The Impact of Multiple Anthropogenic Stressors on the Colour Change and Antipredator Behaviours of the Common Shore Crab, *Carcinus maenas*

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Abstract

The marine environment is increasingly subject to environmental change driven by anthropogenic stressors, which may alter species' key behaviours and necessitate rapid behavioural and phenotypic plasticity. Such stressors rarely occur in isolation, yet our understanding of their potential interactions and the resultant effects not only on individual species, but upon trophic interactions, is still relatively limited. Here I study the combined impacts of a major global stressor, temperature increase, and a local stressor, anthropogenic noise, upon traits key to the survival of the common shore crab, *Carcinus maenas,* within a laboratory setting. First, I use image analysis and a relevant predatory vision model to determine the impact of concurrent temperature increase and noise pollution on the camouflage and growth behaviours of juvenile *C. maenas*. I demonstrate that anthropogenic noise detrimentally impacts crab camouflage, negating the positive influence of increased temperature, while growth increases under higher temperatures, negating negative effects of noise pollution. With this data, I reveal, for the first time, the potential for mitigative antagonism, with the biological response to one stressor reduced by the presence of the other. Following this, I further extend my investigations by studying the impact of the above stressor interaction on the movement and antipredator retreat behaviours of *C. maenas.* Using a series of behavioural trials, consisting of simulated predatory events and a directional movement trial, I demonstrate that anthropogenic noise pollution reduces likelihood, and increases latency, of antipredator response, whilst also prompting directional avoidance behaviour. I reveal that increased temperatures may have a complex impact upon *C. maenas* movement and antipredator behaviour, with the potential to impair continuity of movement, reducing distances covered and increasing pausing behaviour. This thesis provides novel insight into the cross-modal impacts of a global and local stressor interaction upon an intertidal crustacean which is native to the UK and globally invasive. It is my hope that the themes discussed in this thesis will contribute to the growing body of studies focussing on the impact of stressor interaction upon marine ecosystems, and provide valuable insight into potential management and conservation efforts.

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Chapter 1: Introduction

Multiple Stressors and Impacts on Marine Ecosystems

As the predominance of human populated areas continues to grow, so do the potential impacts of human activity upon the natural environment (Halpern et al., 2008; Hoegh-Guldberg and Bruno, 2010; Slabbekoorn et al., 2010). Areas that may have previously been considered the most isolated from human influence, such as the open ocean, are no longer beyond the reach of pervasive global environmental change (Boyd and Hutchins 2012). These anthropogenic drivers of habitat change, more commonly referred to as stressors (Hofer and East 1998), may be global or local in their range.

Global stressors such as climate change driven changes in sea temperature are among the most well studied challenges facing marine environment. However, stressors which are global in their source are often complex and challenging to mitigate(Crain et al., 2008; Brown et al., 2013). Further compounding the issue, but generally easier to manage, is the addition of so-called local stressors, which affect the environment within a limited range from their source. The impacts of these stressors upon the marine environment are varied, and despite the recent growth of awareness and subsequent research effort, remain, for the most part, poorly understood.

It is rare for stressors to occur in isolation in the natural environment, particularly in marine ecosystems, where the ability for a given stressor to propagate widely is vastly increased by the physical properties of water and by natural movements of currents and trophic interactions (Boyd and Hutchins 2012). This means that species and habitats may be concurrently exposed to combinations of global and local stressors which may interact and prompt species to adapt in order to survive, , and therefore study of such interactions is vital for the development of effective conservation attempts (Brook, Sodhi and Bradshaw, 2008).

My study aims to create the first assessment of stressor interaction between a global and local stressor upon the key survival adaptations of a marine intertidal crustacean. Drawing upon previous studies which have tested the impacts of temperature change and noise pollution individually (Wale, Simpson and

Radford, 2013a, b; Mynott, 2018; Carter, 2019; Carter, Tregenza and Stevens., 2020), I examine the impact of the interaction between these two stressors upon the camouflage and antipredator behaviour of the common shore crab *(Carcinus maenas).*

Climate Change as a Global Stressor

Anthropogenically driven changes in climate and subsequent sea temperature rise are perhaps the most pervasive and best studied of global stressors currently threatening marine ecosystems. Current predictions of end of century warming vary depending upon emission scenarios and potential implementation of management and mitigation measures, but studies have predicted that by the end of the century, global sea surface temperature will rise by 0.3-4.8ºC (Collins et al., 2013; Przeslawski et al., 2004).

As a global stressor, no area of the ocean is fully isolated from these effects and, if current emission levels continue, temperatures across global Marine Protected Areas (MPAs) could rise by an average 0.035ºC per year, with a further rise of 2.8ºC by 2100 (Bruno et al., 2018).These temperature changes may be further influenced by extreme fluctuations due to natural forcing through El Nino Southern Oscillation (ENSO) and Atlantic Multidecadal Oscillation (AMO) acute climatic events (Huber and Knutti, 2014; Chylek et al., 2014), with unpredictable outcomes compounding difficulties of successful mitigation attempts.

Associated with global climate change may be alterations to ocean circulation resulting from sea level rise and decreased salinity (Hurrel et al., 2002; Solomon et al., 2007), reduced oxygen levels (due to solubility changes), and increased solar radiation, potentially providing further challenges for marine ecosystems (Coles, Jokiel and Lewis, 1976). These additional stressors, along with the global nature of temperature rise as a stressor mean that *in situ* studies are challenging, and it may be difficult to separate and quantify effects of particular stressors (Coles, Jokiel and Lewis, 1976; Crain et al., 2008, Nishizaki and Carrington, 2015).

Species at different trophic levels and in different functional groups have been observed to differ vastly in their response to temperature increase, and this may lead to the disruption of trophic energy transfer. For example, raised temperatures may cause phenological changes to vital reproductive events, which may contribute to temporal mismatches between predators and prey (Lawrence and Soame, 2004; Durant et al., 2007; Hipfner, 2008; Genner et al.,2010) (known as the match-mismatch hypothesis (Cushing, 1974; Cushing 1990)), affecting recruitment into consumer populations.

It is important to consider species at lower trophic levels, such as invertebrates, when considering climate change led alterations in community structure (Przeslawski et al., 2008). In particular, smaller species at lower trophic levels are more likely to be ectotherms, and will therefore be more sensitive to thermal stressors (Paaijmans et al., 2013). Such foundation species form a vital food source, and their decline has the potential for dramatic ecosystem effects if species are unable to adapt to new conditions. For example, climate change has been linked with a breakdown of the association between temperature and photoperiod, which, in intertidal and estuarine habitats, may disrupt environmental cues vital to invertebrate reproduction, causing a mismatch between shorebirds and their prey and subsequently leading to population declines (Lawrence and Soame 2004). The potential for plasticity in timing of reproductive events, or spatial alterations is vital in such instances to help to mitigate these effects, however this is not always possible (Lawrence, 1996).

Though there is some evidence of long-term adaptation to increasing temperatures, this is highly variable among species and is seemingly linked with natural levels of local heterogeneity of temperature conditions (Coles, Jokiel and Lewis, 1976; Fitt et al., 2001). Some motile organisms, however, may leave the affected habitat as opposed to acclimating to new conditions. As habitats become unsuitable, reducing reproductive success and increasing mortality, shifts in range of affected species may be observed, to remain within optimal temperatures (Last et al., 2011; Tanaka et al., 2012; Smale and Wernberg, 2013). Such poleward shifts of marine species may present a host of issues, including, but not limited to, temporal mismatches between predator and prey species presence and the introduction of novel predators, parasites or diseases (Sorte, Williams and Carlton, 2010; Wallingford et al., 2020).

Studies of intertidal communities in the UK have revealed poleward range shifts of up to 50km per decade as a result of climate change (Helmuth et al., 2006), with northerly distributional shifts in invertebrate species (e.g. *Phorcus lineatus* and *Steromphala umbilicalis*), as well as decreases in body size (Mieszkowska et al., 2006a; 2007), resulting in community changes and potential alterations to trophic energy transfer. As many invertebrates represent foundation species within their ecosystems, their importance as indicator species for climate change related thermal stress must not be underestimated.

Anthropogenic Noise as a Local Stressor

Human disturbances to marine soundscapes have increased dramatically over the past century, with anthropogenic noise pollution resulting in a 10-12dB increase in average sound levels in the Northeast Pacific since the 1960s (Andrew et al., 2002; McDonald Hildebrand and Wiggins, 2006). Sound propagates more effectively in the marine environment than on land, travelling long distances, especially at low frequencies, which may reach five times further underwater than in air (Slabbekoorn et al., 2010; Montgomery and Radford, 2017). Anthropogenic additions to ambient noise levels in the marine environment introduce novel, low frequency sounds that often overlap with species' natural auditory and vocalisation ranges, and have the potential to disrupt or mask natural cues for communication, foraging and navigation, causing increased stress in marine organisms and secondary issues including distraction, reduced predator vigilance and reduced predatory success (Wright et al., 2007a,b; Tyack, 2008; Slabbekoorn et al., 2010; Purser and Radford, 2011; Francis and Barber, 2013).

Offshore activities including sonar and pile-driving produce infrequent, loud bursts of low frequency noise which have been observed to produce acute behavioural responses in nearby organisms (Brandt et al., 2011; Dolman et al., 2011; Merchant et al., 2020), such as changes to movement behaviours (e.g. Herbert-Read et al., 2017). Alterations to locomotive behaviours, such as schooling behaviour could have severe consequences to predator prey dynamics, and may alter migration patterns. For example, a reduction in school cohesion was noted within shoals of bluefin tuna (*Thunnus thynnus*) when exposed to ship noise, and fish also exhibited directional avoidance behaviour away from the source of the noise (Sarà et al., 2007).

Infrequent bursts of loud short term noise can cause severe behavioural alterations to local populations, however, arguably more extensive are the effects of mid-range noise stimuli that can propagate over huge distances (Slabbekoorn et al., 2010), as produced by ever growing shipping activity, responsible for average peak frequencies of around 500Hz or less (Wale, Simpson and Radford, 2013b; Gazioglu and Okotan, 2016; Rolland et al., 2012; Ross, 2005), through low frequency engine noise, and higher frequency propeller cavitation (noise resulting from the collapse of bubbles formed during propeller movement) (Hildebrand, 2009; Gazioglu and Okutan, 2016).

Recent expansions in shipping activity and growth of global fishing fleets have been responsible for dramatic changes to ocean soundscapes worldwide, and ship noise is now recognised as a major global pollutant (Wale, Simpson and Radford., 2013a), responsible for a 10dB rise in ambient noise levels off the coast of California between 1994 and 2001 (when compared with baseline noise levels recorded in the area in 1963-1965) (Andrew et al., 2002). The peak frequencies of this kind of noise place it within the likely auditory ranges of a vast range of marine species (E.g., Veirs, Veirs and Wood, 2016), and one of the most well studied resultant impacts is the masking of cetacean vocalisations (Erbe et al., 2016).

In the presence of ship noise, whales have been found to exhibit altered foraging activity (Blair et al., 2016), and show signs of chronic physiological stress (Rolland et al., 2012) and noise avoidance behaviours (Tyack, 2008). Although right whales have demonstrated the ability to raise the frequency of their calls in order to avoid overlap with ship noise, calling at higher amplitudes and with less frequency in noise polluted areas (Parks, Clark and Tyack, 2007; Parks et al., 2011), it is not yet known what the long-term costs of this adaptation may be to whale energy budgets and communication efficacy.

Though there is an ever-growing body of work concerning the impacts of noise pollution upon charismatic marine vertebrates as demonstrated above, the impacts of noise on species at lower trophic levels, particularly invertebrate species, remains poorly understood, despite the fact that many species are crucial to food webs and provide vital ecosystem services as food sources and decomposers (Morley, Jones and Radford, 2014). It has previously been demonstrated that noise pollution may result in changes in invertebrate development, antipredator behaviours, stress and foraging activities, among other impacts (Nedelec et al., 2014; Chan et al., 2010; Wale, Simpson and Radford., 2013a,b). The detrimental impact of noise on behaviours crucial to species persistence is extremely concerning and could result in population declines without sufficient research and subsequent mitigation. if gaps in our knowledge are allowed to persist, and informed mitigation measures are not implemented.

Stressor Interaction

Given that the majority of studies seeking to understand the impacts of stressors upon the marine environment often involve an individual species, exposed to a single stressor, and take place within a laboratory setting, large gaps remain in our knowledge of how increasing human population expansion may impact whole ecosystems in a real-world setting (Crain et al., 2008). Multiple stressor studies have become more frequent in contemporary literature, and with this, a concerning overview of the impacts of stressor interaction upon the marine environment has begun to emerge.

Generally, stressor interactions may be classified into one of three groups; synergistic, additive, or antagonistic. It was previously assumed that the combined effect of two stressors upon an organism would be equal to the sum of their individuals effects (additive) (Folt et al., 1999), however, although this kind of interaction has been demonstrated (E.g. Reich et al., 2001; Zavaleta et al., 2003), this is not always the case. More often, stressors are found to react in a multiplicative way, with their resultant effects several magnitudes more severe upon affected species (Crain et al., 2008; Côté, Darling and Brown, 2016). This synergism produces unpredictable effects which occasionally result in so-called “ecological surprises” (Paine, 1998), and give rise to serious conservation concern for affected species. One of the most commonly studied such examples is that of a possible synergism between UV exposure and temperature rise upon coral mortality risk, which is compounded by their interaction, far more so than their individual additive effects would suggest (e.g. Bhagooli and Hidaka, 2004).

Management of synergistic stressor interactions can be relatively straightforward, with the removal or mitigation of even one of the interacting stressors in these scenarios likely to be successful in aiding population persistence (Brown et al., 2013). Unfortunately, this is not the case when combined stressors are found to react antagonistically, with their combined impacts being less than the sum of their individual impacts, or, in extreme cases, where one dominant stressor entirely negates the effects of another (termed mitigative antagonism) (Folt et al., 1999).

To create robust predictions of stressor interactions, it has been suggested that, wherever possible, studies should seek to employ the most ecologically relevant methodology. This could be further aided by considering interactions among different trophic levels within the same ecosystem, and by employing factorial designs with full control treatments (Crain et al., 2008). Studies that have included organisms at different trophic levels have revealed differential susceptibility to stressors among organisms within the same ecosystem, for example, diatom productivity is enhanced under increased exposure to UV, due to the detrimental effect of UV damage to their grazer population (Bothwell et al., 1994; Boyd and Hutchins 2012). The scale of response accounted for in a study may therefore affect the concluded interaction between stressors, with studies at the population level being more likely to predict extreme outcomes, which could contribute to the differentially high numbers of synergistic conclusions within current literature (Crain et al., 2008; Darling and Côté, 2008).

Potential susceptibility to detrimental effects of stressors may also be influenced in part by environmental heterogeneity, combined with the likelihood of the presence of local versus global stressors (Boyd and Hutchins, 2012; Russell and Connell, 2012). Intertidal environments in particular experience highly variable environmental conditions, which may predispose inhabiting organisms to increased plasticity and tolerance to stress (Tomanek and Helmuth, 2002; Hewitt, Ellis and Thrush, 2016). This may confer higher probability of rapid adaptation when faced with novel stressors, in addition to the potential for fine-scale stressor mediation through the variation of natural local conditions. This may be observed in intertidal communities in Canada, where threats to kelp diversity from rising temperatures were mitigated in areas with local refuges, created by increased wave exposure, with the highest temperature related biodiversity losses occurring in locations with little wave action (Starko et al., 2019). The importance of local wave action gradients upon intertidal communities has long been associated with decreased susceptibility to desiccation and thermal stress (Helmuth et al., 2002), and illustrates the importance of considering local fine-scale environmental conditions when studying the interactions between stressors and informing policy (Witman and Lamb 2018).

Antipredator Adaptation

With studies suggesting that species at differing trophic levels may react in different ways when encountering stressors, interactions between different species, and particularly between predators and prey may be altered. The impact of stressor interaction upon key survival adaptations has the capacity to directly alter predation success, with implications for predator and prey. This may fundamentally shift trophic energy transfer through an ecosystem, and therefore is key to building holistic predictions of ecosystem level responses to stressor combinations.

An important behaviour to be considered in this area is the ability of prey to evade predators. With a large proportion of predators relying on visual stimuli for successful hunting, many organisms have evolved antipredator defences to reduce their likelihood of visual detection within their environment (Stevens and Merilaita, 2009a; Troscianko et al., 2017; Merilaita, Scott-Samuel and Cuthill 2017). Most commonly, antipredator evasion may comprise of physical movement to a sheltered location (hiding), or cryptic coloration to facilitate hiding in plain sight.

Camouflage

The concept of adaptive animal coloration conferring protection from predatory detection through camouflage has long been recognised (Cott, 1940; Stevens and Merilaita 2009, 2011; Stevens, 2016; Troscianko et al., 2016), and in recent times, sensory ecologists have aimed to quantify the efficacy of such coloration in preventing detection, not only from the perspective of human vision, but by relating camouflage techniques to the advantage conferred in ecologically relevant settings by mapping coloration to predatory visual systems (Stevens, 2007; Troscianko and Stevens, 2015).

Coloration for predator evasion (cryptic coloration) is most commonly divided into two dominant forms; disruptive coloration (the presence of markings, often at the edges of the body, which break up obvious prey-shaped outline) and background matching (coloration that closely matches either one specific background within the native habitat (specialist), or alternatively that matches less closely with several backgrounds within the environment (generalist), and this may occur through changes to pattern, coloration, luminance, skin texture, material decoration or choice of settlement position (Kettlewell 1955; Cuthill et al., 2005; Stevens and Merilaita, 2009a,b; Smithers, Wilson and Stevens, 2017; Stevens and Ruxton, 2019).

The phenotypic appearance of organisms that display cryptic coloration is not always fixed, and certain species exhibit temporal, fine-scale changes in their appearance in order to best match their background at any given point in time (Stevens, Lown and Denton, 2014; Stevens, 2016). Adaptive coloration may occur through ontogenetic changes at different life stages (Todd, Qui and Chong, 2009; Nokelainen et al., 2019; Booth 1990), temporally to adjust to seasonal changes in habitat (Zimova et al., 2018), or over shorter timescales, diurnally (Stevens, Rong and Todd, 2013), or in hours, weeks or days (Umbers et al., 2014; Duarte et al., 2017).

Alterations in coloration occur through the functioning of specialised chromatophore cells, and is particularly common throughout the marine environment, where animals such as cephalopods (Hanlon et al., 2007), crustaceans (Stevens, Rong and Todd, 2013) and fish (Smithers, Wilson and

Stevens, 2017), can modify the expression of coloration of their body surface using contraction and dispersion of pigment from chromatophores (Powell, 1962; Stuart-Fox and Moussali, 2009; Umbers et al., 2014; Caro, Sheratt and Stevens, 2016), in order to better match their background over short timescales, or to signal to conspecifics. The expression of this pigment over short timescales, such as in cuttlefish and squid, is most commonly controlled through neuromuscular action (Loi et al., 1996; Wardill et al., 2012), while slower changes are mediated through hormonal changes via the endocrine system or morphologically (via moulting) (Rao, Fingerman and Bartell, 1967; Umbers et al., 2014).

The prevalence of dynamic coloration in the marine environment, and particularly among intertidal species may be attributable to the highly heterogeneous habitat, which undergoes frequent fine-scale changes in quality and appearance due to prevailing environmental conditions, perhaps facilitating greater necessity for phenotypic plasticity amongst its inhabitants (Tomanek and Helmuth, 2002; Hewitt, Ellis and Thrush, 2016), and driving the persistence of dynamic colour change despite the likely energetic cost (Rodgers et al., 2013). Fiddler crabs (*Uca spp*.) and chameleon prawns (*Hippolyte varians*) change their coloration following circadian rhythms (Brown and Webb, 1948; Keeble and Gamble, 1900; Stevens et al., 2013), to better match their background under diurnal changes in light conditions, becoming lighter and more translucent at night. Additionally, *H. varians* may choose to settle on substrate that best matches their own coloration in order to maximise camouflage, as well as preferentially choosing substrate that they are best matched to and exhibiting colour change over long time-scales in order to better match novel backgrounds (Green et al., 2019).

Common shore crabs (*Carcinus maenas*) exhibit highly heterogeneous patterning, which varies associated with habitat, particularly in juveniles (Hogarth, 1978; Todd et al., 2006; Price et al., 2019: Stevens, Lown and Wood, 2014a), which possess the ability to change carapace coloration, patterning and luminance (Powell 1962; Stevens, Lown and Wood, 2014b) over relatively short timescales. This species also displays ontogenetic changes in coloration, with the carapace of adult crabs becoming a uniform intermediate green colour, conferring a more generalist level of camouflage, and owing to the calcification of the carapace with age (Nokelainen et al., 2019).

With the recognition that these camouflage strategies are essential to species survival, a growing body of work has emerged, focussing on possible impacts of novel environmental conditions and anthropogenically driven changes to habitat use upon an organism's ability to camouflage successfully. However, these studies have been, for the main, limited to the direct impacts of stressors upon the visual environment, and thus, by extension, the camouflage ability of the species, or the detection ability of predators. For example, there has been evidence that changes in seasonality associated with climate change may cause temporal mismatch between prey camouflage and environmental conditions, (Zimova, Mills and Nowak, 2016; Zimova et al., 2020). On the contrary, there has been only limited investigation as to how the direct influence of stressors upon an organism may link to changes in its ability to exhibit camouflage as a predatory evasion technique.

Juvenile *C. maenas* have been demonstrated to exhibit impaired colour change and background match ability when exposed to anthropogenic noise pollution (Carter 2019; Carter et al., 2020), whilst increases in temperature cause rates of colour change in this species to increase (Powell, 1962; Mynott, 2018). However, at extreme temperatures impacts become more complex. Mynott (2018) revealed that background matching of crabs to a white background ceased improving above a threshold temperature of 25ºC, while those on black backgrounds continued to change in appearance. Alternatively, Powell (1962) demonstrated that at extreme temperatures, white pigment dispersed regardless of the colour of background substrate (Powell, 1962). These studies indicate that environmental stressors may directly influence predator evasion in some species and therefore, further study is needed in order to better inform conservation practices, particularly concerning invertebrate camouflage and environmental stressors.

Movement

Under immediate threat from a predator, even an animal that is well-matched to its background will need to employ a fight, flight or freeze response to evade predatory attack (Eilam, 2005; Soares et al., 2012; Rupia et al., 2016). These behaviours are mutually exclusive, and therefore prey species will be selected to perform the most appropriate given their physiology and the immediate source of predatory threat, which may often be variable in more commonly predated species occupying lower trophic levels (Metcalfe et al., 1987; Eilam, 2005). Although these behaviours may not be performed in conjunction, they may become more effective when combined with cryptic coloration, thereby maximising survival probability. In many prey species, the ability to effectively and efficiently retreat from a predator comprises of directional movement to available shelter, however, this movement, commonly known as "refuging" may incur costs to the individual, such as reduced foraging and reproductive opportunities, increased likelihood of detection whilst moving, as well as energetic costs of physical movement. Therefore, the distance at which a prey animal decides to initiate a flight response from a predator must be a trade-off which maximises efficiency (Ydenberg and Dill, 1986).

There are, therefore, observable trade-offs evident in several species which adapt to enable efficient predator evasion techniques, with the decision of whether to freeze or flee from a predator dependent upon several factors, including the proximity of the predator and the distance between prey and suitable shelter (Eilam, 2005). For example, choice of habitat type determines flight behaviour in some lizards, with those individuals spending a higher proportion of time in open areas possessing longer legs and faster sprint speeds than those residing primarily in sheltered habitats, where speed is traded for increased endurance (Vanhooydonck and Van Damme, 2003; Gifford, Herrel and Mahler, 2008). In this instance, lizards in open areas also exhibit delayed flight initiation responses, relying on their cryptic coloration until an attack is imminent, whilst those lizards with higher endurance initiate flight far sooner in response to a predatory threat (Vanhooydonck et al., 2001). Similarly, a study by Hennig, Dunlap and Gallup (1976) concluded that anoles were more likely to freeze where there was no shelter nearby and a predator was in close proximity, while in more structurally complex (sheltered) landscapes, anoles froze more when predators were situated further away, perhaps relying more on crypsis to avoid predator detection than direct flight from the threat. However, this relationship is not clear cut, and studies in fish found no correlation between flight initiation and distance to shelter (McClean and Godin 1989), although flight response was negatively correlated with morphological differences in body armour possessed by target species.

The ability to move effectively and in an energy efficient manner is not only important for antipredator evasion. Many species, particularly in the marine environment, rely on locomotion for a host of other key behaviours, including successful foraging (Siemers and Schaub, 2010), mate encounters (Mizumoto, Abe and Dobata, 2017), migration to breeding grounds (Hines et al., 1995), or migration from nursery sites to adult populations (Montgomery et al., 2006). The potential compromise of these behaviours in the presence of anthropogenic drivers of environmental change, and the resultant potential for mortality risk, must not be underestimated. Indeed, recent studies have revealed disruption to key movement behaviours in a range of species under environmental stressors (E.g., Cotton, 2003; Miksis-Olds et al., 2007, Miksis-Olds and Wagner, 2011; Tennessen, Parks and Langkilde, 2014), leading to potential deleterious population level outcomes. Pelagic larvae of fish and decapod crustaceans use sound cues from potentially kilometres away to locate reefs, and therefore, masking of these navigational cues via anthropogenic noise pollution could result in enormous energetic costs (Montgomery et al., 2006), with boat noise known to impact larval settlement rates on coral reefs (Simpson et al., 2016a).

