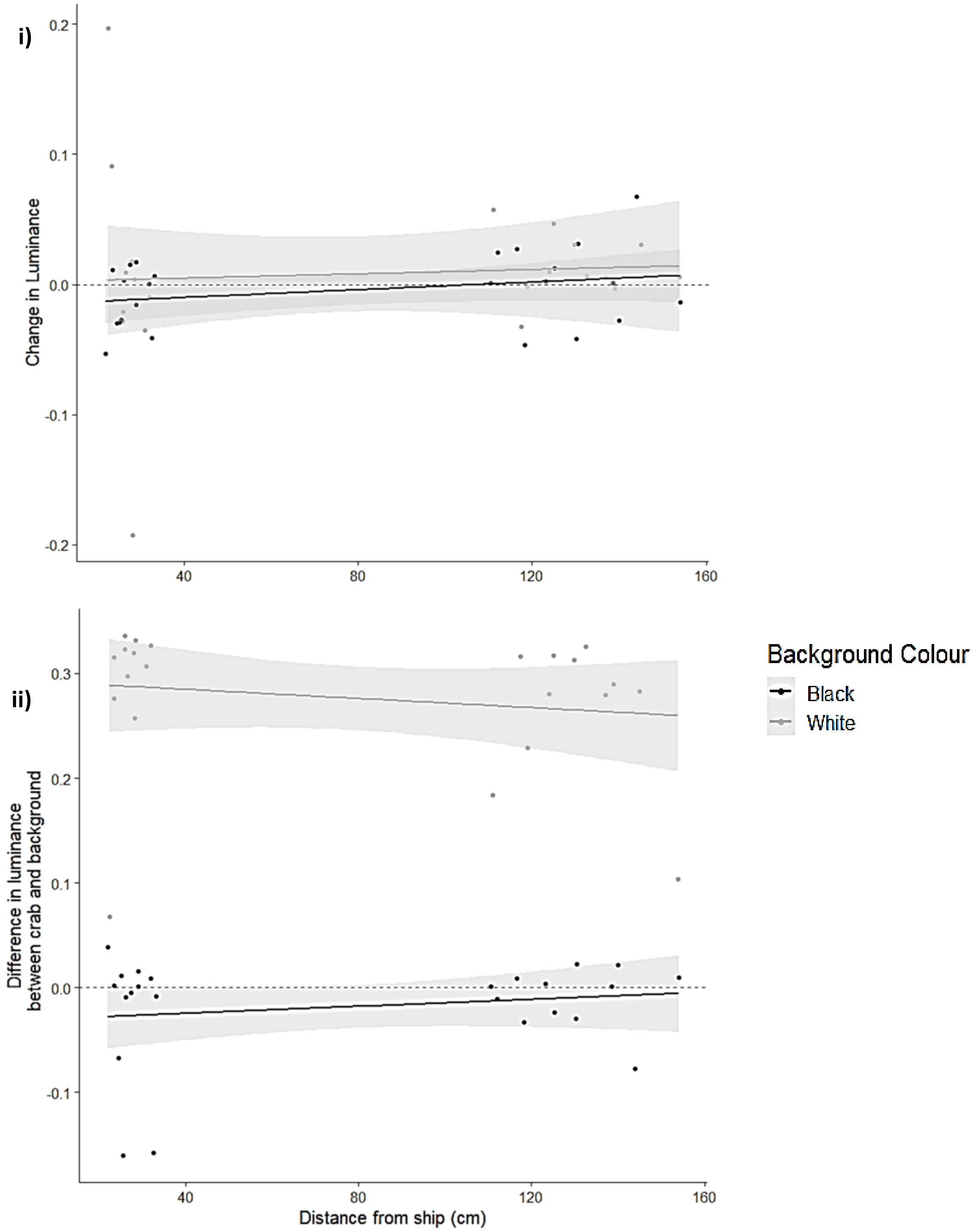


Figure A1: 24 hours. Luminance change (i) and consequent background matching (ii) after 24 hours, in relation to the distance from the shipping noise source, with individuals separated based on background colour.