Changing environmental conditions may also impact antipredator movement through alteration of predator detection rates, or behavioural changes to predator or prey strategy. For example, predatory activity and foraging success decreased in the greater mouse-eared bat when exposed to traffic noise (Siemers and Schaub, 2010), and cichlid fish displayed reduced antipredator defence behaviours in the presence of noise pollution (Bruintjes and Radford, 2013). However, the impact on antipredator response of noise exposure is not consistent among species, with response latency decreasing in sticklebacks exposed to noise pollution, but not in minnows (Voellmy et al., 2014a,b), while crabs retreat more slowly to shelter when exposed to ship noise (Wale, Simpson and Radford 2013b; Carter 2019), and juvenile eels' response is similarly affected, with individuals also showing signs of increased stress (Simpson, Purser and Radford, 2015).

Similarly, warming temperatures have been demonstrated to impact movement behaviour across many species, and in turn to impact species interactions. Increases in temperature may differentially affect movement speeds in predators and prey, producing difficult to predict consequences for trophic energy transfer (Kruse, Toft and Sunderland, 2008; Dell, Pawar and Savage, 2014). At higher temperature, rates of prey encounter and subsequent consumption may increase if both predator and prey become more active (Öhlund et al., 2015) although these behaviours vary among species. Such differences in species movement and antipredator response as a result of varying environmental conditions illustrate the need for more thorough investigation into the effects of not only noise and temperature, but other environmental stressors upon species at different trophic levels, particularly where stressor interactions may be present.

Tolerance to Multiple Stressors

Novel stressors are being introduced into the marine environment at a rapid and unrelenting pace, necessitating plasticity in behaviour and morphology or rapid evolutionary adaptation for populations to persist (Hoffman and Sgrö, 2011; eg. Bitter et al., 2019). Adaptation and tolerance in the face of stressors can fundamentally change impacts of stressor interaction upon ecosystems and for this reason, adaptation potential in the face of novel stressors (and fitness costs of such adaptation), is a key factor to consider when conducting multiple stressor studies to gain accurate insight as to the true impacts of environmental change upon an ecosystem.

It may be difficult to reliably quantify acclimation to novel conditions, with a lack of response to a given stressor not necessarily indicative of there being no effect upon the organism, rather it may be that the individual is too unfit to respond, or it is too energetically costly to continue to do so. It is similarly difficult to determine whether a large behavioural response to a stressor results from a large effect upon the organism, or simply through a lack of cost associated with response (Wright et al., 2007a,b). For example directional movements away from stressors, through range shifts or smaller scale avoidance behaviour, such as that noted in bluefin tuna (*Thunnus thynnus*) in response to anthropogenic noise, where shoals of tuna preferentially navigated away from areas of high noise (Sarà et al., 2007), may indicate that the source of the noise was a particularly stressful stimulus for the fish, or simply that there was little to no direct cost associated with moving away from the area into quieter waters.

Certain species may exhibit a natural predisposition to tolerance in the face of stressors, for example, individuals with lower metabolic rates are known to be more resistant to stress (Parsons, 1991), and some populations may also exhibit co-tolerance to certain combinations of stressors, where the tolerance to one stressor is associated with tolerance to another, such as in aquatic species where resistance to acidification is concurrent with resistance to UV exposure. This may be driven by stressors that commonly co-occur, as well as potential for increased resistance among those communities previously exposed to the stressor in question (Vinebrooke et al., 2004; MacLennan and Vinebrooke, 2021).

Organisms are not always observed to build up acclimation to stressors over time, and in some cases there have been notable trade-offs between tolerance to stressors, for instance, marine copepods exposed to thermal stress over several generations did exhibit increased thermal tolerance, however, this was associated with decreased fecundity, and they did not exhibit any acclimation to changes in salinity, in fact, under concurrent increased temperature and salinity, thermal tolerance decreased. This was attributed to competing energy demands resulting from a synergism between the two stressors (Kelley et al., 2015) and illustrates the difficulties of reliably predicting stressor response and capacity for acclimation.

Research Aims

Large gaps remain in our knowledge of how stressors interact to impact behaviours vital to the survival of species in the marine environment. Although there is existing research into the impacts of both climate change and noise pollution on marine invertebrate species, this remains limited, particularly so when considering colour change for camouflage, and fails to account for the potential interactive effects known to occur between global and local stressors.

Prioritisation of management strategies for drivers of environmental change should be informed by robust scientific study and, given the lack of study of the impacts of multiple stressor interactions upon key marine invertebrates, further research in this field is crucial. This study aims to determine the impact of the combination of a global stressor (climate change driven sea temperature rise) and a local stressor (anthropogenic ship noise) upon the camouflage and antipredator behaviour of an intertidal species, the common shore crab (*Carcinus. maenas*), using a factorial, laboratory-based experiment.

A species commonly found on European coastlines (Crothers, 1968), with invasive extensions to its range throughout the world (Yamada, 2001), *C. maenas* inhabits highly heterogeneous environments, exposed to combinations of a host of environmental stressors and provides key functions in intertidal food webs (Elner, 1978; Rangeley and Thomas, 1987; Moksnes and Montfrans, 1998).

When confronted with a predator, juvenile *C. maenas* have fewer morphoplogical defences against predation than mature adults of the species, making their ability to avoid predators key to survival. Exhibiting highly variable coloration, associated with habitat (Hogarth, 1978; Todd et al., 2006; Price et al., 2019: Stevens, Lown and Wood, 2014a), with the ability to change carapace appearance over short timescales (Powell 1962; Stevens, Lown and Wood, 2014b), *C. maenas* can match their background and effectively avoid being spotted by predators. This ability, coupled with timely directional retreat from a potential predator is crucial to the shore crab’s survival, and therefore potential environmental impacts on such traits could directly influence the success of the species.

Further, in inhabiting the intertidal zone at the barrier between terrestrial and marine environments, populations of *C. maenas* are increasingly exposed to human influence. Major ports operate close to, or directly on top of rock pool habitats, making them subject to the disturbance of regular ship traffic. Combined with exposure to broader scale changes in environment such as sea temperature rise, this intertidal invertebrate makes an interesting study species. Indeed, *C. maneas* has previously proved a model organism for studies investigating individual impacts of noise pollution (Wale, Simpson and Radford, 2013a,b; Carter 2019; Carter, Tregenza and Stevens, 2020) and temperature (Powell, 1962; Mynott, 2018), with juveniles proving to possess the greatest colour change ability, perhaps owing to their variable habitat, small size and lack of morphological predator defences (Powell, 1962; Nokelainen et al., 2017). Juvenile C. maenas therefore provide a logical choice for the study of combined stressor impacts of temperature rise and noise pollution.

Previous studies have revealed the impacts of solitary stressor treatments upon survival adaptations of *C. maenas*. Studies by Wale, Simpson and Radford, (2013a,b) and Carter (2019; Carter, Tregenza and Stevens, 2020) have demonstrated that shore crabs exposed to noise pollution exhibit increased stress responses, are less likely to respond appropriately to predators, and have reduced camouflage ability. Conversely, *C. maenas* exposed to increased temperatures have been observed to exhibit generally faster rates of colour change, although mismatches have been observed at high temperatures (Powell, 1962; Mynott, 2018). This thesis directly builds upon and extends knowledge developed through the studies mentioned here, employing methodology consistent particularly with that used by Wale et al. (2013a,b), Carter (2019; Carter, Tregenza and Stevens, 2020) and Mynott, (2018). In doing so I investigate the impacts of stressor interaction above and beyond the known impacts of these stressors in isolation, and create the first study of a global and local stressor interaction upon *C. maenas*.

In Chapter 2 I examine the impacts of ship noise and temperature rise upon the camouflage of *C. maenas*, using photographic analysis of carapace luminance and subsequent background match. My aim is to determine what kind of interaction, if any, exists between these stressors, and its resultant impact upon vital camouflage behaviour. I place this camouflage in the context of an ecologically relevant predatory visual system model, through the use of digital image analysis techniques (Hart, 2002; Stevens et al., 2007; Troscianko and Stevens, 2015), and also monitor growth activity, as colour change in this species may be heavily impacted by morphological changes (moult behaviour). Through Chapter 3, I study the effect of this stressor combination upon the movement and antipredator behaviours of *C. maenas*, using a series of trials adapted from previous methodology (Wale, Simpson and Radford, 2013b; Carter 2019), focussing on response to a simulated predatory threat (retreat to shelter or burial behaviour), and on directional movement when exposed to ship noise at different temperatures, with a view to revealing any noise avoidance behaviours. These behavioural trials also aim to determine whether individuals acclimate to noise treatments, through the use of individuals with varying experience of previous noise exposure. Both of these chapters use the same factorial design, incorporating two temperature treatments (14ºC to represent an average ambient temperature as may be experienced by *C. maenas* populations in the UK, and 25ºC to present an extreme temperature scenario, taking into account both current climate projections (Collins et al., 2013; Przeslawski et al., 2004)and temperatures currently tolerated by *C. maenas* in certain locations across its invasive range (Compton, Leathwick and Inglis 2010; deRivera et al., 2007)) and two noise treatments (three ship noise tracks, to represent regular passing of ships, and three ambient noise tracks, representing natural soudnscapes, played at the same amplitude ((Wale, Simpson and Radford, 2013 a,b)). This design allows full control treatments, while also facilitating separation of any potential interactive effects between the two stressors, compared to their individual impacts. In the final chapter, I summarise these findings and place their importance in a wider context, presenting suggestions for further research in the field.

Chapter 2: Crab luminance change, background matching and growth under multiple stressors

Abstract

Organisms inhabiting the intertidal zone are exposed to some of the harshest and most rapidly changing of all marine environments. Many such species already live close to their tolerance limits, and therefore additional stressors that alter their environment may have severe consequences for survival and community composition. Further, the majority of studies considering stressor impacts have tested individual sources of stress in isolation. Increasingly, it is being recognised that concurrent exposure to multiple stressors is more common in the natural environment, and that the interactions between these stressors can cause unpredictable consequences for affected species. The common shore crab *(Carcinus maenas)* is an intertidal species known to be impacted by anthropogenic changes to their environment. Previous studies have revealed that changes to auditory or thermal environments may cause alterations to key survival behaviours directly linked to organism mortality, such as camouflage and antipredator escape response. In this chapter, I demonstrate that the combined stressors of ship noise pollution and sea temperature rise interact antagonistically to impact camouflage and growth activity of juvenile *C. maenas* in a factorial experiment. To do this, I used a suite of combined treatments in a controlled setting to monitor crab camouflage and growth over a six-week period. I used image analysis techniques to monitor changes in luminance and resultant background match from the point of view of a predatory vision model *(Pavo christatus).* Following the six-week experimental period, crabs exposed to acute elevation of temperature and ambient noise treatments were better matched to their background than crabs in any of the other treatments. This result might indicate an antagonistic stressor interaction, with the opposing impacts of stressors working against each other such that the negative impacts of ship noise negated the positive influence of temperature rise on camouflage ability. Conversely, growth behaviours were predominantly impacted by temperature, not by noise treatment, with crabs growing fastest under raised temperatures. My findings raise important considerations for conservation, strengthening the argument that stressors should be studied concurrently to mitigate for surprising and unpredictable consequences for affected species.

Introduction

Marine species are increasingly subject to complex environmental changes wrought by concurrent exposure to multiple stressors, often anthropogenic in source (Halpern et al., 2008; Hoegh-Guldberg and Bruno, 2010; Slabbekoorn et al., 2010). Predicting the effects of such stressors upon organisms is complex (Craine et al., 2008) and variable according to the trophic level of species, as well as their life history stage, morphology, physiology, distributional range and habitat heterogeneity (Parmesan, 2007; Boyd and Hutchins, 2012; Nye, Gamble and Link, 2013; Voellmy et al., 2014a,b; Sunday et al., 2015). Due to the ever growing range of anthropogenic sources of stress upon the natural environment, and the often difficult task of accurately monitoring marine species' responses, particularly *in situ*, large gaps remain in our knowledge of the impacts of multiple stressors. This could give rise to serious cause for conservation concern (Cote, Darling and Brown, 2016), especially where interactions between stressors cause unpredictable consequences and so-called "ecological surprises" (Paine, 1998).

Sea surface temperature, driven by global changes in climate resultant from anthropogenic forcing and natural climatic events, is rising at an unprecedented rate (Hughes, 2000), leading to alterations in species behaviour and physiology. Increases in temperature have been linked to mass coral bleaching events (e.g. McGowan and Theobold, 2017), increased susceptibility to disease (Shish and Duklow, 1994), shifts in species range (E.g. Helmuth et al., 2006), altered growth and timing of reproductive events, potentially leading to temporal mis-matches between predators and prey (E.g., Lawrence and Soeme, 2004).

The effect of temperature increase on invertebrate species has been investigated perhaps most in sessile invertebrates such as corals, or in pelagic larvae, a key stage of many marine species (e.g. Hoegh-Guldberg 1999; Hoegh-Guldberg et al., 2007; Ainsworth et al., 2016), however, organisms in intertidal zones may be more exposed to extreme impacts related to climate change than other groups of marine species (Tomanek and Helmuth, 2002; Hewitt, Ellis and Thrush, 2016). Similar to shallow reef environments, the littoral zone is subject to high exposure to ultraviolet radiation (Fleischmann, 1989;

Tedetti and Sempéré, 2006), and shallow pools of water isolated from the sea at low tide undergo rapid and extreme temperature changes (Harley, 2008). As interfaces between terrestrial and marine environments, intertidal habitats are subject to both terrestrial and marine temperature input, and by extension, to the impacts of climate change acting upon both of these environments (Helmuth et al., 2002).

Intertidal organisms may respond to changes in environmental conditions by shifting their distributions, or through rapid adaptation or behavioural plasticity (Helmuth et al., 2006; Clark et al., 2013; Ng et al., 2017) and these reactions may differ between trophic levels (Morelissen and Harley, 2007). In the UK alone, range shifts have been observed in key intertidal invertebrates (Mieszkowska et al., 2006a,b), and 2021 was the fourth hottest year on record for ocean temperatures in the northern hemisphere (NOAA National Centers for Environmental Information, 2021). Coastal shelf sea warming at a rate of 0.26°C per decade has been linked to alteration of key survival behaviours including growth and reproduction (Przeslawski et al., 2004; 2008), with a further rise of 1.5-4°C predicted by the end of the century (Hughes, 2000; Holt et al., 2010; Ådlandsvik, 2008; Collins et al., 2013; Przeslawski et al., 2004).

Temperature rise is not the only stressor linked to direct fitness consequences in marine organisms. Noise pollution is now regarded as a pervasive global stressor in both terrestrial and marine environments (World Health Organisation (WHO), Theakston and Weltgesundheits, 2011) Owing to the physical properties of water as a medium, anthropogenic noise pollution may detrimentally affect species many kilometres from the source of the noise (Slabbekoorn et al., 2010; Brandt et al., 2011; Dolman et al., 2011; Brandt et al., 2013; Merchant et al., 2020). Unlike temporary sources of noise pollution such as pile driving and sonar activities, sound from commercial shipping results in a wide ranging, chronic impact upon even the species most isolated from coastal urbanisation, (Slabbekoorn et al., 2010; Rolland et al., 2012; Wale, Simpson and Radford, 2013a,b). Shipping noise has been responsible for a global rise in ocean sound levels of 1-2 dB every year (Ross 2005) and often produces low frequency sounds that overlap with the auditory detection ranges of a plethora of marine species (Packard, Karlson and Sand, 1990; Tautz and Sandeman, 1980; Popper et al., 2003; Popper and Fay, 2011; Casper, Halvorsen and Popper, 2013).

Given the prevalence of reliance on auditory cues across taxa, impacts are not solely confined to those species most well-known for using auditory signalling. In invertebrates, ship noise has been associated with increased stress, reduced reproductive success, and altered growth and foraging behaviours, resulting in potentially severe impacts upon survival (Chan et al., 2010; Wale, Simpson and Radford, 2013b; Nedelec et.al., 2014; Di Franco et al., 2020) The potential for noise to affect behaviours not directly related to auditory perception or vocalisation illustrates the pervasiveness of this stressor, and has prompted further research into the impact of noise upon other key survival behaviours, including predator evasion.

A very common antipredator defence strategy is camouflage (Cott, 1940), and many species display body patterning or coloration developed to aid them in evading visual detection by predators (Cuthill et al., 2005; Stevens and Merilaita 2009a,b). The highly heterogeneous habitats of marine ecosystems have resulted in the development of camouflage strategies across taxa, modified at fine spatial scales to maximise concealment in the native habitat (e.g., Hanlon et al., 2007; Stevens, Rong and Todd, 2013; Smithers, Wilson and Stevens, 2017). This is increasingly recognised among intertidal species, where habitats are both spatially and temporally variable, and where organisms are subject to both terrestrial and marine predators, necessitating robust antipredator defence strategies and resulting in strong phenotype-environment matches (Stevens, Lown and Wood 2014a,b). Many species of crustacean display colour change for antipredator defence, with species such as the fiddler crab, the chameleon prawn and the horned ghost crab performing colour change to better match their backgrounds (Brown and Webb, 1948; Keeble and Gamble, 1900; Stevens, Rong and Todd, 2013).

Carcinus maenas, the common shore crab is a well-studied intertidal species native to UK coasts, and present on shorelines around the world, and an example of a species that uses specialised chromatophores to regulate medium- and short-term colour change to improve its camouflage and successfully evade predators (Todd et al., 2006; Stevens, Lown and Wood, 2014a,b; Mynott, 2018; Price et al., 2019; Nokelainen et al., 2019). Juvenile common shore crabs are extremely variable in carapace coloration and patterning, and demonstrate the ability, when transplanted onto different substrates, to alter their luminance to achieve a better overall level of background match with respect to predatory vision (Stevens, Lown and Wood, 2014a). Given that juvenile shore crabs may spend a large proportion of time inhabiting a comparatively small area of the littoral zone during periods of low tide, (or risk immediate exposure to predators during travel to an adjacent rockpool over land), the ability to perform fine-scale, rapid and reversible changes in appearance to better match their environment is directly related to their survival. It therefore follows that any alteration to environmental conditions that may impact this ability could result in reduced population resilience.

Although anthropogenic drivers of environmental change in the marine environment are well known and increasingly well studied, there continues to be a lack of knowledge as to how the interaction of stressors impact marine species, with invertebrate species particularly under-studied. Given that in modern natural settings, marine environments are unlikely to experience any one stressor in isolation, the reliance on lab-based studies of individual stressor impact, and their use to inform conservation strategies, remains concerning (Crain et al., 2008). Here I study the combined effect of these two commonly occurring stressors – temperature change and noise pollution, upon a key survival behaviour of the juvenile common shore crab, camouflage.

Previous studies have aimed to quantify impacts of both temperature changes and noise pollution independently upon the common shore crab. Indeed, *C. maenas*' success as an invasive species has previously been linked to its wide thermal tolerance range (Kelley, de Rivera and Buckley, 2013). Larval development in this species occurs between 10-23°C (with peak survival at 12-20°C) with adult thermal tolerance even wider and this facilitates survival at temperatures anywhere between 0-30°C (de Rivera et al., 2007; Compton, Leathwick and Inglis, 2010). Studies manipulating temperature conditions experienced by *C. maenas* have demonstrated that the rate of crab carapace luminance change (and subsequent camouflage ability) increases with increased temperature (Powell, 1962; Mynott, 2018). However, the efficacy of this background matching may be affected at extreme temperatures, for example, one study found that at 25°C, crabs on light substrates stopped changing luminance to match their backgrounds, whilst the background match of those on dark substrates continued to improve (Mynott, 2018). Meanwhile, another noted that at 30°C, white pigment dispersed regardless of background colour, resulting in crabs becoming mismatched on darker backgrounds (potentially due to an attempted albedo effect) (Powell, 1962).

Exposure to anthropogenic noise pollution has been demonstrated to result in both physiological and behavioural alterations in adult *C. maenas.* When exposed to playback of ship noise, shore crabs exhibited a stress response, consuming more oxygen dependant on their size (Wale, Simpson and Radford 2013a). Additionally, adult shore crabs displayed reduced foraging rates and impaired response to a simulated predatory attack (Wale, Simpson and Radford 2013b). It is possible that the stress resultant from exposure to ship noise in this scenario caused distraction from vital foraging and antipredator behaviour, as further indicated by faster righting rates of crabs which were turned on their backs whilst experiencing ship noise treatments (Wale, Simpson and Radford 2013b). Further to this work, juvenile *C. maenas* have also been shown to display increased response latency to predatory threat under conditions of noise pollution (Carter, 2019). In addition, a further cross-modal physiological effect was noted in this study, with crabs exposed to ship noise exhibiting compromised rate and efficacy of luminance change for background match compared with those crabs exposed to ambient (natural) noise at the same amplitude. Crabs were also observed to moult less often and have reduced size change per moult under ship noise than those under ambient noise (Carter, 2019; Carter, Tregenza and Stevens, 2020).

Using a factorial experiment in a laboratory setting, I test the impact of four treatments, combining raised temperatures and ship noise to answer the following questions; 1) Do juvenile *C. maenas* exposed to the combination of ship noise and raised temperatures still exhibit luminance change and improved background matching and is this impacted by stressors? 2) Are juvenile *C. maenas* growth behaviours impacted by the combined ship noise and raised temperature treatments? 3) Do stressors interact additively, antagonistically or synergistically to impact *C. maenas* camouflage and growth? To quantify this camouflage in an ecologically relevant context, digital image analysis techniques are used, allowing images to be viewed through a predatory vision model (*Pavo christatus*), and estimating the real-world efficacy of this camouflage for evading detection, and its conferred survival advantage. I also monitor growth activity under the four treatments, with particular emphasis on moult behaviour, a key factor in the morphological regulation of the long-term colour change of this species.

It is apparent that there is currently a lack of knowledge concerning the potential interactions between the two stressors studied here, and it is therefore challenging to predict what kind of interactive effect, if any, may occur. Based upon previous findings from studies by Mynott (2018), where it was demonstrated that raised temperatures increased rates of juvenile *C. maenas* luminance change and by Carter et.al. (2020), where crabs exposed to ship noise exhibited impaired luminance change, I hypothesised that crabs at high temperatures in the absence of ship noise would exhibit the best level of background match by the end of the experiment, and those experiencing ship noise treatments at cold temperatures would display the lowest level of background match.

Methods

Crabs were collected from mudflats alongside the tidal Penryn River creek, Penryn, UK (50.168944, -5.097639 (Figure1.1a)), at low tide, between February and October 2019. Juvenile shore crabs of between 5 and 13mm were selected as they exhibit the greatest levels of colour change ability, with adult carapace cuticles becoming increasingly calcified with age (Powell 1962). Owing to a uniform dark mud substrate, crabs collected at this location had largely homogenous dark carapace coloration upon collection (Figure 1.1b). Crabs were transported in grey buckets, filled with seawater, to the Animal Housing Facility at The University of Exeter's Penryn Campus.

The common shore crab is not a protected species and all work was carried out in accordance with the University of Exeter's Ethics policy (application no. ECORN001803).

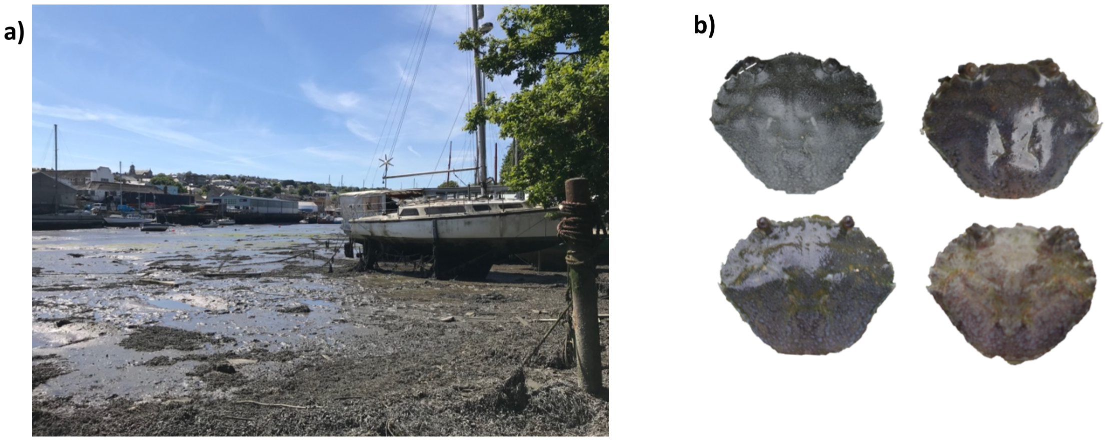

Figure 1.1: a) Collection site at low tide (50°10'08.2"N 5°05'51.5"W); b) Example crab carapace coloration upon collection.

Husbandry:

Crabs were held in glass aquarium tanks (Clear-Seal, Birmingham, UK) measuring 900x445x300mm, with approximately 350mm depth of dechlorinated saltwater mixed to a salinity of between 30-35ppt (Aquarium Systems Instant Ocean Salt, Instant Ocean, Blacksburg, Virginia). Initial tank temperatures were maintained at 14±1°C. Each tank was fitted with a filter (Classic 600 filter, Eheim GmbH & Co., Deizisau, Germany) and a chiller (DC 300, D-D The Aquarium solution LTD. Ilford, UK), with outflow dispersed evenly throughout the tank using white PVC plumbing tubing, interspersed with holes, with one large outflow at each end of the tank to facilitate maximum water flow throughout the system. Tanks were illuminated by two aquarium lights (TMC Grobeam, Aquaray) – one UV and one natural white light, on a 12:12 cycle, to mimic natural daylight. Each tank also contained an airstone, which was supplied with air flow through a pump (Airtech value pump, 230v, Pets at Home). Bubble wrap lined the internal surfaces of tanks to minimise sound reflection from glass surfaces, and both bubble wrap and 30mm thick polystyrene lined the outer surfaces and the base to provide sound insulation (Figure 1.2a,c).

Upon arrival at the lab, crabs were placed, within the holding tanks described above, in individual black PVC housing units measuring 60x60x60mm, with fine grade 2mm mesh on the base and top, allowing maximum water flow and noise transmission. The pots were lined to between 15-20mm with black aquarium gravel (Aquarange “aqua substrate” gravel- black, 6mm, Maidenhead Aquatics), to mimic the dark substrates of the collection location. Crabs were housed individually to prevent cannibalism and to minimise stress caused by potential conspecific competition (Figure 1.2b).

Each crab received three sinking food pellets (Hikari Crab Cuisine) every 48 hours. Approximately 30 percent of tank water was replaced twice a week to maintain water quality, and water was tested once a week for the presence of ammonia, nitrate, nitrite and for PH, in order to maintain stable parameters. Surfaces within the tank were also cleaned during water changes to remove any algal growth.

Throughout the luminance change monitoring experiment, substrate luminance was maintained through the changing of gravel when it became visibly discoloured by algal growth. This was assessed every 48 hours when crabs were fed. Following feeding, each row of crabs was rotated one position clockwise within the treatment tank, to control for potential differences in sound levels throughout the tank.

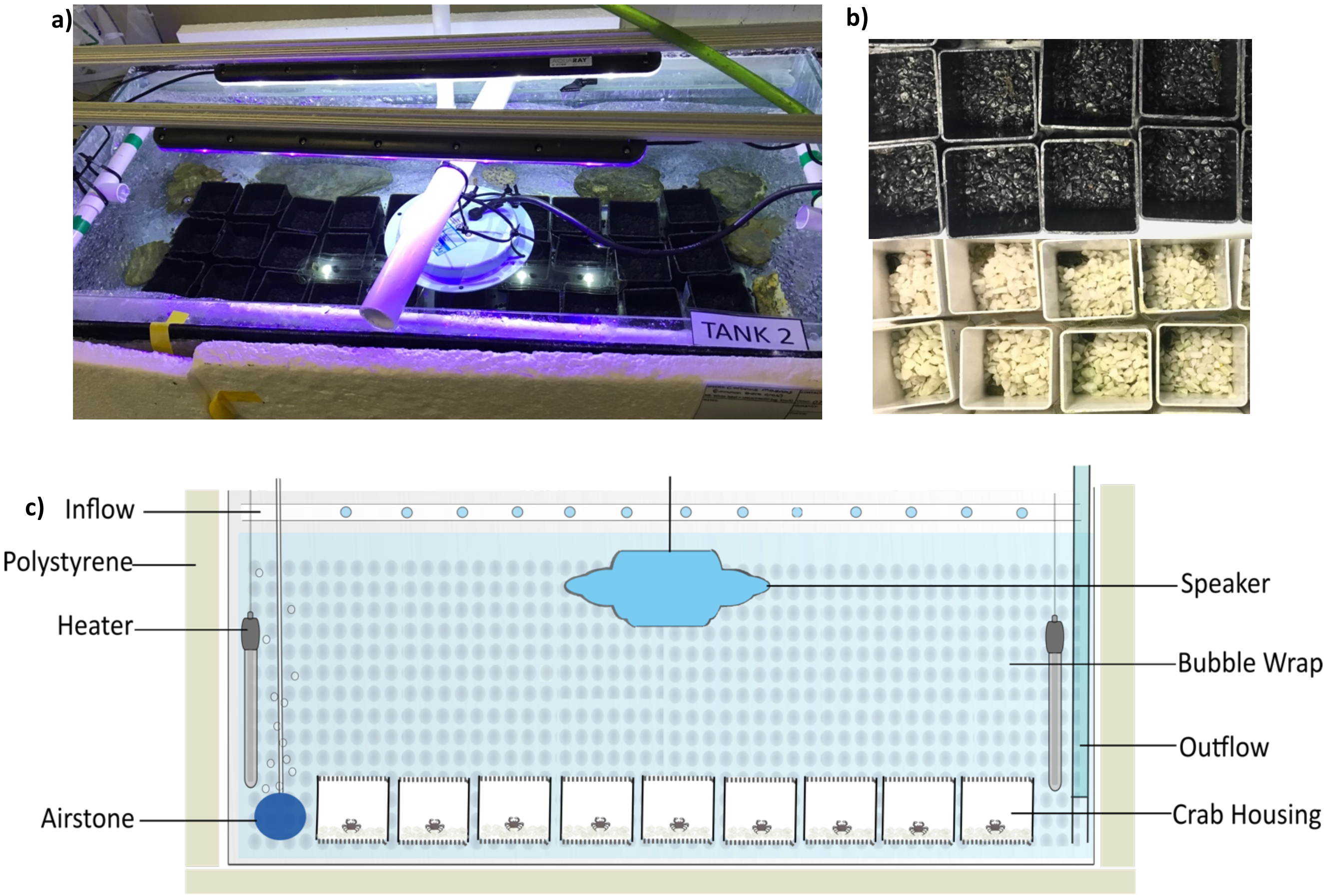

Figure 1.2: a) Photograph of tank set-up during acclimation period; b) Example crab housing during acclimation week (black substrate) and during experimental period (white substrate), c) Cross section representing tank set-up during experimental period (position of individual crab housing was rotated throughout the experiment).

Experimental set-up:

To ascertain the luminance change response of crabs exposed to the combination of anthropogenic noise and temperature change, a 2x2 factorial experiment was designed, with the following treatments:

Table 1.1: Experimental treatments

1) 14±1 °C : Ship noise playback	2) 24±1 °C : Ship noise playback
3) 14 ±1°C : Ambient noise playback	4) 24±1 °C : Ambient noise playback

These treatments were designed to incorporate both a control and an experimental treatment for temperature and noise, and to allow investigation of both the individual effects of treatments upon crab luminance change, as well as their interactive effect. The control treatments were based upon those used in previous similar experiments (Mynott, 2018; Carter et.al., 2020), and in this case, 14±1 °C was considered the control temperature, and 24±1 °C the raised, experimental treatment, while Ambient noise playback was considered the control noise treatment, and Ship noise playback the experimental treatment (noise and temperature treatments described below).

These treatments will hereafter be referred to as:

1. **"Cold-Ship"**
2. **"Hot-Ship"**
3. **"Cold-Ambient"**
4. **"Hot-Ambient".**

Due to husbandry requirements and laboratory space restrictions, only two holding tanks could be maintained at any one time. The four experimental treatments were therefore carried out in two batches, with initial Hot-Ship and Cold-Ship treatments being carried out in February-April 2019, and subsequent Hot-Ambient and Cold-Ambient treatments carried out in May-July 2019. To account for potential impacts of seasonality upon responses to treatments, a repeat was carried out, with ship noise treatments at both temperatures occurring between August- October 2019 and ambient noise treatments completed between October and December 2019. Hot and cold treatment tanks were switched between experimental batches to control for individual tank effects. Any crabs that escaped or died at any point throughout the experimental period were removed from the study.

Total sample sizes for each treatment (including both repeats and following removal of any escaped or dead individuals) were as follows; Hot-Ship: n=50, Cold-Ship: n=64, Hot-Ambient: n=52 and Cold-Ambient: n=56.

Temperature Treatments:

Following initial collection, crabs were held for a one-week acclimation period, to minimise stress prior to commencement of the experimental period. During this time the water temperature in the Hot temperature treatment tank was raised by 2°C per day for five days (using aquarium heaters (2x Deltatherm 100w, Interpet Ltd, UK), until it reached 24°C, with an additional 24-hour resting period once this target temperature was attained.

Ambient temperature tanks were maintained at 14±1°C to mimic a natural yearly average temperature as might be expected to be experienced by intertidal shore crabs at the chosen collection location. To study the effect of an increase of temperature upon colour change behaviour, a temperature treatment of 24±1°C was chosen. Shore crabs are a persistent invasive species in many other regions of the world, and have therefore demonstrated an ability to tolerate extremely variable local temperature conditions across their extensive range, from the cold waters of Nova Scotia and west coast America, to high temperature extremes around the coast of Japan, and east coast US, with larval development occurring between 10 and 22.5°C (Compton, Leathwick and Inglis 2010; deRivera et.al., 2007) (see discussion). This temperature has also proved to be within UK shore crab tolerance limits and is comparable with those conditions used in previous studies on the species (Mynott, 2018; Halsey et.al., 2015, McGaw and Whiteley 2012; Naylor 1963; Powell 1962 (see introduction)). Tank temperature was maintained as close to the chosen temperature as possible, however, occasional fluctuations of up to ±1°C occurred due to external lab air temperature changes.

Sound treatments:

Sound recordings were provided by Wale, Simpson and Radford from their 2013 studies (Wale, Simpson and Radford 2013a,b). Originally taken at the UK ports of Plymouth, Portsmouth and Gravesend, recordings were made at each location to capture ambient background noise, as well as the sound of a ship passing at a distance of approximately 200m (of an LPG tanker, container ship and ferry respectively). For full details of recording and sound modification procedures, see Wale et al., 2013a,b. Further sound treatment modifications were made in accordance with a study by Carter (2019; Carter, Tregenza and Stevens, 2020), in which it was demonstrated that ship noise playback negatively affected luminance change and subsequent background match ability of juvenile shore crabs, when compared with those exposed to ambient noise played at the same amplitude.

The six recorded tracks were individually modified in Audacity ® (Audacity Team, 2020) so that all played at a comparable amplitude. Individual tracks were looped to create six 5-minute playbacks, each with a 30 second fade in and out. Throughout the ambient treatments, ambient soundtracks played continuously, in an unpredictable order, while ship noise treatments consisted of this same ambient noise playback, with the addition of a ship noise track played once every hour, again in an irregular order.

Sound playback occurred through a UW30 underwater speaker (University Sound Diatran Omni-directional Underwater Loudspeaker, 100-10,000Hz), using MP3 players (RUIZU X02 MP3 Player, 8GB) connected via an amplifier (Kemo Electronic; 18W; frequency response: 40-20,000Hz). MP3 players were fully charged every 24 hours using a portable battery (EC technology power bank, 22400mAh), to ensure there was no break in sound transmission. The speaker was suspended from a PVC pipe placed across the centre of the tank, so that it was situated just below the surface of the water, approximately 300mm above the base of the tank (see noise playback methods below).
In-tank playback was recorded using a hydrophone (D-Series hydrophone, JrF audio supplies) and recorder (Zoom handy H1 recorder, 441kHz), with recordings taken approximately 60mm above the base of the tank, in the centre, in the far left and far right extremes of the tank, and mid-way between these points, in the left and right quartiles of the tank, to reveal a mean level of sound transmission throughout the tank. Recordings were analysed using the WavStats function in Audacity ®(Audacity Team, 2020) and amplitude is given, as it is considered the most appropriate SPL measurement in this case (Table

1.2) given that shore crabs primarily sense sound through particle motion (Popper, Salmon and Horch 2001).

Table 1.2: Mean sound levels of each combined treatment recorded 60mm above tank base, averaged across the centre, far left and far right of the tank. RMS(A): Root Mean Squared Average, A-weighted (A-weighting is commonly used in environmental pollution studies to standardise sound with respect to human hearing response); dbFS: decibels relative to full scale.

Noise	*RMS (A)*	*RMS dBFS*	*Peak dBFS*
Ambient	-40.65	-41.13	-19.29
Ship	-37.96	-40.8	-21.3

Photography:

To monitor changes in crab carapace appearance under the four treatments, photographs were taken periodically throughout the experimental period.

Crabs were photographed for the first time following the one-week acclimation period. This was considered their starting appearance and marked the commencement of the six-week colour change experiment. Following the first photography, crabs were placed in individual white PVC housing units measuring 60x60x60mm, with fine grade 2mm mesh on the base and top, lined with approximately 15mm depth of white gravel substrate (Natural White Aquarium Gravel by Pets at Home). At this point, sound treatments commenced. Crabs were subsequently photographed once every two weeks (at weeks 2,4 and 6), at which point the trial was ended and this was considered final luminance.

Crabs were removed from holding tanks individually, immediately prior to photography, to avoid unnecessary stress. Their carapace was gently dried using soft paper tissue, to reduce spectral reflectance, and their carapace width measured (from spine to spine) and weight recorded. Photographs were taken using a Nikon D7000 camera fitted with a 105mm coastal lens and a remote shutter release, mounted on a tripod (Figure 1.3). The camera had undergone quartz conversion to enable full-spectrum sensitivity. Crabs were placed onto a uniform grey background (EVA craft foam) inside a ring of translucent PTFE (which acted to diffuse light evenly), alongside a 93% and a 7% photographic reflectance standard (Spectralon®, Labsphere) and a unique identity label. An arc lamp (Ventronic, EYE Color Arc Lamp, Venture Lighting Europe Ltd. Hertfordshire, UK), that had had its UV/IR filter removed, was used to illuminate the subject. Two photographs, in RAW format, with manual white balance and fixed aperture, were taken of each crab (Figure 1.3a and b), one with a UV band-pass filter (Baader U filter, 300-400nm) and one with a human visible filter (Baader UV/IR filter, 400-700nm), with care taken to ensure the crab had not moved between photographs, to allow maximum alignment of UV and human visible images. Photographs of the white substrate were also taken, to be analysed for background luminance.

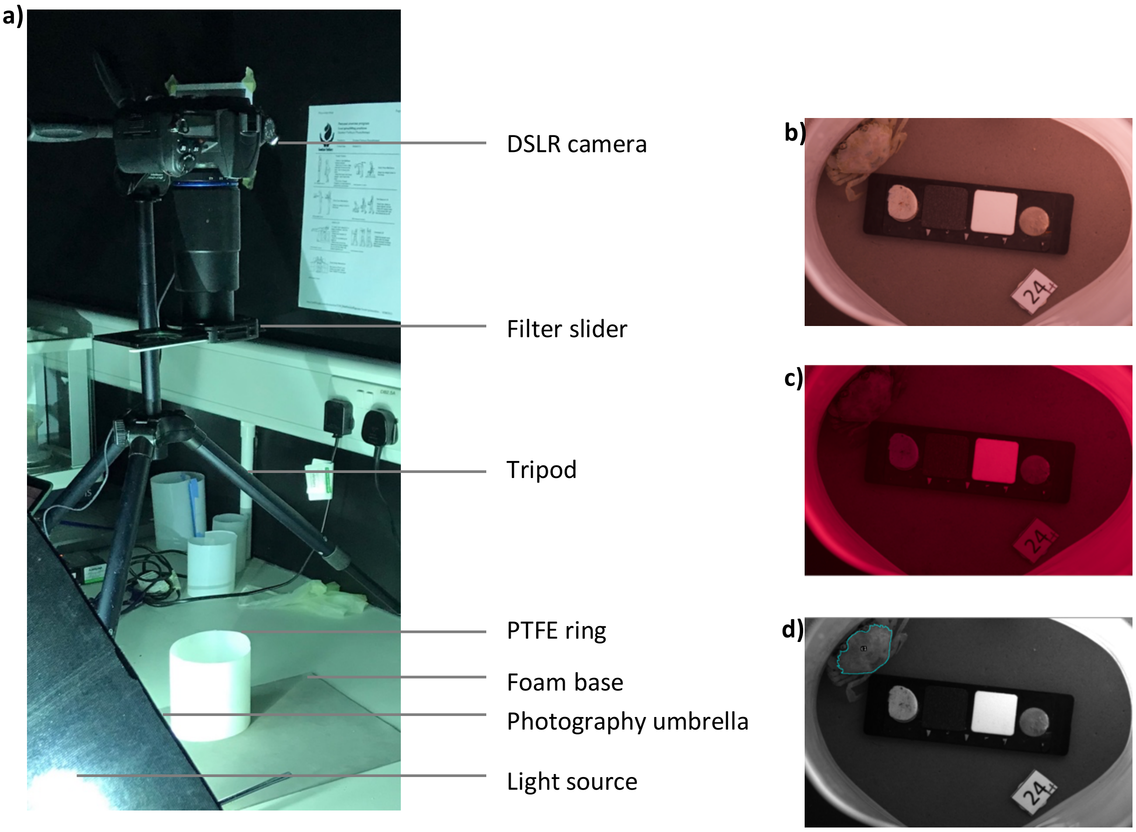

Figure 1.3: a) Photography set-up; b) Human visible photograph, c) UV photograph, d) Multispectral image with crab carapace selected as a region of interest.

Growth:

Crab growth was monitored throughout the experiment, with crab weight, carapace width, and moulting being recorded. Crab moults were counted as and when they occurred throughout the treatment period. The number of moults that occurred during the acclimation week was also noted per treatment. Size and weight data were collected during the photography process every two weeks, to minimise unnecessary stress.

Following the six-week monitoring period, crabs remained in holding tanks at their acclimated temperatures, and sound treatments were stopped. Crabs were subsequently monitored during a series of behavioural trials (Chapter 2).

Image Analysis:

Image analysis was carried out in Image J (version 1.52k, National Institute of Health, NIH), using the MICA toolbox plug-in (version 1.22, Troscianko and Stevens 2015). UV and human visible images were aligned and overlaid to create a normalised multispectral image stack. Images were first linearised (Stevens, 2007, Troscianko and Stevens 2015), and in each photo, 93% and 7% reflectance standards were identified, to allow the image to be standardised, accounting for any variations in illumination between the images, and the crab carapace was selected as a region of interest (Figure 1.3d). Images were scaled to the 16 bit maximum of 655535.

To understand how changes in carapace luminance correspond to real world camouflage against predators, images were analysed with respect to an avian predatory vision model (Peafowl, *Pavo christatus*). *P. christatus* has a violet shifted visual system (Violet Sensitive, VS) capable of perceiving UV light (Hart 2002, Ödeen and Håstad 2003), and provides an ecologically relevant visual system model, comparable to many avian potential predators of juvenile shore crabs (Crothers 1968). Multispectral images were analysed using the Batch Multispectral Image Analysis function in the MICA toolbox, employing a highly accurate polynomial mapping technique (Stevens 2007, Pike 2011, Troscianko and Stevens 2015) to convert the image to peafowl colour space, with luminance values perceptible to peafowl given by double cone values, and output cone catch values falling between 0 and 1.

Cone catch values for luminance were also taken across multiple photographs of the white substrate, allowing the calculation of an average substrate luminance. Background matching was then quantified as the absolute difference between crab carapace luminance and this substrate luminance value (Stevens et al., 2013). Crab carapace hue was not measured, due to the achromatic nature of the chosen background, and luminance analysis has been demonstrated as a more appropriate choice in previous similar studies (e.g. Carter, Tregenza and Stevens, 2020).

Statistical Analysis:

All statistical analysis was carried out in RStudio (version 1.2.5042, Rstudio Inc.).

Carapace coloration and size of crabs upon collection was naturally variable, and therefore, to reveal any initial differences in mean carapace luminance between treatment groups, a Kruskal-Wallis test (Kruskal and Wallis, 1952) was carried out to assess for significant differences in carapace luminance, crab weight, or carapace width, between Hot and Cold treatment groups, at Week 0 of the colour change experiment (following the acclimation week (noise treatments had not yet commenced at this time)).

Crab luminance and growth at week 6 (the end of the experimental period) were analysed for each group using the methods below. **N.B.** Photography and growth measurements were carried out at 0, 2, 4 and 6 weeks to preserve data should any loss of sample size occur, however only final trait values were used for the purposes of statistical analysis,

Data were analysed with generalised linear models, GLM’s, using the Gamma family (for luminance, background matching, carapace width and weight), and the binomial family (for moult data), with background match data undergoing a square root transformation in order to meet the assumptions of the model. Data were evaluated for normality using the Shapiro-Wilk test (Shapiro and Wilk, 1965), as well as by visual inspection of plots, and background match data were transformed (square root transformation), in order to meet the assumptions of a Gamma GLM. The full models for luminance and background matching data initially included temperature, noise, and their interaction, as well as week, crab size (carapace width and weight), and moult behaviour (moult- yes/no; number of moults), with the full models for growth data adapted from this, excluding focal terms as necessary. The model simplification method (Crawley, 2011) was employed and non-significant terms removed. Models were assessed for best fit using the Aikake Information Criterion (AIC) and the model with the lowest AIC chosen, with a threshold difference of ≥ 2 (Burnham and Anderson, 2004).

Post-hoc testing was carried out on luminance and background matching models using the lsmeans package (Lenth, 2016) to provide an indication of which combined treatment groups drove changes in camouflage ability, with p-values adjusted according to the Tukey method for comparing a family of four estimates.

To explore the impact of the interaction between temperature and noise treatments upon moult behaviour, a Cox Proportional Hazards model was employed using the Survival package (Thernau, 2015). Cox proportional hazards are regression models that enable investigation of the impact of multiple variables on the rate of a given event occurring at a certain time point, referred to as the hazard ratio (Cox, 1972). In this case, the model was employed to explore the relationship between combined treatment and the likelihood of moulting at any given day throughout the experimental period (Carter et.al., 2020). The model simplification method was used as above, and the simplified model was assessed using the Cox.zph function in the Survival package to ensure that the assumptions of proportional hazards were met. Pairwise contrasts between combined treatment groups were obtained using the Survminer package (Kassambra, Kosinski and Biecek, 2018).

Results

Carapace luminance

Starting luminance:

There was a small but significant difference in the starting luminance of crabs, which was first recorded following the one-week acclimation period, with a higher mean luminance of Hot treatment crabs (Kruskal Wallace; $\chi^2_{(1)} = 6.28$, p=0.01). This may have been influenced by the acclimation week, where the gradual increase of temperatures in Hot treatment tanks over the 7-day period could have prompted disproportionate premature lightening of crab carapaces, compared with those in cold temperature treatments (see discussion).

Luminance at 6 Weeks:

Luminance was significantly higher in all groups at the end of the six-week period, compared to week 0 (glm: $\chi^2_{1,434}$=65.0, p=<0.001). The magnitude of luminance change was significantly impacted by the interaction between temperature and noise ($\chi^2_{1,432}$=1.59, p=0.018).
Crabs in Hot-Ambient groups exhibited significantly higher carapace luminance at week 6 than those in Cold-Ambient treatment groups (Tukey; Z=3.2, P=0.008 (contrasts given on the inverse scale)). However, there was no significant difference in final luminance between crabs from the Hot-Ship and Cold-Ship treatment groups (Z=-0.169, P=0.998).

Individually, noise treatment did not have a significant effect on crab luminance ($\chi^2_{1,433}$=0.470, p=0.197).

Crab moult behaviour was significant in luminance change ability (moult y/n $\chi^2_{1,432}$=1.07, p=0.052; moult no. $\chi^2_{1,432}$=3.29, p=<0.001). Crab carapace width, weight, and the interaction between week, temperature and noise were all controlled for in the model.

Background matching

Background match at 6 Weeks:

Background matching (the discrepancy between crab carapace luminance and substrate luminance (Figure 1.4b)) was significantly improved in all groups at the end of the six-week period, compared to week 0, (glm(SQRT): $\chi^2_{1,432}$=0.096, p=<0.001) and this was impacted by the interaction between temperature and noise ($\chi^2_{1,430}$=0.004, p=0.03).

As above, background matching was significantly improved in those crabs experiencing the interaction between raised temperatures and ambient noise (Hot-Ambient), and less so in Cold-Ambient groups (Z= 3.23, P=0.007). But there was no difference when comparing Hot-Ship and Cold-Ship groups (Z=-0.001, P=0.999). Individually, noise treatment did not have a significant effect ($\chi^2_{1,430}$=0.002, p=0.112).

Background match was also impacted by crab moult behaviour (moult y/n $\chi^2_{1,430}$=0.01, p=0.001; moult no. $\chi^2_{1,430}$=0.0208, p=<0.001). Carapace width, weight, and the interaction between week, temperature and noise were all controlled for in the model.

Key Findings:

- Crabs in Hot-Ambient treatment groups achieved the greatest increase of carapace luminance, and consequently were better matched to their background, by the end of the 6-week experiment than those in the three other combined treatment groups.