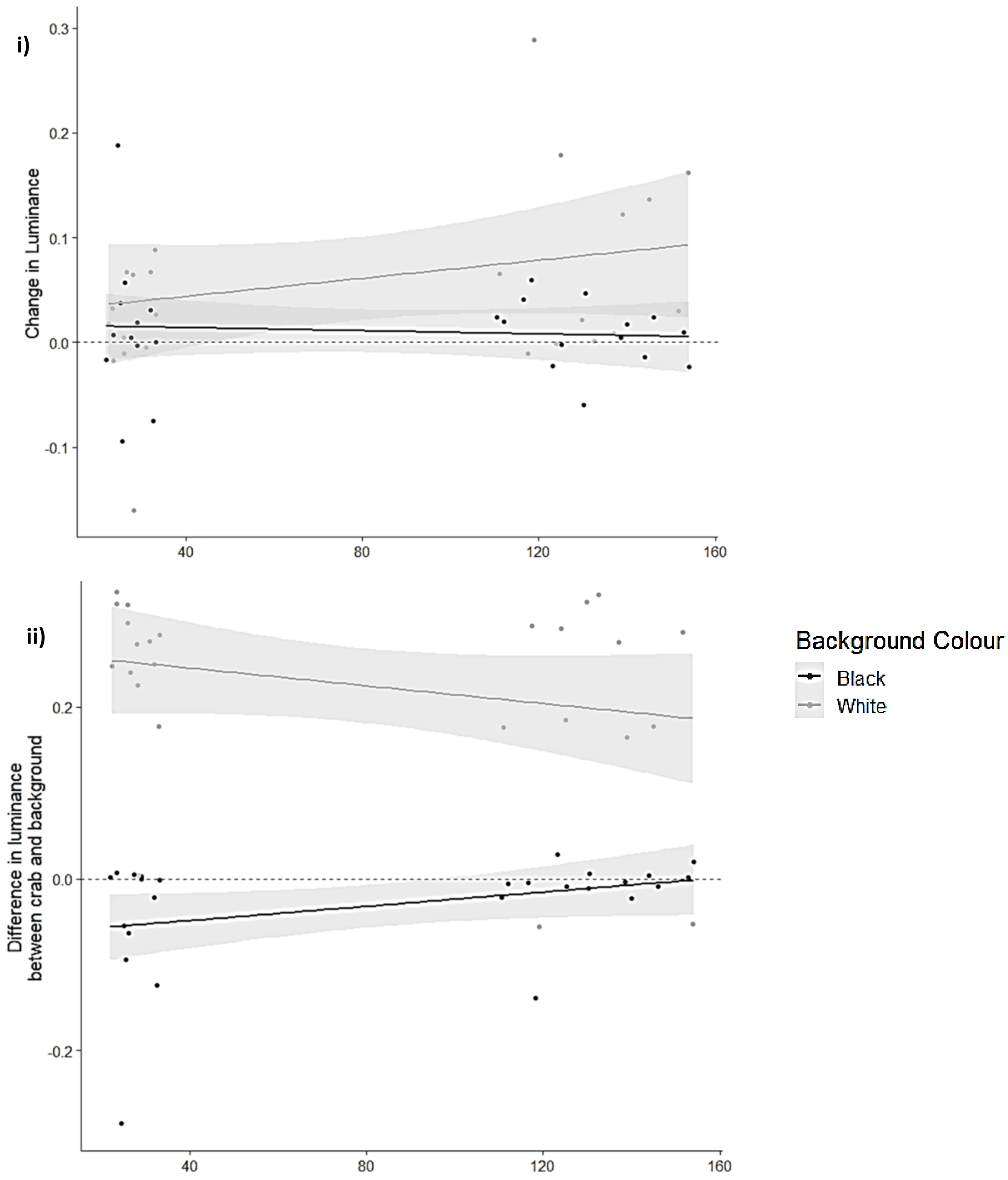


Figure A2: 4 weeks. Luminance change (i) and consequent background matching (ii) after 4 weeks, in relation to the distance from the shipping noise source, with individuals separated based on background colour.

Appendix B: Noise Structure

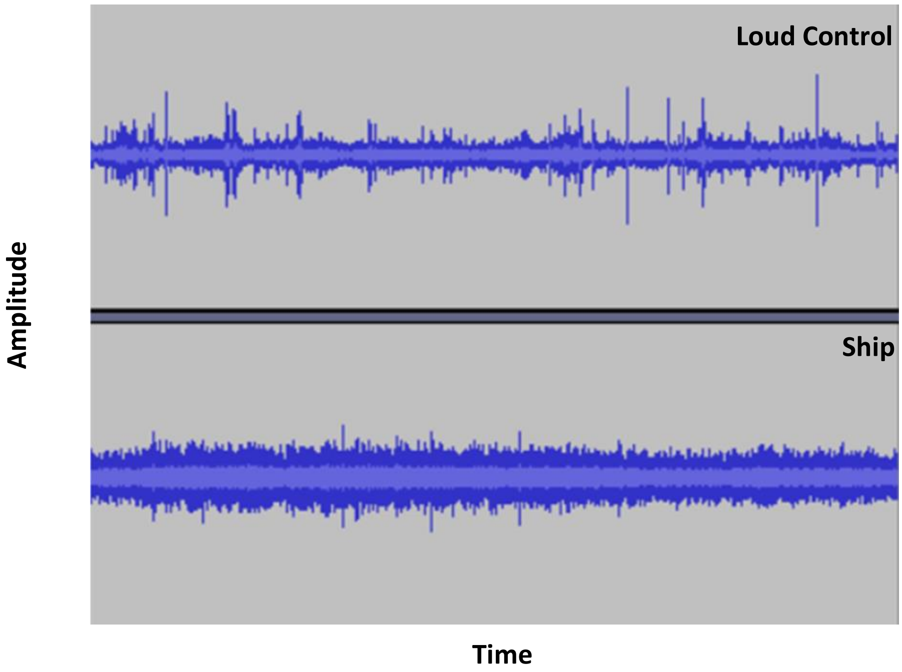


Figure B1: Waveform plot of a sample of the loud ambient and ship noise treatments.

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