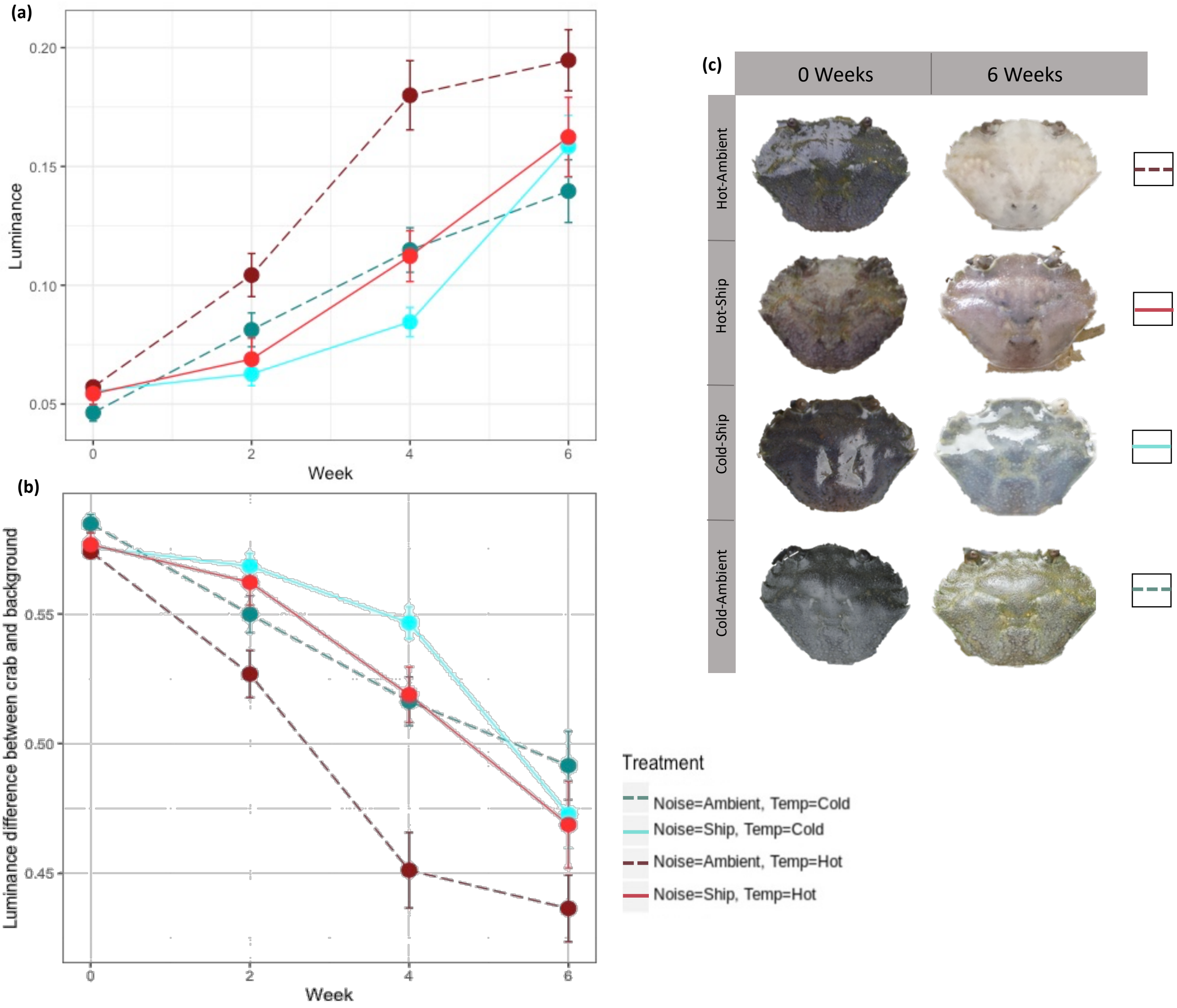

Figure 1.4: Crabs held at 24°C ("Hot") and experiencing ambient noise playback exhibited faster rates of luminance change (a), and better subsequent background match (b) than those experiencing both ship noise treatments, or ambient noise at 14°C ("Cold").

a) Mean luminance at 0, 2, 4 and 6 weeks, with standard error. **b)** Mean difference in carapace luminance and substrate (background) luminance, with standard error. Lower values indicate a better level of background match. Solid lines denote ship noise treatments and dashed lines denote ambient noise treatments. ***NB***: *Week 0 represents the start of the experimental period, following a 1-week acclimation for all treatment groups.*

c) Example crab carapace appearance at the start and end of the experimental period among treatment groups. Note that end carapace luminance and patterning was highly variable, and therefore images shown are intended to depict a potential example observable phenotype among treatment groups.

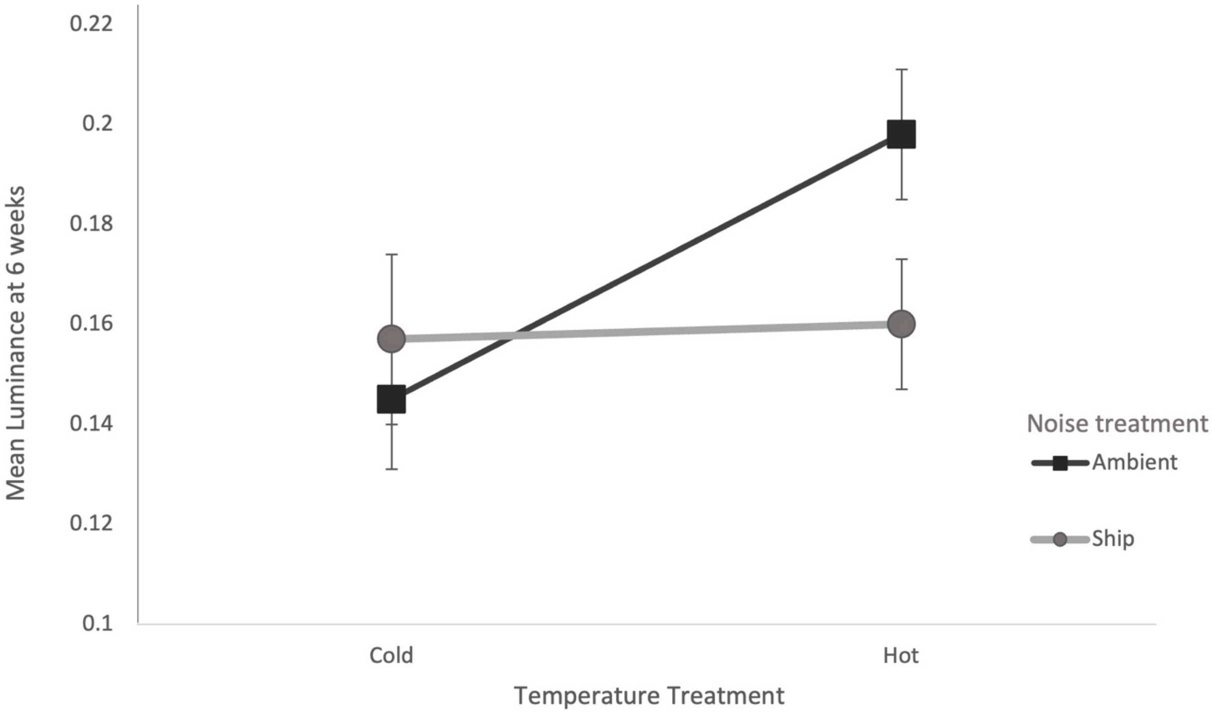

Figure 1.4d: Noise and temperature treatments interacted to influence mean luminance of crabs at the end of the experimental period (6 weeks). Mean luminance values are given for each treatment at 6 weeks, with standard error.

Growth:

Starting Size:

Weight and carapace width of crabs (Figure 1.5) at the start of the experimental period (following one-week acclimation), were not significantly different between hot and cold treatment groups (Kruskal-Wallis: weight χ^2_1= 0.001, p= 0.979; carapace width χ^2_1= 0.110, p = 0.740).

Size at 6 Weeks:

The final weight of crabs following the 6-week experimental period was significantly impacted by temperature treatment ($\chi^2_{1,215}$=0.907, p=0.033) and by crab moult behaviour (moult y/n $\chi^2_{1,212}$=1.08, p=0.020; moult no. $\chi^2_{1,215}$=3.180, p=<0.001), with no significant impact of the interaction between noise and temperature, or noise individually (glm $\chi^2_{1,213}$=0.040, p=0.655; $\chi^2_{1,213}$=0.034, p=0.680 respectively).

Crab carapace width after the 6-week experimental period was significantly impacted by temperature ($\chi^2_{1,215}$= 0.250, p=0.003) and moult behaviour (moult y/n $\chi^2_{1,215}$=0.229, p=0.004; moult no. $\chi^2_{1,215}$=0.505, p=<0.001). Noise treatment, and the interaction between noise and temperature did not have a significant effect ($\chi^2_{1,213}$=0.002, p=0.777, $\chi^2_{1,212}$=0.014, p=0.479 respectively).

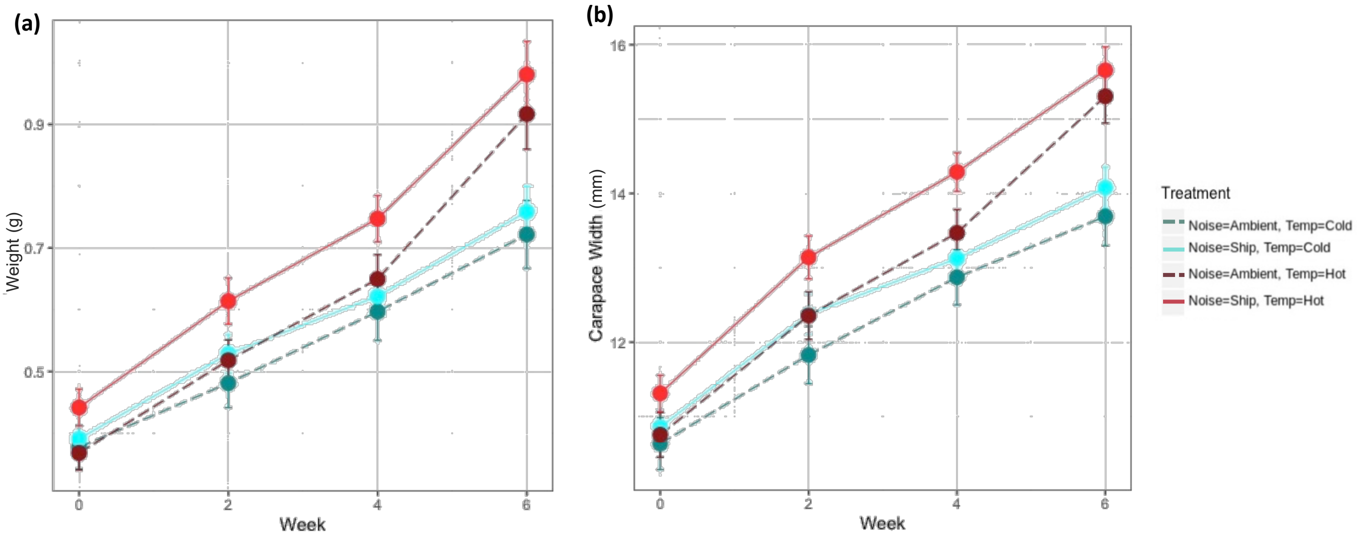

Figure 1.5: Crabs grew faster and attained a greater overall size in 24°C (“Hot”) treatment groups.

a) Mean weight (g) after 0, 2, 4 and 6 weeks, with standard error. **b)** Mean carapace width (mm) after 0, 2, 4 and 6 weeks, with standard error. Solid lines denote ship noise treatments and dashed lines denote ambient noise treatments.

***NB:** Week 0 represents the start of the experimental period, following a 1-week acclimation for all treatment groups.*

Moulting:

During the acclimation week, prior to the experimental period, an average of 35% of crabs in Hot treatment groups were observed to have completed a first moult, compared with 21% in Cold treatment groups.

Across treatment groups, the percentage of crabs to moult at least once throughout the experimental period was similar: Cold-Ship=77%, Hot-Ambient=73%, Hot-Ship=69%, Cold-Ambient=67%. Occurrence of secondary moults was highest in the Hot-ship treatment (21%), compared with the lowest in Cold-Ambient treatment (7%).

There was no significant effect of noise, temperature, or their interaction upon whether a crab moulted or not by the end of the six-week experimental period ($\chi^2_{1,434}$= 0.223 p =0.637; $\chi^2_{1,434}$=0.069, p= 0.793; $\chi^2_{1,433}$=1.03, p=0.311 respectively), or how many times each crab moulted ($\chi^2_{1,434}$= 0.038, p =0.951; $\chi^2_{1,434}$=0.231, p= 0.631; $\chi^2_{1,433}$=0.668, p=0.414 respectively).

The likelihood of a crab moulting at any given time point (Figure 1.6), was not significantly affected by treatment. There was no significant impact of the interaction between noise and temperature treatments (H=0.587 p=0.078), or of noise, or temperature treatment individually (H=1.175, p=0.285; H=1.084, p=0.593 respectively).

Key Findings;

- Crabs grew fastest and attained a greater overall size under Hot treatment groups, regardless of noise treatment.
- There was no observable effect of any of the combined treatment groups upon crab moult behaviour.

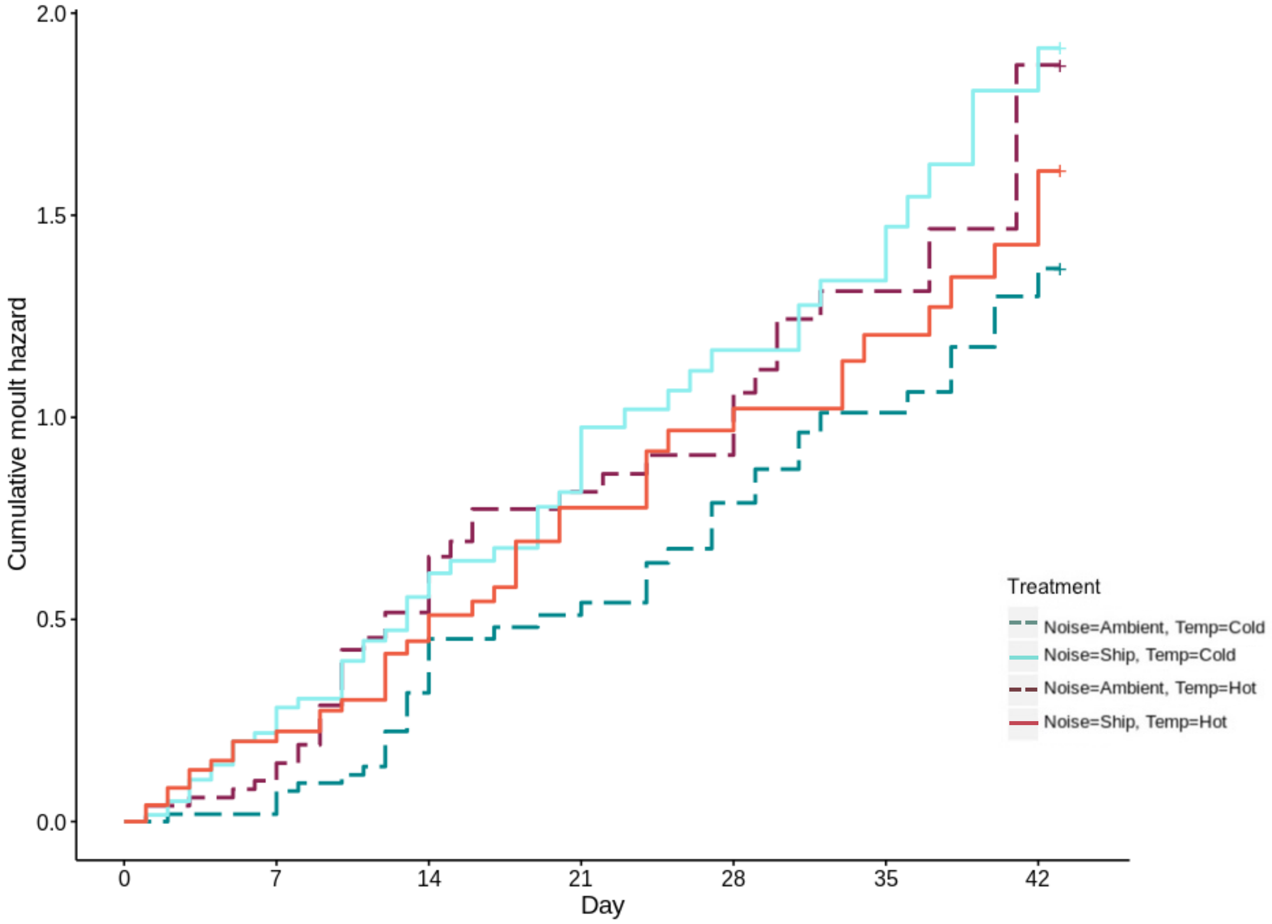

Figure 1.6: Hazard ratio of crab moult over the experimental period. Combined treatment group did not impact the likelihood of a crab moulting on any given day throughout the experiment. (All four groups contain censored individuals – those that did not moult during the experiment (denoted by +). NB: Day 0 represents the start of the experimental period, following a 1-week acclimation for all treatment groups.

<u>Discussion</u>

My study is the first of its kind to demonstrate that when applied in combination, temperature rise and ship noise interact in their effects on juvenile *Carcinus maenas* camouflage and growth behaviours. My findings illustrate that this interaction could be antagonistic in nature and may have differential outcomes upon different behaviours. When acting in combination upon crab camouflage, ship noise was sufficiently detrimental to negate the positive impact of increased temperatures upon luminance change. Meanwhile, when considering growth behaviours, higher temperature increased crab growth rates regardless of noise treatment.

Crabs in all treatment groups demonstrated the ability to improve their background match with respect to the experimental substrate over the long term. The rate and magnitude of this ability was impacted under the combined and individual effect of thermal and auditory stressors. As expected, those crabs experiencing 25°C temperatures with ambient noise playback in the Hot-Ambient treatment group exhibited the highest rates of luminance change and achieved better overall levels of background match than crabs in any of the other three treatments (Figure 1.4). However, crabs exposed to ship noise pollution exhibited lower rates of luminance change and poorer overall background matching at the end of the 6-week experimental period than those experiencing ambient sounds played at the same intensity, regardless of treatment temperature. The results produced here appear to present a mitigative antagonism between the two stressors, with anthropogenic ship noise becoming the dominant stressor over temperature when applied in combination. The significant reduction in rate and efficacy of background match in ship noise treatment groups may result in severe fitness consequences for juvenile shore crabs.

The results presented here could also be indicative of a simple additive effect, however, in this case it could be expected that an observable difference in luminance would be apparent between “Hot-Ship” and “Cold-Ship” treatment groups. It is possible that altering the magnitude of the stressors, either by modifying playback amplitude of soundtracks to simulate different passing distances of ships, or by presenting more extreme high or low temperatures, could reveal whether ship noise remains dominant over temperature regardless of stressor extremes, or whether the results observed here are due to an additive effect.

Increased temperatures have long represented a source of stress in the marine environment, particularly given that the majority of marine species are ectothermic and already live close to their thermal tolerance limits (Sunday et al., 2015). Raised temperatures have been associated with increased disease risk (Shish and Ducklow 1994; Holmquist, Walker and Stahr, 1983), mass die-off events (McGowan and Theobold, 2017), predator-prey mismatches (Lawrence and Soame, 2004; Durant et al., 2007; Hipfner, 2008; Genner et al.,2010), reduced oxygen availability (Coles, Jokiel and Lewis, 1976) and premature maturation (Lange and Greve 1997). However, the camouflage ability of settling juveniles and the subsequent generalised green coloration of mature individuals enable *C. maenas* to function as a habitat generalist, and as such, wide tolerance ranges of biotic factors within the environment are key to its survival. It is therefore perhaps to be expected that *C. maenas*, and indeed other intertidal organisms, are able to adapt and acclimatise to changing temperatures, particularly given that rockpool temperatures may be higher than those of subtidal environments due to increased exposure to sunlight and reduced water renewal.

Although the results of this experiment suggest that when considering camouflage and growth behaviours, an increased temperature of 25°C may have been beneficial to *C. maenas* exhibiting these traits, temperature has previously been linked to increased stress in exposed crabs, with metabolic and behavioural responses indicative of deleterious effects (Wallace, 1972; Pörtner, 2010; McGaw and Whiteley 2012; Halsey et.al., 2015). Additionally, shore crab thermal tolerance has been attributed to restrictions in range, particularly in invasive populations. Therefore, the use of the term stressor when regarding temperature remains the most logical choice, as it cannot be known what the wider, or longer term impacts of this exposure would be, and the quantificartion of this was not possible within the bounds of this study. Adult *C. maenas* have been revealed to possess wide thermal tolerance ranges from 0-30°C, while larval survival peaks between 12-20°C (Kelley, de Rivera and Buckley, 2013). Studies specifically focussed upon the thermal tolerance ranges of settling juveniles have not been performed, however, a study by Mynott, 2018, suggested 15-25°C as the optimum temperature at which background matching was achieved upon black backgrounds, whilst crabs camouflaged to white backgrounds best between 15-20ºC. The invasive success of *C. maenas* in extending its range has been attributed, in part, to this wide thermal tolerance range, however, there has been some debate over whether native *C. maenas* may be genetically different to their invasive counterparts, particularly those populations inhabiting areas at different temperature extremes (Rossong et al., 2012; Tepolt and Somero 2014). At a more local scale, intraspecific differences in thermal physiology and resulting tolerance ranges have been noted among *C. maenas* in different locations in the Pacific (North vs South) (Kelley, deRivera and Buckley, 2011). Such genetic differences between populations inhabiting different thermal gradients could be suggestive of long-term evolutionary adaptation to climatic conditions.

There was a small but significant difference noted in the starting luminance of crabs, with a slightly higher mean luminance in Hot treatment crabs (Figure 1.4). During the acclimation week, temperatures were slowly increased in Hot treatment tanks to minimise unnecessary stress prior to the start of the experiment, and this could have caused premature increases in carapace luminance. Although crabs were held on dark substrates at this time, in an attempt to control for any differences in luminance prior to the official start date of the experiment, it has been demonstrated previously that at extreme temperatures, dark pigment may condense within crab chromatophores, causing carapace lightening regardless of background substrate (Powell, 1962). However, it should be noted that this observation was recorded after acute, short term, exposure to extreme temperatures, as opposed to a more gradual increase as was used in this experiment.

Additionally, differential camouflage ability related to substrate colour, and expression of black versus white pigment has been previously observed to be impacted by temperature, with those crabs in the Mynott study (Mynott, 2018) matching their substrate better at 25°C when the substrate was dark, than on light substrates, whilst Powell (1962) observed impaired match of crabs held on dark substrates at 30°C. Crab camouflage response to temperature has by no means been studied exhaustively, and differences in acclimation protocols and husbandry conditions between studies vary greatly. However it has been suggested that different mechanisms may be responsible for matching different hues/luminance (Duarte, Flores and Stevens, 2017; Mynott, 2018).

If energetic cost is a determining factor in luminance change ability, it may be that available food plays a role in the results seen here. Individuals in all treatments were offered three food pellets every forty-eight hours, which was deemed to be an adequate to surplus amount, and is higher than that offered in previous, similar studies (Wale, Simpson and Radford 2013a,b; Rodgers et al., 2013; Carter, 2019; Mynott, 2018). Organisms experiencing higher temperatures are known to have altered dietary requirements, and although this trend has not always appeared linear amongst crab species (Wallace,1973), it may be that the natural response to higher temperatures would be to become more active, increasing foraging activity and thus consuming more food. This may have contributed to the higher rates of luminance change in those crabs in Hot-Ambient treatments, compared with those in cold treatments. Crabs experiencing ship noise may have experienced a further increase in metabolic rate due to stress associated with the noise pollution (Stansfeld and Matheson, 2003), this could explain why those crabs in Hot-Ship treatments had lower rates of change, as there was no more food available to them to offset these costs. Future work could aim to explore the interaction between metabolic rates, food consumption and resistance to stressors more fully.

The effects of noise pollution upon non-auditory mediated physiological and behavioural traits have been explored in depth through human studies. Noise pollution has been linked to increased blood pressure and heart rate, as well as affecting endocrinological responses, resulting in raised adrenaline and cortisol (Stansfeld and Matheson 2003). Although such studies upon invertebrates are fewer (Di Franco et al., 2020), noise pollution has been similarly associated with stress in crustaceans (e.g. Wale, Simpson and Radford 2013a). Given that chromatophore function in crustaceans is generally believed to be mediated either neurologically or endocrinologically, changes to the endocrine response in crabs exposed to ship noise treatments, and resultant alterations to hormone regulation could be responsible for the lower rates and efficacy of background match in crabs in these treatments (Fingerman, 1970; Duarte, Flores and Stevens, 2017; Carter et al., 2020). The mechanisms involved in colour change and resultant susceptibility to stressor impact warrants further study to enable impacts of anthropogenic pollutants to be more successfully predicted and managed.

Increased stress in affected crabs could reduce available energy budgets for chromatophore function (Fuhrmann et al., 2011). Luminance change has previously been suggested to be an energetically costly behaviour (Rodgers et al., 2013), and therefore a trade-off between necessity for camouflage and maintenance of other vital life history traits, such as growth, could have occurred. This could explain the observed impacts of treatment group upon crab growth behaviours.

Crab growth rate and overall weight and carapace width were highest under raised temperature treatments by the end of the 6-week experimental period, with no impact of noise treatment. Prioritising growth could have a number of advantages for juvenile organisms, not least in shortening generation times, intraspecific competition, foraging ability and development of more robust morphological antipredator defences. Despite this, individuals in all treatment groups exhibited higher overall width, weight and better background match by the end of the experiment, suggestive of prioritisation, but not sacrifice of any particular strategy. As a generalist species, this conservative allocation of resources may be crucial in aiding survival in rapidly changing climates, particularly given that a complete lack of camouflage ability could directly result in juvenile mortality, more so than at other life stages.

Alternatively, the lack of impact of noise treatment upon growth rates could indicate that the mechanisms negatively impacted by ship noise when considering chromatophore function are not vital for organism growth. This may, again point toward an endocrinological impact of noise pollution, as opposed to simply the alteration of metabolic rate (Fuhrmann et al, 2011).

There was no evidential impact of any of the four treatments upon the moult behaviours of crabs. Given that this process forms a major component of luminance change, it is perhaps surprising that it was not found to have been affected by treatment even while crab luminance was. Particularly considering that prior study has posited a link between exposure to noise pollution and reduced moult likelihood (Carter, 2019; Carter, Tregenza and Stevens, 2020). It could be that the stressor interaction has altered this effect. As mentioned above, the dominant stressor from the interaction between temperature and noise was different dependent on each behaviour studied. As moult behaviour is crucial for both growth and luminance change, it may be that the opposing interactive effects prevented the impacts of the stressors upon moult behaviour from being clearly seen. Future studies could aim to explore the impacts of different magnitudes of each stressor to determine whether one stressor will persistently dominate the other, or whether this is simply due to the balance of stressors used in this study.

The emergence of a dominant stressor from a stressor combination is consistent with Leibig's Law of the minimum, an assumption, based upon nutrient levels and growth, where only a single limiting factor may be effect-producing at any given time (Bruland et al., 1999; deBaar, 1994; Folt et al., 1999; Boyd and Hutchins, 2012). Long present in literature, these mitigative antagonisms are consistent with comparative effects models. For example, sedimentation, UV exposure and temperature rise are all stressors individually associated with coral bleaching events, however, when sedimentation was studied with concurrent UV and temperature rise, it was found that coral mortality was decreased compared to when only UV and temperature were studied, possibly due to the increased suspended sediment reducing water clarity, or providing food for bleached coral (Anthony, Connolly and Hoegh-Guldberg, 2007). Such complex interactions pose challenges for policy makers in that, in order to have maximum efficacy, both/all involved stressors would need to be controlled to ensure a positive improvement in conditions, as the removal of only one stressor in a mitigative antagonism could in fact have a negative effect. This becomes particularly difficult when there is a mix of global and local stressors, which may require international cooperation of management strategies and where management of local stressors has the highest impact where there are synergistic reactions (Brown et al., 2013).

Although rate of luminance change and growth were impacted by combined stressors, by the end of the experimental period, the absolute difference between the treatment groups had narrowed. This could indicate a long-term acclimation, which has previously been studied in relation to both temperature and marine noise pollution, and will be explored further in chapter 3. However, care must be taken when interpreting potential acclimation to place it in ecological context, particularly when considering key survival behaviours. Although the end difference of luminance and growth rates between treatment groups was not as substantial as at earlier intervals, the radical early reduced background match and growth could result in death in the natural environment, for example by failure to evade predators, or to compete with conspecifics respectively. Given the highly heterogeneous small-scale environment of the intertidal zone, the ability to change luminance as rapidly as possible is key to enable juveniles to take advantage of changing habitats and forage successfully. Therefore, the concept of camouflage rates “catching up” through acclimation in the long term may not hold such significant ecological relevance, and alternative strategies such as relocation to avoid the stressor may be more appropriate (as explored in chapter 3).

Conclusions:

At the time of writing, my study is the first to explore the interaction between marine noise pollution and sea temperature rise on an intertidal crustacean. These two stressors commonly interact and are pervasive in marine habitats across the world. Studies of multiple stressors are becoming more common, and the interactions revealed have important implications for conservation. Here I demonstrate that crab luminance change and growth behaviours are affected by the antagonistic interaction between noise pollution and temperature change, with one stressor having a dominant impact upon each behaviour. The results presented here form an important step in understanding more fully the impacts that multiple stressors may have on key survival behaviours not directly linked to the stressor itself. Chapter Three will further build upon this knowledge by studying another key survival behaviour, antipredator movement.

Chapter 3: The impact of multiple stressors on crab movement and antipredator behaviours

Abstract

Throughout the natural world, movement behaviours form one of the most basic and vital components of organism success. An essential part of life history strategies of many species, effective movement drives mate encounter, foraging behaviours, migratory patterns and avoidance of predators (Siemers and Schaub, 2010; Mizumoto, Abe and Dobata, 2017; Hines et al., 1995; Montgomery et al., 2006).The decision of if, how and when to flee from an approaching predatory threat is directly linked to organism mortality, and therefore effective and timely responses are key. Speed, fluidity and continuity of movement must all be optimised to facilitate successful evasion and may be affected by environmental stimuli (Eliam, 2005; Rupia et al., 2016). Environmental change may result in non-typical conditions which distract or preclude an organism from behaving normally, potentially impairing optimum movement, particularly when multiple stressors interact (e.g., Cotton, 2003; Miksis-Olds et al., 2007, Miksis-Olds and Wagner, 2010; Tennessen, Parks and Langkilde, 2014). In this chapter I tested the impacts of combined ship noise and temperature rise upon the antipredator response and movement behaviours of the juvenile common shore crab (*Carcinus maenas*). Successful and timely response to predators is of vital importance for this species, particularly at juvenile life stages where predators may range from rock pool fish to seabirds. Using a series of behavioural trials, I explored whether combined stressor treatments impact the likelihood of antipredator retreat and burial behaviours, as well as monitoring response latency when compared with control treatments. I also investigated movement behaviours in the context of noise avoidance and fluidity of movement in the face of this stressor interaction. The results presented here illustrate a complex and variable impact of stressor interaction upon *C. maenas* movement. Consistent with previous studies, crabs exposed to ship noise treatments were less likely in all cases to retreat to a predatory attack, regardless of temperature, however temperature did impact response latency. Further, temperature affected continuity of movement, with crabs in Cold treatment groups moving further and pausing less often than those in Hot treatment groups, with no impact of noise treatment. My results are the first to quantify impacts of combined noise and temperature stressors on the movement and antipredator behaviours of a key intertidal crustacean, and form

an important step to understanding the impacts of stressor interaction upon behaviours directly linked to survival.

Introduction

Movement behaviours are necessary over short temporal scales to enable efficient foraging and antipredator evasion. Often, these behaviours are intrinsically linked, and response latency and refuging in response to predatory threat has a direct impact upon time available for feeding or for mate encounter (Ydenberg and Dill, 1986). However, the ability to sense and respond to an imminent predatory attack may be impaired under conditions of environmental stress.

Noise pollution has been associated with masking cues and signals of both predators and prey (Erbe et al., 2016, Templeton, Zollinger and Brumm, 2016), as well as impacting behaviours not directly linked to auditory sensing, resulting in increased stress and distraction in some species (Wale, Simpson and Radford, 2013a,b ; Wysocki, Dittami and Ladich, 2005; Smith, Kane and Popper, 2004). For example, noise from nearby vessel activity has been associated with impaired parental care in a range of reef fish, leading to reduced offspring survival (McCloskey et al., 2020; Nedelec et al 2017; Bruintjes and Radford, 2013; Picciulin et. al., 2010), with increased noise causing intensified vigilance behaviours in some fish species (McCloskey et.al., 2020; Nedelec et al., 2017) and reduced antipredator defences in others (Bruintjes and Radford, 2013).

Latency of response to imminent predatory threat has also previously been studied in relation to noise pollution, with differing results, even among species sharing the same environmental niche (Voellmy et al., 2014a,b). Under exposure to ship noise, common shore crab response latency increased following a simulated predatory threat (Wale, Simpson and Radford, 2013b; Carter et al., 2020; Carter, 2019), possibly associated with increased stress as a result of additional noise (Wale, Simpson and Radford, 2013a). These effects may be further complicated under the addition of other environmental stressors, such as changes in temperature, which are also known to alter predator-prey relationships, with movement of ectotherms directly associated with local thermal gradients (Breder, 1951; Fry, 1971).

Activities of keystone predators such as echinoderms have been found to correlate with fluctuations in temperature, driven by climate change and major climatic events, with increased consumption of mollusc and crustacean prey resulting from increased search effort and subsequent encounter frequency at higher temperatures (Barbeau & Scheibling, 1994; Sanford, 1999). Similarly, predator vigilance may also increase among prey species exposed to increased temperatures (Weetman, Atkinson and Chubb 1998). Increased speed and frequency of movement behaviours among organisms at higher temperatures may result in higher incidence of predator-prey encounters, and subsequently severe consequences for trophic interactions.

Migratory marine animals may inhabit and experience a range of different habitats, risking exposure to the anthropogenic influence upon each of those habitats (Witt et al., 2011) and posing a challenge for conservation efforts, particularly considering global stressors such as climate change, and economically driven local stressors such as fishing pressure (Boyd and Hutchins, 2012; Russell and Connell, 2012). Global changes to sea surface temperature and resultant alterations in current formation have been linked with shifts in the migratory routes and behaviour of many marine species (Hoar, 1953; Bates et al., 2014; Poloczanska et al., 2016), with overall distributional ranges shifting significantly poleward (Sorte, Williams and Carlton, 2010). This may be due to temporal mismatches between predator and prey, for example where blooms of primary productivity may occur earlier, resulting in foraging grounds being depleted upon arrival by migrating species (Post and Forchhammer, 2008).

Further, initial onset of migration is known to be impacted under changing thermal conditions and climate change driven differences in timing of major climatic events. Migration of long veined squid (*Loligo forbesii*) is associated with thermal forcing of NAO events, and early migration has been observed under increased sea temperatures (Sims et al., 2001). Altered local environmental conditions may also impact migration behaviour, with pollution from nearby shipping activity linked to impaired navigation movement and settlement of juveniles to adult habitats in some reef fish (Simpson et al., 2016a).

Additionally, such shifts in behaviour may be indicative of a directional avoidance behaviour in response to untenable conditions in the natural range. Such avoidance behaviours have previously been studied in marine taxa, not only exemplified by range shifts in response to changes to the thermal environment (E.g., Last et al., 2011; Tanaka et al., 2012; Smale and Wernberg 2013), but in response to stressors such as noise pollution. Some schooling fish have been observed to alter their immediate location in response to ship noise, descending to greater depths in a directional movement away from the noise source (Sarà et al., 2007).

This has also been found in several other taxa, including manatees, which altered their choice of foraging grounds in accordance with daily tourist boat activity. Furthermore, not only did manatee foraging ground choice change under anthropogenic noise, their foraging activity also varied in the presence of noise pollution (Miksis Olds et al., 2007; Miksis-Olds and Wagner, 2011). Other studies have also addressed the potential impacts of stressors upon foraging activities across taxa, often revealing differential impacts upon predators and prey, resulting in potential mismatches.

Pollution from ship noise affects foraging activities of harbour porpoises, reducing prey capture success, echolocation frequency and altering dive behaviours (Wisniewska et al., 2018), and prey species may be similarly impacted. Antipredator movement was directly altered in seabass exposed to anthropogenic noise pollution, which, when faced with a predator, failed to employ their natural freeze response. These fish also displayed increased vigilance and reduced predator inspection behaviours under additional noise (Spiga et al., 2017), behavioural changes synonymous with those noted in other species (E.g., Bruintjes and Radford, 2013).

It has previously been proposed that long term exposure to stressors may prompt rapid adaptation and the development of tolerances in those species commonly affected (Byrne et al., 2020; Donelson et al., 2019). This theory has been demonstrated across several species, and is particularly well-studied in response to changing thermal gradients, with adapted thermal tolerance ranges in species exposed to both long and short-term changes in temperature environments (Coles, Jokiel and Lewis, 1976; Fitt et al., 2001), although the potential physiological costs of this acclimation are not fully understood (Windisch et al., 2011; Enzor and Place, 2014). However, tolerance to stressors is hard to predict, and studies of acclimation to anthropogenic noise pollution in marine species yield mixed results, with long-term exposure to additional noise associated with chronic stress in right whales (Rolland et al., 2012), despite the rapid adaptation of communication signals in response to masking by noise pollution (Parks Clark and Tyack, 2007; et al., 2011).

Further, acclimation probability is increasingly hard to predict in the face of stressor combinations. In the event that multiple stressors act in conjunction, their interactive effects may further complicate acclimation likelihood. Co-tolerances have been demonstrated in some species, where tolerance to one stressor naturally creates a predisposition to tolerance to another, thereby conferring increased resilience in affected organisms (Vinebrooke et al., 2004; Burleson and Silva, 2011; McBryan et al., 2013). The opposite may also occur, with negative co-tolerances resulting from exposure to combined stressors thereby reducing community acclimation compared to stressors experienced in isolation. However, the outcomes of stressor interactions upon tolerance ability are challenging to predict, generally lacking thorough study (McClanahan, Graham and Darling, 2014).

In common with studies concerning physiological impacts of stressor combinations on marine species, the investigation of stressor impact on movement behaviour is generally dominated by marine vertebrate focussed studies, and particularly those concerning mammals. However, the lower trophic level positions occupied by many invertebrate species, and the subsequent dependence on effective movement behaviours for survival against predators, mean that the impacts of stressor combinations upon invertebrate behaviour must not be underestimated. Indeed, as demonstrated above, studies have linked changes in sea surface temperature and noise pollution individually to a host of deleterious impacts in invertebrate species, and in some cases, these impacts have appeared more severe upon invertebrates than on species at higher trophic levels (e.g., Nye, Gamble and Link, 2013). Playback of ship noise has also been associated with increased oxygen consumption by common shore crabs, indicating a stress response (Wale et al., 2013a), and *C. maenas* exposed to ship noise displayed reduced foraging behaviours, potentially indicating distraction. Furthermore, crab antipredator response has been demonstrated to be impaired in the presence of ship noise, with crabs less likely to respond to a simulated predatory event and taking longer to retreat to shelter under ship noise exposure than under ambient noise conditions (Wale et al., 2013b; Carter, 2019; Carter et al., 2020).

In this chapter, I use a combination of noise and temperature treatments, synonymous with those employed in Chapter 2, in a series of behavioural trials, to answer the following questions; 1) Do juvenile *C. maenas* exposed to the combination of ship noise and raised temperatures still exhibit evasive behaviour in response to predatory attack, and is the likelihood and speed of this behaviour impacted by stressors? 2) Are the characteristics of juvenile *C. maenas* movement behaviour impacted by the combined ship noise and raised temperatures? 3) Do individuals exhibit directional movement away from the source of noise? 4) Do stressors interact additively, antagonistically or synergistically to impact *C. maenas* movement and antipredator behaviours? Based upon previous findings from studies by Wale et al., (2013a,b) and by Carter et.al., (2020), where crabs exposed to ship noise exhibited reduced response to simulated predatory attacks, and from studies demonstrating increased crab locomotor activity (in the short term) under increased temperatures (Warburg, Goldenberg and Rankevich, 1982; Weinstein 1998), I hypothesised that crabs experiencing ambient noise at high temperatures would be most likely to respond to a predatory attack, and would likely exhibit greater speed, and reduced continuity, of movement, while those experiencing ship noise treatments at low temperatures would display the lowest levels of antipredator response, and have the longest response times and increased movement continuity.

Methods

Following the six-week colour change experiment (described in Chapter 2), crabs remained in their holding tanks at their acclimated temperatures (14±1°C or 24±1°C) to be studied in a series of behavioural trials to measure their antipredator and noise avoidance responses under the different treatment conditions as used in Chapter 2 (Table 2.1).

Table 2.1: Experimental treatments

1) 14±1 °C : Ship noise playback **(“Cold-Ship”)**	2) 24±1 °C : Ship noise playback **(“Hot-Ship”)**
3) 14 ±1°C : Ambient noise playback **(“Cold-Ambient”)**	4) 24±1 °C : Ambient noise playback **(“Hot-Ambient”)**

The common shore crab is not a protected species and all work was carried out in accordance with the University of Exeter’s Ethics policy (application no. ECORN001803). Following these behavioural trials, all crabs were released to their original collection location on the mudflats on the Penryn River creek.

Antipredator Response Trials

To measure responses to a simulated predatory event under combined noise and temperature treatments, crabs were monitored in a behavioural trial where they were exposed to either ambient or ship noise at their acclimated temperatures (14±1°C or 24±1°C), and their response to a simulated predatory event (retreat or burial) was monitored.

The approach to the experimental procedure, outlined below, was informed by the work of Wale et al. (2013b), and further adapted according to a study by Carter (2019), both of which served to demonstrate the apparent detrimental impact of ship noise upon antipredator retreat in shore crabs, and is used here to investigate whether this difference in behaviour is similarly present under the combined noise and temperature treatments presented here.

General set-up:

In order to ensure trial conditions were as close to holding conditions as possible, and thus reduce the impact of any other environmental factors upon response times, and to minimise stress, trials were carried out within holding tanks. To create a trial arena, holding tanks were divided in two portions – a larger holding area (measuring two thirds of total tank volume) and a smaller trial portion (one third), with the division sound-proofed using a fitted polystyrene dividing wall lined with bubble wrap. This prevented sound transmission between the two areas. A grey plastic tray (100x300x440mm) was fitted in the trial portion of the tank as a trial arena.

Noise treatment playback occurred through a UW30 underwater speaker (University Sound Diatran Omni-directional Underwater Loudspeaker, 100-10,000Hz), using MP3 players (RUIZU X02 MP3 Player, 8GB) connected via an amplifier (Kemo Electronic; 18W; frequency response: 40-20,000Hz), with the speaker suspended underwater, to the left of the trial arena, where it would not cast overhead shadow during trials. Prior to trial commencement, water movement in the trial portion of the tank was halted to control for any disruption by additional sound and movement stimuli.

Sound recordings were taken in both the trial arena and holding area using a hydrophone (D-Series hydrophone, JrF audio supplies) and recorder (Zoom handy H1 recorder, 441kHz. Analysis using the WavStats function in Audacity®(Audacity Team, 2020) confirmed that trial soundtracks were not detectable within the holding portion of the tank at any point throughout the trials.

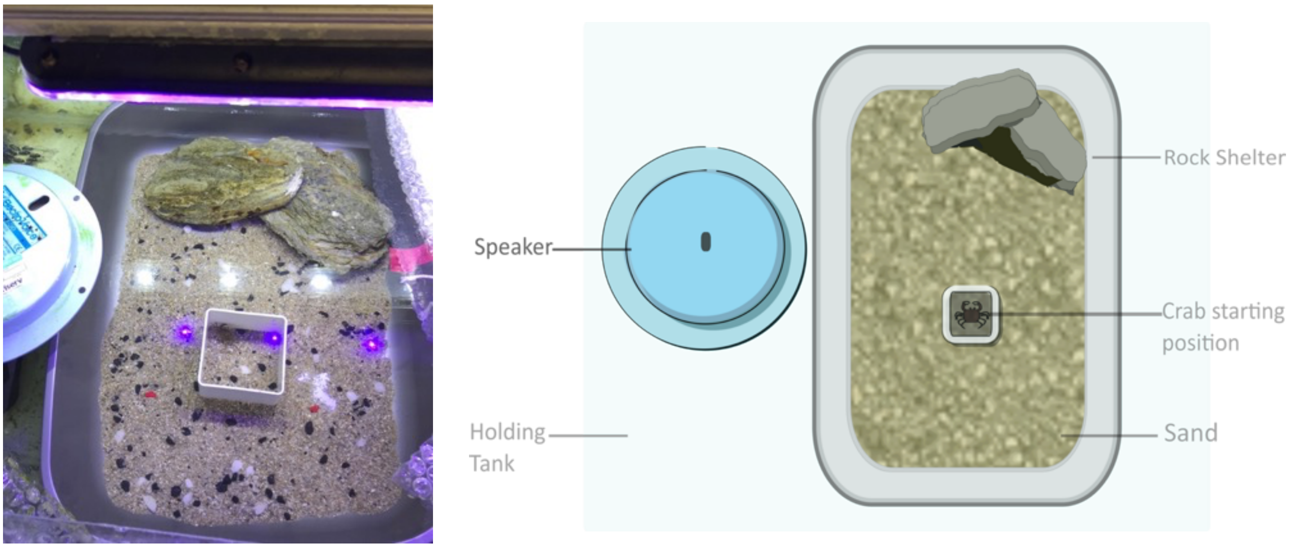

Figure 2.1: Experimental arena for antipredator response trials, featuring <3mm mixed gravel and a rocky shelter. Sound treatments were played through a UW30 underwater speaker elevated to the left of the arena.

Antipredator Retreat

Set-up:

The trial arena was lined with a fine layer of mixed sand (Sand Mix aquarium Gravel, Pets at Home, <3mm depth to prevent burial) and two rocks were arranged as a shelter (measuring approximately 50x80x180mm) in the far-right corner of the tray (Figure 2.1).

All crabs were exposed to one trial under ship noise and one trial under ambient noise, with a five-minute break in between trials. Ship and ambient noise tracks were manipulated in Audacity® to play at the same amplitude, and each track was looped to create a track that was 3 minutes long, with a 30 second fade in and out. Specific tracks played were played in an unpredictable order using the shuffle function on the MP3 player.

Trial:

Crabs were placed in the centre of the experimental arena inside a 60x60x60mm white PVC ring, where they were allowed to acclimate for 1 minute. After 15 seconds the noise treatment was started.

After one minute had elapsed, the holding ring was lifted straight up and out of the water, effectively releasing the crab into the arena. Ten seconds after release, a metal dowel rod was plunged into the water three times (once per second), in order to simulate a predatory attack. The time taken for the crab to respond by retreating to the rock shelter was recorded, with retreat having taken place when the crab had successfully hidden at least half of its body (carapace and legs) underneath the shelter (Wale, Simpson and Radford, 2013a; Carter, 2020).

Crabs were rested between trials for at least five minutes, and once they had completed two trials, were returned to the holding tank.

Antipredator Burial:

Following the antipredator retreat trials described above, a further antipredator response trial was conducted, following the same method, but with a modified set-up for the trial arena. Acting upon observations that crabs in the retreat trial had, on occasion, exhibited burial behaviour following attack (unsuccessfully owing to the very shallow depth of sand), as opposed to fleeing from the predator, a reduced number of trials were conducted to investigate whether burial was an alternative antipredator response, that could likewise be impacted by the interaction between noise and temperature treatment. To investigate this, a repeated antipredator retreat trial was carried out as above, however the arena was lined with a 15-20mm depth of sand and did not feature a rock shelter.

Following a simulated predatory attack, the time taken to exhibit burial behaviour was monitored. Burial behaviour was quantified as the crab remaining stationary, whilst moving the legs and chelae in such a way that it displaced the substrate on top of its’ carapace, effectively concealing itself from view (McGaw, 2005).

Statistical Analyses:
Statistical analyses were carried out in RStudio (version 1.2.5042, RStudio Inc.).

Data were analysed with GLM's, using the binomial family (for response; Yes/No) and the Gamma family (for time taken to respond). Data were evaluated for normality using the Shapiro-Wilk test (Shapiro and Wilk, 1965), as well as by visual inspection of plots. The full models for antipredator response initially included temperature, noise, and their interaction, as well as an interaction between these treatments and prior noise exposure, in order to investigate any potential acclimation to ship noise. The specific track played was also included in the model, to account for any differences in sound profile between the different kinds of ship noise. The model simplification method (Crawley, 2011) was employed and non-significant terms removed. Models were assessed for best fit using the Aikake Information Criterion (AIC) and the model with the lowest AIC chosen, with a threshold difference of ≥ 2 (Burnham and Anderson, 2004).

Post-hoc testing was carried out on models using the lsmeans package (Lenth, 2016) to determine which combined treatment groups drove significant changes in antipredator response, with p-values adjusted according to the Tukey method for comparing a family of four estimates.

In order to explore the impact of the interaction between temperature and noise treatments upon moult behaviour, a Cox Proportional Hazards model was employed using the Survival package (Thernau, 2015). Cox proportional hazards are regression models that enable investigation of the impact of multiple variables upon the rate of a given event occurring at a certain time point, referred to as the hazard ratio (Cox, 1972). In this case, the model was employed to explore the relationship between combined treatment and the likelihood of retreat at any given time throughout the trial (Carter, 2019). The model was assessed using the Cox.zph function in the Survival package, which revealed a violation of the assumptions of proportional hazards. The model was then adjusted accordingly, using strata, which allows for non-proportionality of covariates, and the proportional hazard of response was modelled with respect to noise, stratified by temperature.

Noise Avoidance

To measure movement responses to combined noise and temperature treatments, crabs were monitored in a behavioural trial where they were exposed to either ambient or ship noise at their acclimated temperatures, and their movement monitored. As in antipredator trials (described above), noise avoidance trial methodology was informed by a study by Carter (2019), in which it was demonstrated that crabs exposed to ship noise actively chose to settle farther away from the source of noise playback than those experiencing playback of ambient noise.

In order to allow investigation of potential acclimation to ship noise, prior exposure to noise treatments during the luminance change experiment (Chapter 1) was taken into account here. Playback of ship noise to crabs during the short antipredator response trials was not considered sufficient exposure to prompt acclimation and, in order to maximise naivety to ship noise in those crabs that had previously experienced only ambient noise treatments during the luminance change experiment, movement trials were carried out at least 48 hours after antipredator response trials.

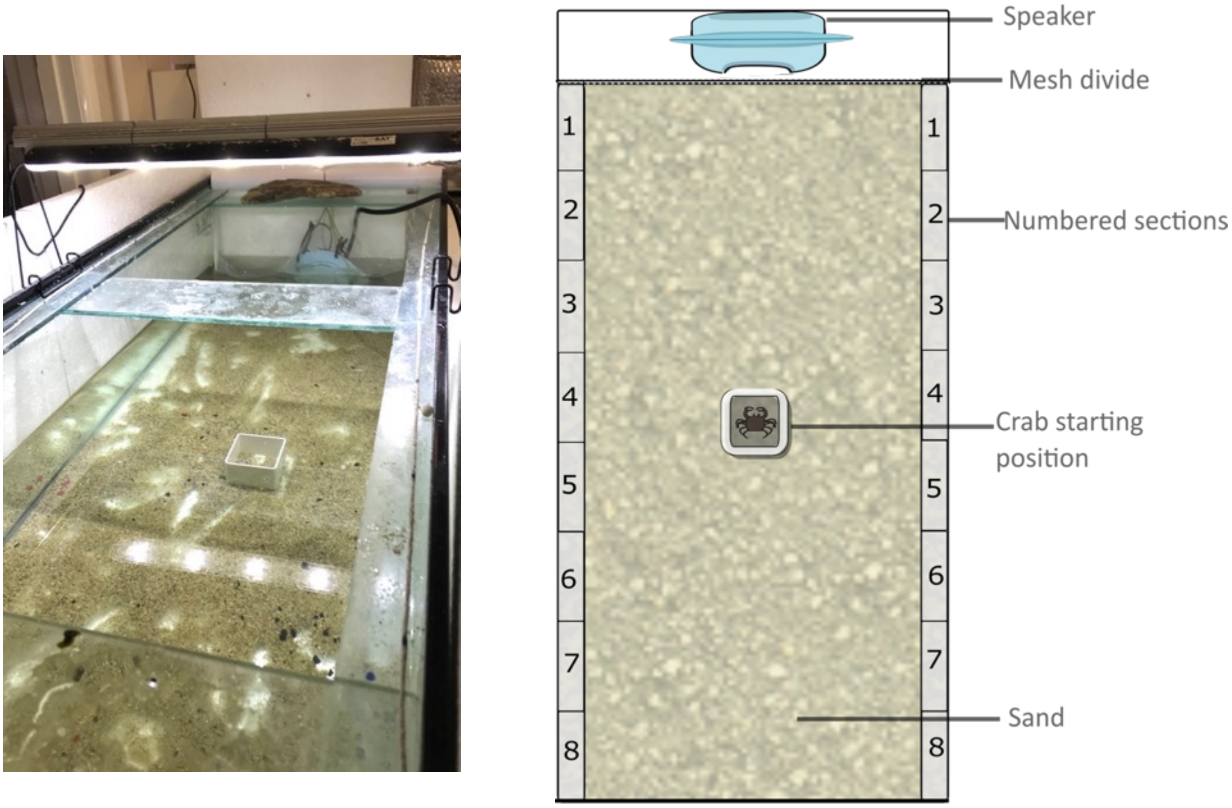

Figure 2.2: Experimental arena for noise avoidance trials, comprising a 1200mm long trial tank split into eight sections with a speaker situated at one end, separated from the trial area by a mesh barrier.

Set-up:

A trial tank (Clear-Seal, Birmingham, UK), measuring 1200x445x300mm was fitted with a filter (Classic 600 filter, Eheim GmbH & Co., Deizisau, Germany) and a chiller (DC 300, D-D The Aquarium solution LTD. Ilford, UK) with the intake and outflow placed at opposing ends of the tank to facilitate maximum flow through the system. A UW30 (University Sound Diatran Omni-directional Underwater Loudspeaker, 100-10,000Hz) speaker was placed at one end of the tank, behind weighted mesh netting to prevent crabs being able to interact directly with it. Noise treatment playback occurred through a UW30 underwater speaker (University Sound Diatran Omni-directional Underwater Loudspeaker, 100-10,000Hz), using MP3 players (RUIZU X02 MP3 Player, 8GB) connected via an amplifier (Kemo Electronic; 18W; frequency response: 40-20,000Hz).

The tank was filled with approximately 250mm depth of saltwater at a salinity that matched holding tank (between 30-35ppt salinity (mixed using Instant Ocean aquarium salt, Instant Ocean)). To mimic temperature treatments of holding tanks, the trial tank water was either maintained at 14±1°C using the chiller, or heated overnight to 24±1°C using aquarium heaters 2x Deltatherm 100w, Interpet Ltd, UK), prior to commencement of trials. The base of the tank was lined with an even layer of mixed fine sand (Sand Mix aquarium Gravel, Pets at Home) at <3mm depth to prevent burial. The trial tank was lit by a single light (TMC Grobeam, Natural Daylight, Aquaray) placed above the tank centre. The tank was divided into eight equal marked sections using string placed on the top glass lips of the tank (Figure 2.2). Prior to trials commencing, the filter and chiller systems were switched off to minimise potential noise and movement disruption caused by water flow.

Noise treatments:

Tracks were modified to play at a similar amplitude using Audacity® (Audacity Team, 2020), and looped to create a 11-minute long playback with a 30 second fade-in and out. Playback was recorded using a hydrophone (D-Series hydrophone, JrF audio supplies) and recorder (Zoom handy H1 recorder, 441kHz), at both ends of the tank (close to and far from the noise source) and analysed using the WavStats function in Audacity® (Table 2.1).

Table 2.1: Sound levels of each combined treatment recorded near to, and far from, the noise source; RMS(A): Root Mean Squared Average, A-weighted(A-weighting is commonly used in environmental pollution studies to standardise sound with respect to human hearing response); dbFS: decibels relative to full scale.

Noise	*Distance from noise source*	*RMS (A)*	*RMS dBFS*	*Peak dBFS*
Ambient	Near	-32.9	-33.6	-6.3
	Far	-41.2	-41.9	-13.9
Ship	Near	-24.9	-26.1	-10.7
	Far	-31.9	-32.9	-16.76

Trial:

Trials were carried out at the holding temperature that crabs had experienced for the duration of the previous six-week colour change experiment.

20 trials were carried out for each holding tank, for each of the four treatments, with two repeats (following the two experimental runs completed for each combined treatment, to account for season when the crabs were collected). At each time, for each tank, 10 trials were carried out under ship noise and 10 under ambient noise, with treatments carried out alternately. Specific tracks were selected in an unpredictable order using the shuffle function on the MP3 player. This resulted in a total sample size of: Cold-Ambient; 41, Hot-Ambient; 40, Cold-Ship; 39, Hot-Ship; 40.

Each crab was removed from its’ holding tank immediately prior to the trial and transferred directly to the trial tank to minimise unnecessary stress. Crabs were placed within a 60x60x60mm white holding ring in the centre of the tank at section four to acclimate for 2 minutes prior to trial commencement. After one minute the noise treatment was started. After two minutes, the ring was lifted directly upward and out of the water, effectively releasing the crab into the trial tank, and the stopwatch was restarted. The position of the crab within the tank was noted every 30 seconds for ten minutes. After ten minutes, the noise treatment was stopped, and the crab removed from the trial tank and replaced into the holding tank (Carter, 2019).

Statistical analysis:

Statistical analyses were carried out in RStudio (version 1.2.5042, Rstudio Inc.).

Statistical analyses aimed to determine whether treatment temperature and the impact noise treatment effected crab noise avoidance and movement behaviours. To assess whether crabs preferentially avoided the noise source under differing treatments, the time each crab spent far from the noise source (in sections 6-8) was calculated, and their ultimate settlement position (the section of the tank where they remained stationary for the longest consecutive number of recordings) was recorded, and then assigned a binary value of either 0 (sections 1-4) or 1 (sections 5-8), in order to denote settlement in proximity to, or at distance from, the noise source. To investigate whether treatment affected the movement behaviour of crabs, the number of times that a crab remained in the same section for two or more consecutive recordings was recorded, to generate a number of pauses for each crab. Further to this, the amount of time that a crab spent stationary during the trial, when paused in such a manner, was also calculated. Finally, the number of steps moved between each 30 second recording was recorded as a potential indication for speed/ erraticism of movement.

Data were analysed with GLM's, using the binomial family (for settlement) and the Gamma family (for time far from noise source, number of steps moved, number of pauses and time stationary). Data were evaluated for normality using the Shapiro-Wilk test (Shapiro and Wilk, 1965), as well as by visual inspection of plots. The full models for all factors initially included temperature and noise treatment, as well as their interaction and an interaction between these and prior noise exposure, in order to test for any potential acclimation to noise treatments. Trial number and crab carapace size were also included, as well as specific track played, to account for any differences in sound profile between the different kinds of ship noise. The model simplification method (Crawley, 2011) was employed and non-significant terms removed. Models were assessed for best fit using the Aikake Information Criterion (AIC) and the model with the lowest AIC chosen, with a threshold difference of ≥ 2 (Burnham and Anderson, 2004).

Post-hoc testing was carried out on models using the lsmeans package (Lenth, 2016) in order to determine which combined treatment groups drove significant changes in noise avoidance or movement behaviours, with p-values adjusted according to the Tukey method for comparing a family of four estimates.

Results:

Antipredator Retreat

Retreat Likelihood:

Crabs exposed to ship noise treatments took refuge in response to a simulated predatory attack significantly less often than those crabs experiencing ambient noise (glm $\chi^2_{1,291}$=4.45, p=0.035 (Figure 2.3a,b)). Neither the interaction between temperature and noise treatments, nor temperature alone, had a significant effect ($\chi^2_{1,289}$=0.081, p=0.776; $\chi^2_{1,290}$=2.06, p=0.151 respectively). Prior noise exposure, and the interaction between noise treatment, temperature and prior exposure, as well as the specific track played during trials, were also originally included in the model, but were removed as they did not significantly affect the model's deviance.

Retreat Time:

Of those crabs that responded to simulated predatory attack, time to retreat was significantly impacted by the interaction between temperature and noise treatment ($\chi^2_{2,118}$=10.3, p=0.002 (Figure 2.4a,b)), with crabs in Cold-Ambient treatment groups retreating significantly less quickly than those in Hot-Ambient treatment groups (Z= -2.73, P=0.032). When single stressors were analysed without regard to an interaction, neither overall noise or temperature treatment alone had a significant effect upon response time ($\chi^2_{1,119}$=1.19, p=0.305; $\chi^2_{1,119}$=2.06, p=0.138, respectively). Specific track played during trials, prior noise exposure and the interaction between treatment, noise and prior noise exposure were all initially included in the model, but were ultimately removed as they did not affect the model's deviance.

Key findings:

- Crabs were less likely to retreat to shelter in response to a simulated predatory attack when exposed to ship noise playback than those exposed to ambient noise.
- Crabs were slowest to retreat under the combination of Cold temperatures and Ambient noise playback.
- Crab retreat behaviour revealed no evidence of acclimation to ship noise based on prior exposure during the 8-week luminance change experiment.

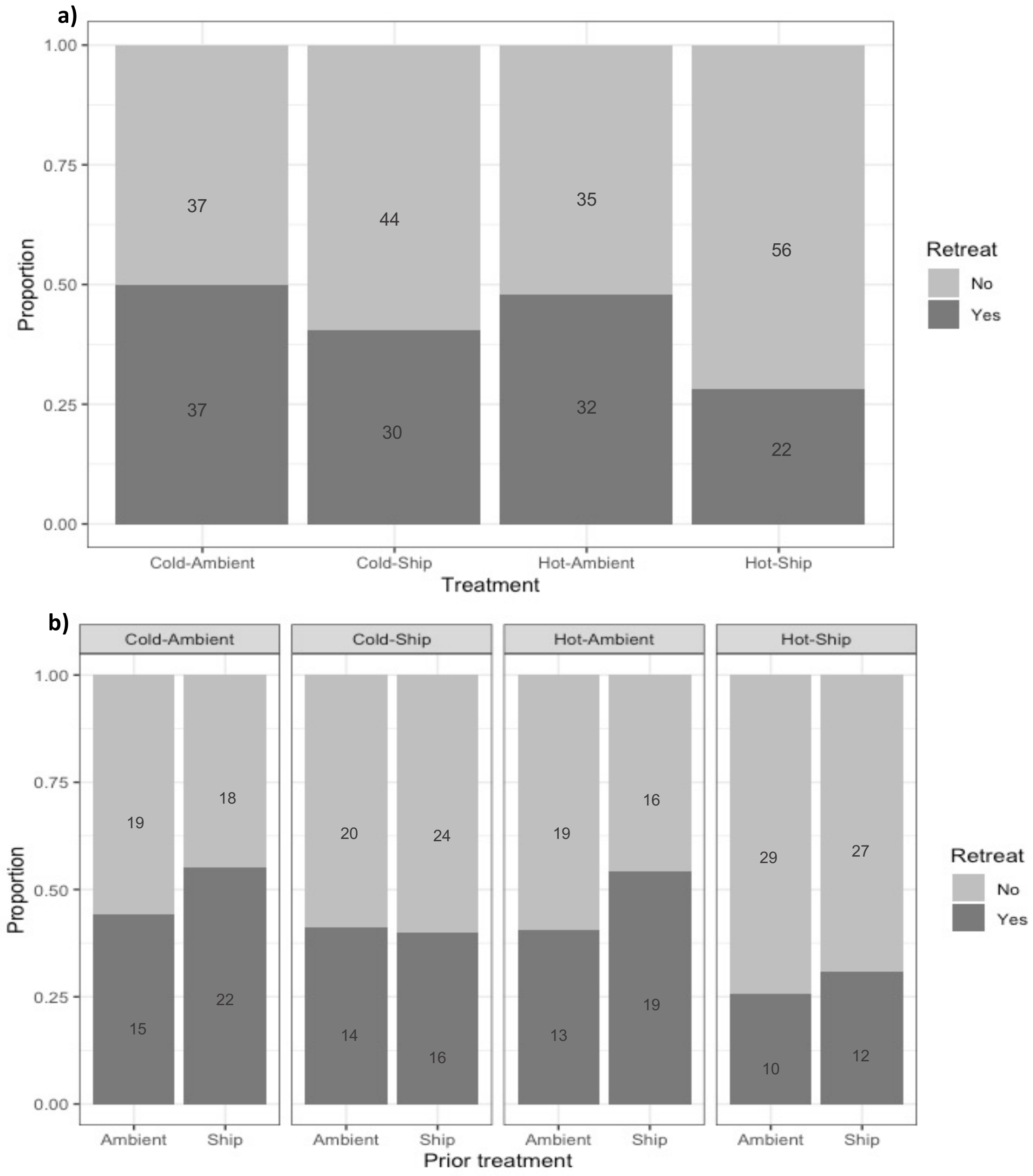

Figure 2.3: Crabs exposed to ship noise were less likely to respond to a simulated predatory attack by retreating to shelter than those exposed to only ambient noise. Of the four combined treatment groups, crabs in Cold-Ambient groups were more likely to retreat than crabs exposed to hot temperature treatments, and/or ship noise (a), and this response was not significantly impacted by prior exposure to noise treatments (b).
a) Proportion of crabs exhibiting retreat behaviour in response to a simulated predatory attack, or displaying no response, with **b)** accounting for prior noise exposure. *Sample sizes given.*

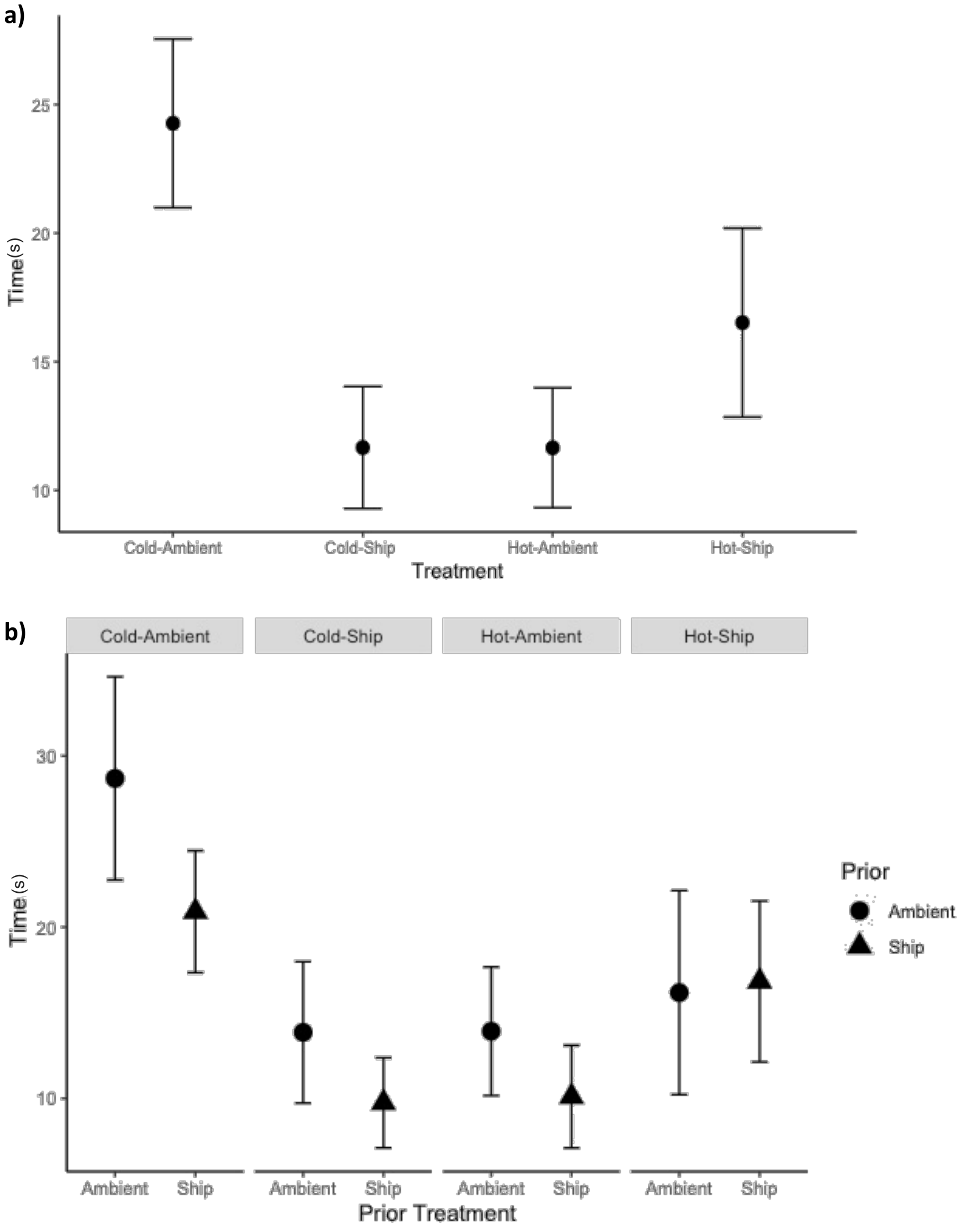

Figure 2.4; Of those crabs that displayed retreat behaviour in response to a simulated predatory attack, crabs exposed to cold temperatures and ambient noise responded slower than crabs exposed to hot temperatures and/or ship noise. There was no impact of prior noise exposure upon time taken to retreat.

- **a)** Mean time to retreat to shelter among crabs that responded to a simulated predatory attack, with standard error
- **b)** Mean retreat times among crabs that responded, with standard error, separated by prior noise exposure during the 8-week luminance change experiment. Triangular points represent individuals that had previously been exposed to ship noise, and circular points denote individuals previously exposed to only ambient noise.

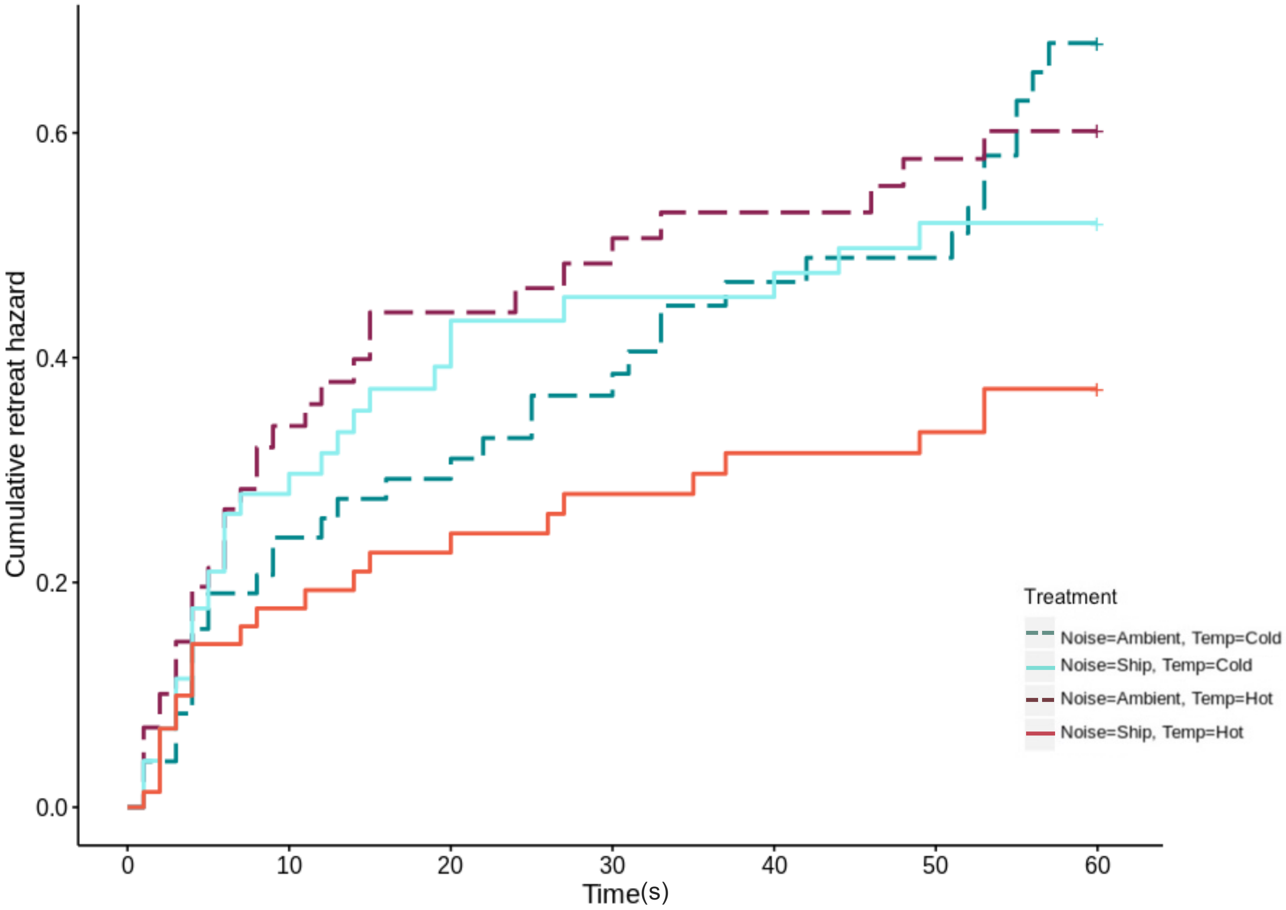

Figure 2.5: Proportional hazard ratio of crab retreat over the 60 second trial period. (All four groups contain censored individuals – those that failed to retreat during the experiment (denoted by "+").

A proportional hazard model testing the significance of the interaction between noise and temperature treatment upon likelihood of crab retreat at any given time point was employed but found to violate the assumptions of proportionality. When stratified by temperature treatment, noise did not significantly affect retreat likelihood (H=0.7284, p=0.082).

Antipredator Burial

Burial Likelihood:

Temperature significantly affected how likely crabs were to respond to a simulated predatory attack by exhibiting burial behaviour (glm $\chi^2_{1,156}$=4.19, p=0.041), with crabs in Hot treatments less likely to bury. Crabs that had previously been exposed only to ambient noise were also less likely to bury ($\chi^2_{1,156}$=11.59, p=<0.001) (Figure 2.6a,b). Noise treatment during trials did not have a significant effect ($\chi^2_{1,154}$=0.290, p=0.590). The interaction between noise treatment, temperature and previous exposure, as well as the specific track played during trials were also originally included in the model, but were removed as they did not significantly affect the model's deviance.

Burial Time:

Of those crabs responding to the simulated predatory attack, there was no significant impact of noise or temperature treatment, or their interaction, upon the time taken to exhibit burial behaviour (glm $\chi^2_{1,20}$=0.034, p=0.827; $\chi^2_{1,20}$=0.159, p=0.637, $\chi^2_{1,17}$=0.080, p=0.738 respectively (Figure 2.7a,b)). The interaction between noise, temperature and prior noise exposure, as well as specific track played and prior noise exposure individually were also investigated, but were removed from the model as they did not significantly impact the model's deviance.

Key findings:

- Crabs were less likely to bury in response to a simulated predatory attack when exposed to Hot temperature treatments than those in Cold temperature treatments.
- The time taken to exhibit burial behaviour was not impacted by trial treatment conditions.
- Crabs that had previously been exposed to ship noise during the 8-week luminance change experiment were more likely under all trial treatments to exhibit burial behaviour than those that had previously been exposed to only ambient noise.

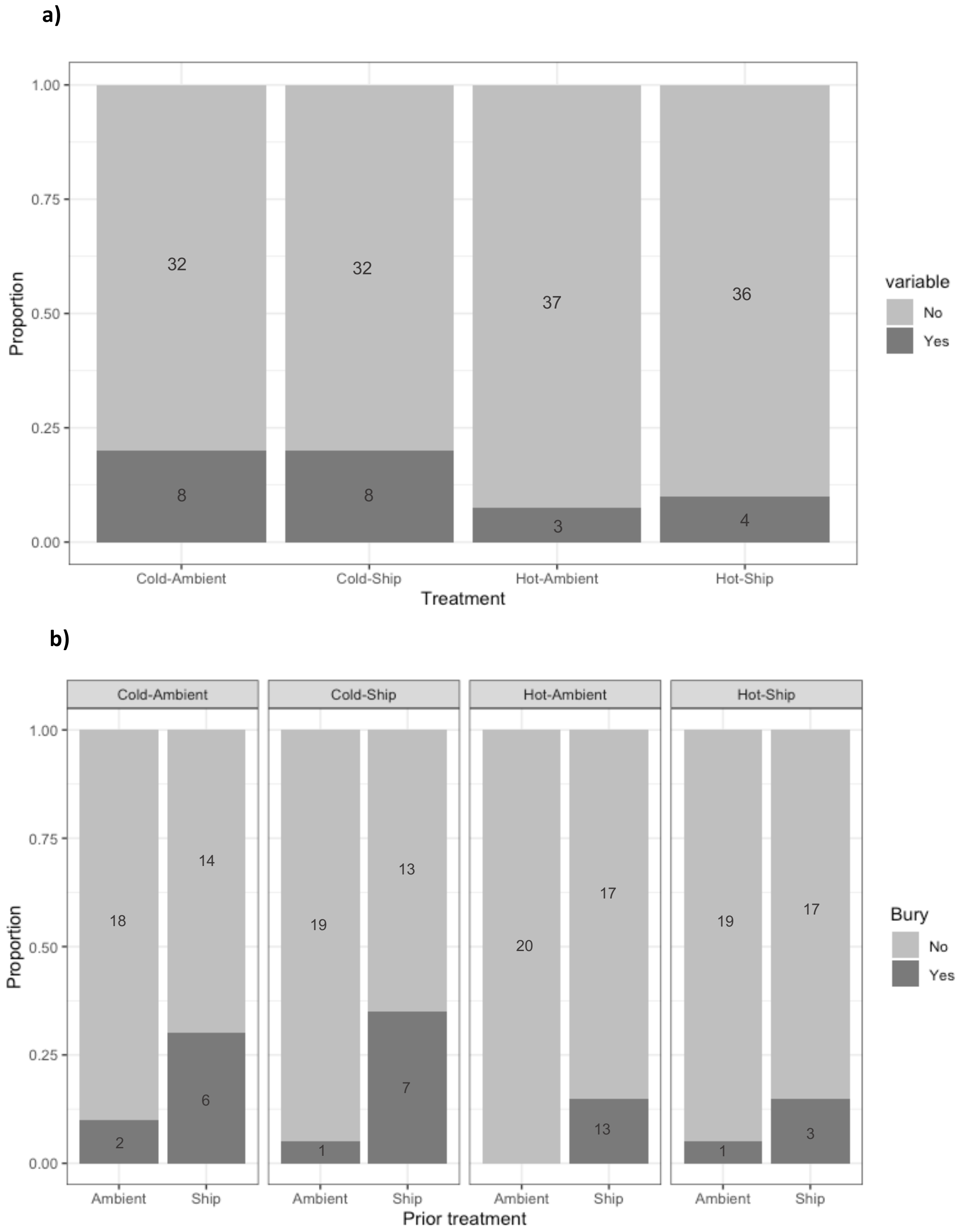

Figure 2.6: Crabs exposed to warm temperatures during a simulated predatory attack were less likely to respond by exhibiting burying behaviour than those exposed to Cold temperatures (a), with those having previously experienced ship noise (b) being more likely to bury than those previously exposed to only ambient noise*.*

a) Proportion of crabs exhibiting burial behaviour in response to a simulated predatory attack, or displaying no response, with **b)** accounting for prior noise exposure. *Sample sizes given.*

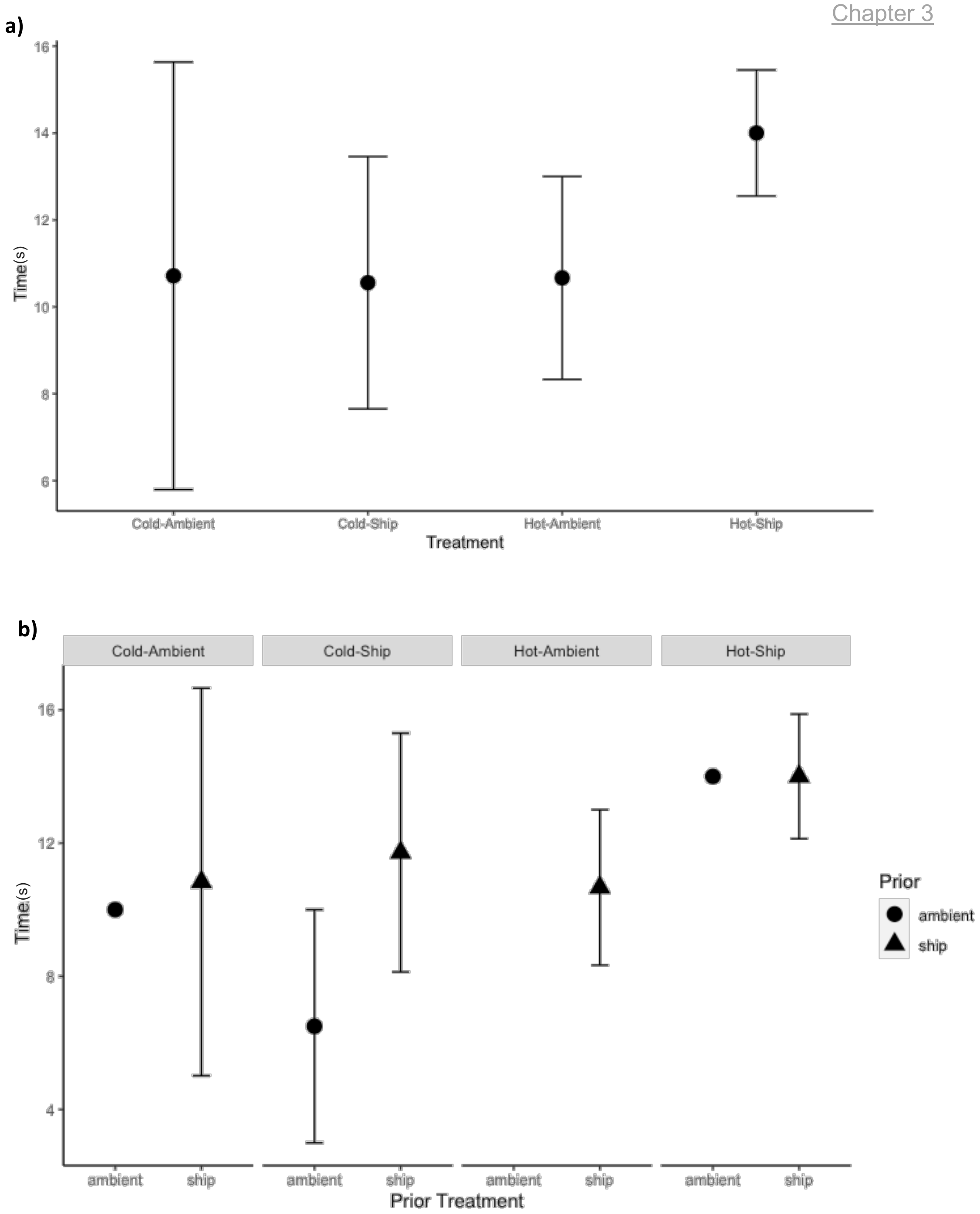

Figure 2.7 Of those crabs that did exhibit a burial response to the simulated predatory attack, time to bury was not influenced by the combination of temperature treatment and noise exposure (a), or by prior noise exposure (b)

a) Mean time to exhibit burial behaviour among crabs that responded to the predatory attack, with standard error.

b) Mean burial response times among crabs that responded, with standard error, separated by prior noise exposure during the 8-week luminance change experiment. Triangular points represent individuals that had previously been exposed to ship noise, and circular points denote individuals previously exposed to only ambient noise.

Noise Avoidance

Settlement position:

Crab ultimate settlement position (near/far from noise source) was significantly impacted by noise treatment ($\chi^2_{1,139}$=4.24, p=0.040), and by the specific track played during trials ($\chi^2_{5,136}$=12.3, p=0.031), with crabs exposed to ship noise settling, on average, further from the noise source than those exposed to ambient noise. Temperature was also significant, and crabs in Hot temperature treatment groups settled closer to the noise source than those in Cold temperature groups ($\chi^2_{1,141}$=19.9 p=<0.001).

The possibility of acclimation to noise treatments was investigated by the inclusion of prior treatment in the model, and there was a significant impact of the interaction between temperature treatment, noise treatment and prior noise exposure upon settlement position ($\chi^2_{3,136}$=9.22, p=0.027). Both Cold-Ambient and Cold-Ship groups that had previously experienced ship noise settled further from the noise source than Hot-Ambient and Hot-Ship groups (that had also previously experienced ship noise) respectively (Tukey: Z=3.13, p=0.037; Z=3.26, P=0.024) Figure 2.8)).

The interaction between temperature and noise did not significantly impact settlement position ($\chi^2_{1,106}$=0.091, p=0.763), and was removed from the model as it did not impact model deviance. Crab carapace size and trial number were also investigated, but were similarly removed as they did not significantly affect the model's deviance.

Time far from noise:

The amount of time spent far from noise was significantly impacted by the interaction between temperature treatment, noise played, and prior noise exposure ($\chi^2_{4,104}$=3.31, p=0.044). Both Cold-Ambient and Cold-Ship groups chose to spend more time farther from the noise than Hot-Ambient and Hot-Ship groups respectively (Z=-2.57, P=0.051, Z=-2.65, P=0.041), with the largest difference apparent between the responses of Hot-Ambient and Hot-Ship groups (Z=2.85, P=0.023).

The interaction between temperature and noise ($\chi^2_{1,142}$=0.061, p=0.699) did not significantly impact the amount of time spent far from the noise, nor did noise alone ($\chi^2_{1,145}$=0.025, p=0.801), and both were removed from the model as they did not impact model deviance. Crab carapace size, trial number, and specific track played were also investigated, but were removed as they did not significantly affect the model's deviance.

Key findings;

- Ship noise playback caused crabs to be more likely to settle in areas of the treatment tank farthest from the noise source than those exposed to only ambient noise.
- Crabs exposed to Hot temperature treatments settled closer to the noise source and spent less time far from the noise source, under both ship noise and ambient noise playback than those exposed to Cold temperature treatments.
- Crab noise avoidance behaviour was impacted by the interaction between trial treatment and prior noise exposure, however this was not suggestive of acclimation to ship noise over time.

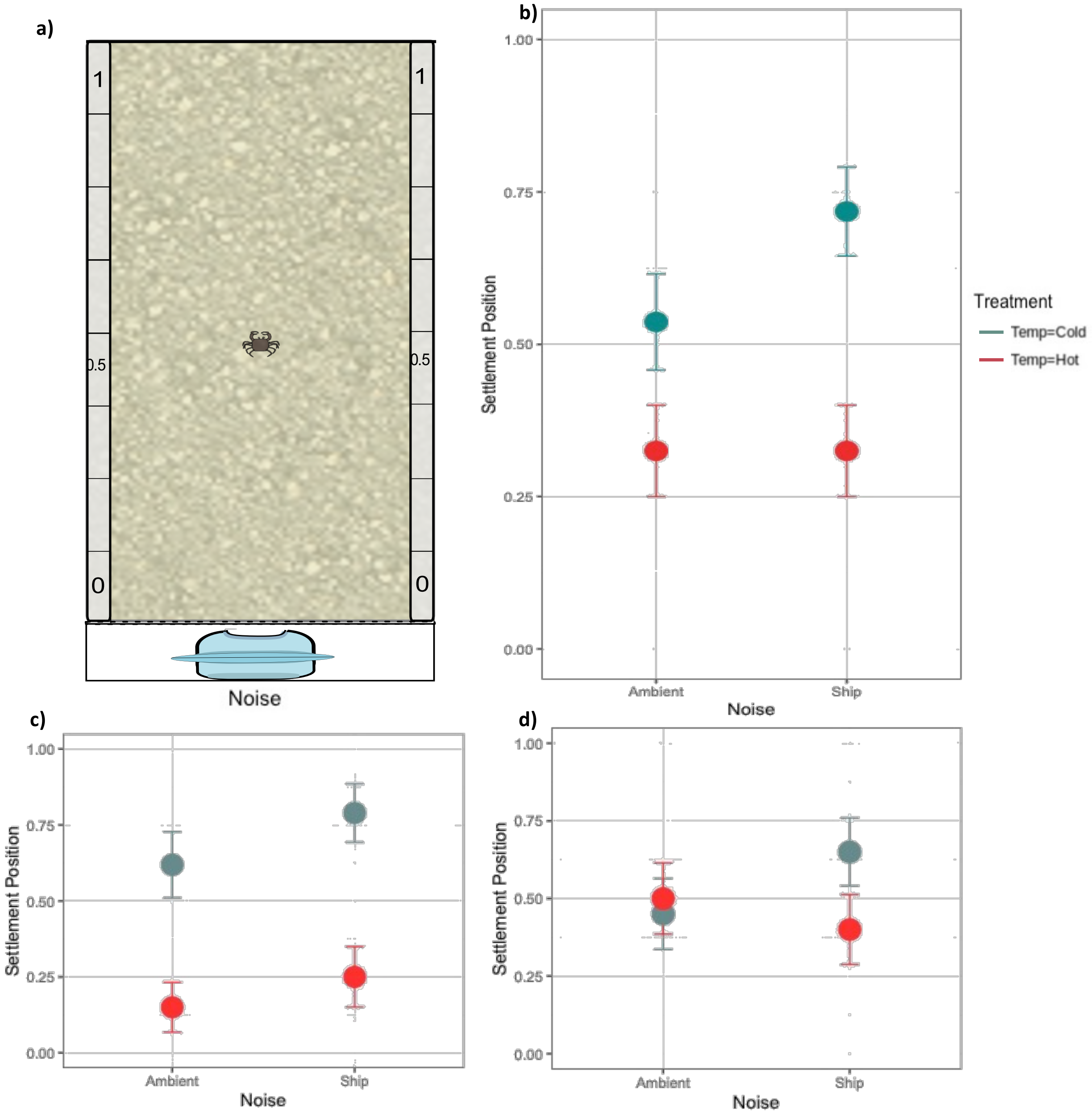

Figure 2.8: Crabs settled closer to the noise source at higher temperatures (b). Crabs that had previously been exposed to ship noise showed a greater disparity in settlement position between treatments, with Hot treatment crabs settling, on average, closer to the noise source than Cold treatment crabs (c). This disparity was less apparent in those crabs that had previously only experienced ambient noise (d).

(a) Crab ultimate settlement position within marked tank sections was assigned a proportional value between 0 and 1, with 0 representing settlement closest to the noise source, and 1 representing a settlement position at the furthest distance from the noise.

b) Mean settlement position among crabs from Hot and Cold treatment groups, in trials conducted under either Ambient or Ship noise.

c) Mean settlement position of crabs that had previously been exposed to Ship noise during the 8-week luminance change experiment.

d) Mean settlement position of crabs that had previously been exposed to only Ambient noise.

Movement

Steps moved:

Crab carapace size affected the mean number of sections moved by crabs between each 30 second recording interval ($\chi^2_{1,141}$=7.72 p=0.005), with larger crabs moving further than smaller crabs. Crabs under cold temperature treatments also travelled a greater number of steps than those under hot temperatures ($\chi^2_{1,145}$=2.56, p=0.007 (Figure 2.9a)).

Noise played during trials did not significantly impact the number of steps moved ($\chi^2_{1,145}$=0.466, p=0.246). Trial number, prior noise exposure and the interaction between temperature, noise and prior exposure, as well as the specific track played, were also investigated, but were removed as they did not significantly affect the model's deviance.

Pausing:

The interaction between noise, temperature and prior noise exposure did not significantly impact the number of times crabs paused during the trial period ($\chi^2_{5,141}$=1.03, P=0.35). Noise played during trials also had no effect ($\chi^2_{1,145}$=0.008, p=0.836) nor did temperature or prior noise exposure individually ($\chi^2_{1,145}$=0.171, p=0.324;) $\chi^2_{1,146}$=0.387, P=0.138 respectively).

Trial number, crab carapace size, the interaction between temperature and noise, as well as the specific track played, were also investigated, but were removed as they did not significantly affect the model's deviance.

Time stationary:

Noise did not significantly affect the maximum amount of time that crabs spent stationary in one section ($\chi^2_{1,130=}$0.176, p=0.187) (Figure 2.9b). However, time spent stationary was impacted by temperature, with crabs in Cold treatment groups spending significantly less time stationary than those in Hot treatment groups ($\chi^2_{1,131}$=1.68, p=<0.001). This response was also impacted by prior noise exposure ($\chi^2_{1,145}$=0.838, p=0.003), though pairwise comparisons did not reveal any significant differences between those crabs experiencing ship noise for the first time combined with either Hot or Cold temperature treatments, compared with those that had previously been exposed to ship noise during the 8-week luminance change experiment (Z=-2.94 p=0.065). The largest difference in time spent stationary was notable between those crabs under Hot treatments, having previously experienced only Ambient noise, and those crabs under Cold temperatures, having been previously exposed to Ship noise (Z=-5.03, p=<.0001).

There was no significant impact upon time spent stationary of the interaction between temperature and noise ($\chi^2_{1,144=}$0.006, p=0.806), or between temperature, track and prior noise exposure ($\chi^2_{4,141=}$ 0.730, p=0.095). Trial number and crab carapace size, as well as the specific track played, were also investigated, but were removed as they did not significantly affect the model's deviance.

Key Findings;

- Crab movement was generally slower and less efficient under Hot temperature treatments than Cold temperature treatments, with Hot treatment crabs covering shorter distances, and remaining stationary for greater periods of time during trials.
- Movement behaviour was not affected by the different noise treatments played during the trials.
- Crab movement behaviour did not suggest acclimation to ship noise over time.

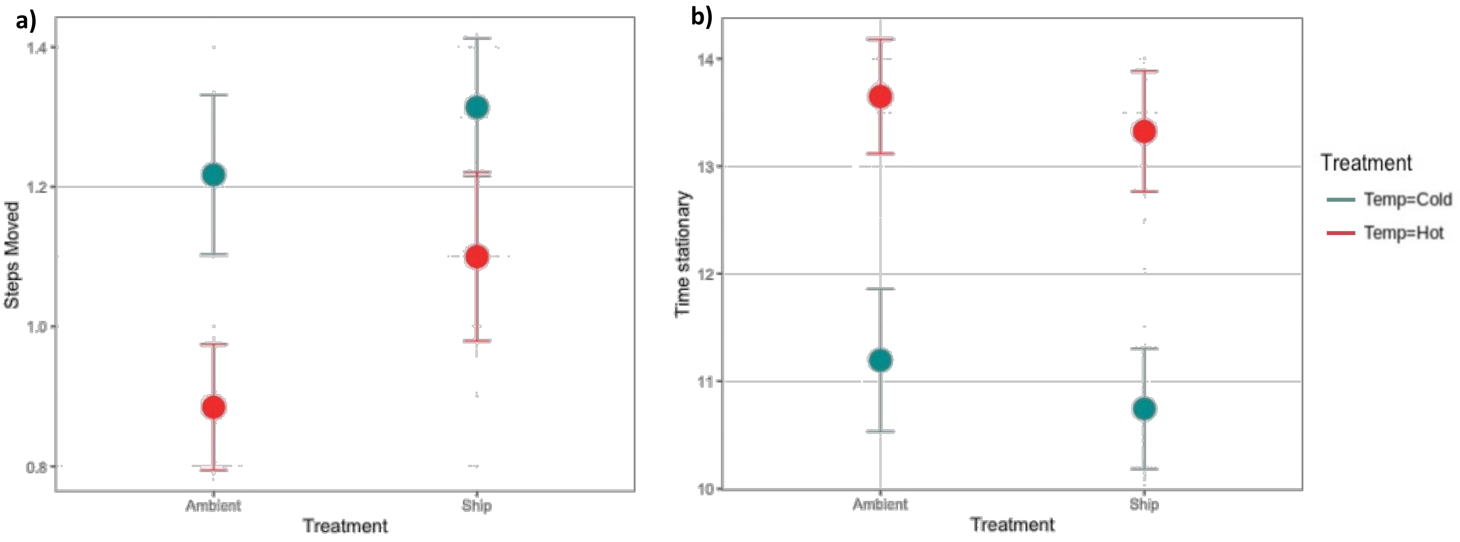

Figure 2.9: Crabs in Cold treatment groups moved further per recording interval, and spent less time stationary, than crabs in Hot treatment groups, under both noise treatments.

a) Mean number of steps moved per 30 second recording interval.

b) Mean number of times crab remained in one section for two or more consecutive recordings.

Discussion

The combined stressors of temperature and noise had a significant and complex impact on crab movement and antipredator behaviour. In accordance with previous studies (e.g. Carter, 2019), those crabs experiencing ship noise playback were less likely to retreat from a simulated predatory attack than those exposed to ambient playback at the same amplitude (Figure 2.3). However, retreat times of crabs that did respond were slowest in Cold-Ambient treatment groups (Fig. 2.4), suggesting that lower temperatures have the potential to increase response latency. Crabs exposed to the stressor combinations did exhibit noise avoidance behaviours, which were impacted also by temperature, with crabs in Cold treatments settling further from the source of noise than those in Hot (Fig. 2.8). Crab mobility was also impacted by treatment temperature, and crabs in cold treatments travelled longer distances between recordings and remained stationary for shorter periods of time during trials (Fig. 2.9). The results presented here demonstrate complex impacts of stressor interaction upon juvenile *C. maenas* movement behaviour, which could have direct consequences for crab survival.

Maladaptive responses to stressor exposure are particularly concerning when they affect behaviours key to survival. As in Chapter 2, the results presented here clearly reveal the impacts of noise pollution upon a non-auditory reliant behaviour, also known as a cross-modal sensory effect (Halfwerk and Slabbekorn, 2015). The reduced ability of crabs to respond appropriately to predators in the presence of ship noise could result in mortality, and has now been demonstrated across multiple studies (Wale, Simpson and Radford 2013b; Carter, 2019) and in a range of other species (e.g. Siemers and Schaub, 2010; Bruintjes and Radford, 2013; Simpson, 2014; 2016a,b). It has been posited that the physical qualities of ship noise in comparison with natural sounds distract attention from antipredator vigilance behaviours, which reduces capacity for predator detection (Chan et al., 2010; Wale, Simpson and Radford 2013b; Carter, 2019), and they could also result in the favouring of vital noise avoidance behaviours to preserve sensory systems. This theory is supported by the results described above, with crabs exposed to ship noise treatments choosing to settle farther from the noise source, an effect which has also previously been recorded (Carter, 2019).

It is feasible that increased stress resultant from noise pollution incurs a metabolic cost, and therefore available energy for flight response may be reduced (Wale, Simpson and Radford 2013b; Simpson, Purser and Radford, 2015; Ruiz-Ruiz et al., 2019). In this event, it would be even more important for individuals to avoid false responses to predatory attack, which could reduce available time for vital activities such as foraging or mate encounter (Vanhooydonck and Van Damme, 2003; Eilam, 2005; Gifford, Herrel and Mahler, 2008;). However, increases in response latency are directly linked to organism mortality, with predation risk increasing the longer the prey remains in the open (Vanhooydonck and Van Damme, 2003; Gifford, Herrel and Mahler, 2008).

It has previously been suggested that noise pollution induces a cognitive response in affected animals (Chan et al., 2010; Hasan et al., 2018), particularly those that rely on auditory cues to sense predators and may mistake additional noise for imminent predatory danger (Klump and Shalter 1984, Gyger et al. 1990; Quin et al 2006). However, this is perhaps a less likely explanation than increased stress levels, due to the fact that novel anthropogenic noise stimuli are unlikely to align with predatory search image.

Further, crabs in Hot treatment groups under both ship and ambient noise responded less often than those in Cold groups. Higher metabolic rates in crabs experiencing higher temperatures may prompt increased energy demands and foraging necessity, meaning that the trade-off between remaining in the open and the possibility of being predated is more heavily weighted in favour of foraging opportunity (Wallace 1972). This motivation is, however, difficult to extrapolate from this study. Although some crabs were observed to be sifting the substrate in search of food, no food was provided, so it is unclear whether crabs given the opportunity to forage successfully within the trial period would have prioritised this over predation likelihood or not.

Of those crabs that did retreat from a predator, it is perhaps surprising then that Cold-Ambient treatment crabs recorded the slowest response times. It is possible that those crabs that did respond and register the predator were more stressed under conditions of high noise, and so responded faster than those crabs experiencing only ambient noise. Lower temperatures are also commonly associated with slower movement and reduced metabolic rates in crustaceans (Weinstein and Full, 1998), and so this could have served to further increase response latency.

Many species of crab are also known to exhibit burial behaviour as a form of antipredator defence (Bellwood, 2002). In initial retreat trials, a number of crabs were anecdotally noted as performing such behaviours, resulting in them being recorded as not responsive to the predator, or extending the recorded time it took them to reach shelter. Subsequent trials focussing on burial behaviour illustrate an impact of temperature upon burial likelihood, with crabs in Hot treatment groups less likely to bury than those in Cold treatment groups. However, overall numbers of crabs that responded to a predatory attack by burying were very low.

Buried crabs exhibit lower cardiac activity, ventilatory and metabolic rates than non-buried crabs, and the behaviour is often performed for extended period of time to allow crabs to enter a torpor-like state, where energy reserves may be protected. This has been documented as occurring mainly under colder temperatures (Rebach, 1974). It may be that the lower temperature in Cold treatment groups made crabs more pre-disposed to choose this behaviour in response to a predator, serving the dual function of conserving energy and avoiding predation.

Additionally, it has previously been found that burial of hermit crabs under conditions of raised temperature can result in shell abandonment and reduced survival (Valère-Rivert et al., 2017). During burial, crabs continue to respire, though the rate of respiration is reduced (McGaw, 2005) It may be that under conditions of increased temperature, and thus decreased dissolved oxygen, the ability to oxygenate sufficiently while buried is reduced, reducing crab likelihood of choosing this behaviour to escape predators.

It may also be the case that crabs in Hot treatment groups were simply more active due to higher metabolic activity (Wallace, 1972), and therefore were more likely to reach shelter, while Cold crabs were more likely to simply remain in place for longer, increasing the likelihood of burial behaviour. In ectothermic species, temperature, combined with body size, is a key factor in antipredator movement, with larger individuals remaining more inactive at lower temperatures than smaller individuals at high temperatures (Cury de Barros et al., 2010).

However, antipredator behaviours under increased temperatures vary among species, for example, guppies at high temperature have been observed to form tighter schools, swim faster and display increased predator inspection behaviours than at cooler temperatures (Weetman, Atkinson and Chubb 1998). Meanwhile under increased temperature, antipredator flight initiation distances of certain bird species decreased, possibly due to increased costs (heat stress) associated with potential movement (Fernández-Juricic, Jiminez and Lucas 2002).

It is feasible that crabs which failed to respond by either burying or retreating to shelter were in fact responding to the predatory attack in different ways not recorded in the data. It could be that crabs relied on a freeze response and their camouflaged carapaces to hide from visually guided predators in plain sight, rather than risk creating a visual cue by fleeing. However, as all crabs had been held on white substrates for 6 weeks prior, non were particularly well camouflaged to the mixed sand substrate of the trial arena and so this seems improbable. It is also possible that crabs were directionally fleeing from the predator, not seeking to hide, but simply to leave the area as quickly as possible, only to be hindered by the enclosed sides of the arena. Directional movement trials could shed light on impacts of noise and temperature on flight responses to simulated predatory attacks. Expanded study in this area could help to fully investigate these behaviours and to reveal preferred methods of predator evasion under different conditions.

The results of predation trials using model predators are always difficult to extrapolate to impacts in natural environments. The model predator used here was a dowel rod to simulate a beak strike by a predatory seabird- a common predator of juvenile crabs. Crab detection of such a predator would commonly be via visual cues rather than chemical as may occur with some underwater predators such as fish. However, it is possible that over the previous 7-week trial period, crabs could have become less sensitive to overhead shadows due to essential maintenance and husbandry by research staff. Previous studies have also suggested that where predators are removed, crabs perform antipredator behaviours less readily (Reznick et al., 2008). Future study on in-situ predation of crabs affected by stressors could help to investigate these ideas at ecosystem level, perhaps through the use of mesocosm style experiments. However, this becomes challenging when applying multiple stressors, hence the methods chosen in this study.

It could also be suggested that, presented with an open arena, crabs may have been distracted from predatory threat under conditions of anthropogenic noise, and instead perform direction movement behaviours to escape potentially damaging conditions. Noise avoidance behaviour may reduce damage to sensory systems caused by extreme stimuli and therefore this may take precedence over, or at least provide distraction from, predator detection. Indeed, in the mobility trials performed here, crabs exposed to ship noise chose to settle farther from the source of the noise than those exposed to ambient noise. Treatment temperature also significantly impacted this behaviour, with crabs in Cold treatments spending more time, and ultimately settling, further from the source of noise than those in Hot treatments (Fig. 2.7).

Continuity of movement was also found to be impacted by temperature and also by size, but not by noise treatment (consistent with findings by Carter (2019)). Crabs in Cold treatments moved further between readings, as did larger crabs, and also spent less of the trial period stationary than Hot treatment crabs (Fig. 2.8). The impact of temperature upon movement behaviours noted here is complex, and may help to predict or explain *C. maenas*' invasive potential across different thermal gradients to its native range. The movement data in this trial are in contrast with the faster response times of Hot temperature treatment crabs found in the antipredator trial. It is possible that in the absence of a predator, the cost of movement (i.e. heat stress as previously discussed (Fernandez-Juricic, Jiminez and Lucas 2002)) were too high, causing the lower rates of movement seen here.

The results presented here do not suggest any positive acclimatisation to ship noise over time, with those movement behaviours that were negatively affected by ship noise being equally impacted whether crabs had previously been exposed to it during the 6-week colour change experiment in Chapter One or not. It is possible that the constantly variable nature of *C, maenas'* intertidal habitat could prevent them from being predisposed to acclimatisation over time, simply because twice a day conditions are refreshed and stressors acting upon individuals change. This could explain why noise avoidance behaviour persists in this highly motile species, as movement is likely a faster and more efficient way to avoid stressors than gradual acclimatisation, which could result in increased predation risk. Many shallow water and intertidal species have been recorded using movement behaviours or relocation to avoid unfavourable conditions, such as range shifts of key intertidal invertebrates (Mieszkowska et al., 2006a,b), or polyp bail-out in corals (Fordyce et al., 2017).

The crabs in this study had previously experienced ship noise exposure for six weeks, whilst in a previous study, crabs were still not found to have acclimatised after a period of eight weeks (Carter, 2019). Although longer term studies could investigate this more thoroughly, for juvenile *C. maenas,* it is unlikely that acclimatisation after this period of time would confer any ecologically relevant advantage, as the likelihood of predation would be high. It is also unlikely that ship noise would be consistent enough over this time period to prompt acclimatisation. Distinction has been made between the likelihood of acclimation in response to continuous versus infrequent exposure to anthropogenic noise (Smith, Kane and Popper, 2004; Wysocki, Dittami and Ladich, 2006; Masini et al., 2008), and given that noise is a local pollutant in the marine environment, commonly caused by transient shipping activity, the emerging evidence that ability to acclimatise may be impaired under sporadic exposure warrants more thorough investigation.

Conclusions

The impact of marine noise pollution upon predator-prey interactions is increasingly being explored, however a lack of knowledge persists for invertebrate species in particular, and studies investigating interaction of multiple stressors upon locomotion and predator evasion are scarce to non-existent. In this chapter, both ship noise and temperature rise were found to differentially impact movement and antipredator behaviours of *C. maenas*. Ship noise impacted antipredator response of juvenile crabs, with potentially severe consequences to mortality. Whilst impacts of temperature were more varied and complex, they nonetheless form an important step in predicting how interaction between stressors may affect community structure in an ecologically relevant context.

Chapter 4: Discussion

Key findings and Implications for Multiple Stressor Studies

My thesis presents the first exploration of the impacts of a combination of local and global stressors upon the camouflage and antipredator behaviour of an intertidal crustacean. In Chapter 1 I present evidence of an interaction between anthropogenic noise and raised temperature on crab morphology and physiology. Crab camouflage after 6 weeks was less effective under the influence of ship noise, with this stressor dominating over the impacts of increased temperatures, whereas crab growth increased under higher temperatures, regardless of ship noise. While stressors interacted antagonistically in their impacts on growth and camouflage ability, impacts on mobility and antipredator defence behaviour were more varied. Crabs exposed to anthropogenic noise were less likely to demonstrate antipredator avoidance behaviours, with crabs in Cold temperature treatments exhibiting increased latency of response. Noise pollution also prompted directional avoidance behaviours, which were affected by temperature, with increased temperatures reducing continuity of movement.

Multiple Stressors and *Carcinus maenas.*

My study demonstrates that two opposing stressors of elevated temperature and anthropogenic noise act antagonistically upon camouflage and growth in the common shore crab, *Carcinus maenas*, such that a possible stressor dominance is seen in each response variable. Dominance of a single stressor resulting from stressor interaction has been demonstrated across several other studies, perhaps most notably by Folt *et al*. in 1999, but also in contemporary work. For example, the two stressors of fishing pressure and coral bleaching might be assumed to be synergistic, based on their individual detrimental impacts on coral cover, however, bleaching was found to be the dominant stressor when applied in combination, resulting in an overall “antagonistic or weakly additive” interaction (Darling, Mclanaghan and Cote, 2010).

When tested in isolation, temperature increases rates of luminance change in *C. maenas* (Mynott, 2018). Although shore crab camouflage does not directly rely on temperature cues, higher temperatures are known to increase rates of protein synthesis and may mean that more energy is available for production of chromatophores and pigments (Whiteley, Taylor and El Haj, 1997; Mynott, 2018). However, this pattern is only consistent where slow acclimation to temperature in employed, as seen in this study and that by Mynott (2018). Acute increases of temperature are associated with reduced neuromuscular function, physiological deterioration and respiratory stress (Stephens 1957; Powell, 1962; Winch and Hodgson 2007; Jiang et al., 2018). In this way, temporal manipulation of stressor introduction may have significant impacts on response and studies should seek to employ ecologically relevant timescales of stressor presence and development where possible.

Outcomes of stressor interaction may also be heavily impacted by temporal variability of stressor introduction (Molinos and Donahue, 2010; Hiltunen, Ayan and Becks 2015). While crabs in this study were allowed an adequate acclimation period to reach higher treatment temperatures as described above, ship noise treatments were applied immediately at the commencement of the experimental period. In natural environments, these stressors would likely have different rates of introduction, with sea surface temperatures gradually increasing over time and ship noise being a highly variable and sudden source of stress. Consideration of temporal introduction of stressors, particularly in laboratory settings, may help studies better represent ecologically relevant effects of stressor interactions.

Intertidal species, more so than many other marine species, are commonly subjected to extremes of environmental factors, including temperature, which could prompt predisposed tolerance of changing thermal environments (Whiteley, Taylor and El Haj, 1997). However, this variability may also mean that intertidal species are more likely to already live close to their thermal tolerance limits, and therefore be increasingly vulnerable to end of century warming scenarios (Stillman and Somero, 2000). Studies have presented temperature as a source of stress for many intertidal species (e.g. Winch and Hodgson 2007; Jiang et al., 2018), resulting in community level impacts and prompting shifts in species range (e.g. Mieskowska et al., 2006).

Temperature ranges experienced by intertidal species also vary according to species position on the shore, with those species inhabiting the mid-high region of temperate rocky shores exposed to significantly higher temperature ranges, spanning approximately 0°-32°C, than those inhabiting the low shore (Stillman and Somero,1996; 2000). This range varies diurnally and seasonally, and it has been suggested that ectothermic species adjust physiological traits according to seasonal temperature patterns (Paaijmans et al., 2013). My study tested crabs collected across seasons to minimise this effect, particularly given that previous studies have discovered that critical thermal maximal temperature (CTMax) differs significantly in crabs collected in different seasons, and this difference is not mitigated by acclimation under laboratory conditions (Cuculescu, Hyde and Bowler, 1998).

Juvenile *C. maenas* most commonly inhabit the mid to higher reaches of rocky shores, and as such are subject to the most wide-ranging temperatures. Their exceptionally wide thermal tolerance has seen them labelled as a eurythermal species and this ability is commonly associated with their success as a globally invasive species (Kelley, de Rivera and Buckley, 2011, 2013, 2015; Lehnert et al., 2018). CTMax has been noted to differ between invasive populations (Kelley, de Rivera and Buckley, 2014), indicative of long-term adaptation to different temperature scenarios. This adaptation has been linked to the emergence of genetically distinct populations of invasive *C. maenas* over relatively short timescales, with morphological differences in traits such as size also noted (Kelley, de Rivera and Buckley, 2011).

C. maenas' presence in non-native environments can have devastating effects on host ecosystems, and also impact socio-economic activities (Garbary et al., 2014; Floyd and Williams, 2004; Lafferty and Kuris 1996). Increased focus on the thermal tolerance ranges and physiological differences between disparate invasive groups may help to reveal the drivers behind the species' global spread. Perhaps more importantly, studies into stressor combinations and susceptibility between different populations could explore whether invasive crabs may have developed more resilience than their native counterparts in order to enable them to continue to expand their range to novel conditions, potentially helping to guide future mitigation efforts.

Cross-modal implications of stressors have not been studied in depth, but are particularly important to consider. As yet relatively understudied, but demonstrated clearly in this study and in several others (e.g. Wale, Simpson and Radford, 2013b; Hasan et al., 2018; Carter, 2019, Carter, Tregenza and Stevens, 2020), the effects of stressors on behaviours not directly related to them can be dramatic, but often less immediately obvious. Noise pollution has perhaps been linked to more cross-modal sensory impacts than other stressors and although suggestions have been made that intertidal species may be more resilient to noise pollution, by virtue of living in environments subject to constantly fluctuating noise (Leduc et al., 2021), the dominance of noise as a stressor presented in my study contradicts this. Further study into cross modal sensory effects is essential, particularly in the face of stressor interactions, where prediction of impacts becomes increasingly complex.

Given the relatively short timescales of response to thermal stress noted in this species, it is possible that in this study, crabs in high temperature treatment groups acclimatised sufficiently to warmer temperatures throughout the six week colour change period, such that in behavioural trials effects of temperature as a stressor were more difficult to extract. However, fluctuations in environmental factors and stressor combinations have been associated with reduced rates of development of antipredator defences, and this has been demonstrated in microbial communities (Hiltunen, Ayan and Becks, 2015). Antipredator defence development is also impacted by predator density (Laurila et al., 2004; Lima and Bednekoff, 1999), a factor which was not present in my laboratory-based study. For this reason, mesocosm or field studies of stressor interactions may help reveal more ecologically applicable ecosystem level effects, although these kinds of studies present methodological difficulties, amplified with the introduction each additional stressor (Crain et al., 2008).

Tolerance to Stressor Interaction

My study found evidence of noise avoidance behaviours in *C. maenas* in response to anthropogenic noise pollution, a behaviour previously noted in juveniles of this species (Carter, 2019) and in other marine species including cetaceans (Kok et al., 2018) and terrestrial species such as songbirds (Liu, Slabbekoorn and Reibel, 2020). Avoidance behaviours may also occur in response to other stressors, such as changes in temperature, or predation or fishing pressures (Siepielski and Beaulieu, 2017; Adams et al., 2018), and are not confined to motile species, with even sessile marine species such as corals able to perform polyp bail-out to avoid adverse conditions (Fordyce et al., 2017).

Avoidance of adverse conditions may enhance the short-term survival probability of affected species, reducing the need for energetically costly phenotypic plasticity, or the risk of physiological damage, and could explain the lack of camouflage ability under conditions of anthropogenic noise seen in Chapter 1. However, species shifts result in community level impacts that can have severe impacts upon trophic energy transfer, disrupting predator-prey interactions and impacting timing of reproductive events (Sorte, Williams and Carlton, 2010; Kharouba et al., 2018)

Long term exposure to adverse conditions may prompt irreversible shifts in species range, a behaviour particularly evident in the face of climate change, with global distributions of marine species shifting by ever larger increments and introducing new, potentially invasive species to different habitats (Mieskowska et al., 2005; 2006; Sorte, Williams and Carlton, 2010; Wallingford et al., 2020), resulting in not only ecological, but also socio-economic implications (Madin et al 2012). Alternatively, range shifts may allow some species to survive the imposition of global stressors which are not possible to manage effectively. Stressor-driven range shifts in predatory species may confer a survival advantage to those prey species which remain within the native range, provided that the arrival of novel predators does not negate this (Francis et al., 2009).

For behaviours directly impacted by stressors, such as oral signalling and communication under noise pollution, mechanisms for coping with these factors may be simpler and are often more apparent. For example, whales alter their call amplitude in response to masking by ship noise (Parks, Clark and Tyack, 2007, Parks et al., 2011) and songbirds in areas of high anthropogenic noise may alter the frequency and amplitude of their calls in order to cope with masking effects, however, it is not known whether this is associated with changes to call transmission efficiency or efficacy, or increased predation risk and energy expenditure (Read, Jones and Radford, 2014). Further study into both adaptation in the face of cross modal sensory effects and into the costs of phenotypic plasticity is vital to drive effective and focussed conservation efforts.

Life stage may also be a contributing factor in stressor susceptibility. Adult *C. maenas* have wider thermal tolerances than larvae (de Rivera et al., 2007; Compton, Leathwick and Inglis, 2010). Juveniles are less well studied but this study, among others, suggests that their thermal tolerance ranges may be comparable with adults of the species (Kelley, de Rivera and Buckley, 2013; Mynott, 2018) This may be in part, driven by the different micro-habitats experienced at different life stages. Pelagic larvae experience comparatively narrow but frequently fluctuating thermal ranges throughout their developmental period in the open ocean, and these thermal cues impact development and settlement behaviour (Metaxas and Saunders 2009; Kelley, de Rivera and Buckley, 2013). Therefore, disruption to thermal environments may be detrimental to survival. Settling juveniles, on the other hand, experience rapidly changing, harsh environments of the upper and mid-shore intertidal environment, where they are only sporadically immersed, and may spend long periods out of water, or in shallow pools which overheat quickly. Immersion period has previously been linked to thermal tolerance in other crustacean species such as porcelain crabs, where longer immersed species had narrower thermal tolerances than those that spent greater periods of time out of the water (Stillman, 2002). Studies should aim to explore the impact of stressors across life stages, to create more reliable predictions of potential species tolerance and plasticity.

The potential to cope with stressors may in itself be impacted by the presence of multiple stressors as opposed to stressors in isolation. Certain species have been observed to exhibit positive co-tolerance where the addition of a second stressor increases tolerance to the first, and this may lead to community level tolerances to stressor combinations (Vinebrooke et al., 2004). Brown et al (2013) posited that stressor co-tolerance in itself may drive stressor interactions toward antagonistic outcomes, and this further elucidates the importance of considering long term developmental and behavioural changes in the face of combined, ecologically relevant stressors, as opposed to solo stressor studies.

The quantification of impacts of stressors and resultant changes in phenotype exhibited by study organisms are often difficult in the natural environment, especially in marine ecosystems. However, it should be noted that acclimation to stressors may be more likely under laboratory conditions than in natural settings due to the increased regularity and predictability of experimentally manipulated stressors, and this could create false conclusions regarding acclimation ability of communities (Wright et al., 2007a,b). Therefore, care must be taken when applying results of laboratory-based studies into wild populations (Slabbekoorn et al., 2010).

Implications and Future Study

As contemporary study increases focus on stressor interaction as opposed to solo stressor studies, emergence of growing evidence for synergistic reactions has been noted. Synergisms present particular cause for immediate conservation concern, as impacts are magnified compared with when stressors are experienced in isolation. A review by Crain et al., (2008) found that the most common interaction concluded across all studies reviewed was synergistic, and that the likelihood of finding this effect further increased if a third stressor was added to a combination. This is of course very concerning, however there has been some debate as to whether synergisms may be overpredicted in scientific literature (Darling and Côté, 2008; Crain et al., 2008; Côté, Darling and Brown, 2016).

The vast majority of stressor impact studies, including this one, are carried out in controlled laboratory environments. This enables isolation of stressor impacts and clarity of results. However, it also means that there is a predisposition to choose stressors which have the most severe impacts and are therefore more likely to interact synergistically (Crain et al., 2008). The conclusion of both synergistic and additive effects must therefore be based upon thorough and ecologically relevant studies, in order to avoid any over-catastrophised estimates of current ecosystem health, and to promote positive action among policy makers.

Studies of three or more stressors are few and far between, not least due to the physical difficulties of experimental set-up of combined treatments, however, it is very common for more than three stressors to occur in the natural environment (Crain et al., 2018). It is possible that the addition of other environmental factors also experienced by *C. maenas* in both native and non-native habitats, such as ocean acidity or microplastic pollution, could result in unpredictable interactive outcomes for camouflage and antipredator behaviours. Understanding these interactions more fully could aid studies in predicting trends of *C. maenas* range expansion as an invasive species.

With synergistic outcomes between local and global stressors, management efforts should be focussed on mitigating local stressors, where global stressors are impossible to mitigate for, as this can reduce the magnitude of impacts upon ecosystems dramatically. Despite this, studies combining global and local stressors are few (Brown et al., 2013) and the issue of stressor management becomes more complicated when interactions between stressors have an antagonistic effect. In this scenario, the removal of one stressor may in fact worsen the overall impacts of environmental change on an ecosystem (Cote and Darling, 2010). For example, sedimentation is known to reduce coral survival, however, in conditions of extreme UV exposure, increased sedimentation may actually block harmful impacts of UV and prevent coral bleaching. Therefore, mitigation of sedimentation may in fact turn out to be more devastating for coral reefs than if the stressor is allowed to persist (Anthony, Connolly and Hoegh-Guldberg, 2007; Brown et al., 2013). However, it is unknown how the addition of other stressors may affect this relationship, for example pressures of overfishing or ocean acidification could interact synergistically with sedimentation and therefore reduce the benefit of allowing this local stressor to persist. This highlights the importance of studying stressor interactions at an ecosystem level and using knowledge to guide effective management strategies.

Studies that have included organisms at different trophic levels have revealed differential susceptibility to stressors among organisms within the same ecosystem, for example, diatom productivity is enhanced under increased exposure to UV, due to the detrimental effect of UV damage on grazer populations (Bothwell et al., 1994; Boyd and Hutchins 2012). Therefore, it is perhaps more likely that responses at a population level may be more extreme and easier to interpret than ecosystem level responses (Darling and Côté, 2008), which could contribute to the differentially high numbers of synergistic conclusions within current literature (Crain et al., 2008).

In order to create the most robust predictions of stressor interactions, it has been suggested that, wherever possible, studies should seek to employ the most ecologically relevant methodology by considering interactions among different trophic levels within the same ecosystem, and by employing factorial designs with full control treatments (Crain et al., 2008). Mesocosm or field studies are far fewer, but have been found to be less likely to result in synergisms, and are more capable of studying stressors at the community level (Crain et al., 2008), and therefore further efforts to develop methodologies to enable more ecologically relevant stressor interaction studies are essential.

Conclusion

Contemporary studies are increasingly examining the effects of multiple stressor interactions on study species, with the realisation that species in natural environments are subject to stressors that vary in source, as well as spatially and temporally. Most commonly studied stressors in ocean study systems include temperature, hypoxia and ocean acidification (Gunderson et al., 2016), all of which may be considered global stressors, and often occur in conjunction with one another. This study is one of the few of its kind to combine both a local and a global stressor to test their interaction. Future stressor interaction studies should continue to combine local and global stressors and seek to study their potential impact on behaviours not directly related to the stressors in question. In an ever-changing world, where anthropogenic drivers of environmental change are fluctuating and complex, ecologically relevant study of stressor interaction and cross-modal impacts is crucial to drive effective conservation efforts. I hope my study forms an important contribution to the still relatively novel but growing body of scientific literature on this topic.

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